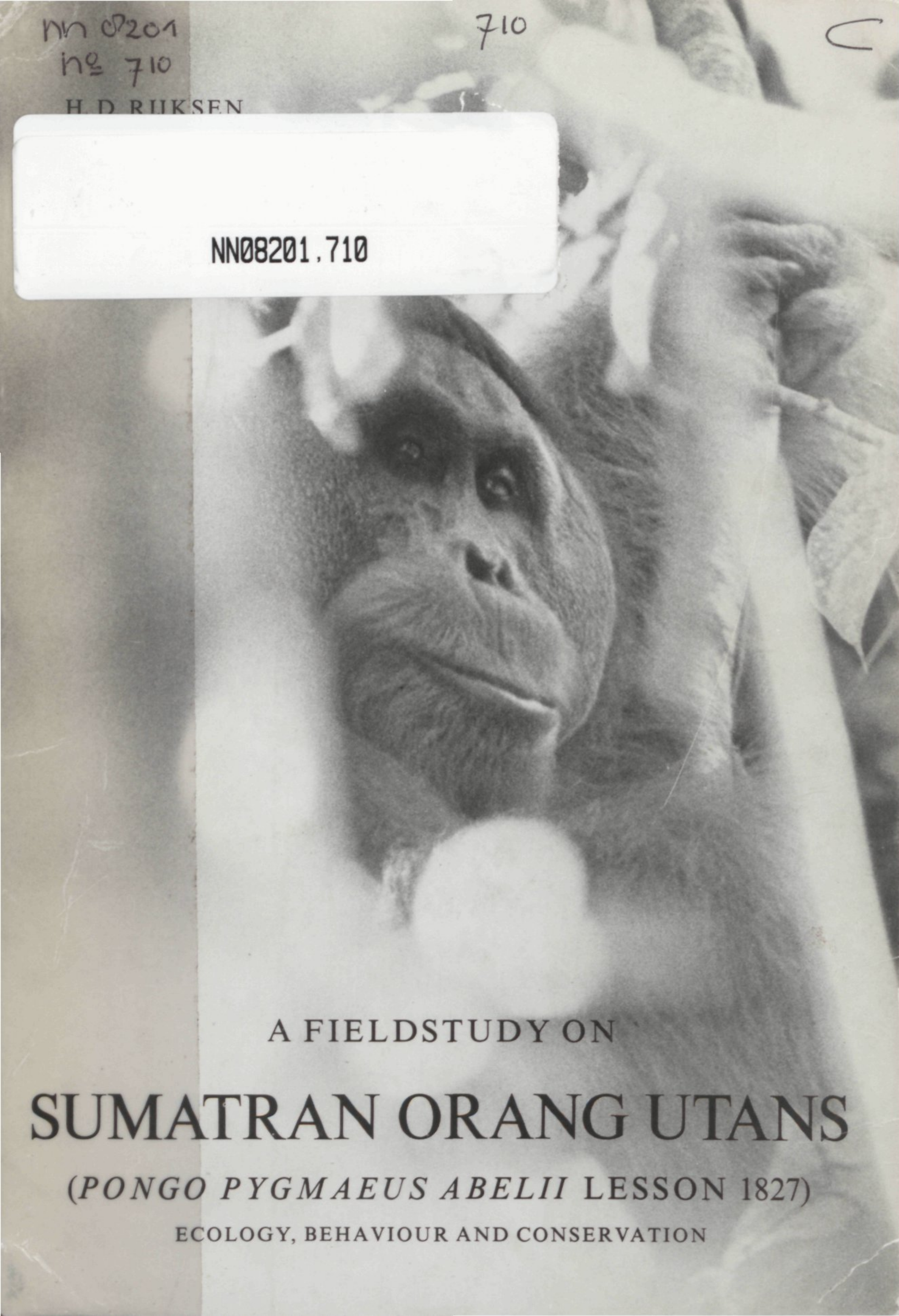
H. D. RIJKSEN



A FIELDSTUDY ON

SUMATRAN ORANG UTANS

(*PONGO PYGMAEUS ABELII* LESSON 1827)

ECOLOGY, BEHAVIOUR AND CONSERVATION

A FIELDSTUDY ON SUMATRAN ORANG UTANS
(*PONGO PYGMAEUS ABELII* LESSON 1827)

ECOLOGY, BEHAVIOUR AND CONSERVATION

Dit proefschrift met stellingen van

HERMAN DIRK RIJKSEN

doctorandus in de diergeneeskunde, geboren te Zeist, op 9 januari 1942, is goedgekeurd door de promotoren dr. M. F. Mörzer Bruyns, hoogleraar in natuurbehoud en natuurbeheer, en dr. J. A. R. A. M. van Hooff, lector in de vergelijkende fysiologie.

De Rector Magnificus
van de Landbouwhogeschool,
H. C. VAN DER PLAS

Wageningen, 24 oktober 1977

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H. D. RIJKSEN

A FIELDSTUDY ON SUMATRAN ORANG UTANS (*PONGO PYGMAEUS ABELII* LESSON 1827)

ECOLOGY, BEHAVIOUR AND CONSERVATION

PROEFSCHRIFT
TER VERKRIJGING VAN DE GRAAD
VAN DOCTOR IN DE LANDBOUWWETENSCHAPPEN,
OP GEZAG VAN DE RECTOR MAGNIFICUS,
DR. H. C. VAN DER PLAS,
HOOGLERAAR IN DE ORGANISCHE SCHEIKUNDE,
IN HET OPENBAAR TE VERDEDIGEN
OP VRIJDAG 3 FEBRUARI 1978
DES NAMIDDAGS TE VIER UUR IN DE AULA
VAN DE LANDBOUWHOGESCHOOL TE WAGENINGEN

H. VEENMAN & ZONEN B.V. – WAGENINGEN – 1978

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STELLINGEN

I

Het terugwennen van in gevangenschap gehouden orang utans aan het leven in wilde staat in gebieden waar geen wilde soortgenoten voorkomen, is uit het oogpunt van natuurbescherming verre te verkiezen boven rehabilitatie in door soortgenoten bewoonde gebieden.

II

De beweringen dat orang utan populaties geen nadelige invloed zouden ondervinden van de commerciële bosexploitatie[1], en dat deze exploitatie zelfs een gunstig effect zou hebben op het habitat voor de Zuid-Oost Aziatische mensapen[2], zijn gebaseerd op incidentele en/of onnauwkeurige waarnemingen.

1. STOTT, K. and C. J. SELSOR, 1961. The orang utan in Borneo. Oryx 6: 39–42.
HAILE, N. S., 1963. Orang-human co-existence in North Borneo. Sarawak Mus. J. 11: 259–261.
2. CHIVERS, D. J., 1972. The siamang and the gibbon in the Malay peninsula. In: Gibbon and Siamang, Basel: 103–135.
WILSON, C. C. and W. L. WILSON, 1975. The influence of selective logging on primates and some other animals in East Kalimantan. Folia Primatol. 23: 245–274.

III

Bij het botanische onderzoek van het tropisch regenwoud zou naast het plantengeografisch en het plantensystematisch onderzoek méér aandacht moeten worden besteed aan de vegetatiekunde in relatie met zoöoecologisch onderzoek.

IV

Het inventariseren van bedreigde diersoorten met een bijzondere economische waarde, om een idee te krijgen van de te beschermen relict-populatie zal, indien niet tegelijkertijd afdoende beheersmaatregelen getroffen (kunnen) worden, in vele gevallen de aanzet zijn tot een versnelde uitroeiing.

V

Voor een oecologisch verantwoorde leefwijze is het animisme de meest aanvaardbare godsdienst. De activiteit van missionarissen en zendelingen in 'primitieve' gemeenschappen verdient dan ook niet de instemming die het bij een breed publiek nog altijd geniet.

VI

Het is waarschijnlijk dat jachtgedrag van mensen voor een belangrijk deel zijn drijfveren vindt in aggressie, omgericht naar niet tot de groep van de jager behorende individuen, en dat zulk gedrag een aanzienlijke selectieve invloed heeft gehad in het ontstaan van *Homo sapiens*. Men kan constateren dat vele als zeer 'beschaafd' bekend staande personen nog steeds onder invloed staan van die met recht 'primitief' te noemen drang tot doden.

VII

In het huidige beleid met betrekking tot 'ontwikkelingshulp' aan zogenaamde derde wereld landen ligt het accent duidelijk op ontwikkeling. Zolang in dat beleid onvoldoende aandacht besteed wordt aan een zinvolle oecologische begeleiding, is het zeer de vraag of de 'ontwikkeling' die de donorlanden voor ogen staat wel als 'hulp' gezien mag worden.

VIII

Zolang natuurbescherming niet hand in hand gaat met, en actief steun verleent aan geboortenbeperking, blijft het een activiteit gericht op het bestrijden van symptomen, in plaats van oorzaken.

IX

De grootscheepse bestrijding van vectoren van dierziekten in savannegebieden is een maatregel die op korte termijn een welvaart versterkend effect kan hebben voor de plaatselijke bevolking; op lange termijn kan het effect echter desastreus zijn doordat het verleidt tot progressieve overbegrazing met als gevolg erosie en woestijnvorming.

X

De wilde fauna van Oost Afrika, die in toenemende mate het savanne habitat moet delen met gedomesticeerde dieren, wordt door veehouder en dierenarts in het algemeen gezien als een belangrijk reservoir van veeziekten. Het tegendeel is eerder waar; het vee kan een belangrijke ziektenbron zijn voor de wilde fauna.

XI

Het internationale massatourisme naar ontwikkelingslanden is één van de oorzaken van de steeds snellere desintegratie van het daar voor touristen nog zo aantrekkelijke milieu.

XII

De pessimisten onder natuurbeschermers zijn nog maar zelden bedrogen uitgekomen.

H. D. Rijksen
Wageningen, 3 februari 1978

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PART I

INTRODUCTION

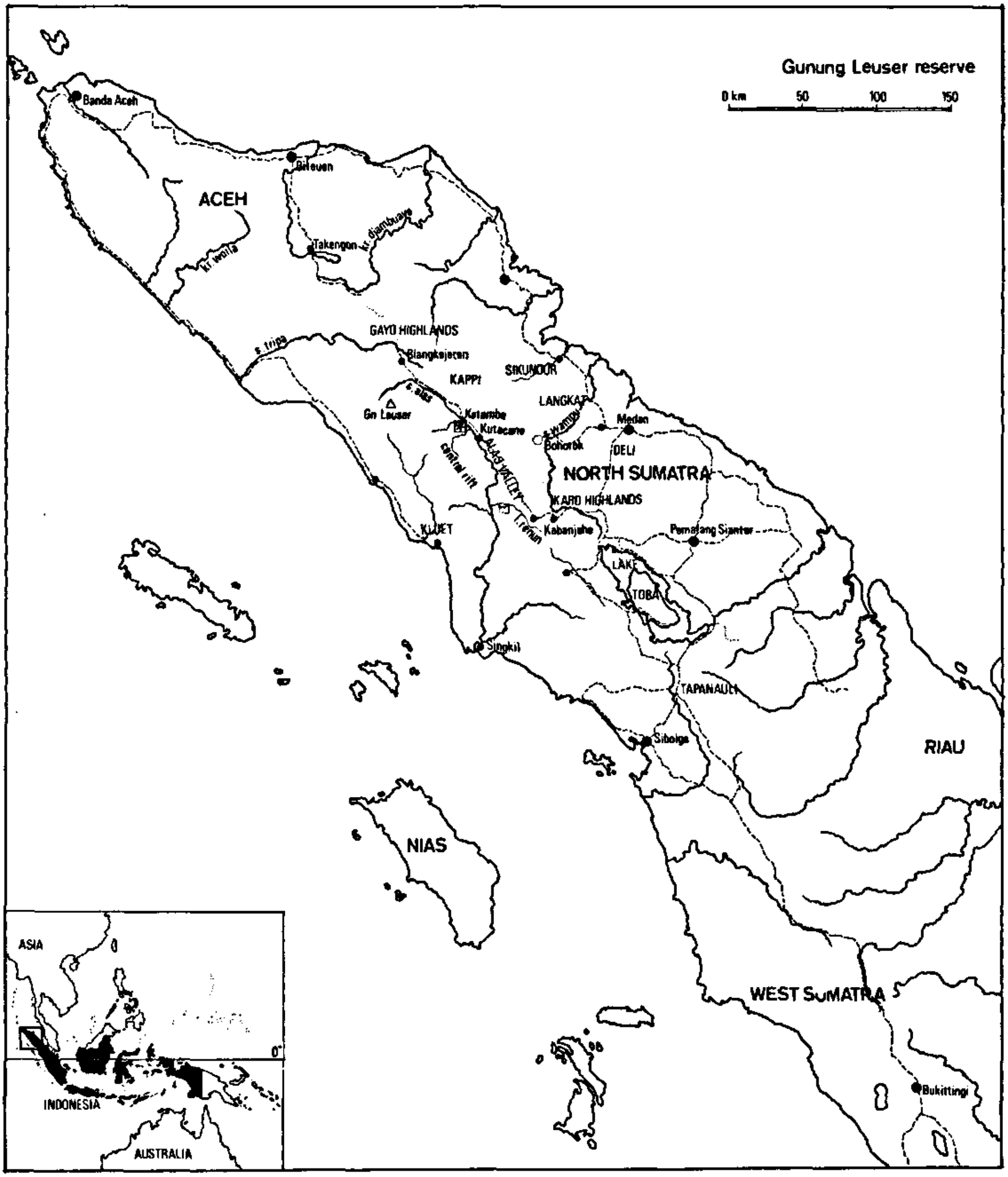

FIG. 1. The Gunung Leuser reserve, North Sumatra, and the location of the Ketambe study area.

1. INTRODUCTION

1.1. BACKGROUND

Information on the ecology and the behaviour of the species in its natural environment is essential if we are to ensure the survival of the orang utan under the pressure of imminent destruction of the Sumatran and Bornean rainforest habitats. Since the Sumatran orang utan (*Pongo pygmaeus abelii*, LESSON, 1827) had not previously been the subject of a systematic study in its natural habitat, the present research was intended to (a) add to fundamental knowledge of the biology of this ape, and (b) to investigate the conservation problems concerning this species.

Supported financially by the Netherlands Foundation for the Advancement of Tropical Research (WOTRO), and in close cooperation with the Netherlands Appeal of the World Wildlife Fund (WWF), the present study commenced in the Gunung Leuser reserve in June 1971, under the supervision of Prof. Dr. M. F. MÖRZER BRUYNS, of the Nature Conservation Department, Agricultural University, at Wageningen.

Following two preliminary surveys in the reserves in 1969 (by Dr. R. SCHENKEL), and in 1970 (by Dr. F. KURT; WWF/IUCN project 596); a tripartite agreement between the Indonesian Directorate General of Forestry, Nature Conservation and Wildlife Management Service (Dinas PPA); the Netherlands Gunung Leuser Committee; and the World Wildlife Fund was drawn up in order to improve the management and conservation of the Gunung Leuser reserves (Decree of the Sekretariat Kabinet Republik Indonesia No. 641, 4 April 1971; WWF Project No. 733/1971). One of the conservation actions to be undertaken in WWF Project 733, was the establishment of a rehabilitation station for orang utans, parallel to the present study.

On instigation of Dr. F. C. VAN HEURN, the Gunung Leuser reserve proper (416,500 ha) was established in 1934; soon extended with the adjacent Kluet reserve (20,000 ha) in 1936, and the Sikundur, South- and West Langkat reserves (some 200,000 ha) in 1938 (VAN HEURN, 1955). Recently, in 1977, the Kappi area (some 100,000 ha) was included in the Gunung Leuser reserve. This complex of contiguous reserves is summarized here as 'Gunung Leuser reserve' (fig. 1), with its more than 7500 km.sq. area of tropical rainforest being the largest reserve in South East Asia. The Gunung Leuser reserve is of a mountainous character; the Mount Leuser reaches as high as 3466 metres. Large sectors of the reserve are well over 1000 metres; apart from the few lowland regions, two high plateaus are of significance specially for wildlife, namely the Kappi plateau (1000–1500 m) and the spaceous Central rift valley (1200–1500 m) (fig. 2), only recently discovered by a geological survey in the inaccessible interior of the reserve (HELMKAMPF, 1973 pers.comm.). The area of the reserves and their surroundings harbour a rich and divers fauna (see

Fig. 2. The recently discovered central rift valley in the Gunung Leuser reserve; Mount Leuser in the background.

HOOGERWERF, 1936–'38; CHASEN, 1940), which includes several rare and endangered mammals, such as Sumatran tiger (*Panthera tigris*), Sumatran rhinoceros (*Didermoceros sumatrensis*), and orang utan.

1.2. OTHER FIELD STUDIES ON ORANG UTANS

A limited amount of information on the behaviour and the ecology of orang utans, especially of the Bornean subspecies, was available since the earlier decades of the last century (see e.g. SCHLEGEL and MÜLLER, 1839–1844). Yet, most naturalists aimed at collecting as many specimens as possible and much of their information on this ape's behaviour is scattered amongst exhaustive, yet largely irrelevant information on their heroic collecting efforts. The first study, carried out without a weapon, was by G. SCHALLER (1961), who conducted some two months of fieldwork in Sarawak; in 1964 followed by a six months field study in Sabah by DAVENPORT (1967). Since then, the wild Bornean orang utan has been the subject of several long term field studies. HORR (1972; 1975) spent some 25 months in East Sabah in the period 1967–1969; MACKINNON (1971; 1974) also conducted some 16 months of field-research in Sabah in the period 1968–1970; and RODMAN (1974) observed orang utans for approximately 14 months, dividing his time between Sabah and East Kalimantan (Kutai) in the period 1969–1971. Only BIRUTE and ROD GALDIKAS-BRINDAMOUR (1975) conducted a field study lasting several years in South East Kalimantan from 1971 onwards.

One of the earliest detailed accounts of some aspects of the behaviour of Sumatran orang utans, though also originating from a collecting expedition, has been given by HOOGERWERF (1936–'38). Except for MACKINNON (1973), who devoted approximately 7 months to a field study on the Sumatran orang utan, the present project is the first long term research which concentrates on the Sumatran subspecies. Earlier, much shorter surveys, mainly concerning the distribution of orang utans in Sumatra have been conducted by CARPENTER (1938) and by MILTON (1964).

1.3. THIS STUDY

The present study deals mainly with the relationship between the orang utan's behaviour and its environment. Before the actual fieldwork had started, the main questions leading to this study centred around how this ape behaved in the wild, since at that time (1970) little data had been published on the subject. I was intrigued by the reported low densities of orang utans in the vast and, as regards humans, only sparsingly inhabited rainforest. I wondered if information on the animal's behaviour and its immediate environment contained clues about the ape's highly endangered status. Furthermore it seemed that a detailed study might provide information on how to improve the ape's status.

During three years (i.e. from June 1971 until August 1974), observations were made on a wild orang utan population in a selected area of tropical rainforest at Ketambe. In addition to the intensive study in this study area, ecological surveys were made in other parts of the orang utan's range in Sumatra. In 1974, I made two trips to Borneo, one to Sepilok reserve in Sabah, and another to Tanjung Puting reserve, Kalimantan Tengah, in order to gather some comparative information on the subspecies from that island.

After the fieldwork in Sumatra was completed, I made brief visits to Central and East Africa in 1975 to observe wild mountain gorillas in their natural habitat at Mount Visoke-Karasimbe research station (Parc des Virungas in Rwanda), and to observe and discuss chimpanzee behaviour and social organization at the Gombe Stream research station (Gombe Stream National Park) in Tanzania. Again, in December 1975, a two weeks visit was made to the Ketambe study area where additional data were gathered, and a film on orang utan behaviour could be completed.

The observations on orang utan behaviour gathered during this study, supplemented by the numerous reports on other primate field studies and in particular on the other apes, made me wonder why the orang utan, which shows so many behaviour patterns very similar to those of its closest relatives, had 'chosen' just that option in the array of possible lifestyles to assure a maximal 'fitness'; a lifestyle which makes the orang utan exceptional among the primates, being the heaviest arboreal animal and living a 'solitary' lifestyle.

At the present time (1977) several studies on this ape have been completed. Without exception they give detailed information on its behaviour and are valuable contributions to our insight into the complex social organization of the orang utan. Yet, in my opinion, they do not give a sufficiently shaded and comprehensive conclusion on the important relationship between the complex rainforest ecosystem and the orang utan's behavioural adaptations. In this report I do not pretend to give the definitive conclusions in this highly complex matter. The mainly qualitative descriptions of the variables involved do not allow conclusions beyond a tentative level.

Yet, the present study attempts to contribute to the discussion by providing speculations which emphasise the selective pressures that have led to the orang utan's anomalous but – by virtue of its survival value – very efficient life style.

This thesis is arranged as follows. After an introduction and a general description of the study area and study methods, a detailed analysis is given of the orang utan's habitat, its feeding behaviour in that habitat and information on the size and density of the orang utan population. In the third chapter I present a qualitative description of the animal's behaviour in relation to conspecifics and its social organization.

The discussion compares the selection pressures which may have influenced the orang utan's biology, with similar behavioural and ecological variables affecting the allopatric African apes. Finally, in Part IV, I discuss the conservation of the orang utan and its habitat: The tropical rainforest. A detailed account is given of the ape's present status and of the threats to which it is exposed. This chapter also includes an evaluation of the measures to protect this ape and discusses the role of rehabilitation in this protection.

Since this study continued for only a little over three years, it is obviously too short to clarify all aspects of the behaviour of a long-lived animal such as the orang utan. Gathering supplementary information over a much longer period will be necessary to validate the tentative conclusions and speculations which are presented here.

1.4. THE REHABILITATION PROJECT

As a welcome consequence of a successful fundraising campaign by the WWF Netherlands Appeal in 1970, a rehabilitation project for confiscated orang utans was started at Ketambe in conjunction with the research on wild apes.

The aims and background of orang utan rehabilitation have been discussed by HARRISON (1963) and by DE SILVA (1971), and are to be reviewed on p. 367. In brief, the rehabilitation of orang utans attempts to reintroduce confiscated orang utans that have been held captive illegally, to living under wild conditions.

Already at the onset of the study, even before a suitable study site had been chosen, the Dinas PPA offered us several confiscated orang utans to take into the project. We regarded it as advantageous to have such tame orang utans close at hand in order to acquire a better insight into this ape's behavioural repertoire. The daily contact with rehabilitant orang utans of different ages and sex made us familiar with the characteristics of each stage of development and thus made it easier to assign the wild orang utans to their appropriate age class. We were able to make regular observations on rehabilitants when unable to locate wild orang utans. Moreover, the ease of contact with the rehabilitants enabled us to carry out simple experiments in order to clarify questions with regard to the interpretation of certain behaviour elements observed in the wild population.

2. THE STUDY AREA

Following two months of surveying the Alas valley in search of a suitable research area, the comparatively flat country close to the confluence of the rivers Alas and Ketambe, situated within the boundaries of the Gunung Leuser Reserve, was selected (Fig. 3).

The criteria for the choice were: The area had to be a representative habitat for the orang utan and it had to be accessible from a road or river. For the establishment of an orang utan rehabilitation station the area had to be located within the boundaries of the Gunung Leuser reserve and the area preferably had to be bordered by natural boundaries so that released orang utans would not come into contact with human settlements; and the terrain of the study area had to be such that it could be easily traversed.

The Ketambe area, which was recommended by a local guide, was found to fit most of these criteria at first sight. Preferred orang utan food trees were plentiful (i.e. *Ficus* sp. and *Durio* sp.); orang utans were observed relatively frequently and the terrain was relatively flat. The area was separated from neighbouring villages by the Alas river and was accessible by 4 wheel drive vehicle most of the year from the Kutacane-Blangkejeren road.

2.1. TOPOGRAPHY

The Ketambe study area is situated at an altitude of approximately 350 m above sea level, with elevations to 450 m. The area is enclosed by the escarpments of the high massives of the Gunung Mamas (west of the study area), the Gunung Kemiri (north of the study area) and the Gunung Bandahara (east of the study area). The Alas valley, some 100 km in length, runs in a south-eastern direction, dividing the Gunung Leuser complex of reserves into two parts: The Serbaulangit-Langkat reserve, and the Gunung Leuser reserve proper.

In the south, near Lao Pakam, the valley is approximately 15 km wide but it narrows to the north where the Leuser mountain complex as a sector of the Bukit Barisan range traversing Sumatra, meets the Serbaulangit range near the village Aunan.

In topographical terms, the study area is located at latitude 3°40′ north, and longitude 97°40′. It is situated on the eastern bank of the Alas river, opposite the village of Balelutu on the Kutacane-Blangkejeren road, some 4 kilometres north of Aunan village, and 32 kilometres north of the township Kutacane (fig. 3). The area is bordered on two sides by rivers, i.e. the Alas river on the north-eastern side, and the Ketambe river to the north-west. The area is drained by numerous small streams, some of which dry up in the dry seasons. Some parts of the area are badly drained, resulting in small swamps.

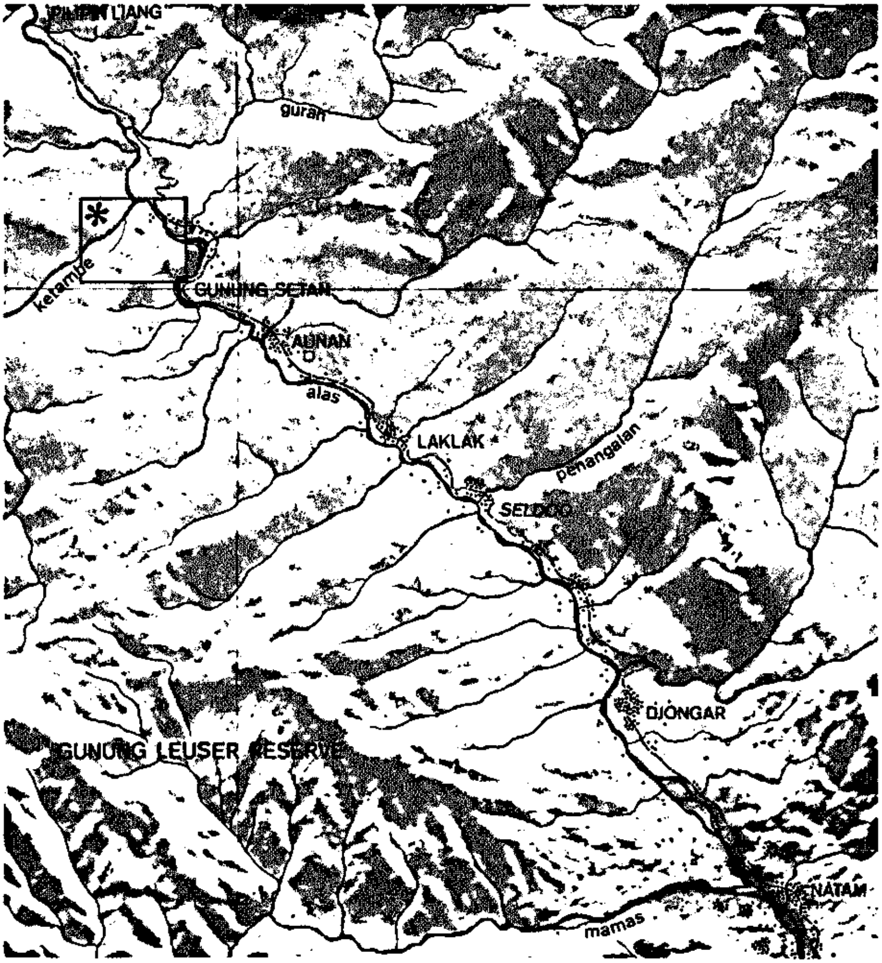

Fig. 3. Topography of the northern sector of the Alas valley; the asterix denotes the Ketambe study area (radar map).

The northern sector of the study area is traversed east-west by a local ridge, rising 70 metres above the surrounding land.

A base camp was established on the bank of the Alas river (see fig. 5) from where a system of trails was developed to facilitate the search for orang utans.

No official maps of any accuracy exist of this part of North Sumatra, but in 1974 a large scale mapping programme by means of air-photography was carried out with the aid of the Australian airforce. As yet, however, accurate topographical maps and air photographs have not been made available.

2.2. SIZE OF THE STUDY AREA

In order to make searching for orang utans as efficient as possible, it was decided to chose a relatively small study area of 1.5 square kilometre. To understand the social life of a species one needs to make frequent observations on certain recognized individuals. By confining the study area we hoped to get a better picture of the whereabouts of known individuals.

When choosing a larger study area, one is inclined to follow more animals for a shorter time each and the disturbing effect of observers will be higher because habituation proceeds much slower (see MACKINNON, 1971).

For the description of the ecology, social organization and individual behaviour of orang utans the size of the study area proved to be satisfactory. Yet for answering detailed questions such as those concerning the size of home range of the different age-sex categories a considerable extension of the study area would be necessary.

2.3. GEOLOGY AND SOIL

The geological basement of a large part of the Ketambe area is a terrace conglomerate consisting of sedimentary deposits laid down by the Alas river. The fact that the Alas river has cut into its unconsolidated deposits, which at some places (Ketambe, Gurah, Penangalan) are 25 metres deep, indicates a recent uplift of the area ('mass-elevation'). The terrace conglomerate consists of sandy deposits containing black marl, sandstone, and crystal tuff (HELMKAMPF, pers. comm. 1973).

The soil underlying the humus layer of the Ketambe forest consists of sand in the sectors bordering the rivers. Further inland the soil is composed of coarse grained red lateritic earth, alternated in some places with loamy yellow earth. The humus layer on top of the soil is shallow, varying in depth from 5–30 cm. The rootsystems of most trees are almost exclusively anchored in this layer. When large trees toppled over during storms, their flat rootsystem, usually no more than 50 cm in depth, stood up like a wall at right angles to the forest floor. A relatively thin leaflitter layer, 2–5 cm deep forms the top of the humus layer.

2.4. HISTORY OF THE REGION

A small sector of the Ketambe area, along the Alas river in the North had reportedly been felled and used for agriculture in 1940–1941, but the people left the area after an epidemic in 1941. The species composition of the forest in that sector is typical of secondary growth or forest-fringe habitats, including such species as *Macaranga diepenhorstii*, *Bisschofia javanica*, *Turpinia laxiflora* and *Erithrina subumbrans*. Moreover, this area is badly drained and often turns into swamp. Apart from this small scale human influence some 30 years ago, there is no evidence of other human encroachment in the study area. VOLZ (1912) mentions that the footpath from Reket Goip (close to Blangkejeren) to Bambel (Kutacane) followed the Alas river along the western bank between a place some ten kilometer south of Geumpang and Rambung Teledaq (Seldoq) and in its course crossed the Ketambe river. This indicates that this path led through the present Ketambe study area in the first decade of this century. The present Kutacane-Blangkejeren road has followed the opposite (eastern-)bank of the Alas valley since 1920.

2.5. THE CLIMATE

The weather in the Ketambe area usually permitted a rather comfortable mode of fieldwork. Though subject to season, rainshowers usually occurred during the late afternoons, when the actual search for orang utans had already been abandoned. Rain could add considerable discomfort to the fieldwork, especially during the searching.

The climate of North Sumatra is subject to a certain degree of seasonality, mainly caused by annual periods of increased rainfall. This annual regime is variable between years. Both seasonal and diurnal regimes are influenced by topography and vegetation cover, which affect cloudcover, and thus solar radiation, precipitation, air humidity, wind and evaporation. Within the Alas-valley considerable variation in climatic conditions can occur in different localities.

The seasonal variation in precipitation in the Ketambe area induced the occurrence of seasonal rhythms in the vegetation as well as in the behaviour of certain animals, notably the birds. The seasonal variation was most marked in 1972; the dry period of January-February was extreme with only 64 mm rainfall. During these months, the forest had an exceptional dry appearance: Shrunken and dehydrated leaves hung from the branches and the normally moist forest floor was cracked. A remarkable phenomenon was the exceptionally abundant growth of algae (*Cladophora* sp.) submerged on boulders in the, then, shallow Alas river.

Maximum, minimum and noon-temperature was registered daily. Occasionally relative humidity readings were taken with a sling psychrometer at various points in the study area.

In general, the daily temperature fluctuated within a range of approximately 10°C in the shady environment close to the forest-floor. The temperature reached a maximum around noon, (average 29.2°C : n = 384 days), and remained high during the early afternoon. The highest temperature, measured in the shade, was recorded in the months February and March 1972 (34.2°C); the lowest temperature, recorded during a night in March 1973, read 17°C. The highest and the lowest temperatures were reached prior to the first wet season (April–May). In general the daily temperature was relatively low on days with a permanent cloud cover.

As a rule, the relative humidity in the Ketambe area was high, and varied from 62%, measured during the driest months, to almost 100%, during – and immediately after – the frequent rains. Taken from 134 day-readings, distributed throughout the day, the mean daily value is 86.9%. When differentiated into the three categories morning (8–12 a.m.) midday (12–2 p.m.) and afternoon (2–6 p.m.) the average relative humidity fluctuated from 94%–79%–88% respectively, throughout the day. On some days, usually at the end of a rainy season, when both the temperature and the relative humidity were high under a cloudy sky, the atmosphere was far from pleasant. It was remarkable that all animals, including the orang utans, seemed to be less active on such days.

In general, wind velocities in and around the Ketambe area were low. During some months, usually February and March, strong squalls of wind sometimes preceded torrential downpours of rain or thunderstorms during the late afternoon. These squalls were typically of short duration, but could reach very high velocities. Large trees or sometimes even groups of trees fell during such storms. The places most affected were often the same as those affected by earlier storms, with the result that patches of secondary succession occurred where the primary forest-cover had been destroyed throughout the years. As the Ketambe area is a valley between high mountain escarpments the wind direction was undoubtedly influenced by the topography of the area.

Rainshowers occurred almost every day in the Ketambe area; the average number of rainy days per months is considerable (fig. 4). Most rain fell in

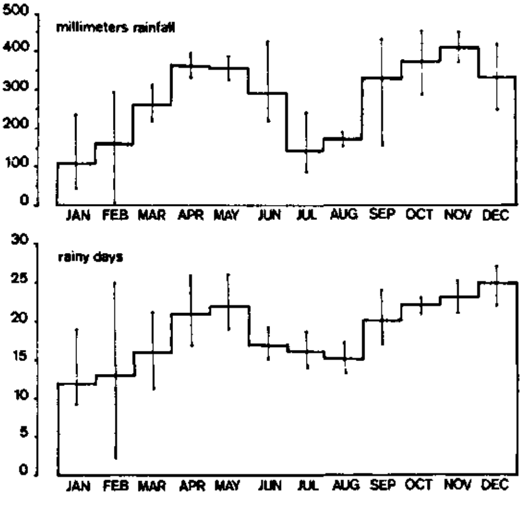

FIG. 4. Mean monthly precipitation and number of rainy days in the Ketambe area, 1971–74.

the late afternoon or during the night, but in the wet seasons the rain could start in the early morning and last all day, with only occasional dry spells. Such long-lasting rains were typically light; torrential downpours rarely lasted all day. On certain days the drizzle was so slight that it left unmeasurable amounts of precipitation in the rain-gauge; such days are consequently not included in the table. Roughly two dry seasons can be distinguished, namely: January-February, and July-August. Still, even in these periods nightly rain-showers were common.

In the rainforest, precipitation generally exceeds evaporation throughout the year. When the monthly rainfall is less than 10 cm, the area becomes liable to drying out. (CHARTER, 1941, in RICHARDS, 1952). In the Ketambe area, such conditions only occurred once, in a period of 4 months during 1971–1974 (see fig. 4). The forest then had a very dry appearance and the rivers had a very low water-level.

During the early wet season (March-June) especially, the rains had the character of thunderstorms; showers usually occurred during the nights and strikes of lightning in high trees, notably large fig-trees were not uncommon. The maximum amount of rainfall measured in one day during the study period was 143 mm (in April 1974).

The yearly amount of precipitation was around 3000 mm. VAN STEENIS (1937) has reported 2544 mm annual rainfall in Kutacane for the period 1926–1928; the corresponding figure for Blangkejeren amounted to 1736 mm. Similar to the present situation he reports that the early wet season started in March, reached its peak in April and May and ended in June; the late wet season was characterized by a larger amount of precipitation. It starts in September, reaches its peak in November and ends in December.

After heavy rains in the upper courses in the Gn. Leuser- and Gn. Mamas massives both the Alas and Ketambe rivers might become torrential streams and flood their banks (‘*banjir*’). Within a short time, fifteen to thirty minutes after the characteristic colour-change that accompanies a ‘*banjir*’, the water level of the Alas river could rise more than 1.5 meter.

The torrential rivers contained a large amount of suspended matter and could carry along floating logs or entire trees. Typically the Ketambe river adopted a reddish brown, the Alas river a yellowish brown colour when torrential, indicating the differences in soil types in their respective upper courses. In periods of heavy flooding the vegetation along the river-banks could be severely affected.

The forest structure in the Ketambe area with its relatively open canopies allowed comparatively good illumination of the lower strata, resulting in an abundance of herb vegetation covering the forest floor in some places.

Incident light-measurings during a cloudless day with a diffusor on a (Gossen Lunasix 3) exposure meter at a height of 1.5 meter from the forest floor, varied for different places from Lux 11 to Lux 88 (footcandles approx. 1–8).

These data correspond with measurements taken in other, similar rainforest areas (RICHARDS, 1952).

During the dry season with no cloud cover, the amount of daily sunshine could exceed 8 hours; however, even during the dry season, clouds usually appeared during the course of the day, reducing the direct sun-radiation considerably.

3. THE STUDY METHODS

3.1. SEARCHING METHODS AND SURVEYS

Searching for orang utans within the research area along the existing network of animal trails, as attempted in the early stages of the study, appeared to be impractical. The difficulties of keeping to the right trail while scanning the canopy were such that orang utans were often overlooked. Moreover it was impossible to walk silently enough to prevent disturbing the orang utans from a distance so that they were able to hide before our arrival. As an alternative, a system of trails approximately 1 metre wide was cut, traversing most of the 1.5 km^2 research area. These paths were regularly cleared of vegetation.

Orang utans were located by traversing the research area, walking at a slow pace, approximately 1 km/hr., along these trails, covering an average distance of 5.9 km per day. The daily searches were carried out by one or two men.

In the early stages of the study we also tried to locate orang utans by scan-

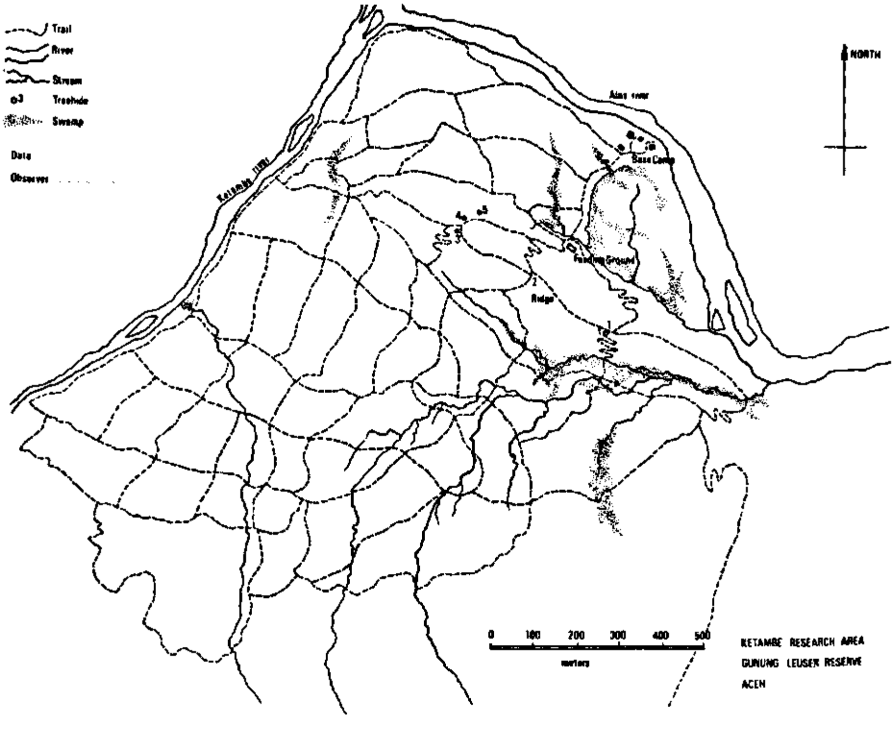

FIG. 5. The Ketambe study area, showing the base-camp and trailsystem.

ning the canopy from platforms built in high trees on vantage points on top of the ridge. We assumed that the orang utans would betray themselves by movement of the vegetation, as they travelled. However, the number of sightings was disappointing and the method was abandoned after some months. The most satisfactory results came from walking through the area, watching the canopy for movements.

Signs which betrayed the presence of orang utans were swaying trees, the accompanying rushing sound (which was audible from a greater distance than visual observation permitted), the typical smell of orang utans, discarded fruit-shells or wadges from epiphytic plants (fig. 6), orang utan faeces and the occurrence of freshly made nests.

During the early stages of the research, it was not unusual for several days of intensive searching to pass without a single orang utan being sighted. As long as an ape moved about or fed, he was easily detected, but an immobile or hiding orang utan was extremely difficult to find, notwithstanding its large size and conspicuous coloration. Even when there was evidence of an orang utan's presence in a particular place, it was often impossible to detect him. It was also difficult to sit out the patience and endurance of a found, hiding orang utan, and it was not easy nor pleasant to keep up with a fleeing individual.

Unless certain trees were in fruit, when observations were focussed there, the whole research area was searched in a random fashion. Still, the searching pattern was probably often influenced by the sub-conscious expectation that

FIG. 6. A discarded wadge of *Rhaphidophora foraminifera* stem.

orang utans might be found at certain locations, and was determined by the practicability of certain trails, especially during the rainy seasons. Although searching activity was spread as evenly as possible over all hours of the day, especially in the earlier stages of the study, it soon became apparent that the number of animal sightings was considerably higher during the morning. This was probably due to the animals being more active and the observers more alert before the daily temperature reached its maximum.

On average some 6–7 hours each day was spent in the field, of which at least 4 hours were devoted to the searching of orang utans.[1] Since we were primarily concerned with the dispersal of individuals over the area, and their social organization, rather than with individual behaviour and daily activity patterns, solitary ranging individuals were usually not followed.

As only very scant data were available on the general distribution of the orang utan (see p. 33) several surveys were made to other localities within the presumed distribution range of the Sumatran orang utan in 1971 and 1972. During these surveys almost every accessible road in the northern part of the island was covered and in localities where orang utans could be expected, additional safaris on foot were made into the forest in search of nests. In addition, several surveys on foot penetrated deep into the Gn. Leuser and Langkat reserves. On one occasion I was able to use a helicopter to explore some inaccessible places deep in the interior of the Gunung Leuser reserve. Finally, local information was gathered, both verbally and in writing, concerning the distribution of the orang utan in the Northern part of Sumatra. For this aspect, the help of the Forestry Department (Dinas Kehutanan) and Nature Conservation Service (Dinas PPA) was indispensable.

3.2. OBSERVATION METHODS

The total time spent observing wild orang utans exceeds 2000 animal hours. In addition, at least 3500 animal hours were spent observing the free roaming rehabilitant orang utans.

For a detailed study of the social organization of the Ketambe population it was necessary to recognize individual animals. Although orang utans show striking individual differences in facial features, voices and other characteristics, recognition was not at all easy under field conditions. The observation distance is often quite large and the view often obscured by foliage. Only after prolonged and close contact can an observer recognize an individual animal's features. Lone females and adolescent orang utans were especially difficult to recognize. Females with offspring could sometimes be recognized individually by the sex

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[1] During 1973 and 1974, the fieldwork was intensified with the assistance of a student of the Nature Conservation Dept. of the Agricultural University, Wageningen, and with the additional help of two students from Indonesian Universities (Universitas Gajah Mada, Yogyakarta and Universitas Padjadjaran, Bandung) who carried out separate field research on the hylobatids, but aided in locating and following orang utans.

and approximate age of their young. The recognition of certain individuals was aided by comparing photographs of the animals; this procedure was particularly convenient with animals which were seen again after long intervals.

The distance of observation and the light intensity often affected the apparent colour of an orang utan's coat considerably; therefore coat colour could not always be considered a reliable criterion for recognition. Obvious features such as scars and mutilated or stiff fingers, reportedly common among wild Bornean orang-utans (HORNADAY, 1885; MACKINNON, 1972; GALDIKAS-BRINDAMOUR, pers. comm. 1974) and among captive Sumatran orang utans (BRANDES, 1938), were not observed in the Ketambe population.

Due to our exceptionally close and intensive contact with the rehabilitant orang utans, recognition of these animals was very easy, even from considerable distances and when the animals were partly obscured by foliage. Only in the later stages of the study (1973–1974) we were able to recognize the habituated wild orang utans with the same ease. Some of these individuals could then be recognized from their vocalizations alone.

After finding an orang utan, the observer was usually unable to remain undetected for long, even though orang utans appeared to be considerably less inquisitive and alert then, for instance, siamangs and gibbons.

During the early stages of the study, the presence of an observer invariably disturbed the normal behaviour of an observed orang utan. Unhabituated animals were never persistently followed and if habituated orang utans showed clear signs of disturbance, the observations were usually abandoned.

It took several months of regular contacts before the orang utans gradually began to tolerate human presence and carried on their normal routine when being observed. It was late 1972 before it became possible to follow some individuals for a longer time.

The presence of the free roaming rehabilitant orang utans in the area facilitated the habituation of some wild individuals. Four wild orang utans frequently visited the feeding area of the rehabilitation station, situated at the edge of the study area (see fig. 5). Visiting wild orang utans were provisioned on a limited scale, meant to encourage subsequent visits but to discourage the apes from hanging around the feeding site.

Apart from their accelerated habituation, a phenomenon which has also been described for chimpanzees (VAN LAWICK-GOODALL, 1968), the regular visits of these particular individuals to the feeding area made them easy subjects to follow, while their interactions with the rehabilitants added considerably to our insight into orang utan behaviour.

3.3. RECORDING METHODS AND EQUIPMENT

After cutting the trails, an accurate map of the area (scale 1:8000) was drawn with the help of a 20 metre line and a compass (fig. 5). Copies of this map were used in the field daily.

During every searching trip through the area a detailed record was kept of all mammal sightings and in particular of all primates along the trails. The route followed, the time of the start and duration of the search, the exact location, the direction of movement, the time of contact and the activity of an encountered orang utan were recorded on the maps. When contacted, an orang utan was followed for at least 90 minutes and a detailed record was made of its behaviour (sampling method; the activity was recorded twice every five minutes). Depending on the animal's activity and several other factors such as time of day, the earlier experience with and 'mood' of the individual under observation, and the presence of fruit sources in the area, the orang utan either was followed for a longer period, or the observer left to search for other individuals.

When groups of orang utans were found or whenever a fruit tree attracted associations of orang utans, the individuals were followed for whole days, or as long as social behaviour could be anticipated. Then, a detailed record of their behaviour was made every minute. A dry cell operated electronic timer was used to time the intervals between observations. The behaviour was recorded in a detailed though simple short-hand code denoting the maintenance activities, e.g. the mode of locomotion, the type of food (and the species when known), and social behaviour, including which animals initiated interactions. Full analysis of all available data is not yet complete but I have used some representative samples to support qualitative information obtained on the social behaviour and the ecology of the Sumatran orang utan.

All wild and rehabilitant orang utans were given names, and these will be used in the text. Names are used because they express the individuality and 'personality' of the different orang utans much better than impersonal numbers or codes.

Although most of the behaviour shown by rehabilitant orang utans was indistinguishable from that of wild animals and some rehabilitants were well integrated with the local wild population, a clear distinction between the two categories 'wild', i.e. without previous human contact, and 'rehabilitant', i.e. previously subjected to various degrees of human contact, is made, and all aspects referring to rehabilitant individuals are clearly denoted as such.

Whenever possible food items of the orang utans were collected and preserved. Plants and vegetable material were dried between newspaper and sent to the Rijksherbarium, Leyden, for identification, as were numerous fruits, preserved in spirits or 70% alcohol. Insects and freshly collected orang utan faeces were preserved in alcohol-formalin solution. Faecal samples were examined for certain food-remains (i.e. seeds, insects and perhaps vertebrates) and for endo-parasites.[2]

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[2] The ants, termites and some of the crickets were identified by staff members of the British Museum of Natural History, London. Ecto-parasites were identified with the help of staff members of the AZU Hospital, Dept. Dermatology, in Utrecht; the examination of the faecal samples and the identification of the endo-parasites was done by myself, with the facilities provided by the Veterinary Faculty of the State University, Utrecht.

Whenever the lighting conditions in the forest and the habituation of the animals permitted, a photographic record was kept of individuals and of behavioural elements. For stills photography several 35 mm single lens reflex cameras were used with a variety of lenses. Lenses with focal lengths of 200 mm, 400 mm, and 500 mm were used most frequently to record orang utan behaviour. Lenses with a focal length shorter than 200 mm appeared to be impractical for recording orang utan behaviour in the field due to the exceptional long distances over which observations were made. Lighting conditions and the use of the long lenses made the support of a tripod necessary. The film used was as sensitive as available in the circumstances, and was home developed. Even with pushed sensitive film, i.e. ASA 1200 for black and white, and ASA 200 for color slides, the lighting conditions in the forest usually prescribed very slow shutter speeds (i.e. 1/4–1/15th second), and consequently often resulted in blurred pictures. Cinefilm of behaviour was shot on Super 8 and occasionally on 16 mm color film. The film cameras both accepted interchangable long telelenses. The lenses most frequently used for cinefilm were of 85 mm, 135 mm and 200 mm focal length.

Apart from a jungle knife (*parang*) we did not carry weapons during the fieldwork.

4. THE ORANG UTAN

4.1. LIFE STAGES

It is possible to distinguish several stages in the life of the orang utan. These are characterized by certain physical and behavioural features which differ between the two sexes. A distinction of these stages facilitates the understanding of the social behaviour and the social organization of the population observed in the Ketambe area.

A differentiation is made into the life stages of infancy, juvenile-hood, adolescence, sub-adulthood in males, and adult-hood. In particular the last three categories have special relevance for understanding the orang utan's sociology. Table 1 lists the physical and behavioural criteria used in the field to assign an individual to the appropriate stage (modified after MACKINNON, 1972) (see also fig. 7).

4.2. TAXONOMY

There has been considerable confusion about the nomenclature of the African and Asian apes since their 'discovery' by Western scientists in the 17th century; for instance, the now accepted name *Pongo* LACEPÈDE, 1799 has been derived from the name of a supposed Angolan ape, described by BATTELL in 1613, but presumably founded on an orang utan specimen (GROVES, 1971). Similarly, NICOLAAS TULP in 1641 erroneously described a chimpanzee from Angola as *Satyrus indicus* supposing that it was the same animal as the orang utan which, as SAMUEL BLOEMAART, a merchant of the VOC (Dutch East Indies Trading Company) had told him, displayed great interest for feminine grace in the East Indies (VISSER, 1975).

In a posthumously published work, the physician JACOBUS DE BONDT describes his observations on an orang utan in the East Indies (BONTIUS, 1658), but according to his illustration it is likely that he refers to a local woman suffering from hyper- or para-trichosis; nevertheless CAMPER (1782) has referred to it as the first description of the orang utan. Again in 1718 the orang utan is described by captain D. BEECKMAN in his book *Voyage to and from Borneo*; but the illustration in the book is strongly inspired by (if not copied from) TULP's illustration of the *Satyrus indicus* (the chimpanzee) and lacks typical orang utan characteristics. Also HOPPIUS (1763) based the name *Simia pygmaeus*[3] on a

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[3] It is interesting to notice that CAMPER writes about HOPPIUS' nomenclature: 'Al wat derhalven over de Afrikaansche gezegd wordt, of al wat opgegeven is door de Reizigers van Pangos, Jockos enz., is op den onzen niet toepasselijk, ook konnen wij niet aanneemen 't gene door de algemeene Naamrol-Schrijvers deswegens is opgegeeven, van LINNAEUS bijvoorbeeld, en van zijn leerling HOPPIUS als enkel op zeer oppervlakkige gissingen, gebrekkige onderrigtingen en valsche beschrijvingen gebouwd. Zij hadden den Orang van Borneo, als zij hunne Naamrollen schreven, niet gezien en dwaalden, tegen hunnen wille, omdat zij nergens eene nette beschrijving aantroffen van dit vreemd, en allerzeldzaamst voorkomend gedierte.' (pp. 25–26).

TABLE 1. Life stages of the orang utan.

Life stage	Estimated age	Estimated weight	Physical characteristics	Behaviour characteristics
Infant	0–2½ years	2–6 kg	light pigmented zones around eyes and muzzle contrast with darker facial pigmentation; hair surrounding face long and standing out.	always carried by mother during travel; largely dependent on mother for food; sleeps in nest with mother.
Juvenile	2½–5 years	6–15 kg	facial characteristics as in infant.	still mostly carried by mother, but makes short exploratory trips alone within her field of vision; plays, often alone or with peers; initially still sleeps with mother, but later it builds own nest close to mother; towards the end of this stage mother may bear a new infant and attention for juvenile weakens.
Adolescent	5–8 years	15–30 kg	hair surrounding face still long and standing out; initially facial coloration has the obvious light patches, but changes to completely dark; changes teeth; male and female are difficult to distinguish unless there is full view of anogenital region.	frequent contact with mother; seeks contact with peers, plays with them and moves about with them in adolescent groups; cautious during contacts with adults, especially adult males; sometimes still travels with mother; starts showing sexual behaviour; females are sexually mature at about 7 years.
Subadult male	8–13/15 years	30–50 kg	facial coloration completely dark, with hard rims of undeveloped cheek flanges; beard starts to develop; hair surrounding face short, not standing out but flattened against the skull; testicles completely descended.	this stage commences with sexual maturity and continues until individual is socially mature; avoids contacts with adult males.
Adult female	8+ years	30–50 kg	old females may develop a beard, and are difficult to distinguish from subadult males, if not accompanied by offspring, nipples enlarged.	usually accompanied by offspring.
Adult male	13/15+ years	50–90 kg	extremely large animals; maximal development of secondary sexual characteristics; cheek callosities, beard, throat pouches and long hair.	sexually and socially mature, travels alone, moving cautiously; characteristic vocalization is loud calling: 'long call' (MACKINNON, 1971).

specimen described by Edwards (1758), which probably came from Sumatra, but from which he erroneously supposed the type locality to be Africa (Elliot, 1913).

During the last decades of the 18th century, the works of Arnout Vosmaer and Petrus Camper cleared the confusion surrounding the description of the orang utan. The first live orang utan arrived in Amsterdam on 29 July 1776; the animal had been captured at the request of Vosmaer, director of the Natural History collection of the Stadtholder Prince Willem V. He published a very good account of the behaviour of this animal, an adolescent female, including the first accurate drawing of an orang utan in *Beschrijving van de zoo Zeldzaame als Zonderlinghe Aap-soort, genaamd Orang-outang, van het eiland Borneo* (1778). When the animal died on 22 January 1777, presumably from pneumonia, he had it mounted for the Prince's cabinet, although it had been promised to Camper for anatomical dissection. Through his relation with the VOC, Camper obtained several preserved orang utans about which he gave public lectures in Groningen since 1770.

Then in 1782 Camper published the first extensive and accurate anatomical description of the orang utan in *Natuurkundige Verhandelingen over den Orang-outang*, in which he named the orang utan *Homo sylvestris* after De Bondt, although he strongly opposed the idea that this ape was related to man as was proposed by some of his contemporaries.

All orang utans that reached Europe in the 18th century must have been young animals, and consequently accounts of enormous orang utans of more than *vijf Rijnlandsche voeten* (approx. 1.50 m.) told by people returning from the East, were regarded as fables.

When in 1779 during his voyage in the interior of Borneo the merchant Willem Adriaan Palm managed to shoot an adult male orang utan (Radermacher, 1780), the first account of this ape's behaviour in his natural environment was given.[4]

The animal, which had a height of 4 'rijnlandse voeten' (approximately 1.25 metres), was preserved and shipped to Java where Baron F. von Würmb, secretary of the Bataviaansch Genootschap, dissected and described it (Von Würmb, 1781). This specimen was finally sent to Vosmaer to be placed in the collection of Prince Willem V. Camper considered this specimen to be a new species, as did many other scientists after him (Visser, 1975).

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[4] ...'dien ik' des morgens 8 uren in het vizier kreeg. Lang hebben wij bezig geweest, met allerhande middelen uit te denken om in de diepste wildernis, omtrent halverwege Landak dit verschrikkelijke gedierte levendig te vangen. Zelfs hebben wij dien dag om geen eten gedacht, om hem maar bezet te houden: teffens zorg dragende dat wij van hem niet geraakt wierden; terwijl hij onophoudelijk zware stukken hout en groene takken afbrak en ons daarmede smeet. Dit spel duurde tot in den achtermiddag om 4 uren wanneer wij besloten hem den kogel te geven, hetgeen mij ook zoowel gelukte, en beter dan ik nog immer naar een schijf geschoten heb, want de kogel ging juist in de zijde en in het bovenlijf en dus is het dier weinig geschonden. Wij brachten hem nog levendig in de prauw, bonden hem aan de stijlen van de kaaimatten die ons tot ene tent dienden: alwaar hij, in den morgenstond, aan zijne bekomene wonde overleed' (Radermacher, 1780, p. 43).


a


b


c


d

FIG. 7. The life stages of the orang utan (a) adult female/infant (Bin and Ans); (b) juvenile male (Koen); (c) adolescent male (Mos); (d) sub-adult male (Roba); (e) adult male (O.J.).


e

In 1826, C. ABEL published his account of a large male orang utan of a height over 1.50 metres, which had been sent to him by Commander CORNFOOT who had collected the specimen in Sumatra in 1825.

In 1844, the first monograph on the orang utan was published as a chapter in the excellent work of TEMMINCK (see SCHLEGEL and MÜLLER, 1839–1844), based on MÜLLER's surveys in Borneo during 1828–1836.

The orang utan became increasingly the subject of collectors' attention in the nineteenth century. BECCARI (1856) collected 24, WALLACE (1865) 17, and HORNADAY (1885) as many as 41 orang utans during their respective expeditions and killed an even greater number that were often just left in the trees 'as young animals are of comparatively little interest' (WALLACE, 1869; p. 40).

The disputes over the number of different species or geographical variants bloomed. SELENKA (1896) described as many as 8 different species from Borneo and 2 from Sumatra. It appears that many of the distinctions between the different species were based on age and sex differences, particularly on the sexual dimorphism of males, although the German biologist RUDOLPHI had already demonstrated in 1824 on the basis of anatomical features that the large dimorphistic males belong to the same species as the smaller females (VISSER, 1975). The three most commonly mentioned Bornean 'species' were *Simia Morio*, *Simia satyrus* and *Pongo Würmbii*, while the Sumatran forms were known under the names *Pongo Abelii* or *P. sumatranus*. Based on his experience and collecting efforts in 1855, WALLACE (1865) concluded that at least two different species existed on Borneo. He disputed that these correspond with the three different types of orang utans the local 'Dyaks' distinguish, and he reckoned the vernacular types to be different age-sex classes rather than different species.

Thus, the nomenclature concerned with the orang utan has been remarkably confused, possibly aggravated by the fact that several of the earliest accounts on this ape were written and published in Dutch. The name *Simia satyrus L.* 1766, has gone out of use since STILES (1926) demonstrated that LINNAEUS' pupil HOPPIUS had described this ape three years earlier and hence the correct name should be *Pongo pygmaeus* (HOPPIUS, 1763) (see also GROVES, 1971).

Recent assessments of the geographical variants recognise *Pongo pygmaeus pygmaeus* (HOPPIUS, 1763)[5] from Borneo, and *Pongo pygmaeus abelii* LESSON, 1827 from Sumatra as sub-species. Both races can be distinguished by their general appearance, the shape of the facial mask of adult males and the distribution of hair on the body (CHASEN, 1940; VAN BEMMEL, 1969) and by different morphological characteristics of the hair (MACKINNON, 1974). GROVES (1971) has summarized the main characteristics of the Sumatran orang-utan as:

> '...being larger and lighter coloured than the Bornean sub-species; males have a well developed beard and moustache, also females may have a short beard (and moustache); the face is flatter, more elongate and O shaped (rather than prognathous and 8 shaped...; male's cheek pads are flat and covered with downy tufts of hair (rather then curving forward and being sparsely haired); animals tend to be more muscular or 'linear' in build (rather than tending to obesity – in captivity –); ......; facial colour greyish (rather than blueish...)' (GROVES, 1971).

The indigenous name for the orang utan is *máwas* in Sumatra and *maias* or *mias* in Borneo. Different ethnic groups of the interior of Borneo used other, local, names, such as '*kahieo*' among the Ngadyu (Central Kalimantan), '*keoe*' among the Dusun, and '*kogiau*' among the Kenyah. The local name in Aceh sounds '*máwèh*'.

Although the word orang utan is of Malay origin and literally translates as 'man (from the) forest' (*orang hutan*), it almost certainly never has been used to denote this ape in the regions where *Pongo pygmaeus* occurred (see also NAINGGOLAN, 1931). It appears that JACOBUS DE BONDT first mentioned the name 'orang-outang' (BONTIUS, 1658; see also CAMPER, 1782), which was probably the translation his Malay interpreter gave for the local name. Yet, another possibility is that, since the word 'orang hutan' is used in general to denote a madman or savage human in Malay, BONTIUS actually referred to the strange looking woman shown in his illustration. It was quite remarkable that when we referred to *P. pygmaeus* as 'orang utan' in Borneo and Sumatra, the local people did not understand that we meant the ape, while in Java people only knew the ape as 'orang utan' and did not understand the Bornean or Sumatran names.

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[5] To make the confusion complete; the account on the specimen described by EDWARDS (1758), used by HOPPIUS (1764) to name the orang utan 'pygmaeus' was most likely based on a Sumatran orang utan (ELLIOT, 1913).

4.3. TYPOLOGY

Two morphological types of orang utans in Sumatra

Several authors who describe the Sumatran orang utan from brief field observations, mention two and sometimes even three different types (SELENKA, 1896; VOLZ, 1912; HOOGERWERF, 1936–'38; MILTON, 1964), but these types have not been mentioned as such in the more recent taxonomic accounts (NAPIER and NAPIER, 1967; GROVES, 1971).

The Gayo people, the local inhabitants of much of the Sumatran orang utan's range, distinguish two different types which they call *mawas kudö* (or horse orang utan) and *mawas pròk* (or squirrel orang utan). This differentiation is based on the size, general appearance and colour of the animal (pers. comm., see also HOOGERWERF, 1936–'38). It is an acknowledged fact that size, general appearance and colour can change considerably during the successive life stages, however, the distinction the Gayo people make cannot entirely be attributed to differences related to the stage of development, as WALLACE (1869) has argued for the vernacular 'types' of the Bornean subspecies.

During my own three years of field observations on wild orang utans, and on the basis of close contact with semi-wild and captive animals, I found that, apart from differences related to development, two different types of orang utans can be distinguished within the same range of the subspecies in Sumatra. In their most extreme forms, the two types may be described as follows:

(1). The dark-haired, long-fingered type (fig. 8a).

These animals have without exception dark hair, brown to maroon in colour; their skin and facial colouration is dark brown to blackish. In general appearance they are rather delicately built, with slender extremities, long fingers and toes. They possess a distinct and well-developed thumb and hallux, which both always bear a nail. This type does not attain the enormous size and bulky appearance of the next type, but remains smaller and lighter in weight.

(2) The light-haired, short-fingered type (fig. 8b).

These animals have a reddish-cinnamon to rusty-red hair colour; their skin and facial colouration is light to dark greyish brown. In general appearance they are more heavily built with stouter limbs. Their fingers and toes are short and thick; they have a small or rather rudimentary thumb and hallux. On the thumb the nail may be missing; on the hallux it is always absent.

As far as hitherto ascertained, many intermediates seem to exist between these two extreme forms. Some light haired individuals may show comparatively long fingers and toes while their thumbs and hallux may bear nails. During observations on more than 80 Sumatran orang utans in this study I never met the typical characteristics of the light- or short-finger type orang utan in a truly dark pigmented individual. In other words, while the lighter coloured orang utans may show considerable variation in characteristics, such as long fingers etc. the dark form shows a great consistency in its characteristics and all dark individuals had long slender extremities and invariably had nails on both thumbs and hallux.

FIG. 8. The two types of Sumatran orang utans (a) hands of the long-fingered, dark haired type; (b) face and hand of the short-fingered, light haired type.

One female of the wild Ketambe population (Mif), which showed the characteristics of the long-finger type, had an adolescent son showing clear characteristics of the other, light type. Thus, in the Ketambe population both types co-existed, and indeed even occurred within one kinship-line. In the observed population (n = 22) the individuals displaying the long-finger type accounted for 25%; when regarding all observed Sumatran orang utans, (i.e., wild + Zoo kept + rehabilitant: n = 88) the percentage of long-finger type individuals was 29.5%. (This percentage roughly accords with the 60% of museum specimens lacking the terminal phalanx of the hallux and the nail as in the short-finger type, reported by SCHULTZ, 1956, (see also TUTTLE & ROGERS, 1966). The consistency of the characteristics in the long-finger type, and its relative occurrence throughout the population suggests that its quality is inherited by means of a recessive factor.

A remarkable aspect of the distinction between these morphological variants is, that in their extreme forms, they seem to display marked differences in temperament and in the quality of their behaviour. These differences were most *striking in the rehabilitant orang utans, but where comparisons could be made* concerning certain behaviour complexes, such as for instance 'play', the findings from wild individuals confirmed suggestions derived from observing the rehabilitants' behaviour.

In an attempt to characterize the nature of the short-finger type orang utan, one could say that they are more 'friendly', extrovert and playful, they are often more obviously 'afraid' of new stimuli, and they show 'bluff-behaviour' towards other orang utans and humans more readily. On the other hand, the long-finger type orang utans seem more introvert. They tend to threaten, and attack (see p. 279) rather than display bluff-behaviour, and in particular dark phase rehabilitants demonstrated a striking technical interest and technical skill, and seemed to enjoy solving technical problems. Moreover, we had the impression that they engaged less in social contacts, i.e. they seldom initiated social play. Courtship display preceding copulation was not observed for this type, but again we had the impression that they were more direct in their approach.

It was common knowledge among the former local orang utan hunters that the dark (long-finger type) orang utans made less desirable pets than the lighter ones, because they were assumed to become unpredictable, unmanageable and even dangerous animals in captivity.

Rehabilitant long finger type orang utans (e.g. Usman and Bujong) showed more ready, more intelligent and better coordinated use of primitive tools for a large variety of actions, including the opening of boxes, the forcing of locks, the breaking into a cage (from the outside when the doors were open with no apparent incentive other than the challenge of the problem itself), as well as reaching or 'fishing' for food, for drinking facilities and for inaccessible branches during locomotion. In contrast to these 'technical' applications, the short-finger type orang utans were only observed to use objects in a more crude, imitative and exclusively 'playful' context, that is during intimidation and play activities (see p. 292).

Differentiation between the sub-species

The difference in hair colour was believed to be one of the distinguishing marks between the Sumatran and the Bornean orang utan (VAN BEMMEL, 1968), but as a dark colour variety also occurs in the Sumatran sub-species, such a characteristic largely loses its value.

Our own observations on Bornean orang utans, in the wild state in Tanjung Puting reserve, Kalimantan, in the Sabah rehabilitation station, and in several Zoos, though small in number (n = 31), suggest that this sub-species is generally characterized by dark pigmented skin, a more sturdily built body with correspondingly heavy extremities and short, stout fingers and toes. GROVES (1971) and MACKINNON (1971) mention that Bornean orang utans have a tendency to become obese, and show a more sparse distribution of body hair with males typically naked-showing areas on the face and on the chest.

As the dark coloured Sumatran orang utan typically has the slender build and long fingers, these features could possibly distinguish the dark maroon coloured Sumatran orang utan from its Bornean counterpart. Yet, the observations of WALLACE *(1856) and several other naturalists and taxonomists* (e.g. SELENKA, 1896; HORNADAY, 1885) suggest that the Bornean subspecies may also show considerable variation in morphological features; variations which are reflected by the many different tentative 'species' of Bornean orang utans suggested in the 19th century. It seems therefore rather premature to generalize about the Bornean orang utan in order to give distinctive characteristics distinguishing it from the (variable) Sumatran subspecies.

PART II

ECOLOGY

1. DISTRIBUTION AND POPULATION SIZE

1.1. GEOGRAPHICAL DISTRIBUTION

Today, the two sub-species of the orang utan (*Pongo pygmaeus*) are found only on the islands of Borneo and Sumatra. Prehistoric remains of orang utans, found in caves in the southern provinces of China, North Vietnam, Sumatra and from excavations in Java (for a review, see GROVES, 1971), indicate that the animal's distribution was much greater in ancient times, and probably covered the entire South East Asian peninsula extending into the so-called Sundaland region (DE TERRA, 1943).

Literature concerning the distribution of the orang utan on both islands is comparatively scarce; extensive surveys to assess the ranges have not been conducted yet and most of the former data were based on incidental observations supplemented with information by others. The size of the islands, especially Borneo, and the inaccessability of large parts of its hinterland make such surveys time-consuming and expensive and as such largely impracticable.

Concerning the Sumatran orang utan, SCHLEGEL and MÜLLER (1839–1844) have reported on a live specimen, that S. MÜLLER observed in Padang, south of the equator, and on another, dead specimen collected in Jambi province (p. 5). BECCARI (1904) mentioned that orang utans occur in the northern part of Sumatra only and he explicitely noted Tapanuli province as the most southern region of the range. He also described a specimen collected near Sibolga (BECCARI, 1904; p. 205). VOLZ (1912) reported a distribution range covering the Gayo- and Alas-lands in Aceh and extending into Tapanuli province to the south.

A useful report on the distribution range of the Sumatran orang utan has been given by VAN HEURN (1935). Based on his own long term field experience in the region, on accounts of hunters and planters, and on several references he describes the orang utan's distribution as covering a large part of the Jambu Aye tributary, extending northwards into Aceh province past the (present) Bireuen-Takengon road, and to the south into the Gayo-lands. To the west it included the mountain forest region to Meulaboh in the north, and followed the west coast of Aceh south to Singkil; from there orang utans were found across the Alas (Simpang kiri) river into Pakpak country and Tapanuli province. Of particular interest is his reference to an isolated population south-east of Lake Toba. He also gives references of accounts of sightings of orang utans in the Tapanuli region near Sibolga, and near the Asahan river (i.e. NEUMANN, 1885–1887; HAGEN, 1890 and SCHNEIDER, 1905). An extensive inquiry, carried out by CARPENTER (1938) revealed the orang utan's distribution range to lie almost entirely within the boundaries of Aceh province; he makes no mention of the occurrence of orang utans south-east of the Alas river.

Additional information on the orang utan's range in Sumatra can be found in the reports of several surveys conducted in North Sumatra; unfortunately these were mainly confined to the Alas valley (e.g. HOOGERWERF, 1936–'38, MILTON, 1964 and KURT, 1970).

For Borneo, which is a much larger region, accounts of the distribution of *Pongo pygmaeus pygmaeus* are even scarcer. For a large part of the Kalimantan region, the account of ZONDAG (1931), reviewed by WESTERMANN (1938), is available. In addition there are reports on the surveys and short studies conducted by zoologists (e.g. SCHALLER, 1961; DAVENPORT, 1967; YOSHIBA, 1968 and MACKINNON, 1971, etc.) and other expeditions and surveys (e.g. NIEUWENHUIS, 1907; BUYS et al., 1925), which give an impression of the presence or absence of orang utans in certain localities.

1.2. SURVEYS

In the course of this study, several surveys were made in order to estimate the present distribution range of the Sumatran orang utan and to get an impression of possible changes in the situation since VAN HEURN's (1935) and CARPENTER's (1938) reports.

We travelled by car along almost every accessible road north and west of Lake Toba, in the districts (*kabupaten*) of Tapanuli, Dairi, Karo and Aceh province (formerly Atjeh). From these roads we made short surveys on foot in places where the existence of primary forest suggested the possible presence of orang utans. In fig. 7 the surveys are shown on a map of the northern part of Sumatra with the relevant data concerning the orang utan's distribution.

During these surveys inquiries were made among local people concerning the orang utan's presence in the neighbouring forest. Additional inquiries were made via the Dinas PPA (Nature Conserv. Service) and the Dinas Kehutanan (Forestry service). One survey was made by helicopter to reach the remote and inacessible mountainous area in the south west part of the Gunung Leuser reserve. Several landings were made in small rivers, from where short recces on foot could be conducted. Much of the north eastern part of the Gunung Leuser reserve (Langkat) and the Kappi area was covered during a 12 day march. Similar safaris were made to the Kompas and Renun regions.

The main concentrations of orang utans within the present distribution range are (1) the lowland- and swamp-forests between the Sungei Simpang kiri (southern Alas river) and the Indian Ocean, extending to the north into the Benkung- and Kluet-areas in the southern part of the Gunung Leuser reserve, and (2) the mountainous forest of the volcanic Kappi-plateau extending to the north into the vast mountain forests of the Serbojadi mountain ridge and the lowland forests of the Jambu Aye tributary (see fig. 1).

The northern boundary of the distribution range is the line between Laut Tawar, Krueng Peusangan and Krueng Woya in Aceh. CARPENTER' record (1938) of sightings north-east of this line, as well as VAN HEURN's record (1937) of sightings north of this line were not confirmed in the present study.

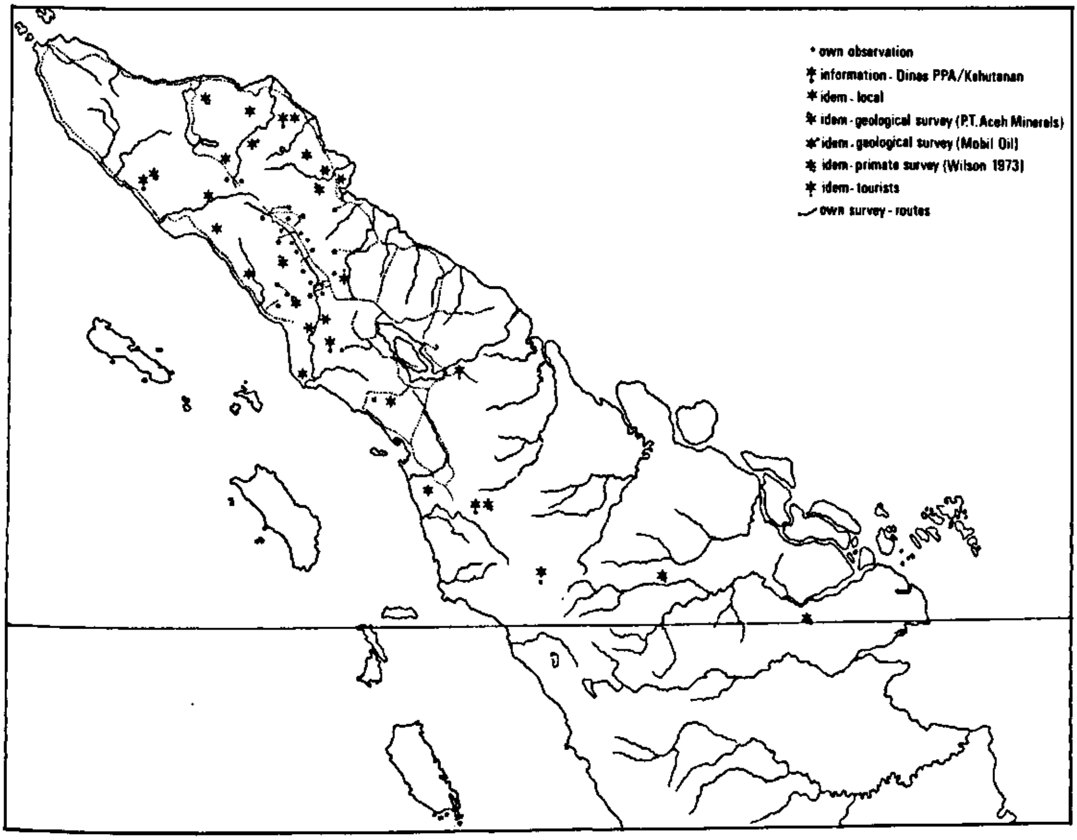


FIG. 9. Map showing the surveys, conducted in North Sumatra in order to assess the orang utan's distribution, and locations of orang utan finds.

The western boundary of the distribution range is a line which roughly follows the road from Keude Pasi through Meulaboh to Tapaktuan and Bakongan some 2–5 kilometers inland. From Bakongan to Singkil and Barus the boundary line follows the seashore. The eastern boundary of the distribution range roughly follows the road from Biruen, through Lhoksukon to Pangkalanberandan, some 4–10 km inland, depending on the degree of disturbance of the forest, and from there it follows the boundaries of the Gunung Leuser reserve (i.e. the Sikundur-Langkat region) to the Sungei Wampu. To the southeast, the limit of the orang utan's distribution is probably the Sungei Wampu, as local informants stated that these apes have not been seen recently in the forests of south Langkat in the Karo district, east of the said river. Nor have orang utans been seen recently in the forest of the Karo highlands around Berastagi and in the Simalungun district. The apes have probably been hunted to extinction in these regions. Only one informant reported to have seen a female orang utan with infant near the village of Torajabernah, but it was not clear whether the locality was north-east, or south-west of the Wampu river. The distribution limits to the south are still not clear. Probably some relict populations still survive in remote regions of the Bukit Barisan mountain ridge in Tapanuli and even further south. During a survey along the west coast of Tapanuli, local informants along the road from the village Pakkat to Barus stated that occasionally orang utans were seen and hunted in the primary forests bordering the road. During a subsequent expedition on foot, one orang utan nest was indeed found in the area.

With regard to the location south-east of Lake Toba, i.e. the Asahan river region, that was mentioned by VAN HEURN (1935), the account of an agricultural expert on a sight-seeing trip with his family to the Asahan region is of particular interest. This informant saw a large red ape slowly climbing a tree in a ravine by the road along the Asahan river in March 1972 (STAALDUINEN, pers. comm. 1972). It is unlikely that the large red haired ape was a gibbon (*Hylobates agilis*), while the described 'slow' locomotion lends weight to the suggestion that the observed animal was an orang utan. A subsequent visit to the region by myself gave no further indications of the orang utan's presence in the Asahan region. Most of the forest in the area has been subjected to considerable disturbance and only scattered patches remain. Yet, this incidental information deserves further investigation as to whether orang utans still occur in that region.

Forestry authorities in West Sumatra reported that orang utans had been seen in the swamp forest of the Batang Toru region, west of Padangsidempuan, as well as in the mountain forests near Hutabaru, south of this large city. It might be argued that the reported sightings concern siamangs, as this hylobatid is often confused with the orang utan in this region. Yet, details given with some of the reports, such as 'red haired', etc., suggest that at least two of these sightings were of orang utans.

Local information gathered during a primate survey conducted by W. and C. WILSON in 1972, also revealed that orang utans were reported from three localities south of Lake Toba, i.e. near Rimbo Pantai reserve, near Kota Badak, north of Pakanbaru, and near Sungei Kampar, south of Pakanbaru. The last two localities are in Riau province.

If we consider both VAN HEURN's and CARPENTER's accounts, we can see that the distribution range of the Sumatran orang utan has shrunk by 20–30% since 1935–1938. The rainforest, especially on the periphery of the ape's former range has been subjected to extensive habitat destruction, mainly by 'ladang' practices. The more recent timber exploitation will accelerate this destruction proces considerably (see chapter: Conservation).

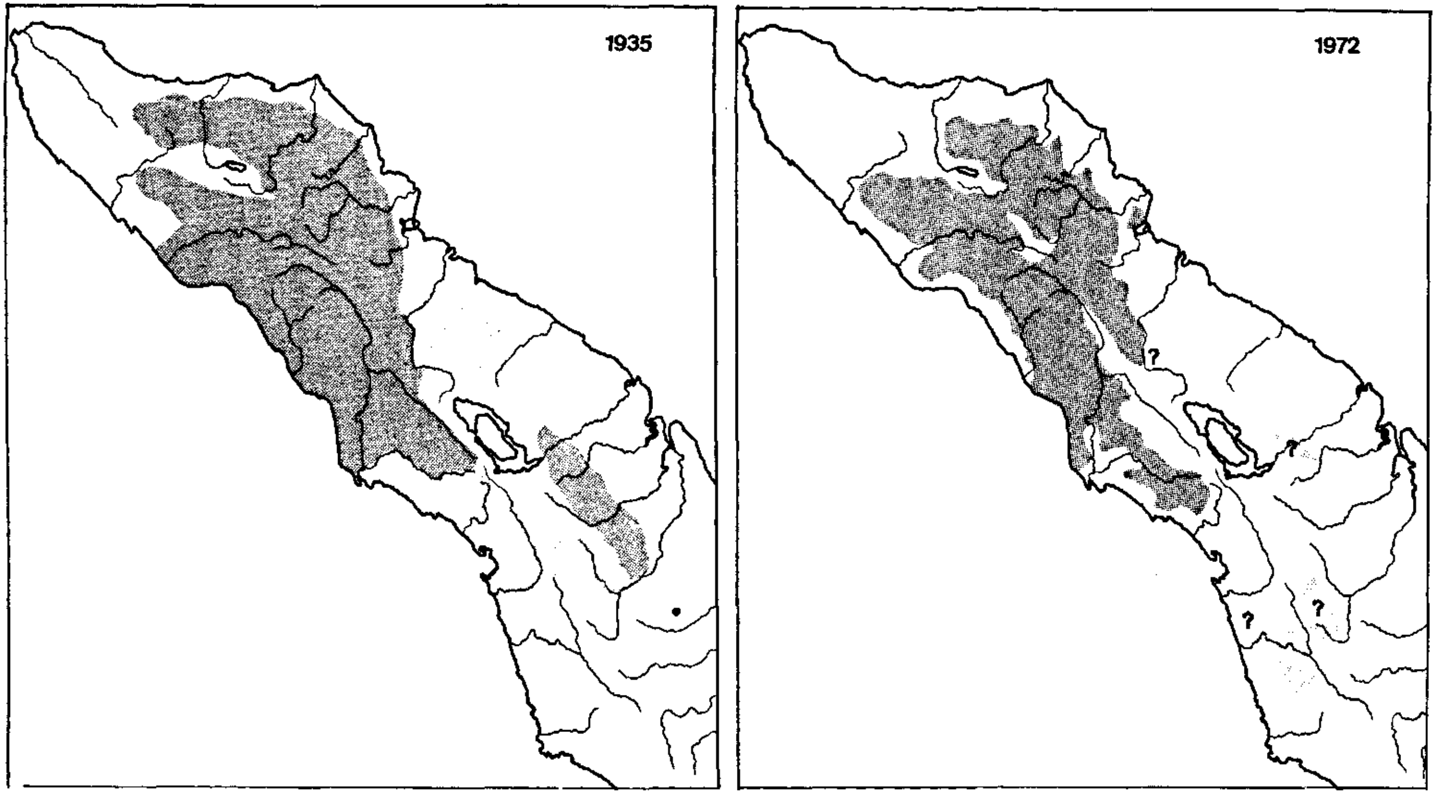


FIG. 10. The change in orang utan distribution; (a) situation in 1935 (after VAN HEURN, 1935 and CARPENTER, 1938); (b) present situation.

1.3. ALTITUDINAL ZONATION

Nearly two thirds of the present distribution range of the Sumatran orang utan is mountainous country including vast mountain complexes and wide plateaus at altitudes between 1000 and 2000 meters (e.g. Gunung Leuser, Gn. Kemiri, Gn. Mamas, Gn. Bandahara and Gn. Goh Lembu).

Surveys into the mountainous parts of the orang utan's range revealed that this ape can occur at altitudes well over 1000 meters. Several authors have considered the 1000 m altitude to be the upper limit of the ape's range (SCHALLER, 1961; CARPENTER, 1937; KURT, 1971) though there are some accounts of observations from higher altitudes (BANKS, 1931; GUAN ANAK SURENG, 1961; MILTON, 1963). Orang utans occurred on the Kappi plateau (1000–1400 m) as well as in the Central Rift Valley of the Gunung Leuser reserve (1200–1500 m). From the number of nests found and animals seen there is no reason to assume that the population density at this altitude was significantly less thans elsewhere. In the mossy forest on the escarpment of the Gn. Mamas massif, a calling orang utan male was found at an altitude of approximately 1700 m, while nests seen in that region indicated the occurrence of more of such apes. The occurrence of *Ficus* sp. (strangling figs), several species of *Fagacaea*, rattans and other vines and an abundance of many different species of epiphytic plants in mountain forest (see also RICHARDS, 1952) may provide convenient habitat conditions for the orang utan's existence. It is possible that the absence of certain specific food plants, notably strangling fig species, at higher altitudes, rather than climatic conditions limit the orang utan's distribution. The orang utan's abilities to store fat and to conserve body heat during the night by using a nest cover, (see p. 153), probably enable it to stand the intensive cooling off during the nights high in the mountains.

1.4. VARIOUS ORANG UTAN HABITATS

Considering his distribution range, it appears that the orang utan is well adapted to several different primary forest types, from the swamp- and lowland (Dipterocarp) forests at sea-level to the hill- and mountain forests at higher altitudes.

Orang utans were observed in the extensive swamp forests of the Kluet reserve, and they are known to occur in many other swamp areas throughout their distribution (SCHALLER, 1961; GALDIKAS-BRINDAMOUR, pers. comm., 1974). Orang utans generally were not afraid of open water, especially when it was stagnant. A sub-adult male orang utan, encountered in the swamp forest of Kluet reserve fled along partially flooded ground. In Borneo, orang utans have been observed to wade waist deep in swamps and streams in order to collect certain fruits, i.e. *Pandanus* (HORNADAY, 1885), or feed from certain grasses (GALDIKAS-BRINDAMOUR, pers. comm., 1974).

It has often been attempted to estimate the population density of orang utans in certain regions on the basis of nest-countings along transects (e.g., HARRISSON, 1961; SCHALLER, 1961; MILTON, 1964; KURT, 1970). The number of individuals per kilometre square was then calculated by means of the equation:

$d = N/x.\,c$

in which (d) stands for the population density; (N) for the number of found nests; (x) for the distance surveyed; and in which (c) represents a factor, being the product of the observation distance on either side of the track and the number of nests built by one individual orang utan in the period that an average nest remains visible (KURT, 1970).

It is noteworthy that the above authors all used different figures for the period they assumed a nest to remain visible. The figures range from 2 (KURT, 1970), and 4 (MILTON, 1964), to 6 months (SCHALLER, 1961). With respect to the number of nests built per day, they agreed unanimous upon 1 nest per orang utan per day. Thus, the factor (c) alone showed a discrepancy, exaggerated by a factor 3.

We tried to find a figure for the durability of orang utan nests in the Ketambe area by mapping 30 nests on the day that they were built, and checked these at monthly intervalls. In fig. 11 the results are shown, indicating the trend that nests stay visible for approximately $2^{1}/_{2}$ months with a variation ranging from two weeks to more than a year.

The durability of an orang utan nest in the Ketambe area depended on the individual orang utan's construction technique, his size and weight, and probably on his 'mood', on the tree where it was built and on the location, on the prevailing weather and on the chance that it was pulled to pieces and destroyed by another orang utan or by long tailed macaques in search of insects.

In at least five occasions we noticed that nests were re-used and rebuilt, or were provided with a new lining. As will be described on p. 151, orang utans might build more than one nest per day. Such nests were either resting- or play-platforms; young orang utans especially, might build a large number of such nests per day. From a number of 36 orang utan days, we calculated that an

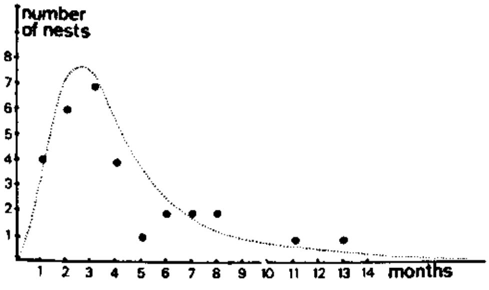


FIG. 11. The life-time in months of orang utan nests (n = 30).

orang utan builds an average number of 1.8 nests per day (range 0–6). Thus, when arbitrarily taking the average observation distance in rainforest on both sides of a trail to be 25 metres, the factor (c) amounts to 6.75.

The above equation is based on a number of assumptions, notably that (a) orang utans distribute their nests randomly over an area, and consequently that (b) an observer will have a high probability of finding a representative number of such nests. However, orang utans do not distribute their nests in a random fashion over an area; the distribution pattern may be related in particular to the spatial distribution and the seasons of certain preferred fruit trees, and to the topography of the region. Orang utans appear to prefer vantage points for their nest location (fig. 12), as has also been reported by KURT (1970). Consequently, the probability of finding a representative number of nests does not only correlate with the skill and experience of the observer, but also with his familiarity with the area. Conservation surveys are usually carried out by observers who are not familiar with the regions for which the data are needed. Consequently, they may result in consistently too low figures for (N).

In order to test the variation in (N), we made several nest counting surveys in

FIG. 12. An orang utan nest at a vantage point.

the Ketambe area, in particular because the population density was known and the observers were very familiar with the area. The surveys can be grouped in three categories, (a) those by an inexperienced observer (either a guest, or myself during the earliest stages of the study), (b) those by experienced observers, and (c) those carried out simultaneously by two observers (October 1973) and by three observers (December 1973) on one day along different routes. The results are shown in table 2 (also fig. 13). It illustrates the variation in numbers of nests per kilometre (range 1.2–27.8) in one area, dependent on the date of surveying and on the chosen route through the area. The census conducted in October 1973, that led past a large esteemed fruit tree gave a result of 24 nests per kilometre more than another one on the same day, only 400 metres away from the first (see fig. 13). A total of 30 nests were counted in the immediate vicinity of the fruit tree, most of which served the apes as resting- or play-platforms. None of these nests, however, had been used for sleeping at night, although even an experienced observer would not have noticed the difference. Similar clumpy distribution of a large number of orang utan nests has been reported by MACKINNON (1974); KURT (1970), who noticed such concentrations of nests near Seldoq, in the Alas valley, even spoke of 'villages'. Obviously, such large numbers of nests do not indicate a high local orang utan density; it illustrates that caution is needed in interpreting the data. With reference to the best estimate for the population density (5 orang utans per km.sq.; see p. 159) the application of the data from table 2 to the equation gives density figures which are on average a factor 15 too small.

Thus, nest counting surveys, notably those leading through unfamiliar country cannot be used *per se* for proper assessment of the population density

TABLE 2. Variation in the calculated orang utan population density based on different nest counting surveys in the Ketambe study area.

census date	distance covered (x)	number of nests per km.	'calculated' density (d) of orang utans/km.sq.
a. inexperienced observers			
Sep. 1971	5000 m.	1.2	0.2
Dec. 1971	5000 m.	1.8	0.3
May 1974	4390 m.	1.8	0.3
b. experienced observers			
May 1972	1450 m.	2.1	0.3
Mar. 1973	3200 m.	2.5	0.4
Sep. 1973	5350 m.	1.9	0.3
c. several experienced observers (see fig. 13)			
Dec. 1973	1120 m.	6.3	0.9
Dec. 1973	1510 m.	11.3	1.5
Dec. 1973	1600 m.	6.3	0.9
Oct. 1973	1550 m.	3.9	0.8
Oct. 1973	1220 m.	27.8	4.1

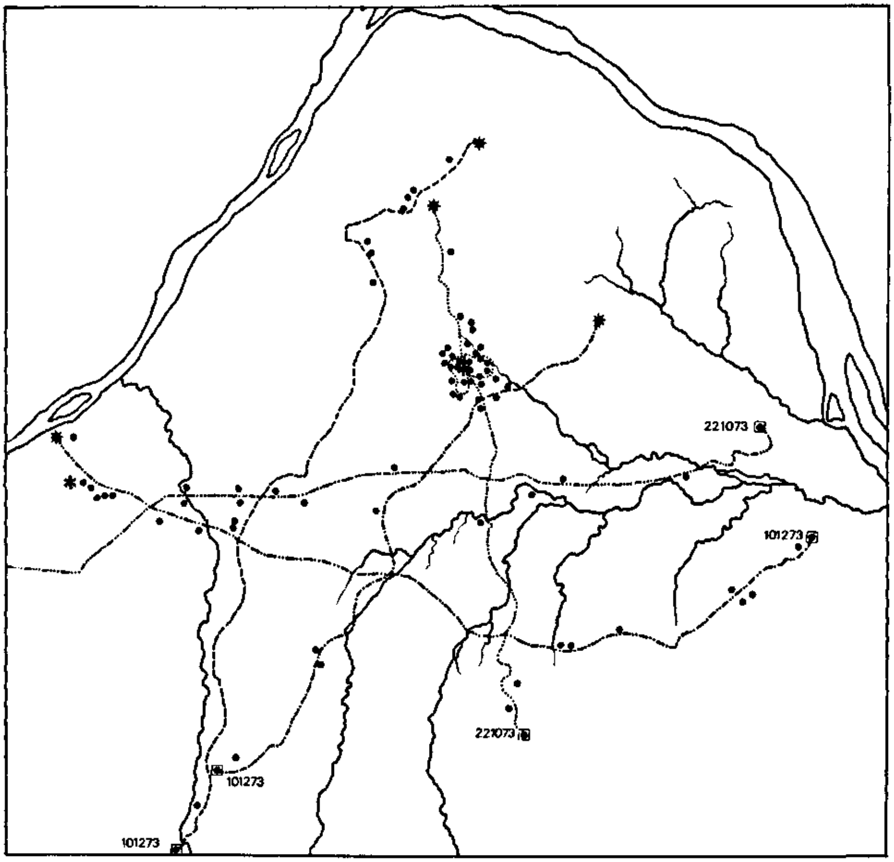


FIG. 13. Distribution of orang utan nests along 5 transects.

of orang utans, unless a method is developed to cover a large, and statistically representative sector, the results of which are computed in an equation that includes most of the variables. In practise, nest counting surveys only give an answer to the question whether or not orang utans are present in a certain area. However, in conservation practice, nestcounting surveys may have some value in comparing densities in the same area in different periods, e.g. before and after disturbance. Such surveys provide a comparatively easy method to assess the effects of disturbance in particular when time is a limiting factor for conducting alternative, more sophisticated populations studies.

1.6. POPULATION ESTIMATES

In 1960, the total wild orang utan population in the world was estimated at around 4000 individuals (HARRISSON, 1960); a figure entered in the IUCN Redbook (SIMON, 1966) which gave the orang utan the status of a 'highly endangered species'. The figure appears to be biassed by a very proper concern for the excessive pressures on this ape in the form of hunting for the animal trade and the starting boom in timber exploitation, as well as by inadequate data from the field concerning distribution range and population density.

As for the Sumatran orang utan, only very scant data have been available until now. In 1963, after a two months survey in the Alas valley, MILTON (1964) estimated the entire orang utan population in Sumatra to be between 800 and 1500 individuals. It is interesting to note that he calculated that at least 140 orang utans were smuggled out of Sumatra annually; a figure which, since mothers are killed to capture their young, implies the yearly loss of at least 280 individuals (30–50%) from the estimated wild population. This would have meant that for a slow-breeding ape like the orang utan, the entire population would have been eradicated by 1970.

Unfortunately, it is often necessary to exaggerate the endangered status of a particular species to achieve urgent conservation measures to save relict populations. However, gross underestimates of population size may have the opposite effect in that anti-conservation interests can exploit any inaccuracy that comes to light, to query the endangered status of the animal.

After a three months' stay in the Alas valley in 1970, KURT (1970) estimated a total of approximately 5000 Sumatran orang utans, of which some 930 were reported to live within the boundaries of the Gunung Leuser reserves. MACKINNON (1973), who studied the Sumatran orang utan for approximately 6 months, does not give estimates for the total Sumatran population but gives density figures for several areas he surveyed. These figures are in the order of less than one to a maximum of two animals per square kilometer.

While in earlier studies and surveys the orang utan population densities were estimated to be as low as 0.1 to a maximum 1 individual per square kilometre (see SCHALLER, 1961; MILTON, 1964; KURT, 1970, etc.), more recent studies on the orang utan's behaviour and ecology (this study; RODMAN, 1973; GALDIKAS-BRINDAMOUR, pers. comm.) have shown that orang utan density may, in some places, be as high as 3–5 animals per square kilometre. The discrepancies in the estimates may be due to differences in the carrying capacity of the different areas, or due to the consistently low population density figures obtained by means of the nest counting method.

Taking into consideration our own impressions acquired during comparative surveys throughout the animal's distribution range, and the figures given by other authors, it seems reasonable to estimate a density of 0.5 to a maximum 1.5 orang utan per square kilometer as a standard for the entire range. The present distribution range of the Sumatran orang utan (see fig. 14) covers approximately 30,000 km.sq., of which some 20,000 km.sq. is mountainous with summits reaching over 3000 m altitude which is no suitable habitat for orang utans. If we consider that, of the total area of the distribution range, only one third is suitable orang utan habitat, the total number of orang utans in Sumatra can be estimated to be in the region of some five to fifteen thousand individuals.

As at least two thirds of the forest within the distribution range of the Sumatran orang utan is liable to imminent destruction due to recently awarded timberconcessions and a steady increase of slash and burn agriculture, this estimate must be regarded as critically small for a population that represents a distinct subspecies (see also the chapter Conservation).

Because of the unstable conservation situation in Indonesia, I would recommend great caution in interpreting the data presented here for the orang utan's population size. Certainly there is little cause for complacency or optimism about the future of this species.

Concerning the Bornean orang utan earlier reports only mention that this ape is rare in almost every location (ZONDAG, 1931; WITKAMP, 1932; DAMMERMAN, 1937; WESTERMANN, 1938). During a two months' survey SCHALLER (1961) estimated the total population present in Serawak as between 450 and 700 individuals, mainly distributed along the boundary with Indonesia (Kalimantan). In a preliminary survey in Sabah, OKANO (1965) reported that orang utans were relatively numerous in that country although he saw only one animal in 52 days. DAVENPORT (1967) reports that the orang utan in Sabah is becoming increasingly rare, a statement which appears to be at least partly based on local information. The subsequent longer studies carried out by MACKINNON and by HORR revealed population densities of orang utans of less than 1 to 2 animals per square kilometre respectively (HORR, 1972; MACKINNON, 1971), though the figures given by MACKINNON may even be obscured by the fact that he studied a temporary situation in a population that appeared to 'wander over enormous areas' (MACKINNON, 1971: p. 184). MACKINNON (1971) has estimated the total orang utan population in Sabah to be between two and three thousand individuals.

The distribution range of the orang utan on the island of Borneo is insufficiently known to give reliable estimates. In some regions orang utans reportedly do not occur: thus between the Barito and Mahakam river – south-eastern part of Kalimantan – orang utans have not been seen since historical times (ZONDAG, 1931). The area north-west of the Kutai region, (see fig. 14), has rarely been visited by explorers interested in wildlife (e.g. BUYS et al., 1927) and hence the ape's presence in that region has never been reported (WITKAMP, 1932; HARRISON, 1961), although the distribution pattern to the south (Kutai) and to the north (Sabah state) would suggest a continuous range.

From the absence of orang utans in regions which are known to have had the longest human inhabitation, it may be postulated that this ape has been, and probably still is subjected to human persecution in some areas. In addition, the large scale timber exploitation which threatens to destroy most of the Bornean rainforest ecosystem within the near future (see p.350) cannot be monitored with

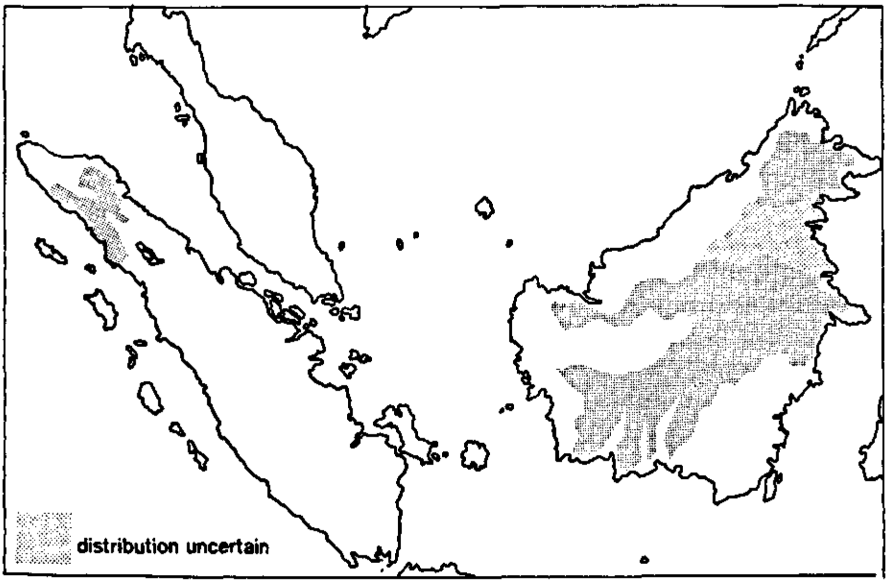


FIG. 14. The present distribution of orang utans in Sumatra and Borneo.

regard to the extent of destruction, illegal hunting and other violations against the regulations. Thus, it is impossible to give an estimate of the Bornean orang utan population, although the estimated area of orang utan distribution suggests that the total Bornean population could be as much as six times larger than the Sumatran population.

Since even the very small proportion of habitat that has a reserved status on Borneo (some 3%) is liable to extremely destructive commercial logging (MEIJER, 1974; KARTAWINATA, 1974) the situation concerning the status of the orang utan is as grave as ever, notwithstanding the fact that the numbers of still surviving orang utans may be considerably higher than previously suggested.

2. THE HABITAT

In order to compare the orang utan's habitat in the Ketambe area with other primate habitats, I present some of its most characteristic features. As yet there has been no intensive study by a trained botanist to give a proper description of the complexity of the rainforest habitat in Ketambe and this section can do no more than present a limited and rough picture of the situation.

The data used in this description come from several different sources; the food plant collection has been identified by staff members of the Rijksherbarium in Leyden, and is stored there. In addition, they kindly made provisional identifications of several plants and herbs from colour slides. The vernacular names were provided in the field by Mr. G. AMAN SAR of Seldoq, and were transcribed with the tree list of HILDEBRAND (1950).

2.1. HABITAT CHARACTERISTICS

The forest in the Ketambe area (fig. 15) can be classified as a mixed rainforest association, belonging to the upland, or hill category (RICHARDS, 1952). Characteristics of this type of forest are the absence of dominance by a single tree species, stratification in which the lower strata (B or C) form a closed

FIG. 15. The Ketambe area seen from the West (aerial photograph).

canopy and abundant herbaceous ground-covering vegetation (RICHARDS, 1952).

As may be conjectured from the travel journal of VOLZ (1912; p. 150), there has probably been some human influence in the Ketambe area for a century at least (see also p. 11). Therefore it seems appropriate to use, instead of the term 'primary forest', the description for rainforest given by POORE (1968) as a '... complex mixed forest with a fluctuating mean composition which has remained in dynamic equilibrium with its environment' (p. 145–146). Yet, the strong similarity in physiognomic aspect (and in general terms in species composition, at least as far as orang utan food-plants are concerned) of the Ketambe forest and of some forests in remote regions (e.g. the Mukap area in the Central part of the reserve) suggests that human influence has taken place on a limited scale only.

2.2. FOREST STRUCTURE

In order to describe the forest structure in the Ketambe area, the distribution of three arbitrarily chosen forest types were mapped. The chosen types were:
1) high forest: composed of a variety of trees among which those with girth larger than 80 cm occur in a density of 5 or more in the field of vision, and most trees are higher than 35 metres.
2) medium forest: composed of a variety of trees among which those with girth larger than 80 cm occur in a density less than 5 in the field of vision and most trees are higher than 20 metres.
3) low forest: mainly containing small trees of girth less than 80 cm; most trees do not reach 20 metres height.

Typically, high forest was comparatively easily to traverse, with a less dense ground cover including saplings and scattered bushes of *Elatostema rostratum*. The medium forest had abundant herb and bush vegetation at groundlevel, while the low forest was a dense tangle of smaller saplings, lianas and bushes that was difficult to penetrate in places. Fig. 16 shows the distribution pattern of these forest types. It appears to follow a pattern that can be related to the soil conditions in the area, as well as to the profile of the region, although the latter is not consistently detectable from the profile figures drawn from the transects (fig. 17). The medium forest was predominant on the steeper slopes in the area, and also connected the low forest vegetation of badly drained regions ('swamps') with the high forest on the drier parts of the area. The lowest forest type was mainly found on the sandy riverdeposits and in the swampy regions, where high trees appeared to be liable to topple over during violent rainstorms.

All stages of the regeneration cycle, typical of the rainforest, are found in the Ketambe area. Gaps in the vegetation were almost exclusively caused by the fall of large trees. Such gaps could be very wide (30 × 50 metres) because a falling tree dragged several others down and also damaged those on which it fell.

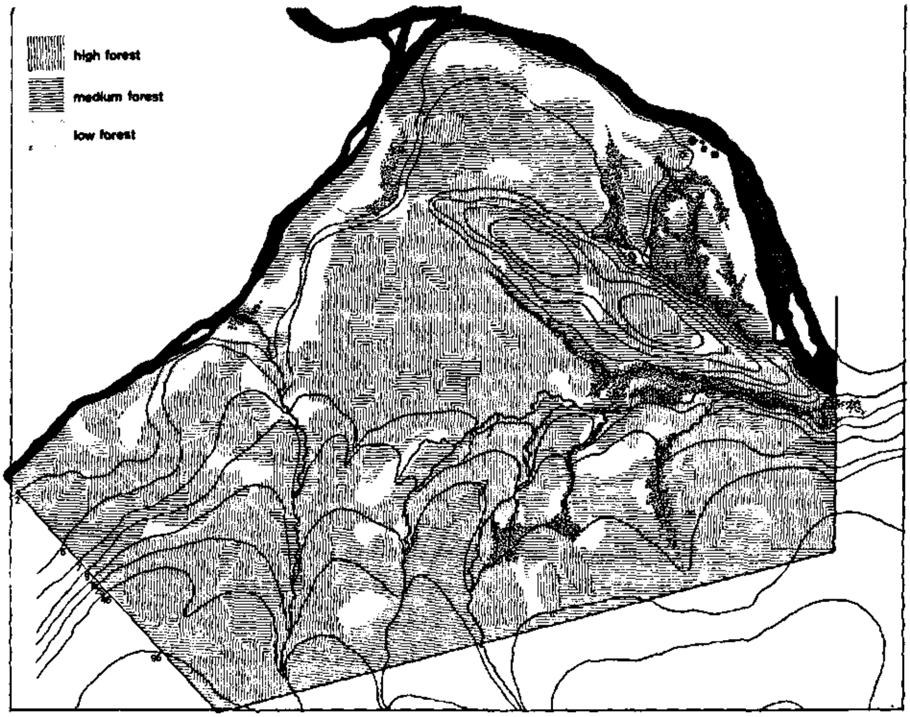


FIG. 16. The distribution pattern of three forest types in the Ketambe area.

In general, the vegetation cover in the Ketambe area is mainly composed of high forest (35–50 m. height), interspersed with large patches of medium forest (20–35 m. height). A very characteristic aspect in many sectors of the area is the almost continuous ground-cover of herbaceous vegetation.

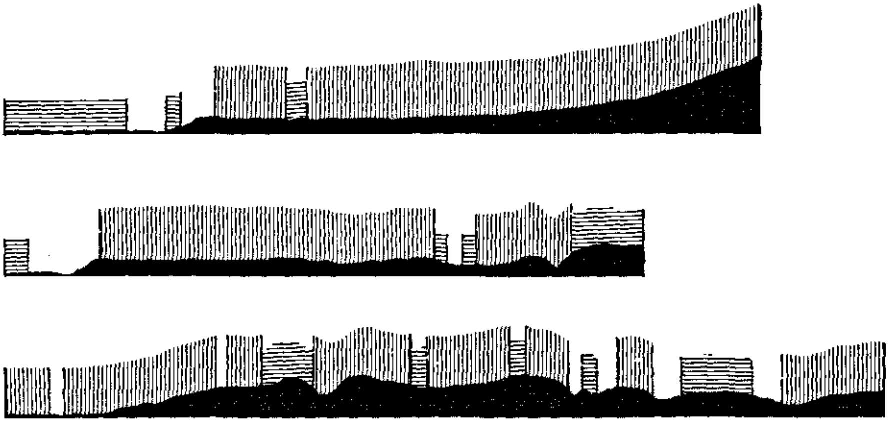


FIG. 17. Forest types along three transects (see fig. 27); profile diagramme.

2.3. SPECIES COMPOSITION

To characterize the species composition, and illustrate the pattern of diversity of tree species throughout the Ketambe area, inventory samples were made along three different transects that traversed the entire study area. All trees with a diameter greater than approximately 15 cm, which stood within 5 meters of both sides of the trail were mapped and recorded by vernacular names. Although this is a rather inaccurate method, it allows one to make useful comparisons with different primate habitats sampled by a similar technique (cf. MACKINNON, 1971; 1973).

The average number of trees with a diameter wider than 15 cm per hectare is 475 on a sampled area of 4.5 ha. A total of 2,137 trees were recorded, of 111 vernacular 'species'. It was noted that the the local tree expert showed the greatest consistency in naming those tree species that have edible fruits for man (and orang utan), and those that are considered as common, (valuable) timber trees.

In cross checking the vernacular names with the scientific names of the collected food-plant species, it becomes apparent that one vernacular name may be used for several species in a genus. Moreover, vernacular names such as *balik angin* (which literally means 'turn in the wind'), and *pagar anak* ('children's fence') were used for several species of different genera (see also HILDEBRAND, 1950). The number of species will probably be considerably higher than the 111 described by the tree expert. The tree expert could not give vernacular names for 6.8% of the recorded trees.

Although the number of individual trees corresponds closely, the number of species is rather low when compared with some other South-East Asian rainforest areas. For instance, a total of 559 trees per hectare, of 227 species has been recorded for a lowland rainforest near Kuala Lumpur, Malaysia (WYATT-SMITH, 1949); the most abundant species accounted for less than 7% of the total. However, in his study in Sabah (Borneo), MACKINNON (1974), who also had to rely on vernacular names, found a tree density of 436 trees per hectare, belonging to 'over 88 different species' (p. 9). This may indicate that in structural aspect, the Segama- and the Ketambe habitats are rather similar; however, in species composition as well as in physiognomic aspect, the areas differ markedly (MACKINNON, pers. comm.).

From descriptions in the literature (WYATT-SMITH, 1952; POORE, 1968; WHITHMORE, 1975), and my own impressions from other rainforest regions, the density of *Dipterocarpaceae* in the northern Alas valley in general, and in the Ketambe area in particular, was low, possibly due to the higher altitude of the region (i.e. over 350 metres).

Dipterocarpaceae (3.6%), *Bombacaceae* (i.e. *Durio spec.*, 0,8% and *Bombax valetonii*, 0.2%) and some extremely large strangling fig trees (3.1% of the total tree species: e.g. *Ficus benjamina* and *F. drupacea*) were among the main emergents in the Ketambe area. Such trees only rarely combined in a closed canopy.

Among the most common genera in the area are *Aglaia* (11.4‰) *Mastixia* (8.5‰), *Walsura* (4.2‰), *Litsea* (4.1‰), '*medang*' (cf. *Lauraceae*) (4‰) and '*djerik*' (cf. *Eugenia*) (3.8‰); these form the main elements of the middle canopy layer. Common genera in the lower stratum are *Xerospermum* (4.8‰), *Castanopsis* (3.1‰), '*babi kurus*' (cf. *Drypetes*) (2.5‰), *Macaranga* (2.2‰) and *Garcinia* (1.9‰) (data from FERNHOUT, unpublished report, 1974).

Gaps in the vegetation, whether caused by fallen trees or human activity, particularly when wider than 8–10 m in diameter, gave rise to a secondary succession in which *Macaranga diepenhorstii* was predominent. In older secondary growth, reaching over 15 meters high, other genera such as *Mallotus* (*Euph.*), *Bischofia* (*Staph.*), *Eugenia* (*Myrt.*) and *Turpinia* (*Staph.*) were common. Apparently these had been able to displace the pioneer vegetation of *Macaranga* (*Euph.*).

The abundance of the genus *Ficus*, both in species and in individuals is a major feature of the South-East Asian rainforest (CORNER, 1952), as is the abundance of climbers and lianas (RICHARDS, 1952), two elements which play an important part in the structure and physiognomy of the forest. Several different species of *Ficus* were found in the Ketambe area, displaying all the highly interesting life forms so characteristic of this genus (see CORNER, 1952) (see table 3). Thus several species grew as (a) free standing trees, usually these were cauliflorous; others occurred as (b) terrestrial shrubs, sometimes growing in (c) epiphytic style on others. Some species grew like (d) climbers covering the trunk of their host with dense bushes. Yet the most impressive, and from the orang utan's point of view, most important group was (e) the strangling figs. At least eight different species of strangling fig grow in the Ketambe area. The seedlings of the large strangling figs usually germinate on the tall emergent of the upper storey, sometimes on the higher trees of the middle storey (CORNER, 1952). Apart from their importance for orang utans, strangling figs also play a major role in the diet of several other animals, notably the hylobatids (CHIVERS, 1974) and the hornbills. The relative abundance of strangling figs in the tree inventory amounted to 3.1‰, which groups them among the common genera in the Ketambe area. Additional remarks on this important genus are to be given on p. 67 and 364–365.

TABLE 3. The different life-forms of *Ficus* species found in the Ketambe area.

Free-standing trees	Terrestrial shrub	Climbing-creeping shrub	Strangling trees	Epiphytic shrub
F. racemosa *F. glandulifera* *F. pubinervus* *F. benjamina* 2 spp. indet.	*F. obscura* (3 varieties)	*F. parietalis* *F. subulata*	*F. benjamina* *F. glaberrima* *F. annulata* *F. virens* *F. elastica* *F. sundaica* *F. drupacea* *F. stupenda*	*F. obscura*

Although no quantitative data on the synusiae of the lianas and woody climbers were gathered in the Ketambe area, their abundance in species as well as in individuals was evident. Lianas have always been regarded as weeds by foresters (Fox, 1969) and their systematics and ecology remains considerably less well-known than that of the economically more valuable tree species (Jacobs, 1976). Illustrative of this comparative ignorance is the fact that one liana occurred among the orang utan food plant collection (i.e. *Brousonetia kurzii*; *Morac.*) that had not been reported previously for the Malesian region (De Wilde, pers. comm.; Jacobs, 1976). The woody lianas may constitute more than 8% of all flowering plants in the Indo-Malayan rainforest (Schenck, 1892 quoted in Richards, 1952); the percentage of true lianas in the sample of utan food plants (which is clearly a biased sample) amounts to 17.6%. A liana common in the Ketambe area in places where fallen trees had opened up the canopy and allowed secondary succession, was *Acacia pennata* (*Legum.*).

A large number of trees in the Ketambe area served as hosts for climbers and epiphytes, a phenomenon perhaps correlated with the altitude of the region, with the relatively open canopy structure and with the microclimate governed by two confluencing rivers. The most abundant climbers of the lower and middle storeys belong to the genus *Aracea*, notably *Rhaphidophora foraminifera.*

The most commonly occurring herbaceous shrub in the Ketambe area is *Elatostema rostratum* (*Urtic.*: '*sesirung*'). Among the herbaceous ground-covering plants, the most common genera are *Cyrtandra* (*Gesn.*), *Strobilanthes* (*Acanth.*), *Forrestia* (*Comm.*), *Pilea* (*Urtic.*) and *Asystasia* (*Acanth.*).

In open places and clearings along the rivers a ground-covering *Graminae* (*Centhoteca latifolia*) is found, while in clearings (e.g. feeding site of the rehabilitation station) and open places deeper in the forest, the grass *Axonopus compressus* soon sprouted and could form a fast closing mat.

3. FOOD

3.1. FOOD IDENTITY

Even the earliest accounts of wild orang utans mentioned that these apes were predominantly frugivorous. SCHLEGEL & MÜLLER (1839–1844) even specified the diet; they noted that orang utans display a preference for certain fruits, notably '*Pohon tielap* (*Ficus infectoria*), *Pohon doeatak-banjoe* and *Pohon kampoeak*' (p. 20). They continue:

> 'Behalve deze en meer andere vruchten, voornamelijk vijgen, bestaat het voedsel van den Orang-oetan in vruchtknoppen, bloesems en jonge bladeren van verschillende boomen, heesters en struiken' (p. 20);

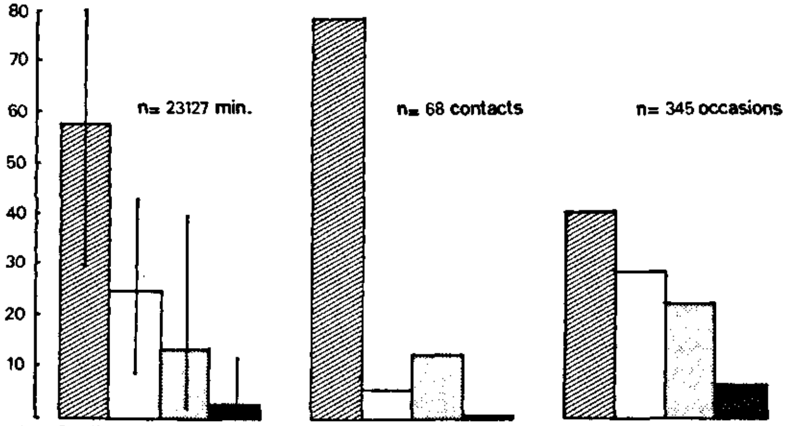
thus, apart from stressing the importance of several species of *Ficus*, making mention of buds, flowers and leaves. Moreover they reported strips of bark and several intact seeds of *Sandoricum indicum* in the stomach contents of a collected adult male specimen. In 1856 BECCARI (1904) added insects to this list of food categories. Recent studies, notably MACKINNON (1974) have extended and specified the list of food plant species. Thus, the food of the orang utan can be grouped according to five main categories, namely: fruits, leaf material, 'bark', insects, and miscellaneous food items.

The orang utans in the Ketambe area were observed to feed on 92 different kinds of fruit, 13 different kinds of leaves, 22 sorts of other vegetable material such as top-sprouts, pseudobulbs of orchids (fig. 18), flowers and the growth layers of certain trees, 2 kinds of aerial roots and stems of climbers and at least 2 species of epiphytic fungi. In addition they ate at least 17 species of insects, bird's eggs, cob webs and several leaf-galls. Occasionally earth from termite mounds or soil was ingested in small quantities.

FIG. 18. Feeding on pseudobulbs of an epiphytic orchid.

The apes drank water from natural bowls in trees where rainwater had collected, or they licked rainwater directly from leaves or from the hairs of their arms during the frequent rains.

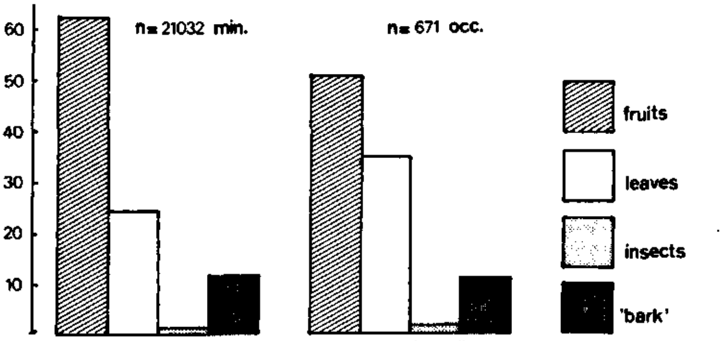
Fruits, leaf-material, insects and 'bark' were the most frequently recorded categories for which the quantitative data are given in fig. 19. The histogram shows the relative frequencies of feeding time for these four categories throughout the year 1973. On a total of over twenty-three thousand minutes of recorded feeding, 58% of the time was spent feeding on fruits, 25% on leaf material, 14% was spent in search for insects and some 3% represented feeding on bark or chewing on wadges. The time spent in actually feeding on insects, especially small insects, is almost impossible to record from the average observation distance in the forest. Consequently, I recorded the time spent in searching for and collecting insect food, rather than the actual feeding time. This implies that



% feeding time per category KETAMBE area

feeding activity per category at moment of first contact

occasions of feeding per category



% ‹time›
KUTAI region Borneo
from RODMAN 1973

‹occasions of feeding›
ULU SEGAMA region Borneo
from MACKINNON 1974

FIG. 19. Comparison of the relative frequencies of feeding duration and other measures of feeding activity for 4 food categories between Bornean and Sumatran orang utans (Bornean data after MACKINNON, 1974 and RODMAN, 1973).

the heading 'feeding on insects' in the table includes a relatively larger proportion of searching behaviour than the other headings concerned with fruit-, leaves- and 'bark'-food. These data differ slightly from those reported for Bornean orang utans by MACKINNON, (1974), and RODMAN, (1973); (see fig. 19).

Bornean orang utans apparently spend more time feeding on 'bark' than Sumatran animals, but the latter appear to spend more time searching for insect food. The orang utans observed by MACKINNON (1974) showed a higher incidence of feeding on leaf-material than either those studied by RODMAN (1973) or those from the Ketambe area. Perhaps these differences reflect local trends in food availability, although the different sample methods used by MACKINNON and RODMAN make comparisons highly tentative.

In appendix 1, a list is given of all collected food plants with their reference number in the collection of the Rijksherbarium in Leyden. Approximately 90% of the food plants are 'primary' forest species. Of the 114 collected food plant species from the Ketambe area, some 53% are trees, including treelets, and 7% are strangling figs; some 28% are lianas, rattans and climbers; some 8% are epiphytes and only 4% are herbaceous plants and grasses. In addition, the rehabilitant orang utans fed on 4 more herbaceous plants.

Of the food plant items, 32% occur in the highest canopy stratum, 51% in the middle stratum and only 17% occur in the layers close to the ground.

3.2. FOOD CATEGORIES

Fruits

The orang utans in the Ketambe area utilized a large variety of fruits, ranging from the contents of the heavy and spiny durian fruit (*Durio* spp., *Bomb.*) to the tiny figs of *Ficus obscura* (*Mor.*). Most of the fruits eaten were medium sized (about 1–2 cm). Only two fruit types were quite large, those of *Durio* spp. and of *Artocarpus elasticus* (*Mor.*) (about 15–20 cm long).

The most frequently eaten fruit type was figs, especially those of the strangling *Ficus* spp. Of all observations on fruit eating by orang utans, 54% concerned feeding on figs. Most figs of the strangling species are medium sized (i.e. *Ficus benjamina*, *Ficus virens*, *Ficus sundaica*); *Ficus drupacea* has larger oval shaped figs (2 × 4 cm); and only two species have quite large figs (3 × 6 cm), namely *Ficus annulata* and *Ficus stupenda*. The figs of the creeping *Ficus* spp. (i.e. *F. parietalis* and *F. subulata*) as well as those of *F. obscura* and *F. obscura var. borneensis* were small, i.e. less than 0.5 cm in diameter.

A fig fruit is in fact a curiously shaped, widened inflorescence stalk, resembling a hollow pear with the flowers lining the inside (CORNER, 1952). Figs contain a number of specific fig wasps (*Blastophaga*) which effect their pollination. Undoubtedly these insects, ingested by a consumer of the fruit, provide the eater with an incidental source of animal protein.

Figs usually had a rather dull taste to me, some leaving an adstringent after-taste in the mouth. Others however, like ripe figs of *F. benjamina* and *F. drupacea* had a nice, cherry like taste. It is perhaps not fortuitous that the latter two species are among the fruits 'esteemed' by the orang utans (see p. 61).

Many of the fruits eaten by orang utans consist of a large seed, surrounded by a fleshy substance; e.g. those of the *Meliaceae*, the *Euphorbiaceae*, the *Vitaceae*, the *Sapindaceae*, the *Guttiferae* and several others. Only rarely did the actual seed of a plant appear to provide the nutritional part of the food for orang utans, although many seeds were swallowed incidentally with the rest of the fruit (see p. 97). Thus, only the seed-cotyls of *Spatholobus ridleyi* (*Leg.*), of the *Fagaceae*, the *Sterculiaceae*, *Payena lucida* (*Sapot.*), and *Iodes yatesii* (*Icacin.*) were ground between the teeth and eaten by the apes.

MACKINNON (1974) has already noted that orang utans may feed on several fruit species before these actually ripened. In the Ketambe area, such early utilization was especially apparent with the unripe fruits of *Durio oxleyanus* and with the figs of *Ficus drupacea*, *F. benjamina*, *F. sundaica* and *F. virens*. Unripe figs were eaten when still very young and small. Then there was usually a period when the figs were not eaten at all until they had fully ripened. Undoubtedly, the early exploitation of important food sources which are liable to food competition, plays a role in the niche differentiation of the primates in the area (see also MACKINNON, 1974). Yet, siamangs may also eat unripe figs (CHIVERS, 1974); in the Ketambe area we only saw siamangs feed from unripe *Ficus drupacea*.

Some of the fruits that occur in the orang utan's diet are eaten solely by this large ape, perhaps because of the inaccessability of the contents to other primates and other animals. All fruits with thick, hard and spiny shells from the food plant collection were presumably eaten in the trees by orang utans only, as no other animals were seen to take them. These are *Durio oxleyanus*, *Heritiera elata* (*Sterc.*), *Artocarpus elasticus*, *Strychnos ignatii* (*Logan.*), and *Monocarpia spec.* (*Annon.*). The durian fruit is esteemed by the indigenous people and by a variety of other ground dwelling mammals such as the Malayan sunbear and the tiger. However, these species only eat ripe durian fruits that have dropped onto the ground. Unripe durian fruits have a very nice, fresh walnut-like taste which is unlike the delicious sweet and penetrating taste of a ripe durian fruit. Quite remarkably, the fruits of the *Durio oxleyanus*, growing in the Ketambe area, did not have the obnoxious smell that the cultivated races of *Durio zibethinus* often have.

Leaf material

Throughout the year, the orang utans in the Ketambe area were observed to feed on a relatively large quantity of leaf material, ranging from leaf buds and terminal shoots (top-sprouts) to old mature leaves.

The most frequently eaten leaves were those of the endemic *Alangium scandens* (*Cornac.*) and those of *Acacia pennata* (fig. 20); the most frequently eaten top sprouts were those of the abundantly occurring creepers *Rhaphidophora foraminifera* and *Scindapsis hederaceus* (*Arac.*). There appeared to be a

FIG. 20. Feeding on the small leaves of *Acacia pennata*.

typical selectivity in feeding with respect to the development (age) of the leaves; In some species only the young, newly sprouted leaves or buds were taken, in others only the mature leaves were eaten. Thus leaves of *Ficus subulata* and of F. *glandulifera* were eaten when still very young; for *Acacia pennata* and *Iodes yatesii* the leaves growing on the non-woody climbing shoots were mainly taken, while old, mature leaves were eaten from *Trema cannabina* (*Ulmac.*), the liana *Alangium scandens* (*Cornac.*), the creeper *Pothos rumphii* (*Arac.*) and the epiphytes *Hoya spec.* and *Dischidia spec.* (*Asclep.*).

Asclepidiaceae leaves have a rather abundant latex content, which give the leaves a slightly sweet taste. The young *Acacia pennata* leaves had a slightly sour taste, as did most of the other leaves.

On two occasions it was observed that wild orang utans ate grass. A subadult male was found on the ground feeding from the top sprouts of a grass believed to be *Centhotheca latifolia* (*Gram.*) (AMAN SAR, pers. comm.), and an adolescent female (Jet) was observed to eat the seeds and the top shoots of the grass *Axonopus compressus* (fig. 21), apparently following the example of several rehabilitant orang utans who frequently ate the sprouts of both *A. compressus* and *C. latifolia.*

'*Bark*'

Although orang utans occasionally chewed on bark, this heading also includes feeding on the phloem and xylem layers of certain trees. To reach these

FIG. 21. Feeding on top-sprouts of the grass *Axonopus compressus.*

very thin growth layers the animal had to remove the bark. The xylem layer was then scraped off the exposed wood with the large spade-like incisors, the phloem layer was removed in a similar manner from the peeled-off strip of bark. The amount of material ingested during a feeding bout seems fairly small but the natritional value of this food type is probably relatively high, because of the passage of carbohydrates.

The plant species from which these layers were eaten belonged to the *Moraceae* (*Ficus pubinervus, F. racemosa, Artocarpus elasticus*) (fig. 22), to the closely related *Urticacaea* (*Dendrocnide sinuata*) and to the *Euphorbiaceae* (*Mallotus sphaerocarpus* and *Macaranga diepenhorstii*). Several of these species have a rather sweet tasting latex. The apes also ate the growth layers of another three unidentified plant species, including one liana. Only the bark strips of this unidentified liana were stuffed into the mouth and chewed until they became a fibrous wadge.

Judging by the numerous discarded fibrous masses found in the study area, the orang utans made wadges fairly frequently (fig. 23). These wadges were almost invariably the chewed stems of the large creeping Araceous *Rhaphidophora foraminifera.* Before chewing the creeper's stem, the apes used to peel off the rind (bark), which was discarded. It may be relevant that this creeper sometimes harbours small ant nests in its stem, although we found no evidence that the apes selectively used those parts that contained ant-nests.

Rehabilitant orang utans liked to chew on several different materials,

FIG. 22. Scraping the growth layer off a strip of *Ficus* bark.

FIG. 23. Chewing on the stem of *Rhaphidophora foraminifera.*

especially on cloth and cardboard. On several occasions we noticed that wild orang utans stole pieces of cardboard from rehabilitants to share in the feast. A similar taste of chewing cardboard and other domestic materials has been reported for chimpanzees (VAN LAWICK-GOODALL, 1967).

Insect food

The insects most frequently eaten by orang utans were ants, predominantly of the genus *Camponotus* (at least four species indet.). Most – if not all – insects eaten by the apes are arboreal.

The creeping plants, especially epiphytes, often appeared to provide a niche for the ant species that were caught and eaten by the orang utans. Thus, the roots of several epiphytic ferns, e.g. *Asplenium nidus, Polypodium spec.*, and *Davallia denticulata*, and of several climbers and creepers, e.g. *Cirtandra spec., Poikilospermum spec.*, and *Rhaphidophora foraminifera* provide nesting sites for several species of *Camponotus* ants. Other plant species, e.g. the epiphytic *Dischidia spec.*, and *Myrmecodia spec.* have internal cavernous spaces in their root system induced by the nesting habits of several species of *Polyrhachis* ants. The hollow branches and twigs of the tree *Erythrina subumbrans* also provide nesting space for a small species of ant (indet.) that was eaten by the orang utans.

BECCARI (1904; p. 161) mentioned that orang utans eat the viciously stinging weaver ants (*Oecophyllus* spec.) of the Bornean rainforest. We only once observed an orang utan eating from the leaf-nest of what we assumed to be weaver-ants. The unusual feeding technique of the ape displayed on this occasion is described on p. 89.

The *Camponotus* and *Polyrhachis* ant species eaten by the orang utans both had vicious bites. By contrast, the abundant terrestrial *Camponotus gigas* rarely bit when handled, though its large size suggested a vicious character. Some rehabilitant orang utans ate these giant ants, though the frequency with which they took them did not suggest a preference for this terrestrial species.

We observed that the orang utans ate two species of termites, namely *Nasutitermes matagensis* and *Coptotermes curvignatus*, both concealed living, white, arboreal termites. Presumably these two species represent only a small proportion of the several different species eaten by orang utans. Yet, some arboreal termites were clearly not eaten by orang utans. For instance, the brown termite *Hospitalitermes medioflavus*, that was often observed migrating in endless columns through the forest, was completely ignored by passing orang utans, even when the apes were apparently searching for insects. Also rehabilitant orang utans never ate these termites, not even after we had drawn their attention to them. Rehabilitant orang utans also preferred the white, concealed-living termites and often broke down parts of the quarantine cage in search of these insects. It has been reported that chimpanzees similarly ignore the abundant, migrating arboreal termites in the African woodland savanna habitat, but search for and feed on the concealed living species (VAN LAWICK-GOODALL, 1968; WRANGHAM, 1975).

FIG. 24. Ingesting a bush-cricket.

Other arboreal insects eaten by the apes include crickets, caterpillars of at least two species of moths, insect eggs, and at least two different types of leaf-galls. For the crickets (*Gryllidae*; two species indet.) usually hidden in rolled leaves on terminal twigs, and the bushcrickets (*Tettigoniidae*; at least three species indet.) (fig. 24) among which the giant *Pseudophyllus prasinus*, the orang utans had an elaborate catching technique, which is described on p. 93.

On several occasions we noticed that orang utans, in particular adolescents and juveniles, ate the cob webs they found during their search for insects among the epiphyte vegetation.

Some insects, notably those in leaf-galls, in epiphyte stems, and in figs were eaten incidentally together with the plant material. Especially for figs, the amount of ingested insect matter may be considerable. Sometimes large amounts of fig-wasp remains were found in the faecal samples of the orang utans.

Miscellaneous food-items

The orang utans in the Ketambe area occasionally ate bird's eggs and at least two different species of epiphytic fungi (indet.). We also noticed on two occasions that sub-adult male orang utans chewed on, and presumably ate decaying wood.

Remains of vertebrates were not detected in 108 freshly collected faecal samples that we sieved; MACKINNON (1974) has reported a similar absence of vertebrate remains from his examinations of orang utan faeces collected in Borneo. As orang utans in zoo conditions are known to catch vertebrates and eat them, it seems likely that wild orang utans may eat the young nestlings of certain vertebrates when the opportunity arises. There are some observations (p. 93) which strengthen this suggestion.

Chimpanzees hunt a variety of animals and eat their meat (VAN LAWICK-GOODALL, 1968; TELEKI, 1973). One of the outstanding features of the chimpanzee's hunting behaviour may well be its relevance as a social behaviour (see also TELEKI, 1973; KORTLANDT, 1974; RIJKSEN, in press). As orang utans lack the multi-male group condition in their social organization, I would postulate that hunting will not have evolved in this species and that the only vertebrate food taken, if any, will have been obtained by a 'gathering' method, rather than by 'hunting'.

3.3. FOOD PREFERENCE

The frequency of occupancy of certain food plant species, and the individual ranging patterns and feeding behaviours of orang utans, associated with such trees, clearly suggest that the apes in the Ketambe area displayed a marked preference for certain food-types.

The collected food plants (Appendix 1) are grouped according to three arbitrary categories: Esteemed, preferred and other. Fruit trees in the Ketambe area such as *Durio oxleyanus*, *Nephelium lappacaeum*, *Ficus benjamina*, *Ficus drupacea*, *Heritiera elata*, *Antiaris toxicaria* and *Garcinia bancana*, might attract associations of several individuals at a time. Accordingly, 'esteemed' (+ +) is defined as having attracted temporary associations of two or more orang utans (see p. 168). 'Preferred' (+) is defined as having attracted more than three individual orang utans in one fruiting season. These two categories together will be termed 'important' food-plant species. The third, i.e. 'other' category includes all food plants not meeting the criteria.

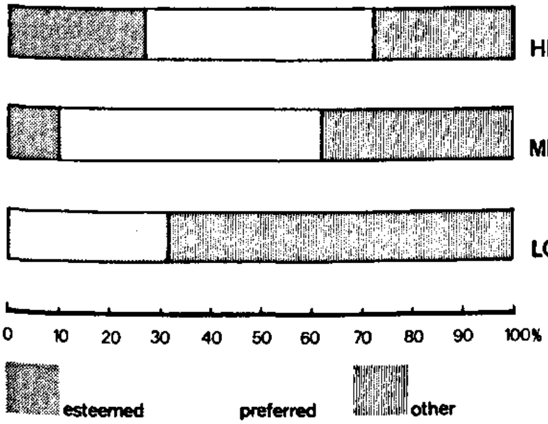


FIG. 25. Distribution of the orang utan's vegetable foods with reference to preference and storey-height.

Already WALLACE (1869) has noted that orang utans have a particular zeal for fruits prized by man, notably the durian (*Durio* spp.). It is noteworthy that nearly all the 'esteemed' fruit species are also favoured by the indigenous peoples of South-East Asia, often to such extent that those living in or near the forest retain very ancient and strict (*adat*) laws regulating the rights of clans, families or individuals to exploit such wild growing trees (see HOSE and MCDOUGALL, 1912; RUTTER, 1929). Violation of that right could result in serious, and sometimes mortal conflicts (see e.g. RAPPAPORT, 1968).

Of the trees utilized by the orang utans in the Ketambe area, 68% is classified as 'important' food-plant species, including 22% 'esteemed'- and 46% 'preferred' food-plants. For the group of lianas and climbing/creeping plants these figures are 63%, 4% and 59% respectively. For the epiphytic plants, only 22% are classified as 'important', the majority of these plants provide only leaf-material, which possibly has a subsidiary function in the diet.

If grouped according to height (see fig. 25), the 'esteemed' fruits occur in the two highest strata, while the lowest storey contains the largest proportion of 'other', i.e. less important food species.

4. FOOD-AVAILABILITY

The availability of food for a frugivorous species in the complex environment of the tropical rainforest is very hard to describe in quantitative terms. In this chapter I shall attempt to give some educated guesses of the food-availability in space, in quantity and in time. Variables of interest in this respect are the number of fruit trees and their spatial distribution, the amount and quality of fruits per fruit-crop, the periodicity of fruiting and the durability of the fruits.

4.1. SPATIAL DISTRIBUTION OF FOOD-PLANT SPECIES

Undoubtedly the South-East Asian rainforest is among the world's richest ecosystems in terms of species composition, as well as in terms of plant-biomass and plant productivity. Yet, food for any particular frugivorous animal component of the system is not equally distributed within its homerange throughout the year. With regard to space, two extremes from the orang utan foodplant collection may illustrate this. The tree *Aglaia speciosa* was about the most common species in the Ketambe area (11.4% in the tree inventory; see Appendix 2) with a density of some 52 trees per hectare on average. By contrast, only one individual could be found of the tree *Heritiera elata* in the entire study area.

To give an impression of the distribution pattern of food-plant species in the Ketambe area, the locations of 15 important species in which we found feeding orang utans have been mapped (fig. 26). In addition, the locations of two important fruit tree genera (*Ficus* and *Aglaia*: '*rambung*' and '*setur*' respectively) recorded during the tree inventory are shown in fig. 27. A comparison of the maps gives a very rough indication of the 'superabundance' of these two potential food-sources with reference to their observed utilization. The map reveals a density of one large strangling fig tree per two hectares, and also shows the unevenly spaced distribution pattern of that species.

The occurrence of several individual trees of different ages in rather discrete patches ('family groups') has been recorded for certain species, notably *Dipterocarpaceae*, from several forested regions in South-East Asia (POORE, 1968; FOX, 1973; WHITMORE, 1975). Such patchy distribution patterns were apparent in the Ketambe area for *Aglaia speciosa, Mallotus sphaerocarpus, Cyathocalyx sp., Turpinia spp., Carallia brachiata, Durio oxleyanus* and different species of strangling fig trees. In some sectors as many as four giant strangling fig trees grew in an area of approximately 0.5 ha (see also fig. 26).

In regions close to the Ketambe area, other tree species were observed to grow in patches. For instance, the very similar looking forest region near Seldoq contained large numbers of clumped *Baccaurea cf. maingayi Euphorb.*: '*bergang*') trees; an orang utan food-plant which was less common and grew rather dispersed in the Ketambe area.

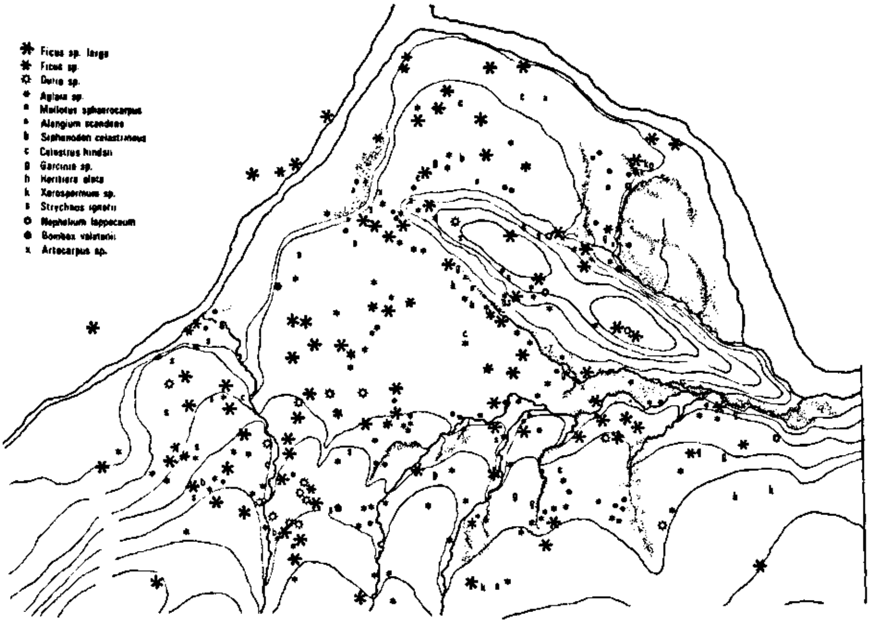


FIG. 26. Distribution of 15 important food-plants in which orang utans were observed feeding.

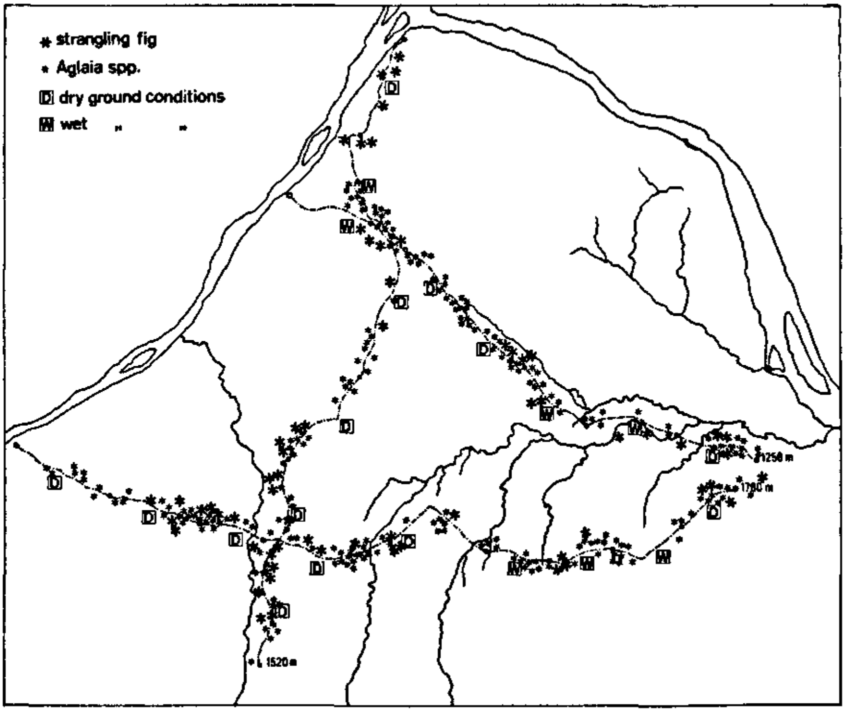


FIG. 27. Distribution of 2 fruit tree genera (*Ficus* and *Aglaia*) along three transects.

From the tree inventory, one can draw a criterion for the dispersal, i.e. 'common' is defined as occurring with a frequency, greater than 1.9% in the inventory, which corresponds with an average density of 9 or more trees per hectare. I estimate that of the 52 important foodplants of the orang utan in the Ketambe area (see appendix 1), only 4 species (8%) may be considered as common and some 29 species (56%) are represented in the area by few, or even by single individual trees. The remaining 36% may be considered as less common species. Allthough some indication of food-crop size is inclusive in the term 'important' food-plants, notably in the proportion representing the 'esteemed' fruits (see p. 61), it is important to realize that the figures presented here concern the spatial distribution of potential food sources and give only one aspect of the food-availability in space.

Some of the fruit tree species that were represented by only one individual tree in the area were quite large and had large fruit crops, providing food for several orang utans for a longer period of time. By contrast, some of the common species (i.e. *Xerospermum spec.*, *Garcinia parvifolia*, etc) were rather small trees providing only moderately large quantities of fruits.

With regard to the spatial distribution, several food-tree species appeared to grow with marked preferences for particular, readily recognizable habitat conditions, an observation which has been elaborated by FERNHOUT in his (unpublished) report on the tree inventory. Thus, the cauliflorous tree *Ficus racemosa* was found to grow exclusively on the banks of large rivers, this tree was nowhere seen further than 20–30 metres from a water course. Another characteristic tree of the riparian forest conditions is *Dillenia indica*, which occurred mainly along the small streams in the Ketambe area, rather than along the large rivers. Similarly, the species *Pometia pinnata* and *Mallotus sphaerocarpus* were mainly found in the badly drained sectors in forest with a medium height, or low canopy; *M. sphaerocarpus* often along small streams, *P. pinnata* usually along rivers. Both the genera *Durio* and *Ficus* (i.e. the strangling figs in particular) were found mainly on dry ground and contributed to the forest type with a high canopy. *Aglaia* shared the preference for dryer ground-conditions, but contributed mainly to a forest type with a medium height canopy, as did *Garcinia parvifolia*, *Cyathocalyx sumatranus*, *Mastixia trichotoma* and *Xerospermum spec.*.

Differences in the distribution patterns of the food-plant species are undoubtedly related to differences in the means of seed dispersal and the degree of seed predation. It has been argued that a widely dispersed distribution pattern enables individual trees of particular species to escape insect-predation of its leaves (JANZEN, 1971). On the other hand, for those species that may occur in clusters, it has been suggested that these contain metabolites which make them less palatable for predators (e.g. JANZEN, 1970, 1971). Several authors have noted the very important role that animals play in the dispersal of rainforest trees (e.g. RIDLEY, 1893; CORNER, 1952; VAN DER PIJL, 1957; 1969); WHITMORE (1975) has argued that animal dispersal is more effective than dispersal by wind under rainforest conditions. In the section 'influence on the habitat' (p.

96) I describe the role of the orang utan in the dispersal of several of its food-plant species.

4.2. SEASONAL CYCLES

Different species of rainforest trees and even different individuals of one species may differ widely in the frequency and abundance of flowering and subsequent fruit production (RICHARDS, 1952). Thus, a frugivorous animal will experience a decidely discontinuous availability of food in particular with reference to quality. In other terms, the availability of any sort of fruit shows a cycling pattern which is characteristic for each plant species. For some (e.g. certain *Ficus spp.*) the cycle was comparatively short, namely 4–5 months, for others it was a year, while some species seemed to have a very variable cycle, bearing fruits at intervals of two to several years (e.g. *Heritiera elata*, *Mangifera foetida*, *Baccaurea maingayi*, *Durio spec.*, etc.). During the period 1971–1974, some 70% of the important food-plant species displayed a more or less regular fruiting cycle (range 4 months–1.5 year).

In his long-term study to monitor the phenology of a tropical rainforest in Malaysia, MEDWAY (1972) recorded only ten (22%) species in a sample of 45 which displayed an annually recurrent floral cycle. The Ketambe sample differs markedly from the Malaysian one in species composition, notably in the absence of *Dipterocarpaceae*, which hampers a meaningful comparison.

Simultaneous flowering and fruiting was especially apparent in *Mallotus sphaerocarpus*, *Aglaia speciosa*, *Durio oxleyanus*, *Tinomiscium phytocrenoides*, *Cyathocalyx sumatranus*, *Celastrus hindsii* and *Macaranga diepenhorstii* throughout the study period. Some species however, showed more or less clear intra-specific differences in fruiting synchrony; thus two individuals of *Syphonodon celastrineus* appeared to have fruit crops in different times of the year, also it was rather unusual that two or more large strangling fig trees of the same species (i.e. *F. benjamina*) were in fruit simultaneously. Particularly in the important group of strangling figs, the diversity in periodicity resulted in a rather even spread of the fruit-availability over the year. Some species had as many as three fruiting seasons per year with great regularity, (i.e. *Ficus racemosa*); some had two seasons per year, most *Ficus* had an annually recurrent fruiting cycle and only a few displayed strong irregularity (i.e. *Ficus glaberrima*). In table 4 I give the observed fruiting seasons of the most important *Ficus* spp. Because I lumped the data for nearly two consecutive years, table 4 gives the impression that figs were available throughout the year. It is true that figs were the most frequently available food-item throughout the year (see also MCCLURE, 1964; 1966; MEDWAY, 1972), but there were periods that figs were available in very small quantities only, or (for short periods) were not available at all. Several *Ficus species*, notably strangling and creeping figs, usually came into fruit at the end of every dry season. The wettest months (April–May) showed a relatively poor availability of figs in each year of the study period. MEDWAY (1972) has concluded that 'despite specific variation in

TABLE 4. Observed fruiting seasons of strangling- and creeping *Ficus* species in the Ketambe area.

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
(strangling figs.)												
Ficus benjamina	.	+	+	+	.	.	.	.	.	+	+	+
F. sundaica	+	.	.	+	.	+	.	+	.	.	.	.
F. drupacea	.	.	.	.	.	.	+	+	+	+	.	+
F. glaberrima	.	.	.	.	.	.	.	.	+	.	.	.
F. elastica	.	+	.	.	.	.	.	.	.	.	.	.
F. virens	+	+	.	.	.	.	.	.	+	.	.	.
F. annulata	.	.	.	.	.	.	+	.	.	.	.	.
F. stupenda	.	.	+	.	.	.	.	.	.	.	.	.
(creeping figs.)												
F. parietalis	.	.	.	.	+	.	.	.	.	.	.	+
F. subulata	.	.	+	.	.	.	.	.	.	.	+	.

phenology the community as a whole exhibited regular seasonality, with single annual peaks of (...) fruiting' (p. 117) (see also WHITMORE, 1975). He found that the inter-specific differences in periodicity maintained a minimum incidence of fruiting at 27% of species in the sample of 45. We had the impression that the percentage of minimum incidence of fruiting with reference to those species providing food for orang utans was higher, possibly in the order of 40–50%. Moreover, the intra-specific variability in periodicity within a large community of trees (i.e. those in the 'common' category; p. 65) may add considerably to the over all availability of food in time.

The seasons with an obvious abundance of fruits in the Ketambe area during

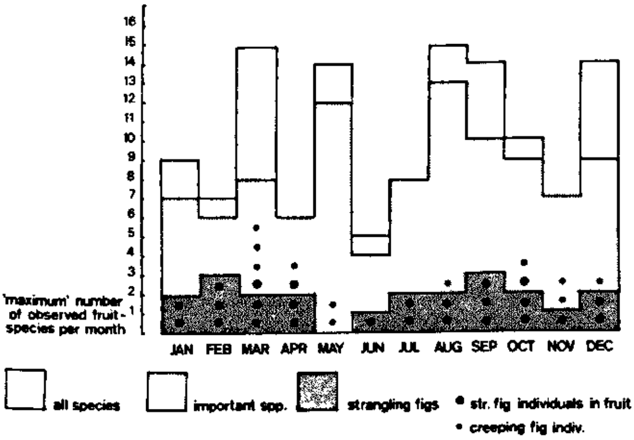


FIG. 28. The total number of observed fruit-bearing food-plant species per month in the period November 1972–March 1974.

this study were December–January, May, and August–September. The period that commences in October and ends in March, i.e. the late wet and early dry season shows the highest diversity of fruit-crops relevant to the orang utan. Fig. 28 shows the total number of observed fruit tree species per month, as derived from the collected data of specimens between November 1972 and March 1974.

4.3. FRUIT-CROP SIZE

One important variable with regard to food-availability is the quantity of ripe fruits of a single food-source. Regularly spaced, small quantities of food will require a completely different foraging strategy than, for instance, irregularly spaced, large amounts (e.g. CROOK, 1970). Crop-size is certainly determined by the age and the volume of the fruit-tree; moreover, it is influenced by the productivity of the tree's immediate environment, by climatic conditions and by the pollinating and/or predatory activity on its flowers by animals. On p. 96, I give an example of the presumed negative effect of the orang utan's foraging technique on the fruiting pattern of one of its important food-sources, the durian tree.

Flowering does not always result in subsequent development of fruits, as was apparent in a giant *Mangifera foetida* tree in the Ketambe area for two seasons. MEDWAY (1972) recorded that the lowest proportion of trees that produced fruits after flowering was 57%.

Of the 52 'important' fruit tree species, 12 (23%) were represented by trees of which the adult individuals were enormous in size and had large fruit-crops. Thus, several strangling figs, notably *Ficus benjamina* and *F. drupacea*, *Durio oxleyanus*, *Heritiera elata*, *Antiaris toxicaria* and *Mangifera foetida* had large crowns with an estimated volume of 1000–4000 m. cubic. Some of these might provide food for several apes for a longer period of time (1–3 weeks).

Of 15 species (29%) the fruit-quantity in general was small and, we presumed, insufficient to feed more than one orang utan.

Combining these estimates directly with those on the spatial distribution of potential foodplant species (see table 5) shows that about half the number of food-plant species (42 %) provide large amounts of food within a limited space, and half the number of food-plant species (58%) offer small and/or scattered quantities of food.

These figures should be interpreted as a rough illustration. Tree species of all ages were represented in the area, which, in combination with environmental factors might cause a rather wide spread of fruit production in different specimens in different periods. Moreover, when growing in close spatial association but in low overall density, several small sized specimens could provide a considerable amount of fruits. For instance, the liana *Tinomiscium phytocrenoides* had a relatively large quantity of fruits in certain sectors of the Ketambe area where it occurred in clumps of several specimens.

Another important variable one has to take into account in assessing the food

TABLE 5. The relation between the estimated degree of dispersion of the 52 most important fruit tree species of orang utans in the Ketambe area, and their estimated crop size potential.

	large quantity	moderately large quant.	small quantity	total
common 9 or more trees/ha	0	4 (8%)	0	4 (8%)
less common 1–9 trees/ha	3(6%)	6 + 6 (23%)	4 (8%)	19 (36%)
dispersed less than 1 tree/ha	9 (17%)	9 (17%)	11 (21%)	29 (56%)
total	12 (23%)	10 + 15 (48%)	15 (29%)	52 (100%)

22 (42%) (large amount of food in limited space)
30 (58%) (small and/or scattered amount of food)

availability is the durability of ripe fruits or the time-span that fruits are available for consumption before they fall from the tree. For instance, the *Heritiera* fruit-crop was almost entirely harvested by the orang utans and only few fruits dropped to the ground because of over-ripeness. By contrast, the large strangling fig trees dropped a considerable proportion of their crop because most figs ripened synchronously and had limited durability of only a few days. The sudden availability of a very large quantity of fruits was usually too substantial for the limited feeding capacity of the assembled arboreal animals. Fallen fruits were eaten by ground dwelling animals such as pigs and the sunbear.

In conclusion, food for orang utans in the Ketambe area is available according to a complex pattern of distribution in space, in quantity and in time. In other words, the Ketambe habitat represents a decidedly discontinuous patchwork of different resources, according to the definition of a 'patchy' environment (PIANKA, 1974).

This study did not aim at giving a quantitative analysis of the food availability in time. It is assumed that the qualitative description given in the present chapter, supplemented with indirect parameters for food availability such as the biomass, the sexual dimorphism, the homerange size, the travelled distance per day, in comparison with the same variables in other species, provide sufficient grounds to speculate about the relation between the orang utan's social organization and the selection pressures provided by the environment.

5. FEEDING BEHAVIOUR

Whereas the preceding chapter gave a description of the relation between the environment and the orang utan, which was mainly based on environmental data, this chapter presents information on the same relation, based on observations of the ape's behaviour. This encompasses the ape's adjustments to availability of food-items, its food choice and preferences for certain items as well as its utilization pattern. The last section describes some simple experiments to test the orang utan's readiness to accept unfamiliar food-items in order to investigate our impression that the wild individuals were conservative in their choice of food-items out of the array of potential foods available in the forest.

5.1. FOOD SELECTION

Diet-variety in the orang utan appeared to be correlated with several variables, of which seasonal availability was inevitably the most obvious one. Within seasons, the animal's feeding behaviour clearly showed a certain selectivity that seemed to aim at optimizing the quality of the daily food-intake. Thus, the individuals displayed a 'preference' for certain food-plant species but still utilized at least 4 different items per day. They showed a daily regime for certain items (notably leaves), and they seemed to discriminate between individual fruits of one crop or between crops. The number of food plant species eaten per day varied from 4–15 (average 7 species).

5.2. SEASONAL VARIATION IN THE DIET

Inevitably, a frugivorous animal has to shift its diet composition according to availability. In general, several major shifts could be distinguished, with reference to the fruiting seasons of certain important fruit tree species, notably those from the 'esteemed' catagory. Such species then provided the bulk of the food for that period. Several authors have already drawn attention to a 'durian season' (e.g. WALLACE, 1856b); DAVENPORT (1967) even recommended this season to be the best period for studying orang utans. Other such seasons in the Ketambe area were the *pepuah* season, when *Mallotus sphaerocarpus* fruited and the *setur* season, when *Aglaia speciosa* was in fruit. In fig. 29, I give an impression of the fruit utilization of 6 important food plant species in the Ketambe area, in the period August 1973–April 1974. Even in the periods that certain plant-species provided the bulk of the food for the orang utans, such food was invariably supplemented with leafmaterial and usually with several other foods as well. The minimum number of observed food-items per day was never less than four.

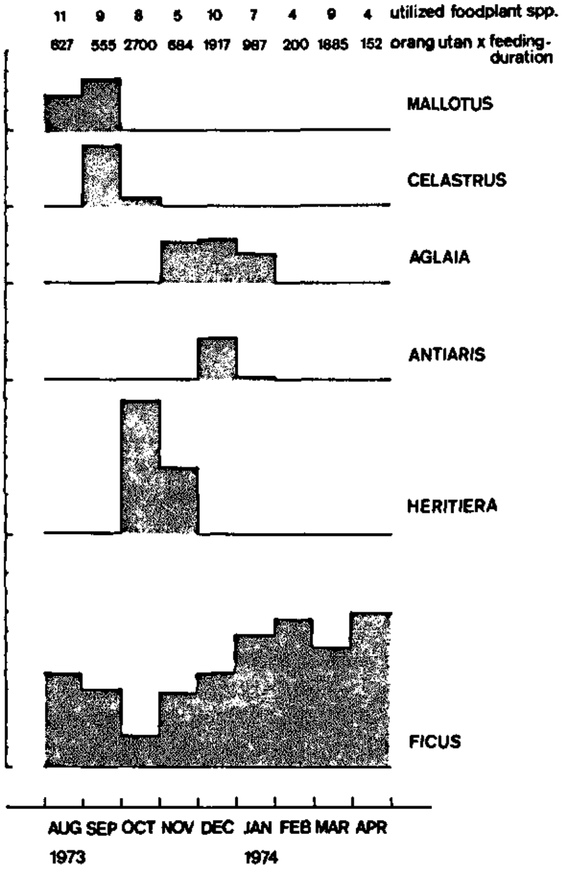


FIG. 29. Relative feeding duration on 6 important fruit species.

The relative frequency of feeding duration on the four main food-categories (fruit, leaf-material, insects and 'bark') are shown in fig. 30 .The month-histograms are based on data from varied (daily activity) samples of different individuals feeding on different items; for fruits ranging from small scattered food-morsels picked up during foraging to clumped, large quantities of high quality foods. In view of the fact that the relatively small sample size represents only a small proportion of the total feeding time of an individual orang utan per month (see the upper 2 rows of figures), the interpretations made must be tentative.

A comparison of fig. 30, with fig. 28 shows that the apes showed a slightly higher incidence of feeding from alternative sources, notably leaves, in the months with a comparatively small offer of different fruit species. Fig. 30 clearly suggests that the relative frequencies of feeding duration per food-category is not consistently correlated with the month. If we would accept that the data are sufficiently accurate, a comparison of the periods January–February

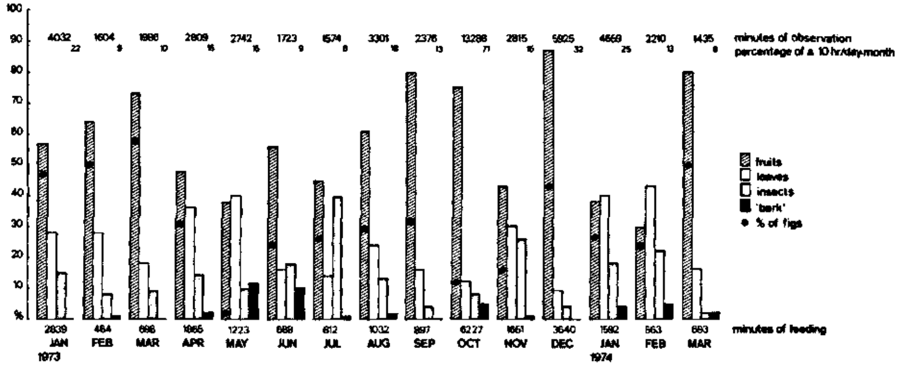


FIG. 30. Relative feeding duration per food category per month.

in 1973 and 1974 demonstrates that there can be a considerable between-year variability, which approaches the order of magnitude of the within-year variability. Possibly the shown variation is largely due to individual variation of the different apes contributing to the data. For instance, the histograms for February 1974 have been constructed from data concerning a group of 4 adolescent individuals, whereas the February 1973 data concern two adult individuals and an adolescent who frequented a large strangling fig tree. These figures contain a warning for a very cautious interpretation of ecological data from relatively short-term samples of a limited number of individuals. Not only are the environmental variables that determine food-availability too many to encompass in a short term study, as I argued on p. 69, the ideosyncrasies and perhaps the differences related to the age and sex of the subjects also appear to add to the complexity of such data.

MACKINNON (1974) has reported that the incidence of bark-feeding in Bornean orang utans strongly increased in certain periods due to a local shortage of fruits. An indication for a similar dietary adjustment in the orang utans of the Ketambe area may be inferred from the data of May 1973 when the availability of figs and other fruits was rather poor and the apes showed some increase in feeding from the growth layers under the bark of certain trees. Such a change of diet towards more widely available food sources was especially apparent in the disabled, adult female Josh in the period August–October 1973 (see p. 140). She showed an obviously higher incidence of 'bark-feeding' than other orang utans. We observed her stripping the bark of a variety of trees and lianas on several occasions and she not only used to scrape off the growth layers but also chewed on the bark. As she could not range over a larger area because of her lameness, she probably faced a shortage of fruits in her restricted range and had to utilize alternative sources.

5.3. TASTE

I already noted on p. 61 that the orang utans in the Ketambe area descriminated between potential food items. I also defined the terms 'esteemed' and 'preferred' foodplant species in terms of utilization pattern, as displayed by the apes. Presumably these also reflect 'taste' and food-quality. Apart from such 'preference', the orang utans sometimes appeared to discriminate between fruit-crops of different individuals, or even between different fruit-crops of one individual tree. This was especially notable for certain *Ficus* species.

For instance, with one particular *Ficus stupenda* tree, we noticed only occasionally in three consecutive seasons that passing orang utans ate its figs, whereas the figs of another *F. stupenda* tree, only some 300 meters apart from the other, appeared to be frequented by the apes; it even attracted temporary associations of several individuals. It is noteworthy that this difference in utilization was not obvious for the other primates eating from these fig trees. Furthermore a large *Ficus sundaica* tree, which had been visited by orang utans during previous fruiting seasons, was not noticeable visited or fed upon by orang utans during its fruiting season in March 1974. Yet, at least five orang utans were known to be present in the Ketambe area during this period and we observed once that an individual passed the tree at close distance. Although occasional visits of orang utans might certainly have passed our attention, the tree clearly did not attract temporary associations nor kept orang utans feeding for any length of time during this season, as it had done previously. An explanation for the noted discriminative utilization of different individuals of the same fruit tree species may be sought in the occurrence of genetic variants. On the other hand, a different distribution of the three flower types of figs (i.e. male, female and gall-flowers; see CORNER, 1952) in one individual in different seasons, or between individuals, may also cause discriminative feeding. It is likely that the taste of the three types is different.

We had the impression that some fruits were only eaten when other, more preferred types were scarce or not available in the near surrounding. For instance, the large figs of the cauliflorous *Ficus racemosa*, that grows exclusively on riverbanks, were never eaten in large quantities. Usually passing apes took some of the abundant figs (fig. 31) but rarely fed for any period of time as they used to do in strangling figs. The fact that *F. racemosa* often had some 5–6 fruiting seasons in two years made it theoretically a considerable food potential.

Often the abundant crop of this fig species fell to the ground without arboreal animals feeding on it. Similarly, the large fruits of *Aglaia elliptica* were only occasionally eaten by passing orang utans. These fruits appeared to be esteemed, however, by giant squirrels (*Ratufa bicolor*), which frequented such trees in the fruiting season.

Several tree species in the Ketambe area, had edible looking fruits that were never eaten by orang utans according to our observations. For instance, the abundant, large figs of the medium sized cauliflorous *Ficus* species (indet.; other than *F. racemosa*) were neither touched by passing orang utans, nor by other

FIG. 31. Eating the figs of *F. racemosa.*

primates, and invariably fell onto the ground to rot away. Although the small, hard, apple-like fruits of *Siphonodon celastrineus* were eaten by orang utans we could not find traces of feeding on almost identical fruits of another unidentified tree species. MACKINNON (1971) has reported that Bornean orang utans feed on the fruits of at least two *Dysoxylon* species. However, the fruits of two *Dysoxylon spp.* one of which had a very bitter and adstringent taste, were not seen eaten by orang utans in Ketambe. Yet, the fruits were eaten by hornbill birds, notably *Aceros plicatus.*

Another example of non-utilization of potential, or edible-looking fruits concerned the medium sized, ovoid shaped, yellow fruits of a liana, somewhat resembling the fruit of *Tinomiscium phytocrenoides.* This fruit was eaten by macaques but orang utans never ate it as far as we could ascertain.

In general, the orang utans in the Ketambe area appeared to utilize a rather limited, fixed set of food items. Our observations on feeding behaviour rarely suggested that the apes 'tried almost everything that looked edible' as has been noted by MACKINNON (1971; p. 164). However, one such observation was made. Once we saw the adolescent male Mos show rather elaborate inspecting behaviour of a food item which he later discarded.

When travelling in the company of his mother (Mif), Mos found a bright red tomato-like fruit of an – unidentified – liana. He initially handled it in a playfull manner. He smelled the fruit, put his protruded lips and tongue to the skin of it and took a very cautious bite: apparently to open it. He again inspected the fruit with protruding lips and the tip of his tongue, but did not take a piece in his mouth. Immediately after this second attempt, he produced excessive saliva and blew bubbles (cf. 'blowing raspberries': HARRISSON, 1971). He then dropped the fruit, elaborately wiped the saliva from his mouth with some leaves and spat several times. His mother who fed close to him, did not show particular interest in her son's behaviour; this in contrast to chimpanzee- and Japanese macaque mothers who may prevent their offspring feeding on unfamiliar food items (WRANGHAM, 1975; ITANI, 1958).

On another occasion, the sub-adult male Roba found a melon like fruit of a climber (cf. *Melothria* sp.). He tasted the fruit and ate it with many visual inspections during his feed. His companion Mos did not eat the fruits, but watched him closely. After this incident both animals moved on without touching the rest of the crop. Discarded shells found on other occasions indicated that orang utans had eaten some of these fruits. Possibly *Melothria* fruits were a familiar, but less preferred food item.

5.4. DAILY RHYTHM

Several authors have published detailed activity profiles of the diurnal life of orang utans. RODMAN (1971) has differentiated patterns according to age and sex classes and he concluded that adult males spend relatively more time feeding to moving than females. MACKINNON (1974) has differentiated the activity profiles of the two sexes according to age-class, to fruiting season and to the weather conditions. He found that 'males and females showed similar activity patterns though females showed significantly more (morning)feeding than males' (p. 24).

Comparing daily activity in seasons with an abundance of fruit and seasons with a paucity of fruits, he found 'that the animals spent more time travelling and less time feeding in the non-fruit season'. MACKINNON also found a marked difference in daily activity patterns for dry and for wet days. On dry days there was a considerable increase in the time spent resting in the midday period, with a corresponding decrease in feeding and travel' (MACKINNON, 1974).

In general the orang utan's daily activity pattern shows two peaks, one in the morning, some two to three hours after the animal has left its night nest, and one less pronounced peak around 15.00 p.m. Feeding activity is most marked in the morning; travelling activity in the afternoon. Midday is usually spent in a resting position.

As mentioned earlier, we did not collect dawn to dusk activity data for the individual orang utans consistently, yet the general impression, supplemented with tallied data from our field notes, correspond with the picture of daily activity as given by MACKINNON (1974). Still, it may be noteworthy that our field notes with reference to the activities of the two adult males O. J. and Mozes, suggest a difference (fig. 32). The male O. J. displayed a daily activity pattern which was almost identical to that of adult females, including the relatively higher proportion of daily travelling. By contrast, the male Mozes spent most of his time in or near the large fruit trees and travelled only small distances, 250–500 metres per day. Such an activity pattern seems more in accordance with RODMAN's (1971) picture for adult males. Several factors are involved in this difference. The data pertaining to Mozes were collected during a period when large fruit-trees had plentiful fruits. Those of the male O.J. how-

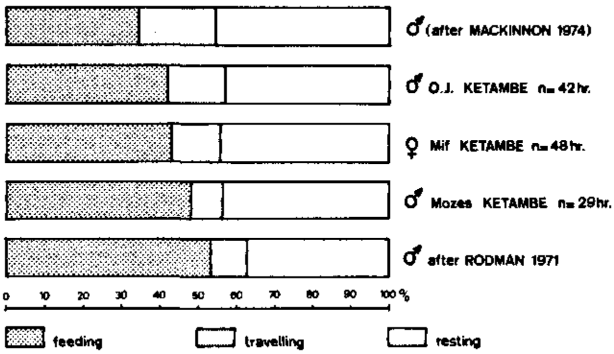


FIG. 32. Comparison of activity profiles of orang utans (Bornean data after RODMAN, 1971 and MACKINNON, 1974).

ever cover a much wider time span, including several different environmental conditions. Another factor perhaps is the dominant status of the first male, which allowed him to be less evasive in his choice of food sources. Nevertheless, these observations may illustrate that great caution is needed in the interpretation of short term, irregularly gathered data. The differences in daily activity patterns of the age and sex classes of orang utans appears to have had insufficient attention. Only a more detailed, long term study on this subject, parallelled by a study of the availability of food resources can provide a firm basis for conclusions on the feeding strategy of this ape. Apart from the rhythm in daily activity with regard to feeding and travelling in general, orang utans showed differential utilization of certain food items. Thus, the daily feeding pattern of the apes in the Ketambe area showed a rather high feeding incidence on leaf material in the early morning and the late afternoon. Feeding on fruits happened predominantly during the late morning hours (8.00–11.00 a.m) while terminal shoots, insects and less abundant fruits were usually taken during the afternoon. Quite remarkable, the leaves of *Acacia pennata* were mainly eaten before 8.00 a.m. or after 15.00 p.m. and orang utans often ignored *Acacia* leaves when they passed these during midday hours. Feeding on *Alangium scandens* leaves nearly always occurred after 16.00 p.m. and such feeding often preceded nesting. After long bouts of feeding on one of the 'esteemed' fruit species, orang utans usually went to a nearest liana or tree with edible leaves and ate from these for some time. Species which were utilized in this manner, next to *Alangium scandens* and *Acacia pennata*, were *Trema cannabina* and *Pothos rumphii*.

Temporal spatiation in the feeding on certain food items has been observed in squirrel monkeys (*Siamiri* spp.) that eat fruit mainly during the morning hours and insects later on the day (BALDWIN and BALDWIN, 1970). Siamangs (BROTOISWORO, pers. comm., 1974) and chimpanzees (WRANGHAM, 1975) eat fruit mainly during the morning hours and leaves mainly in the afternoon.

The nutritional value of leaves, especially with respect to carbohydrate levels, as well as the potential toxic alkaloid contents fluctuate during the day in many plants (ROBINSON, 1974), which suggests that there is an optimal period for harvesting. FREELAND & JANZEN (1974) have demonstrated that the different types and concentrations of plant secondary compounds influence variation in the herbivore's diet. The daily fluctuations of such compounds may well determine the particular utilization patterns of leaves that we observed in the orang utan.

5.5. RANGING IN RELATION TO FEEDING

The usual travelling pattern of the orang utans in the Ketambe area appeared to be influenced by social as well as by ecological factors. Ranging behaviour that was obviously influenced by social factors is described on p. 161.

Since its main food, fruits, is dispersed in space for short periods of availability, the orang utan has to adjust its daily ranging pattern accordingly. We had the impression that 'taste', or preference for particular food items (which presumably relates to nutritional quality) determines much of the ranging behaviour. For instance, a single *Heritiera* tree attracted more orang utans to the study area during its fruiting season, than the most common fruit tree species, i.e. *Aglaia speciosa*, producing a local over-abundance of fruits during its season. Moreover, the availability of alternative foods in the surroundings of the study area did not differ notably in these two cases. It is assumed that the nut-like *Heritiera* fruits are qualitatively better than the watery flesh around the stones of *Aglaia* and that the apes selected for quality, even though this meant crowded situations around the single tree with inherent risks of agonistic encounters.

In fig. 33 the travelling patterns of the adult male O. J., the adult female-infant unit Mif/Mug and the sub-adult male Roba are shown. Map a shows some of the travel-routes of the female Mif in the period that the tree *Heritiera elata* was in fruit. Map b shows some of the travel routes of the same female during the period that two large esteemed fruit trees (i.e. *Ficus drupacea* and *Antiaris toxicaria*) were in fruit. Map c shows some of the travel routes of the adult male O. J. during a period of widely dispersed availability of *Mallotus sphaerocarpus* in small scattered quantities. In the same period, three strangling fig trees came into fruit which attracted associations of several individuals in which O. J. only occasionally participated. In map d some of the travel routes of the sub-adult male Roba are shown in a period which was characterized by the fruiting of a large strangling fig tree and the onset of fruiting in the *Heritiera* tree.

Some of the travel routes in the maps are straight, for instance the routes of the female Mif made on 14.10.1973, on 19.10.1973 and on 22.10.1973 were directed linearly from the *Heritiera* tree, while her way of travel gave the impression as if she was after some goal. It could be twice ascertained indeed that she went towards a *Ficus drupacea* tree which was in the process of ripening. After such visits she sometimes, i.e. on 14.10.1973, returned to the *Heritiera*

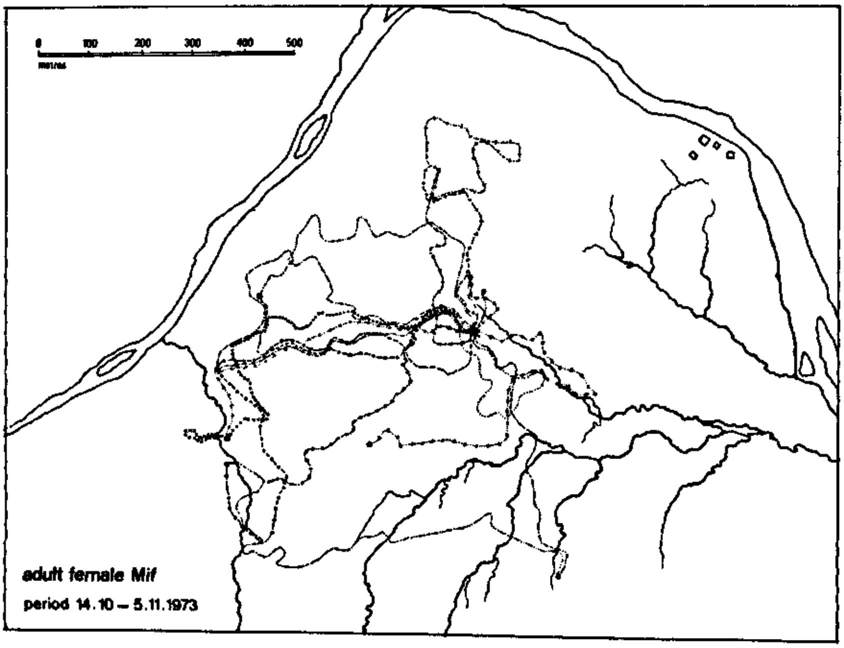
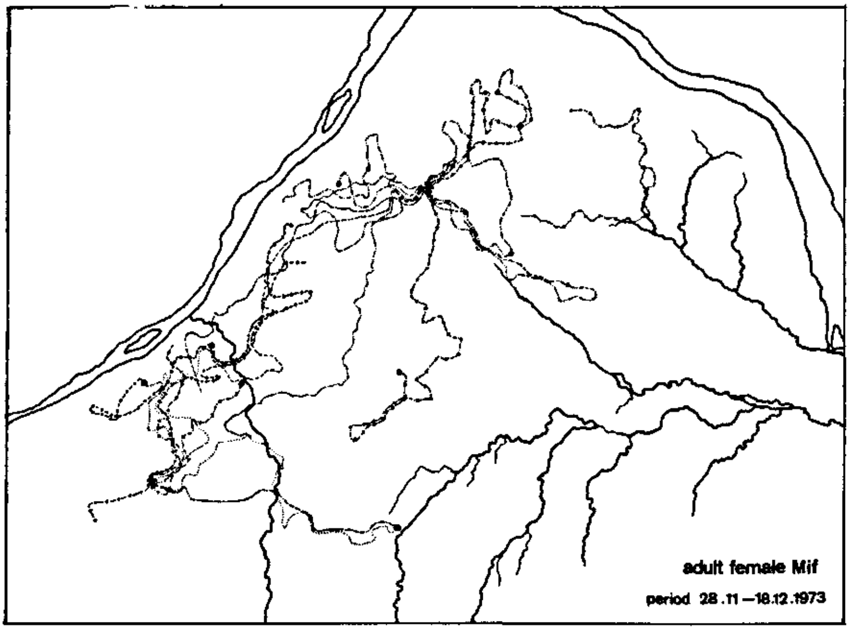
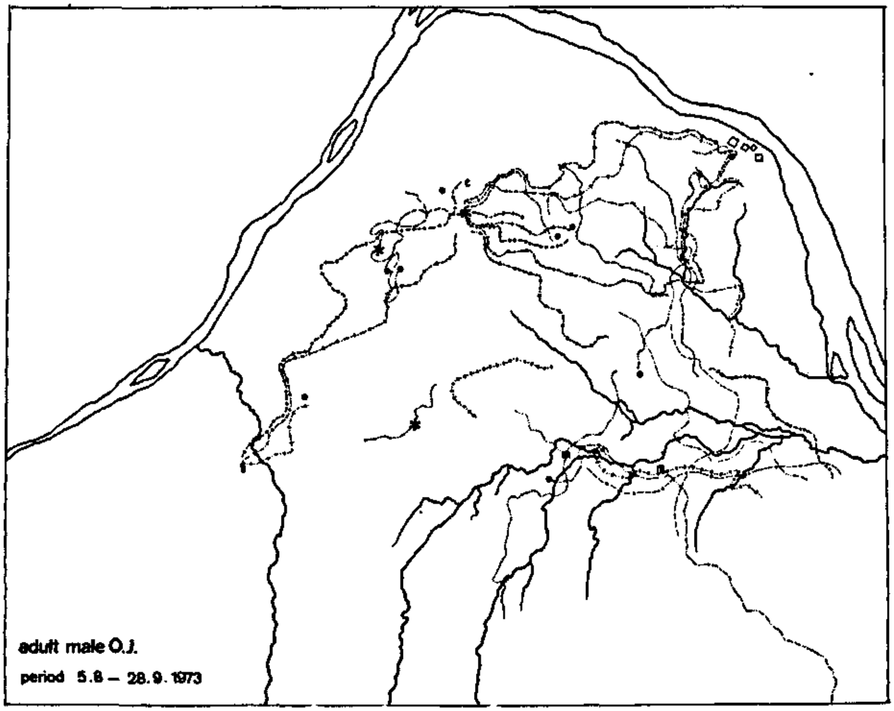
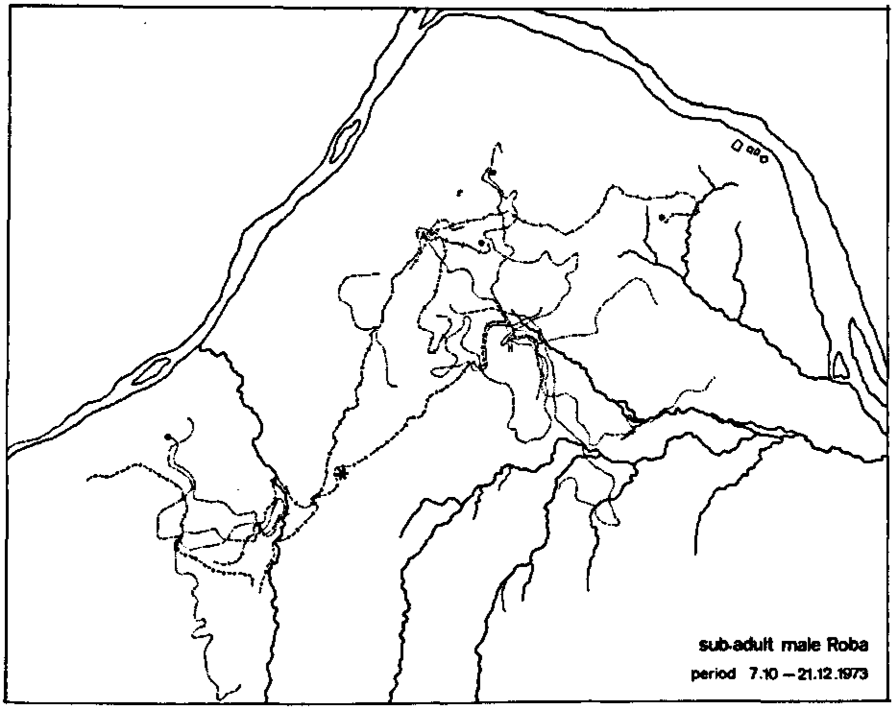


FIG. 33. Travelling patterns of 3 orang utans: (a) and (b) the adult female Mif; (c) the adult male O.J.; and (d) the sub-adult male Roba.




adult male O.J.
period 5.8 – 28.9.1973


sub-adult male Roba
period 7.10 – 21.12.1973

tree in a straight line again. At other times she left the *Heritiera* tree in the late afternoon to nest in a nearby location, and did not return to the fruit tree the next morning, but set out on a route seemingly aimless through the study area. Such round trips usually lasted one or two days after which her path led back to the fruit tree again, where she stayed for another one or two days to feed from its fruits.

A similar alternating pattern of utilization and abandoning the food source was apparent in all individuals when feeding in a tree with a large crop which remained available for several days. Thus, an orang utan might leave an esteemed fruit tree vacant for several days, even when he fed there entirely alone amidst a wealth of food. MACKINNON (1974) has also reported that Bornean orang utans sometimes left areas that still contained fruit in plenty. He does not mention however, whether such leaving animals returned to the tree after some time, nor if such behaviour was an usual ranging pattern, as it was in the Ketambe area.

Thus, two types of ranging may be distinguished; (a) a direct course in which the individual would not, as a rule, stop when passing potential food items along the way, and (b) a more or less meandering course in which the individual might feed from many different kinds of food-items along the way. These different types may be interpreted as the individual moving (a) after some goal, either to seek the company of a social partner, or to check other, important food sources on their state of productivity; and moving (b) at random through his home range in order to acquire general information on food availability, or food potential. This is not to imply a conscious awareness of the individual to match his diet to standards of quality. It is conceivable that a tendency to abandon food in plenty supply is caused by temporary satiation and a mounting aversion against one particular taste.

The ranging patterns of orang utans in the Ketambe area appeared to differ between individuals, which possibly reflects a difference between age and sex classes. The patterns differ in (a) spatial coverage of the range, and (b) the speed of travel and the duration of staying in any one location. Thus, the adult female Mif covered much of her home range, usually at a comparatively leisurely pace. She travelled an average distance of 550 metres per day (range 180–1250 m.). The ranging pattern of the adult male O. J. by contrast, suggests that he covered more the outskirts of his range and travelled less through the central sector (see also fig. 33c). This suggestion of a more or less circuitous route was strengthened by the fact that we often encountered O. J. in the same locations with regular intervals. O. J. travelled an average distance of 480 meters per day (range 100–1800 m.). The ranging pattern of the sub-adult male Roba basically resembles that of the female Mif, yet it differred in that he consistently covered a much larger area in a shorter time and stayed in any one location for shorter periods. This sub-adult male travelled an average distance of 890 metres per day (range 300–2000 m.). We had the impression that the ranging pattern of younger apes, including sub-adult males, was influenced stronger by social factors than that of adult individuals. Young orang utans might travel a considerable distance apparently in order to meet a particular companion. On one such occasion (9.11.1973), we noticed that the sub-adult male Roba set out for a travel of some 1100 meters, in a straight line towards the adolescent male Mos. Halfway he passed a large strangling fig tree with a wealth of fruits, and in which no other apes were present. The following day we found both orang utans feeding in the fig tree that Roba had passed. Both stayed together in a bond that lasted several days. Similar instances of the remarkable locating ability of orang utan individuals is reported on p. 251.This anecdotal event may even bear the suggestion that Mos benefitted from information about a food source acquired by the sub-adult male.

5.6. How foods are found

As I described in the preceding paragraph, orang utans gave a strong impression of being familiar with the topography of their range and in particular with the location of large fruit trees. A very similar impression has been reported by MacKinnon (1974) in terms of 'excellent knowledge of local geography' (p. 16). On several occasions we followed individuals heading straight for a fruit tree in which we had not seen them in the previous days. To achieve this they sometimes covered distances equalling a normal day range, i.e. 500–1000 metres. Similarly, we noticed that certain *Camponotus* ant nests were visited with some regularity by some individuals. They went there by a direct route. The same applied to the natural bowls where rainwater became trapped. I once followed the adolescent female Jet, who suddenly separated from her social group, to travel some 80 metres towards such a bowl. She drank there and subsequently returned to the group.

Another important source of information, particularly relevant to the detection of strangling fig trees with ripe fruits, appeared to be the hornbill birds. Orang utans were observed to react to the flight patterns of these large, noisy birds. Most of the larger hornbill species, especially the genus *Aceros*, have a very conspicuous flight noise which has been described as a 'metallic or resonant swish, which can be heard at an increadible distance' (Smythies, 1968, p. 326). Orang utans can probably tell the location of a ripe fig tree from the direction of the flight of flocks of these birds, as well as from their loud feeding calls. Several times we noticed that orang utans watched overflying hornbills. We observed on at least four occasions that an ape set out in the same direction and headed straight for the strangling fig tree, in which he had not been seen the previous days. We also found that orang utans can even be deceived by this means of information acquisition. For instance, the female Mif twice set out after the flight direction of a large flock of Blyth's hornbills but was halted in her travel by the Ketambe river; the strangling fig tree was situated at the other bank of the river. That she was deceived a second time, two days later might have been due to the fact that another large fig tree, though out of season, occurred in the study area, opposite the inaccessible fig tree in fruit.

Apart from this method of acquiring information on the availability of food, the orang utans sometimes gave us the impression of having awareness of the temporary patterns of food distribution. As I described in the preceding section, the female Mif seemed to check a large strangling fig tree on two occasions that we followed her. It is conceivable that an orang utan who travels through his home range with some regularity, obtains information on the state of productivity of particular potential food trees. He may recognize such trees by means of their morphological characteristics as well as by their location.

5.7. FEEDING POSTURES

Postures displayed by orang utans during feeding have been described in many earlier accounts, and most extensively by MACKINNON (1974); the descriptions closely correspond with those observed in the present study. A frequently observed feeding position in strangling fig trees consists of a hanging by one arm and one leg from a branch, while the two free extremities are used for reaching, holding on, and gathering the twigs laden with figs. This position closely resembles the foodgathering positions of other apes, notably the siamang (pers. observ., see also CHIVERS, 1974) and the chimpanzee (WRANGHAM, 1975), under similar circumstances.

An important derivate form of this posture in orang utans is that the ape hangs by three extremities, which are all secured on branches which have no immediate interconnection. We noticed that for its locomotion, as well as for its food gathering the orang utans often did not depend on one supporting branch, as most other primates in the Ketambe area, but that this ape typically distributed its weight over several supporting branches and/or lianas. Thus, two or three small branches, which separately would not have been strong enough to support the animal, were used simultaneously. The anatomical adaptations of the orang utan enable it to hang in almost any position for a prolonged period of time with a minimum of effort (NAPIER and NAPIER, 1967). By means of this technique the orang utan is able to reach the outer skirts of many trees (fig. 34). Moreover, the orang utan bends or breaks fruit bearing branches towards itself so that he is able to crop the terminal twigs of food trees which are inaccessible to many other animals. A similar technique has also been described for the chimpanzee (WRANGHAM, 1975), indicating that the Pongids are less restricted in foodcompetition than their weight and size would lead one to predict.

FIG. 34. Reaching for a terminal branch.

5.8. FEEDING HABITS AND FOOD MANIPULATION

The orang utans in the Ketambe area showed individual variation in handling and processing of food items. For instance, we noticed that some individuals frequently collected fruits to eat them some distance away from the harvesting site while others were never observed to do so. Also, some individuals appeared to swallow the seeds and stones of fruits, whereas others meticulously removed the flesh from the stone.

The orang utan's anatomical adaptations, namely good manipulative ability of the hands and feet, extremely mobile and sensitive lips and large broad incisors, aid in processing food. The processing techniques for some important foods items will be described below.

5.8.1. *Fruits*

Durian fruit (*Durio spp.*).

The spiny shell of the fruits of e.g. *Durio oxleyanus* pose a problem to everybody who attempts to reach its highly esteemed flesh. Humans are only able to open the fruits with tools. The spines of the wild *Durio oxleyanus* and some other *Durio spp.* are so sharp that it is painful to carry the fruits (500–700 grams) in the unprotected hand. Younger orang utans also appeared to find it painful to touch this spiny fruit. Up to the stage of sub-adulthood, most orang utans were unable to pluck and to open durian fruits efficiently.

Adult apes plucked the fruits by rotating the fruit around the stalk or by biting through the stalk. Only adult males were seen to pull the fruits off the branches. Adult orang utans often collected several durian fruits at a time and took these to some comfortable place where they could concentrate on the processing technique. Such a place might be a large branch near the centre of the crown or a nest. Some orang utans (notably sub-adult males) left the tree with their load to open the fruits in a nearby tree.

Durian fruits were carried by holding the stalk between the teeth or by holding one or several fruits in the opened hand; on the bent arm; kept between the arm and the body, and sometimes in a foot.[6] An adult orang utan might be able to transport 3 to 6 durian fruits at a time. To open a durian fruit, an adult orang utan gently took it in both hands, thus covering a large portion of the shell and so dividing the pressure over as many spines as possible. He then cautiously took one or two of the sharp spines between his large, slightly protruding incisors. The ape pulled out these spines and this process was repeated until several spines were removed so that he could bite away the tough skin without hurting his lips and reach the soft aril. Younger orang utans usually collected only one fruit at a time. They rarely employed the method of pulling the fruit away from their mouth by means of their hands, as the adults did. Often they placed the fruit against a trunk, in a small crevice or in the fork of a branch, pushing it into place with their hands and then pulling out the spines one by one with their incisors. Once we observed that the sub-adult male Doba held a durian fruit into a small crevice by pushing it with a piece of dead wood, thus using a crude hand-protecting device. He had collected the tool some 15 meters from the place where he used it.

Rehabilitant orang utans usually opened provided durian fruits in a similar fashion. Some rehabilitants however displayed a more ready use of tools to facilitate processing. Thus, the rehabilitant David used pieces of paper, leaves, and once a gunny sac to protect his hands while holding the spiny fruit. Another rehabilitant (Usman) tried to open the fruit by using a pointed stick that he especially collected for the purpose; he repeatedly stabbed into the fruit (see fig. 35). Usman only succeeded in blunting most of the fruit's spines, with the ultimate result that he could hold the fruit much easier. Both wild and rehabilitant juveniles and some adolescents did not succeed at all in opening this esteemed food item.

Heritiera fruits (*Heritiera elata*).

The small nut-like *Heritiera* fruits have a hard, tough skin which was cracked by orang utans with their premolars. These fruits were probably inaccessible to other primates in the Ketambe area; no other primate species were observed to feed from them.

Sometimes orang utans collected fruits by breaking off laden twigs and eating their harvest in a nest. Four times adolescents were seen to carry such a twig with them when they left the tree to follow their companions in a social

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[6] Note that these techniques closely resemble those employed by chimpanzees in transporting similar sized objects (ALBRECHT and DUNNET, 1972).

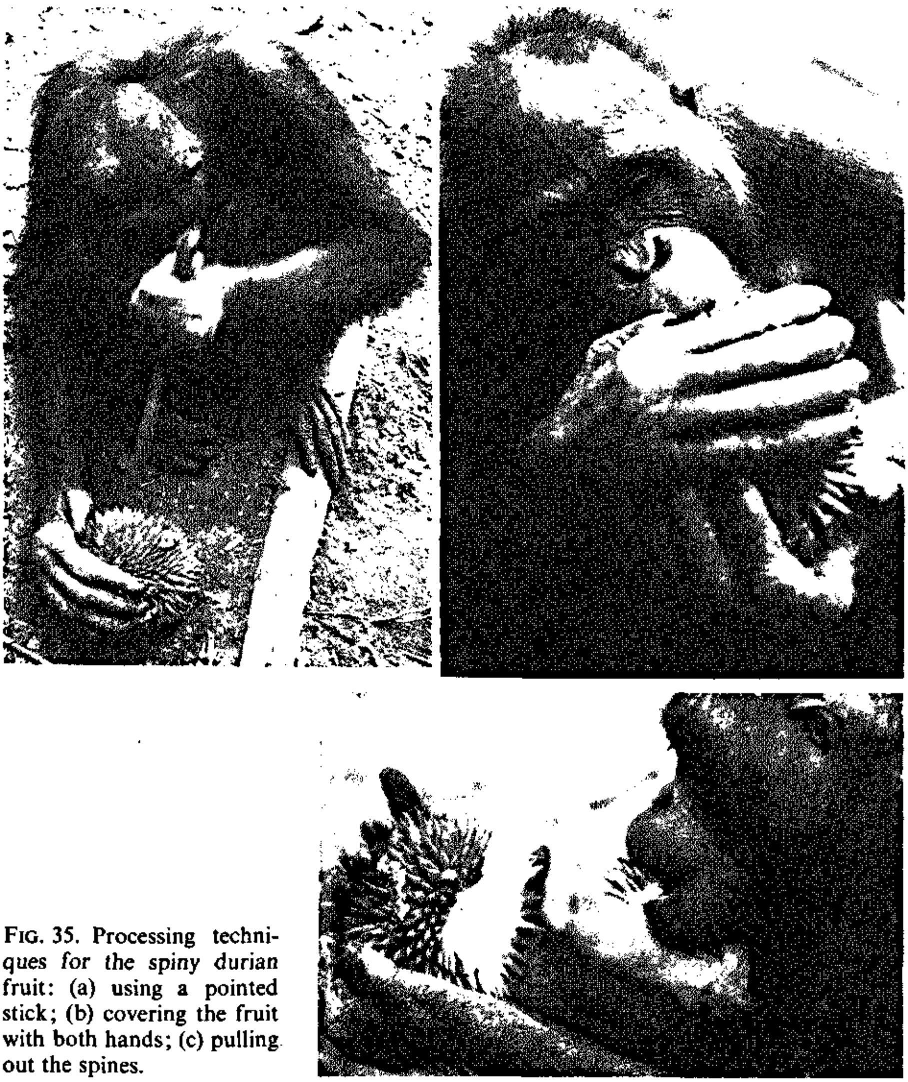

FIG. 35. Processing techniques for the spiny durian fruit: (a) using a pointed stick; (b) covering the fruit with both hands; (c) pulling out the spines.

group. They fed from the fruits as they travelled. One twig was carried some 150 meters from the parent *Heritiera* tree.

While feeding on this fruit the orang utans usually sucked the hair on their arms and sometimes their legs after every feeding bout of several fruits (fig. 36). All animals did this and one adolescent even sucked the hair on the back of his peer who fed next to him. The cause of this behaviour has to remain obscure, but a possible explanation is that the apes sucked salty sweat from the hairs to enhance the taste of the fruits. Perhaps its function is to recycle a valuable resource (NaCl), which is quite scarce in some forested regions such as the Ke-

FIG. 36. Sucking on the hair of the arm during feeding on *Spatholobus* fruits.

tambe area. Such hair sucking behaviour was also observed in connection with the utilization of a variety of other fruits, e.g. some figs, *Antiaris toxicaria, Scaphium javanicum, Combretum latifolium* and *Spatholobus ridleyi.* Apart from the figs and the *Antiaris* fruits, all mentioned species had a somewhat adstringent taste and were of a dry texture.

Figs

Many types of figs were eaten without special processing and were swallowed, but some, notably the large *F. stupenda* fruits were usually subjected to elaborate preparation. The apes removed and discarded much of the tough, hairy skin as well as a considerable proportion of the inner contents, i.e. the seeds, of such figs with their teeth and lips.

Fruits with large seeds

Sometimes seeds with firmly attached flesh e.g. those of *Nephelium lapaceum, Aglaia speciosa, Tinomiscium phytocrenoides,* were swallowed whole. Such seeds passed the digestive tract undamaged. It was remarkable that some individuals took greater care in processing fruits than others. This difference in behaviour was also apparent with the provided seed containing bananas (*Musa spp.*). Some orang utans swallowed the entire fruit including the seeds, others carefully removed the seeds. Those orang utans who processed their food more carefully inspected their mouth contents more often by peering at their protruding underlip (fig. 37).

FIG. 37. Inspection of mouth-contents.

5.8.2. *Foodplants with poisonous qualities*

Orang utans may eat certain fruits and plants which contain poisonous secondary compounds. The orang utans in the Ketambe area often fed on the fruits of *Strychnos ignatii*, and also ate large quantities of the fruits of *Antiaris toxicaria*. *Strychnos ignatii* is a woody liana containing quantities of the alkaloid strychnine. The orang utans seemed unaffected by these toxins, apart from producing excessive saliva. Similarly, chimpanzees in East Africa feed on three allopatric Strychnos spp. with no apparent ill-effects (see VAN LAWICK-GOODALL, 1968; WRANGHAM, 1975; and pers. observ.).

The tree *Antiaris toxicaria*, of which the fruits are among the 'esteemed' foods of orang utans, contains a toxic alkaloid (*ipoh*), used by native hunters throughout South East Asia as an arrow poison. Several ethnic groups in Borneo mixed the latex of *A. toxicaria* with the resin of *S. ignatii* to get a very potent toxin for their blow-pipe darts (see MÜLLER, 1857; LESCHENAULT, 1810). They reportedly hunted orang utans, amongst others, with these blow pipe darts.

Prior to eating the *antiaris* fruits, the Ketambe orang utans wiped the plucked fruits along branches. This elaborate rubbing technique, applied to the breaking point of the stalk may have removed most of the exuding latex, containing the toxin. However, it is noteworthy that orang utans applied a very similar rubbing technique to several non poisonous fruits exuding latex (e.g. the unripe figs of *F. drupacea*). Whether the latex of *A. toxicaria* is indeed poisonous when ingested is obscure; it is not very likely as Malay children are also known to eat the

FIG. 38. Feeding on the leaves of *Dendrocnide sinuata*.

unprocessed *Antiaris* fruits (see CORNER, 1952). Chimpanzees eat the same (*A. toxicaria*) fruits in Tanzania (WRANGHAM, 1975) and the bonobo (*Pan paniscus*) feeds on the fruits of an allopatric species *A. welwitschii* (MACKINNON, 1976).

Apart from these truly poisonous plant species, the orang utans fed on the shoots, the inflorescence and the leaves of the treelet *Dendrocnide sinuata* ('*latong gajah*') (fig. 38). A touch of the leaves of this large stinging nettle (*Urticaceae*) on human skin has a very unpleasant burning effect which may last for several days. Contact with this plant may even cause an inflammatory reaction accompanied by mild fever. Orang utans were apparently less affected than humans by this plant. Younger animals had a cautious way of eating this particular food item. They appeared to avoid touching the leaves with their lips, often cautiously removed the large mature leaves and frequently rubbed their hands and muzzle after feeding on this item. It is interesting that, according to our informant, '*latong*' had been utilized as a common vegetable in ancient periods (G. AMANSAR, pers. comm., 1972). RAPPAPORT (1968) has listed the closely related (if not identical) genus *Laportea*, (and several other non-identified *Urticaceae*) under the non-domesticated resources, used as food by the Tsembaga people in Papua-New Guinea. Similar utilization of a viciously stinging nettle (*Laportea alatipes*) has been reported for the mountain gorilla (see SCHALLER, 1963; FOSSEY, 1972).

5.4.3. *Insects and other animals*

Many of the insects eaten by orang utans are colonial and possess a defence mechanism consisting of an attack by a mass of viciously biting and/or stinging individuals. When feeding on the arboreal non-flying colonials ants (e.g. *Camponotus*) the ape hung or sat on a branch or liana which had no direct connection with the vegetation supporting the insect's nest. Usually the orang utan disturbed the nest, holding the back of his hand against it and allowing some insects to crawl onto the hairs of the hand and the wrist (fig. 39). Such ants were then picked off with the lips one after the other. Ants biting the lips were apparently ignored, whereas those which bit the toes or fingers were usually hurriedly removed. Sometimes an orang utan kept a handful of ant nest material in a firmly clenched fist, and by relaxing his grip a little he allowed a limited flow of ants to crawl out. These were then picked off with the lips and eaten. Once we observed an orang utan tear off a twig containing an ant nest constructed of leaves presumably of an *Oecophyllus* sp. Grasping with his hand around the twig, just below the nest, the ape suddenly jerked towards the nest, thus stripping off a number of leaves from below the nest. These leaves apparently served as a cover between the ants' nest and his hand. By holding this bundle of leaves, containing the nest, in his clenched fist, he could regulate the number of escaping ants. These were picked off one by one with the lips.

The small ants of the genus *Crematogaster* were eaten quickly after the orang utan had torn off a part of the cardboard-like nest and stuffed it in its mouth. The orang utan then usually retreated hurriedly some meters to avoid the mass of tiny ferocious ants, swarming out of the remnants of the nest. Young inexperienced rehabilitants sometimes did not retreat fast enough and were covered with a swarm of biting insects, which caused them considerable discomfort.

Ant nests which were easily accessible, such as those of some arboreal *Camponotus* species and *Polyrhachis villipes*, built in the root systems of epiphytic plants, were completely destroyed by orang utans (fig. 40). The nests of some other *Camponotus* species and of *Polyrhachis hector* ants, which were built under the bark of certain trees or inside dead or live trees (*Myrmecodia*), and consequently difficult to reach, were visited regularly by orang utans. During these visits the orang utans consumed small numbers of ants which they from around an entrance or breaking a branch wherein a nest was situated. The branches of the tree *Erythrina subumbrans*, for instance, often contained such nest extensions.

Termites, especially the white termites *Coptotermes curvignatus* and *Natusitermus matagensis* were collected in a similar manner to ants. These insects were usually exposed more easily than ants but more difficult to find initially. The orang utans often bit off large pieces of dead or decaying branches (fig. 41) or poked their fingers in the earth-covered mounds and crevices leading to such dead branches. Rehabilitant orang utans sometimes poked small sticks into deeper termite tunnels; the tool was used as a lever, or as a probe (fig. 42) (cf.

FIG. 39. Catching *Camponotus* ants leaving their nest entrance under the bark of a large tree; (a) keeping the wrist against the tree, allowing the ants to crawl onto the hairs; (b) picking the ants off with the lips.

FIG. 40. Raiding a nest of *Camponotus* ants in an epiphytic fern.

FIG. 41. Biting off pieces of dead wood to expose the white termites beneath.

FIG. 42. Using a small stick in order to disturb an *Camponotus* ant nest under the bark of a tree.

chimpanzees; (VAN LAWICK-GOODALL, 1968).

Whereas Bornean orang utans reportedly eat *Meliponid* bees (MACKINNON, 1974), the abundant sweat bees of the genus *Trigona*, which live in colonies in the trunk of large emergent trees and make characteristic waxen funnel-like entrances to their nests, were of no apparent interest to orang utans. Nor did the rehabilitant orang utans ever show any interest in the conspicuous entrances of the *Trigona* nests. The only animal in the Ketambe area which was able to expose and raid these nests, was the Malay sun-bear.

Orang utans in the Ketambe area sometimes raided the small exposed nests of *Ropalidia* wasps. These nests are situated against tree trunks or large branches, usually near or under epiphytes, only few metres from the ground. An orang utan approached to within arm length distance of the nest, suddenly grabbed a piece and quickly stuffed it into his mouth. Either he then quickly retreated in upwards direction in order to avoid the attacking wasps, or he sat motionless. The sting of these wasps is painful but of short effect.

Once an orang utan female with infant was persistently followed and attacked by a swarm of bees, probably of the genus *Megapis*. It was not clear whether she had raided the nest of these bees, as orang utans in Borneo do (MACKINNON, 1974), or whether she just had collided with the swarm, as is a comparatively 'normal' experience for a rainforest traveller (see e.g. VAN STEENIS, 1937). She tried to get rid of the insects by piling twigs on top of herself, and at times moved at a fast pace to another tree, repeating the procedure. She also waved and hit with twigs at the bees swarming around her, while crouching over her infant and shielding her eyes with her other hand. Her attempt to hide under a shield of twigs seems to give credit to the assumption, made by BRANDES (1937) saying that the orang utan's habit of putting vegetation on its head (cf. 'self-decoration'; p. 187) has derived from an escape mechanism from stinging insects.

Orang utans caught crickets and caterpillars by inspecting rolled, crincled and funnel shaped leaves. They unrolled such leaves with their lips and hands, catching the emerging insects in their mouth. If an orang utan spotted a bush-cricket, he quickly grabbed it, opened his clenched fist cautiously, finger by finger, close to his mouth to catch the emerging insect between the teeth.

We had the impression that adolescent orang utans spent considerably more time in foraging on insects than adults. The fact that all examined faecal samples of adolescents contained insect remains, whereas these were absent from some stools of the adult age category may lend some weight to this impression. Orang utans of all ages ate insects. The most frequently found insect remains were those of the ant genus *Camponotus*. Of 96 examined faecal samples, 76 contained insect remains. Of the 20 faecal samples lacking insect remains, 70% were from males. This suggests that males may have a lower incidence of feeding on insects than females. Chimpanzees show a sexual difference with regard to eating of insects, i.e. females feed on ants and termites more frequently than males (WRANGHAM, 1975).

As I noted on p. 52, on two occasions I noticed that wild orang utans raided bird nests. In addition, the rehabilitant male David was seen to raid bird nests on another two occasions (fig. 43). Once the adult male O. J. raided the nest of a bronzed drongo (*Dicrurus aeneus*), and swallowed the contents. On another occasion the adolescent male Mos happened upon a nest of a fairy bluebird (*Irena puella*) in the fork of a tree. When the orang utan moved onto the branch bearing the nest, the bird flew off. This apparently attracted the apes's attention; he moved towards the nest, pulled it down, peered at the contents and pushed his muzzle inside the nestcup, presumably to scoop up the contents. Mos dropped the nest and made chewing movements. He discarded nothing which suggests that if he ate the eggs, he also swallowed the shells. Rehabilitant orang utans always chewed on, and swallowed the shells of hens' eggs, as did the adolescent female Jet during an experiment to test her readiness to accept eggs as food. Orang utans were not observed to use vegetable matter in connection with egg consumption, as has been reported for chimpanzees (KORTLANDT, 1966; VAN LAWICK-GOODALL, 1968).

On several more occasions we noticed that both wild and rehabilitant adolescent orang utans inspected, and sometimes pulled, nest material from crevices and holes in trees. On one such occasion, the adolescent female Jet destroyed the nest of a pygmy squirrel (*Callosciurus tenuis*). The squirrel had just transferred its young to another nest site. Perhaps the squirrel had attracted the attention of the orang utan during one of its moving trips. Although we did not see the apes find any edible contents in the nests in these cases, this inspec-

FIG. 43. Raiding a bird's nest (probably of the blue naped flycatcher).

tion of potential nesting sites of birds and small mammals suggests that they may occasionally catch and eat small vertebrates. Similar inspection of tree holes and nests has been noticed for Bornean orang utans (MACKINNON, pers. comm., 1976).

Several times rehabilitants used sticks to poke into the burrows of rats (*Rattus* spp.) near the feeding site. On one occasion the rehabilitant male David showed particular interest in a burrow which a rat had just entered. He peered into the tunnel, poked into it and then stamped the ground near its entrance. The rodent suddenly emerged and ran away whereupon the orang utan jumped back and immediately climbed a tree.

5.4.4. *Drinking behaviour*

Several authors have commented on the techniques employed by orang utans to drink water; MACKINNON (1971) has given fairly extensive descriptions of these techniques. He noted that most of the water required by this large primate may come from the fruits and shoots eaten; many of the fruits in the ape's diet have a high water content. According to my observations, however, young orang utans drank water at least once every day. Usually they obtained the water from natural bowls in trees where rainwater had collected (fig. 44). The sites of such water bowls appeared to be known by most individuals in the area and they sometimes made obvious detours to drink at such places.

The orang utans in the Ketambe area sometimes profusely sweated and probably this loss of water had to be supplemented with drinking-water when

FIG. 44. A juvenile drinking rainwater from a natural bowl.

the liquid content of the diet was insufficient. The apertures of the natural bowls were not always wide enough to allow an individual to suck up the water directly. Then the ape might dip his hand or some fingers into the liquid and suck the water off them. Orang utans also sucked water from surrounding leaves and from the hair of their arms during and immediately after the frequent rains.

Although we did not see orang utans come to the ground to drink from streams, the footprints of the adult male O. J. found beside a small tributary suggest that orang utans in the Ketambe area might do so on occasion. As many of the natural bowls have only small entrances which are even too small to allow the hand of a young orang utan to pass, the adult males with their large, heavy built hands may experience a comparative shortage of such arboreal drinking sites and have to exploit alternative sources.

5.4.5. *Eating soil*

The orang utans in the Ketambe area occasionally ate small quantities of soil. We did not see the apes come to the ground for this purpose, as they do in Borneo and parts of North Sumatra (i.e. in the Renun- and the Kompas region where they enter cave-like depressions in the limestone rock where elephants and other animals ingest the mineral rich substratum; see also MACKINNON, 1974).

The orang utans in the Ketambe area sometimes ate the reddish clay-like substance that covered termite tunnels on the trees. Feeding on termite soil has also been reported for chimpanzees (WRANGHAM, 1975). Termite soil contains a higher mineral content than randomly collected forest earth, because of the added excretion products of the small insects. Rehabilitants sometimes picked up the small mounds of soil deposited near earth worm burrows and swallowed them.

5.9. INFLUENCE ON THE HABITAT

Every animal influences its habitat to a degree related to its biomass, i.e. to its size and weight and to its population density. In particular the influence of large mammals may result in dramatic changes to the environment, e.g., man (see also p. 327) and elephant (MUELLER-DOMBOIS, 1972; LAWS, 1970). When there is a combination of the two, the habitat may degrade to savanna or even desert (see e.g. BUECHNER and DAWKINS, 1961; GLOVER, 1968 and LAWTON and GOUGH, 1970). Gorillas too may have considerable influence on their habitat; maturing male gorillas may make very heavy use over parts of the range where they begin to establish individual rights (see FOSSEY, 1974).

Orang utans exerted several different influences on their immediate surroundings, they had a conspicuous and immediate destructive influence on the vegetation, and a longterm dispersing effect on certain food-plant species. When feeding in certain fruit trees, the apes often broke branches in order to reach otherwise inaccessible fruits. They also might construct nests to eat collected quantities of fruits. Trees which were particularly vulnerable to such destructive feeding behaviour were *Garcinia sp., Durio sp., Bisschofia javanica, Mangifera foetida*, and *Dendrocnide sinuata*. Several months after orang utans had been feeding in such trees, the broken, dead branches still gave it a battered appearance. The marked difference between the fruiting patterns of the grove of *Durio* trees in the Ketambe area which did not fruit for at least 4 years from 1972, and the durians in the village on the opposite bank of the Alas river, which fruited every second year, may have been caused by the Ketambe orang utan's destructive feeding behaviour during the 1972 season. Perhaps this had an effect that inhibited rapid succession of fruiting seasons. Destructive behaviour of orang utans in fruit trees has also been noted for Bornean orang utans (MACKINNON, 1974).

As I described on p. 56, the apes sometimes removed the bark of certain tree and liana species to feed on the growth layers. Occasionally trees were entirely stripped of their bark, and were killed. The tree species thus utilized in the Ketambe area were *Artocarpus elasticus, Mallotus sphaerocarpus, Macaranga diepenhorstii, Ficus pubinervus* and two unidentified species. If the damage was limited, the trees usually survived.

When searching for insects, orang utans often tore loose large numbers of epiphytic plants, and detached climbers and lianas. Such vegetation was dropped after inspection and the fallen plants usually died on the forest floor. Some climbing *Araceae* had a remarkable bushy shape with numerous side-branches. This formation appeared to have been brought about by the frequent removal of terminal shoots by orang utans (fig. 45). Epiphytes exhibiting this shape always grew in easily accessible places, whereas those in inaccessible locations retained a normal shape.

FIG. 45. Feeding on the terminal shoots of *Scindapsus hederaceus*; note the bushy shape of the creeper.

Rehabilitant orang utans, notably males, often broke large branches and saplings, and bit through or detached lianas in playful displays. They also did so during their social play and while performing 'gymnastics'. Such behaviour was infrequent among wild adolescents and sub-adult males. The destructive influence of orang utans is well illustrated by the fact that in the immediate surroundings of rehabilitation stations the abnormally high density of these apes result in the destruction of most of the vegetation.

As many other mammals (see RIDLEY, 1893), primates can have a very important influence on their habitat through the selective distribution of food plant species. This is well known for man of course; it has also been described for gorillas (JONES and SABATER PI, 1971) and for vervet monkeys (*Cercopithecus aethiops*) (GARTLAN and BRAIN, 1968). MÜLLER already has reported the occurrence of seeds in the gut contents of a collected male orang utan specimen (SCHLEGEL and MÜLLER, 1839–'44) thereby possibly implying that this ape may play a role in the dispersal of certain food-plant species. The relatively large amounts of intact seeds of *Aglaia speciosa*, *Mallotus sphaerocarpus* and *Xerospermum sp.* in orang utan faeces, and the comparatively high incidence of groves of these fruit tree species in the Ketambe area, suggest that this ape plays an important role in their distribution. Of the 96 examined faecal samples 44% contained intact seeds.

It is noteworthy that the large seeds of the esteemed *Durio oxleyanus* are severely damaged by orang utans during processing. For this species the larger ground walking mammals, such as man, the sun-bear, and possibly the tiger, seem to be the main dispersers.

5.10. EXPERIMENTS WITH UNFAMILIAR FOODS

Some experiments were carried out with several habituated wild orang utans in the Ketambe area to test their readiness to accept unfamiliar food items. All tests were carried out on, or in the immediate surroundings of the feeding place of the rehabilitation station (see fig. 5).

An orang utan first smells an unfamiliar food item (fig. 46), and examines it from all sides. Then he touches it with the tongue and protruded lips in a kiss-like gesture or takes a very cautious bite, often with the buccal side of the mouth. After such initial testing, the ape may take a small bite and chew on the piece, frequently inspecting his mouth contents on his protruded underlip (fig. 37). If the smell or taste does not appeal, he drops the item and usually ignores it further.

Rehabilitant orang utans were present in some of the experiments. Most of the tested food items were familiar to them and consequently they sometimes may have influenced the experiments.

Altogether 10 different foods were tested on 8 different wild individuals, some of whom only entered a single experiment (i.e. Mif, and Mos), while others (i.e. O. J., Jet, Doba and Bor) were subjected to more than 20 tests. Due to the provisioning scheme for rehabilitants, which some of the latter individuals attended at times, the most frequent tests were done (either advertedly or to-

FIG. 46. Smelling an unfamiliar food item (sugar cane).

gether with the provisioning of the rehabilitants) with cultivated bananas and cooked rice, the staple food for the rehabilitants.

Bananas (*Musa violascens*) are endemic plants in Sumatra (Holttum, 1954). However, they did not occur in wild, or cultivated forms in the immediate surroundings of the Ketambe area, and for several reasons it seems unlikely that bananas were included in the diet of the wild orang utans in the study area. Eight orang utans were tested for their readiness to accept cultivated bananas. Four individuals accepted the fruits on the first occasion, namely the sub-adult males Doba and Roba, and the adolescents Jet and Mos. The adolescents were tested in the absence of rehabilitant orang utans; both showed the elaborate testing procedure described above. The sub-adult males both took the bananas but first ate the fruits after the rehabilitant female Bin had begged with them. Two individuals, the adult male Mozes and the adult female Mif did not show any interest in the bananas during the first experiment. A second test with Mozes gave the same negative result; a second test with Mif was not attempted.

The other two orang utans participating in the experiment, namely the adult male O. J. and the sub-adult male Bor, both ignored the bananas on the first, and on a number of subsequent occasions. However, later, when either of them was present at the feeding site when the rehabilitants were fed, both O. J. and Bor appropriated bananas from rehabilitant females, after the second and fourth attended provisioning respectively. On subsequent occasions they readily accepted bananas and even competed with rehabilitants in order to obtain them.

Cooked rice was tested on five wild orang utans. At first all wild individuals ignored the food. After some occasions when rehabilitants were provisioned with cooked rice, four individuals took some left over grains which they sniffed and carefully tasted. Again, none of them ate the grains which were discarded after the probe. On a subsequent occasion, the adolescent female Jet immediately took a clump of rice, examined it carefully and dropped it. However, she picked it up again when rehabilitants showed an interest in her share. Although she did not sniff nor taste the piece, she carried it around for some five minutes before the female Bin succeeded to appropriate it. When Bin ate the rice, Jet showed begging behaviour, and on the next occasion, some 5 days later, Jet immediately accepted rice and ate it. The sub-adult males Bor and Doba (who consorted the rehabilitant female Bin) accepted rice after a similar procedure, again instigated by Bin. For Doba it took 6, and for Bor 8 trials before they ate the food.

The other fruits or vegetables (i.e. papaya fruit, avocado fruit, carrots, papaya stem, sugar cane) were only tested incidentally. Both the sub-adult males Doba and the adult male O. J. who could be tested most elaborately with most of the above items, did not accept any of the offered foods. Also Bor and Roba did not accept papaya fruits. It is noteworthy, however, that the adult male O. J., after having rejected 5 offered papaya fruits during subsequent tests, some months later raided a papaya tree in our garden; quite remarkably he merely plucked the fruits and did not eat them.

Three wild orang utans were tested for their response to white hen's eggs. Only Jet immediately accepted the eggs and ate them, the two others (Doba and O. J.) did not. Even O. J., who had been observed to eat the contents of a drongo nest, ignored the conspicuous, large white eggs. It is noteworthy that some rehabilitants were very fond of hen's eggs, to such an extent that it became impossible to breed chickens near the base camp. All eggs were collected from under the hen early every morning by the rehabilitants David and Seamus, who could eat large numbers in a day. The female Jet was the only wild orang utan who, apparently in response to seeing rehabilitants do the same, immediately drank milk when we offered it to her.

These observations raises the interesting point that the sight of other orang utans eating an unfamiliar food initiates interest in the item and induces the individual to investigate its potential value. In the cases where active competition occurred, either in the form of begging or in attempts by others to appropriate the food item still to be tested, the wild orang utans were more ready to accept the food and often ate it without the typically elaborate probing. A similar phenomenon was observed among rehabilitants who sometimes eagerly accepted and ate less favoured food when others competed for it.

The conclusion which can be drawn from the experiments is that younger individuals (adolescents) most readily accepted unfamiliar food, while older orang utans often completely ignored it and responded to some of the offered food items only after repeated trials. This seems to concur with the fact that immature individuals of other primates have also been shown to react to novel stimuli and accept unfamiliar food more readily than adults, e.g. Japanese macaques (see KAWAI, 1965). The ignorance of potential food items displayed by adult individuals during the tests, which was expressed far more obviously in their behaviour than the results indicate, suggests that adults were as conservative in their diet choice as the other apes (see KORTLANDT, 1966).

We had the impression that the more an unfamiliar food item resembled a familiar food (fruit) in shape, size and colour, the more likely it is to be accepted as a food. However, our experiments are too few in number and too inconsistently conducted to draw a firm conclusion. It also remains obscure to what extent orang utans from different regions learn to utilize particular foods, while other, possibly edible food items remain untouched because of unfamiliarity. These preliminary experiments may suggest that although some form of 'ecological imprinting' (cf. IMMELMANN, 1975) may play a role in the diet choice of orang utans, notably young individuals are sufficiently susceptible for new stimuli (from feeding conspecifics) to adjust to a limited amount of change according to local conditions. This is certainly advantageous for youngsters who leave their mother's home range in order to find a suitable location for settling, where they may encounter other food-species.

6. FAUNA

In addition to orang utans, a rich and diverse fauna exists in the Ketambe area. In Appendix 6 I present a list of all reptile, bird and mammal species observed during the study period. This list will be far from complete. Several smaller animals as well as some rare and temporary visitors to the Ketambe area will have escaped notice, the more so because our attention mainly focussed on orang utans.

The knowledge that a tiger (*Panthera tigris sumatrensis*) regularly roamed through the study area, as indicated by fresh pug marks along the trails, often added an uncomfortable sensation to the daily searches, especially when these were carried out by a lone observer. No tiger was seen nor heard during the study period, yet, the regular occurrence of tracks indicated that the large cat visited the area almost every other month for several days. It is noteworthy that the local Gayo people claimed to be not particularly afraid of tigers when going into the forest, but they feared encounters with Malay sunbears (*Helarctos malayanus*), in particular females with cubs. Two Malay sunbears were resident in the Ketambe area. On several occasions these animals were observed together; the total number of encounters with sunbears was 14. On a few occasions such encounters were unintentionally close, with both parties becoming aware of the other at a distance as little as 3 meters. In all these instances, the bears startled back and fled after giving a loud barking vocalization.

Of the cat species, only the small sized Bengal jungle cat (*Felis bengalensis*) and the medium sized golden cat (*Felis temminckii*) were directly observed – once each – during the daily surveys. Usually the presence of felid predators in a forested region can only be ascertained by finding the pug marks or other traces, i.e. scratch marks on certain trees. Two trees with deep and high reaching scratch marks were found in the Ketambe area, presumably these trees had been used by a tiger as a scratching pole.

Some tracks found in the area could be indicative of the presence of leopard (*Panthera pardus*)[7], but the occurrence of this cat species in Sumatra has never been confirmed by the collecting of museum specimens (see HOOGERWERF, 1970).

6.1. REACTIONS TO GROUNDWALKING MAMMALS

Pigs (babi hutan)

Orang utans generally did not react when pigs (*Sus scrofa*) fed beneath their fruit tree; in eight observed cases, only once did a female orang utan start a short-lasting and not very intensive display towards a sow with piglets. Some reha-

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[7] The plaster cast of the pug marks of this track is kept at the Zoological Museum Amsterdam under no. 2564.

bilitants were more easily upset when seeing pigs. On five occasions we observed that a rehabilitant sub-adult male (David) displayed at pigs, and in particular at pig groups. Such displays included 'breaking and dropping of branches', and 'kiss' sounds. On two such occasions the rehabilitant made a vocalization like a 'lork call' (p. 232).These observations correspond with those of MACKINNON (1972); in Borneo however, wild orang utans seemed to react more intensively to the presence of these suids.

Pigs are the most important scavengers in the tropical rainforest, but it is unlikely that they constitute a threat to a groundwalking orang utan.

Cats and dogs

Some rehabilitant orang utans were – unintentionally – confronted with a caged clouded leopard. Presumably most of them had had some experience with this predator; experience which ranged from visual contact to having been mauled severely, when the leopard was still free. Nearly all rehabilitants stayed at a considerable distance from the cage with the cat (i.e. 8–15 m.). Those in the trees immediately above it expressed curiosity alternated with long lasting bouts of displays consisting of swaying the vegetation, and breaking and dropping branches until the cage was covered with debris. This behaviour was accompanied with 'kiss sounds' and 'grumpf' vocalizations (see p. 232).

The female Yoko, who was still recovering from wounds inflicted by the predator two months earlier, even tried to break into the cat's double fenced enclosure. When we witheld her from forcing the lock on the door, she poked with long sticks through the wire, arousing the clouded leopard into defensive reactions. When the cat struck out at the pole, she jumped back and immediately fled high up a tree.

When a tame infant leopard cat (*Felis bengalensis*) was introduced to the rehabilitant female Djahe, she caught it and handled it for some time. She seemed to appreciate the tactile sensation of the cat's soft fur as she repeatedly stroked the animal and rubbed it along her face and her clitoris. Gradually her handling became rougher and she dragged the cat by its tail along the ground. As she was about to climb a tree with it, the cat bit her. She startled, released it and then followed the fleeing cat with a stiff approach locomotory pattern dragging a branch behind her. (At this point the experiment was terminated.)

When this cat was older and had reached near adult size, a second confrontation took place. Another rehabilitant (Seamus) immediately approached it with short stiff steps, and as he advanced he threw two stones and a stick in the cat's direction. At this the cat fled into the vegetation. The other rehabilitants present reacted by branchwaving from the trees and giving occasional kiss vocalisations.

The introduction of a domestic dog pup to a groundwalking, Bornean adolescent male rehabilitant[8] evoked a series of bluff and threatening behaviours by the orang utan. The ape's behaviour showed several similarities

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[8] The confrontation took place in the Tanjung Puting Orangutan Project (see GALDIKAS-BRINDAMOUR and BRINDAMOUR, 1975) during our visit there.

FIG. 47. Reaction towards a playful puppy dog; note tense mouth facial expression, piloerection and the use of the stick.

to that reported for chimpanzees towards a disturbance (KORTLANDT, 1965; 1968; ALBRECHT & DUNNETT, 1971), including the use of sticks and the throwing of objects such as stones in the direction of the dog. The ape's piloerection and tense mouth facial expression (see fig. 47) indicated an agonistic attitude; the orang utan frequently sought reassurance in clinging to his attendant. The puppy, however, clearly expressed a 'playfull' tendency.

The offensive reactions of the rehabilitants towards the dog and the cat were probably facilitated by the observer's presence and by the fact that in the case of the dog, the experiment took place on an open field which gave the orang utan hardly any other alternative; the normal reaction of an orang utan to such potentially dangerous factors may well be avoidance (climbing a tree) rather than any offensive display. Yet, MACKINNON (1974) has described that an adult male orang utan 'voluntarily' climbed down to face two dogs. There are several other stories describing adult male orang utans attacking and sometimes killing dogs (GAUN ANAK SURENG, 1960). The circumstances surrounding these incidents are usually not very accurately described and in most cases the orang utans may have been met by men with dogs during hunting parties; probably the apes were wounded or forced down to meet their fate, rather then really taking the initiative.

Experimental introduction of a tame serow (*Capricornis sumatrensis*)

Both the wild adolescent female Jet and several rehabilitant orang utans obviously avoided a tame black mountain goat (*serow*), by climbing higher up a tree and displaying at it by means of 'breaking and dropping of branches', and 'kiss' sounds (see p.236).The goat had the rather frightening habit of suddenly dashing out from the bushes, sometimes preceding this behaviour by a whistling sound. Apart from reacting to these explosive outbursts of activity, the orang utans at other times also avoided the serow when it was browsing peacefully.

Humans

The reaction of orang utans to man has been described in numerous accounts since the earliest collecting expeditions in the forests of Borneo and Sumatra (RADERMACHER, 1780; ABEL, 1826; BROOKE, 1866; WALLACE, 1869; BECCARI, 1904; HORNADAY, 1885). On many of these expeditions, however, the orang utans were not allowed much time to perform any elaborate display behaviour as they were shot on sight. Moreover, most authors showed a remarkable tendency to describe their own displays with greater accuracy than that observed along the barrel of their weapons. Good accounts of the reactions of orang utans towards people can be found in HOOGERWERF (1936–'38); SCHALLER, (1961); DAVENPORT (1967) and MACKINNON (1974).

The behaviour patterns shown by orang utans towards groundwalking disturbances, and towards humans in particular, are variable and may range from clear avoidance, sometimes even giving the impression of panic flight, through apparent inquisiveness, to obvious threat.

Although some adult females were shy in encounters with me, it was mainly the adult females which gave conspicuous displays including elements such as 'breaking and dropping of branches', 'branchwaving' and 'kiss' (fig. 48) or 'grumpf' vocalizations. This corresponds with WALLACE's observations in 1855 (ibid, 1869; p. 43); he noted that 'it was however always the female Mias who behaved in this way' (throwing down branches).

Adult males seemed less easily aroused to display towards humans. Usually they simply sat still and stared at the disturbance. Some even tried to hide from the observer's view. The large adult male Gorm used to hold his arm before his face and peer over this hairy mass, so that his face was partly concealed. Adult males seldom gave kiss vocalizations when encountered, and some only kissed when apparently expressing their annoyance with my persistent following (e.g. the adult male O.J.).

Some sub-adult males readily gave displays towards humans (e.g. Bor), others kept silent or tried to escape observation like the adult males (e.g. Doba, Roba and Bobby). Only once did the habituated adult male O.J. direct an 'ostentatious approach' display at me; the context of this behaviour suggested

Fig. 48. A female orang utan giving 'kiss sounds'.

annoyance with my presence during a presumed socio-sexual interaction with the adolescent female Jet (see also p. 288).

Local information did not reveal any accounts of adult male orang utans ever threatening humans in the northern part of the Alas valley. This is in contrast to accounts from the Bornean subspecies. MacKinnon (1974; p. 34) reports having been chased by adult male orang utans on several occasions. Yet, from the numerous encounters between people and wild orang utans it can be surmised that in the majority of cases a tendency to avoid contact with humans is far stronger than a tendency to react in any agonistic way. Aggressive behaviour seems more likely when the human observer betrays an interest that can be interpreted as offensive by the ape; e.g. if he persistently observes ('stares') or follows the ape.

In most cases if an orang utan detects an observer before he is seen himself, he will attempt to hide, either by cautiously moving into dense foliage, or by just remaining immobile. Consequently an observer will quite often fail to detect such an animal at all. Therefore, we may conclude that, although arboreal, the orang utan has a whole set of reactive behaviours available for ground-walking disturbances. Humans are particularly powerful releasers of such behaviours.

6.2. REACTIONS TO REPTILES

On two occasions we observed a wild orang utan encountering a snake in the trees. When the adolescent female Jet detected a moving green *Dendrophus pictus*, she startled back and moved to another tree in great haste. The adolescent male Mos showed a similar avoidance reaction towards a *Coluber oxycephalus* snake which suddenly moved away from him.

In the 8 instances that a rehabilitant's reaction to snakes could be observed, these were similarly characterized by avoidance. During experiments, when rehabilitants were confronted with snakes, they also showed only avoidance reactions. None of the apes directed offensive behaviour at the reptiles in the experiments, which were carried out with a large *Coluber oxycephalus* and with a large *Python reticulatus*. Theoretically a large python can manage a prey of the size of a juvenile or small adolescent orang utan. In the research area however pythons were only encountered on the ground, and although they are skilled climbers and may catch their prey from vantage points, some 1–3 metres above the ground, this large constricting snake is probably not a significant predator of orang utans.

On two occasions I noticed more defensive and even inquisitive behaviour towards reptiles. For instance, we observed that two rehabilitant orang utans, namely Seamus and Bobo, cautiously approached a small densely foliated bush, attracted by a persistent squeaky noise. The noise appeared to originate from a medium sized tree frog that had been caught by a *Zaocys fuscus* snake. The apes peered into the foliage from close quarters, i.e. 1.5 metre away. Then Seamus, who stood in front, bent aside some twigs in order to have a better look. When he saw the snake he shook the twigs. His partner Bobo, who had rested his hand on Seamus' back, jumped back. When the snake moved, Seamus immediately followed his partner by retreating some 3 metres, but still fixing his gaze on the snake. He picked up a small stick and threw it with an underhand sway in the direction of the snake. The situation did not change and both orang utans left the scene after three minutes. Yet, Bobo returned to the same spot some two hours later. He approached through the trees and intently peered at the bushes from his high standpoint; after one minute he descended and investigated the place from the groundlevel.

The sub-adult male rehabilitant Usman once detected a badly wounded but still live monitor lizard (*Varanus salvator*) lying on the ground and partly hidden under vegetation. The orang utan displayed at the 1.5 metre long lizard from the trees, dropping branches and making kiss vocalizations. Then Usman climbed down and walked along a dead log towards the reptile. As he drew close the ape pushed aside the herbs to get a good view and peered intently at the immobile reptile. The monitor lizard had a large gaping wound in the side of its neck exposing part of the vertebrae; apart from its breathing the reptile was motionless. The orang utan pulled out some herbs and tore off other vegetation then threw these at the reptile with an overhead movement (fig. 49). Many

FIG. 49. Reaction towards a dying monitor (*Varanus salvator*): (a) and (b) throwing herbs; (c) investigating with a stick; and (d) sniffing the contact point of the stick.

of these projectiles hit the lizard, but caused only a slight reaction. The ape then pulled a small sapling out of the ground and, holding it by the crown he hit and slapped the *Varanus* several times with the roots. When the monitor did not react to this display, the orang utan moved some 12 metres away, selected a 1.2 m long stick from a pile of broken vegetation and returned to the reptile. He poked the stick carefully at the head and into the large gaping wound, then turned the stick round to sniff the place of contact (fig. 49d). Usman then seemed to lose interest and moved away.

6.3. FOOD COMPETITORS

Several animal species, i.e. birds and mammals, appeared to have a dietary overlap with the orang utan. Although there are several food items which may be utilized solely by orang utans, these are considered to be of minor importance in the ape's overall nutritional intake. Figs may be regarded as the most important food for orang utans, and especially figs are eaten by a large number of animals. For some of these, i.e. the hylobatids and a number of hornbill species, figs also constitute the main pirtion of their diet.

Several mammals other than primates, such as squirrels (at least 4 species), civets (possibly 3 species), rats (possibly 2 species), and several fruit bat species, were observed to feed also on figs. In addition, several bird species, other than hornbills, were observed to eat figs; in particular several fruit dove species (*Ptilinopinae*), several bulbul species (*Pycnonotidae*), and the fairy bluebird (*Irena puella*). As these species usually operate in small flocks or solitary (i.e. have a small biomass), and their food requirements probably do not significantly decrease the available crop, they are left out of this discussion on food competition. Only those animals which, through their numerical presence or otherwise, can be regarded as serious food competitors for orang utans are discussed in this section; especially the biology of the five sympatric primate species is to be treated in some detail.

Hornbills (Bucerotidae), 'burung enggang', 'rangkok'

The size of hornbills, and the fact that some species operate in large flocks, make them serious competitors for the orang utan. Eight species of hornbill were observed in the Ketambe area; of these, four species were sometimes seen in large numbers to take figs: Blyth's hornbill (*Aceros plicatus*), wrinkled hornbill (*Aceros corrugatus*), rhinoceros hornbill (*Buceros rhinoceros*) and helmeted hornbill (*Rhinoplax vigil*). Blyth's hornbill might invade large strangling fig trees in flocks containing more than thirty birds. Although the rhinoceros hornbill and the helmeted hornbill were usually observed in pairs in the Ketambe area, and appeared to be territorial in certain seasons, large numbers (i.e. 7–15) of these birds congregated in fruiting strangling figs at other times of the year. The four species of hornbills were often observed in mixed associations; the largest observed mixed flock contained 58 birds.

The great hornbill (*Buceros bicornis*) was observed infrequently in the Ketambe area. Yet, because it is one of the largest hornbills, it may be a food competitor for the orang utan in regions where it is more common.

Fruit-bats (Chiroptera), *'kelawar'*

Of the numerous fruit eating bats of the Indo-Malayan region, especially the flying fox or *kalong* (*Pteropus vampyrus*) may, at times, be an important foodcompetitor for orang utans with respect to fig fruits in particular. The *kalong* is the world's largest bat, with a wing span of 1.5 metre and a weight of 650–1000 grams (MEDWAY, 1969). It roosts gregariously in trees; sometimes several hundreds of bats congregate at one location.

Like other bats, the *kalong* is a nocturnal mammal. In the evening it may travel very long distances to reach a feeding site, and may periodically shift its roost in response to food availability (MEDWAY, 1969). On the other hand, some localities are known where the *kalongs* have roosted for several decades, e.g. in the *Kebun Raya* in Bogor. During certain months (July-August-September), thousands of these bats flew over the Ketambe area every evening in a steady stream heading north-west. In September 1973 a colony, containing at least 300 *kalongs* settled for two months in the Ketambe area. Before that event, *kalongs* were occasionally seen in the area, feeding from fruits – most of which were not eaten by orang utans –, and from the flowers of *Durio* spp. and *Bombax valetonii*. After they had settled in the area, however, they invaded particular strangling fig trees 'en masse' on several occasions and exhausted the crop in a few days. Thus, the presence of these bats in the area caused a temporary increase in foodcompetition, especially as regards figs. Moreover, we got the impression that orang utans avoided the trees in which the fruit bats were roosting and feeding. A large *Ficus elastica* tree in fruit, which during earlier seasons had attracted associations of several orang utans, was only fleetingly visited by single orang utans on four occasions after the bats had invaded the tree. Many *kalongs* stayed in the fig-tree during the day and every now and then individuals clambered around, fed, flew up and circled around the tree before returning to roost. Possibly the commotion and raucous noise produced by the roost of bats repelled the orang utans, although the apes were usually quite indifferent to the even larger hornbills flying near them in such fig trees.

Bear (Helarctos malayanus), *'beruang'* and *bear-cat (Arctitis binturong)*

On two occasions we observed that a Malay sun-bear fed on figs in the crown of a large strangling fig tree (*F. benjamina*). No primates were present on these occasions, but as several primate species were observed to feed in the tree before, and after these incidents, one wonders to what extend the feeding bear repelled other animals.

These few observations, may indicate that sun-bears only occasionally enter fig trees to feed from the fruits. The sun-bear is predominantly terrestrial and the numerous traces, i.e. pugmarks and faeces at the base of large strangling fig trees that had large fruit fall, indicated that the sun-bear mainly utilized this food-source by means of clearing away the waste of the arboreal species.

Bear-cats or *binturong* were observed to feed in fig trees on 8 occasions, and like the bear, *binturong* usually fed alone in the tree. Two times we saw a *binturong* feed in association with hornbill birds, yet we did not observe them with primates. Certainly these figures are too small to generalize, but twice we actually saw a *binturong* leave a fig tree when an orang utan entered. On one such occasion, the *binturong* moved towards an old orang utan nest and stayed there, only to return to the fig tree after the orang utan had left again. These observations suggest that *binturong* are repelled from a common feeding site by the presence of orang utans.

Primates

Thomas' leaf monkey *(Presbytis thomasi)*, *'kedih'*

At least four groups of Thomas' leaf monkeys, totalling approximately 40 animals were found in the Ketambe area (fig. 58). Leaf monkeys were found to live in a one-male group system; supernumary males congregated together in separate all-male groups. Occasionally lone males, male pairs or a male with two females were observed in the area between groups' ranges. Similar variation within the social organization of one species has been reported for African Colobines (DUNBAR and DUNBAR, 1976). The size of a group range of *Presbytis thomasi* was approximately 30 hectares; the average group size of five groups was 9.4 individuals. This leaf monkey seems to occupy exclusive ranges (possibly 'territories'), the limits of which are defined by characteristic complex vocalizations in which different members of the group participate.

Fights between males were observed on four occasions, presumably when supernumary males attempted to transfer into an established group. On one such occasion one of the fighting partners sustained serious injuries, i.e. deep wounds and a broken arm, and lost much blood. The injuries had been aggravated when both animals fell from the canopy onto the ground during their fight. The established male, who was the winner, proceeded to chase the badly wounded battered challenger along the ground for some 20 meters, but the chase ceased at sight of the observer.

Leaf monkeys are primates who diverge most from the orang utan in their feeding habits. Their diet consists predominantly of shoots and leaves, supplemented with fruits and insects. Figs did not figure predominantly in their diet. Orang utans and leaf monkeys were observed in close proximity relatively infrequently; this is probably an indication of the divergence in the species' ecological needs (see also p. 123). On the 27 occasions that the two species were observed within 50 metres of eachother they appeared quite indifferent to the other's presence. Orang utans did not react to the alarm calls of *Presbytis thomasi.* Apart from a few individuals of the group which included the feeding site of the rehabilitation station within its range, the leaf monkeys remained unhabituated until the end of our study period.

Long tailed macaque *(Macaca fascicularis)*, *'kera'*

At least three groups of long tailed macaques, totalling approximately 57 individuals, were found in the Ketambe area (fig. 58e). The long tailed macaque typically occupied the niche close to the rivers (e.g. WALLACE, 1869). *Macaca fascicularis* was found to live in multi-male groups (KURLAND, 1973) in which a clear dominance hierarchy was apparent. Young and low ranking males often trailed behind a group and adult males were observed to transfer from one group into another. Immigration of females seems probable as indicated by the appearence of a 'new' female (clearly recognisable by a collar and a mutilated tail, sure signs of earlier captivity), in one of the regularly observed groups. On several occasions solitary males were seen. Sometimes such lone males stayed for prolonged periods at the feeding site of the rehabilitation station and took food from young rehabilitants by threatening them. On several occasions lone long tailed macaques were found to associate fairly permanently with pig tailed macaque groups: 6 out of 7 pig tailed macaque groups observed during this study (6 groups outside the study area) contained at least one male long tailed macaque.

The *Macaca fascicularis* groups typically came to the river every afternoon, around four o'clock. Sometimes the adults sat on stones and allogroomed while the young animals played near or in the water. At other times the group moved slowly along the bank in a terrestrial mode towards their sleeping site. Long tailed macaques are excellent swimmers; they are able to cross wide, fast

FIG. 50. A group of long tailed macaques.

flowing rivers and can stay submerged for some time. The groups in the Ketambe area seemed to have regular sleeping sites. Most groups had more than one site, some of which were used more frequently than others. They slept in large trees close to the river. In the Ketambe area the night trees were often *Ficus racemosa.* At night the groups were often disturbed at their sleeping sites and some nights were punctuated with frequent screams and calls. It never became clear whether commotion was aroused by inter-groups skirmishes or by the appearance of a predator.

The long tailed macaques utilized a wide range of food-plants, and appeared to be predominantly frugivorous. Rather than travelling between fruit-trees, the animals' ranging pattern gave the impression of moving through the home-range over a wide front with dispersed individuals who foraged for many different items along the way. A considerable amount of time per day was spent in search of insects. Although long tailed macaques and orang utans may show considerable overlap in diet, the smaller macaque kept to the riverbank habitat and seldom moved inland for more than 300 metre.

Proximity of orang utans and long tailed macaques was observed on 32 occasions, and both species were seen in association in large strangling fig trees several times. Occasionally orang utans reacted to the presence of long tailed macaques. Three times a female orang utan gathered her infant and adopted a 'posturing' stance when a *kera* approached and started feeding close by. On two occasions I observed juvenile orang utans move towards long tailed macaques with a 'stiff approach' locomotory pattern, once a macaque threatened back with an 'eyebrow raise' gesture. Yet, when feeding together in a large strangling fig, macaques usually passed very close to orang utans, sometimes even coming within touching distance, without any apparent interaction. A lone long tailed macaque male, that stayed around the feeding ground

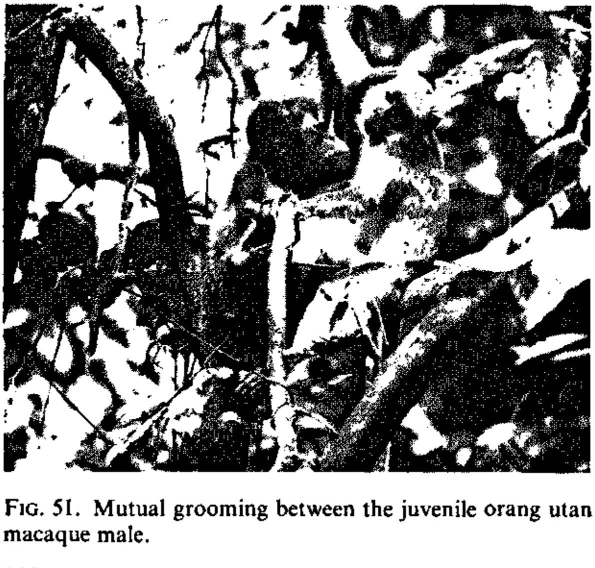


FIG. 51. Mutual grooming between the juvenile orang utan (Barby) and a wild long tailed macaque male.

of the rehabilitation station for some months, engaged in friendly interactions with some rehabilitants. Particularly interesting was the fact that the macaque induced allogroming in two rehabilitant orang utans (see fig. 51).

Long tailed macaques appear to be able to adapt to a relatively high degree of vegetation disturbance. In several parts of South-East Asia this monkey can be found in city parks, in suburban gardens and in temple-complexes. Since the riverbank habitat is most frequently and most severely disturbed by natural causes (e.g. flooding), it is quite conceivable that adaptability to changing environmental conditions is of selective advantage in long tailed macaques. Two groups of long tailed macaques were habituated during the course of this study.

Pig tailed macaque *(Macaca nemestrina)*, *'beruk'* (fig. 52)

Only one group of pig tailed macaques totalling some 23 animals was present in the Ketambe area. The pig tailed macaque's social organization showed similarities with that of the long tailed macaque. *Macaca nemestrina* was found to live in a multi-male group system, as a rule foraging in small widely dispersed sub-groups. Intra-group skirmishes were seen and heard much less frequently than with long tailed macaques, probably due to the larger inter-individual distance of this species as has also been reported for captive pig tailed macaques (ROSENBLUM et al., 1966; BERNSTEIN, 1969).

The small sub-groups, probably family units, often contained at least one adult female and some younger animals. On one occasion it was ascertained that the group was dispersed over an area of at least seven hectares of forest. Pig tailed macaques kept in contact during their dispersed foraging by uttering a soft, low sounding moaning vocalization, which could be heard at distances varying from 30–80 metres. On the occasions that sub-groups were stalked, animals spent a large proportion of their daily activity in searching for miscellaneous food items.

The number of animals foraging in the trees was larger than that of animals searching for food on the ground. Yet, pig tailed macaques travel mainly along the ground. The macaque group seldom stayed in one location for long. Their daily travelling covered approximately 600 metres. The observations on feeding pig tailed macaques suggest that they may, at times, be serious food competitors for orang utans, in particular with respect to certain fruits such as figs. Both long tailed – and pig tailed macaques appeared to be rather wasteful in their feeding habits; often they dropped more fruits than they consumed, unripe as well as ripe fruits. Strangling fig crops in particular could rapidly be exhausted after a few visits by macaque groups.

Occasionally we encountered solitary pig tailed macaque males in the forest. In the Ketambe area such males appeared to stay in one small sector of the area for a longer period of time, i.e. several weeks.

For example, a lone male stayed at the feeding ground of the rehabilitation station for several consecutive months in 1973 and 1974. He became fully habituated (fig. 52), even to the stage that he threatened the attendants and terrorized the orang utans, both rehabilitant

FIG. 52. A pig tailed macaque.

and wild, in order to obtain provisioned bananas. This *beruk* had the habit of lunging in the direction of a feeding orang utan (fig. 53); the ape usually fled, often losing some bananas. The only orang utan who ignored such offensive behaviour was the wild adult male O.J. In the course of the first fake attack by the *beruk* at the wild male, he stopped short at two metres from the ape and moved off again. The orang utan male did not show a reaction to the macaque's bluff. On other occasions, the *beruk* cornered juvenile rehabilitants and snatched away their share. One such incident, which evoked aggressive support from another rehabilitant is described on p. 282.

Several adolescent orang utans, both wild individuals and rehabilitants, directed agonistic displays at the macaque, also in situations when no food was provided. The macaque might respond by threatening back by 'eyebrow raise' threats and short, incomplete lunges. Usually, however, he ignored the apes.

The interactions between some orang utans and the pig tailed macaque were of particular interest as it showed an intelligent way to outwit the macaque. The orang utans (adolescent female Jet, sub-adult male Doba and rehabilitant female Bin) positioned themselves in one of two particular large trees that stood some 5 metres apart. Both trees were interconnected with one long pendulous liana loop, hanging from their crowns. When the macaque chased the orang utan female Jet, she used the loop to sway towards the other tree. Then she bit through the liana so that it became one long loose hanging rope between both trees.

On several subsequent occasions the female used this liana as a rope to swing from one tree to the other, dependant on the *beruk*'s position. As pig

FIG. 53. A pig tailed macaque threatening the wild subadult male orang utan Bor in an attempt to appropriate the ape's (provisioned) bananas.

tailed macaques are apparently not agile in moving along swaying lianas, the *beruk* had to cover the distance between these trees either along the ground or through the canopy. Every time the macaque approached the eating orang utan, she swung to the other tree. Perhaps by imitating this technique, the male Doba and the rehabilitant female Bin were observed to use the same rope in a similar situation.

'Proximity' between orang utans and pig tailed macaques was observed on only 6 occasions; usually the apes were just leaving a fruit tree in which *beruks* were about to enter. We were struck by the fact that other primates feeding in large strangling fig trees suddenly left a short time before a pig tailed macaque group entered it, as though the other primates were deliberately avoiding close proximity with the *beruks*. Pig tailed macaques were not seen to feed in association with the other primate species except for the long tailed macaque males which associated with pig tailed macaque groups, and one observation when the adult male O.J. continued feeding while three pig tailed macaque females passed by at a distance of 3 metres.

Pig tailed macaques appeared very difficult to habituate when within their group. Upon noticing an observer they immediately fled. They typically rushed to the ground and disappeared in the herb layer. Individuals that fed in the canopy, jumped down into lower vegetation or dropped straight to the ground some 20 to 30 meters below.

The *beruks* in the Alas valley were notorious for their habit of raiding local vegetable gardens.

White handed gibbon *(Hylobates lar vestitus)*, *'owa-owa'* (fig. 54)

Three groups of white handed gibbons, totalling 14 animals occurred in the Ketambe area (fig. 58). In addition two adjacent groups of approximately 8 gibbons lived along the edges of the research area.

Gibbons live in family units consisting of a male, a female and one to three offspring. These family groups are territorial; the size of the territories in the Ketambe area was approximately 40 hectares. The ranges of the groups usually overlapped slightly; the families defended their territories by characteristic loud structured calling sessions, and only rarely by physical combat. Gibbons are truly arboreal primates; in the Ketambe area they were never seen closer to the ground than 3 metres.

The gibbon's day started before dawn when the group moved to the nearest fruit tree to feed, and then rest and groom one another. Around 9 o'clock the group usually moved in the direction of the territory boundary and might become involved in a territorial conflict. Usually the female led the group in travel, and she might induce the conflict, but apart from joining in the calling

FIG. 54. A white handed gibbon female in a *F. elastica* tree (photograph A. K. C. FERNHOUT).

she refrained from any physical threatening. The territorial conflict calls lasted for an average of 16 minutes on 42% of the observation mornings. There appeared to be a variation in calling frequency between groups, which may have reflected the degree of hostility between the groups and their neighbours. Most calling occurred between 8.30 a.m. and 10.30 a.m., with a peak around 9.30 a.m. After a calling session, the animals usually travelled to another food source. The gibbons appeared to use well-known arboreal routes. The average distance a gibbon group travelled in the Ketambe area was some 1250 m per day (n = 10 days). At about 16.00 p.m. the group settled for the night. The gibbons slept in different trees every night, usually close to the centre of their territory, and not far from a fruit tree. Gibbons do not build a nest; they sleep in a sitting, or lying position on a terminal branch. The gibbons in the Ketambe area were frugivorous with a preponderance of figs in their diet (47%) (see fig. 56). Most of the data from the Ketambe area, gathered by Y. WANGSADINATA (unpublished report, 1974) concur with those from other areas (i.e. CARPENTER, 1940; ELLEFSON, 1967; CHIVERS, 1972).

During the surveys in the Gunung Leuser reserves, gibbons were not found above 800 m altitude. The gibbons and siamangs in the Ketambe area lived in (inter-specifically) overlapping territories in which they tolerated one another to a certain extent. Yet, siamangs sometimes actively displaced gibbons in certain trees, particularly in *Ficus sp.* It was also observed however that both species living in the same area, at times had friendly relations (see p. 119).

Associations between orang utans and gibbons were observed relatively frequently, especially in large strangling fig trees. On the 41 occasions that 'proximity' between orang utans and gibbons could be ascertained, both species appeared generally indifferent to eachother's presence. On only one occasion hostility was noted when the adolescent male Mos persistently tried to supplant a male gibbon in a large *Ficus* tree. He even followed the gibbon when it left the tree. The orang utan's following behaviour showed some clear sighs of the 'ostentatious approach' locomotion of adult males. I got the impression that the adolescent's behaviour expressed a playful self-assertive attitude towards a substitute. The gibbon's group-members did not interfere and followed the male when it left the fig tree.

Gibbons were observed to threaten long tailed macaques on two occasions; once this ended in a short chase. Yet, in general gibbons shared the food resources within their territories in peaceful coexistence with the other primate species.

The gibbons in the Ketambe area were very shy and even prolonged exposure to observers, who refrained from all potentially provocative behaviour, such as looking directly at the animals with binoculars and pointing cameras with telelenses etc. did not result in successful habitation.

Siamang *(Hylobates syndactylus)*, *'imbo'*

Five groups of siamangs, totalling 20 animals were found in the Ketambe area, and two groups (9 individuals) (fig. 58) lived along the fringes of the research area. Similar to gibbons, siamangs live in family groups with a maximum number of 6 individuals. The eldest sub-adult offspring is probably gradually expelled from the parents' territory, although the observed instances of agonistic behaviour between parents and such older offspring were rare. The siamang is about twice the size and weight of a white handed gibbon, but the siamangs in the Ketambe area occupied territories which were roughly half the size (21 ha) of those occupied by the gibbons. The territories of adjacent groups showed more overlap than those of the gibbon groups, and large fruit trees in the overlapping area were often visited by both siamang groups, but at different times of the day. Siamang territories were also defended by ritualized displays including loud chorussing of the entire group.

Siamangs are arboreal primates; a siamang was observed on the ground on only one occasion. This animal crossed a gap in the vegetation by descending and running along the ground over a distance of some 10 metres. The animal ran bipedally and balanced with his arms held high. Usually siamangs stayed in the canopy and were rarely observed feeding below three metres above the ground. The siamang day started after dawn, usually between 6.00 a.m. and 6.30 a.m. The siamangs in the Ketambe area showed the distinctive pattern of diurnal activity which is characteristic of the hylobatids, with a mid morning peak of activity and a gradual decline towards an early settling for the night, (ELLEFSON, 1967; CHIVERS, 1972). The siamangs in the Ketambe area spent more time in certain parts of their range than in other parts depending of fruiting patterns of certain trees. The siamangs' daily range varied from 450–980 metres (average 748 m: n = 16 days). We gained the impression that, like the gibbons, siamangs travelled along a network of established pathways. During travel, mothers might 'bridge' (p. 206) for their juvenile offspring to cross gaps too wide for the youngster to cross alone. As in the gibbon family, the female usually led the group during travel; the sub-adult usually followed in the rear. Siamangs had fixed sleeping sites, at 2 to 5 different locations, usually situated in emergent trees or in trees on vantage points, and often situated near the periphery of the territory.

During territorial defence, the male often led the group, while the female hung back. The male and the sub-adult son, when present, actively defended the territory. Territorial calling sessions lasted for an average of 17 minutes on 27% of the observation mornings, but some sessions lasted well over 30 minutes. The calling rate seemed to be influenced by the weather conditions. On several occasions siamangs were heard calling during the night; these calls were different from the territorial callings and were presumably caused by a disturbance (i.e. alarm calls). Most calling occurred between 10.30 a.m. and 11.30 a.m. with a peak around 11.00 a.m., about one and a half hour later than the gibbons. The siamangs in the Ketambe area are frugivorous primates. As for the orang utan and the gibbon, figs were the most important fruits of the diet. The frugivorous habit of the Ketambe siamangs appears to contrast with the findings on Malayan siamangs which were predominantly folivorous (CHIVERS, 1974). Siamangs bent branches to obtain fruits which were out of reach, but they were never observed to break branches, as orang utans may do.

From all associations between orang utans and other primates, orang utans and siamangs were most frequently observed together, usually in large strangling fig trees. In contrast to most of the associations between other primates and orang utans, those between siamangs and orang utans were not always accompanied by indifference (or unnoticed avoidance). In general, siamangs appeared to be comparatively intolerant towards other animals. CHIVERS (1972) even noted 'extreme intolerance' of siamangs towards gibbons in Malaysia. On three occasions when orang utans and siamangs were encountered together the siamangs attacked the orang utans. The victims were either young animals or adult females. In addition, the behaviour of the adult female Mif on two occasions suggested that she hid from approaching siamangs.

One of the attacks was particularly interesting as the male of a siamang family group of three (male, female and infant), lunged straight at and bit two orang utans from a group of four, who passed through the siamang's sleeping tree. The orang utans, an adolescent female (Jet) and a sub-adult male (Bor) screamed and fled, followed by the other group members. Yet, orang utans usually did not avoid encounters, but in most instances entered fig trees in which siamangs were feeding without hesitation. Often both species fed in association without signs of agonistic behaviour. Agonistic interactions were not only observed in the study area; another four agonistic encounters between siamangs and orang utans were observed in other areas. Of particular interest was the encounter reported by MACKINNON (1973, p. 238) from the Renun region, which was witnessed by me. On this occasion both the male and his sub-adult son out of a family group of five siamangs, seemed to coordinate their actions by attacking a sub-adult male orang utan from two opposite directions simultaneously. The orang utan hurriedly descended the tree and fled from the scene.

Considerable individual variation in inter-specific aggression was apparent among the siamangs in the Ketambe area. Some groups were comparatively tolerant whereas others were readily aroused into agonistic behaviour during encounters with other primates, and particularly towards gibbons and orang utans. For instance, one of the groups, namely the one that was most readily habituated, maintained a non-agonistic relationship with the gibbon group that shared its range. The interaction pattern involved coordinated movements (sometimes travelling together for periods up to three hours), and even allogrooming and play between the youngsters of both groups. Yet the same gibbon group was harrassed on several occasions by the other siamang group with which it shared common territory. The level of intra-specific aggression between groups also seemed to vary considerably.

Some siamang groups in the Ketambe area became comparatively rapidly habituated.

Many of the quantitative data given were gathered by E. BROTOISWORO (unpublished data, 1974).

7. ECOLOGICAL INTERRELATIONS OF THE PRIMATES

An important factor affecting the orang utan's biology is competition, notably for food, with other animal species. As I mentioned in the preceding chapter, a large number of animal species in the Ketambe area appear to have a strong overlap in dietary needs with the orang utan, notably for one of the latter's most important food sources, namely figs. Primates play a major role in this competition.

Merely identifying potential competitors is only a preliminary step towards achieving some insight in this complex ecological problem. It is necessary to determine the extent of competition to investigate its significance. To give some preliminary insight in the the latter problem, I shall consider some data on the respective primate species with reference to (a) their population density and biomass, (b) their distribution in three dimensional space, and (c) the niche differentiation in terms of their food supply. Clearly, a mainly qualitative description, such as the present one, can only provide tentative conclusions. Perhaps it can generate ideas for further, more detailed ecological research.

7.1. POPULATION DENSITY AND BIOMASS

A striking aspect of the South-East Asian rainforests is the relatively high density of several primate species, as well as their relatively frequent spatial association (MCCLURE, 1964; BERNSTEIN, 1967). Even for an inexperienced observer walking through the forest, primates appear to be the most abundant mammals, and indeed are often the only animals to be seen.

During the period August 1973–August 1974, the locations of all primates and other mammals encountered in the daily search were recorded systematically on day-maps. A total of 1250 contacts were made with 'units' or 'groups' of the six primate species. In addition to ecological considerations, it may be of conservational interest to add some details to the scant and inconsistent information presently available for rainforest species in the South-East Asian region. Therefore I shall also give some of the raw data from the daily surveys, although these are not particularly relevant for the population density and biomass calculations.

Of a total of 167 day surveys, only 3% showed a complete lack of success in finding primates, 22% resulted in a complete lack of orang utan sightings, while during 6% of the surveys, no primates other than orang utans were seen.

The frequencies of finding the respective species and other results of the surveys are shown in table 6.

The figure given under 'noticed number of individuals', are estimates, apart from those for the orang utan, which are actual counts. In fact they are under-

TABLE 6. Total number of contacts with primates during 167 search days. The average distance covered per day was 5.9 km.

species		number of contacts	noticed n. of individ.	mean n. of individ./group	real average group size		enc. group/km	n/km
orang utan	(P.p.)	144	284	1.97	1.91*		0.15	0.29
siamang	(H.s.)	175	572	3.29	4.16	(n=6/27)**	0.17	0.58
gibbon	(H.l.)	183	607	3.32	4.50	(n=4/18)	0.14	0.62
leafmonkey	(P.t.)	196	779	3.97	9.40	(n=5/15)	0.19	0.79
l.t. macaque	(M.f.)	134	858	6.40	19.20	(n=4/11)	0.13	0.87
p.t. macaque	(M.n.)	70	283	4.04	(23)	(n=1/ 1)	0.07	0.28

(*, see p. 166; ** the (n=6/27) code refers to 6 different groups which, together, were counted on 27 different occasions)

estimates; they represent the number of individuals noticed in the often fleeting contacts during the searchings. On the occasions that proper counting of particular groups was possible, considerably higher figures were found. These are presented in the table as 'real average group size'.

For the conservation of rainforest regions, it may be of particular interest to have a factor for calculating the density of certain animal species from data gathered in the course of conservation surveys which are usually short term. It should be kept in mind however that such a factor is highly observer-specific. The data show that there is a large discrepancy between the actual number of individuals and those noticed during surveys. The discrepancy may even be larger in areas that are unfamiliar to the observer. Except for orang utans, roughly half the actual number of individuals in a group is usually noticed during a survey encounter. The macaques show the greatest discrepancy between noticed individuals and real average group size, which reflects this species' widely ranging foraging technique.

Using – occasionally possible – accurate countings of all group members in the spatially and temporally rather stable groups of the primates in Ketambe, it is possible to calculate their respective population densities. For the orang utan, this was only possible on the basis of long term data from recognized individuals (see p.157). These densities and the educated guesses of the biomass of the primates in the Ketambe area are given in table 7.

The population density of orang utans is lower than that of the other primates by a factor of 2–3. Therefore it is quite remarkable that the scores of 'number of contacts' with this ape per covered kilometer are in the same order as that of the others. Perhaps this relatively high score reflects a concentration on orang utan in the searches, even though we attempted to keep bias as small as possible. The density of primates in the Ketambe area is approximately 125 specimens per square kilometer (i.e. 1 primate per hectare).

Most of the figures representing the 'best estimate of the biomass' fall within

TABLE 7. Population density and the educated guesses of the biomass of the primates in the Ketambe area.

species	density n/km²	estimated weight in kg			G*. (kg)	best estimate of the biomass. (kg/km²)
		female		male		
P.p.	5	30	–	75	28	140
H.s.	15	10	–	13	8	120
H.l.	11	6	–	8	5	55
P.t.	27	5	–	7	5	135
M.f.	48	3	–	6	3	144
M.n.	(19)	6	–	14	7	133

(G*. represents a calculated mean weight of a specimen, taking into account the age sex composition in the observed groups; e.g. for the siamang the calculation was as follows: the sum total of 4 adult males (52 kg), 4 adult females (40 kg), 2 adolescents (16 kg), 3 juveniles (12 kg) and 2 infants (1 kg), divided by 15. This figure is entered as the calculation of the 'best estimate of the biomass'.)

(For reference to weight, see NAPIER and NAPIER, 1970.)

a remarkable close range, namely 120–144 kg/square kilometre. Only the figure for the (white handed) gibbon shows a striking discrepancy. The gibbon biomass is less than half of that of similar sized primates (long tailed macaque, Thomas' leafmonkey), and that of the closely related siamang and the orang utan, which show the strongest resemblance in dietary needs to the gibbon. A similar discrepancy in the biomass of gibbons and other primates appears to be present in other areas such as Malaysia (CHIVERS, 1972) and Kalimantan (RODMAN, 1974). Typically a low gibbon biomass seems to coincide with the sympatric occurrence of either the siamang or the orang utan, or both. In areas

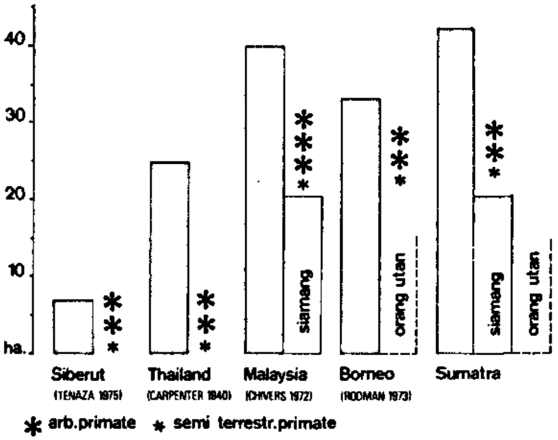


FIG. 55. Comparison of the size of territories of different hylobatids with reference to the degree of food competition from other primate species, notably apes. The shaded blocks represent the gibbon's territory.

where the gibbon is the only ape, the territory size is considerably smaller and hence its biomass larger. Thus gibbons in Thailand (*H. lar*; CARPENTER, 1940) have a territory (25 ha), some 38% of the area occupied by a Sumatran, Bornean or Malayan gibbon (*Hylobates lar*, *Hylobates muelleri*). Kloss' gibbons (*Hylobates klossi*) occupy even smaller territories (7 ha: TENAZA, 1975, to 14 ha: TILSON, 1975); with an estimated population density of 25 to 30 individuals per square kilometre (TENAZA, 1975); this gibbon has a biomass which is within the range of most of the Ketambe primates (120–145 kg/km^2) (see fig. 55).

7.2. NICHE DIFFERENTIATION WITH RESPECT TO FOOD PREFERENCE

The niche differentiation among the primates in the Ketambe area is achieved by a complex of specific physiological and behavioural adaptations. The most obvious one is of course related to food conversion and expressess itself in food selectivity (c.q. food-preference), between, as well as within food categories. Although we only made a very rough analysis of the diet of the primates, based on a limited number of observations, it is possible to make a tentative differentiation concerning the species' respective food-selectivity with reference to fruits and leaves (fig. 56). Thus, Thomas's leafmonkey is clearly distinguished from the others by being predominantly folivorous (54% leafmaterial in its diet). The other primates however, are remarkably similar, especially concerning the proportion of fruit in their respective diets (average 52–60%). Based on the estimated proportion of figs in the diet, the macaques may be distinguished ecologically from the apes. This distinction is further supported by the observation that macaques foraged widely dispersed while the apes usually fed from more or less localised food sources.

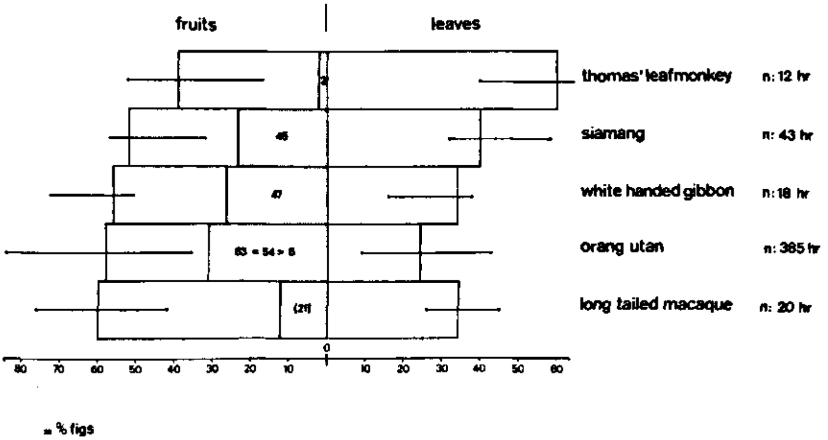


FIG. 56. Comparison of the relative frequency of feeding durations (mean and range) with respect to fruits and leaves for 5 sympatric primate species in the Ketambe area.

As mentioned before, figs, and in particular those of the strangling *Ficus* spp., are the most important food, in quality as well as in quantity, for both the hylobatids and the orang utan (fig. 56) (see also CHIVERS, 1972; 1974, and MACKINNON, 1974). The observations on the apes' feeding behaviour clearly showed that the relative proportions of the main food categories have a considerable variation (see fig. 56) so that, in relation to availability, a frugivorous ape may switch temporarily to a more or less folivorous diet or to a relatively higher proportion of other items i.e. 'bark,' insects, etc.). A comparison of the relative frequency of orang utan food-items from several different study-sites (i.e. RODMAN, 1973; MACKINNON, 1974) clearly demonstrates the variance in such shifts, may be as an adjustment to local conditions. Similarly, siamangs in Malaysia are reportedly folivorous (CHIVERS, 1974), whereas those in the Ketambe area were predominantly frugivorous.

The observations on gibbon feeding behaviour in the Ketambe area (RUCHIYAT, pers. comm., 1973, and pers. obs.) strongly suggest that gibbons are more selective feeders than the other apes. In their study on the synecology of Malaysian primates, MACKINNON and MACKINNON (in press) have found that white handed gibbons utilized 99 food items, and siamangs 112. They noted that 'the similarity between the diet of *Hylobates lar* and *H. syndactylus* is almost as great as that expected between two samples of the same species'. As I reported on p. 52, the orang utans in the Ketambe area were observed to utilize 152 different food items, which suggests that this heavy ape is the least selective feeder, if the data drawn from the present study and from Malaysia are compatible. It certainly accords with our impression of the feeding behaviour of the three species as observed in the Ketambe area.

When making an arbitrary differentiation according to food selectivity between, and within food categories, my impression ranks the long tailed macaque and the orang utan at one extreme, and the gibbon and leaf monkey at the other, representing the more opportunistic feeders and specialists respectively.

Perhaps the figures for the biomass also reflect this trend, i.e. the long tailed macaque scoring highest (144), followed by the orang utan (140). The folivorous leafmonkey presumably experiences the least degree of food competition of the primates in the region, score just below the latter (i.e. 135). However, the hylobatids, having a large overlap in dietary needs with other frugivores and especially with the orang utan, score lowest. The more offensive siamang approaches most closely to the biomass of the others; the gibbon, as said, well below.

Food selectivity obviously determines to a large extent the spatial distribution of the primates. Thus, one would expect that those species which have the greatest dietary overlap are to be found most frequently in one another's proximity, unless there exist repelling forces. Before describing the spatial distribution pattern I shall first examine some other factors involved in niche differentiation, namely food gathering and (energy) storage.

Food gathering

Weight and size in arboreal mammals are variables which give differential access to particular feeding sites (GRAND, 1972). Consequently, accessibility to the terminal twigs and slender branches, where most of the fruits grow, may play an important role in the food competition between different age and sex classes in primates (KUMMER, 1971), and may be equally important in the niche separation of sympatric arboreal species (GARTLAN, 1966; CROOK, 1970). Yet, this factor seems to be of less importance for the differentiation between the Sumatran apes. The siamang may bend, and the orang utan may bend and break the terminal branches towards itself in order to reach such otherwise inaccessible regions of a food tree. These specialized feeding techniques of the other apes reduce some of the possible advantage a gibbon might have in such situations on the basis of its lighter build.

The relation between size and energy expenditure

A large animal is able to harvest a relatively larger proportion of a non-durable fruit crop than a smaller one. Thus, especially when excess energy can be stored in the form of fat, being of large size can be seen as a particular strategy under particular environmental conditions. That is, temporary availability of large quantities of food, which occur regularly in time, and a special position with regard to predatory pressure.

On the other hand, the amount of food an animal requires to stay in a fit condition, is undoubtedly related to the animal's body size and to the amount of energy it expends (COELHO, 1974). Several factors determine the total energy expenditure of an individual. Next to the maintenance of homeostasis, a mammal spends energy in (a) the performance of activity, both maintenance activity, and social activity, and (b) in its reproductive status, e.g. pregnancy and lactation.

Consequently, it is impossible to use the mean length of day journeys of species with a different mode of life for an inter-species comparison, e.g. between gibbons and orang utans. However, in a comparison between species with a similar mode of life, such as siamangs and gibbons, the use of this parameter may give an indication of the difference in feeding strategy. It is remarkable that the average distances travelled per day by the two Sumatran hylobatids seem almost inversely proportionate to the size and weight of the animals. The small gibbon (6–8 kg) covers some 1250 metres per day (RUCHIYAT, unpublished data, 1974), the medium sized siamang (10–13 kg) some 750 metres per day (BROTOISWORO, unpublished data, 1974) (N.B. the heavy orang utan (28–75 kg) also travels some 700 metres per day).

That in an area which supplies almost the same food for the three closely related species, the small sized gibbon (i.e. some 10% of the orang utan's weight), covers a distance which is approximately 60% longer than that of its close relative the siamang, and of the orang utan, clearly indicates a different feeding strategy in the three apes.

On the basis of theoretical models, SCHOENER (1971) has suggested that larger animals tend to be less selective in their diet, this accords with our impression of the feeding behaviour of the three apes, as I noted in the preceding section. It may follow that food selectivity is the main variable that determines the ecological segregation of the three Sumatran apes. However, it is not selectivity as regards different food-plant species, but selectivity in quality of fruits within the same crop of a fruit tree species, that seems to play the major role.

Obviously, the small, more agile gibbon can have 'best choice' among the quantity available every day in any given stretch of forest, provided it has the same information on the distribution of quality food as the other apes. The fact that gibbons rise one hour ahead of the others may even add to their 'best choice' capability. At the other extreme, the large, heavy orang utan can, whenever food of high quality is available in large quantity, harvest a considerable proportion of the crop and store the excess energy in the form of fat, as MACKINNON (1974) has suggested. The siamang's active competition may well express its difficult in-between position. It is possible that the food competition of the gibbon, taking the highest quality food, and of the orang utan, reducing the quantity, has forced this medium sized hylobatid to adapt to a more folivorous diet in the course of the sympatric evolution of these ape species.

7.3. DISTRIBUTION IN THREE DIMENSIONAL SPACE

The rainforest habitat provides a complex arboreal substratum and offers a patchily distributed supply of food for frugivorous primates. Foraging determines much of the spatial distribution of animals. The vertical distribution of fruits of different food plant species may be more similar than the overlap of food-species in the respective diets of the primates indicates. Hence the vertical distribution of foraging primate species will probably not differ much between these species and only those who employ entirely different feeding strategies can be distinguished from the others. Estimates of the height at which the 6 primate species were encountered on the average are shown in fig. 57. The histogram shows that a comparatively different use of the vertical space of the rainforest only stands out markedly for the pig tailed macaque. It weakly, if at all, displays a differential use of the strata between the white handed gibbon, the siamang and the Thomas' leafmonkey which were all encountered mainly in the higher middle strata. The orang utan and the long tailed macaque were found most frequently in the lower middle strata and only the pig tailed macaque ranged from the higher middle strata to the ground level. Due to the way of data collection, these conclusions only concern the mode of travel (and avoidance) of the respective primates. They do not reflect the impression that canopy use during feeding by white handed gibbon, siamang and orang utan are extremely similar. It is clear that only a method of observation which makes use of more refined parameters, can reveal the subtle differences and similarities in the vertical spatial distribution patterns of the six primate species more precisely.

The horizontal distribution of food-plant species is very complex and the variety of species per unit-size (e.g. a hectare) may be enormous. Hence it is difficult to draw firm conclusions on the ecological inter-relations of different

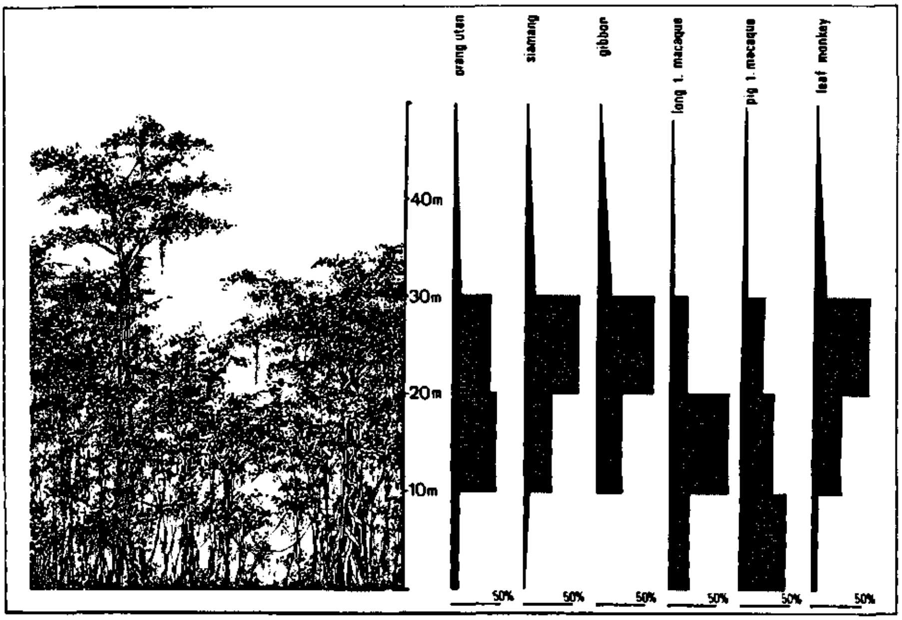


FIG. 57. Vertical spatial distribution of 6 sympatric primate species. First moment of contact.

primate species from data on their horizontal spatial distribution. Such data, however, can give a rough idea of habitat preference, and can indicate whether different species tend to congregate, are indifferent or tend to avoid each other.

In order to detect any possible differentiation in horizontal distribution all locations of the different primate observations gathered in the course of this study were plotted on a map (fig. 58). The plotting confirms that, for instance, long tailed macaques occupy the riverbank habitat, it also concurs with RODMAN's observation (1973) that pig-tailed macaques have some preference for regions at the foot of slopes and hills. The territories of the hylobatids are evenly spread over the area, filling most of the available space. Disregarding the home-ranges of individual orang utans by lumping all sightings together, the map showing these locations (fig. 58) reveals concentration regions, and in general shows a distribution pattern quite similar to that of siamangs and leaf-monkeys. The regions of concentration coincide with stands of certain fruit-trees (compare with fig. 26), as could be expected. Thus, the similarities in distribution patterns of the different primate species seem to correlate with the overlap in their respective diets.

As mentioned earlier, we often had the impression that several primate species were encountered within the same region at the same time, as if they associated. Thus, when finding an orang utan, siamangs and sometimes other primate species were often nearby. Certainly, such associations were mostly

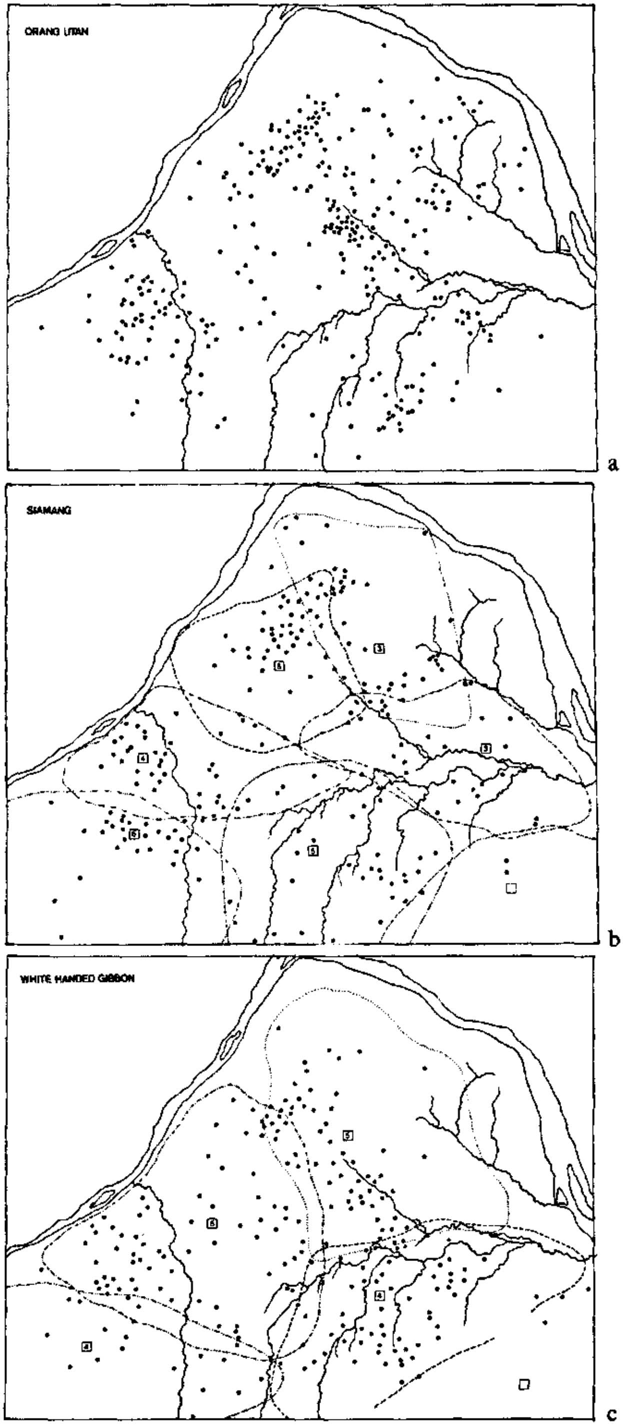
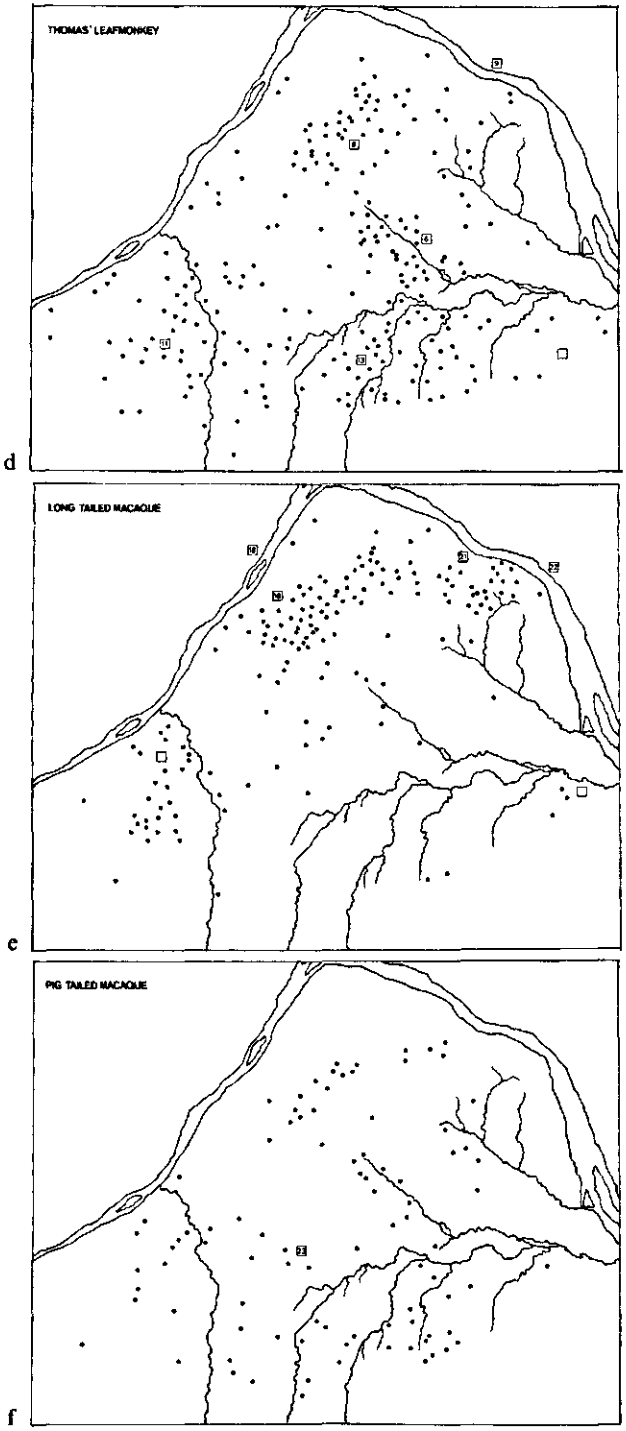


FIG. 58. Horizontal spatial distribution; all locations where the respective primate species were encountered in the study area: (a) orang utan; (b) siamang; (c) white handed gibbon; (d) Thomas leaf-monkey; (e) long tailed macaque; (f) pig tailed macaque.


THOMAS' LEAFMONKEY
9
8
6
11
13
d
LONG TAILED MACAQUE
19
18
21
22
e
PIG TAILED MACAQUE
23
f

in or in the near surroundings of a large strangling fig tree, or another common food-source.

The method of lumping all sightings together disregards the time factor, and consequently does not show if species exhibit temporal avoidance when utilizing the same food source. For instance, as I noted on p. 117, the daily activity pattern of the white handed gibbon appears to be ahead of that of the siamang (see also CHIVERS, 1972), which suggests that the small gibbon takes the initiative in the competition for quality-food; it also suggests that aggregations between the two species would be relatively seldomly met with.

To investigate a possible differentiation in horizontal distribution in time, 227 day-maps (1:8000), which show the rather precise location and the time of contact with the respective primate species, were treated as follows. A circular device of 0.8 cm radius (the converted measure for a circular region with a radius of 50 meters in the field, the distance at which the presence of another species is clearly detectable) was used to scan the maps in order to count all sightings of primates that fell within that space. This gives a rough measure of the temporal proximity of two or more different species within a region of some 0.78 ha. In table 8, the frequency of findings concerning species in 'proximity' is compared with the total number of encounters with the respective species. The table shows that the three apes and the long tailed macaque are found in 'proximity' most frequently; the siamang was found to be close to another species on almost half the occasions we encountered it. The total number of encountered combinations was 161 (composed of two species) + 24 (composed of three species) + 8 (composed of four species). Thus of all recorded encounters with primates in the Ketambe area during 227 days (n = 1250), 15.5% contained at least two different species in eachother's proximity. In Table 9, the 'proximity' of respective species is specified according to the found combinations. The most frequently observed combination in the total sample was orang utan/

TABLE 8. The relative occurrence of each primate species in 'proximity' of one or more others (X) as compared with the total number of sightings of each of the species.

Total number of encounters	P.p.:292	H.s.:211	H.l.:247	P.t.:230	M.f.:176	M.n.:94
	(P.p.+X)	(H.s.+X)	H.l.+X)	(P.t.+X)	(M.f.+X)	(M.n.+X)
Combination of two species	92	72	63	38	41	16
Combination of three species	20	20	14	5	13	0
Combination of four species	7	7	8	3	6	1
Total number of sightings in 'proximity'	119	99	85	46	60	17
Percentage	40%	47%	35%	20%	34%	19%

TABLE 9. The number of combinations found in 'proximity' in 227 days (total number of encounters with primates: 1250).

animal combinations 2 species		3 species		4 species	
P.p. × H.s.	25	P.p. × H.s. × H.l.	6	P.p. × H.s. × H.l. × P.t.	1
P.p. × H.l.	24	P.p. × H.s. × P.t.	3	P.p. × H.s. × H.l. × M.f.	4
P.p. × P.t.	21	P.p. × H.s. × M.f.	7	P.p. × H.s. × H.l. × M.n.	1
P.p. × M.f.	17	P.p. × H.l. × P.t.	1	P.p. × H.l. × P.t. × M.f.	1
P.p. × M.n.	5	P.p. × H.l. × M.f.	3		
H.s. × H.l.	26	H.s. × H.l. × P.t.	1		
H.s. × P.t.	6	H.s. × H.l. × M.f.	3	H.s. × H.l. × P.t. × M.f.	1
H.s. × M.f.	12				
H.s. × M.n.	3				
H.l. × P.t.	5				
H.l. × M.f.	5				
H.l. × M.n.	3				
P.t. × M.f.	4				
P.t. × M.n.	2				
M.f. × M.n.	3				
Total number of encountered combinations	161		24		8
Frequency of the total (n = 1250)	12.8%		2%		0.6%

siamang (47 times), immediately followed by siamang/gibbon (43 times) and by orang utan/gibbon (41 times). These results clearly reflect the extensive dietary overlap, i.e. the close ecological relationship of the Sumatran apes. All combinations containing more than two species were found in, or in the immediate surroundings of large strangling fig trees; they invariably contained an ape-species, either an orang utan or a siamang.

7.4. CONCLUSION

The data presented in this section give only a rough idea of the niche differentiation of the primates in the Ketambe area. Three main groups can be distinguished; (a) the predominantly folivorous leaf monkey, (b) the macaques and (c) the apes. It seems quite remarkable that only one species has adapted to a food-item which seems so over-abundantly present in the rainforest, namely leaf material, whereas for the dispersely available fruits 5 primate species and numerous other animals engage in competition.

The macaque species appear to be segregated mainly on the basis of differential use of the vertical and horizontal space. Long tailed macaques were largely arboreal and confined to the riverbank habitat, pig tailed macaques were semi-terrestrial and preferred the dry ground at the foot of hills and slopes. The differentiation between the three ape species is much more complex, however.

Animals with identical or very similar ecological needs, whether from the same or from different species, have to find ways to survive competition. There are several options, constrained by specific factors, by which an individual can do this. Competition, especially for food, is more often manifested as the effect of harvesting, rather than as direct interference. It is therefore remarkable that siamangs sometimes displayed agonistic behaviour towards the other apes, particularly during associations in strangling fig trees. Orang utans and gibbons, who possibly have an even higher preference for figs, rarely, if ever, supplanted other species in such trees.

The three sympatric apes have morphological differences, notably in body size, which may ultimately account for the mechanisms underlying their ecological segregation. One of the ways by which the hylobatids segregate is by their temporally spatiated use of the same area. This may add to a high degree of selectivity by gibbons with respect to quality food. Food selectivity with regard to quality may be a determinant factor in the ecological segregation of the three ape species; the orang utan may well be the least selective, which is in accordance with the large number of potential food items as compared with the hylobatids.

The tropical rainforest ecosystem consists of an immensely complicated network of subtle relationships between the many different components. As the present study only focussed on the comparatively minor aspect of the orang

TABLE 10. Summary of the feeding strategies of the three sympatric apes in the Ketambe area.

Species characteristics	Approximate time of rising	Speed of travel	Distance covered per day	Quantity of food taken and (the number of food-items)	Ecological option
GIBBON Weight 6–8 kg territorial terr.size: 40 ha	5–6 a.m.	very fast	large 1250–1500 m	small (99)	first choice selective feeder fruit/leaves: 56%/34%
SIAMANG Weight 10–13 kg territorial terr.size: 20 ha	6–7 a.m.	fast	medium 400–800 m	medium (112)	aggressive competitor fruit/leaves: 52%/40%
ORANG UTAN Weight 30–70 kg Overlapping home ranges home range size: 200–1000 ha.	7–8 a.m.	very slow	medium 500–900 m	very large (152)	least selective feeder, stores excess energy as fat-tissue fruit/leaves: 60%/34%

utan's biology, it is quite understandable that this network can only very roughly be unravelled. The synecology of the primate species of the Ketambe area certainly deserves a much more detailed approach than the meager facts presented here; it requires a detailed analysis of the respective species' feeding behaviour, their energy balance, as well as a close monitoring of natural changes in the habitat conditions from day to day for each species. Yet, notwithstanding the paucity of firm conclusions from this chapter, it can be stated that the orang utan is exposed to a considerable degree of food competition from a variety of mammals and birds. This particularly concerns his staple food, figs.

8. DISEASES AND MORTALITY FACTORS

8.1. Predation

Of the predatory animals, found in Sumatra, only the tiger, the clouded leopard, (perhaps the leopard), the hunting dog (dhole) and the crocodile are capable of preying upon orang utans.

In 1975, a freshly killed, past prime adult male orang utan was found in the Gunung Leuser reserve (Van Strien, pers. comm., 1975) (fig. 59). The corpse had bruises and deeply penetrating scratches on the back and in the neck region and a large part of the abdomen and the legs had been eaten. Pug marks near the corpse indicated that a tiger had caught and killed the male. All that was left of the corpse after one month were scattered tufts of orang utan hair.

In July 1974, a tiger broke into the night quarters of the juvenile rehabilitants and killed one male orang utan. The predator had made a considerable effort to get into the cage. Attempts to break through the wire mesh had failed (in the process the cat tore off two nails), but the tiger finally succeeded in breaking two of the boards of the sleeping-cage's floor. During the same period a tiger had tried to break into a small house in the village Balelutu, opposite the Ketambe area. Presumably this was the same animal.

Scattered amounts of orang utan hair were found in two localities outside the study area, whether these represented remains of a predator's kill or of animals that died from another (natural) cause is obscure.

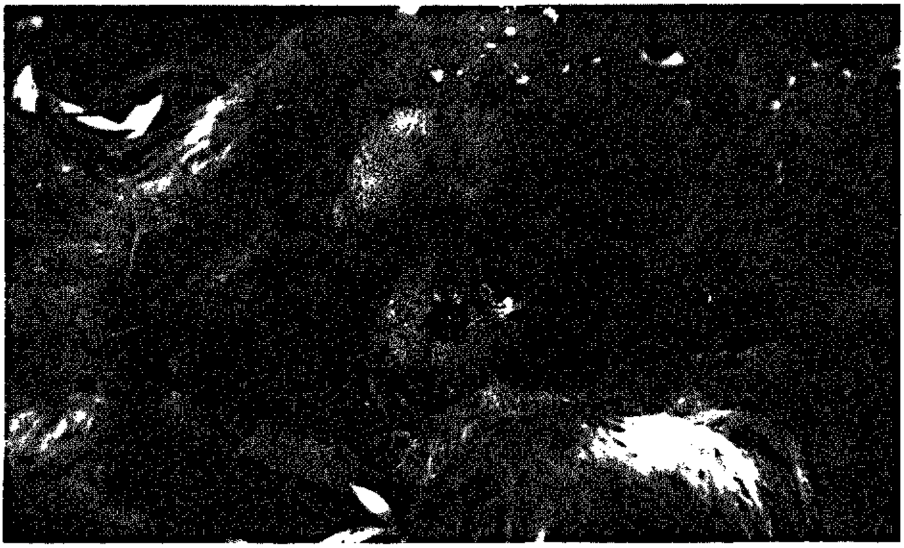


Fig. 59. An adult male orang utan, past his prime, killed by a tiger (photograph N. J. van Strien).

Notwithstanding these observations, it seems unlikely that tigers constitute a major threat to orang utans. It is possible however that the alleged lower frequency of travel on the ground by Sumatran orang utans in comparison with their Bornean cousins (see MACKINNON, 1974) is due to the presence of this large predator in Sumatra.[9]

A clouded leopard set back the rehabilitation project in 1972 by killing 7 juveniles and wounding several adolescent orang utans. The rehabilitants that disappeared and presumably were killed, were all less than 10 kg of weight. Larger individuals, i.e. adolescents and sub-adult males were attacked and wounded but not killed outright. Only one adolescent female died from a deep cut perforating her abdomen, presumably caused by a striking claw. Another female was severely mauled and was only saved with elaborate surgical treatment. The fact that some adolescents were wounded but not killed may indicate that the clouded leopard operates a hunting technique where the prey is not pursued after the initial strike. Two times it happened that two juvenile rehabilitants disappeared in one day. The cat returned to the feeding ground of the rehabilitation station at intervals of two to three weeks, as could be deduced from the disappearance of rehabilitants and the finds of pug marks. There were indications that several of the killed rehabilitants were caught while moving on the ground. These observations suggest that a clouded leopard is too small a predator[10] to prey successfully upon orang utans larger than adolescent size. As young orang utans, prior to adolescence, stay in the protective vicinity of their mothers, it seems unlikely that this cat is an effective predator on the species, except in isolated instances.

The occurrence of the Asian hunting dog (dhole) could not be ascertained in the Ketambe area, but tracks of this dog were found in other parts of the Gunung Leuser reserve (see KURT, 1970). From the very scant data on this canid species (see HOOGERWERF, 1970) it is impossible to speculate about its predatory effect on orang utans.

There is a large number of indigenous tales about the struggle between the crocodile and the orang utan, usually told among Bornean peoples (see e.g. WALLACE, 1869; DAMMERMAN, 1937). Since orang utans occasionally may move

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[9] The tiger does not occur on the island of Borneo, and possibly never occurred there. The finding of one prehistoric canine tooth, attributed to *Panthera tigris*, in the Niah cave deposits (HOOYER, 1962), is insufficient evidence for the tiger's former occurrence on the island. Moreover, several tiger-remains, usually skulls or canine teeth are known to have been used as tokens by several different ethnic groups in Borneo (e.g. PERANIO, 1959). The origin of these artefacts is uncertain, but the indigenous owners often claim that they come from 'heaven', rather than being obtained through hunting. As most of the ethnic groups of Borneo originally migrated from the South-East Asian continent, it is likely that these artefacts originated from the mainland and have been brought to Borneo along the pre-historic trade routes (see: VAN HEEKEREN, 1959) or by the invaders themselves.

[10] A clouded leopard weighs 7–12 kg (MEDWAY, 1969). The Ketambe animal's weight was 10.5 kg. The clouded leopard male was caught in a live-trap, baited with (well protected) rehabilitant orang utans and a young goat. While awaiting a transport licence, the animal died of sepsis in his transport cage.

close to, or even go into water in places where crocodiles are expected to have occurred, these stories may be based on facts. At the present time the crocodile is either very rare or has been eradicated in most parts of Sumatra and Borneo.

No evidence of predation on orang utans by the Malay sun-bear, as suggested by KORTLANDT (1972), was found in the present study; examined bear faeces from several different locations in the Gunung Leuser reserve never contained recognizable vertebrate remains.

In summary it can be said that, despite occasional casualties due to predation by larger felids, these predators exert little influence on the population density of orang utans.

8.2. HUNTING PRESSURE

To understand the extent of human influence on the orang utan's biology it is necessary to look at much of what is known of human history in South-East Asia. The heaviest predatory pressure on the orang utan may have been exerted by humans. The remains of orang utans, found in limestone caves in Southern China, Vietnam, Borneo and Sumatra (see DUBOIS, 1897; HOOYER, 1948; 1961), often in large quantities and in many cases coinciding with traces of prehistoric man, may indicate that this ape has been hunted since at least 30,000 years B.C. The finds of prehistoric orang utan remains in close association with those of *Homo erectus* in the Kendeng formation at Trinil, Java (DENINGER, 1910; VON KOENINGSWALD, 1931) may indicate that this hunting pressure was of a much earlier date (i.e. 500,000 years B.C. or earlier; see HOWELLS, 1966). The extinction of the orang utan in Java, which presumably occurred during the late Pleistocene (but see CAMPER, 1782)[11], strongly suggest that early man had some, if not a major influence on the ape's fate (see also MACKINNON, 1974). Apart from the extant great apes, all other close relatives of man (e.g. the Australopithecines, *Gigantopithecus*, *Ramapithecus* and several *Homo* spp.) have become extinct; many during the late Pleistocene. The finds of mutilated skulls of *Homo erectus* at Choukoutien (China) (WEIDENREICH, 1943) and similarly fragmented skull parts of Australopithecines and of *H. erectus* in Swartkrans (S. Africa) (BROOM and ROBINSON, 1952) suggest that these relatives have been hunted to extinction by more advanced forms, perhaps as a result of head-hunting or cannibalistic traits. NIEUWENHUIS (1907) has noted that the head-hunting raids of the Dayaks in Central Borneo aimed at taking heads of the tribes which were formerly supplanted from an invaded region. Perhaps a range or food competitive attitude may have played an important role in such behaviour.

Similarly, for at least one large, extinct African primate (i.e. *Simopithecus*), the finds strongly suggest that it had been hunted (MARTIN, 1966); several other

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[11] In 'Natuurkundige Verhandelingen...', CAMPER (1782) cites the physician RELIAN, who claimed that orang utans were still to be found in some remote places in Java in the eighteenth century.

large prehistoric primates (i.e. *Parapapio*, *Dinopithecus*, *Cercopithecoides*) also became extinct during the late Pleistocene, for which early man may also have been responsible (see also MARTIN and WRIGHT, 1967).

It has been suggested that the prehistoric skeletal remains of orang utans found in some caves (i.e. Padang Highlands) are not the result of human activity, since evidence of human habitation has not been found there (see HOOYER, 1962; MACKINNON, 1974). This implies that the orang utans had either entered the caves on their own account and died there, or that they were deposited there by other – predatory or scavenging – animals. Rehabilitant orang utans will occasionally enter cave-like depressions to shelter for the night[12] (see HARRISSON, 1969), and wild orang utans may enter similar (but well lit) depressions in hills to eat saline soil (MACKINNON, 1973; and pers. observ.), but it is very unlikely that a wild diurnal primate will wander fort into a pitch-dark limestone cave. The larger predatory animals of the South-East Asian region, notably the tiger, are not known to transport nor store their quarry in caves (cf. SCHALLER, 1967). The most common scavengers in the South-East Asian forest are pigs, which usually scatter the remains of their quarry and are also not known to enter caves. Hence the most likely explanation for the presence of the skeletal remains is that they have been deposited there by humans, the only species known to have used caves to store its implements, its religious artefacts and its food, including vertebrate prey, in the South-East Asian region.

The remains found in the Asian and in the Sumatran caves show a 'normal' age/sex composition, whereas those found in the Niah cave deposits in Borneo are predominantly of female origin (HOOYER, 1961). Such a phenomenon may be explained by regarding the metaphysical value which some cultures may have attributed to male orang utans in particular. It is noteworthy that several head-hunting tribes in Borneo took their most prized skulls with them when a clan moved to another location, while they might leave other, less prized ones behind (see HOSE and MCDOUGALL, 1912; also, for Papuan peoples, SCOFIELD, 1962). In other words, the discrepancy in age/sex composition of the prehistoric orang utan remains from the Niah caves may be due to the fact that the hunters removed the male's,[13] and left the female's and youngs's behind. This suggests that orang utans have not been considered as food (only), but as a 'substitute' in the head-hunting and/or cannibalistic practice of earlier inhabitants (see also RIJKSEN, in press). There is sufficient evidence in the ethnographical literature on the South-East Asian region (see p. 335) supplemented with artefacts stored in ethnological musea and other collections (see fig. 60) to lend weight to this suggestion.

It is almost certain that several of the earlier human invasions into the present Indonesian region came from the Asian continent, notably the East Indian

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[12] The 'cave dwelling' rehabilitant orang utan 'Arthur' (HARRISSON, 1969) had been reared in and around a house and consequently was familiar with the peculiarities of cave-like structures and their value for shelter.

[13] Of the 4 orang utan skulls, used in veneration ceremonies in Dayak rituals that I was able to examine, 3 were of adult male specimens; (see also fig. 60, and HARRISSON, 1960).

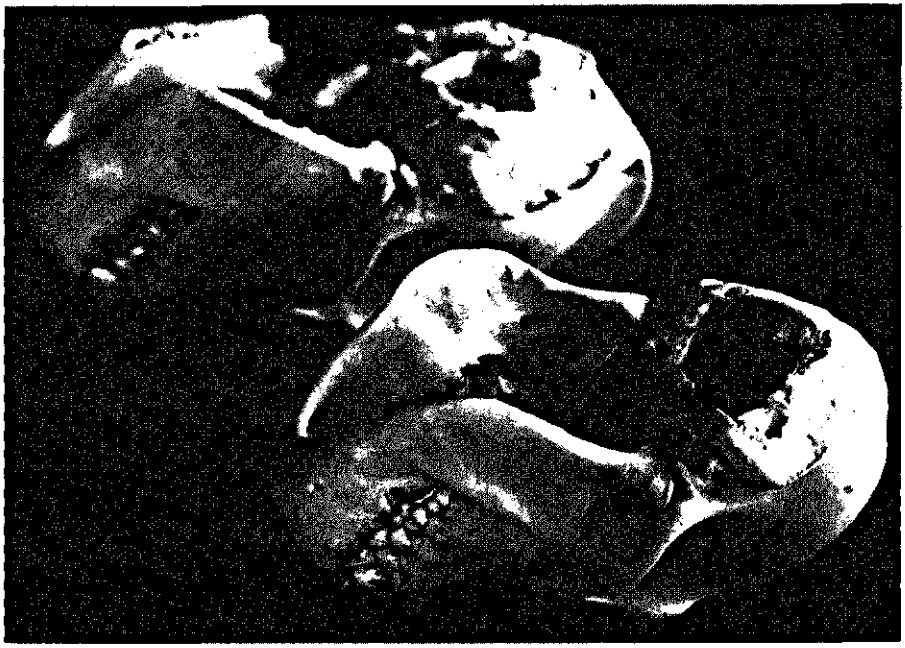

FIG. 60. Orang utan skulls with enlarged *foramen occipitale* which have been used in veneration ceremonies of Dayak people during the last century (the skulls have been cleaned, bleached and uncovered from their customary rotan and grass baskets).

region (see e.g. HOSE, 1926). The major climatic and geological influences, notably the effects of glaciation, resulted in considerable fluctuations of the sea level. Thus, during some periods, areas now flooded were above sea level and formed 'Sunda land', connecting the islands west of Wallace's line with the Asian mainland (DE TERRA, 1943). At other times, when the sea-level rose again, this region was flooded so that the landmass was restricted to approximately the extent of the present Malesian region (see VERSTAPPEN, 1975). In either condition, the land was under rainforest cover, presumably dispersed with patches of slightly more open woodland (PETERSON, 1970; VERSTAPPEN, 1975). In one of the periods of the Sunda landmass condition, *Homo erectus* presumably entered the South-East Asian region and may have been forced to higher land (i.e. Java) when the sea level rose again. It is likely that subsequent invasions of the more advanced *Homo sapiens* types followed the same routes traversing the vast Sunda-landmass. In fig. 61 the tentative migration routes of these earlier invasions are reconstructed. The map shows the drainage lines in the region where the large rivers cut through the land and also shows some of the locations where implements, indicating a Paleolithic culture, have been found. On the basis of observations of the present-day travelling modes of people in unfamiliar rainforest regions, supplemented with observations of the 'migratory mode' of African chimpanzees (see IZAWA, 1970) one can easily assume that

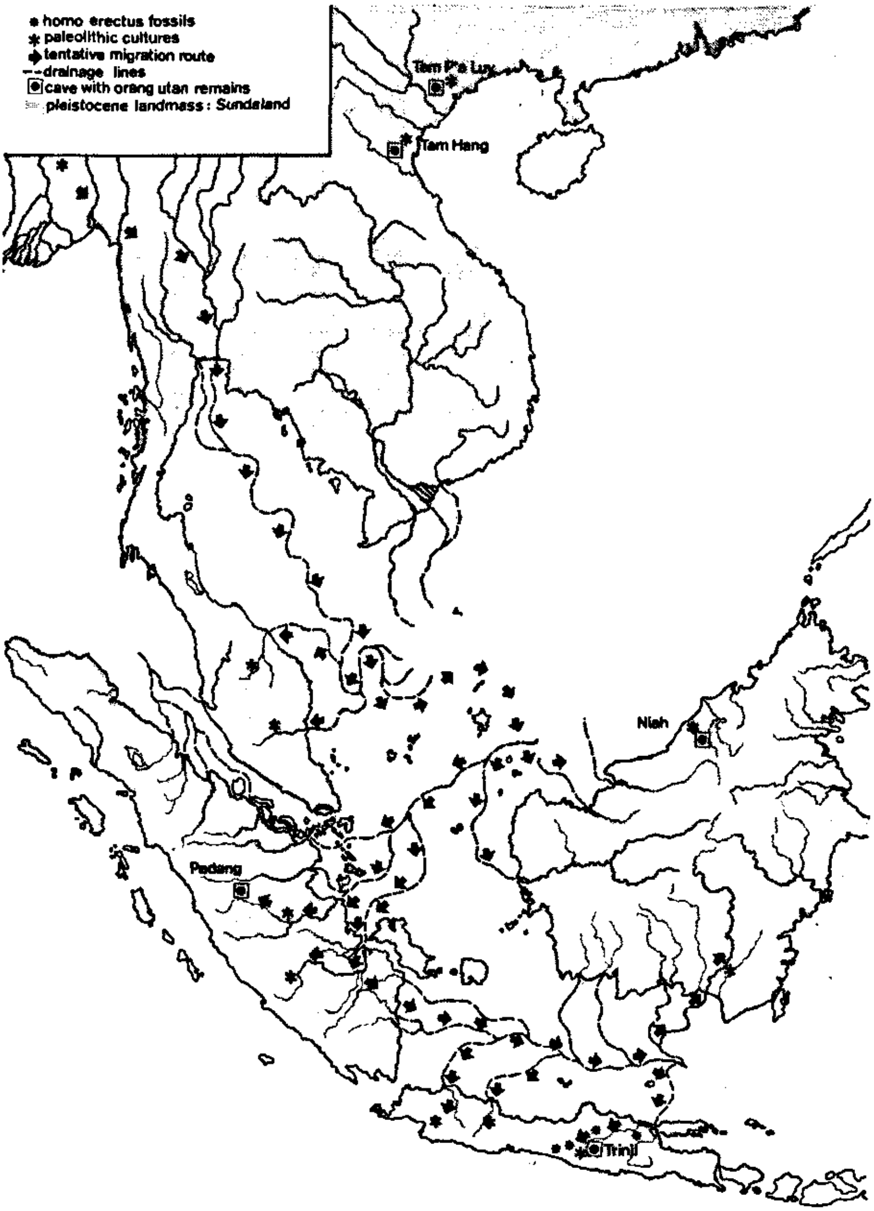

FIG. 61. Sunda land; the main river drainage and tentative migration route of the hominids into the region (see also SARTONO, 1972).

early man followed the courses of the larger rivers when penetrating into the vast Sunda-land area. This may explain the dispersed nature of the finds of artefacts disclosing early man's presence in the region (see fig. 61). Most of the evidence of man's history in South-East Asia is probably burried in the shores of the drainage system of Sunda-land, presently constituting the bottom of the China sea. When assuming that early man lived a predominantly – fruit – gathering life, he probably had a preference for the same habitat-types as the orang utan, i.e. river valleys, hill country and swamp edges. This certainly led to clashes of interest and competition for food.

It is noteworthy that in those regions in South-East Asia, where the occurrence of man seems to date back to early times, some 20,000 to 30,000 years B.C., orang utans are absent; e.g. in South-East Kalimantan, between the Barito and the Mahakam river, where the geologist H. KÜPPER found Late Pleistocene pebble tools and flake implements in 1939; in South Sumatra, where HOUBOLT discovered similarly ancient mono-facial tools in the same year (VAN HEEKEREN, 1959); in the region around Niah caves (HARRISSON, 1959); and in Java, orang utans have not occurred since historical times.

8.3. FALLING

On at least twelve occasions during this study orang utans were seen to fall accidentally from a tree. In five instances the falling animal was a wild orang utan, in seven cases a rehabilitant. In addition fifteen 'near-falls' were also seen. The heights from which the apes fell varied from 3 to some 30 metres. The adult male O.J. once misjudged the strength of a branch, and he fell some 6 metres on the ground. It did not seem to affect the animal very much. He stood up, looked at the broken branch and walked along the ground for some 12 metres before he climbed another tree and continued his journey. On another occasion I saw him fall some four metres because a large liana broke loose under his weight. He landed on his back in a small muddy stream and did not show any apparent ill-effects. He simply waded to the bank and continued his travels. The rehabilitant adolescent Bobo fell from the canopy (about 30 m height) after an apparent miscalculation of the strength of a large branch. In his fall the orang utan held on to the branch, which broke the impact of his fall. The animal was unconscious and laid for about a quarter of an hour, having some difficulties with his breathing. A superficial check revealed that he had no bones broken; the animal had recovered completely after three hours. Another rehabilitant juvenile (Bas) also fell from the canopy (some 12 metres) and after a short recuperation period, the animal showed no further distress. When this animal died about a year later (of *peritonitis-orchitis*), autopsy revealed that he had sustained a skull base fracture. The rehabilitant adolescent Pon fell out of a tree from only 5 metres height; he died instantly and autopsy revealed that he had broken his neck.

In August 1973 the wild female Josh was found with both her legs paralysed.

Fig. 62. The disabled orang utan female Josh; note her swollen feet.

The symptoms (*paraplegia cruralis* combined with *incontinentia*) strongly suggested a traumatic incident affecting the lumber vertebrae. The female's only remaining mode of locomotion was brachiating (fig. 62). Any vertical locomotion appeared to be very strenuous, she had to pull herself up by her arms alone, and frequently used her teeth and chin to get a hold. She lived for only two months after the first observation of her incapacity, and was found dead sitting on the ground in a very crude ground nest (fig. 63). During her last days her paralysed legs were severely infested with *myiasis*. For several days she did not brush away the numerous flies on her legs but every now and then took one of her feet in her hand and peered at it. It is assumed that her *paraplegia* was the result of a fall.[14]

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[14] A similar case of *paraplegia* caused by an accidental fall in a wild gorilla has been described by MALBRANT and MACLATCHY (1949).

FIG. 63. The female Josh, dead on the ground; the white patches are aggregations of fly eggs.

Examined museum specimens of orang utans contained a high percentage of healed bone fractures (34%: SCHULTZ, 1956). This fact, and the number of accidental falls observed, suggest that an arboreal lifestyle poses considerable risks for such a heavy primate. Strong selective factors must have forced the orang utan into arboreality.

8.4. PARASITES

Orang utans may become infested with a large number of different parasites; only a few of these are potentially fatal under normal circumstances.

Myiasis/wounds

Infestation of wounds with fly maggots is a common phenomenon for forest living mammals. Rehabilitant orang utans who acquired even very small wounds out of reach of their grooming activity, very easily became infested. On two occasions rather intensive veterinary care was necessary to save an infected animal. Very weak and undernourished orang utans, such as newly acquired rehabilitants, sometimes became infested with myiasis through the unbroken skin[15]; especially between the fingers, between the toes, in the arm pits and in the groin, where the microatmosphere is moist. Without appropriate veterinary care these animals soon developed sepsis and died. The scratch wounds inflicted by the clouded leopard on the rehabilitants were especially liable to infestation.

Rehabilitant orang utans sometimes acquired serious bruises and wounds on their hands and feet. Presumably these were caused by conspecifics in attacks or during physical combat. Such wounds were often very deep. BRANDES (1939) has noted that in wild caught Sumatran orang utans, the adult males showed a high incidence of scars and stiff or apparently bitten off fingers and toes. The wounds on accessible places were usually treated by the animals themselves; they often inspected, sucked and groomed such wounds and were very cautious in using a hurt extremity. Scratches and wounds usually healed remarkably fast in healthy orang utans and it was very rare that a wound, that the individuals could groom themselves, became inflamed.

Leeches

Two species of land leeches are common in the forests of the Gunung Leuser reserves below 500 to 700 metres altitude. Leeches also occurred at higher elevations, but their distribution was more patchy and probably correlated with a local abundance of ungulates. Thus, in certain sectors of the Kappi area (1100–1200 m) leeches were quite common, whereas elsewhere they were absent. The brown leech (*Haemadipsa zeylanica*) reportedly occurs at altitudes over 2000 metres (WITKAMP, 1933). Both the brown leech and the green and yellow coloured jumping leech (*Haemadipsa cf. picta*) attach to and suck blood from almost every bypassing mammal they can reach.

Rehabilitant orang utans, who frequently travelled on the ground were often bitten by these leeches. Even though they carefully groomed the leeches from their body a few were easily overlooked. Some rehabilitants even groomed the leeches from their companion's body, or from the attendant's legs. The rehabilitants rubbed the sticky animal between their fingers to dispose of them. Some rehabilitants actually attempted to kill adhered leeches by rubbing them over a hard surface or by biting and tearing them in two parts (fig. 64). The small wounds inflicted by a leech's bite rarely became infected.

Infected leech's bites occurred more frequently in people who appeared to be particularly susceptible to secondary infections in any wound acquired in the forest. Yet, in most people the small wounds usually caused no long lasting inconvenience. Regular contact with leeches throughout the entire study period caused no serious long term ill effects nor parasitic diseases in the observers (see also VAN BENTHEM JUTTING, 1932; PIETERS, 1933; MOORE, 1938; MEDWAY, 1959).

It is tempting to speculate that the occurrence of this very abundant ectoparasite in the South-East Asian rainforest could have influenced the degree of

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[15] The flies responsible for primary myiasis through unbroken skin are the *Calliphorid* flies; these responsible for the secondary myiasis, via wounds, are the *Sarcophagid-* and *Muscid* flies. (See also Appendix 4).

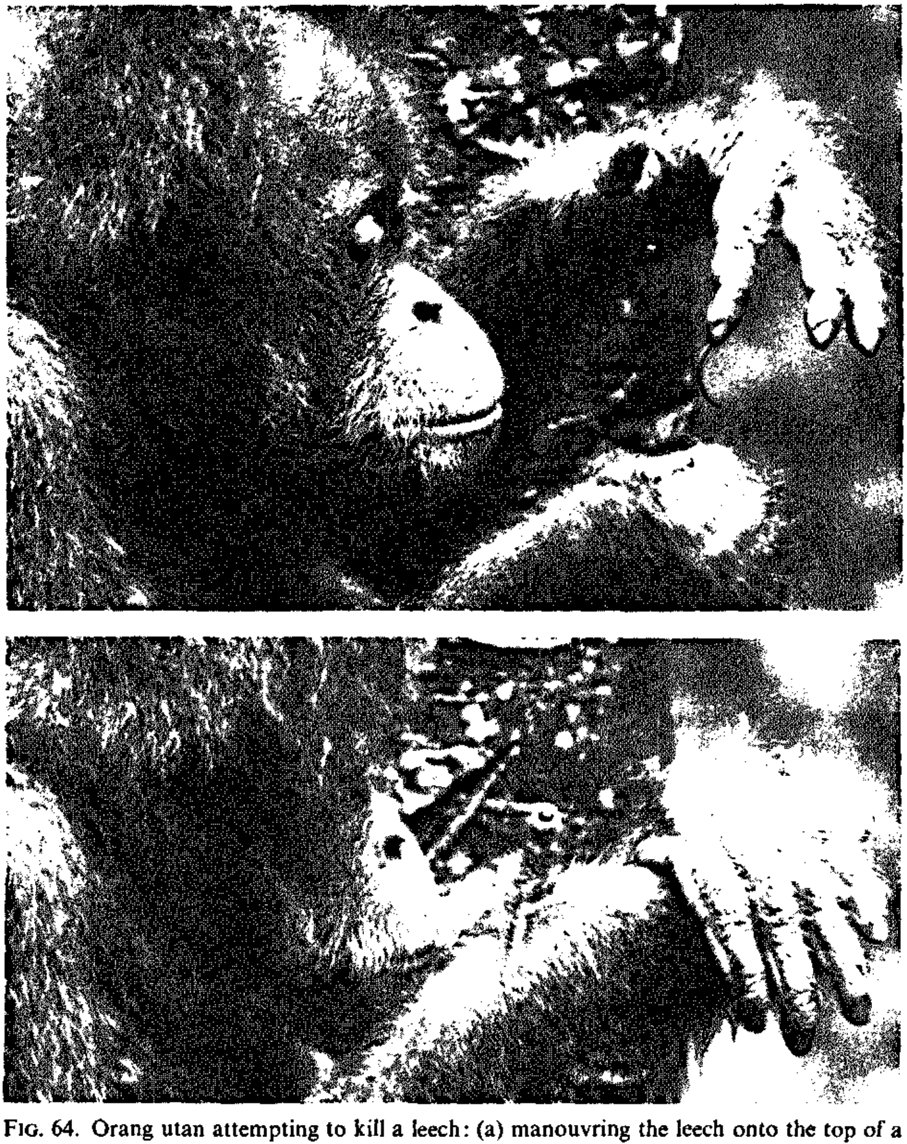

FIG. 64. Orang utan attempting to kill a leech: (a) manouvring the leech onto the top of a finger, (b) subsequently rubbing it between both hands.

arboreality of orang utans, but the absence of ill effects from leech bites refutes this suggestion.

During 1975, the rehabilitant female Tjali often bled profusely from her nose. The bleeding appeared to be caused by two large leeches (cf. *Dinobdella ferox*), which were removed from the orang utan's nasopharynx under sedation (DE WILDE, 1975, pers. comm.). *Dinobdella ferox* invades pharynx and sometimes the upper respiratory tract of mammals, including man. The infestation of the host usually occurs while drinking from pools and streams and the leech may stay attached for months (FLYNN, 1973). The rehabilitant orang utan often travelled on the ground which could explain her infestation. This leech species is a widespread parasite in South East Asia, and it has been reported to be a common parasite in wild macaques obtained for laboratory experiments (PRYOR, et al., 1970). Infestation with some of these leeches causes symptoms of restlessness, epistaxis, anaemia, weakness, asphyxiation and is sometimes mortal (FLYNN, 1973).

Endo-parasites

Most orang utans were infested with intestinal parasites. This seems remarkable for an arboreal primate, as one would expect them to rarely come in contact with their own faeces or those of conspecifics. The most frequently found parasites in the faecal samples were *Trichuris trichuria* (22%), *Enterobius cf. buckleyi* (16%) and *Abbreviata caucasica* (17%). If we considered all collected samples together (n = 96), and not attributing samples to recognised individuals, 56% contained eggs of endo-parasites. This percentage accords remarkably well with the infestation rate of wild mountain gorillas (53%: SCHALLER, 1963) and is a little higher than that of wild chimpanzees (48%: VAN LAWICK-GOODALL, 1968).

However, if we look at the samples from the Ketambe orang utan population individually, it appears that most examined individuals (18 of the 20: 90%) were infested with endo-parasites. Yet the percentage of positive samples in all individually known faecal samples (n = 65) lumped together, again gives a percentage (55%) similar to that for the entire collection. It is noteworthy that several samples of infested individuals appeared to be negative on examination. From the three infants it was impossible to collect faecal samples. Yet, on the basis of the two other infant's positive findings it is likely that these three infants were infested like their mothers.

During the collecting, it was observed that helminth larvae, presumably *Strongyloides spp.* and/or *Enterobius buckleyi*, were present on the surface of eight fresh faecal samples. The helminth eggs found in the faecal samples were identified as: *Trichuris trichuria, Enterobius cf. buckleyi, Abbreviata caucasica, Strongyloides cf. stercoralis, Oesophagostomum cf. blanchardi.* In addition some eight other species were found which were not positively identified but included cf. *Pithecostrongylus sp.*, cf. *Trichostrongylus sp.* and cf. *Gasterodiscoides sp.*

Several rehabilitants were heavily infested with *Ascaris lumbricoides*, a parasitic nematode not found in the samples of the wild orang utans, but a common endo-parasite of people. Also the rehabilitant's infestation with *Ankylostoma brasiliensis* probably was due to their former close contact with humans. Infestation with hookworm (*Ankylostoma*) caused a very serious decline in the physical condition of affected rehabilitant orang utans; the apes showed symptoms of listlessness, severe anaemia, and often loss of hair.

Infestation with *Trichuris* in orang utans (22% of the total sample collection) may be important since this parasite can cause severe enteritis and sometimes result in death, as has been reported for chimpanzees (THIENPONT, et al., 1962). It is interesting to note that an autopsy on the juvenile rehabilitant Bas, who died suddenly, revealed a very high degree of infestation with *Trichuris* in the caecum and colon. The parasites had caused a very extensive nodulous colitis that resulted in perforative enteritis and subsequent peritonitis and orchitis, the cause of his sudden death. The animal had shown listlessness only the day before his death; it had also displayed atypical locomotion and a slightly enlarged, painful scrotum for some days, but in general his condition and behaviour prior to death had not given any indication of the infestation. *Trichuris trichuria* may occur in the large intestine of man and other primates e.g. the long tailed macaque (REARDON & RININGER, 1968) and the white handed gibbon (CARPENTER, 1940). In chimpanzees an incidence as high as 28% infestation with *Trichuris* has been reported (REARDON & RININGER, 1968).

On two occasions, the symptoms shown by ill rehabilitants suggested a parasitaemic infestation i.e. high fever, listlessness and yellowish conjunctivae. The first affected ape was treated with high doses of antibiotics (Ampicillin) for four days, but despite initial improvement, the fever returned every second day for four cycles. The ape seemed to recover spontaneously after 20 days as he showed no further symptoms afterwards. Another rehabilitant who showed similar symptoms was treated with a single dose of chloroquine (1000 mg) and recovered completely after this treatment. Although the facilities in the Ketambe station did not allow specialized diagnosis, the symptoms shown by both orang utans and the positive effect of the chloroquine treatment strongly suggest that the apes had been affected by a tertiary malarial parasitaemia, presumably caused by the specific *Plasmodium pitheci* (GARNHAM et al., 1972). In Appendix 4, a list is given of the endo-parasites known to affect orang utans, and their occurrence in the Ketambe population.

Ecto-parasites

Nearly all closely examined orang utans in Sumatra appeared to be remarkably free of ecto-parasites. Yet, superficial scratches and small scars on rehabilitant orang utans usually became infested with large numbers of very small red chiggers (*Eutrombicula wichmanni*). These acarids did not seem to affect the wound healing, nor to cause discomfort to the orang utan. As all rehabilitants readily acquired these chiggers, it is likely that the wild orang utans were similarly affected. Like other mites, *Eutrombicula* may transmit *Rickettsia*-parasites, causing Q-fever in mammals.

On several occasions rehabilitant orang utans appeared to be affected by ticks (*Haemaphysalis cornigera*), that typically adhered to the ape's eyelid. Surprizingly, the orang utans did not show any discomfort from the tick's presence. *Haemaphysalis* ticks may transmit *Coxiella* and *Rickettsia* parasites. It is possible that the occasional infestation of rehabilitants with this parasite is due to their high incidence of ground travel. The small ticks were not detected on the few wild orang utans that allowed rather close examination.

In human societies ecto-parasitic infestations are more common and in relation to this two cases are of particular interest: The introduction of a young ex-captive siamang, who afterwards appeared to be heavily infested with human head-lice (*Pediculus corporis*), to the rehabilitant orang utans did not result in any infestation of these apes although they had been in close contact on several occasions. In contrast, the human attendants became heavily infested through such contacts.

During our visit to the rehabilitation station at Sepilok (Sabah) in 1974, it became apparent that some rehabilitant orang utans were infested with scabies (*Sarcoptes scabei*), which had caused dermatosis and extensive alopecia (i.e. loss of hair). Photographs of some of these rehabilitants taken in earlier years (see MACKINNON, 1972, p. 183) give the impression that this infestation has affected some animals over a long period. It seems likely that the rehabilitants acquired the scabies through frequent and intensive contact with humans, before or after they had been taken to the station. Scabies in orang utans has been described by WEIDMAN (1923); the typical symptoms are thickening of the skin (parakeratosis), alopecia and often pruritis.

One adolescent female rehabilitant (Tjali) acquired a persistent fungal infection on the side of her foot, resembling *Blastomycosis*. The animal did not seem to be troubled by the infection, which disappeared spontaneously after six months. Earlier attempts to treat the infection with fungicides were unsuccessful. A *Blastomycotic* dermatitis in captive orang utans has been described by BINKLEY (1959).

Diseases

Orang utans appeared to be particularly susceptible to ailments of the respiratory and digestive tract. At the onset of the wet season the symptoms of a common 'cold', i.e. sneezing and sometimes coughing, were often heard from wild and rehabilitant orang utans alike. Similar symptoms have been reported for wild mountain gorillas (SCHALLER, 1963), and for wild chimpanzees (VAN LAWICK-GOODALL, 1968).

Of particular interest were diseases which seemed to spread from the human population onto the orang utans. An influenza-like disease, characterized by symptoms of listlessness, loss of appetite, head-ache,. rhinitis and sometimes diarrhoea in people, seemed to pass from the small villages along the road, via the attendants to the rehabilitants and eventually to at least two wild apes. In the orang utans the symptoms were a thick mucous discharge from the nose, listlessness, coughing and diarrhoea; the animals recovered spontaneously. Similar transmission was apparent with a human originated conjunctivitis; fortunately only rehabilitant – and no wild – orang utans became affected. Such epizootic spreading of diseases is particularly important when considering the function of rehabilitation programmes for apes. An evaluation of this important ecological factor is given in chapter Conservation (p. 367).

One aspect of the diseases of rehabilitant orang utans is of particular interest. Late adolescent- and sub-adult male orang utans were usually reported ill by the attendants only when their disease was already in an advanced stage. This phenomenon that animals try to simulate physical fitness as long as possible, seems remarkable for a 'solitary' animal. In gregarious animals such simulation may have the effect of keeping up social status as long as possible, since physical weakness may readily result in loss of prestige.

In Appendix 4, the diseases known to affect orang utans are listed together with those diagnosed in the Ketambe area.

In conclusion there are several factors which can influence an orang utan's state of health and hence affect its survival or individual fitness. Under normal circumstances, neither parasitic infestations nor diseases will take a significant toll of the population, but in most cases only result in a temporary decrease in physical condition of the individual affected. The risks of acquiring a serious disease as well as the rate of degree of infestation with common blood and intestinal parasites may well be of a similar magnitude to that, described for other animals, especially the African apes.

9. NESTING BEHAVIOUR

Among the primates, only some prosimians and the great apes build nests in which to sleep and deliver their young. Orang utans also build nests in which to rest and play during the day time (fig. 65). Detailed descriptions of nest constructions (e.g. MÖBIUS, 1893) and nestbuilding techniques have been given for caged orang utans by BERNSTEIN (1969) and JANTSCHKE (1972); for rehabilitant orang utans by HARRISSON (1969); and for wild orang utans by SCHALLER (1961) and MACKINNON (1972). Therefore only those aspects of nesting behaviour that have had little or no attention are described in this chapter.

Nest heights correspond closely with those of Bornean orang utans (see DAVENPORT, 1967; SCHALLER, 1961 and MACKINNON, 1974) and though there appears to be a generally preferred nest height of 13–15 meters, the nest height often seemed to depend on the forest structure at a particular site. Among the Sumatran orang utans (including rehabilitants) the location played a major role in nestbuilding; many nests were constructed at typical vantage points, and usually in such a way that it enabled the animal to have a good, unobstructed view over a large stretch of forest. Thus nests were often constructed on slopes and usually at the very edge of a gap in the vegetation (see fig. 12). These observations correspond with those of several other studies in Borneo (HARRISSON, 1969; MACKINNON, 1974) and Sumatra (KURT, 1971), and also concur with

FIG. 65. Sleeping in a very comfortable day nest; note the support behind the female's back.

observations on the distribution pattern of nests in a chimpanzee community (VAN LAWICK-GOODALL, 1968).

All wild orang utans made nests for their night repose, usually at a different site from the one used the preceding night. Occasionally orang utans used the same nest on two or more nights; in such cases they invariably reconstructed the inner lining. Individuals differed with respect to their repeated use of nests and nesting sites. Thus, the adult male O.J. was observed to re-use, and rebuild nests on earlier used sites on several occasions whereas such behaviour was seldom (Jet, Doba) or never ascertained for other wild orang utans. Such idiosyncratic patterns were even more clear among rehabilitants. For instance the female Yoko was observed to re-use one particular nest for 18 consecutive nights; towards the end of this period she collected twigs for the inner lining at distances of some 15–30 metres away from the nest-site (fig. 66).

While some nests were re-used the following evening, for instance when located near a preferred fruit tree and in the case described above, re-use of a nest or reconstruction at a particular site usually occurred after some time (sometimes after considerable periods of time; 2–8 months). In these cases, the animal's preference for a particular location was evident.

FIG. 66. Suitable twigs for a lining or raincover are sometimes collected at considerable distance from the nest.

For example, the adult male O.J. built a nest in a particular tree standing along the trail that was used by the attendants to provision the feeding site of the rehabilitant group. The nest was situated just above the trail and assured the owner of an excellent view; it was impossible to miss the provisioning from here. O.J. re-used the same nest on several occasions during his later visits to the station, and re-built it at the same spot after it had been destroyed by passing long tailed macaques. For seven mapped nesting sites of the adult female Mif a mean distance of 142 metres from the food tree was measured.

Sometimes orang utan nests were found in food trees; however, these were invariably 'day-nests', used for short day time rests (fig. 65), for comfortably processing collected fruits, or for social play. Thus in contrast to MACKINNON's observation, that orang utans 'frequently... nested in or near the last food tree of the evening' (MACKINNON, 1974; p. 47), the orang utans in the Ketambe area were rarely if ever found to make their night nests in or near a tree with ripe fruits. The only possible exception was a nest, found in a large *Garcinia* tree in which the adult male Moses had been feeding late the previous evening. As the male was seen again in the immediate surrounding of the tree early next morning this may have been his sleeping nest. The fact that the male Moses was presumed to be the highest ranking adult male in that particular region (see social behaviour p. 287) might have allowed him to choose a nest location in such an attractive place as a preferred fruit tree. We namely had the impression that one possible reason for the reluctance of most orang utans to build their sleeping nests in attractive places such as preferred fruit trees, could be the risk of agonistic encounters if they did so. The risk for agonistic encounters with conspecifics of higher social status seems evident, but there may also be a risk of agonistic encounters with other species, in particular with man, who regards several of the 'preferred' fruit tree species of the orang utan as private property (see p. 338) and may kill competitors.

Day-nests were found in especially those trees of which the fruits need rather elaborate processing, i.e. *Durio* sp., *Heritiera elata*, *Garcinia* spp. and *Mangifera foetida*, but never in *Ficus* sp. Sometimes clumps, varying from 6 to as many as 32 nests were found in the immediate vicinity of preferred fruit trees in the Ketambe area, a phenomenon also reported by KURT (1970) and by MACKINNON (1971) for other regions. On two occasions the cause of such clumps could be observed: the members of an adolescent-sub-adult male group built a total of 9 nests in one day in the immediate vicinity of a large fruit tree. Most of these nests served as platforms to play on and during the play-activities two of these nests were destroyed again. In the course of the fruiting period of the *Heritiera elata* tree, 12 such play-nests were constructed and/or rebuilt. An additional 20 nests in the vicinity of this tree were built by different individuals in order to eat gathered fruits at leasure, or to rest during the heat of midday. In particular adult females with dependent offspring might build several nests per day in which to rest. Other orang utans usually just lay down on a large branch to rest (fig. 81) or constructed a very flimsy platform that might not even be recognized as a nest by an inexperienced observer.

Already MÜLLER (SCHLEGEL and MÜLLER; 1839–1844) has described that Bornean orang utans may cover themselves with leaves during rainy nights in order to remain dry (see fig. 67). Also WALLACE (1856) and BECCARI (1904) have drawn attention to this remarkable behaviour although they did not observe it themselves but referred to local Dayak informants. In the wild caught Sumatran orang utans kept in the Dresden Zoo, BRANDES (1937) observed such raincovers. Recently MACKINNON (1974) confirmed the use of 'umbrellas' from his observations on wild Bornean orang utans. A similar phenomenon has been reported for Sumatran orang utans by HOOGERWERF (1936–'38), who observed a female using a leafy branch as a shade against excessive sun shine.

The orang utans in the Ketambe area always sought shelter of overhanging branches when caught in a sudden downpour of rain and often broke off several twigs which they held above the head while sitting in a hunched position. Also to avoid excessive sun shine, an animal might hold a twig or leaf above its head, or drape vegetation around his neck and head.

In the rainy season, even on dry evenings, the orang utans often covered themselves with loose branches and twigs while lying in their sleeping nests (fig. 68). Such twigs were usually broken from the surrounding vegetation when the orang utan had finished the nest construction and sat or laid down in the

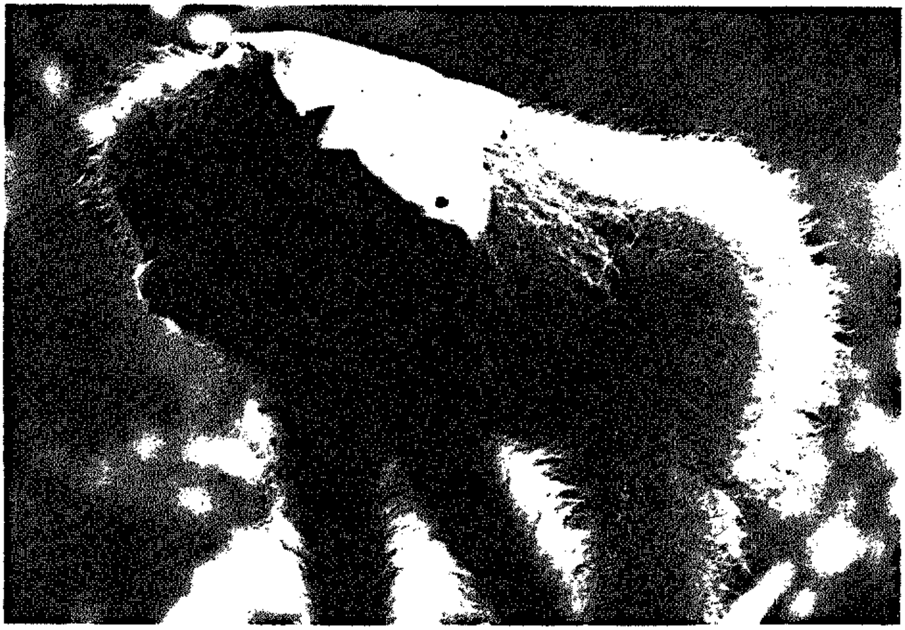

FIG. 67. A large *Alocasia* leaf being used as a raincoat; (note also the wadge in the female's mouth.

FIG. 68. A night nest with rain cover; the adult male has just lifted the cover from his head in order to have a look.

nest, but on some occasions individuals left their nest, apparently specifically to collect vegetation for use as a cover. On one such occasion an orang utan collected his cover some 15 metres away from his nest (fig. 66). The cover was usually loosely draped over the occupant of a nest but in such a regular fashion that the broken ends of the twigs were pointing inwards-up and the foliage direction outwards-down, thus assuring an effective deflection of the water. The cover was often held with one hand and frequently rearranged during the rain, suggesting that the animal adjusted it to stop leaks. The effectiveness of such covers could be assessed from the fact that the orang utans usually had a completely dry appearence after rain. Also imitations of such covers, made by myself during unexpected rainshowers, proved to be surprisingly effective. Apart from keeping the occupant of a nest in a dry condition, such covers may also reduce heat-loss during cold nights.

Overhead shelters, such as described by DAVENPORT (1967) for Bornean orang utans have not been observed in the Ketambe area.

The construction of a functional, comfortable tree nest appears to be dependent on learning and experience (see BERNSTEIN, 1969; HARRISSON, 1969). A 6 week old rehabilitant infant bent pieces of cloth, newspaper and cardboard under himself and patted them down with cupped hands into a crude nest-like construction; yet this animal was hardly able to sit upright without support.

Some older rehabilitants – adolescents and sub-adult males – were not able to construct a proper tree nest when first released. Some spent several nights in rather uncomfortable positions in the trees, balancing on a large branch or sitting hunched in a fork. Others slept on the bare ground or on shelves in the (open) feeding cage. After some time most individuals had learnt to build a reasonably comfortable platform; yet for some individuals, in particular for those who became accustomed to using old nests or to supplanting others from newly constructed nests, this process took many months.

PART III

SOCIAL BEHAVIOUR

1. SOCIAL STRUCTURE

1.1. THE STUDY POPULATION

The wild orang utan population within the Ketambe study area from August 1971 till August 1974 consisted of at least 24 different individuals, of which 22 were seen with such regularity that they were recognized individually. Occasional observations of strangers, that is those not recognized by the observers, the irregularity of observations of several known individuals, and their interactions support the idea that the 22 known individuals were only portion of a larger, local population or deme.

The population observed in the Ketambe area showed a comparatively normal composition, containing individuals in almost every age category (Table 11). Only visibly old orang utans, e.g. adult males past their prime, were not seen in the area. A presumably past-prime, old male was observed on the other side of the Alas river, opposite the study area.

The overall sex ratio of the Ketambe population was 1.3, that is, 4 males to every 3 females. The male-female ratio of sexually mature individuals (i.e. adult- and sub-adult males: adult females) was 1.2, and the sex ratio of socially mature individuals was 0.5, that is, 1 adult male to every 2 adult females. Notwithstanding the fact that the sample of individuals is small, these data indicate an almost equal birth ratio between males and females, with perhaps slightly more males than females.

A larger sample of randomly collected individuals, i.e. those taken into the rehabilitation station (n = 31), shows a sex ratio of 1.06. The male-female ratio of all orang utans observed in Sumatra during the present study (i.e. wild + zoo kept + rehabilitant orang utans: n = 88) is 1.04.

Two births and two deaths were recorded in the wild population in the course of the present study. The adult female Josh was found dead on October 16, 1973, (p. 140: and fig. 62). The other individual presumed dead was the infant Dummy, whose mother was seen without him in September 1973.

1.2. POPULATION DENSITY

Estimates of population densities of orang utans in earlier fieldstudies revealed that large areas of rainforest were only sparsely populated. Densities given were in the order of less than 0.1 to a maximum of 1 individual per square kilometer. On p. 39 I have commented on the methods used to reach estimates (i.e. nest countings in unfamiliar regions) which appear to be rather inaccurate.

Given the restrictions imposed upon an observer by the nature of the habitat and the habits of the ape, it is difficult to give an exact figure for the density

TABLE 11. Orang utan individuals observed in the Ketambe area during the period August 1971–April 1974.

Name	Life stage		Estimated age in 1973 (or year of birth)	Number of encounters			Estimated % of time spent within the Ketambe area in 1973–1974
				in the study area 1971/72	in the study area 1973/74	feeding ground 1971–74	
Gorm	M	adult male	20+ years	15	19	2	20%
Mozes	M	adult male	20+ years	10	42	3	45%
O.J.	M	adult male	15+ years	24	64	47	70%
Mif	F	adult female	20+ years	?	79	1	85%
Mug	i	infant male	(early 1973)	–	79	1	85%
Mos	a	adolescent male	5–6 years	?	69	1	75%
Josh	F	adult female	20+ years	24	25*	2	30%
Jet	A	adolescent female	7–8 years	15	64	176	70%
Jane	F	adult female	15+ years	9	4	–	5%
Jimmy	j	juvenile male	(early 1971)	9	4	–	5%
Rim	F	adult female	15+ years	5	7	–	10%
Rom	j	juvenile female	(early 1971)	5	7	–	10%
Bel	F	adult female	10+ years	1	17	–	20%
Bol	i	infant male	(end 1972)	–	17	–	20%
Daisy	F	adult female	10+ years	1	10	–	10%
Dummy	i	infant	(1972)	1	–**	–	–
Bor	S	sub-adult male	12–14 years	–	14	20	15%
Roba	S	sub-adult male	9–11 years	7	40	2	45%
Doba	S	sub-adult male	8–9 years	5	59	135	65%
Bobby	S	sub-adult male	9–10 years	–	5	1	5%
Sin	A	adolescent female	5–7 years	3	17	–	20%
Gin	A	adolescent male	5–7 years	–	46	–	50%
			Total	134	696	390	760%

* Adult female Josh was found dead on 16 October 1973.

** Infant Dummy was not seen with his mother in 1973 and was presumed dead.

of orang utans in an area. The number of orang utans found in the Ketambe area on any particular day might vary from 0 to 11 individuals (e.g. 22-9-1973). Even with the small size of the study area, the traversability of the terrain and our familiarity with the region, it was still impossible to get an accurate picture of the presence of all individuals in the area in any given day.

In order to calculate the population density of orang utans in the Ketambe area, we estimated the percentage of time spent by each individual within the study area during 1973 and 1974. This estimate is based on the frequency with which each individual was encountered in the area during that period, assuming that the most frequently met individual, the female Mif, had spent 85% of her time within the Ketambe area. This is certainly an arbitrary percentage,[16] chosen on an intuitive basis. We felt that it would not be realistic to assume that she spent 100% of her time in the study area since occasional observations on 'stranger' orang utans in the study area suggest that individuals do not remain in one particular region all the time. They may make excursions into adjoining regions every now and again. We have not tried to make comparable estimates of the percentage of time spent in the area during 1971 and 1972, because of difficulties in recognizing all individuals encountered during the early stages of the study. Only individuals who were recognized with certainty have been listed in table 11. The sum total of the percentages of time spent by all recognized individuals in the Ketambe area is 760, which, in a study area of 1.5 square kilometre, gives a population density of approximately 5 orang utans per square kilometre.

That orang utans in Ketambe may spend most of their lives in one area is illustrated by the case of an adult male who was seen on several occasions on the opposite bank of the Ketambe river. He showed excessive fear every time he saw humans, while other orang utans in that area were far less intimidated under similar circumstances. According to a local hunter, an expedition to capture orang utans had visited that particular region during the sixties, and two of the captives had managed to escape again. One explanation for the fear of the adult male could be that he had been one of the escapes. If this assumption is correct, it could imply that, despite this rather traumatic incident, the animal had stayed in the same area since his youth.

The population density of orang utans in the Ketambe area is approximately 5 individuals per square kilometre. At least 5 animals, the individuals O.J., Mif, Mug, Mos and Jet were known residents during 1973 and 1974 (fig. 69). Though there are few data for the earlier study period, due to uncertainty in recognizing individuals, it is almost certain that the resident population was different during the period 1971–1972. Then the adult female Josh occupied the resident place that was taken by Mif in the latter half of the study. Moreover, in the last few months of the present study, the resident place of the adolescent male Mos seemed to be taken by the sub adult male Doba.

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[16] The same percentage, namely 85%, for the time spent in a particular region has been used to define the concept of 'core-area' in coatis (*Nasua narica*) (KAUFMANN, 1962) and in chimpanzees (WRANGHAM, 1975).

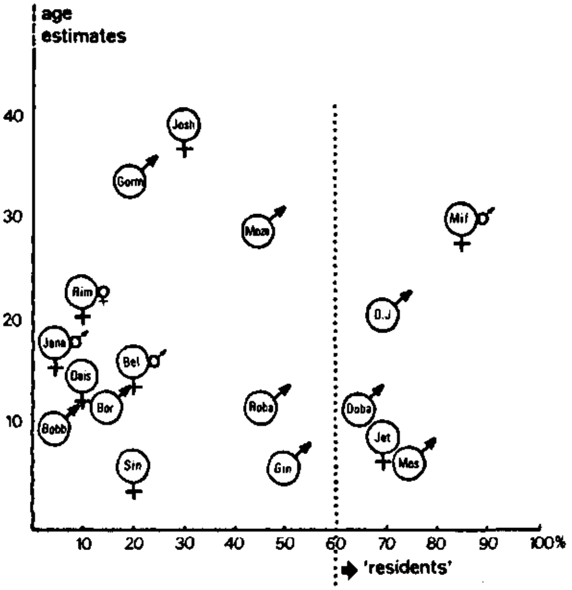

FIG. 69. The build up of the Ketambe orang utan population; relative frequency of encounters with individuals in the study area in the period 1973–'74.

The ranging pattern of residents and the observations on regular visitors indicates that resident animals occupied a core area (see KAUFMANN, 1962) which covered the study area almost entirely. It was clear that these core areas were not used exclusively, but were parts of a number of overlapping home ranges of different individuals of both sexes. The extent of overlap of core areas of different individuals is no doubt related to the carrying capacity of that sector. The Ketambe area may be an exceptionally rich habitat. This implies that the surrounding regions do not necessarily have a similarly high population density of orang utans. From surveys through the distribution range of the Sumatran orang utan, it seems that rivervalleys can support more orang utans than other areas.

In order to arrive at a maximum estimate, the percentage of time spent in the area by the most frequently observed individual could be assumed to be almost 100%. This gives a maximum population density of 6 orang utans per square kilometre.

Minimum population density is estimated by dividing the total number of observed individuals in a large sample of searching days (O) by the total number of searching days (d), multiplied by the size of the area in square kilometres (1.5); i.e. min. density = O/d × 1.5. On a number of 227 searching days, we made 588 independent observations of orang utans. Thus, the minimum estimate of the population density is: 588/227 × 1.5 = 1.8 individuals/km^2.

The population density of orang utans in the Ketambe area seems to be considerably higher than the densities reported for other regions and may be

TABLE 12. Population densities of orang utans in different regions throughout the distribution range as reported by recent authors.

Sarawak	:	0.2 orang utans / km²	(SCHALLER, 1961)
Sabah (Lokan area)	:	2.1 orang utans / km²	(HORR, 1975)
Sabah (Segama area)	:	1.5 orang utans / km²	(MACKINNON, 1974)
Kalimantan (Kutai area)	:	3 orang utans / km²	(RODMAN, 1973)
Sumatra (Renun area)	:	+1 orang utans / km²	(MACKINNON, 1974)
Sumatra (Ketambe area)	:	5 orang utans / km²	(this study)

as high as the population densities reported for the African apes, especially the chimpanzee in some areas. Table 12 summarizes the population densities of orang utans as reported by recent authors.

1.3. HOME RANGE

Altogether 22 individually recognized orang utans used the 1.5 square kilometre large study area fairly regularly. Some of these apes appeared to be resident in the area, others were occasional, yet regular visitors. Other animals appeared as irregular visitors; I will not deal with them here as they were not recognized individually. Both adult males (see fig. 70) and adult females were seen at locations spread over almost the entire study area. This indicates that

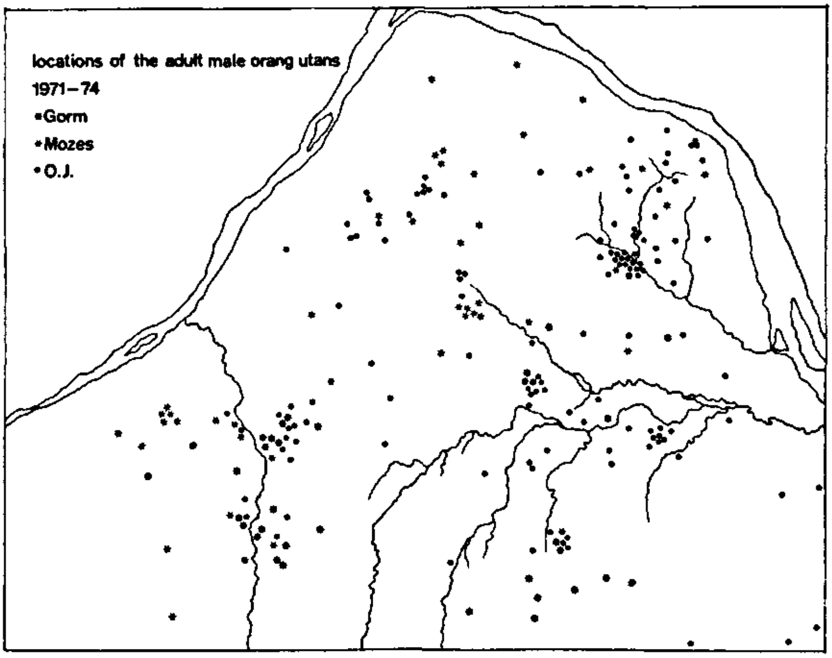

FIG. 70. Observed locations of the three adult male orang utans in the Ketambe study area.

the orang utans in the Ketambe area have overlapping ranges which are larger than 1.5 square kilometre for most individuals. A few known orang utans were also seen at irregular intervals during the three years of the study in the region north-west of the Ketambe river. This suggests a similar situation there, as in the Ketambe area.

The core areas of the two adult residents in the Ketambe area, the male O.J. and the female Mif, were estimated by drawing a boundary around the area that included all observations on these two individuals throughout 1973 and 1974. Mif ranged through an area of approximately 1 square kilometre. Part of the core area of the adult male O.J. was outside the study area, but from regularly observing his ranging pattern and occasionally following him into the region south-east of the study area I estimate that he covered a core area of approximately 2 square kilometres (see fig. 71).

From spot sightings and the observed ranging pattern of the female Josh it seems that she too covered an area of approximately 2 square kilometres during the first half of the study period (1971–1972). However, during the latter half of 1972 and early 1973 she appeared to have shifted her core area in south-western direction. She returned to her former core area in 1973, where we found her badly crippled in August 1973. In the two months prior to her death, she ranged over a very small area, approximately 40 hectares, which was obviously too small to provide her with sufficient high quality food. It was quite remarkable that this invalid female was able to supplant the female Mif, while ranging in the latter's core area.

The frequency of observations on the adult females Rim and Daisy suggests that they both occupied core areas contiguous with the study area. Towards the end of the present study, in 1974, the adult female Bel was seen fairly frequently in the former core area of the dead female Josh. Yet further investigations (FERNHOUT, pers.comm. 1975, and SCHÜRMANN, pers.comm. 1976) have as yet not indicated that Bel had become a resident in the study area.

As I described in section 5.5. the ranging patterns of the adult male O.J. and the adult female Mif, differed in some important respect; the female appeared to cover most of her core area with her ranging pattern, while the male seemed to travel in wide circles along the edges, and less often covered the central parts of his core area (see fig. 71).

For the non resident individuals, the picture is more complex and far more speculative. The male Mozes, for instance, stayed two months within the Ketambe area in 1971. He then disappeared and was not seen again before the end of 1973, when he stayed for another four months in a sector of the study area that overlapped at least one third of the core area of the adult male O.J. (fig. 71). During these months he appeared to displace the resident male. Mozes then disappeared again, but was seen in the Ketambe area in December 1975 by myself. Although some of this male's visits to the Ketambe area might have passed unnoticed, the few clumped encounters with this individual suggest that his range was several times larger than the study area and/or that the

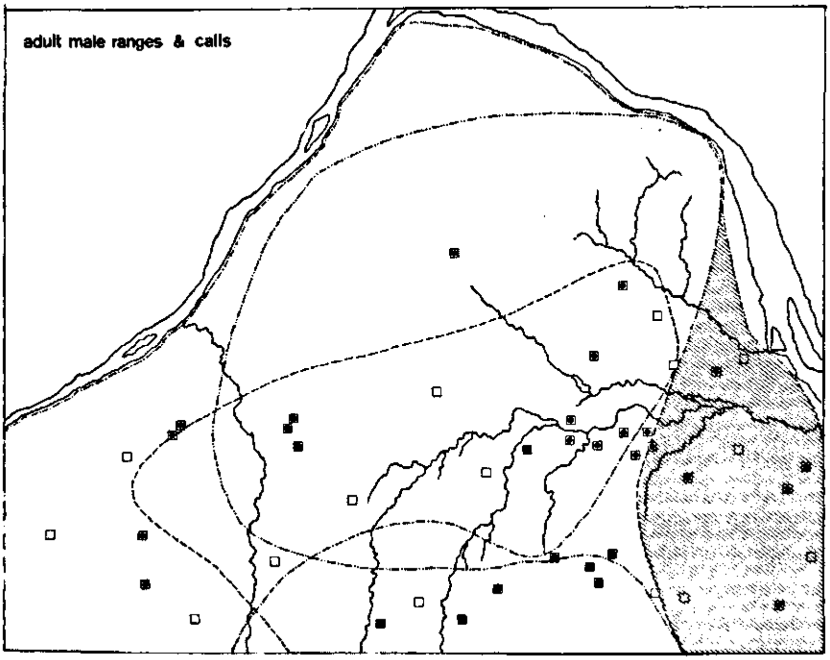

FIG. 71. The ranges of the three adult male orang utans and locations where their calling ('long call') was heard. The squares represent calling-locations; the symbols correspond with fig. 70.

sector of the study area in which he was seen constituted an unimportant part of his contiguous, but not necessarily large range.

It is also difficult to asses the size of the range of the adult male Gorm. This male was a regular, though infrequent visitor to the study area. Whereas the male Mozes invariably appeared to enter and leave the region from south-western direction, along the Ketambe river, Gorm entered and left the area from the south-east (see fig. 71). Gorm's visits seemed to coincide with the ripening of large esteemed fruit trees such as *Ficus drupacea* and *Durio oxleyanus*. During his visits he also covered about one third of the range of O.J.; the four agonistic encounters between these males that we witnessed indicated that the resident O.J. was subordinate to Gorm. The ranges of these males are shown in fig. 71.

The ranging pattern of adolescent individuals is even more difficult to reconstruct from the available data. The adolescents Mos and Jet were residents in the Ketambe area. Jet was observed throughout the entire study period and was still present in the area in 1976 (pers. observ., SCHÜRMANN, pers. comm. 1976). After the adolescent male Mos had become independent of his mother, he was seen to travel alone or in the company of the sub-adult males Doba (fig. 72) and Roba on several occasions. He was then observed in sectors outside his mother's range. Mos has not been seen in the study area since

1974 (SCHÜRMANN, pers.comm. 1976); yet his mother still occupies much of her former core area.

During 1973 the two sub-adult males Doba and Bor were seen in the study area for the first time and became regular visitors. Another unidentified sub-adult male and an unidentified lone adult female visited the Ketambe area in 1974. This may suggest that some individuals, and in particular sub-adult males, do not stick to a relatively small core area but have a fairly large home range and temporarily settle in sectors where the social and other conditions are favourable. Yet, the two sub-adult males Roba and Bobby were observed at regular intervals throughout the entire study period and have been seen again during 1975 and 1976 (pers. observ., SCHÜRMANN, pers.comm. 1976), which suggests that they are residents in a contiguous core area, or have a very small range.

One observation may illustrate how young orang utans can extend their homerange far beyond that of their mother's core area and into regions that were formerly unfamiliar to them. Once we saw a late adolescent orang utan male cross the Ketambe river by using a temporary bridge formed by the overhanging branches of a fallen tree. This crossing was approximately two kilometres upstream of the Ketambe area. Since this fairly wide river forms the natural boundary between two populations for several kilometres upstream under normal conditions, this incident shows that an individual may transfer into an almost certainly unfamiliar population. The observations on experimental introductions suggest that youngsters can enter a strange population with little risk of agonistic interactions.

From the data presented here it is possible to construct a model for the development of an individual's home range and core area. Obviously, different individuals may show considerable variation in the occupancy and use

FIG. 72. The adolescent male Mos travelling together with his 'bond' partner, the sub-adult male Doba.

of a familiar range. This variation seems to be influenced by the age, and most likely by the sex and social relationships of the individual involved. Thus, a dependent orang utan youngster becomes thoroughly and exclusively familiar with his mother's core area for the first four years of his life. As a result of his acquaintanceship with peers from adjacent core areas and his participation in peer groups, the growing adolescent extends his range beyond that of his mother's core area. This proces probably continues well into sub-adulthood until he eventually has become familiar with quite a large area, and consequently with a large number of residents. Within this area the late sub-adult male may attempt to settle into a sector where the social and other conditions are favourable. It may well be that there is considerable competition for such areas; and then it becomes dependent on the individual's ability to come to terms of co-existence with residents of either sex, whether he is able to settle or whether he has to become a wanderer through his large range. It is likely that the latter strategy emphasizes survival rather than reproductive succes, whereas the sedentary strategy allows for better reproductive succes. Of course, this picture represents the two extremes of a continuous range, and individuals are probably able to merge one strategy into another according to the circumstances and local conditions.

The range occupancy of Bornean orang utans (see HORR, 1971: 1975: MACKINNON, 1971: 1974: RODMAN, 1973) appears to differ in some aspects from the picture sketched above. Yet, many of the observations on ranging behaviour seem to be consistent with those observed in this study. RODMAN (1973) found that adult male orang utans in the Kutai region (Kalimantan) maintained discrete, non-overlapping ranges of approximately twice the size of female ranges. The adult females had overlapping ranges of approximately 0.4–0.6 square kilometre in extent. These ranges were mostly occupied by female-offspring units and thus can be compared with the core area in this study. Apart from the smaller size of the Bornean ranges (which suggests a greater richness in food-resources than found in the Ketambe area), it is interesting that the size of the female ranges seems to be rather constant in RODMAN's study area. Perhaps the length of his study period did not allow the detection of major changes in the ranging behaviour of the observed individuals. The same applies to the ranges of adult females in Sabah (East Malaysia) which HORR (1971) estimates to be 0.64 square kilometre or less. The ranging behaviour of adult males in HORR's study showed more resemblance to that observed in the Ketambe area. Male's ranges had some overlap and their size was 'considerably larger, – perhaps 2.5–5 square kilometres in extent, – than those of female-offspring units.'

MACKINNON (1971: 1973; 1974) has reported a wide variation in ranging behaviours. Concurring with the reports of SCHLEGEL and MÜLLER (1839–'44, p. 20), and HORNADAY (1885, p. 444), MACKINNON emphasises the non stationary nature of the orang utans he observed. A very interesting aspect is his account of group nomadism in response to seasonality of food species. In particular Sumatran orang utans appeared to be 'centred around single, large calling males, to form dispersed but recognizable groups' (MACKINNON, 1974; p. 18). No indications for such behaviour could be found in the Ketambe orang utan population. MACKINNON (1972) supposes the ranges of his studied populations to be 'very large, at any rate considerably larger than the study area' which was approximately 5 square kilometres.

1.4. GROUP SIZE

The observed wild population of 22 known individuals consisted of 15 independent units (see table 11). The term unit includes both lone individuals and mothers travelling with their offspring. Adolescent offspring accompanying their mothers have consequently been included in the mother-unit, while if the same adolescents were encountered separately they have been considered as independant units. The average size of a unit was 1.47; RODMAN (1973) who used the same criteria, found an average unit-size of 1.83.

In the period of August 1971 till April 1974 a total of 658 observations of the units, corresponding with 829 observations of individuals, were made in the Ketambe area. In addition, another 42 observations of units (i.e. 62 independant observations) on Sumatran orang utans were made outside the study area, mostly in the area on the opposite bank of the Ketambe river.

A unit observation has been defined as the observation of one unit in one day, irrespective of the number of times it was met that day. Thus, if the unit was encountered on *n* consecutive days, this was scored as *n* unit observations.

Apart from the 658 unit observations in the study area, some 390 unit observations were made on wild orang utans who visited the immediate surroundings of the rehabilitation station. The four most frequent visitors to the station's feeding area (fig. 58a, the shaded area), were the adult male O.J., the sub-adult males Doba and Bor, and the adolescent female Jet. Data concerning these visits have not been included in the tables on group size and group composition,[17] because the presence on a feeding place represents an unnatural situation which may have influenced the ape's behaviour to a certain extent (cf. WRANGHAM, 1974). Encounters with rehabilitants away from the rehabilitation station, have not been included in the quantitative data on group size and group composition.

Units were found to have associated in groups on 141 occasions; these correspond with 355 unit observations. A 'group' is defined as a combination of two or more independent units which stay together for a period longer than necessary for just passing by, and in which the individuals have been able to see one another clearly (i.e. a distance of less than approximately 50 meters). Table 13 shows the frequency with which various groupsizes were encountered

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[17] Except for the first day of any longer lasting episode of visiting by these wild apes after an interval of at least one month. Thus, whenever an individual returned to the feeding ground after an absence of one to 30 days, it was not scored as a new 'unit observation'.

TABLE 13. Frequency of encountered group sizes (average group size: 1.91).

Individuals per group	Number of groups	% of total (n = 434)
(1)	(235)	(54%)
2	97	22%
3	59	14%
4	18	4%
5	9	2%
6	8	2%
7	6	1%
8	2	1%
	434 (comprising 829 indiv.)	100%

in the Ketambe area. On the 141 occasions that units were found together also the age-sex composition of these groups was determined. The following groups have been distinguished:

adult groups, containing adult female(s) (with offspring) and/or adult male(s);
sub adult-adolescent groups, containing sub-adult (males) and/or adolescent(s) of either sex;
adult/sub-adult-adolescent mixed groups, containing both adult male(s) and/or adult female(s) (with offspring), and sub adult(s) and/or adolescents.

In table 14, the frequency with which the various types of groups were encountered in the research area is listed, and Table 15 shows the different age-sex classes composing these groups.

TABLE 14. Frequency of encountered group types.

Type of group	Number of groups	Number of units involved	Frequency of encounterd group types
Lone indiv.	235	235	36%
Mother/offspring units	68	68	10%
Subtotal	303	303	46%
Adult groups	37	77	12%
Subad/adolesc. groups	32	81	12%
Mixed groups	62	197	30%
Subtotal	141	355	54%
Total	434	658	100%

Of all 658 unit observations in this study, 355 (54%) formed part of groups. This figure is considerably higher than the 10% frequency of observations of (secondary) groups, which RODMAN (1973) found for Bornean orang utans, using similar criteria. Perhaps the difference in sociability is due to differences in composition of the population studied in Kutai. RODMAN's report shows few observations on sub-adult males and adolescents; consequently all combinations of primary units must have been those we have described in this study as adult groups. The frequencies for adult groups is very similar in the 2 areas (12% in this study – 10% in Kutai). Groups may also be commoner in Ketambe because of the higher population density there. It is difficult to compare the figures of Table 14, with those given by MACKINNON (1972), because his methods of counting sub-groups were different.

1.5. GROUP COMPOSITION

Groups, i.e. associations of individuals other than mothers with offspring, were observed on 141 occasions (see Table 14). These groups can be divided into two major categories, namely:

a. *social groups*, consisting of individuals moving about together, within view of one another, and showing coordination of movements, and

b. *temporary associations*, groups of individuals feeding in the same fruit tree, but separating into independent units after feeding.

Temporary associations were seen to develop into social groups and there is of course no absolute distinction between the two categories. When in doubt, we described a group as a temporary association. Individuals that met in fruit trees for instance were invariably seen to react to one another in some way. As I shall describe on p. 296 such reactions included avoidance movements,

TABLE 15. The number of units and frequencies of the different sex-age classes encountered in groups and solitary.

	Adult males		Adult females		Sub-adult males		Adolescents		Total	
Total number of observed units	174	100%	181	100%	130	100%	173	100%	658	100%
Solitary units	108	62%	86	46%	54	42%	55	32%	303	46%
Units in groups	66	38%	95	52%	76	58%	118	68%	355	54%
Attendance to social groups	8	5%	11	6%	32	24%	58	33%	109	17%
Attendance to temporary associations	58	33%	84	46%	44	34%	60	35%	146	37%

TABLE 16. Distribution of the different age-sex classes in the composition of the various types of observed groups.

Lone individuals		Mother units		Adult-groups		Sub-adult/ adolesc. groups		Adult/sub-adult/adolescent mixed groups					
								male(s)/sub-adult(s) and/ or adolesc.		female(s) and sub-adult(s) and adolesc.		male(s) and female(s) and sub-adult(s) and adolesc.	
M	108	Fi	31	MM	1	SS	2	MS	1	FS	3	MFS	2
F	18	Fj	14	MMF	1	SSA	1	MMS	1	FiS	3	MFiS	1
S	54	Fa	8	MF	12	SSAA	1	MSS	1	FjS	1	MFiaSS	1
A	55	Fia	15	MFi	10	SSAAA*	1	MSA	1	FiaS	3	MFFiS	1
				MFj	2	SA	12	MSAA	1	FFiaS	1	MFA	1
				MFa	2	SAA	5	MA	6	FjFjSA	1	MFiaSA	1
				MFia	3	SAAA*	2	MAA	5	FiSA	3	MFiaSAA	3
				MFFj	1	AA	6			FiaSAA	2	MFiaSSAA	1
				MFjFj	1	AAA*	2			FiSSA	2	MFFiFjA	1
				FFj	2					FiaSSA	1	MMFFiAA	1
				FFia	1					FiaSSAA	1		
				FaFia	1					FFiSSAAA	1		
										FSSAAA*	1		
										FA	1		
										FiA	4		
										FiaA	1		
										FiAA	1		
										FiaAA	2		
										FiaAAA*	1		
Total	235		68		37		32		16		33		13
											62		

M: adult male.

F: adult female, Fi: female-infant unit, Fj: female-juvenile unit, Fa: female-adolescent unit, Fia: mother offspring unit containing infant and adolescent.

S: sub-adult male.

A: adolescent male or female, A*: group contains the rehabilitant female Bin.

submissive gestures and vocalisations and sometimes aggression. Occasionally individuals might engage in brief social interactions involving body contact (i.e. play). Nevertheless, such groupings have been classified as temporary associations if the individuals left the tree independently.

In Table 15, I have listed the frequencies with which the various age/sex classes were observed together in social groups and in temporary associations. Of all unit-observations, 54% were observed as part of a group. Of these only 17% can be considered as real social groups, the other 37% were associations of individuals attracted to the same fruit tree. Whereas all sex/age classes showed a similar amount of time spent in temporary associations, they differed with respect to their participation in social groups (Table 16). Sub-adult individuals, in particular adolescents spent the most time in social groups while adults, both males and females, scored least. RODMAN (1973) found that only 4.3% of all observed orang utan units occurred in real social groups. This is not only considerably lower than the average 17% found in the Ketambe area, but even lower than the percentage for the least social of the age/sex classes (i.e. adult males; 5%). This might indicate a difference in sociability between the Sumatran and Bornean sub-species, as has been suggested by MACKINNON (1974). However, the different frequencies may also be due to different population compositions in the two study areas.

2. ELEMENTS OF SOCIAL BEHAVIOUR

2.1. INTRODUCTION

Adult orang utans maintain an exceptionally large inter-individual distance which has long been defined as a 'solitary' lifestyle and until recently most studies have reported a striking paucity of social behaviour in this ape. For instance, several authors have reported that orang utans in Borneo often showed no detectable response to a conspecific's presence during aggregations in fruit trees (MACKINNON, 1971; HORR, 1972; RODMAN, 1973); for this reason HORR (op.cit) even characterised such situations as 'ships that pass in the night'. However, it is not always clear from their descriptions whether the observation conditions were sufficient to allow the detection of the often remarkably subtile signals that may be exchanged between individuals. In Sumatra at any rate such instances of complete mutual ignorance were never observed. The individuals usually showed some kind of interaction, albeit often very subtle and inconspicuous.

In this chapter I describe the social behaviour of the orang utan individuals observed in the Ketambe and adjacent areas. To describe the continuous stream of actions and physiognomic changes that comprise an animal's social behavioural repertoire is only possible by breaking up this stream into arbitrary units. The smallest units looked at in this study have been called 'elements', which constitute limited groups of actions and postures in the individual in relation to the presence of a partner. The second level of description concerns 'complexes' of behaviour. It is clear that elements are not randomly clustered into any possible combination (VAN HOOFF, 1968). Instead some more of less distinct combinations tend to occur with great regularity. Due to the conditions of the fieldwork, and to the pioneer-like nature of the study, it was not possible to gather sufficient quantitative material at the elementary level of behaviour to allow the use of objective quantitative analyses of the organizational structure of behaviour. The categories presented here are based on an intuitive appreciation of the temporal contingencies in the observed behaviour and its functional significance. In doing so, I have tried as much as possible to take into account the conventional standards set by other authors, especially those concerned with the description of the behaviour of the allopatric apes (SCHALLER, 1963; GOODALL, 1965; VAN LAWICK-GOODALL, 1968). Two different methods have been used to describe the chimpanzee's behavioural repertoire. As the method based on intuitive appreciation of the observer (i.e. VAN LAWICK-GOODALL, 1967; 1968), gives very similar results to sophisticated cluster analysis (i.e. VAN HOOFF, 1971), this provides confidence to an observer who cannot but rely on the former for practical reasons.

An obvious characteristic of the orang utan's activity pattern is that it proceeds at a typical slow pace; consequently the orang utan's nature has been described as 'introvert' (YERKES and YERKES, 1931).

Even in the orang utan's social behaviour, this slow pace is often notable; consequently, behaviour elements might occur with a comparatively large temporal spatiation. Also, as a consequence of the large inter-individual distance of this ape-species, several interactions were often exchanged over a comparatively large distance. Moreover, many social interactions were characterized by avoidance rather than by contact-seeking elements. These details may account for the statements cited above, concerning the paucity of social behaviour in this ape-species. Yet, when aware of these subtle reactions and inconspicuous interactions, it became possible to assess the relationships of the animals. Consequently, the third level of description concerns the interactions between the individuals composing the studied deme; i.e. those patterns of actions (complexes of behaviour) exchanged in reaction to one another. By trying to relate these to the sex and age catagories of the participants I hoped to detect the general characteristics of the social relations in the deme and thus, to construct a model of the Ketambe deme's social organisation.

The behavioural elements observed in wild and rehabilitant orang utans described in this section add to earlier accounts, of which the study of MACKINNON (1971; 1974), mainly on the Bornean sub-species, and the studies of BRANDES (1939) and JANTSCHKE (1972) on zoo orang utans have provided the most detailed information to date. Reference will be made in particular to comparable elements in the chimpanzee's – (VAN LAWICK GOODALL, 1968a and b, and unpublished[18]: VAN HOOFF, 1971) and gorilla's social behaviour SCHALLER, 1963; FOSSEY, 1972).

The elements have been grouped into 4 main categories, based on morphological features and relational aspects; they have been listed in an arbitrarily chosen order. When elements are referred to elsewhere in the text, they will be designated by means of inverted commas: an alphabetical list of the elements will follow this section of descriptions.

2.2. TYPES OF LOCOMOTION

With a few notable exceptions, orang utans in the wild restrict their locomotion to the arboreal strata of the mature tropical rainforest. Thanks to his particular anatomical adaptations the orang utan can practise a wide variety of locomotor modes (NAPIER & NAPIER, 1967: TUTTLE, 1970). A detailed description of the types of locomotion observed in wild and rehabilitant orang utans has been published by MACKINNON (1972; 1974); other good accounts have been given by SCHALLER (1961) and DAVENPORT (1967). Their observations are in agreement with mine on the Ketambe population.

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[18] Unpublished illustrated behaviour glossary, in use in the Gombe Stream Research Station.

In this paragraph I present a general description of the main types of locomotion based on my own observations, and I only refer to other sources when their data differ from my own.

When searching for food items in an apparently random fashion, the orang utans of the Ketambe area travelled over considerable distances through the upper storeys of the forest, where most of their food sources are situated (see p. 62). When fleeing from humans, the orang utans also use the upper storeys of the forest, whereas a flight from a conspecific was always directed downwards, sometimes ending on the ground. Ground-walking was only rarely observed in the wild Sumatran orang utans (fig. 73). When they did, individuals descended with great caution and moved from one tree to another at a fast pace. While ground-walking, orang utans would stop at every next treelet, large liana or tree, and holding on to this support, often with one foot raised, would scan the surroundings. Only after some time would a ground-walking orang utan then move to the next tree, where the procedure was repeated until eventually the animal climbed up into the canopy again. The average distance between two such stops was some 9 meters (n = 11) and seemed to depend on the diameter of the trees along the route; animals only chose easily ascendable trunks.

A few instances when one animal pursued another gave us the strong impression that orang utans excel at evaluating the multivariate aspects of

FIG. 73. An adult male orang utan (O.J.) walking along the ground; note that he uses a fallen log for a path.

FIG. 74. A female orang utan (Bin) retaining a bitten through liana in order to secure an escape route while feeding.

choosing the optimal route. For instance sub-adult males regularly chose escape routes through arboreal pathways that heavier pursuers (e.g. an adult male) could not possibly use. Another remarkable aspect of this skill was that a fleeing individual often retained the lianas he had used to swing across a gap (fig. 74) so that the pursuer had to make a detour to cross the same gap.

When entering a preferred fruit tree, most orang utans seemed to recognize immediately where the best potential escape routes were, and generally they fed close to such exits. Some individuals avoided or rarely visited isolated food trees that allowed acces from only one direction. Sometimes one orang utan waited in an adjoining tree while his companion fed in the isolated tree. The adolescent male Mos, for example, did not follow his mother into such trees but waited for her to rejoin him. This ability to foresee the possible difficulty of escape if he should become involved in an agonistic encounter is highly adaptive for the orang utan since the animal's size and weight make rapid travel or jumping dangerous. Yet, such rare fleeing behaviour as jumping was observed on two occasions in this study. In both instances orang utans fled in response to my persistent following. The animals, a sub-adult male and a mother with infant, displayed behaviour which gave the strong impression of panic. The male jumped across a gap of some two metres, the female dived 8 metres in a free fall from the canopy into lower vegetation and continued to flee.

Much of the orang utan's locomotion is performed with an upright body position, in a typical climbing-hanging-clinging mode. When travelling along large horizontal branches, adolescent and older orang utans used to walk on top of the support. Although orang utan feet have the ability to grasp even large branches, the apes often walked along such supports with their toes curled inwards, similar to their locomotory mode on a flat surface (i.e. the ground). A similar non-grasping mode of locomotion can be seen in chimpanzees, who, instead of grasping large supporting branches with their flexed hands, usually proceed in the typical groundwalking 'knuckle' position when walking quadrupedally along large boughs. Whereas chimpanzees thus extend their feet and flex their hands when walking on a spaceous support, orang utans were never observed to hold their hands in the typical clenched-fist groundwalking position but they extended their hands in a grasping mode when walking quadrupedally along large branches.

It was notable that young orang utans, namely infants and juveniles, often used a hanging type of locomotion, in which both the hands and the feet grasped the supporting branch and the body was positioned horizontally beneath the support. Such preference may be due to a lack of experience in balancing on a moving substrate. Rehabilitant orang utans, who had not had much climbing experience, sometimes showed the typical infantile (i.e. hanging) locomotor pattern during their first weeks in the station.

Brachiating was a common locomotor pattern among the Ketambe orang utans (fig. 75). In particular when an individual increased its speed or started a 'show off' display (i.e. 'ostentatious approach') for other orang utans or

FIG. 75. A brachiating adolescent male.

people, it would change over to this mode. The speed-increasing effect of brachiating has already been described by BECCARI (1904). Brachiating typically occurred in bouts, alternated with short spells of rest during which the animal hang tri-manually or quadrumanually, scanning the surroundings. Adult- and young orang utans of both sexes did not seem to differ with respect to the form of brachiating or the context in which it was performed.

A specialized method of locomotion, which may be employed by all age-sex catagories, but typically by adult males, is tree swaying. For this mode large saplings and small trees are used. The elasticity of these trees in combination with the animal's weight makes for a very economical way of locomotion.The ape pulls in the crown of a small tree, then transfers his body onto the crown and lets go (fig. 76). The tree swings back past the perpendicular amplitude, amplified by the animal's active shift of momentum. At the end of the arc he grasps the next tree from where the procedure is repeated. The transfer of weight during this type of locomotion requires good timing so that the swaying tree will bend in the right direction. Adult male orang utans can move at a considerable speed employing this method, a speed which may equal that of an observer walking on the forest floor.

The only disadvantage of this method is that it is very conspicuous. It is possible that some males, in particular lower ranking adult individuals prefer ground-locomotion under certain circumstances (i.e. when higher ranking

FIG. 76. A sub-adult male (Doba) progressing by means of 'tree-swaying'.

males are present in the region) to avoid this conspicuous alternative.

Adult orang utans can climb very thick tree-trunks; the apes do not always depend on epiphytic or parasitic vegetation to ascend large trees. The mode employed has been described as 'bear climbing' by MACKINNON (1974), yet some aspects of this locomotor type, observed in the Ketambe area may be added to his account. On two occasions we observed the adult female Mif ascend a fruit tree with a trunk diameter of some 70 cm. The ape clung with her belly against the tree while embracing the trunk with her arms and legs. Her armspan reached an approximate 270° sector of the trunk. She then alternately moved both arms and both legs, meanwhile pushing her body upwards by pressing her chin and muzzle against the tree and bending her head downwards, in time with the stretching action of her legs. In one cycle she moved up as little as 15 to 20 cm; the procedure was obviously quite fatigueing, for she paused frequently. The adult male Moses was observed to ascend an even thicker tree with the same technique.

The locomotor patterns described above were classified on the basis of their morphological aspects; most of them constitute aspects of maintenance activities. Yet, in the social context, many of the same locomotor patterns can vary in tempo, intensity and direction with regard to a partner or to other environmental aspects. Together with the manner in which these patterns are integrated with other behaviours, the afore-mentioned variables contribute to their communicative significance in social interactions. Thus, in the social context separate classification is required, based on the relational aspects of these particular behaviour patterns.

2.2.1. *Locomotor patterns with a specific taxis component, clearly with reference to, if not directed at a partner*

Approach

This element, performed by an animal moving towards another orang utan and stopping within contact distance, may be divided into several sub-elements.

a. *Stiff approach*

The actor approaches another orang utan with exaggerated stiff movements. When walking quadrupedally, the back is rounded and the head is slightly pulled back between the shoulders; the actor looks at the partner. Sometimes this element could abruptly change in the 'loutish approach'.

b. *Loutish approach*

The actor moves towards a partner with exaggerated slouched movements; the back in a quadrupedally walking individual may be rounded and he may dangle his head and arms (fig. 77). Some times short bouts of 'gymnastics' may be performed in connection with this element.

Both the 'stiff-approach' and the 'loutish-approach' often precede 'gnaw-

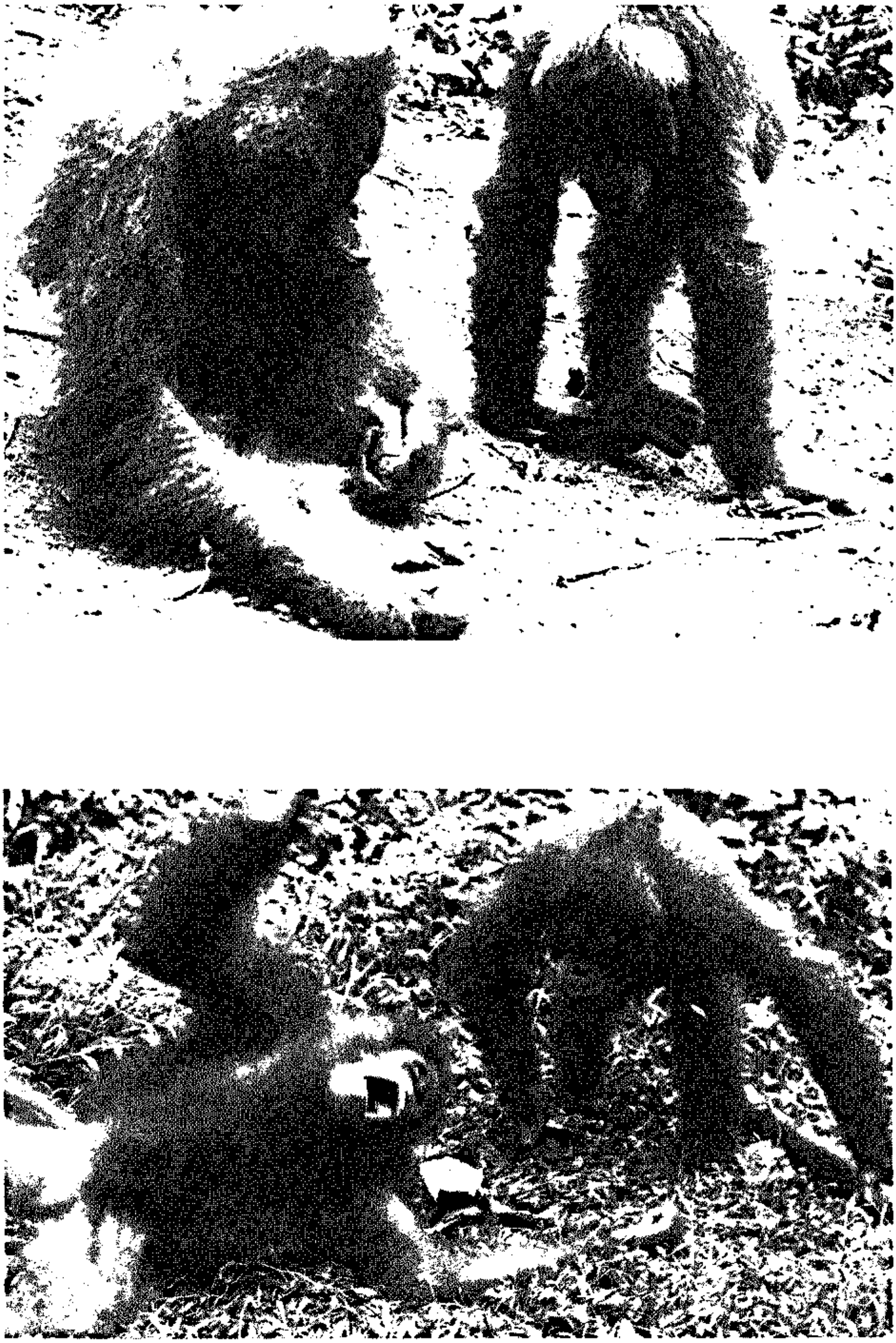

FIG. 77. 'Loutish approach' (a) the sub-adult male David initiates play; (b) the female Yoko accepts the invitation, note her 'wide open-mouth face'; she will make the first grasp.

wrestling' (fig. 77b): they therefore may be considered as invitations to play (sometimes referred to in the text as 'play approach'). A similar play approach can be observed in captive gorillas (see also HESS, 1974).

c. *Hesitant approach*

This behaviour differs only slightly from 'approach', in that the actor occasionally or regularly interrupts its pace; this element often occurred in connection with the 'stiff-approach', and in connection with 'ostentatious approach'.

d. *Ostentatious approach* (agonistic display)

The actor moves in the direction of the partner with abrupt and exaggerated movements, which cause the vegetation to sway and shake more than during normal locomotion. This display pattern often starts with the animal rising from a sitting position and then (from the erect standing position) making a short dive towards the next over head branch support (fig. 78). Hanging onto that support with both hands, he pulls vigourously at the vegetation or proceeds with a short bout of brachiating. It appears as if the animal hangs onto the supporting branch with all his weight during every part of the locomotor pattern. After a short distance the animal may pause and hang or stand silently ('posturing') before approaching closer. The elements 'stare', 'look away', 'bark biting', and 'branch waving' may precede and/or alternate with this ap-

FIG. 78. The adult male O.J. starting an ostentatious approach; note the massive appearence of his arms, effectuated by 'piloerection' (he still keeps a fig in his mouth).

proach pattern. When high ranking adult males performed this display, it was sometimes followed by a 'long call' vocalisation.

Although this pattern was clearly aimed at an other individual, I never observed both interactants to come within contact distance. In this respect 'ostentatious approach' does not entirely accord with the definition of 'approach'. Yet, the reason for the large inter-individual distance in my observations was clearly due to adequate flight reactions of the others; observations on Bornean orang utans have revealed that following such approaches both animals may engage in a fight (HORR, 1972; GALDIKAS-BRINDAMOUR, 1975).

In particular the hesistant aspect of most observed 'ostentatious approach' patterns indicates that in many individuals the expression of this behaviour is governed by aggressive- and flight tendencies.

Advance

The actor moves in the direction of a partner and either stops at a distance from him, which is greater than contact range, or he continues past the partner.

The essential difference between the 'approach' and 'advance' patterns is that in the first the locomotion is understood to be aimed at (contact with) the partner, whereas in the second case it is not aimed at contact with the partner, but often at another aspect of the immediate environment. The pace of the actor is usually the normal climbing-walking gait.

This pattern may be sub-divided into another element which in view of the context in which it was observed, clearly suggests a submissive meaning (i.e. only females and adolescent orang utans were observed to perform this element when advancing towards adult males and the actors often showed a 'silent pout' facial expression and frequently made 'squeak' vocalizations during this pattern). This typical advance pattern I termed:

a. *Hesitant advance*

The actor regularly or occasionally interrupts his pace, or breaks off his advance for a short while and sits down at some distance from the partner(s). The pace of the actor is slow and he gives the impression of being cautious.

Typically this element was shown by individuals who entered a fruit tree in which another (higher ranking) individual was already feeding. When coming into full view of the other, the actor might stop, look away and wait for some time before advancing again. Whenever the partner reacted in any way, the actor would make a 'squeak' vocalization. Any further initiative by the actor would also be accompanied by a 'squeak' vocalization.

Follow

The actor coordinates his movements with his partner, often moving closely behind the other in the same direction, but also coordinating other activities such as feeding etc.

Leave

The actor leaves the immediate surrounding of the partner at a normal, smooth pace, without any clear indication that his departure is determined by an agonistic attitude of the partner.

Avoid

In this element all locomotor patterns are included which are consistently directed away from the partner, beginning when both partners have come close enough together to notice one another. The locomotion is not performed at great speed, and sometimes it is determined by a preceding agonistic interaction ('threat') between the partners.

One particular aspect of avoidance in orang utans deserves special attention. On several occasions I noticed that individuals changed course, some time before another orang utan came into view. For instance, such behaviour was seen when individuals who had been travelling in a straight line towards a ripe fig tree, suddenly lingered and turned away from it at some 50–100 metres distance. In all instances, another orang utan was already present in the tree; the known relationships between some of the potential interactants in such cases (often a sub-adult male moving towards a tree containing an adult male) clearly suggest that the actor was avoiding a potentially agonistic interaction. Still, how the approaching animal noticed the other from such distances was not always clear, (see also p. 251).

Hesitant avoid

The actor moves in a direction away from the partner after they have seen each other. Doing so, however, he lingers, sometimes sits, waits and looks back at the partner. On other occasions the locomotion is sufficiently hesitant to enable a pursuing partner to catch up and eventually make contact. This behaviour was commonly observed during play-sessions of adolescent orang utans. Adult females, who were pursued by sub-adult males, also sometimes showed hesitant avoidance before being raped; meanwhile they often made frequent 'squeak' vocalisations.

Flinch:

This behaviour consists of a ducking of the head and upper part of the body, often accompanied by the raising of one arm (seldom both arms) across the face and by withdrawal or retreat movements of the actor. The retreat may be performed by crouching backwards. This pattern has been observed in response to sudden stimuli, (e.g. sounds), particular animals (e.g. snakes) or sudden threats from a conspecific or human. Flinching may develop into 'flight' or 'avoidance'; it may also be followed by 'hiding' or by seeking reassurance from a partner. In the latter case, the animal may peer at the disturbance after a while and relax; make a sweeping movement in that direction ('hit away'); or wave a branch ('branch waving') or even eventually approach and investigate it. A similar behaviour pattern has been described for chimpanzees as the 'startle reaction' (cf. VAN LAWICK-GOODALL, 1968), while some fractions of this behaviour resemble the element 'parry' (cf. VAN HOOFF, 1971).

Groundwalking rehabilitant orang utans showed flinching behaviour towards approaching higher ranking animals comparable to 'bending away' in chimpanzees (cf. VAN LAWICK-GOODALL, 1968).

Brusque charge

The actor suddenly rushes towards his opponent, silently and in a straight line. The head is withdrawn between the shoulders and the animal often shows piloerection of the shoulder- and upper-arm region. The pace is either smooth and very fast (noticed on five occasions when an apparently high ranking animal attacked or tried to attack a lower ranking one), or this element is performed more slowly with rather stiff steps (observed in rehabilitant orang utans on the ground; in one case an adult female rehabilitant approached me in this manner and tried to bite my leg).

As a rule, the 'brusque charge' was accompanied by 'frowning', and a 'tense-mouth' facial expression; it was often proceded by 'fixed gaze', 'chomping', and 'bark biting' behaviour.

When catching up with the partner, the actor may grasp an extremity and bite. Judging from the reaction of the partner, such bites seemed to be rather painful and, indeed, in some cases 'bites' inflicted rather serious wounds. The 'brusque charge', performed with stiff steps, bears some resemblance to the chimpanzee's 'stamp-trot' (VAN HOOFF, 1971). The smoothly performed 'brusque charge' pattern corresponds with the 'attacking charge' (cf. VAN LAWICK-GOODALL, 1968) or 'brusque rush' (cf. VAN HOOFF, 1971) of the chimpanzee.

Fleeing

The actor moves as fast as possible, away from the partner or from some source of disturbance. In 'fleeing', the animal may seem to lose its normal caution and rush through the vegetation without testing the strength of supporting branches and liana's beforehand. It may jump from one branch to another, drop from branches, or jump into lower vegetation. A fleeing animal may frequently urinate and sometimes defaecate; the faeces may resemble diarrhoea. If the actor was fleeing from a conspecific with whom he had not had contact, he repeatedly uttered loud 'squeak' vocalizations. Where the 'fleeing' had been caused by an attack, the actor often showed the 'bared-teeth facial expression' and uttered 'scream' vocalisations. Unhabituated orang utans showed fleeing behaviour when they were persistently followed by an observer. On several occasions such fleeing was accompanied by 'grumpf' vocalizations.

We had the impression that it is practically impossible for an equally large or larger actor to catch up with a fleeing victim under normal circumstances.

2.2.2. *Locomotor patterns, faciliated by – if not released by – a partner, but which are not clearly defined in terms of a taxis component with reference to that particular partner*

Diving

Towards disturbances on the ground (e.g. people), the orang utan may show a lunging behaviour of dropping the upper part of the body, head down and arms extended while holding on to the supporting branch with the feet. The whole act thus results in an extended upside down hanging position (fig. 79a).

'Diving' resembles some initial fractions of the 'ostentatious approach' pattern, but lacks the clear taxis component and locomotion. 'Diving' also bears some resemblance to 'dangling', which may be considered to be a play-inviting behaviour pattern. These similarities in two differently motivated behaviour patterns may suggest that 'diving' expresses an intention to play (or, make contact) with a self-assertive (threat) undertone. This spectacular pattern has been described earlier by ABEL (1826) and by DAVENPORT (1967).

FIG. 79. The adult male O.J. displaying (a) 'diving' and, during his descent, (b) a facial expression which may possibly be interpreted as a 'wide open mouth bared teeth face'.

Hide

Sometimes orang utans moved silently behind a tree trunk or into dense epiphytic vegetation, and remained immobile when they saw another animal moving in their direction. This behaviour has been interpreted as an attempt to avoid contact; every now and then the actor might cautiously peer towards the advancing animal.

On some occasions when unhabituated orang utans detected an observer who deliberately did not look in their direction, they 'hid'. Also habituated animals observed for prolonged periods sometimes suddenly tried to escape from view and 'hid'. In such cases the animals often retreated to an old nest, built a new nest, or moved to the top of an emergent tree and sat there silently. Twice orang utans were observed to 'hide' upon hearing the sound of an approaching helicopter.

Rehabilitants sometimes withdrew from their group and 'hid' under fallen logs or in dense shrubs with their share of provided food, apparently in order to eat it undisturbed.

Gymnastics

This behaviour consists of various activities and locomotor patterns, which may occur separately or in sequences. The activities generally give the impression of being non-functional, while the locomotor patterns are not oriented in a particular way with respect to a partner. Gymnastics include various ways of handling and biting objects (fig. 80) or vegetation; the ensueing locomotion may consist of climbing, dangling from the vegetation by hand(s) and/or feet, swinging on lianas and jumping. On the ground gymnastics by rehabilitant orang utans include somersaulting, pirouetting and bipedal running. Suitable lianas were sometimes transformed into sway-ropes by biting then through.

Gymnastics are performed as a sequence of activities by an individual on his own. However, this behaviour seems social as it was never performed by lone individuals; the performer was always near his fellows. Regularly two – sometimes even more – individuals performed 'gymnastics' more or less synchronously. When such animals came close, gymnastics could sometimes merge into 'gnaw-wrestling'. Gymnastics were typically performed by young (juvenile and adolescent) individuals.

This pattern corresponds closely with 'acrobatics' (BIERENS DE HAAN, 1952), 'locomotor play' (REYNOLDS & REYNOLDS, 1965) and 'gymnastics' (VAN HOOFF, 1971) in the chimpanzee and the gorilla (see SCHALLER, 1963).

Circling

This behaviour was typically shown by males in a socio-sexual context, i.e. in the presence of a female and another male. While following the female, the actor attempted to keep position between the female and the other male. On some occasions this resulted in repeative circling around the female. In doing so, the male's movements were exaggerated, in several morphological aspects resembling an 'ostentatious approach', though not apparently aimed

FIG. 80. The use of objects during gymnastics; the adolescent male Bobo balances a piece of wood on his head while trying to climb up; note his open mouth facial expression which strongly resembles a form of 'play face'.

at either of the two companions. Yet, such circling displays could easily change into an 'ostentatious approach' display, aimed at the other male.

We first observed this behaviour when two sub-adult male rehabilitants, namely David and Sibujong, met the wild female Jet. David supplanted the other male with this display, occasionally emphasizing his intentions with fierce bouts of 'wrestling' with his male companion. It may be relevant that both males had a friendly relationship, which remained unchanged after this incident. Other observed circling displays never contained such 'wrestling' bouts.

On another occasion the wild adult male O.J. performed a circling display covering an arc of only 270° around the female Bin, which suddenly changed into an 'ostentatious approach' directed at the female's consort mate Bor. On yet another occasion a similar display by the same male (O.J.) was directed at myself. I found O.J. in the presence of the adolescent female Jet, feeding in a large *Nephelium* tree. When the – fully habituated – adult male detected me, he performed part of a circling display around the female, then sat down and subsequently changed to an 'ostentatious approach' in my direction. I left the scene. It seems certain that it was my presence which had released this behaviour, as previously, when both animals were still unaware of my presence, they had been feeding close together without any sign of arousal.

The examples suggest that a male signals a claim on a female to a possible rival male, by means of a 'circling' display.

The 'slow sway' display, reported by MACKINNON (1974) for Sumatran orang utans may correspond with this element, although 'ritualised chest-rotating movements' (MACKINNON, 1974) were not observed in this pattern.

A similar behaviour pattern may exist in gorillas. SCHALLER (1963) describes how a male may circle around a female with a 'strutting-walk' display (p. 280) in the course of an attempt to initiate copulation. Yet, the strict hierarchical organization in a gorilla group does not suggest the need for a male to claim a female.

2.3. GESTURES AND POSTURES

2.3.1. *Gestures, postures and movements involving no clear taxis component with reference to a social partner, but directed towards self or inanimate objects in the environment (if directed at all)*

Rest

The animal sits or lies down in a relaxed inactive manner. It may either watch the surroundings of sleep (fig. 81). Sometimes a nest is built in advance (see also 'nest-building', p. 191).

Ignore

When an orang utan detected another one approaching, he sometimes stopped whatever he was doing and sat down motionless, specifically not looking in the direction of that partner but seemingly ignoring him; though occasionally he might casually glance at the newcomer out of the corners of the eyes. The facial expression during 'ignore' behaviour is blank, often the animal gazes in a slightly upward direction. If the partner 'approached', the 'ignoring' actor might make a 'squeak' vocalisation and a slight 'ducking' movement, yet he would still neither look, nor turn in the partner's direction.

Self-grooming

During self-grooming the actor runs his fingers or the back of his hand through his hair against the direction of growth. He exposes a small area of skin, from which he may remove small particles; he may also inspect small wounds or irregularities, usually with the extended under-lip.

Orang utans would sometimes elaborately pick their nose or their teeth, behaviours which are included in this element. Self-grooming was observed very infrequently: it occurred exclusively during resting and seemingly irrespective of a social setting.

FIG. 81. The adult male O.J. during a midday rest on a large bough.

Scratching

During tense social interactions and when unhabituated orang utans detected an observer, the apes sometimes performed elaborate scratching movements. Areas which were frequently scratched include the upper-arm, the neck, the side of the head, the thighs and – in adult males – the throat-pouch. With the arm raised, the side of the trunk was often scratched, usually with the opposite hand (fig. 82); to scratch the neck of throat-pouch, the animal stretched his neck and held his head high.

This element is distinct from the scratching movements which may occur during 'self-grooming' in that the animal does not look at the treated area. Also the mode of scratching differs; 'scratching' is performed with long elaborate strokes. Individuals varied considerably in how and which part of their body they scratched. Scratching is recognized as a common displacement activity in apes and man (TINBERGEN, 1951).

Self-decoration

Adolescents and sub-adult male orang utans sometimes carried fresh branches, parts of vines or lianas when approaching a partner, especially during their 'stiff approach'. Such behaviour was especially prominent in the rehabilitants who used a great variety of objects in this context. The pieces of vegetation were usually draped around the neck (fig. 83) or on the head, or

FIG. 82. A typical 'overhead' scratching during a tense social situation (Yoko).

were held in an extended arm above the head (see also fig. 112). Also in a non social context, when individuals transported branches from some distance for nest-lining, they sometimes carried these draped over their head or around their neck.

All instances of self-decoration appeared to be of a playful nature. Decorating behaviour in orang utans has been described by BRANDES (1939) and JANTSCHKE (1971); it is also known from the chimpanzee (VAN HOOFF, 1973) and from the gorilla (SCHALLER, 1963).

Self-inspect

Orang utan females sometimes inserted a finger into their vulva and then sniffed it. This behaviour sometimes occurred after a copulation, but also when no sexual interaction had occurred. Males sometimes rubbed their finger, their hand, or foot along their erect penis, and then sniffed it (fig. 84).

Masturbate

This behaviour consists of either the manipulation of the performer's own genitals in a repetitive movement or rubbing the genitals against objects. Although masturbating is a solitary activity, the animals were only observed to perform it when other orang utans were within view. Both male and female orang utans (fig. 85) performed this behaviour, particularly adolescents; adult

FIG. 83. 'Self-decoration' in a non-social setting (Sibujong).

animals were not observed to masturbate. A few rehabilitants, two wild adolescent females and a wild sub-adult male orang-utan, masturbated relatively frequently. Some of the animals used several different methods and at times used inanimate objects to stimulate their genitalia.

A similar pattern has been described for a rehabilitant Bornean male orang utan (HARRISON, 1961), while it is also known from the chimpanzee (cf., 'clitoris rubbing': VAN HOOFF, 1971 and VAN LAWICK-GOODALL, 1968).

Urinate/defaecate

During avoidance, but especially during 'fleeing', orang utans might defaecate. Also, in situations of social excitement, some orang utans showed repeated excretion of urine in small quantities.

A similar behaviour has been described for chimpanzees (VAN LAWICK-GOODALL, 1968). Also gibbons and siamangs often defaecated during their fleeing from an observer. Siamangs in particular seemed to be able to time their excretion accurately, and they often defaecated when they were directly above the observer.

FIG. 84. 'Self-inspect' after a copulation (Sibujong).

FIG. 85. 'Masturbate' (a) the sub-adult male Sibujong (b) the adolescent female Jet, while drawing the attention of the male Mos.

Yawning

This element consists of a sequence of morphological changes, usually starting with an extreme pouting of the lips, changing to a gradual widening and an opening of the mouth. It ends with a widely opened mouth exposing the gums and teeth. After some time the mouth is closed again. In the course of this sequence, the head is raised and when the mouth is fully opened, the head is held somewhat backwards, only returning to its normal position with the closing of the mouth. Sometimes this last movement is done in a jerky fashion, giving the gesture a nod-like character.

Orang utans sometimes yawned in a non social context, for instance in their nest, just preceding- or immediately after a rest. But males in particular yawned repeatedly in apparently tense social situations. While yawning, the actor typically did not look in the direction of the tension-eliciting partner. Observers sometimes evoked yawning in unhabituated orang utans. One rehabilitant sub-adult male (Bujong) used to yawn immediately after being chased by another animal, and also after having raped a female.

For several primate species it has been noted that males in particular frequently yawn in situations of agonistic arousal or social excitement (CARPENTER, 1934: HALL, 1962: ALTMANN, 1967). HINDE and ROWELL (1962) have suggested that yawning in the Rhesus macaque expresses a conflict situation and may be interpreted as a mild threat. Chimpanzees (VAN LAWICK-GOODALL, 1968) and gorillas (SCHALLER, 1963) show yawning in similar contexts, and especially when in close proximity to human observers.

Nest-building

The technique of nest-building consists of breaking and bending branches and roughly interlacing these to form a platform (see SCHALLER, 1961; DAVENPORT, 1967). Nest constructions varied from very crude small platforms to very sturdy and large nests, capable of supporting a human observer quite comfortably.

Individuals in a group of youngsters might build a nest as part of social play. Between the ensuing 'gnaw wrestling' bouts which take place on or just above such a nest-platform (fig. 86), one or both the interactants might add new nest material to the construction. Thus, some nests became enormous in size, i.e. over 1 meter in diameter. More often however such nests were destroyed in the course of the play. Chimpanzee youngsters may show similar nest building behaviour during their social play (cf. 'play-cushion': ALBRECHT & DUNNET, 1971) and also during sexual behaviour (TUTIN & MCGREW, 1973).

Branch-waving

This behaviour pattern consists of grasping and tugging or shaking a branch or some other piece of vegetation such as vines, lianas and epiphytes. It occurred when orang utans were confronted with some form of disturbance. Branch-waving is an integral part of the male orang utan's 'ostentatious approach' display.

FIG. 86. The youngsters Gin (hanging up side-down) and Roba (only his face and right hand are visible) playing on a crude play-platform between a wealth of epiphytes.

The shaking or waving might be directed towards the disturbance but more often this was not the case. The distance between orang utans performing this behaviour and the source of disturbance varied from approximately two to twenty meters.

Disturbances could be other orang utans (fig. 87) or proximate animals of other species such as a hornbill, a siamang, a binturong. On some occasions the performer would actually shake the very branch on which the disturbing animal was sitting (i.e., hornbills); on rare occasions the disturbing animal was actually hit with the shaken branch, as happened to a Blyth's hornbill. Branch-waving was also released by disturbances on the ground (e.g. human observers), when it often preceded the 'braking and dropping of branches' pattern.

Branch-waving or pulling of vegetation in response to disturbing factors has been reported for many primate species, i.e., baboons (HALL, 1962), the red spider monkey (CARPENTER, 1934), the gorilla (SCHALLER, 1963) and the chimpanzee (cf. 'branching' VAN LAWICK-GOODALL, 1968). This element (i.e. 'branch-shaking') has been described for the orang utan by MACKINNON (1974).

Breaking and dropping of branches

This behaviour element is one of the first behaviour patterns recorded for the orang utan (see BEECKMAN, 1718; RADERMACHER, 1780). It consists of the deliberate breaking of twigs and branches, and biting or tearing other vegetation, such as lianas and epiphytes, which are then, often after some manipula-

FIG. 87. The 'kiss-sound' accompanied by 'branch-waving' (Bin).

tion, dropped or slung to the ground. This behaviour was exclusively seen in response to disturbances on the ground and in particular to humans.

The branches choosen for this purpose were not always small; occasionally quite large and heavy live or dead branches or even boughs were torn loose and pushed down. Because of their weight, such projectiles could constitute a real danger for an individual walking underneath.

The manipulating (slinging) was always performed under-hand. It rarely gave aim to the projectiles.

Elements which were frequently observed in combination with breaking and dropping of branches, were 'branch-waving', 'staring' and a 'tense mouth' facial expression. On all occasions the repeated 'kiss sound' and sometimes also the 'grumpf' vocalization were heard during this activity. The breaking and dropping of branches was common in both wild and rehabilitant orang utans. Some rehabilitants were observed to throw vegetation with good aim (see 'arm wave'). Breaking and dropping of branches has also been observed in other arboreal primates notably forest living chimpanzees (KORTLANDT, 1968).

FIG. 88. 'Bark biting'. The female (Bin) reacts in response to seeing a third orang utan advancing towards her.

Bark biting

This behaviour consists of biting into the bark of a tree, sometimes followed by tearing off long strips of bark (fig. 88). The bark was not manipulated any further, nor was it treated as the bark used in feeding behaviour, but it was dropped immediately. It appeared that any tree was suitable for this behaviour. Lianas and twigs which were bitten through during the 'breaking and dropping of branches' or during 'gymnastics' are not included in this element.

Bark biting behaviour was often accompanied by 'chomping' vocalisations. The contexts in which bark biting occurred suggest that it is an act of redirected aggression, for it was always observed in response to the presence of a conspecific, in a tense situation. In a few cases it preceded an attack. It was performed by both male and female orang utans.

A rehabilitant female showed this behaviour minutes before she attacked me. Another rehabilitant, a sub-adult male (David) showed bark biting behaviour after he had been chased by a higher ranking sub-adult male orang utan (Doba).

There are no reports of a corresponding pattern in the other apes nor has it been reported for orang utans.

Posturing

The performer assumes an extended posture for some time, so that his body is exhibited at maximal size. He may stand on all four limbs, showing the body sideways; he may hang, supported by both arms with limbs fully extended (fig. 89) or he may stand erect, bipedally with extended arms and legs. This last position was observed particularly often in females and sometimes also in sub-

FIG. 89. A hanging 'posturing' stance (O.J.); note his 'tense mouth face'.

adult males. When posturing in an erect stance, females with infants typically lifted and held up the leg on the same side of the body as the clinging infant.

Both the quadrupedal- and the hanging postures were shown in a social context with the performer staring at a the conspecifics. When 'posturing' the secondary sex characteristics of adult males were clearly visible, e.g. the long hair waving from the arms, from the shoulders and from the sides of the back, and the broad facial mask.

The hanging posture often preceded or formed part of the 'ostentatious approach' display. Neither the erect standing posture nor the sideways quadrupedal stance were usually followed by any directed locomotor element. The erect stance was often observed in response to people: this stance resembles MACKINNON's (1974) description of 'posturing'.

The quadrupedal posture, in which the side of the body is presented to the partner, bears strong resemblance to the 'sideway posture', which is part of the 'strutting walk display' of the gorilla (cf. SCHALLER, 1963), and to the 'quadrupedal hunch' of the chimpanzee (cf. VAN LAWICK-GOODALL, 1968).

Temper tantrum

Young orang utans, i.e. juveniles and adolescents, sometimes showed a series of exaggerated and convulsive movements and jerky locomotor patterns (e.g. crawling along branches, hitting with both hands at the branch on which they lay, pressing both hands on their bent head, etc.) (fig. 90). Such temper tantrums were always accompanied by loud 'scream' vocalisations.

An example of this behaviour was observed when a juvenile did not get part of the fruit he begged from his mother. On another occasion an adolescent male had failed to notice that his mother had left a feeding site, while he was engaged in play with a peer. When the play ended, he looked up, and then screemed and showed a series of convulsive movements, dragging himself along to the nest which his mother had just left. He then 'whimpered', but nevertheless calmed down quickly and went back to play with his partner.

Mothers often reacted by conceding part of the desired food item, or by waiting for their offspring to follow and catch up with them. The temper tantrum behaviour is obviously designed to attract the mother's attention and to make her adjust her behaviour or give in. This is also indicated by the fact that a youngster displaying such behaviour continuously watched its mother, glancing at her from under his eyebrows. When the mother at last payed attention, the performer's facial expression changed to a 'pout face'.

Rehabilitant orang utans sometimes directed such temper tantrums at their bondpartner or personal 'friend' when they could not catch up with him; as well as at a human attendant, for instance when a desired food item (e.g. milk) was withheld.

Fig. 90. A temper tantrum by the juvenile female Marga.

Temper tantrum behaviour has been described quite accurately by VOSMAER (1778) for the first live orang utan that reached Europe. YERKES (1943) has also mentioned that chimpanzee infants, performing a temper tantrum, 'furtively glance' at their mother or a keeper.

Throat pouch inflation

Orang utans may inflate the large cavernous pouch that lies anterior to their throat. This behaviour was observed for both males and females, and seemed only to be performed after animals had reached the adolescent stage. Throat pouch inflation did not occur in response to any specific phenomena, yet it seemed to represent a state of general arousal. For instance orang utans performing an 'ostentatious approach' display or a 'circling' display sometimes showed the inflated throat pouch. But also during 'gnaw wrestling' and even on occasions when animals were apparently relaxed and 'resting' orang utans sometimes inflated their throat pouch. Some rehabilitant orang utans would even inflate their throat pouch when they were tickled.

The remarkably large throat pouch of adult males seems to have a function in the calling behaviour by acting as a resonance chamber (BRANDES, 1939). This element has been described in detail by BRANDES and by MACKINNON (1974).

Penile erection

Young orang utan males, especially infants and juveniles, regularly showed erection of the penis during such social excitement as initiating play ('gnaw wrestling'), but also when their mother moved off and they apparently were not able to catch up with her immediately. In the latter case the animals showed signs of distress, as well as penile erection.

In older individuals this behaviour was very rarely observed outside the contexts of copulation and masturbation.

The small size of the erect penis and the hairiness of a male orang utan's abdomen suggest that the erection of the penis cannot function as an important signal in adult socio-sexual interactions, as has been suggested for 'penile erection' in the chimpanzee (VAN LAWICK-GOODALL, 1968; TUTIN & MCGREW, 1973).

Rocking

A rehabilitant female who had lived for a long time with humans prior to her rehabilitation, showed persistent rocking movements whenever she did not get attention from the human attendants. She usually sat crouched on the ground and moved her head and the upper part of he body up and down in a repetitive movement, bouncing on one of her arms. She used to continue such behaviour for several minutes. This particular animal rarely engaged in social interactions with other rehabilitants, and seemed to focus all her attention on humans.

Such rocking behaviour has been described for wild chimpanzees when 'frustrated' (VAN LAWICK-GOODALL, 1967) and for captive chimpanzees, in particular when upset or seriously deprived of social contact (BERKSON et al., 1963).

2.3.2. *Gestures and postures involving a clear taxis component with reference to a social partner*

Watch

During their daily activity, orang utans might stop whatever they were doing, sit down and attentively watch another orang utan 'advancing', suspicuously moving vegetation, or other orang utans nearby during temporary associations or in his social group.

Sometimes individuals climbed to the top of a tree or to another high vantage point and stared in a particular direction for some time. In social interactions, 'watching' often takes the form of unobtrusive glancing towards a partner.

Look at mouth

While holding the face very close to that of the partner, the actor looks intently at the other's chewing mouth (fig. 91). The actor's underlip is often slightly protruding and he may hold an open hand under the partner's chin, without touching it. The chewing partner may drop some food onto the protruding underlip, or in the hand of the actor. Animals who showed this behaviour were always younger and/or lower ranking than their partners; I saw it in wild juveniles and adolescents directed at their mothers; and also reha-

FIG. 91. 'Look at mouth' (peer begging); note that the female Bin (left), who holds the food, ignores the peering male Bobo.

bilitant adolescents (i.e. the male Usman, and the females Yoko and Bin) showed such behaviour towards the adult male O.J. and towards several wild sub adult males.

This element resembles 'peer-begging', which has been considered a form of greeting behaviour on the part of lower- to higher ranking chimpanzees (WRANGHAM, 1974). Similar behaviour also occurs in the repertoire of baboons and vervet monkeys in a similar context (ALTMANN & ALTMANN, 1970).

Vertical head nod

This behaviour usually consists of a fast upwards jerk of the head or less commonly a rather deliberate nodding (upwards and downwards) movement. It was performed from some distance, (20 or more meters), towards a partner or towards the observer and often occurred together with 'scratching' and 'yawning'.

This behaviour was only observed in two individuals, the adult male O.J. and the adolescent female Jet. Both showed it in tense social situations. During his encounters with the adult male Gorm, O.J. repeatedly made this gesture. Also during prolonged observations, O.J. often head-nodded at me. The female Jet used to nod to her former 'friend' Bin, after Bin had 'stared' at her in a period when the relationship between both females became rather hostile.

This element resembles the 'vertical head nod' of the chimpanzee (VAN HOOFF, 1971).

During the 'kiss' sound orang utans may also move their head, mostly sideways. This behaviour is performed more slowly and the direction of the movement differs from the 'vertical head nod' in which the animal remains facing the partner. The head-movement accompanying the 'kiss' sound is included in that element.

Arm wave

Only ground-walking rehabilitants were observed to make this gesture. Sometimes a rehabilitant orang utan interrupted his 'stiff approach', adopted an erect posture and walked bipedally towards a partner with one arm or both raised above his head. As he neared a partner, he swayed one or both his arms downwards in the partner's direction. Rehabilitants, particularly males, 'arm waved' while walking bipedally towards a partner, preliminary to 'wrestling' or 'gnaw wrestling', and sometimes also when approaching human attendants.

It was my impression that rehabilitants often tried to imitate their human attendants. Perhaps this is reflected in their high frequency of bipedal locomotion when near humans (see also HARRISON, 1961).

As in gibbons (CARPENTER, 1940) the raising of the arms might have a function in keeping balance during bipedal locomation. However, orang utans showed skill in walking bipedally with their arms lowered, and the appearance of this gesture did not at all suggest a balancing function.

The context in which this behaviour was observed suggests that it functions as a playful intimidation. On some occasions orang utans held objects, such as stones or sticks, in their hands during arm-waving. These objects were sometimes released during the downward sway, thus resulting in 'throwing', but quite often they retained the object and hit the ground, respectively their partner with it.

The orang utan's 'arm wave' may bear some morphological resemblance to both the 'arm waving and running' behaviour and with the 'bipedal swagger' of the chimpanzee (VAN LAWICK-GOODALL, 1968).

Throwing (and catching)

Real aimed throwing has only been observed in rehabilitant orang utans: they threw either with an overhand movement (resembling a downsway movement, see 'arm wave'), or with an underhand movement (resembling the 'upsway', VAN HOOFF, 1971). Heavier objects such as stones and branches were usually thrown with the underhand gesture. The underhand throw was aimed more precisely than the overhand throw. Usually orang utans threw whilst on the ground, but on three occasions I observed a rehabilitant throwing pieces of wood from a three metres high platform. Objects thrown were herbs, torn off vegetation, sticks and stones; animals threw at other rehabilitants (2), the attendants (often, usually after playful provocation), a tame jungle cat (1), a tame mountain goat (1), a young domestic dog (2), a dead python (1), a dying monitor lizard (1) and a live snake (1).

One rehabilitant orang utan was very skilled in catching objects that were thrown to him. Experiments with some habituated wild orang utans to test their skill in catching bananas showed that, although all readily responded by attempting to catch the food, none showed immediate skill at doing so. After some trials most of the tested individuals succeeded in catching at least a few bananas. A remarkable aspect of this experiment is that none of the individuals interpreted my throwing behaviour as offensive.

Hold out hand

The actor extends his arm in the direction of a partner and maintains that position for some time. The hand is between a prone and supine position or entirely supine (i.e. with the palm upwards). This gesture might also be performed towards an observer (fig. 92). Even unhabituated orang utans sometimes made this gesture towards me. Perhaps it corresponds with the 'arm and leg saluting' gesture described by MACKINNON (1974).

When their juvenile screamed, mothers held out their hand preliminary to 'gathering' it; the behaviour was then accompanied by a 'squeak' vocalisation from the mother. Altogether, we observed this element 4 times in a social context of wild orang utans; three times sub-adult male directed a 'held out hand' gesture at an adult male, and once the adolescent female Jet stretched her hand in the direction of the approaching male O.J., while making 'squeak' vocalisations. Of particular interest in the latter case may be that she held a twig laden with fruits in her stretched-out hand.

This element was most frequently seen in rehabilitant orang utans who in-

FIG. 92. 'Hold out hand' (Sibujong).

variably performed it towards higher ranking partners or towards me. The context suggested that the actor felt threatened and asked for reassurance by means of this gesture. For instance, the sub-adult male Sibujong directed a held out hand gesture at the adult male O.J., who had chased him. O.J. sat and stared at Sibujong across a gap in the vegetation which he could not traverse because the rehabilitant held the connecting liana on his side. On some occasions, even habituated orang utans made this gesture if I looked at them too intently or when people took photographs in an ostentatious manner. It is noteworthy that this element was also used in an appeasing, rather than a reassuring meaning.

This element is identical to the 'hold out hand pattern' in the chimpanzee (GOODALL, 1963; KORTLANDT, 1967; VAN HOOFF, 1971), which is used as a begging, appeasing and reassuring gesture.

Hit away

This gesture was observed only rarely. It consists of a sweeping movement, resembling an incomplete upsway gesture with the hand and underarm. The sweeping movement is generally directed towards a partner and may be performed at some distance. The hit away gesture was also used against members of other species; I observed it three times directed at a pig tailed macaque, and once at a siamang. Rehabilitant orang utans made the hit away gesture when confronted with a snake and also with live leeches. I observed rehabilitants use this gesture only twice in a social context; on both occasions it occurred when the actor had been engaged in a 'wrestling' bout with a higher ranking partner, and both animals were sitting some 8–10 meters apart. The actors made the gestures when they were about to move off, but when the recipients were not looking in their direction. This element resembles the 'hitting away' (VAN LAWICK-GOODALL, 1968) and 'up sway' (VAN HOOFF, 1971) behaviour of the chimpanzee.

Presenting

This behaviour pattern was exclusively performed by female orang utans. The female hangs, suspended by two limbs (e.g. two arms or an arm and a leg), with her legs wide apart in such a position that her genital region is clearly exposed and close to the face of the male. The genital region of the female orang utan is relatively sparsely haired in contrast to the male's, whose penis is entirely hidden between abundant hair. When 'presenting' some females repeatedly 'scratched', a behaviour which usually indicates a certain tenseness. Once I observed that a female orang utan crouched backwards on a large branch towards an approaching subadult male prior to a rape sequence. This particular crouching closely resembled the 'crouch-presenting' pattern of the chimpanzee. 'Presenting' resembles the 'ventro-ventral presenting' in the female chimpanzee (VAN LAWICK-GOODALL, 1968). Unlike male chimpanzees male orang utans were never observed to present.

2.4. CONTACT BEHAVIOURS

2.4.1. *Smooth and gentle contacts*

Touch and smell

When juvenile and adolescent orang utans met, the first gesture by one of the partners might be a rather slow extending of the arm and hand resulting in a gentle touch with out-stretched fingers. Typically the actor would then withdraw his hand and sniff elaborately at the contact place on his finger (fig. 93). Parts most frequently touched were the head, the shoulder and the ventro-genital region. On some occasions the actor smelled directly at the partner's face or shoulder; this might happen after an initial (indirect) touch and smell procedure. The direct smelling gesture sometimes resulted in nose to nose contact, which was then maintained for a short while. The nose to nose contact was invariably accompanied by a very soft nasal 'uff' vocalisation. Nose to nose sniffing may be restricted to individuals who are very familiar with one another. It was observed frequently in rehabilitants but only once in the wild between a juvenile- and an adolescent animal. Its context is one of friendly inspection.

FIG. 93. 'Touch and smell'; (a) the female Yoko (below) intently peering at the unfamiliar orang utan, Bobby; (b) touching him; (c) smelling the hand that touched.

It may be appropriate to mention in this respect that some orang utans had a distinct body odour, discernible even to me. The body odour of the adult male O.J. for instance was sometimes so strong that it could be smelled a distance of about 15 meters. We noticed that the male's body odour was more powerfull when he was engaged in an agonistic interaction with a conspecific, Similarly, SCHALLER (1963) has reported that he got the impression that male mountain gorillas disperse a stronger odour during their 'strutting walk' display. In comparing the body odours of rehabilitant orang utans, it struck us that young individuals (infants and juveniles) smelled quite different from older ones (sub-adults and adolescents); in our own species a similar difference between very young and older individuals is also discernible. As the orang utan's sense of smell is probably no less accurate than that of humans, it is likely that the 'smell' behaviour provides the actor with socially relevant information. Such information might concern, e.g., the physiological state of a female, or perhaps even a partner's motivational state.

FIG. 94a.

Touching the genital region was sometimes followed by parting the hairs in order to obtain a good view of a partner's sex.

Smelling and touching was not exclusively observed in a social context; it was common when orang utans encountered new or apparently frightening stimuli, such as dead animals or unfamiliar (human) visitors. After the female Jet became habituated, she sometimes approached me and performed the touch and smell pattern; she never did this in the forest, but only at the feeding site of the rehabilitation station (although she often was close enough for such contact in the forest).

A few times we observed that rehabilitant orang utans used a stick or some other tool to touch the subject and then smelled the place of contact. Similar use of tools ('investigation probe') has been reported for chimpanzees (VAN LAWICK-GOODALL, 1968) and for Zoo orang utans (a.o. JANTSCHKE, 1972) (see also fig. 49).

Mouth-mouth contact

The performer cups his hand around the underside of the muzzle (fig. 94a) or holds his hand around the back of the head of a partner and presses his slightly opened mouth on to that of the partner. This behaviour was observed in several different contexts for both wild and rehabilitant orang utans. During provisioning a higher ranked individual often took food from a subordinate's mouth in this fashion. On several occasions it could be ascertained that subordinate partners responded by syphoning over a considerable portion of the food. The two wild sub-adult males that consorted the rehabilitant female Bin both obtained bananas from the female in this way (fig. 94b) while we were trying to avoid provisioning them. Among rehabilitants, such behaviour was

FIG. 94. 'Mouth-mouth contact' (a) the males David (left) and Usman (right); (b) often preceded by hand to mouth, (Doba and Bin).

FIG. 94b.

sometimes preceded by '(gnaw-) wrestling' bouts, initiated by the higher ranking individual. By means of a similar mouth to mouth pattern, orang utan mothers sometimes fed chewed food to their infants (fig. 116). The same behaviour occurs in some human cultures; the Gayo people in Aceh used the word *mēme* for this behaviour.

On several occasions when a mother had no food in her mouth, she pressed her slightly opened mouth laterally against the infant's muzzle in a kiss like gesture, immediately after she had 'gathered' it. This pattern may resemble the 'kissing behaviour' described by MACKINNON (1972).

The mouth-mouth contact pattern was observed in still another context. During play the (wild) adolescent male Mos was observed to take a mouthful of rainwater, from a natural bowl into a tree and, after having approached his partner Gin, syphoned the water over in the other's mouth. Gin sprayed the water from between his compressed lips and spilled it over Mos, after which the procedure was repeated, this time with Gin as the actor. Similar play with syphoned water was observed between two rehabilitant males: David and Bujong. Usually it was the higher ranking male David who initiated the play. On one occasion I observed the male David performing the mouth to mouth pattern with the sub adult male (rehabilitant) Usman while neither individual had anything in his mouth. This gesture preceded a 'gnaw-wrestling' bout: its significance in relation to play is not clear, but in this form it may resemble the greeting gesture of chimpanzees, where mouth to mouth contact can be accompanied by a 'silent-bared teeth-face' (VAN HOOFF, 1972) (c.f. 'open mouth kissing'; VAN LAWICK-GOODALL, 1968). I had the opportunity to witness this 'open mouth kissing' element being exchanged between male chimpanzees who showed excitement during the sharing of a red colobus monkey corpse after a successful monkey-hunt in the Gombe stream Nat. Park. This 'open mouth kissing' thus seemed to be a ritualized display of greeting and reassurance. Apart from the context, the strong resemblance to the orang utan's mouth-mouth contact was evident. Also the forms of mouth to mouth contact related to food seem to have a corresponding pattern in the chimpanzee's behaviour repertoire (c.f. 'mouth-to-mouth', and 'syphoning food'; VAN HOOFF, 1971).

Gathering

This element, which was only shown by mothers towards their infants, consists of a 'hold out hand' pattern, followed by a gesture in which the mother cups her hand around the back of the infant's head and gathers it to her. In most instances the infant reacted to the light pressure on its neck by releasing its grip on the vegetation and clambering onto the mother's hand and/or arm. Only rarely did a mother 'grasp' her infant and gently pull it in order to make it release its grip on the substratum. In a later stage, mothers often simply responded with a 'hold out hand' gesture when their juvenile offspring showed signs of distress (i.e. 'scream', etc.); yet, they still would give a 'squeak' vocalisation in advance as in complete 'gathering'.

HARRISSON (1961) has noted that touching an infant on the neck caused it to cease whatever it was doing, just like the immobility response of many other young mammals upon a neck-touch.

The 'gathering' element corresponds with the 'gather' behaviour of chimpanzees (VAN LAWICK-GOODALL, 1968).

Bridging

Sometimes a mother would remain suspended between two trees, often for several minutes, while her juvenile offspring used her body as a bridge to cross a gap in the canopy. This only happened where the juvenile would have been unable to cross on its own because the distance was too great. Such behaviour was also performed by rehabilitant orang utans who sometimes 'helped' their friend across a gap in this manner. On one occasion I observed a newly introduced rehabilitant (i.e. the juvenile female Linda), who had become trapped in

FIG. 95. The female Bin 'bridging' for her consort mate Bor (below).

a tree, being helped across a wide gap by the rehabilitant female Bin. The latter came to her rescue from some 30 meters away. Surprisingly the animals were still strangers and no clear social behaviour had been observed between them prior to this incident.

During consort relationships, it was observed that the smaller and lighter female, who could venture out onto slender branches, sometimes made bridges for her heavier consort by pulling trees together; she only released her grip after the male had crossed (fig. 95).

It is interesting to notice that siamang mothers also bridge for their juvenile offspring (pers. observ.: BROTOISWORO, 1974, pers.comm.). The bridging behaviour of orang utan mothers has been described by MACKINNON (1974), and bridging behaviour has been reported for several other arboreal primates (e.g. spider monkeys; in JOLLY, 1973).

Embrace

This behaviour pattern consists of placing one or both arms around a partner's body. On two occasions I observed females embrace their consorting male briefly. The context of this behaviour was relaxed with both individuals sitting idle (resting).

Young, juvenile orang utans who suddenly became emotionally aroused, e.g. when they detected me or when another orang utan suddenly approached them, returned quickly to their mother and touched, embraced or clung to her.

FIG. 96. 'Embrace' (Pim and Puk).

Rehabilitant orang utans showed similar embrace behaviour towards their bond-partner or to an attendant, whenever they appeared to be frightened (fig. 96). Embrace could at such times merge into 'clinging' or 'walking/climbing in tandem'.

The context suggests that it is an act to seek reassurance, clearly derived from the juvenile comfort seeking behaviour directed at its mother.

MACKINNON (1973) observed a sub-adult male orang utan putting his arm around the back of a female, an observation which indicates that this behaviour may be initiated by both sexes. GALDIKAS-BRINDAMOUR (pers.comm., 1974) also observed embracing behaviour on the part of Bornean orang utan females towards males. The same behaviour element in a similar context has been reported for the chimpanzee (VAN LAWICK-GOODALL, 1968).

Clinging; walking and climbing in tandem

Rehabilitant juvenile orang utans sometimes showed a behaviour pattern of prolonged embracing or clinging to the partner. The contact varied from holding on to a tuft of hair, or hanging on to the partner's body with both hands, to complete suspensory clinging with full ventral body contact and holding with hands and feet. This could seriously hinder the partner's movements when this behaviour continued during locomotion. Wild juvenile orang utans held on to a tuft of hair after they had fled behind their mothers upon seeing me, and also when they followed their mothers along large boughs.

Clinging behaviour in the wild was only observed in the mother-offspring context and usually concerned infants. Yet rehabilitant orang utans showed clinging behaviour into adolescence; this may be considered a deprivation syndrome. As such it is also known from captive chimpanzees (e.g. McCULLOCH, 1939; VAN HOOFF, 1971). DAVENPORT (1967) has described 'train walking' in wild juvenile orang utans which corresponds with this element. Also, FREEMAN & ALCOCK (1973) have reported a similar clinging/walking in tandem behaviour pattern for orang utans and gorillas during play situations in a Zoo setting.

Grooming

Social- or allo-grooming was rarely observed in wild orang utans. The grooming technique is identical to that described for 'self-grooming', although performed on the body of a partner. On one occasion I observed an orang utan mother briefly groom her infant. On another occasion a female was seen to make brief grooming movements on the upper arm and back of her male consort. On two occasions we noticed that the wild, adolescent female Jet groomed the rehabilitant juvenile female Barby. Among rehabilitant orang utans, allo-grooming was also rarely observed. It occurred almost exclusively between individuals who displayed a strong mutual attraction at all times (bond-partners or friends) (fig. 97). The duration of observed grooming bouts was invariably less than a minute.

The skin and coat of an orang utan is nearly always in beautifully clean condition. This apparently does not depend on particular care by the animal itself or by its partners.

It is noteworthy that some rehabilitant juvenile females (Barby and Puk) readily reacted to the presenting of a wild long-tailed macaque male and engaged in long mutual grooming sessions with this particular monkey (fig. 51).

FIG. 97. 'Grooming' (Seamus and Pon).

Some rehabilitant orang utans appeared to be very inquisitive with respect to small wounds and sometimes also made grooming gestures through an observer's hair.

In Zoo situations, grooming in orang utans may occur more regularly (pers. obs.). LETHMATE & DUCKER (1973) have reported that orang utans tried to remove experimentally applied paint from each other's bodies in an experiment to test self-recognition. On the other hand, JANTSCHKE (1972) rarely observed allo-grooming in Zoo orang utans. It is possible that the degree of early experience with other apes and monkeys contributes to the variation found in the occurrence of grooming at later stages.

Genital inspection

The actor brings his face close to the genital region of the partner or touches that region with a finger. Usually such behaviour was performed by males towards females, and often followed 'presenting' by the female partner. During this behaviour, males were observed to touch or poke the vulva of the female with a finger or with their extended underlip, meanwhile peering intently at that region (fig. 98). I also saw males sniff directly at the vulva or sniff

FIG. 98. 'Genital inspection' prior to copulation (Sibujong and Jet).

the place of contact on their finger after a brief touch. Whereas the genital inspection of a partner usually preceded a copulation, 'self-inspection' occurred after copulation.

2.4.2. *Elements including more or less forceful contact*

Grasp

The actor firmly grasps the partner by the hair or by a limb and holds on. Grasping may occur in a variety of social interactions. It was often observed to follow a 'play approach', and was then the initial contact-gesture in a bout of 'gnaw-wrestling'. This element could be performed by either the play-initiator or by the approached partner. When performed by the partner, the play-invitation was accepted and both individuals engaged in long bouts of 'gnaw wrestling'. The grasp gesture leading to 'gnaw wrestling' was usually directed over the head of the partner to his neck or upper arm region, and could follow an 'arm wave' (fig. 99).

Sometimes the grasp movement was directed at a hand or foot of a passing orang utan without any prior introduction and this too might lead to a play-session. Yet, such grasped partners usually tried to withdraw soon. Following a fast 'approach' which initiates a rape-sequence, the male often got hold of ('grasped') an arm or leg of the fleeing female and then started to 'position' her.

FIG. 99. 'Grasp' (Bin and Sibujong).

Positioning

This term indicates the behaviour by which a male orang utan may pull, push and man-handle a female with some force into a mating position. If the female resists such positioning, this behaviour may come to look like 'wrestling'. It is distinctly characterized, however, by the intentional manoeuvring of the female into a particular position. For mating the female must adopt a position in which she hangs so, that her body is more or less horizontal. When a female was very uncooperative and (or) often interrupted the copulation, the male usually positioned her again with increasingly aggressive actions, bitting her hands and feet (see also 'struggle'). This behaviour may resemble 'man-handling' (TUTIN & MCGREW, 1973) in captive chimpanzees.

Mounting

The male grasps the female with his feet, clasping her round the upper thigh region so that she cannot move her abdomen. This enables him to insert his erect penis into her vagina. During a 'mount' and occasionally during the following copulation females might show a 'tense-mouth facial expression' or a 'pout face' sometimes accompanied by 'whimper vocalisations'.

As in other primate species, mounting was not restricted to male-female interactions. Mounting between two males was noticed on three occasions, which I describe on p. 256. 'Mounting' may also have a communicative function, expressing certain aspects of a (hierarchial) relationship, as it has in gregarious primates.

Copulation

This behaviour sequence, performed by males, starts with intromission, proceeds into thrusting and usually ends with an ejaculation. In most instances, copulations took place while the animals were hanging in trees (fig. 100). The female supported her body weight by at least one hand and one foot. The male usually held on to an overhead branch with one or both hands meanwhile holding the female in a firm grip (see 'mounting').

During copulations a series of slow thrusts, with a frequency of 32–46 per minute (n = 4 recorded copulations) were given by a male. Most observed copulations had a duration of less than 2 minutes, but some lasted much longer, i.e. one recorded copulation between the sub-adult male Bor and the rehabilitant female Bin lasted 14 minutes.

During most of the observed copulations the males were silent. On two occasions sub-adult males had inflated throat pouches; one of these males emitted a series of 'lork call' vocalisations. Females might either be silent during copulation, or they might utter rhythmical, high pitched 'squeals'. Some females chewed on plant shoots, small sticks or other pieces of vegetation during the copulation.

Copulations of orang utans in captivity have been described by several authors. They mention a great variety of positions. Undoubtedly these are to a large extent a result of the restrictions imposed by the cage situation. Except

FIG. 100. Copulation (Sibujong and Jet).

for two cases, all observed copulations in this study took place in hanging positions in trees. Two copulations, performed by a sub-adult rehabilitant male with a wild adolescent female took place in a nest. The female was lying on her back while the male was in a sitting-squatting position. This position strongly resembles one described for adult gorilla copulations (SCHALLER, 1963).

Struggle

This pattern has been defined as an animal's attempts (successful or not) to free himself from the grip or restraint exerted by a partner. Though superficially similar, it differs from the following element 'wrestling' because in the latter the actor actively seeks and engages in body contact. We saw struggling behaviour regularly during copulations when a female began to wriggle and struggle in an attempt to break contact with the male. Struggling was often accompanied by vocalisations of distress or submission and occasionally a female even made biting intention movements towards the males supporting arm.

'Struggle' is one of the elements which defines 'rape' behaviour (see p. 265): only when young, inexperienced sub-adult males were involved in rapes did the female's 'struggling' actually succeed in breaking the body contact.

Gnaw wrestling

This pattern is nearly always shown simultaneously and reciprocally by two (seldom more) individuals. The orang utans engage in an intense form of body contact performed in any possible position (lying, sitting, standing, or hanging). It includes rolling over one another, pushing, hitting, tugging and mock-biting one another's limbs, especially hands and feet. Each partner tries to get a good grip on the other, while at the same time wriggling and wrestling their own limbs free. Gnawing of mock-biting consists of pushing the bared teeth onto a hand, a foot, a thigh or a shoulder of the partner. The face, the throat and the breast are seldomly touched in this manner. During gnaw wrestling both animals pull and tug each other rather forcefully by the hairs of the neck, the head, the shoulders, the arms, the back and the legs (fig. 101). Gnaw wrestling is regularly interrupted by pauses, during which the partners may just sit idle opposite each other, move into another position or rearrange the nest on which the action takes place. A play nest may either be specially constructed, or be an old existing nest. Apart from nests, large horizontal branches are often chosen as play-grounds.

Only rehabilitant orang utans were observed to play on the ground in this study. WALLACE (1869) has reported that he observed two 'half grown orang utans playing on the ground' during his travels through Borneo (p. 46).

When gnaw wrestling up in a tree or on a nest, the individuals held on with one limb, usually a foot, grasping a nearby branch. Even when playing on the ground rehabilitant orang utans showed a similar tendency to secure themselves. Sometimes a rehabilitant collected a liana from some distance away and holding onto with a foot, he dragged the creeper along to his playmate and started to 'gnaw-wrestle'.

The rehabilitant orang utans tended to concentrate their gnaw wrestling at

FIG. 101. 'Gnaw-wrestling' on the ground (David and Yoko).

certain places on the ground. Such places soon became cleared of all vegetation. Usually such 'play-arenas' were close to bundles of lianas which hung to the ground or close to one or more springy saplings which were used for anchorage during the gnaw wrestling bouts.

In the intervals during a gnaw wrestling sequence some individuals manipulated vegetation or another object. On some occasions rehabilitant orang utans even made attempts to drape and wear vegetation around their neck or on their head during a subsequent gnaw wrestling bout (see also 'decorate'). They might also hit their partner with these pieces of vegetation, usually in an attempt to initiate gnaw wrestling again.

Whenever one of the participants attempted to terminate the gnaw wrestling bout he would stop cooperating and would struggle to free himself from his partner's grip. At the same time he would often gently push his extended lips against the muzzle of the partner without biting (see 'muzzle pushing') and would make 'squeak' vocalisations.

During 'gnaw wrestling' both participants regularly showed a 'relaxed open-mouth' facial expression similar to that described for the other great apes (SCHALLER, 1963; VAN LAWICK-GOODALL, 1967; VAN HOOFF, 1967). The gnaw-wrestle pattern of orang utans corresponds in detail with the social play behaviour of the other great apes (see also FREEMAN and ALCOCK, 1973). Gnaw-wrestling was mostly seen in immature animals (juveniles and adolescents). Only once did I see an adult male (O.J.) play with an adolescent animal in the Ketambe area. In zoos adult orang utans may indulge in play behaviour until old age (JANTSCHKE, 1972). When playing with infants older individuals such as mothers and adolescents handled, tickled and poked them very gently.

On two occasions we observed that juveniles in a wild temporary association (see p. 168) initiated gnaw wrestling with another juvenile partner by performing 'gymnastics'. In one such case this behaviour first instigated a gymnastic response in the partner, then, when both had come close together this merged into gnaw wrestling. In the other case the partner reacted with approaching, ensuing in play contact. Similar invitations were seen among rehabilitant orang utans as was also the 'parallel' gymnastics form of coming into contact; e.g. the first contact between the wild adolescent female Jet and the rehabilitant female Bin proceeded in a similar way.

Wrestling

Superficially this behaviour closely resembles 'gnaw wrestling', but it is distinguished on the basis of a passive or clearly uncooperative attitude by the recipient. Other distinctive characters are that the gnawing which constitutes a strongly restrained (mock-) biting in the gnaw wrestling act, is replaced by more forcefull biting which is discernible from the reactions of the partner. The tugging and pulling fractions may also have a much more rough appearance. Hitting was not observed in connection with this behaviour.

Wrestling usually took place in a free hanging position in a tree and rarely on a nest or on a play-arena. When the partner tried to break the contact, it would stop all action and 'duck' or actually flee, urinating and sometimes even defeacating. The vocalisations of the uncooperative individual were frequent 'squeak' vocalisations which could change into 'whimpers' or 'screams'.

The context of this behaviour suggests that it serves in asserting the dominance of the actor. One conspicuous aspect of this behaviour was that the actor would persistently try to force his partner into a lower position in a tree by means of this wrestling pattern (see also p. 259).

The distinction between the more playfull 'gnaw wrestling' and 'wrestling' was sometimes difficult to make. 'Gnaw wrestling' could sometimes merge into more vehement 'wrestling', and vice versa. The same has been noted for other species, e.g. baboons (OWENS, 1973).

Hand-wrestling

This element can be considered as a very leisurely form of 'gnaw wrestling'. When two apes were resting or lying in the same nest or, in case of rehabilitant orang utans, were lying close together on the ground, one individual might extend a hand or foot and touch, tickle or pat the other softly on his hand or foot. The partner might then react by grasping the hand or foot which initiated the act and then both animals would try – without much force – to release the other's grip. Sometimes this pattern proceeded into the more boisterous 'gnaw-wrestling'. If the partner did not want to participate in the hand wrestling, he might gently push his muzzle against the hand or foot which held his own (see also 'gnaw wrestling' p. 214). The hand-wrestling pattern closely corresponds with the 'finger wrestling' (VAN LAWICK-GOODALL, 1968) and/or 'hand-wrestling' (VAN HOOFF, 1971) of chimpanzees.

The patterns 'hand-wrestling', 'gnaw wrestling' and 'wrestling' form a morphological continuum. At one extreme they represent a relaxed and tenseless, playful mood, at the other a boisterous playfulness with occasionally even a tinge of malevolent irritation.

Dragging, pulling

This behaviour pattern was only observed in rehabilitant orang utans. It consists of rather fierce grasping or pulling of a partner, and dragging him along for some distance. The context in which this behaviour was observed suggests a playful motivation. Often a partner tried to release himself by struggling and giving 'squeak' vocalisations, but sometimes the partner reciprocated with gnaw-wrestling. Partners were sometimes dragged along the ground over a considerable distance, usually towards a play-arena. Before performing this element, an actor approached his partner in a way resembling the 'stiff approach'.

Immediately after the morning provisioning the highest ranking rehabilitant male (David) used to drag several of the other rehabilitant orang utans – usually other males – one after the other towards a play-arena and 'gnaw wrestled' briefly with them.

This pattern resembles to a certain extent the 'pulling and shaking limbs', described for captive chimpanzees (VAN HOOFF, 1971). Although this element was observed in a playful setting of rehabilitant orang utans, it sometimes contained elements of vehemence that made it resemble the 'dragging' of group-members reported for the intimidation displays of chimpanzees (VAN LAWICK-GOODALL, 1968).

Ducking

In this behaviour pattern, the animal sits with rounded back, tucking his hands and feet against and partly under the body, while the head is sunk between the shoulders during an interaction. In doing so, the animal tries to shield its hands and feet from the actions of a partner. On two occasions females performed this element when they were approached by a sub-adult male who apparently intended to rape them. Young orang utans often showed this behaviour when another approached them with a 'stiff approach'.

It was quite remarkable that young rehabilitants typically did not flee or climb a tree when suddenly frightened, but 'ducked' instead. By contrast, adolescents immediately climbed trees on such occasions.

'Ducking' behaviour was also effectively used to initiate a pause in a gnaw-wrestling bout or to terminate it.

Hitting

This element consists of a single, more or less forceful, stroke with the extended hand, brought downwards from above and landing on the head or on the shoulder of a partner. Hitting behaviour was most frequently observed in the context of 'gnaw wrestling', especially when this occurred on a flat surface (i.e. in a nest or on the ground). This type of hitting was usually restrained, was often not accurately aimed and usually showed an exaggerated wide arc of the downwards swaying arm.

Forceful hitting was only observed during the artificial provisioning situation in conflicts over food. On seven occasions I observed that females (Bin, Yoko and Jet) hit a higher ranking male who tried to displace them from a good feeding position. On one occasion I was hit by the wild sub-adult male Bor when I was handing out bananas to rehabilitants. The individuals that forcefully hit at others typically did so from higher positions downwards.

'Hitting' has been described as part of the chimpanzee's behavioural repertoire (e.g. VAN LAWICK-GOODALL, 1968). As may be the case in orang utans, chimpanzee females are more likely to show this behaviour than males (BYGOTT, 1974).

Muzzle-pushing

On several occasions rehabilitant orang utans were observed to make movements which could be interpreted as a bite-intention signal. These varied from the more frequent gentle pushing away of the hand, the foot or the head of the partner with the muzzle, showing slightly protruding lips and a slightly opened mouth (fig. 102), to a more rarely, fierce brusque opening of the mouth ex-

FIG. 102. 'Muzzle-pushing' of the juvenile female Marga at the female Yoko (a) starting with pouted lips; (b) changing into an intention bite on the partner's muzzle; note the grasp.

posing the teeth while the head is jerked in the direction of the partner.

This element has not clearly been recorded for other primate species, though it may well occur. In orang utans, at any rate, it is rather conspicuous behaviour affecting the contact phase of certain interaction patterns.

Biting

When biting, the actor closes his jaws abruptly and with force onto some part of the victim's body, usually a hand or a foot. The reaction of the victim was vehement screaming and attempts to withdraw. Biting could sometimes be savage for it was noticed that several bites resulted in bruises or perforating wounds. Such wounds were nearly always rather deep when situated on an extremity. Although biting was observed only rarely, bruises and wounds were rather common phenomena among adolescent and sub-adult rehabilitants.

2.5. FACIAL EXPRESSIONS AND VOCALISATIONS

More intense vocalisations are necessarily associated with more or less conspicuous changes in the facial muscular patterns (ANDREW, 1963; VAN HOOFF, 1967). Apart from these associated facial-vocal displays, some facial expressions can be distinguished which are not linked with particular vocalisations.

2.5.1. *Facial expressions without vocalisations*

Horizontal bared-teeth face

This expression consists of a strong retraction of the mouth corners and lips, thus exposing the teeth and gums, while the jaws are only slightly parted or remain closed. This element was only once observed in a wild juvenile orang utan, but we saw it more often in rehabilitants.

FIG. 103. 'Horizontal bared-teeth face' (Peter).

It occurred when an individual was suddenly startled, for instance by the unexpected appearance of a conspecific. Also sudden threatening gestures made by an observer towards juvenile rehabilitants could evoke this expression (see fig. 103). This element was often shown in connection with 'flinch'. One particular juvenile rehabilitant, that had newly arrived in the station showed this expression in a very intense and prolonged manner when people approached him. Rehabilitants who were startled by people often stretched their arm in a 'hold out hand' gesture immediately afterwards. The context of this element suggests that it is a gesture of submission.

This facial expression corresponds, both in morphology and context, with the 'horizontal bared-teeth face' (VAN HOOFF, 1971) or 'silent grin' (VAN LAWICK-GOODALL, 1968) in chimpanzees, as well as with similar expressions in other primates, notably baboons.

Open-mouth bared-teeth face

Again the lips and mouth corners are drawn back, exposing the teeth (and sometimes part of the gums of the upperjaw), but in this element the mouth is widely opened.

On one occasion a wild orang utan mother in the Ketambe area was observed to react with this facial expression to the 'play approach' of her juvenile son. Other cases involved only younger animals.

FIG. 104. 'Open-mouth bared-teeth face'; Simanis responding to Bobo.

This expression was frequently observed in rehabilitant orang utans. Typically lower ranking individuals reacted to the final phase of a 'play-approach' of a higher ranking orang utan, with this 'open-mouth bared-teeth' facial expression just prior to making contact, apparently as an acceptance of the play-invitation (fig. 104). The individual displaying this facial expression was usually either on a higher standpoint, or had climbed towards a higher elevation than its partner at the first signs of the partner's 'play approach'. The approaching partner then stopped in front of the actor who, still displaying this facial expression, would initiate the 'gnaw wrestling' by grasping the partner around the neck with an overhand ('arm wave') gesture.

Its context suggests that this expression bears an appeasement message by neutralising elements that could look assertive (such as the higher spatial position) or aggressive (such as the 'arm wave' and 'grasp'). In this respect the 'open-mouth bared-teeth face' may be seen as an intermediate between the morphologically closely related 'horizontal bared-teeth face', expressing submission, and the 'relaxed open-mouth-face' expressing a friendly, playful mood.

This expression resembles the 'open-mouth bared-teeth face' of the chimpanzee (see VAN HOOFF, 1971) in morphology and context. There may also be similarities in the meaning of the signals in both these apes. In both species the 'open-mouth bared-teeth face' is a predominantly 'friendly' expression. In this sense it is comparable to human smiling (VAN HOOFF, 1971) (fig. 105).

Though morphologically similar (i.e. the widely opened mouth) to the 'relaxed open-mouth face' this element differs from the latter in context. This

FIG. 105. 'Open-mouth bared-teeth face'; Bobo attempting to continue play with David.

expression functions as a signal preceding contact between two partners whereas the 'relaxed open-mouth face' is exclusively shown during the act of 'gnaw wrestling' and appears to be a functional part thereof in the sense that the typical open mouth posture is the intention movement of the gnawing.

MACKINNON (1974) has described a 'bared-teeth threat' performed by orang utans and refers to the 'open-mouth bared-teeth face' of the chimpanzee (VAN HOOFF, 1971) in this context. His description of the element and its occurrence suggests that it corresponds with the element 'yawning' as performed in tense situations, rather than with the 'open-mouth bared-teeth face'. Moreover, the context of the latter expression, as observed during this study, did not suggest an agonistic ('threat') motivation.

Silent-pout face

In this expression the lips are pushed forwards while they are pressed together at the mouth corners but slightly opened in the middle, to form a small round aperture (fig. 106). The expression may be maintained for some time and may be accompanied by the 'hold out hand' gesture. Actors showing this expression, usually sat down. At any rate they were always stationary. Their

FIG. 106. 'Silent pout face' (Sibujong) directed at an adult male (O.J.).

faces were oriented towards the recipient and with their head slightly bent, they might peer from under their eyebrows.

We observed this facial expression e.g. in a wild adult female (Bel) who entered a strangling fig tree with a 'hesitant advance' locomotor pattern. One adult male and two adult female orang utans were already present in the tree. On entering the tree the female looked in the direction of one of the two other females sitting close to the adult male. She displayed the 'silent pout face' when this female returned her gaze. No further interactions followed and the new arrival started feeding though she still appeared alert. She remained close to the point where she had entered the tree and soon left again.

A rehabilitant sub-adult male (Sibujong) often directed this facial expression at me. The context of this element suggests that it expresses a submissive request for tolerance or appeasement (fig. 106). From observations on rehabilitants it became clear that the 'silent pout face' may be regarded as a low intensity 'pout moan' facial-vocal display. This expression closely resembles the 'silent pout face' observed in chimpanzees (VAN HOOFF, 1971).

Tense-mouth face

In this facial expression the lips are closed tightly so that the mouth looks like a thin slit; the expression is maintained for some time (fig. 107). The 'tense mouth face' is usually displayed during tense social situations or other occasions of uncertainty (e.g. encounters of unhabituated individuals with humans). This expression was often shown in association with elements such as 'vertical head nod', 'branch-waving', 'ostentatious approach' and 'fixed gaze'; it often alternated with the elements 'bark-biting' and 'chomping'.

Much the same facial expression has been described for many different primate species (VAN HOOFF, 1967) and occurs in the chimpanzee (cf. 'compressed lips': VAN LAWICK-GOODALL, 1968) as well as in the gorilla in situations of 'uneasiness' (SCHALLER, 1963).

Bulging lips

In this facial expression too, the lips are pressed together but are pulled slightly inwards between the teeth. It looks as though the individual blows up his lips while pressing them together (fig. 108). It shows a strong likeness with the 'bulging lips' facial expression of the chimpanzee (see VAN LAWICK-GOODALL, 1967; VAN HOOFF, 1971). As far as context is concerned, however, the expressions in both species do not correspond. In the chimpanzee, the 'bulging lips' expression may be regarded as an exaggerated form of the 'tense mouth face', and is shown in situations where the animal is agressively motivated (VAN HOOFF, 1971). In the orang utan, however, the 'bulging lips' expression was exclusively displayed by females during copulation. Sometimes they held small sticks or a leaf between their compressed lips. The significance of this expression is not clear. Yet captive chimpanzee females may show a very similar facial expression during copulation (remarkably named 'grin' by TUTIN & MCGREW, 1973).

FIG. 107. 'Tense mouth face' (O.J.).

FIG. 108. 'Bulging lips' during copulation (Jet and David).

Frowning

In this facial expression the lateral corners of the eyebrows are raised while the median parts appear contracted in a downwards direction. The skin on the forehead thus gets a wrinkled appearance, the eyes are wide open. This element may have been overlooked on several occasions since this subtle expression is only discernible from close quarters. It invariably occurred in connection with the 'brusque charge', and was displayed by the attacker. The best observed attack was aimed at myself. The attacker, a nearly adult female rehabilitant (Simi), showed piloerection of the shoulder and upper arm region and she attacked with a stiff-stepped locomotor pattern. Also on occasions when 'hunched lunges' of the female Bin directed at the female Yoko could be observed closely, 'frowing' accompanied very fast and smooth locomotor patterns. This facial expression seems to express a highly aggressive tendency on the part of the actor.

Fixed gaze (stare)

This behaviour pattern consists of looking intently at a partner, sometimes for several seconds (fig. 109). Typically the actor's body posture expresses a certain tenseness. Remarkably, this direct and intent visual inspection of a partner might, in some individuals, alternate with long spells of apparently deliberate looking-away from the partner. Such looking away was usually in a direction at right angles to the 'fixed gaze' aimed at the partner. In several

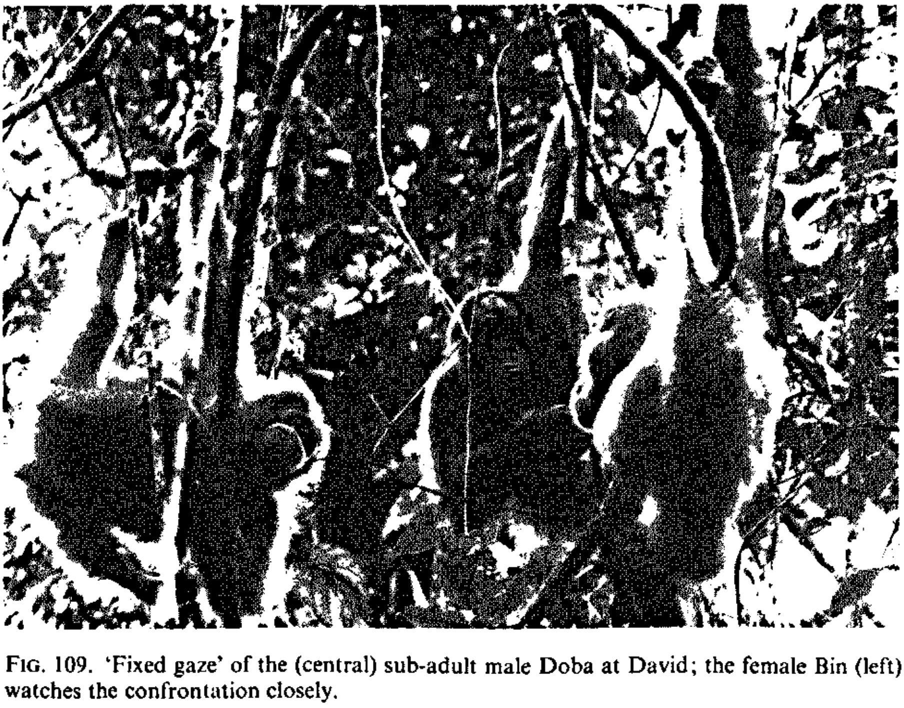

FIG. 109. 'Fixed gaze' of the (central) sub-adult male Doba at David; the female Bin (left) watches the confrontation closely.

instances we observed that the reaction of the partner to a 'fixed gaze' was to move away or to 'avoid' the actor. Sometimes this expression was followed by an 'ostentatious approach' or even by a 'brusque charge' in the direction of the recipient.

The context of this element clearly suggests that it functions as a 'threatening' gesture. As such it corresponds with the staring threat pattern of many primate species (ANDREW, 1963). The combination of this intense gaze with periods of looking away may indicate an ambivalence of attack- and flight tendencies in some individuals. It is noteworthy that the alternating gazing and look away pattern was not only exhibited by lower ranking individuals towards higher ranking ones. In encounters between an adult male and a sub-adult male the adult male invariably showed such alternating behaviour.

Interestingly, a similar alternating behaviour has been reported for the mountain gorilla. In the course of the 'strutting walk display', the actor may stand still in the typical posturing position with stiff limbs and briefly glance in the direction of the opponent. These glances alternate with periods of looking straight ahead (SCHALLER, 1963), i.e. at right angles from the opponent.

2.5.2. *Vocalisations and associated facial expressions*

Squeak

This vocalisation consists of a rather soft sounding, short, one syllable, squeaky tone, presumably made during the expiratory phase. It was the most frequently heard vocalisation in the orang utans. At a distance it is very hard to perceive and it will therefore often have been missed by an observer. The 'squeak' was heard from younger orang utans of both sexes and from adult females. It was seldom heard from sub-adult males and not at all from adult males. We noticed considerable individual differences in the voices of orang utans; these were particularly manifest in this vocalisation, even to the extent that we could recognize some individuals by merely hearing their 'squeak' vocalisation.

The vocalisation was heard in the following contexts. A mother might 'squeak' before she 'gathered' her infant, when the infant showed distress by 'screaming', or immediately after she had broken a branch during feeding or nest-building activity. In the presence of a higher ranking individual, in particular of an adult male, lower ranking orang utans used to 'squeak' upon every move of that individual; moreover they 'squeaked' before every move of their own. When one of two 'gnaw-wrestling' partners attempted to break off the play, he would invariably give soft 'squeaks', while the losing partner in a 'wrestling' bout would give up with loud 'squeaks'. The context of this vocalisation suggests that it functions to express a non-agonistic attitude, sometimes submission in cases where non-dependant individuals were concerned: or possibly reassurance – in particular when a mother directed such behaviour towards her offspring.

'Squeak' vocalisations were not accompanied by a particular facial expression. This vocalisation has been described by several authors who kept, or otherwise came into close contact with young captive orang utans (VOSMAER, 1778; BRANDES, 1939; HARRISON, 1961; ANDREW, 1963; JANTSCHKE, 1972) but rarely by field observers. Possibly this vocalisation corresponds with MACKINNON's 'fear-squeak' (1974).

There seems to be no equivalent of this vocalisation in the chimpanzee's repertoire; nearest to it might be 'pant grunts' (GOODALL, 1965) and/or 'panting' (VAN LAWICK-GOODALL, 1968).

Contact uff

This very soft sound, the production of which is not marked by any particular facial expression, takes the form of short repetitive expulsions of air through the nose. It seems to be a restrained 'squeak' vocalisation. The contact 'uff' can only be heard at very close range; in fact we only noticed it in rehabilitant orang utans, when an individual performed 'touch and smell' behaviour in which it brought its nose close to the face of its partner. Some rehabilitants, in particular the two highest ranking sub-adult males, often 'greeted' me in this manner.

Gnaw wrestle Ahh-relaxed open-mouth face

This vocalisation is exclusively heard in connection with the relaxed open-mouth facial expression. The latter is characterised by the rather widely opened mouth whose corners may be withdrawn. The teeth may remain visible but are often covered by the lips, which may even be pulled inwards over the teeth (fig. 121). In any case the gums remain covered by the lips. This expression is nearly always accompanied by short rhytmic 'Ahh' vocalisations. (It

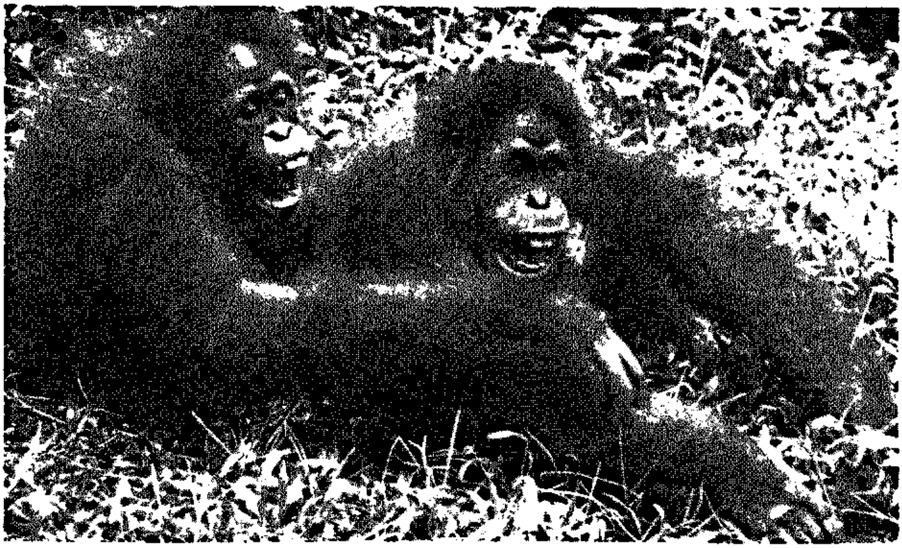

FIG. 110. 'Relaxed open-mouth face' (Yoko and David).

seems possible that this 'Ahh' vocalisation is also a restrained form of the 'squeak' vocalisation.) This facial-vocal complex was typically shown during 'gnaw-wrestling' (fig. 110). Occasionally the 'relaxed open-mouth face' was also observed during 'gymnastics' (see fig. 80); then the 'Ahh' vocalisations were lacking.

This facial-vocal display of the orang utan has been described by numerous authors (BRANDES, 1939; HARRISSON, 1969; MACKINNON, 1971; JANTSCHKE, 1972) for zoo kept or rehabilitant orang utans, usually under the names 'play face', 'play-grunts' or 'Lachen' ('laughing'). An almost identical form is well known in many species of primates; it has been described as 'relaxed open-mouth face' (VAN HOOFF, 1967) or 'play-face' (VAN LAWICK-GOODALL, 1967) in the chimpanzee, and as 'smile and chuckle' in the gorilla (SCHALLER, 1963). A certain contextual and morphological resemblance to human laughter is evident, as had already been noted by DARWIN (1872, in VAN HOOFF, 1971).

Grunt

This vocalisation consists of several repeated low intensity sounds with a dull timbre. Because of its low intensity this vocalisation may often have escaped attention. It was noticed only in rehabilitant orang utans who travelled along the ground for short distances, usually when they were in the company of other rehabilitants.

For several catarrhine primate species, low pitched grunting, coughing or moaning sounds have been noticed in a variety of contexts (ANDREW, 1963). Such grunting noises occur conspicuously during the feeding situation in chimpanzees (VAN LAWICK-GOODALL, 1968) and gorillas (SCHALLER, 1963). The significance of this vocalisation in orang utans is not clear.

Grumbling

This is a soft complex sound with a dull timbre which can only be heard at close quarters. It is as if the animal makes a series of ventriloquized 'grumpf' or 'lork' call vocalisations with its mouth closed. It strongly resembles the first and last strophes of the adult male's 'long call', yet it was heard separately from that call and made by both sexes. We noticed this vocalisation in association with 'bark-biting' and intermittently with the 'chomping' sound; it occurred in an intra-specific agonistic context.

This vocalisation has not been previously reported for orang utans, nor is there any equivalent in the ethography on the chimpanzee; yet, with respect to its form and context, it may bear some resemblance to the 'staccato grunts' (SCHALLER, 1963) or 'pig grunts' (FOSSEY, 1972) of the mountain gorilla.

Pout moan

This vocalisation consists of a soft, melodious whining sound with a duration of approximately one second; it tends to be frequently repeated. The accompanying facial display may vary from a rather neutral expression with only slightly protruded lips to a face in which the median part of the eye-brows

FIG. 111. 'Pout moan' (Puk)

are raised and the lips are pouted in a truly funnel shape (fig. 111). The raising of the eyebrows accentuates a pale coloured zone above the eyes in young orang utans. The pout-moan facial-vocal display was heard most frequently from young orang utans in distress, particularly in feeding situations when they begged from their mother, or, in case of rehabilitant orang utans, from an attendant or peer, and did not obtain a portion of the desired food. In such cases the 'pout moan' element might change into a 'temper tantrum'. On some occasions we observed the 'pout moan' element in females who were subjected to 'positioning' by sub-adult males during a rape. Then the accompanying vocalisation might change into a 'bared-teeth scream' eventually.

The 'pout moan' vocalisation has been described by HARRISSON (1963) as 'whining noise', by MACKINNON (1971) as 'soft hoots', and 'whimpers' and by JANTSCHKE (1972) as 'schreien und wimmern'. This facial-vocal display strongly resembles the 'pout moan' (VAN HOOFF, 1967) and 'whimper' (VAN LAWICK-GOODALL, 1968b) of the chimpanzee, both in morphology and in context.

Bark

This is a short, loud cough-like vocalisation, made with the mouth open. This element was noticed only four times during this study, and was performed by suddenly startled rehabilitant orang utans. A similar 'bark' vocalisation has been described by MACKINNON (1971) and by JANTSCHKE (1972). Yet its social significance is not clear.

Possibly the bark vocalisation resembles the 'soft bark' or the 'hoo call' (GOODALL, 1965) of the chimpanzee.

Mating squeals

This vocalisation consists of bouts of several rhythmically uttered loud squeals. The squeals can be regarded as long drawn-out 'squeak' vocalisations. They are distinct from the 'bared-teeth scream' because of their lower intensity and the different accompanying facial expression (fig. 112). This vocal display was exclusively heard in the context of copulation. Some females habitually squealed whereas others were never heard to do so.

This element has been described by MACKINNON (1974) as 'mating cries'. A similar 'squeal' vocalisation in a copulatory context has been described for chimpanzee females (GOODALL, 1965). while gorilla females may utter rhythmical staccato 'ö-ö-ö-ö...' vocalisations (SCHALLER, 1963).

Scream

This term designates moderately high-pitched screaming vocalisations, either consisting of a single short lasting note or of a series of longer drawn-out

FIG. 112. 'Mating squeals'; note the female's half opened mouth (copulation of Doba and Bin).

FIG. 113. 'Scream' (Pim).

screams. The tonal quality of 'screams' may be described as 'rasping'. The accompanying facial expression consists of a widely opened mouth; the teeth are hardly or not exposed and the lips may be slightly protruded as if in a widened pout-expression (fig. 113). The eyebrows are usually raised, exposing the pale patches around the eyes. This vocalisation was heard from young individuals (infants, juveniles and adolescents) exclusively. In case when 'screaming' consisted of series of long drawn vocalisations these were alternated with choking intakes of air, while the screaming expiration sometimes led to glottal cramps. 'Scream' series typically occurred in connection with a 'temper tantrum'.

The context of the 'scream' suggests that it serves to attract the attention of the mother, as in the case of infants who had ventured some distance from their mother and apparently wanted to re-establish body contact with her. In the case of the 'temper tantrum', 'screaming' in rehabilitant orang utans served to persuade an affiliated partner or an attendant to grant a particular favour. One particular form of this vocalisation, which I was unable to differentiate reliably, seems to represent a transition into the next element. As for its meaning it appeared to express fear or anger. For example, we noticed it being made by a juvenile male rehabilitant orang utan, who was cornered by a male pig tailed macaque in a conflict over provisioned bananas.

This may be the same vocalisation that has been described by HARRISSON (1963) as the 'piercing scream', and by DAVENPORT (1967) as 'squeal'. Morphologically and contextually similar facial-vocal displays have been described for chimpanzees (e.g. YERKES, 1943) and for gorillas (FOSSEY, 1972).

Bared-teeth scream

This vocalisation consists of one or several very loud, high-pitched, drawn-out hoarse screams, each of which may end with a choking sound. The distinctive characteristic of this behavioural catagory is a wide-open mouth with the teeth and gums exposed. This facial-vocal display was given by animals who were attacked and bitten; in such cases the vocalisations last at least as long as the contact. In a less intensive form, the bared-teeth scream was observed during several 'rapes'. On such occasions the female might show this element in connection with 'ducking', 'struggle' and 'flight'.

This behaviour pattern clearly corresponds with the 'bared-teeth scream' (VAN HOOFF, 1971) and 'screaming' (VAN LAWICK-GOODALL, 1968) of the chimpanzee and of the gorilla (SCHALLER, 1963; FOSSEY, 1972), both in morphology and in context.

Grumpf

This is a loud, double-toned, low-pitched belch-like sound, which often occurs in close temporal association with, or follows the 'kiss sound'. I never heard this vocalisation from adult male orang utans. Normally when an individual gave kiss-sounds and grumpf-vocalisations together, I had the impression that he was in a more aroused state than when giving the 'kiss' sounds alone. Moreover, such individuals showed a stronger tendency to flee, also reflected in the head-movements during a 'grumpf', i.e., turning the head away from the disturbance. 'Grumpf' vocalisations alone were noticed in a context which suggested strong annoyance with an attentive partner.

Both the kiss-sound and the grumpf vocalisation have been reported separately or in association under a variety of names by several authors since the first collecting expeditions in the past century. This vocalisation bears some resemblance to the 'pant bark' (GOODALL, 1965) of the chimpanzee.

Lork call

This is a prolonged (in the order of 1 minute) loud vocalisation, composed of 'grumpfs' that follow one another practically without interval. The sound of this vocalisation carries as far as 300 meters in the forest, and as such it is one of the loudest orang utan calls. 'Lork-calls' were mostly heard from adult females and occasionally from sub-adult males (e.g. rehabilitant sub-adult males). The context in which adult (wild) females and sub-adult (rehabilitant) males gave 'lork-calls' differed slightly. Thus the highest ranking rehabilitant (David) was twice observed to give a 'lork call' after detecting a family of pigs. During these events, other rehabilitant orang utans appeared to be attracted towards the caller. They gathered around him, arriving from distances ranging from ten to fourty meters. On another occasion, I noticed that the rehabilitant sub-adult male Sibujong gave a 'lork call' immediately after having copulated with a female. From these scant observations it is difficult to suggest the function of this behaviour in the sub-adult males' behavioural repertoire; with regard to females few more data are available.

The rehabilitant female Bin was once observed to give 'lork call' vocalisations for about 10 minutes after she had become aware of another orang utan travelling through the canopy at a distance of some 200 meters from her. The structure of the forest in that particular region allowed a comparatively good view, though it was impossible to recognize the individual from that distance. My own impression was that the stranger was another female. The female Bin, who was in the company of her consort mate Doba seemed very much aroused and her 'lork calls' were interspersed with 'grumbling' vocalisations and with the elements 'branch-waving' and 'bark-biting'. When the stranger came near it appeared to be the adolescent male Mos, and the female's excited behaviour stopped. She paid no further attention to the newcomer. (On earlier occasions both apes had been seen together during temporary associations and in social groups: see p. 168.) When assuming that the rehabilitant female had the same impression of the stranger as I had myself (adolescents and adult females have a very similar appearance) this observation suggests that the 'lork call' expressed an agonistic state that may serve to space out conspecifics (i.e., females). However, on the six occasions that we observed adult wild females giving a 'lork call' vocalisation, no apparent disturbance could be detected. Also the same rehabilitant female Bin was twice found to give 'lork calls' with no apparent disturbances in her near surroundings. Nevertheless such behaviour elements as 'branch-waving' and 'bark biting' that often accompanied the 'lork call' vocalisation indicated that the individual was in an agonistic mood. Once we observed the adolescent male Mos reunite his mother (Mif) after several days of separation. This reunion took place one day after she had given a 'lork call'. Although far from conclusive, this incident may suggest that the call was functional in reuniting mother and son. These contexts, together with the exceptional loudness of the call, suggest that it functions as a locating advertisement in much the same way as the adult male's 'long call'.

The 'lork call' has been described by MacKinnon (1974); he observed these calls only in the context of 'threat displays'. A similar loud calling almost exclusively emitted by adult females and younger (than adult) males has been described for the mountain gorilla as the 'panting ho-ho-ho...' vocalisation (Schaller, 1963).

Long call

This loud, low-pitched roaring call was only heard from adult male orang utans. It consists of a series of several loud moaning vocalisations interspersed with short inhalatory pauses, filled with a 'bubbling' sound. The call usually starts with a type of 'grumbling' and after some 1–2 minutes also fades out with such a noise. A 'long call' carries some 800–1000 meters in the forest. During the call the lips are protruded slightly and the throat-pouch is inflated. In a minority of cases 'long calls' were accompanied by 'branch-waving' and/or other parts of the 'ostentatious approach', but these were often not directed at any obvious source. The facial expression shows a striking similarity with that of a male chimpanzee during a 'pant hoot' display (pers. observ.).

'Long calls' were usually made after some disturbance, but were also often given spontaneously – or seemingly so. External stimuli that invariably caused an adult male to call were the crashing sound of a falling tree, or awareness of an approaching (lower ranking adult) male. In particular males gave 'long calls' after they had chased a lower ranking adult with an 'ostentatious approach'.

In one instance we were able to induce a long call from the male Gorm, some minutes after he had chased the male O.J. When Gorm had returned to the fruit tree, we approached the tree, coming from the direction in which O.J. had fled the scene, and we made the vegetation to sway by pulling lianas and saplings along the trail. When we came within some 80 meters of the fruit tree, Gorm immediately reacted by beginning an 'ostentatious approach' display over some 4 meters, ending with a 'long call'.

Once I followed an adult male who called repeatedly while following a (for me unfamiliar) lone adult female.

The idiosyncrasies in the calling patterns of different adult males probably enable orang utans in a deme to recognize the calling individual. The observations suggest that the 'long call' represents a long range 'bluff' signal which advertises the presence and location of that particular male (see also sex. behaviour p. 275). The reaction of a recipient will undoubtedly differ, depending on the context, i.e. the social status of recipient males and the sexual receptivity of mature females. Several observations fit this hypothesis. When the second ranking male Moses moved into the range of the resident (but lower ranking) male O.J., the resident remained silent in the area covered by Moses and he only called from a sector which was not visited by the other male (see Home range p. 161). On these occasions when the reaction of the male Moses to O.J.'s calls could be observed, he immediately moved towards the sound, but always stopped his advance at a certain point, long before reaching the calling male, and returned. In the four observed encounters between the two adult males Gorm and O.J., the higher ranking male Gorm invariably called last while the lower ranking male O.J. retreated silently. We did not notice that females ever reacted to the calls of adult males but both HORR (1971) and RODMAN (1974) have described a case when a female was attracted towards a calling male. The three adult males in the Ketambe area were mainly heard to call during the late morning hours coinciding with the peak in their daily feeding activity.

This vocalisation has been described by several authors under different names. The earliest account is from MÜLLER & SCHLEGEL (1839–1840), while the most detailed description has been given by BRANDES ('singen': 1938: 1939). The name 'long call' has been suggested by MACKINNON (1971). This element strongly resembles, both in morphology and in context, the 'pant hoot' display in the chimpanzee (NISSEN, 1931; REYNOLDS & REYNOLDS, 1965; etc.), and the 'hoot series' in the mountain gorilla (SCHALLER, 1963; FOSSEY, 1972).

Loud calls are present in the vocal repertoire of several other forest-living primates, calls which similarly are given more or less spontaneously, though usually at particular times of the day. In most of these species the signals only seem to function in maintaining spacing between groupings (e.g. *Galago demidovii*: CHARLES DOMINIQUE, 1974: *Alouatta* spp.: CARPENTER, 1934: *Colobus* spp.: HADDOW, 1952: *Presbytis* spp.: pers. observ.: *Hylobates* spp.: CARPENTER, 1940; CHIVERS, 1972). Yet, the adaptive effects of the orang utan's 'long call' vocalisation may be more diverse in that, besides maintaining spacing between adult males (see MACKINNON, 1974), it also advertises to the deme and in particular to mature females (within a radius of approximately 800 meters) where the highest ranking adult male is located.

2.5.3. *Expressive sounds and associated facial expressions*

Dependent on the context orang utans may produce several sounds associated with particular facial expressions or with other elements, which cannot be regarded as proper vocalisations since the vocal chords are not involved.

Chomping

This is a sound produced, it seems, by the tongue in the partly closed mouth while the actor makes chewing movements with the jaws. This chewing is rather slow and deliberately performed. This element was only recorded from animals who were quite obviously aggressively motivated. 'Chomping' usually occurred in close association with 'bark biting' and with 'fixed gaze'. On most occasions that a 'hunched lunge' was observed from close quarters this sound was heard to precede the attack. 'Chomping' was rarely heard during the displays directed at groundwalking disturbances.

This element has been described by SCHALLER (1961) and by MACKINNON (1972). No equivalent could be found in the ethography of the chimpanzee or the gorilla; but a very similar 'pumping cheeks with chewing movements' element is a common agonistic signal in hamadryas baboons (KUMMER, 1968).

Spluttering

This sound is produced by strong expulsions of air through compressed or closed and slightly pouted lips. The result is a loud spluttering sound. 'Spluttering' was performed by rehabilitant orang utans who saw, but could not get food, held by the attendants or another orang utan. On some occasions we also noticed it from individuals who were in the possession of food, and directed 'spluttering' towards a partner who was begging for a piece. The meaning of this sound is not clear.

'Spluttering' sounds have been described for caged, wild-caught, Sumatran orang utans by BRANDES (1939) and for rehabilitant Bornean orang utans by HARRISSON, ('blowing raspberries'; 1961). It occurs as an idiosyncratic trait in chimpanzees where 'spluttering' is shown in situations where one might expect lip-smacking (VAN HOOFF, 1971).

Grinding

This sound was only heard from rehabilitant orang utans. It consists of a loud grinding of the teeth, and often occurred alternately with the 'horizontal bared-teeth face'. While grinding its teeth, the actor's eyes were usually wide open and it repeatedly urinated and defaecated, behaviours which seemed indicative of strong fear. 'Grinding' occurred when after its quarantine, a newly arrived rehabilitant was introduced to other rehabilitants within the confinement of the quarantine cage. Usually the largest (and highest ranking) rehabilitant male entered the cage and subjected the newcomer to an encounter including 'wrestling' and sometimes 'rape'-attempts. If a newcomer refused to cooperate and was thwarted in its attempts to escape because of the confines of the cage, 'grinding' might occur. Rehabilitants, recently caught from the wild, also showed such behaviour, while retreating into the farthest corner of the quarantine cage when people came near.

In a similar cage situation, SCHULTZ (1969) has described 'teeth grinding' in orang utans.

Kiss sound

This behaviour consists of sucking in air through pouted lips; it sounds like a loud, sucking kiss. The orang utan might hold its slightly cupped hand in front of its mouth and also while 'kissing' often turned away its head in a smooth jerky fashion, to end up looking away at right angles from the factor that released this behaviour. 'Kiss sounds' were mostly released by, and directed at disturbance on the ground, in particular humans (see fig. 48). Once we saw the rehabilitant sub-adult male Sibujong make kiss sounds in response to the adult male O.J. The adult male reacted immediately with an 'ostentatious approach' and gave a persistent chase to the rehabilitant. On another occasion the wild adolescent female Jet made frequent 'kiss sounds' when she departed from a peer group. During the preceding period she had attempted several times to initiate play with some of the male members of the group but had not succeeded in attracting any attention. After she had travelled some 30 meters away, she stopped, waited and looked at the other animals. When nobody followed her, she moved off, making the 'kiss-sounds'. This sound was often made by unhabituated adult female – and sub-adult male orang utans whenever they noticed me observing them. Adult males seldom made this sound.

As mentioned above, the kiss sound often occurred in close association with the 'grumpf' vocalisation. The context of the kiss sound alone suggests that it expresses annoyance and is made by a mildly aroused individual. At higher levels of arousal the actor made 'kiss sounds' with 'grumpf' vocalisations or 'grumpf' vocalisations alone.

It is difficult to understand the function of this sound merely as a 'threat' towards disturbances on the ground as has been noted by DAVENPORT (1967). It has little deterrent quality, although the accompanying elements, which add to the conspicuousness of the complex, indicate the actor's agonistic attitude. Several times we noticed that the 'kiss sound' did not seem to affect the behaviour of other individuals witnessing the display. This was especially apparent when an unhabituated individual, in the company of habituated orang utans, reacted to my presence. Only once did I observe an adolescent male move into dense foliage and hide there when his mother made loud 'kiss sounds' towards me. This observation might suggest that the conspicuous display including 'kiss sounds' plays a role in diverting the attention so that offspring may escape notice, analogous to the diverting 'broken wing display' of several bird species. However, this explanation does not account for the fact that youngsters usually approached their mothers and either clung to her or engaged in the display with her.

An interesting aspect of this behaviour is that very young orang utans – infants and early juveniles –, seem to be unable to produce a 'kiss sound'. We often saw infants trying to imitate their mothers by pouting their lips and sometimes even performing the head gesture but the sound they produced was either a soft inhalatory hissing or an exploratory spluttering noise. Two juvenile rehabilitants showed the same inability but by imitating other rehabilitant orang utans they had learned to produce a proper 'kiss sound' after 6 months, when both were approximately $3^1/_2$ years old.

The chimpanzee's 'wraa call' (GOODALL, 1966), is given in similar contexts to the 'kiss sound' but is a single, long drawn-out, pure sounding exhalatory vocalisation, rather than a repeated inhalatory sound.

2.6. ALPHABETICAL LIST OF BEHAVIOUR ELEMENTS

advance 180
approach 177
arm wave 199
avoid 181
bared-teeth scream 232
bark 230
bark-biting 194
biting 219
branch waving 191
breaking and dropping of branches 192
bridging 206
brusque charge 182
bulging lips 223
chomping 235
circling 184
clinging: walking and climbing in tandem 208
contact uff 227
copulation 212
diving 183
dragging, pulling 216
ducking 217
embrace 207
fixed gaze (stare) 225
fleeing 182
flinch 181
follow 180
frowning 225
gathering 206
genital inspection 210
gnaw wrestling 214
gnaw wrestling Ahh, relaxed open-mouth face 227
grasp 211
grinding 235
grooming 209
grumbling 228
grumpf 232
grunt 228
gymnastics 184
hand-wrestling 216
hesitant advance 180
hesitant approach 179
hesitant avoid 181
hide 184
hitting 217
hit away 201
hold out hand 200
horizontal bared-teeth face 219
ignore 186
kiss sound 236
leave 180
long call 233
look at mouth 198
lork call 232
loutish approach 177
masturbate 188
mating squeals 230
mounting 212
mouth – mouth contact 204
muzzle-pushing 217
nest-building 191
open-mouth bared-teeth face 220
ostentatious approach 179
penile erection 197
positioning 212
posturing 194
pout-moan 228
presenting 202
rest 186
rocking 197
scratching 189
scream 230
self-decoration 187
self-grooming 186
self-inspect 188
silent pout face 222
spluttering 235
squeak 226
stiff approach 177
struggle 213
temper tantrum 196
tense-mouth face 223
throat-pouch inflation 197
throwing 200
touch and smell 202
urinate/defaecate 189
vertical head nod 199
watch 198
wrestling 215
yawning 191

3. COMPLEXES OF BEHAVIOUR

In the preceding chapter the main elements of the orang utan's social behaviour have been described. These elementary patterns are integrated according to certain programmes and rules. By analogy with species for which detailed analyses have been made concerning the organisational structure of their behaviour (e.g. VAN HOOFF, 1971), one can reasonably postulate that in the orang utan also there must exist a structured hierarchical organisation of behavioural systems and sub-systems which can be interpreted in functional terms. These different behavioural system are not equally used by all individuals of a deme. Certain age and sex categories of animals have a more or less typical behaviour profile. In other words, individuals of a particular age and sex class use specific subsets and distributions of behaviour-elements in interaction with certain fellows: relation-specific aspects of behaviour for which the word 'rôle' seems to provide an adequate coverage (cf. BERNSTEIN, 1966: GARTLAN, 1968).

In the following section, I shall attempt to describe the behaviour of the Ketambe orang utans in terms of the above mentioned organisational complexes. The comparative paucity of quantitative material does not allow me to base this description on an adequate mathematical or statistical treatment. It is therefore by necessity qualitative and, accordingly, many phrasings emphasize the still provisional character of the model presented.

3.1. AFFILIATIVE BEHAVIOUR

3.1.1. *Mother-offspring relationships*

a. Pregnancy and childbirth

Although most of the pregnancy of the rehabilitant female Bin fell after the term of the present study, a number of observations on her behaviour, gathered by A. K. C. FERNHOUT, N. J. C. VAN STRIEN, and W. J. J. O. DE WILDE are reported here because they are the only, rather concise data of feral, (or wild) Sumatran orang utans available at present.

According to the day records, the female Bin was sired in July 1974 by the wild sub-adult male Bor. She gave birth to a healthy female infant (named Ans) on 23 March 1975. An educated guess of the gestation period, based on the dates of observed copulations, and on the assumption that all menstrual cycles of Bin were consistent with the mean from three recorded cycles (see p. 261), gives a number of 248 to 254 days from the date of insemination. The gestation period reported for captive orang utans is approximately eight lunar months with some variation: 233–265 days (ASANO, 1967; VAN DOORN, 1964; LIPPERT, 1974). Figures for longer gestation periods are apparently counted from the last observed menstruation date (VAN DOORN, 1964; CHAFFEE, 1967), instead of from insemination.

The female Bin did not show marked enlargement of the labia majores vulvae as reported to be one of the prominent signs of pregnancy in orang utans (SCHULTZ, 1938; LIPPERT, 1974), She did, however, show enlarged nipples and an increasingly extended abdomen. During the gestation period the female avoided contact with sub-adult males, also with those males which had previously consorted her, and on two occasions she sought the proximity of the adult male O.J., who chased accompanying sub-adult males away. During her last four months of pregnancy she fostered a juvenile rehabilitant male (Bumi). Both orang utans showed strong coordination of movements, the female shared food with the juvenile, she waited for him and helped him across gaps in the vegetation (see 'bridging'). After the birth of her infant, she still tolerated the juvenile close to her, and after about one month her foster child was at times even allowed to suckle together with her own infant.

Parturition has not been observed in the wild orang utan, but several observations on delivering females are available from captive orang utans in zoos (AULMAN, 1932; GRAHAM-JONES and HILL, 1962; VAN BEMMEL, 1963; ASANO, 1967; ULLRICH, 1970; COFFEY, 1971; LIPPERT, 1974) and from a feral rehabilitant female in the Sepilok (Sabah) station (DE SILVA, 1971). From these accounts we know that females in labour are rather intolerant towards human attendants approaching their quarters (ULLRICH, 1970; LIPPERT, 1974). Interestingly, when males witnessed the birth, they became very 'excited and aggressive' towards humans in their view (LIPPERT, 1974). Usually the females withdrew into the comparative solitude offered by their sleeping boxes. A similar tendency was evident in the behaviour of the female Bin. Although in the previous months she had been present almost daily at the rehabilitation centre, she was absent for two days, before she returned with her newly born infant on March 23. It is quite likely therefore, that wild orang utan females, like chimpanzee females (VAN LAWICK-GOODALL, 1968), avoid contact with others in the period immediately preceding parturition.

b. Mother-infant relationship

Few data are available on mothers with very young infants. Only the mothers Bol and Mif were observed for short instances (a total of some 8 hours of observation) in the course of their respective infant's first months. In addition, I give some data, reported by VAN STRIEN (pers.comm., 1975), who has observed the female Bin and her newborn infant during the period March-December 1975.

Mothers were very cautious in their movements during the first weeks; they avoided contacts with other orang utans and the wild females (Bol and Mif) behaved in an unusually evasive manner towards my presence. The females continuously supported their young infants, moving either in a 'hunched gait' locomotor pattern (cf. VAN LAWICK-GOODALL, 1968), keeping one knee bent and thus supporting the ventro-laterally clinging infant with the thigh, or directly supported their infant with one hand. The usual carrying position of orang utans throughout infancy is ventro-lateral (MACKINNON, 1974) (fig. 114); this is apparently best suited to the orang utan's upright ('modified brachiation') locomotion. If not supported during locomotion young infants might gradually slip down along the mother's body. Cautious locomotion and shyness of mothers with small infants has also been reported by MACKINNON (1974) for wild-, and by DE SILVA (1971) for rehabilitant orang utans.

For a period of approximately 5 months after we first noticed the infant Mug (the mother had been seen without him some 4 weeks earlier), his mother Mif was not observed to engage in groupings of any sort. She seemed to avoid all temporary associations. Mif's behaviour during her infant's first year was interspersed with frequent rests for which she sometimes constructed a crude nest. All observed movements of the small infant were very 'wobbly' and had an insecure appearance. Mif frequently handled her infant during resting periods; she often put Mug onto her head or onto her neck region. (A similar behaviour can be observed in captive gorilla mothers; see also HESS. 1972.). On other occasions she inspected and gently groomed him, usually with her lips. The main focus of her attention seemed to be Mug's genital region, and she frequently held the infant upside down for close visual and olfactory inspections. This never caused distress vocalisations or resistance on the part of the infant. Suckling usually occurred during resting periods. The mother sat down

FIG. 114. Infant orang utans cling ventro-laterally onto their mother's belly during travel.

FIG. 115. The mother may initiate suckling by raising her arm, holding on to an over-head support.

and initiated suckling by raising her arm and holding on to an overhead branch, thus clearly exposing her nipple (fig. 115). Such resting periods never lasted long, usually between, 5 to 8 minutes. The length of a suckling bout was usually less than 2 minutes. The longest observed suckling bout lasted 144 seconds, the shortest only 48 seconds. Intervals between suckling bouts in the infant's first year were approximately 40 minutes, the longest observed interval lasted 72 minutes, the shortest 11 minutes. A mother could terminate suckling by moving off, or by gently pushing her infant's head away from the nipple with her muzzle (see 'muzzle pushing'). Most often however, mothers seemed to wait until their infant had stopped suckling before moving off.

The rehabilitant female Bin sometimes performed the 'mouth to mouth' behaviour with her infant Ans; presumably syphoning over chewed food into the infant's mouth (fig. 116). Such behaviour was first observed when the infant was approximately two months old (VAN STRIEN, pers.comm., 1975). A slightly different 'mouth to mouth' pattern was shown by this pair on occasions, immediately after the mother had 'gathered' her infant. She then pressed her muzzle with mouth slightly open, laterally against the infant's muzzle in a fleetingly kiss-like gesture.

As the infant grew older, its locomotor abilities improved. It started to show interest in, and grabbed at food that its mother was eating (fig. 117). In this way it might obtain small scraps. The infant Mug was approximately 4 months old when we first noticed such behaviour. Our observations suggest that imitation plays an important role in learning about foods. We noticed that the youngster plucks, handles and chews only on the food-items that the mother is

FIG. 116. A mother (Bin) feeding her infant with the mouth to mouth behaviour (photograph N. J. VAN STRIEN).

FIG. 117. The infant begs with its mother by initiating 'mouth to mouth' behaviour.

eating. Similar imitative feeding has been described for young chimpanzees (VAN LAWICK-GOODALL, 1968), and gorillas (SCHALLER, 1963).

Concomittant with such exploratory behaviour with respect to food, infants of 4 months of age were observed to touch and handle surrounding vegetation, though remaining in a clinging position onto the mother's body. In contrast to what is reported in the literature on captive orang utans (see AULMANN, 1932; JANTSCHKE, 1972; REDEKER, 1975), captive chimpanzees (YERKES, 1943) and wild gorillas (SCHALLER, 1963), orang utan mothers in the Ketambe area were not observed to stimulate their infants to climb onto surrounding vegetation, nor has such behaviour been reported for wild chimpanzees (see VAN LAWICK-GOODALL, 1968). At the age of 5–7 months, the orang utan infant breaks continuous physical contact with its mother and starts to explore its immediate surrounding without holding on to her. Although the infant's movements still have a rather uncoordinated appearance it can now hold branches firmly with either hands or feet. At this age the infant Mug was first observed to perform 'gymnastics'; these took place within arm's reach of the mother.

When the mother changed position or intended to move off she first 'gathered' her infant. This was usually preceded or accompanied by a 'squeak'-vocalisation. If a mother moved even a short distance from the infant, without 'gathering' it, the infant showed its distress by 'screaming' or 'pout whimper' (fig. 118, a and b). During the exploratory wanderings of the infant, the dis-

FIG. 118. An infant showing distress by (a) screaming, which changes into (b) pout whimper, when the mother shows attention.

tance between it and its mother gradually increases with time. The infant may now move towards a sibling, and sometimes towards another young orang utan. The infant Mug first moved out of his mothers reach without any sign of distress at the age of 9–11 months. Throughout his first year, Mug had enjoyed frequent contacts with his elder sibling Mos, who often touched, stroked, tickled or handled him gently during the mother's resting periods. The sibling also gave special attention to the infant's genital region. On two occasions the mother Mif allowed adolescents other than her own offspring (Sin and the rehabilitant male Bobo) to touch and handle her infant. This happened when Mug was about 9 months old. Mif watched the adolescent closely; either of them appeared cautious during the episode. On four other occasions adolescent females (Jet and Sin) trailed behind mothers with infants. Apparently infants are very attractive to young females. An analogous attraction towards infants has been noted in humans and in several other primate species (SPENCER BOOTH, 1970).

Mothers did not react to the urinating of their infant, and usually the urine spilled freely over their hair. Defaecation by the infant always occurred when the mother rested and when she held her infant in such a way that its anus pointed away from her body. It is not clear whether the mother's handling of the infant released some defaecation reflex, or whether the defaecating position was initiated by the infant itself. Rehabilitant infants also defaecated when their abdomen was lightly pushed outwards by the attendant to whose body they clung; this phenomenon has also been described by HARRISSON (1963). Once we observed that a juvenile orang utan caught her mother's urine in her underlip, and presumably drank it. Some rehabilitant orang utan juveniles had a similar habit, and they occasionally drank the urine of their 'friend'.

Mothers occasionally play with their infant, such play consisted of a gentle 'gnaw wrestling', initiated by the mother. During play bouts the mother usually hangs upside down and holds the infant in front of her face. The mother Mif was observed to play in such a manner with her infant Mug when he was approximately 6 months old; the female Bin played with her infant Ans when it was approximately 8 months old (see fig. 119). Infants of approximately $1^1/_2$

FIG. 119. A mother (Bin) gently 'gnaw wrestling' with her infant.

year old were observed to give some kind of display, including the elements of 'posturing' and 'branch-waving'. Usually such displays were directed at other species (twice at hornbills, once at a long-tailed macaque, twice at me and only once towards another orang utan). Mothers with infants older than one year were seen to engage in temporary associations, so that infants of that age may come into contact with the other members of the deme. Although infants and juveniles are already capable of constructing crude nestlike platforms at the age of one year, they still share the sleeping nest with their mothers.

During locomotion, infant orang utans are carried by their mothers until they are approximately two and a half to three years of age. The separation process resulting in independant locomotion seems to be initiated by the mother and may start when the infant is approximately two years old. At this stage, mothers that moved off reacted to the distress signals of their infants by giving a 'squeak' vocalisation, stopping, looking at it and waiting (sometimes with a 'hold out hand' gesture), but they were reluctant to return and collect the youngster.

c. Mother-juvenile relationship

When a young orang utan was no longer dependent on its mother for locomotion, and was only occasionally carried by her, it was considered as 'juvenile' in this study. As described in the preceding section the mother gradually induces the youngster to travel on its own. When travelling through the canopy, however, mothers helped their juvenile offspring by 'bridging' (fig. 120, a and b) to cross gaps in the vegetation where the youngster would not be able in crossing alone. The mother Jane, who travelled some 10 meters ahead of her son, once waited at least three minutes to help him cross a wide gap in the canopy. The rehabilitant female Bin waited even longer for the adopted juvenile Bumi, when he was some 50 meters behind, to help him across a gap. It is noteworthy that this same female also helped another newly introduced rehabilitant juvenile female who could not cross a gap. Apparently such 'altruistic' behaviour is not necessarily restricted to the mother-offspring relationship.

The young orang utan's exploratory trips become more extensive in the juvenile stage, although juveniles invariably stayed within sight of their mother. Other young orang utans were often the focus of a juvenile's attention. When approximately three years old a juvenile might show 'play approach' towards such other youngsters and 'gnaw wrestle' with them. The encounter behaviour might include elements such as 'touch and smell', sometimes in the face to face form; the meeting animals might also show – 'parallel' – gymnastics before they came into contact.

When mothers were feeding, their juvenile offspring invariably took the same food items. Even when sitting amidst a wealth of fruits, such youngsters often begged from their mothers ('look at mouth') or attempted to take fruits from her.

The observations on suckling are too scant to give conclusions on the pro-

FIG. 120. The mother (Bin) helping the 'adopted' juvenile male Bumi across a wide gap in the vegetation; (a) waiting for the juvenile while holding the vegetation together, and (b) the juvenile crosses the gap.

cess of weaning. In captivity, weaning starts when the offspring is approximately three years of age (CHAFFEE, 1967), although BRANDES (1939) has reported that the youngster Bushi suckled six and a half years on his wild caught (Sumatran) mother Suma.

On one occasion the mother Rim left her four years old juvenile Rom behind in a fig tree for some time. The mother was suddenly chased by the adult male O.J. with whom she was feeding in the same tree. The juvenile did not show signs of distress, even though the large male displayed past it. The male on his part did not take any notice of the small juvenile. After some minutes Rom left the tree and moved in the direction his mother had taken; they met after some 50 meters. The adult male had already returned to the fig-tree. This apparent ignoring of juveniles by adult males may be a general phenomenon, since it was also observed on other occasions. When visiting the rehabilitation station's feeding ground, the adult male O.J. paid no attention to the juveniles present and on some occasions allowed juveniles and even adolescents to come very close. This contrasts markedly with his behaviour towards rehabilitant sub-adult males, who were chased at the slightest signs of provocative behaviour on their part. In a temporary association in a fig tree, the 'scream' vocalisations of the infant Mug did not evoke any visible reaction in the adult male O.J. Also 'temper tantrums' accompanied by 'crying' in rehabilitant juveniles did not evoke any reaction in the same male, though he occasionally looked in the direction of a wriggling and screaming juvenile. The rehabilitant juvenile Koen appeared to be attracted by the adult male O.J. On the occasions when the adult visited the station the small youngster approached and sometimes followed him over some distance.

d. Mother-adolescent relationship

Females were observed with newborn infants when their former offspring was about four years old. Perhaps the hormonal balance of females during suckling inhibits oestrus and ovulation and/or induces a tendency to avoid situations with potential for sexual interactions. Only after the juvenile has been weaned at the approximate age of three and a half, may females engage in sexual interactions again. About half a year after a new baby is born, the older offspring, then about 5 years of age, becomes increasingly independent from the mother.

His appearance changes, and the youngster is considered 'adolescent'. The mother Mif began to show considerably less interest in her adolescent son Mos in the course of 1973, instead she focussed all her attention on her infant Mug. This waning interest seemed to mark the break up of the mother-offspring bond. While the family was mostly found together in the first half of 1973, Mif and Mos were usually found apart in the second half of that year. Mos was still occasionally seen with his mother in 1974, but he appeared to stay with her for only short periods, rarely lasting longer than a day. On two occasions in 1973, i.e. September and October, we noticed that Mif silently moved off at a moment when her son was momentarily out of sight. On both occasions this behaviour resulted in several days of separation of the mother and her son. On one occasion the adolescent showed a 'temper tantrum' when he discovered that his mother had gone.

Often mothers did not wait for their adolescent offspring to catch up with them, as they had done when it was still juvenile. It seems therefore that the separation process is at least partly initiated by the mother. When adolescents rejoined their mothers after a period of several days, they did not show any particular greeting behaviour. Often the two individuals did not even come into physical contact. It was only from their coordination of movements and prolonged proximity that a long lasting attachment could be deduced, when their relationship was not known reliably (as was the case with Josh and Jet). A similar lack of enthousiastic greeting within family units, reuniting after several days of separation has been described for chimpanzees (see VAN LAWICK-GOODALL, 1968).

3.1.2. *Affiliative behaviour between non-related individuals*

Behaviours that can be considered as affiliative are 'touching', 'embrace and 'allo-grooming'; possibly 'mouth to mouth contact' can also be reckoned into this category. Other elements that might express an affiliative bond between individuals were those belonging to the category of reassurance behaviour. For instance an individual might hold out his hand (see also p. 282) in response to a 'crying' partner, possibly a similar response as that between a mother and child. However, an affiliative bond between individuals was more likely deduced from the coordination of behaviour, the continuous proximity and the frequent play-interactions of partners: sometimes also from food sharing. Rehabilitant orang utans often sought comfort or reassurance with their human attendants when they were frightened, in a similar way as wild youngsters obtained reassurance from their mothers. Their behaviour consisted mainly of 'clinging'.

Adolescents, and to a lesser degree, sub-adult males might seek one another's company. Pairs or small groups of young individuals may stay together for several days (see also p. 168) and the members of such groups usually interact in a free and easy manner. Although all known youngsters engaged in such groupings, there seemed to be special relationships or 'bonds' between certain individuals. Such individuals were found together more frequently than they were with others and, especially within large associations or social groups, such bond partners played more frequently together and for longer periods than they did with other play-mates.

In 33% of the 55 occasions that the sub-adult male Roba was observed in a group with other immature wild orang utans, he formed a 'bond' with the adolescent male Gin (see table 17). They showed strong coordination of movements, sometimes continuing after the group had broken up, they played more frequently with one another than with others, and on one occasion we even

TABLE 17. The number and frequency of occasions immature wild orang utans were observed in groups.

	Number of occasions	Frequency					Total
		Roba	Doba	Mos	Gin	Jet	
Roba	55	–	16	24	33	27	100%
Doba	52	17	–	33	29	21	100%
Mos	58	23	29	–	26	22	100%
Gin	75	24	20	20	–	36	100%
Jet	66	23	17	19	41	–	100%

noticed a form of foodsharing, i.e. Gin taking a number of the collected *Heritiera* fruits that Roba was eating, without any sign of aggression. Similarly, the adolescent male Mos engaged in an affiliative bond with the sub-adult male Doba, this was the case in 29% of the 58 occasions Mos was seen in a group with other wild youngsters (fig. 72). It is noteworthy that Mos was also quite frequently found in association with Roba, possibly because the latter at times sought the close proximity of Mos's mother Mif. Notably at the end of the study period, Mos and Roba were often found travelling together and their behaviour suggested an affiliative bond.

During 1973, the adolescent female Jet was engaged in two different affiliative relationships, one with her wild peer Gin, the other with the rehabilitant female Bin (fig. 121). Although Jet and Gin rarely played together or came into physical contact, their frequent togetherness and coordinated movements on such occasions suggested their 'bond'. Of the 66 occasions in which Jet was observed with other youngsters, 41% were with Gin. On two occasions we noticed that Jet left a peer group and travelled in a straight line, some 500–800 meters, to join Gin.

On two other occasions we saw such aimed at travelling also of the wild sub-adult male Roba (see p. 81), and of the rehabilitant sub-adult male David. Neither of the individuals

FIG. 121. Play between the two female partners of a bond (Bin and Jet).

was seen to climb to the top of a tree to scan the surroundings, as orang utans sometimes do. We also had noticed no sounds nor vocalisations that might have betrayed the locations of the peers they joined. Moreover, only the loudest calls, such as the 'long call' and 'lork-call' carry over such a distance in the forest. The rehabilitant male's case is noteworthy as he left a group including several wild peers and travelled some 500 meters to the feeding site at the station. After approximately one hour he returned to his former group, travelling in a purposeful manner along an almost straight path to a place some 200 metres away from where he had left them. To reach this group, he had to cross a ridge which prevented him from any visual (and auditory) checks on the movements of the group.

These observations suggest that orang utans may be able to locate, and perhaps even individually recognize others from a distance beyond their visual and auditory range (if we assume that their hearing ability is similar to a human's auditory range). This sense may also be responsible for the apparently synchronous ranging patterns of the adult males. O.J. and Mozes (see p. 285). The former seemed to avoid the latter although the distance between them was too great for visual checks on the other's progress. Similar remarkable locating ability of conspecifics has been noticed in chimpanzees, notably during instances of 'hunting' and aggressive encounters with 'out group' conspecifics (see BYGOTT, 1974).

Data on the relationship between Jet and the rehabilitant female Bin were not consistently gathered, but the very high incidence of their joint attendance at the provisioning and their subsequent behaviour indicated a strong affiliative relationship. On several occasions we observed that Jet begged food from Bin and we noticed food-sharing in two instances.

Among rehabilitant orang utans affiliative relationships were even more conspicuous. Juvenile rehabilitants in particular usually stayed in pairs. Possibly this age category found a kind of mother-substitute in a bond partner. Bonds between rehabilitants were expressed even more strongly in contact behaviours such as 'embrace', 'clinging and walking in tandem'. Sometimes it included food sharing and rarely 'allo-grooming'. Bonds were easily recognized as the partners were always within sight of each other and loss of contact could evoke 'screaming' and a 'temper tantrum'.

Whereas the bonds between juveniles involved much physical contact, those between older individuals showed themselves more in closeness of proximity and, as in the wild, only during 'gnaw wrestling' and other playful activities (i.e. 'hand wrestling', 'mouth to mouth contact'), did the partners have true contact. Bonding seemed to be independant of the sex of the partners.

These observations indicate that orang utans posess the ability to engage in affiliative bonds with more than one individual at a time, Yet, such behaviour is only manifested during the ape's youth (see also p. 292).

3.2. PLAY

Social play is a category of behaviour which is very difficult, if not impossible (HINDE, 1974) to define. It usually involves mutual and reciprocal physical contact between two or more individuals, and is often preceded by and includes elements of 'meta-communication' (BATESON, 1955). Also it may serve an important function in the establishment and maintenance of a particular relationship between individuals. This complex behavioural repertoire includes the following elements: 'play approach', 'grasp', 'gnaw wrestle' and 'hitting', sometimes also 'mouth to mouth', 'nest-building', 'self-decorate', 'ignore' and 'gymnastics'. Typically the 'relaxed open mouth' facial expression with accompanying 'Ahh' vocalisation is displayed during social play. These elements, together with the 'loutish approach', 'self-decorate' (fig. 122) and the 'open-mouth bared-teeth' facial expression preceding play are clear examples of 'communication about communication' (BATESON, 1955: ALTMANN, 1967), in that they clearly signal the non-aggressive tendencies, and the cooperativeness of the actor and/or his partner.

Immature orang utans were observed to play more frequently than adults. In a period with plentiful fruit, October 1973, a group of 5 youngsters even spent more than 10% of their time in play.

Male orang utans appeared to play more frequently together (44%) than females played together (10%: see table 18). Also there was a stronger tendency in wild, and especially rehabilitant males to 'gnaw wrestle' with other males, rather than with females. On the other hand, females more often attempted to invite males (34%), then males invited females to play (11%).

FIG. 122. 'Self-decoration' in 'play approach'.

TABLE 18. Number, frequency of play invitations, and mean duration of play-bouts between male(s) and/or female(s) over 18 hours of recorded social play.

	number of play-bouts	frequency of play invitations	mean duration of play-bouts in minutes
M M	109	44%	5.4 (3–81)
M F (male initiator)	28	11%	2.7 (1–14)
F M (female initiator)	85	34%	3.9 (1–34)
F F	25	10%	2.6 (1–46)

Usually such play-bouts, ensuing from male invitations lasted shorter (2.7 minutes), than those invited by females (3.9 minutes). Yet, play-bouts between males lasted longer (5.4 minutes) than those between females (2.6 minutes).

Play was more frequent and of longer duration between individuals who formed a bond. For instance, the females Bin and Jet often played together in the period that their relationship was still affiliative (fig. 121).

In addition, there appeared to be a considerable individual variation in frequency and duration of play activities. For instance, the sub-adult male Doba was rarely observed to play. When he did, another individual invariably had initiated it. In general, we had the impression that dark haired, long finger type orang utans – like Doba – rarely initiated, and less frequently engaged in play activities than the light haired, short finger type (see also p. 27).

As mentioned on p. 216, the playful and usually even 'friendly' gnaw wrestling' could very subtly merge into 'wrestling' and vice versa (fig. 123). This phenomenon has also been described for other primates, notably baboons (OWENS, 1973) and chimpanzees (LOIZOS, 1969). From observations on rehabilitant orang utans, it seems that individuals test one another's physical ability and – aggressive – tolerance by means of this repertoire of 'gnaw wrestling', 'wrestling' and eventually perhaps 'bite'. In the rehabilitant group, at least, the social status of each individual became established and seemed to be maintained in this way; i.e. the highest ranking sub-adult male David used to initiate 'gnaw wrestling' with all rehabilitant males, and sometimes with some older females, every morning before, and after the provisioning. With cooperative partners, usually those who were closest to him in status, such play-bouts could last as long as two hours. After his removal from the rehabilitant group, his role was not taken over by the equally old – dark haired – Sibujong, but by the much younger – light haired – adolescent male Seamus. After Seamus' removal, the role was taken over again by a light haired individual, namely Bobo. Yet Sibujong's dominance in competitive situations (over food, or the adolescent female Jet) was beyond doubt. It is noteworthy that the individuals that exerred their social status in play behaviour, also displayed a 'policing' (ROWELL, 1966) or 'control role' (BERNSTEIN, 1969) in the rehabilitant group. For instance, the male David, and later his successors

FIG. 123. The sub-adult males Sibujong and Roba 'gnaw wrestling'.

regularly interfered with 'gnaw wrestling' pairs if one of the participants showed signs of distress. In such cases David dragged away, or initiated 'gnaw wrestling' with the more dominant partner of the two (see also fig. 124), with the result that the distressed individual had a chance to withdraw. He also interfered in inter-specific conflicts (see p. 286). This behaviour had a protective effect, even if it was not meant to be protective; it certainly served a stabilizing function in the rehabilitant group.

In established situations, when the tendencies of both partners may be entirely 'friendly', individuals may stick to enjoyable reciprocal 'gnaw wrestling' and, as said, such sequences could last a long time. At times it was clear that older and stronger individuals adjusted their strength and vigour to that of their play-mate. This was certainly true for the only observed play-interaction between the adult male O.J. and an unidentified adolescent. FERNHOUT (pers. comm., 1974) also observed a fully adult male orang utan, engaged in friendly 'gnaw wrestling' with a small boy in Surabaya zoo.

Still, wild adult orang utans rarely indulged in play activities. One case, concerning the male O.J. is noteworthy. When he was fully habituated and experienced regular contact with humans at the feeding place of the rehabilitation station, he made play-invitation gestures, such as 'loutish approach' and hanging from his feet with dangling arms, towards me on two occasions (see fig. 79). Mothers sometimes gently 'gnaw wrestled' with their infant (fig. 119), an activity in which the older sibling might also participate. Play between fully adult individuals has not been observed.

FIG. 124. The sub-adult male David interfering in the play of two other rehabilitants.

3.3. ENCOUNTER BEHAVIOUR

Orang utans who were familiar with eachother and met after a period of separation, normally did not show any particular greeting ceremony, at least no behaviour comparable to the conspicuous greeting ceremony of male chimpanzees (VAN LAWICK-GOODALL, 1967). On several occasions we noticed that during temporary associations of mothers, the juvenile offspring approached one another and (after a cautious 'touch and smell' ceremony) started 'gnaw wrestling'. On three occasions such juveniles attempted to mount their peer. In one of these, a small juvenile male persistently attempted to mount a somewhat larger female juvenile who resisted. The other cases concerned juvenile males who tried to mount smaller juvenile males. In all instances the partners engaged in long play sessions, which were characterized by frequent chases.

The experimental introduction of rehabilitants to wild individuals evoked various responses. When the sub-adult rehabilitant David was introduced to the mother-adolescent unit Sarah-Jet, both wild orang utans avoided him, perhaps influenced by my presence. David approached the small adolescent female and immediately tried to 'position' her, apparently in order to 'rape' her. The female succeeded in rebuffing the attempt and fled after her mother.

The introduction of the adolescent male Bobo to the wild adolescent male Mos led to a sequence of behaviour elements, similar to those observed in the juvenile-juvenile encounters.

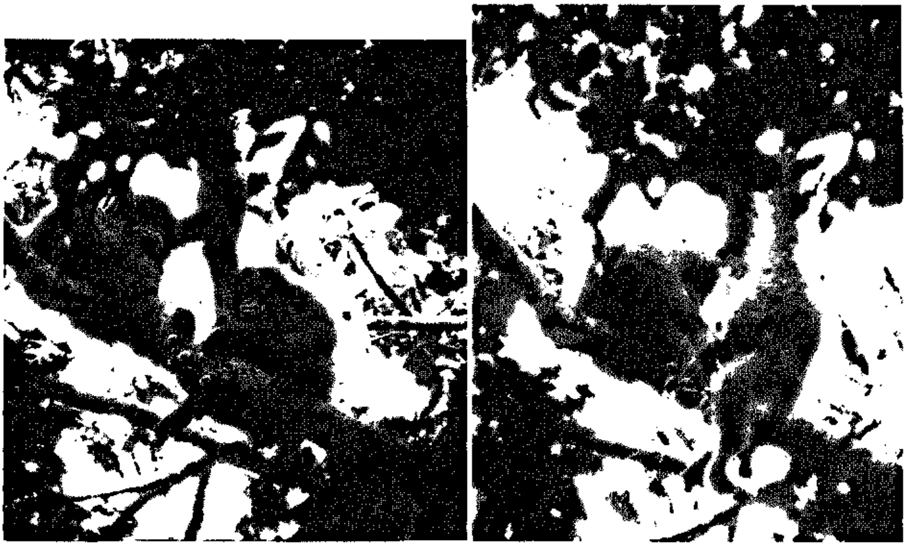

FIG. 125. An encounter situation between the wild adolescent male Mos (left) and the rehabilitant male Bobo (right); (a) Bobo looks intently at his partner (note the twig with *Heritiera* fruits in Mos's foot); (b) Mos touches Bobo's genital region.

It started with 'hesitant approach' of the rehabilitant towards the feeding wild male. Bobo sat down within arms length of the other and 'fixed his gaze' (fig. 125) on the adolescent's chewing mouth. He then stretched his arm in a 'hold out hand' gesture, perhaps begging for fruit. The wild male initially 'ignored' the rehabilitant, then, having finished the fruit he had been chewing, he looked intently at Bobo, who looked away. Mos stretched his arm and lightly touched Bobo's genital region, thereby parting the hairs; he then had a close look at Bobo's erect penis (fig. 125b). The latter made soft 'squeak' vocalisations. Then the wild male grabbed Bobo's foot and both engaged in a short bout of 'gnaw-wrestling' which rapidly changed into a kind of 'positioning' by the wild male and finally led to an attempt to 'mount' the rehabilitant male. After this sequence, both orang utans stayed close together for several hours, feeding and occasionally playing. Apart from 'gnaw wrestling', the play involved a considerable amount of locomotor activity when the wild male followed the rehabilitant through the fruit tree. Unfortunately there is a gap of two days in our observations on this pair and afterwards the rehabilitant male stayed near the fruit tree, but was repeatedly followed, or chased by the wild male, every time he entered it.

It is interesting to note that, although the wild male must have realised that his partner was a male, he nevertheless attempted to 'mount' him. Such behaviour resembles 'dominance mounting', common among groups living primates, including the chimpanzee (for a review see WICKLER, 1969). It may well be that the 'rape' behaviour of sub-adult males towards encountered females, is motivationally related to this 'pseudo-sexual' (dominance) mounting.

One incident involving the wild adult female Mif and the experimentally introduced rehabilitant female Yoko, may illustrate the intolerance between certain females. Mif was feeding in a large fruit tree which attracted a large number of orang utans throughout its fruiting season. The rehabilitant female had followed me into the study area. She entered the tree, in which two wild orang utans with whom she was acquainted (Jet and Doba) were feeding, next to the female Mif, her infant son Mug and her adolescent son Mos. Yoko seemed to ignore the others and started feeding. After approximately 12 minutes, Mif gathered her infant and suddenly rushed at the rehabilitant female who sat with her back towards her. Mif attacked the rehabilitant, and bit her several times. Yoko fled screaming from the tree, pursued by Mif. Perhaps the unfamiliarity of the rehabilitant had aroused aggressiveness in the female Mif, and this may have been aggrevated by the complete lack of submissive signals from Yoko on entering the association. Mif was seen to feed in peaceful association with the adolescent female Jet on several occasions during the same fruiting season. Jet, however, used to 'squeak' every time Mif made a move and she might approach quite close to the adult female.

Newly introduced rehabilitants orang utans were always immediately faced – and inspected – by the sub-adult male David. When smaller individuals, such as juveniles or adolescents, were introduced, David approached them rather gently, often bringing his face close to theirs in a direct 'smell' gesture, accompanied by the 'uff' vocalisation. Usually he then initiated a short 'gnaw wrestling' bout, after which he usually left them alone. To facilitate the genital inspection, he sometimes turned small juveniles upside down. At times the victims showed clear signs of distress during such treatment, they 'squeaked' loudly and often 'struggled' to free themselves. Confrontation with older confiscated individuals of approximately his own size usually led to a somewhat rougher interaction pattern; 8 such encounters were observed in detail. If the introduced individuals gave 'squeak' vocalisations during David's approach, he usually forced them to 'wrestle' in a fairly non-violent manner after an initial 'touch and smell' ceremony. Such wrestling often terminated when the newcomer presistently tried to give up by 'ducking', accompanied by 'squeak' vocalisations or by 'whimper' vocalisations. Such 'whimper' vocalisations might change into 'screaming' when the individual attempted to avoid contact with the resident male. The victims frequently urinated and sometimes defaecated. Introduced individuals of approximately equal size, who showed no signs of submission at David's approach, were usually subjected to a short 'attack'. In the three such confrontations observed, namely those with Usman, Sibujong and Simi, David sat silently for some time glancing at the newcomer then looking away, while making 'chomping' sounds. Suddenly he approached at a fast run, immediately 'grasped' a hand or foot and 'bit' it hard. From the reactions of the victims such bites seemed quite painful, although open wounds were never seen. Such initial contacts were immediately followed by a rather violent form of 'wrestling', which usually lasted until the newcomers showed clear signs of distress and withdrawal. With the female Yoko, who was subjected to a less violent encounter and with the female Simi, the 'wrestling' soon merged into 'positioning', and the sub-adult male made clear attempts to rape the females. He failed to achieve intromission on these occasions although he repeatedly forced the victims into suitable positions and was obviously dominant.

After confrontations with introduced males of approximately equal size, David followed them and repeatedly forced them to 'wrestle' again. Such behaviour sometimes lasted several days (e.g. in the case of the introduction of Sibujong). Typically, the newcomer was not tolerated at a higher level in the trees during the first few days. When such an individual climbed up past the sub-adult male, the latter immediately followed and forced the newcomer down by 'wrestling' and biting his hands or feet. On one occasion David forced the newly introduced subadult male Sibujong onto a small terminal branch that broke when David forcefully tugged at it. Sibujong fell some 8 meters to the ground. After both individuals had settled their status, their interactions became less tense and the 'wrestling' changed in 'gnaw-wrestling' in which Sibujong seemed to reciprocate and eventually even might take the initiative.

It is noteworthy that the rehabilitant female Bin showed encounter behaviour with several females which was similar in some aspects to the 'rape' behaviour (fig. 126) shown by subadult males (see p. 265 for details). She showed no interst in introduced males. Bin was the highest ranking female in the rehabilitant group and this may have been of significance in the expression of this behaviour. Bin sometimes appeared to compete for access to introduced females with the highest ranking male David, and when David had been removed from the group, she took over the role of encountering female newcomers completely.

Encounter behaviour as described here was not observed during temporary associations in the wild population. This suggests that the individuals who took part in these associations were already familiar with one another.

FIG. 126. The rehabilitant female Bin manipulating a newly introduced female's genitalia with her right hand, while masturbating with the hallux of her left foot.

3.4. SEXUAL BEHAVIOUR

3.4.1. *Development of sexual behaviour*

The first genital stimulation an infant orang utan experiences is caused by the actions of its mother and sibling. They frequently show interest in its genital region by touching, sniffing, licking and stroking it during resting periods. Such behaviour, directed at the infant's genitals was observed much more frequently than grooming activity directed at other areas of its body. It may be significant that young infant female orang utans have a rather conspicuous and prominent clitoris which superficially resembles a small penis (fig. 127; see also FISCHER, 1898). The phenomenon that mothers and siblings show interest in an infant's genitals has been described for the other apes (VAN LAWICK-GOODALL, 1967; HESS, 1974) as well as for several other primate species (ROWELL, 1972).

Infant orang utans showed genital manipulation, either in the form of actual stroking or by rubbing or thrusting on their immediate surrounding, e.g. their mother, their sibling, or onto branches or other parts of the vegetation. While male orang utans were observed to 'masturbate' from about the time that they broke continuous body contact with their mother (at 6–7 months) in females such behaviour was observed to emerge at a later stage: about when they become juvenile, at 2 years. Also in rehabilitant females we noticed masturbation at the estimated age of two years (for more details see p. 262).

Learning and experience play an important role in the development of socio-

FIG. 127. Genitalia of a young female orang utan.

sexual behaviour in the apes (ROGERS and DAVENPORT, 1969). During infancy, orang utans may already have witnessed socio-sexual behaviour at close quarters, when the youngster's mother had been the victim of a'rape' (p. 266). Infants also peered very intently at, sniffed at, and touched their mother's – or their sibling's genitals, though this behaviour was less frequent than the reverse. Juvenile orang utans may experience their first sexual contacts outside the family unit during temporary associations of mother-offspring units, when they may seek contact with their peers.

From adolescence onwards, the female orang utan, like all other female primates, has a regular short-interval sexual cycle, characterized by menstrual bleeding (BLAKLEY, 1969). Orang utan females do not show a swelling of the ano-genital region before and during their oestrus period as is seen in chimpanzees and some Cercopithecidae. Due to the absence of such overt signs, it was difficult to gather regular data on the sexual cycle of wild female orang utans. Occasionally menstruation was ascertained from a small patch of bloody discharge around the vulva. In the wild adolescent female Jet we only once noticed menstruational discharge. Three consecutive cycles of the rehabilitant female Bin lasted 31, 36 and 30 days respectively. In this female menstruation remained visible for two days.

Records for captive orang utans show an average length for the sexual cycle of 30 days (BLAKLEY, 1969). Initially, during late adolescence, the cycle may be very irregular with intervals of 32–64 days (ASANO, 1967).

In the female Jet, as well as in the rehabilitant female Bin, the first observed menstruation occurred at the estimated age of 7–8 years, which is about the same age(6–8 years) as has been described for the other great apes (RIOPELLE, 1963).

Females may not be fertile immediately after they show their first menstrual cycles: possibly during many of the initial cycles ovulation does not occur. The female Bin did not conceive for at least one year after we first noticed her menstrual bleeding, yet she often mated in that year. The wild female Jet showed an even longer period of infertility, and at the time of writing (1976) she still has not conceived. These observations accord with records for captive orang utan females. ASANO (1967) has reported that conception in zoo kept orang utans occurred some 1–2 years after the first observed menstruation.

It was noted that, when the female Bin became sexually mature, she became increasingly less tolerant towards other – late-adolescent – females in her immediate surroundings (see p. 292). Intolerance was especially manifest when she was consorted by a male, in particular if the male showed attention for other females.

The changes in behaviour connected with maturation were regularly observed only in this one rehabilitant individual. Whether increasing intolerance towards other females (i.e. sexual rivals) is a general characteristic of the social attitude of this species remains questionable. Reports on intolerance between captive females in zoos are rare and no systematic observations seem to be available. Yet, JANTSCHKE (1972) has reported that agonistic interactions between adult females do occur in zoos. Moreover, the Yerkes R.P.R.C. Bulletin (ANON., 1969) reports the 'stabilizing function' of an adult male orang utan with respect to two convened adult females who engaged in fierce aggressive interactions in the absence of the male.

In the course of maturing, females also appeared to change their attitude with respect to males. Juvenile females did not show any sexual interest in males, and also rarely initiated other forms of body contact (i.e. play) with their peers. Adolescent females, on the other hand, were frequently seen to try to initiate play with males. It was quite obvious that such adolescent females showed a preference for initiating play with older adolescent, or with sub-adult males, rather than with their peers. Males were usually not particularly interested, and often played only briefly with such inviting females, before turning back to their male play-companion. When they reached sexual maturity, adolescent females might actively 'present' in the course of their play activities with sub-adult males; occasionally such invitations resulted in a copulation. The observations suggest that young adult (primiparous) females are not particularly attractive to adult males, and only when they present persistently do the males show any interest in them (fig. 134, a and b).

During the male's adolescence, which lasts until his eight's year, he has the same appearance as females: long projecting hair surrounds the face. Females retain these features for a long period into adulthood, but the male's physiognomy changes when he reaches adulthood. Observations on reactions of other orang utans suggest that the neutral 'un-male' like appearance of the male adolescent allows him to go near to even unfamiliar adult male orang utans during temporary associations and hence become acquainted with the roles of these adults in a non-agonistic manner. This also may allow an adolescent male to wander into areas outside his mother's range.

At sexual maturity, the male's appearance changes rather dramatically. His testicles descend completely and he becomes a sub-adult male (fig. 139). In chapter 6 (p. 298) I describe in detail the role of the sub-adult male in the socio-sexual behaviour of orang utans; sub-adult males show heightened interest in adult females. At about the age of 15 years, the male's appearance changes again. He becomes increasingly less tolerant towards his peers and no longer shows the active interest in females which was so obvious during his sub-adulthood.

Masturbation and non conformistic sexual behaviour

Several wild orang utans, especially youngsters, were observed to stimulate their own genitals, either manually or by means of inanimate objects. Female orang utans might masturbate by rubbing their fingers, their foot or an object along their clitoris (fig. 128), or they might insert their hallux or objects into their vagina. One adolescent female (Sin) was observed to suck and wet the finger she used during her masturbation. Males usually rubbed their fist or

FIG. 128. Female masturbation by means of objects, (a) a small protruding stump on a tree trunk, (b) a bitten off piece of liana.

relaxed foot along their erect penis (fig. 85). Although the use of objects in masturbation was by no means restricted to rehabilitants, they did so more often than their wild counterparts. For instance, the sub-adult male Sibujong often pushed a hole through a leaf with his finger, which he then used to move up and down his erect penis. Young male rehabilitants might also insert their erect penis into small holes and crevices in branches and tree trunks along the way and make thrusting movements.

The context in which masturbation occurred differed between the sexes. While male orang utans, older than infants, usually masturbated during resting periods or at times when social excitement was absent, females showed such behaviour mainly during social excitement (fig. 86). Thus. the female Jet often masturbated intermittently when 'presenting' to males. One exception was the sub-adult male Doba, who was observed to masturbate some minutes after he had been chased away from his former consort Bin by her new consort Bor. Perhaps the motivation of masturbation in this particular case may be called 'frustration'.

Some rehabilitant orang utans showed certain patterns of sexual behaviour that were not observed in their wild counterparts. For instance, the female Bin displayed the peculiar sexual activity of poking her finger or thumb into a newly introduced (rehabilitant) female's vagina and meanwhile masturbating with her own hallux (fig. 126). During such incidents, which could occur at frequent intervals for two or more days, the victim struggled to free herself, but Bin often succeeded in holding her captive for a considerable time (once as long as 12 minutes). Perhaps these incidents are a female equivalent of the sub-adult male's 'rape' behaviour (see p. 266, see also p. 259). On the introduction of the ex-captive female Simi into the rehabilitant group, the female Bin immediately took over when the sub-adult male David ceased 'positioning' Simi, and she persistently tried to insert her thumb into the vagina of the 'ducking' and 'struggling' newcomer. Although all female victims more or less strongly resisted this treatment, some of them later established an affiliative relationship with Bin (e.g. the female Linda).

On some occasions males engaged in homo-sexual relationships. When they were temporarily caged together, the sub-adult male Sibujong playfully forced the adolescent male Bobo into a convenient crouching position to have ano-genital contact. Afterwards, when both individuals were roaming free, a second homo-sexual interaction between them was observed. In both cases the sub-adult male ended the contact after ejaculation.

Another remarkable type of sexual behaviour was shown by the sub-adult male rehabilitant Usman, who frequently caught the adolescent male reha-

FIG. 129. Oral-sexual contacts of the rehabilitant sub-adult male Usman with (a) rehabilitant male Pon, and (b) wild adult male long tailed macaque.

bilitant Pon and sucked his penis (fig. 129). Interestingly, the adolescent became very attached to the sub-adult male, and after a while followed him wherever he went. He showed 'temper-tantrums' (p. 196) when the sub-adult male did not wait for him to catch up, or when he lost sight of the sub-adult. After Usman had moved to another area, the adolescent established a new, very firm bond with his peer Seamus. Within this new bond similar behaviour developed, although Seamus had never before displayed such behaviour. Some days after the bond had been established we saw that Seamus forced his partner to accept oral-sexual contact by inserting his erect penis into Pon's mouth while holding him captive with his feet. Later on this behaviour was seen several more times but with more cooperation on the part of the latter.

On the occasions that male orang utans were forced into non-conformistic sexual behaviour, they generally submitted to their partners. This was in marked contrast to most females who usually struggled and screamed violently when forced to engage in sexual contacts with their male peers.

3.4.2. *Sexual interactions between mature individuals*

It has been reported that copulations between captive orang utans, especially those initiated by sub-adult males, can have a rather violent character (see Seitz, 1969; Jantschke, 1972). MacKinnon (1971, 1974) confirmed such violent copulations, reported as 'rapes' among wild orang utans.

The orang utans of the Ketambe population showed two rather distinct patterns of male-female sexual behaviour; one sequence of behaviour elements I called 'rape' after MacKinnon (1971), the other sequence of elements I called

Table 19. Total number of observed combinations of sexually mature males and females and their sexual interactions.

Combination		Number of combinations	Number of consortship combinations	'Rapes'	Total number of copulations (incl. rapes)
male	female				
M	Fi	23	–	–	–
M	F(j)	27	2	–	–
M	Af	23	2	–	–
S	Fi	25	1	1	1
S	F(j)	10	3	4	4
S	Af	41	–	–	–
M	RAf	(52)	1	–	–
S	RAf	(183)	2	6	17
RS	Af	(176)	1	11	19
RS	RAf	many	1	5	17

M: wild adult male; S: wild sub-adult male; RS: rehabilitant sub-adult male; Fi: wild female-infant unit; F(j): wild female-juvenile unit and lone potentially receptive female; Af: adolescent female; RAf: rehabilitant adolescent female.

'cooperative mating'. In its extreme form, the 'rape' is a straightforward copulatory act, initiated by sub-adult males, in which females usually display distress and a lack of cooperation. In its most extreme form, 'cooperative mating' is an interaction, usually initiated by the female, in which both partners show considerable coordination of movements before, during and after the copulation, while copulation itself is performed cooperatively.

Inevitably there were a number of cases that were difficult to classify. Even in 'rapes' some coordination and some form of cooperation was discernible. It is noteworthy for example that females subjected to 'rape' behaviour usually waited for a sub-adult male to approach or they moved away using a 'hesitant avoid' locomotor pattern, which enabled the male to catch up. Contact would certainly not have been achieved if the female really avoided or even fled. On the other hand, some matings were observed that showed close coordination and cooperation of both partners in the initial stages, but turned into 'struggling' and 'screaming' on the part of the female participant, followed by fierce 'positioning' on the part of the male.

During the present study, a total of 58 instances of sexual behaviour between sexually mature individuals, leading to copulations, were observed in the Ketambe area. Of these, 5 occurred between wild individuals; in another 36 a wild and a rehabilitant partner were involved, and the remaining 17 were between rehabilitant orang utans. Most of the observations on sexual behaviour involved rehabilitants, apparently because the smaller ranges of these individuals, the predictability of their whereabouts and the provisioning scheme greatly increased our chances of meeting associations and/or consortships. It was thus possible to study pair bond stability and quality of a consort relationship involving rehabilitants, in much more detail and over a much longer period than would have been possible for entirely wild pairs.

The participation of the different age classes in the two types of sexual interactions for wild and rehabilitant orang utans is specified in table 19.

The circumstances of 'rape' behaviour

On 5 occasions 'rapes' were observed between wild orang utans. These, as well as 22 'rapes' observed in encounters of wild- and rehabilitant orang utans were carried out by sub-adult males. Adult males were not observed to perform anything the like, although adult males were more frequently seen in association with adult females, than sub-adult males with adult females (see 'number of combinations' in table 19).

It is noteworthy that associations between a sub-adult male and a female-infant unit were seen about twice as frequent than those containing a sub-adult male and a female-juvenile unit, while adult males were seen as frequently with the former as with the latter. These data, strengthened by few observations on ranging behaviour of female-juvenile units (p. 267) suggest that those females, most likely to be receptive (i.e. lone females or females with juvenile offspring) avoided sub-adult males. As only one female, accompanied by an infant, out of 25 encounters of sub-adult males with such females, was raped, and 4 females accompanied by juveniles out of the 10 encounters, it seems that the latter category is especially liable to such violent copulations. The situation is more complicated however, because certain individual females seemed more prone to rape than others, perhaps dependent on their social status.

'Rape' behaviour typically occurred during encounters, i.e. when both partners had not been in contact for at least one day. Overt social behaviour between the partners before the male's initiating 'approach', and after the 'copulation' was absent in most observed 'rape' interactions (see fig. 132).

In 30 of the 35 observed combinations of wild sub-adult males and wild females, no 'rapes' followed. On six occasions the observed interactions between a female and the 'advancing' sub-adult male indicated that the female was dominant over the latter, and no further interactions followed. Usually such males suddenly 'avoided' such females when coming within close quarters, e.g. during feeding. Twice we even saw females actually display agonistically at sub-adult males who 'advanced'.

As noted, on three occasions females actively avoided encounters with sub-adult males. The female-juvenile unit Rim/Rom once made an obvious detour as they travelled in the direction of a large strangling fig tree where the sub-adult male Doba was feeding. Similarly, Bol/Bel avoided an unidentified sub-adult male in another fig tree. On another occasion we saw a lone adult female on the opposite bank of the Ketambe river suddenly retrace her steps when she came in sight of a fig tree which a sub-adult male was entering.

The following observations are typical for the various circumstances of 'rape' behaviour: A feeding female might stop feeding, sit down and wait when she spotted an 'advancing' sub-adult male. When such a male entered the fruit tree, she might make a 'squeak' vocalisation and remain immobile, or move in a direction away from the male, uttering 'squeaks'. In the latter case her locomotion was usually characterized as 'hesitant avoid'. Thus, the female Daisy, 'approached' by the sub-adult male Doba, responded by moving away some meters, but then stopped and actually 'presented'. On another occasion, the adult female Rim 'presented' almost immediately in a rather a-typical crouch-like position[19] when the sub-adult male Doba approached her during a temporary association.

During 'positioning' the females usually uttered 'squeak' vocalisations, which might grade into 'whimper' vocalisations and even 'screaming' during the copulation.

An unsuccessful attempt to rape was observed when the sub-adult male Roba approached the adult female Mif during an encounter in a large fruit tree.

The female sat on a nest, facing the approaching male, and the male's behaviour obviously lacked the straightforwardness so typical of a 'rape' encounter. He 'positioned' Mif so that he could inspect her genital region. She allowed him to handle her, but she once grasped Roba's hand and made a brief bite-intention movement. Roba followed Mif for several days

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[19] This particular form of 'presenting' strikingly resembled 'crouch-presenting' of female chimpanzees (see VAN LAWICK-GOODALL, 1968).

after this episode, but the self-assured behaviour of the female seemed to rebuff the male's attempt; no signs of overt hostility were observed.

Although Mif was seen in several temporary associations with different sub-adult males, this was the only observed attempt to 'rape' her. Another sub-adult male, namely Doba, who often associated with her son Mos, and was consequently quite frequently in her proximity, always avoided to come close. Yet, Doba was seen to rape two other females.

Sometimes very complex situations occurred. Thus, when two females with consorting sub-adult males, met during a temporary association, the males of each consortship pair (i.e. Doba and Bor) 'raped' the female (i.e. Bin and Daisy) of the other. This case is illuminating since it demonstrates that it is not merely some hypothetical 'built up sexual urge' that causes a sub-adult male to 'rape' a female; because the male Doba, at least, had ample opportunity to copulate with his own consort Bin.

On another occasion the same two sub-adult males, who both consorted with the rehabilitant female Bin, met the female-juvenile unit Rim/Rom who were feeding in a large strangling fig tree.

The younger sub-adult male entered the fig tree first. He rushed at the adult female and 'raped' her, but before he could finish his copulatory act he was supplanted by the other sub-adult male who had approached in the meantime. The 'raped' female struggled and screamed vehemently but immediately after the separation all individuals fed in the fruit tree peacefully without any indication of the preceding commotion.

This was also typical of the other observed rapes; after the completion of a rape both partners behaved rather indifferently towards eachother.

It appeared that, unless disturbed, the males ended their copulation during a rape sequence with ejaculation. On two occasions, we observed sperm drip from the female's vulva after a rape.

Sub-adult rehabilitant males raped every newly arriving (adolescent) female. Usually the rape was performed by the highest ranking individual, and on some occasions he prevented other, lower ranking males from gaining access to the female. When the wild adolescent female Jet visited the feeding ground of the rehabilitation station, she was often raped by the highest ranking male present. It is interesting that she usually refused to copulate, if in the absence of one of the higher ranking males a lower ranking individual (Bobo) attempted to rape her.

The circumstances of consorting and cooperative mating.

'Cooperative matings' occurred most commonly between partners who showed coordination and cooperation in many aspects of social behaviour, and who stayed and travelled together for days, sometimes even for months. Such relationships were termed 'consortships' (cf. WASHBURN and DE VORE, 1961; see also MACKINNON, 1971).

It has been noted by SCHALLER (1961) and by MACKINNON (1974) that (sub-adult) male orang utans display a strong tendency to consort with sexually mature females. The observed consortships in the Ketambe area, that included sub-adult males, were in all 4 instances initiated by the males (3 were preceded by 'rapes'), while consortships including adult males were on all 4 instances initiated by the female. The individual initiating a consortship was clear in all cases from its active role in the elements 'following', 'approach' and 'presenting'.

Altogether 8 instances of 'consortship' were observed between wild orang utans; in addition 3 were seen outside the Ketambe area. In none of these consortships we observed overt sexual behaviour such as copulations. Numerous instances of consortship between the rehabilitants and wild orang utans were seen. Within the context of these semi wild/wild consortships, a total of 19 copulations were observed.

The circumstances relating to consortships are best presented by describing the few observed cases in some detail.

In 1973 we noticed that the adult female Daisy entered a large strangling fig tree, followed by the sub-adult male Bor. Both apes stayed close together during the entire 3 hours period of observation, and they left the tree together as well. The female was not accompanied by her small infant, born a few months earlier and the infant was presumed dead. During the next three days, the animals continued to consort; the male usually following the female. Some four months later, in 1974, both were seen again, but although they were still in close proximity, the female Daisy now followed the adult male Gorm with Bor travelling at some distance from the couple. The adult male showed no particular interest in the female, who frequently sought his immediate proximity and twice 'presented' in front of him, but he frequently focussed his attention on the sub-adult male. Several times he made short 'ostentatious' chases in Bor's direction, but Bor kept his distance, some 30 meters ahead of the adult. At times Bor moved in a wide arc around the pair, and usually the adult male changed his position accordingly, keeping himself between the female and the sub-adult male. The next day only the adult male and female were found again; they remained in close proximity, often within contact distance, and, in contrast to the previous day, the coordination of their movements appeared to be reciprocal, with the male also following the female. Unfortunately this consort pair could only be observed for three hours and no mating was observed in that period.

A second episode gives a more complete picture of the socio-sexual relationship of male and female orang utans. The rehabilitant female Bin was followed over a long period of time and much of her sexual development and concomittant sexual relationships with several males were observed with some regularity. In the course of some 18 months, this female engaged in consort relationships with four males (fig. 130 and 131) and during these consortships copulated frequently.

After Bin had returned from a four months stay in the forest in 1973, she was courted by the highest ranking sub-adult male rehabilitant David. The two rehabilitants engaged in a consort relationship for several weeks, during which three copulations were observed. Bin refused to copulate with other, lower ranking rehabilitants. When the rehabilitant pair met the wild sub-adult male Doba during a temporary association, the wild male chased David away and the female actively followed the wild sub-adult male for the next two days. On several occasions she approached Doba very closely and twice we saw her performing 'touch and smell' behaviour; we did not notice that she 'presented' during these two days. After four days we observed that, instead of the female, the sub-adult male adopted the active 'fol-

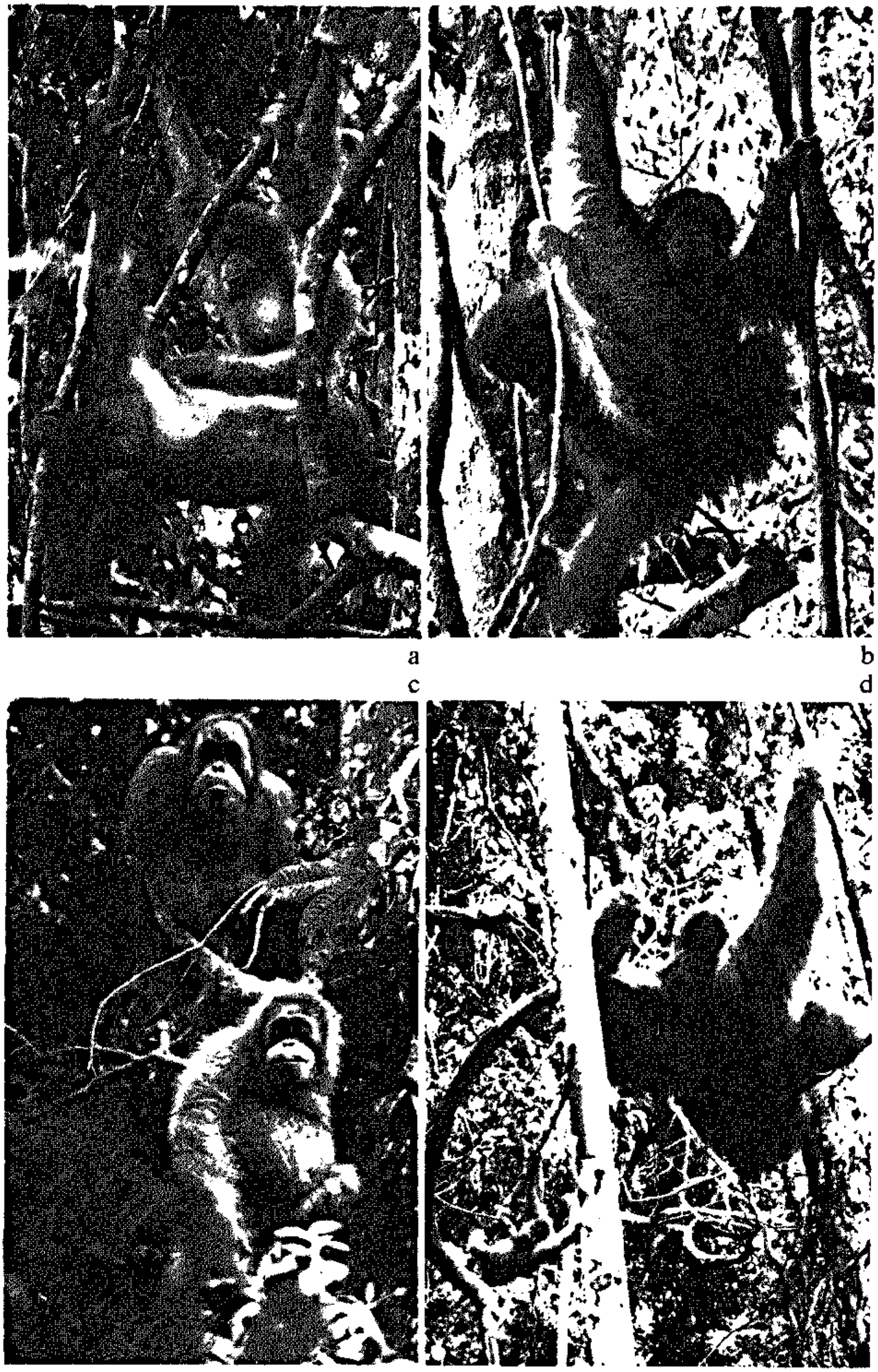

FIG. 130. The consort relationships of the rehabilitant female Bin, (a) Bin presenting for the sub-adult male David; (b) copulation of Bin with the sub-adult male Doba; (c) Bin with the sub-adult male Bor; (d) attracting attention of the adult male O.J.

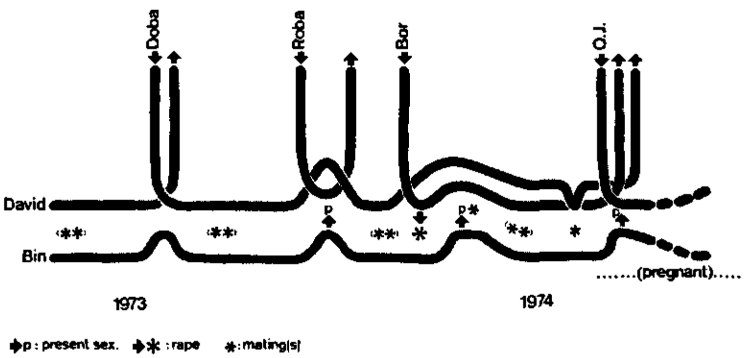

FIG. 131. Diagramme of the socio-sexual relationship of the female Bin and her subsequent consort-mates.

lowing' role, though most movements were coordinated reciprocally. Bin and Doba formed a consort pair which lasted for over seven months; in this period several cooperative matings were observed. The copulations were sometimes initiated by the female who 'presented' for the male. On other occasions the mating was initiated by the male who 'approached' the female and gently investigated her genital region. Copulations with rehabilitants, including her former partner, were not observed though interactions in the form of play occurred almost daily. Bin resisted strongly when a rehabilitant attempted to position her, and her partner's almost continuous proximity apparently prevented rehabilitant males from insisting. Once, however, the pair came into close contact with the wild sub-adult male Roba who visited the feeding ground of the rehabilitation station. Roba clearly supplanted Doba in a provisioning situation and immediately after this incident the female Bin focussed all her attention on the newly-met male, 'approached' him and even 'presented' in front of him. Roba seemed to ignore the female and no particular interactions followed this event. Some months later the female Bin was raped by the older sub-adult male Bor. This incident, in which her own partner raped the consorted mate Daisy of the other male, is described on p. 268. Bin's partner Doba clearly avoided the larger sub-adult male, and Bin again switched her attention towards the newly met Bor. She followed him, 'approached' him and once 'presented' to him during the rest of that day. When Bin and Bor were seen again five days later, both showed strong coordination of movements. This consortship lasted some three months. The former consort Doba trailed behind the couple and stayed in close proximity during this entire period. On several occasions Doba was observed to approach Bin closely and at times he attempted to copulate with her. Such instances usually occurred when her regular consort Bor was at some distance and fed or focussed his attention elsewhere. Twice Doba succeeded in copulating with the female who behaved cooperatively.

On at least one of these occasions the sub-adult male Bor obviously saw the copulating couple but he gave no reaction and continued feeding. However, on occasions that Doba showed active attention for Bin, he usually reacted by 'threatening' or even chasing his rival. These observations suggest that apparently the courting, i.e. the exchange of reciprocal attention between two potential sexual partners, is of more importance in arousing aggressive action in a third party concerned than the actual copulation. Observations on similar situations in a chimpanzee (see VAN LAWICK-GOODALL, 1968) and a gorilla community (see SCHALLER, 1963) seem to support such a supposition.

In the period that the female Bin and the sub-adult male Bor consorted, their pairbond seemed to break on at least three occasions. The male left the female for periods of 6–13 days and she did not follow him. On one such occasion we noticed that Bin was menstruating; it is not certain whether this event was the cause of the temporary break up.

Cooperative matings between the sub-adult male Bor and the female Bin were seen five times.

After three months of consorting, the pair met the adult male O.J. during a temporary association. The adult male instantly directed aggressive behaviour, in the form of 'ostentatious approach' at the sub-adult male, who withdrew some distance. Again, the female switched her attention to the dominant adult male. She attempted to attract his attention from some 15 metres by performing 'gymnastics' which included elements of 'presenting' postures held for a long time and by making very peculiar, drawn out and soft sounding 'kiss sounds' (p. 270). After some time she approached closer and actually 'presented'. The adult male, however, did not seem to be much interested in the female and focussed most of his attention on the sub-adult male Bor. Typically, also O.J. positioned himself between the female and the sub-adult male. The next day O.J. and Bin were seen in close company and showed coordination in their movements with the female still taking the active following role. In the short period that this consortship could be observed, mating did not take place. When the female was seen two months later, however, her attitude towards males was one of active avoidance, and she appeared to be pregnant.

The incidents described involving the female Daisy and the rehabilitant female Bin, strongly suggest that sexually receptive female orang utans have a strong preference for the more dominant or more impressive male available to them at any given time. She stimulates this male to follow her and engage in a number of copulations.

A more detailed picture of the sequences of behaviour elements in the context of 'rape' and 'cooperative mating' is given in fig. 132. Both diagrams represent some of the observed typical forms in each behaviour sequence. 'Cooperative mating' includes more neutral elements such as 'nest building', 'play', 'grooming' and 'masturbation'. Inspection of the female's genital region by the males is always included in the sequence of 'cooperative mating', but often absent in 'rapes'. 'Self-inspection' by both partners after copulation usually occurred in 'cooperative mating' but the females never 'self-inspected' after 'rape'. Also the element 'positioning' may be absent in 'cooperative mating', especially in the initial phases because the female actively coordinates her position according to the male's.

The distinction between 'rapes' and 'cooperative matings' is based on mainly qualitative evidence from a limited number of observations. Nevertheless we have the strong impression that the two types of mating are comparatively distinct with reference to the circumstances of mating in other primate species. Descriptions of sexual behaviour of other primate species indicate that the male's approach may vary from brusque coercion on the one hand to inviting and compliant on the other. Female sexual behaviour may vary correspondingly from resisting and yielding to soliciting. In some species the coercive male behaviour may have longer-lasting effects on the behaviour of his partners. Such behaviour may even have become functionally adapted as an instrument to regulate relationships and have become a dominance signal (see WICKLER,

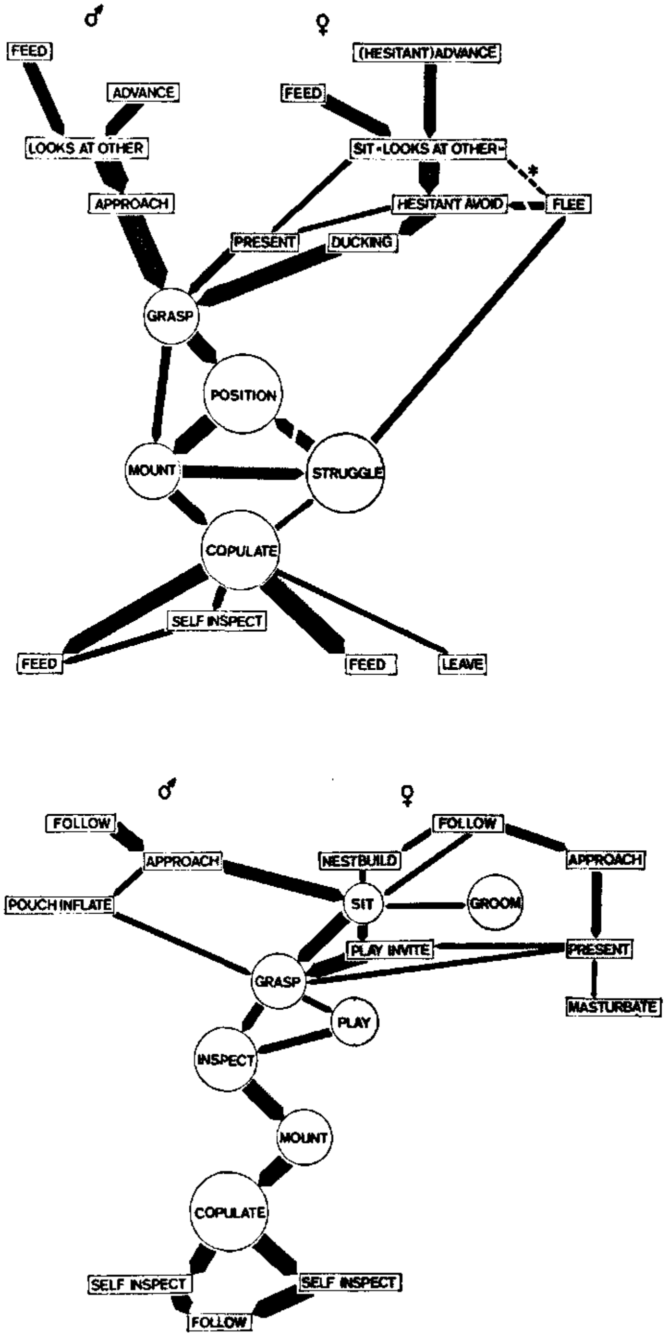

FIG. 132. Flow-chart diagrams of (a) a 'rape' sequence (n = 6), and (b) a 'cooperative mating' sequence (n = 4) (the shaded regions represent female activities; the circles show the contact-elements).

1969). Variability in sexual behaviour is evident also in chimpanzees (e.g. VAN LAWICK-GOODALL, 1967) though the distinction into separate types may be more gradual than I suspect to be the case for the orang utan. There is no firm evidence for a forceful, coercive type of sexual behaviour in the gorilla, although the sequence in which the male gorilla takes the initiative with a strutting walk display, changing to wrestling and chasing as described by SCHALLER (1963) may represent such a variant. In humans such a variant is certainly present in the behavioural repertoire of certain male categories. A very important causal factor in the rape behaviour of orang utans is the fact that the female is newly met or met again after a period of separation. The differences in observed interactions between partners in situations that had the potential for a 'rape', in 'rape-attempts' and in completed 'rapes' suggest that such behaviour is important in the establishment or maintenance of social relationships with the maturing male in the active role.

3.4.3. *The sexual strategy; conclusion*

From our observations the following picture of the orang utan's socio-sexual behaviour emerges. The observations leave no doubt that adult male orang utans can easily displace sub-adult males in consort relationships. Sub-adult males appeared to be sexually more alert and active than adult males, a finding which is in accordance with observations from other areas (see MACKINNON, 1974). When meeting an adult female, sub-adult males may attempt to rape her. Their success in this depends on several factors in which the age, the earlier relationships and the subsequent reactions of the female play a major role. Through this raping process the male may assert his dominance, and acquires information on the reproductive state of the female. Because he advertises himself rather pertinently, the male may establish particular, more individual aspects of a relationship that may be the basis of a personal attachment in the sence that the female may come to prefer one particular male individual over rivals.

Females clearly have an important, if not the determining role in sexual selection, in that they show a preference for certain males (fig. 133). Their choice seems influenced by the age and social status of the male. Our limited number of observations suggest that the orang utan female, when she comes

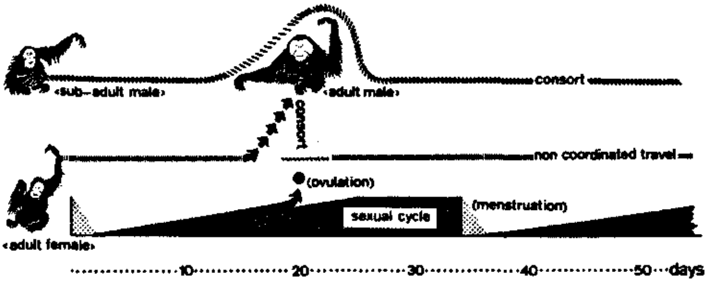

FIG. 133. A model for the socio-sexual behaviour of Sumatran orang utans.

into oestrus, actively seeks out the highest ranking male present and induces him to consort and copulate with her. Such consortships were initiated as a rule by the female but were often short lasting, possibly because they led quickly to pregnancy. As such consortships are largely maintained by the female, a change in her attitude will easily break the pairbond. Adult males seemed to be interested in a female only after she had actively initiated sexual behaviour usually by 'presenting' (fig. 134). The observed 'inspecting' behaviour of males suggest that possibly subtle visual and olfactory stimuli (pheromones) from the female's genital region play a role in the arousal of sexual interest of the adult male orang utan.

If a female orang utan has to seek out a high ranking male in the short period that she is in oestrus, it is vital that she can locate and find such a male quickly. It is likely that the far ranging 'long calls' of adult male orang utans may help to locate them. As only the highest ranking individual in any region was ob-

FIG. 134. The adolescent female Jet (a) attracting the adult male O.J.'s attention and (b) 'presenting' for him.

served to call, such calling includes information on the status of the caller. Animals did, however, seem to have information on the whereabouts of conspecifics which, in view of the dense vegetation and considerable distances must be independent of visual or auditory stimuli (see p. 292). Females who were under observation when long calls were heard did not react to these calls. This is understandable because they all carried dependent offspring, and almost certainly were not in a reproductive, i.e. fertile, state. RODMAN (1973) has described a case in which a female was attracted to the calling male, and MACKINNON (1971) has noted that 'the Bornean natives traditionally believe that the function of the call is to attract females' (p. 170), although he rejects this suggestion on the basis of his observations.

If we compare the morphological features and behaviour related to sexuality in the three great apes, we find interesting differences as well as some similarities between the species. The chimpanzee is exceptional among the apes in that females have a conspicuous ano-genital swelling at the onset of ovulation.[20] This feature almost certainly has adaptive significance in the socio-ecology of the chimpanzee. This ape lives in a highly dispersed group system with many different temporary combinations or sub-groups; they seldom engage in stable groupings including all individuals. By means of her obvious ano-genital swelling at the onset of ovulation, a female chimpanzee broadcasts her reproductive state and from some distance away a male may predict a female's willingness to copulate. As a result females from another community, who transfer temporarily (i.e. immigrate), are guaranteed 'safe conduct' because of their reproductive status. The ano-genital swelling may divert a male's potentially aggressive tendencies towards 'strangers' (see BYGOTT, 1973) into sexual interest.

In gorillas with their relatively stable social groupings, (intra-group) sexual competition is almost non-existent because of a stable hierarchy and the close and continuous proximity of the group members. Perhaps subtle visual and olfactory stimuli are sufficient to stimulate sexual behaviour.

Orang utans live in an even more loosely organized social system than chimpanzees and sub-groupings are relatively rare. It seems that the change in a female's behaviour and her active choice of and approach to certain males is a sufficiently effective strategy to ensure her reproduction. In theory, the acquisition of information on the quality of male-fitness in orang utans is more complex and perhaps less reliable than in the more gregarious African apes since orang utans are not in continuous visual proximity. Possibly the very marked sexual dimorphism in orang utans, some characters of which may even be considered as a 'handicap' for this species's mode of life, is a way to advertise a male's quality (cf. ZAHAVI, 1975), alternative to the information acquisition resulting from continuous proximity.

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[20] A conspicuous ano-genital swelling appears to be a characteristic of females living in a multi-male group structure (cf. macaques, baboons).

3.5. AGONISTIC BEHAVIOUR

The behaviour patterns included in this category are (a) assumed to be mainly assertive or coercive in function, and, as a reaction to such behaviour, are (b) of submissive nature or appeasing in function.

To allocate particular behaviour elements to this category is not so easy. Dependent on the context and the relationship of the interactants certain behaviour elements may be mobilized, or applied in different behavioural programmes, in order to fulfil different functions. Whether a given element should under all circumstances be considered to be submissive (or aggressive) is uncertain. 'Genital presenting' for example can occur as an element in a programme with a submissive function (cf. WICKLER, 1969) in a programme with a sexual function, and as a gesture expressing the intention to make non-provocative, neutral contact (cf. HANBY, 1976).

In an evaluation of the social behaviour of chimpanzees, based on a quantitative analysis of the temporal contingencies of behaviour elements, VAN HOOFF (1971; 1974) distinguished three sub-categories of aggressive behaviour, namely 'bluff', 'threatening' and 'attack'. Although we have not consistently collected the quantitative data, necessary for a similar analytical treatment, I suppose that analogous categories can be determined in the orang utan's behavioural repertoire.

For behaviours with a submissive, appeasing of reassuring function, which are conspicuously represented in the chimpanzee's behavioural repertoire (see (VAN LAWICK-GOODALL, 1968; VAN HOOFF, 1971), categorization is even more difficult because of the scarcity of observations in the context of overt defeat. Perhaps this even stems from the rarity of such elements in the orang utan's behavioural repertoire at large.

3.5.1. *Bluff behaviour*

This heading includes a number of elements which are characterized by their boisterous, vigorous and conspicuous nature. Such behaviour may be displayed towards conspecifics as well as towards sources of disturbance such as humans.

Behaviour elements which seem to be characteristic for this 'bluff' category are 'posturing', 'self-decorate', 'stiff approach', 'vertical head nod' and perhaps 'yawning' (fig. 135). The exaggerated and conspicuous nature of the movements is often enhanced by swaying the surrounding vegetation. Towards groundwalking disturbances and in particular towards humans, an orang utan may perform a sequence of elements, consisting of 'branch waving', 'posturing', 'branch braking/dropping' and 'kiss sounds', with or without the 'hand to mouth' gesture.

Sometimes the tendencies to attack and flee, which are supposed to be the underlying simultaneous motivations of 'bluff' behaviour, are clearly noticeable. When the tendency to flee was predominant, the individual's 'kiss sound' was often followed by, or entirely replaced by the 'grumpf' vocalisation.

FIG. 135. The adult male O.J. yawning, only seconds before he directed an ostentatious approach at the observer.

On several occasions we noticed that 'bluff' behaviours shaded into 'gymnastics', not only in young individuals but also in adults, especially in the course of their displays towards me. Thus the play-intention movements of the adult male O.J. directed at me (see p. 183), containing such elements of 'gymnastics', were once preceded by a display lasting several minutes of 'posturing' with frequent 'vertical head nods'. If two individuals displayed 'bluff' behaviour which shaded into gymnastics simultaneously, they might approach eachother and contine with 'gnaw wrestling' or 'wrestling'. Similarly, adolescent and especially sub-adult male individuals often included 'bluff behaviour' elements in their play approach. This was even more apparent among the rehabilitants, who displayed bluff behaviour in a playful context towards their peers as well as towards their attendants.

This suggests that the essence of bluff behaviour in a social context is to subdue or check aggressive impulses present in the behaviour patterns of interactants by impulses of a socially positive nature (i.e. play). Whether the behaviour has a predominantly attracting or repelling effect might depend on the context and the relation of the recipient with the actor. The 'long call' vocalisation and perhaps the 'lork call' vocalisation may also fit into this category.

3.5.2. *Threatening*

This behaviour category includes the elements 'fixed gaze', 'bark biting', the 'chomping' vocalization and 'ostentatious approach'. The elements mentioned in the 'bluff' behaviour are closely associated with the elements used in 'threatening', but in the latter category they are likely to lead to actual attack or they announce the probability of attack. The form of the behaviours included in threatening also express impulses to attack and to flee, and the signals clearly seem to focus on self assertion. During a threatening display several rests occurred. This hesitancy seemed to indicate the ambivalent nature of the behaviour. It certainly enables the opponent to remain some distance ahead of the actor and to avoid the aggravation of the confrontation.

Adult males often performed threatening behaviours towards sub-adult males during triadic interactions (see 'circling') in which females were involved. They also threatened other (even younger) orang utans who provoked them with 'kiss sounds', 'swaying branches', or by coming too near without submissive signals. Adult female orang utans may direct 'threatening' behaviour towards other females, and occasionally towards males, especially sub-adult males. Orang utans might also direct 'threatening' towards non-conspecifics (p. 101; also GAUN ANAK SURENG, 1960; MACKINNON, 1971). In contrast to bluff behaviour, the observed instances of 'threatening' lacked attention-drawing vocalisations or sounds.

3.5.3. *Attack*

Attack behaviour was rarely observed. I have included in this category the elements 'brusque charge', 'piloerection', 'frowning' and intense and harsh forms of physical contact, like 'bite'. Such behaviours might be preceded by displays of 'threatening', but often they appeared as an explosive outburst after the animal had sat motionless for some minutes, at times directing a 'fixed gaze' at its opponent. During such preludes, the actor's entire body-posture expressed tenseness. The 'brusque charge' which followed did not always result in actual physical contact, usually because the victim fled. There was never any obvious hesitation on the part of the attacker, as was often apparent in 'threatening'.

As a rule, attacks by females were explosive outbursts, not preceded by 'threatening' signals. By contrast, when we saw males attack this was preceded by fairly elaborate threatening. We never observed the victims of a male attack to be severely bitten; violent body-contacts that resulted in biting were all between females. Yet, the frequent occurrence of bitewounds on the hands and feet of sub-adult male rehabilitants suggests that attacks directed at this age group occur more frequently, or are more intense than our observations indicate. Reports of scars, healed wounds and minor deformities, such as stiff fingers and toes in adult male orang utans in other regions, i.e. Borneo (see MACKINNON, 1971; GALDIKAS-BRINDAMOUR, pers. comm. 1974) and in captive apes from Sumatra (BRANDES, 1938), suggest that this age group may occasionally engage in very serious conflicts.

The difference in male and female attack strategies reported here may represent some general characteristic of primate societies. It has been observed in Sykes monkeys (*Cercopithecus mitis*) and in patas monkeys (*Erythrocebus patas*) that females usually attack by surprise, whereas males usually precede their attack with threatening (NAGEL & KUMMER, 1974).

3.5.4. *Submissive behaviour, appeasement- and reassurance gestures*

Submissive behaviours are elicited as a result of particular behaviour by, and are usually directed at, dominant individuals. There are two more or less distinct situations in which submissive behaviours are displayed by primates:

a) in the more passive sense when the subordinate has been subjected to threatening or to attack by the dominant individual, or finds itself in a situation that is likely to release such behaviour; and

b) in the more active sense when a subordinate draws near, or encroaches the 'personal sphere' (HALL, 1966; MCBRIDE et al., 1969) of a dominant individual.

The former category (a) was less frequently observed than the latter (b) in the wild orang utan population in the Ketambe area, although the relatively low incidence of temporary associations (as compared with e.g. chimpanzees) suggest that it was commonest. When the paths of two adult individuals crossed, one of them would often 'avoid' the other, sometimes even before visual contact had been established. In fact, the dominance rank relationship of some individuals was assessed on the basis of the consistency of their 'avoid'-behaviour with respect to other individuals, even if no obvious interaction between them had been observed.

In the most extreme situation (i.e. attack), the submissive reaction of the victim was 'screaming' and 'fleeing'. More usual submission as a reaction to 'threatening' or 'bluff' behaviours was noticed. In such cases the addressee would 'avoid' the actor, either by moving out of sight, or by staying in view but keeping a large distance. In the latter situation the submissive individual made 'squeak' vocalisations at every move of the dominant, and whenever he moved himself. The subordinate avoided to look intently in the dominant individual's direction (and avoided eye contact), yet he always appeared to keep the latter in the field of vision.

Subordinate orang utans used 'active submission' gestures (b) when about to encroach into the personal sphere of a dominant individual, namely: 'hesitant advance', accompanied by the most frequent element used in any submissive context, the 'squeak' vocalisation. Another element which might accompany 'hesitant advance' is the 'silent pout' facial expression.

Most temporary associations (see p. 168) were characterized by a lack of overt 'threatening', of even 'bluff' behaviours, although the inter-individual distances were often quite small. However, the behaviour of one (or more) of the associates usually expressed more alertness or tenseness than the other, and his movements were frequently accompanied by 'squeak' vocalisations, apparently directed at the more dominant individual. By contrast, the atmosphere within mother-offspring units, between consort partners and within youngster-groups was usually more relaxed and 'squeak' vocalisations were less frequently heard.

One of the most obvious appeasement gestures in primates is 'presenting' (ALTMANN, 1962; HALL, 1962; JAY, 1965), a posture which has become ritualized from its sexual context. In chimpanzees the presenting posture has acquired a graded quality which relates to the situation and the relationship of the interactants (VAN LAWICK-GOODALL, 1968). The only ritualized 'presenting' observed in this study was the overt 'presenting' posture preceding some 'rapes', which certain females made in response to the 'approach' of a sub-adult male. Such behaviour seemed to be motivated by the need to appease the male; however, presenting as an 'active' appeasement or reassurance gesture was not observed.

The 'hold-out-hand' gesture in orang utans, as it is performed by individuals other than mothers to their infants, seems to represent an appeasing-, rather than a reassuring element. Such 'hold-out-hand' gestures were sometimes directed at a human observer (see also DAVENPORT, 1967; and MACKINNON, 1974), presumably in its appeasing function. Several times we observed this gesture from different subordinate individuals (i.e. sub-adult males and adolescents) towards an adult male orang utan. In most cases, the gesture was accompanied by 'squeak' vocalisations. For example, we noticed twice that sub-adult males who advanced in view of the adult male O.J. 'held out their hand', apparently to appease the adult, before the male (O.J.) had directed any form of aggressive behaviour towards them. In one instance, the adult male nevertheless began 'threatening' the sub-adult male after having 'ignored' him for some 8 minutes. In the other case, the adult male tolerated the sub-adult male (i.e. Bobby) feeding within view. In a similar situation, the adolescent female Jet, 'held out her hand', in which she kept a twig laden with fruits she was eating, towards the approaching adult male.

The situation, where a subordinate seeks reassurance from a third individual after having been subjected to aggression from an associate, or from a human observer, was only rarely seen. The behaviour consisted of approaching and touching, 'embracing', and 'clinging' onto a third partner. Such reassurance seeking behaviour in tryadic interactions was observed only between offspring and their mothers, or from one partner in an affiliative bond towards the other. For instance, the adolescent male Mos reached back and 'embraced' his bond partner Doba, walking behind him, after he suddenly spotted the observer. On another occasion, the rehabilitant sub-adult male David was chased by his rival Doba (see p. 269). The rehabilitant male's behaviour expressed extreme tenseness and in the course of the confrontation, he suddenly turned to me, approached me and sat next to me grasping my hand. This, and our close proximity apparently relieved his tension as he calmed down.

Reassurance giving gestures or touching in a reassuring context, which appear to be regular communication patterns in chimpanzees (see VAN LAWICK-GOODALL, 1967) were rarely observed in the Ketambe orang utans. The 'hold-out-hand' gesture, when performed by a mother preceding 'gathering' may perhaps be regarded as such. Only once did we observe a rehabilitant sub-adult male, Sibujong, direct a hold-out-hand' gesture towards another groupmember (the crying adolescent female Tjali) in a reassurance giving context (see fig. 136).

The act of giving reassurance represents the initial stage of offering physical support to a partner. Other, more clear instances of support-giving have been

FIG. 136. 'Hold out hand' gesture directed at a group member in response to distress vocalisations by the latter (Sibujong and Tjali).

observed among the rehabilitant orang utans. For instance, 'screaming' of a juvenile male (Manis), who was cornered and threatened by a pig-tailed macaque, elicited aggressive support of the sub-adult male David, who rushed to the scene from approximately 60 meters distance and chased the macaque away. However, the reaction of outsiders to screaming was not always supportive. In another case, the 'crying' of a juvenile female (Marga), displaying a 'temper tantrum' at me, caused the young sub-adult male Bobo to chase her. Perhaps this latter case represents a form of 'winner-support', reminiscent of chimpanzee politics (F. DE WAAL, pers. comm. 1977).

Clear indications of submission (including 'squeak' vocalisations alone).

were observed about 20 times as frequent as instances of clear, aggressive types of dominance (including rapes). This may illustrate the low level of 'aggression' in the orang utan population in the Ketambe area. This was obviously due to the adequate spacing of individuals so that they avoided potentially agonistic associations. Gestures and postures that in other primate species are important for maintaining cohesion, such as appeasement and reassurence behaviours, are present, but used only seldom in the orang utan's behavioural repertoire.

4. INTERACTIONS BETWEEN AGE-SEX CLASSES

During this study it was quite clear that the different age-sex classes of orang utans in the Ketambe area played different roles in social interactions. The following paragraphs will deal with the observed interaction patterns in some detail.

4.1. ADULT MALE – ADULT MALE INTERACTIONS

Associations of adult males were not observed in the present study but on four occasions we witnessed brief interactions between adult males that had come into close proximity. All encounters between the males Gorm and O.J. took place in or near large fruit-trees. When we first saw the male O.J. in 1971, his cheek-flanges were not yet fully developed and he was presumed to be the youngest adult male in the area in 1973 and 1974. In size however, O.J. was nearly as large as the adult male Gorm and he was bigger than the adult male Mozes. During the first observed interaction between Gorm and O.J., in April 1972, O.J. left a large durian tree in which he had been feeding when Gorm came in sight. Shortly before Gorm had given a 'long call' vocalisation close by, but O.J. showed no obvious reaction. Two other orang utans, however, had left the tree in haste upon hearing the call. Gorm entered the tree with an 'ostentatious approach', and O.J. moved off rapidly after his companions.

On two other occasions we saw O.J. approaching a large fruit tree in which Gorm was feeding. When Gorm noticed the advancing male, he immediately started an 'ostentatious' approach' display and chased after the fleeing O.J. Gorm stopped his chase after some 100 meters, gave a 'long call' vocalisation and returned to the fruit tree. In both instances O.J. retraced his steps returning to within about 80 meters of the tree. His movements were cautious and he stayed well out of sight of the other male. On one occasion he waited 12 minutes before moving off silently; unfortunately we missed his retreat but it is likely that he walked away along the ground. On an other occasion he waited 28 minutes until the tree was vacant again and approximately 5 minutes after the other male had left he entered it and began feeding.

On a fourth occasion, we watched O.J. who was feeding in a strangling fig tree when Gorm approached. It was remarkable that quite some time before the male came into sight, O.J. showed clear signs of tension. He also made a threatening gesture towards the adolescent male Gin who had been feeding near him. When Gorm was still some 80 meters away and only discernible to us because of the waving vegetation, O.J. suddenly started an 'ostentatious approach' display in the direction of the swaying trees. However, he soon changed his display and fled when the other male reacted with a display and chased him. O.J. fled along the ground, followed by Gorm for approximately 150 meters. After Gorm abandoned his pursuit, he sat in a tree for approximately four minutes, staring in the direction of O.J.'s retreat and then gave a 'long call' vocalisation. A similar agonistic interaction, 'violent and brief' has been reported by HORR (1975); unfortunately he gives no further details of this episode. GALDIKAS-BRINDAMOUR (pers.comm. 1976) has observed a fight between two adult male orang utans.

The following series of events, occurring during the male Mozes's visit to the study area (usually occupied by O.J.), is also noteworthy, though they were not recorded as true interactions. The adult males Mozes and O.J. were found travelling and foraging approximately 50 meters apart on 22-9-1973 (fig. 137, (*)). Although each must have been able to hear the other moving through the vegetation, both males behaved as if unaware of the other's presence. For a period of several months following this incident when Mozes ranged through a large part of O.J.'s homerange, O.J. did not visit preferred fruit trees there. On 16 different days we were able to collect data on the location and movements of both males, matched with respect to the time of day to within one hour. These are shown in fig. 137. Although no interactions were observed by us, the two males appeared to keep well apart. In particular O.J. seemed to adjust his ranging pattern according to the other's movements so that contact was avoided. How both individuals knew of eachother's whereabouts is obscure, the distance between them was usually larger than 400 metres (see also p. 252). During this period, O.J. was only heard to call from places where Mo-

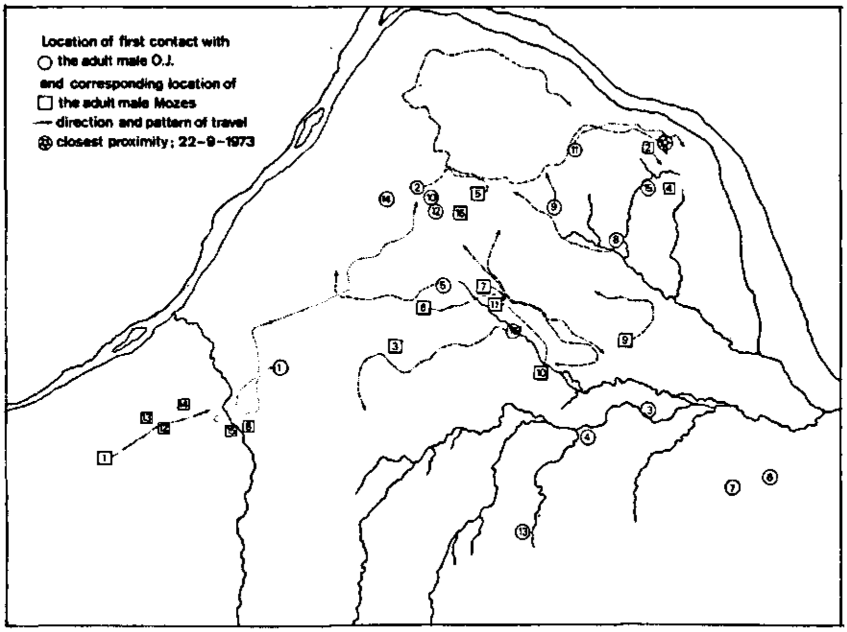

FIG. 137. 16 corresponding locations and some ranging patterns of the two adult males O.J. and Mozes in the period 20-9-1973/29-1-1974.

zes had not been seen, i.e. the south-eastern corner of the study area. On two occasions (fig. 137; (6) and (7)), Mozes reacted to O.J.'s calls by moving some 200–400 meters in the direction of these calls, where-upon he retreated again.

These observations add to the picture of intolerance between adult male orang utans reported in the literature (e.g. SCHLEGEL and MÜLLER, 1839–44; p. 12). Interestingly, MACKINNON (1974; p. 53) reports that 'on seven occasions more than one adult male fed in the tree at once, on three occasions actually arriving at the tree together'. Unfortunately details on these events are lacking in his report.

4.2. ADULT MALE – ADULT FEMALE INTERACTIONS

Adult males and adult females were observed together on 45 occasions. In most cases the encounters took place in or near large fruit trees. The females usually behaved in a submissive manner towards the males. If a female moved to a tree where a male was feeding, she usually entered with 'hesitant advance', making frequent 'squeak' vocalisations. On the other hand, if an adult male entered a tree where a female was feeding, she also would usually make 'squeak' vocalisations in response to his moves. When approached, she would move out of his way.

On one occasion the adult female Mif behaved in a more offensive way towards the adult male O.J., who entered the fig tree in which she was feeding. When the male had approached to within 12 meters of her, she moved a few steps in his direction, silently, then took a 'posturing' stance and fixed her gaze on him briefly. Quite remarkably, the male left the tree. On other occasions however, Mif and O.J. were observed to feed close together without any agonistic interaction.

The same male O.J. once chased the adult female Rom out of the tree in which both had been feeding peacefully for over 30 minutes. Suddenly the male gave a 'long call' vocalisation, started an 'ostentatious approach' directed at the female and chased her. After some 70 meters he gave up and called again. The female fled out of sight, while her juvenile offspring continued feeding during the entire episode.

The adult male Gorm and the female Josh were observed feeding in the same fruit tree for several consecutive days in two different fruiting periods. The two apes moved in close proximity but did not obviously interact other than that the female gave 'squeak' vocalisations when the male made a sudden movement. During the 16 days observation period both animals showed close coordination of movements. Since both individuals were not fully habituated to my presence it is impossible to decide whether their departures from the tree were coordinated avoidance reactions to my presence or represented a 'consort' relationship. I personally favour the former possibility, yet the animal's interaction pattern suggested a relaxed and close relationship.

Our data on groupings in the Ketambe area do not suggest any direct preference of females to gather around certain adult males, as has been suggested by MACKINNON (1974) for Sumatran orang utans. It is interesting, however, that the caution and tenseness, which was normally discernible in female-female associations, was considerably less apparent when an adult male was also present in the temporary association. In such cases females advancing towards a fruit tree showed no avoidance, hiding or waiting. This may mean that adult males have a stabilizing influence in temporary associations (cf. ANON. 1969).

Another phenomenon, perhaps indicative of a stabilizing role of adult males, was the following observation. The pregnant female Bin was seen to seek the close proximity of the adult male O.J. on two occasions when sub-adult males advanced towards her. She showed clear avoidance of sub-adult males during her pregnancy, even avoiding those who had consorted with her some two months earlier. When she sought out the adult male he made 'threatening' actions towards the sub-adult males who left the scene. The female did not display any attention-attracting behaviour towards the adult male, either during the incident or after the sub-adult males had left, as she had been seen to do before she was pregnant (see p. 269). The adult male and the female remained together for several hours; the initiative seemed to be taken by the female (FERNHOUT, pers.comm., 1974).

Several authors have reported on male-female encounters and associations (e.g. MACKINNON, 1971; 1974; RODMAN, 1972; HORR, 1975) but details on the animals' interactions and on the nature of the relationships are few. RODMAN (1972) has reported that an adult female urinated when the adult male she was associating with shook branches and moved. MACKINNON (1974) observed 'aggressive' and/or 'sexual' behaviour in this context, and he stresses the 'lack of interest' and the 'lack of friendly gestures' in other male-female encounter situations (p. 52–53). Interestingly, HORR (1975; p. 314) mentions interactions in which on 'many occasions' females with infants 'avoid or directly threaten adult males' but gives no details.

4.3. ADULT MALE – SUB-ADULT MALE INTERACTIONS

Adult- and sub-adult males were observed in close proximity on 15 occasions. Sub-adult males usually avoided approaching close to adult males and often stayed out of sight altogether. At times sub-adult males waited at some distance from a fruit tree until the adult male had left. On 6 out of 9 occasions when an adult male arrived at a food source where a sub-adult male was already present the latter immediately left the tree, often making loud 'squeak' vocalisations. Twice however, we noticed that the sub-adult male Roba fed peacefully in the same tree as the adult male O.J., once in 1971 and again in early 1972. Similarly, O.J. tolerated the sub-adult male Bobby feeding in the same large strangling fig tree (though at a distance of more than 25 m). The 'hold out hand' gesture made by the sub adult-male in this context is described on p. 281. On two other occasions, however, the same adult male (O.J.) chased the sub-adult male Doba from a large strangling fig tree immediately after the sub-adult male had entered. Apparently, adult males behave differently towards individual sub-adult males. Perhaps the age, as well as the family relationship of the two animals are important in this respect.

During his frequent visits to the rehabilitation station the adult male O.J. usually paid no attention to the rehabilitant sub-adult males, who used to keep at a safe distance. Yet, on two occasions we observed that O.J. directed an 'ostentatious approach' towards a rehabilitant sub-adult male. In one case the display was evoked in response to 'branch-waving' behaviour and several 'kiss' sounds on the part of the rehabilitant; the cause of the other display was obscure. Similar interactions between 'males' have been reported by MACKINNON (1974).

On the occasions when adult males and sub-adult males came into contact through mutual interest in a female, the adult male typically manoeuvred himself between the female and the other male, and, as a rule, supplanted the sub-adult (see 'circling').

4.4. ADULT MALE – ADOLESCENT INTERACTIONS

Adult males and adolescents were observed together on 27 occasions. Adolescent males were cautious in their contacts with adult males: in these associations they always positioned themselves so that they could easily flee from the tree at the slightest indication of aggressive behaviour on the part of the adult male. Once the adult male O.J. was observed to play (i.e. 'gnaw wrestling') with an adolescent in a fruit tree during a temporary association. The adult male hung from his feet above the adolescent male. The youngster took the initiative in the 'gnaw wrestling' bouts several times. Unfortunately, the adolescent could not be identified with certainty because the event took place during the early phases of the study (1971). MACKINNON (1974) has reported an observation of an adult male who 'frightened away an adolescent male by vocalizing at him' (p. 53).

Adolescent females were observed to be less cautious with respect to approaching adult males: they moved within closer range than adolescent males were seen to do and quite frequently approached to within contact distance. Like adult females, adolescents often gave 'squeak' vocalisations when they initiated a move close to an adult male or when the male made a sudden movement.

On four occasions in the period 1973–74, the adult male O.J. was seen in close association with the adolescent female Jet. The animals showed close coordination of movements and appeared to travel together at times. The female seemed to take the initiative by following the male. No sexual behaviour was noticed during these consortships apart from the female 'presenting' once. During one observed consortship the male showed no particular interest in the female, but once he suddenly directed an 'ostentatious approach' display towards me.[21]

[21] A very similar indicent took place in 1977 when VAN HOOFF (pers.comm.) elicited an 'ostentatious approach' and was chased by O.J. in an almost identical situation with Jet.

He had never shown such behaviour before and at that time he was fully habituated to observers. This episode suggests that he was not indifferent about the female's presence and I had the strong impression that he considered me as an unwanted intruder, perhaps even as a rival at that moment. In 1975 the two apes were observed in consort again and a copulation was witnessed (SCHÜRMANN, 1975; pers.comm.).

The males O.J. and Mozes showed no particular interest in the adolescent rehabilitants during their visits to the station. The first visit of the adult male Gorm to the station, however, seemed to result from his interest in the adolescent female Djahe, when she hurriedly returned to the rehabilitation station from the forest (October 1971). Most of the rehabilitant orang utans initially showed fear of the visiting adult males. After several visits by the male O.J. however, some female rehabilitants, namely Yoko, Djahe, Simi and the late adolescent male Usman were observed to have close contact with the adult male. These contacts consisted of approach to within arm's length, and in the case of Yoko and Usman of 'touch-smell' behaviour in the face to face mode. The adult male tolerated the rehabilitants and showed no signs of agonistic behaviour. In general it can be said that adult males appeared to be rather tolerant towards adolescents.

4.5. ADULT FEMALE – ADULT FEMALE INTERACTIONS

Adult females were seen in close proximity on 12 occasions inside-, and on 6 occasions outside the study area. A certain degree of coordination was discernible in a few cases, whereas most combinations had the appearence of chance meetings or temporary associations. Therefore, it seems relevant to discuss them separately.

On eleven occasions, adult females were found together feeding in the same fruit tree. The apes kept well apart during feeding although behaviour effecting increased inter-individual distance was noticed on only three occasions. Once a female was seen to direct elements of 'ostentatious approach' behaviour at the other. Behaviour displayed usually consisted of 'posturing', and 'fixed gaze'. Some adult females were reluctant to come close to certain other females as we saw on three occasions. When the adult female Josh was feeding in a large strangling fig tree, I noticed the female Bol travelling towards the tree, apparently intending to feed there. She suddenly stopped, looked for some seconds in the direction of the tree and then retreated some 20 meters. She waited there, well out of sight of the other female, and after approximately 10 minutes moved in a wide arc before stopping at the opposite side of the tree. After another 30 minutes Josh left the tree along a route which led her close to the place where the other female had waited 30 minutes before. Some 3 minutes after Josh had left, Bol entered the tree and started feeding. A similar incident involved the females Jane and Daisy. Daisy turned back on catching sight of the other female and left the surroundings of the tree altogether. In similar encounter situations on the other bank of the Ketambe river we observed that, although the females obviously avoided contact, their juvenile offspring entered the tree freely and might play with the feeding female's offspring or start to feed themselves. Similar observations have been reported by MACKINNON (1971) who saw juveniles play while their mothers stayed apart or even showed agonistic behaviour.

Females did not avoid temporary associations when an adult male was present in the tree. For instance we twice saw the females Daisy and Jane feeding in associations while the adult male Gorm was present. In one instance where a female was avoiding another she actually returned to the tree when an adult male joined the temporary association (this happened in the region northwest of the Ketambe river).

On two occasions we observed the adult females Rim and Daisy in close association for several hours; they travelled and fed close together and their movements were closely coordinated. The two females even waited for each other during travel. The relationship between these females seemed relaxed. Rim and Daisy may have stayed in each other's proximity for a considerable period. The two occasions we saw them in close coordination were little over a month apart. We also observed such closely coordinated adult female groups on two other occasions outside the study area. MÜLLER has mentioned that adult females with, or without offspring, may be found in groups (SCHLEGEL and MÜLLER, 1839–44; p. 13). RODMAN (1973) is the only recent author to have noted two adult females that fed and travelled in a coordinated manner.

Thus, despite the fact that most adult females appeared reluctant to approach close to other females, some may engage in affiliative bonds. Orang utans of the same age class may have affiliative relations which originated during their social phase of adolescence. Such a relationship existed for a long time between the rehabilitant female Bin and the wild female Jet; obviously such bonds can exist outside a family relationships. Yet, the bond between Jet and Bin broke up because of intolerance on Bin's part, which coincided with her sexual maturation (see p. 292). Perhaps in an atmosphere which lacks the potential for competition for mates, such bonds may re-establish.

4.6. ADULT FEMALE – SUB-ADULT MALE INTERACTIONS

Adult females and sub-adult males were observed together on 33 occasions inside the study area, and on 4 occasions elsewhere.

The socio-sexual relationship of these age-sex classes have been discussed in section 3.4. Some females are dominant over certain sub-adult males, others may be of approximately equal rank, and young adult females seemed to be subordinate to older sub-adult males (see also chapter 5: and fig. 138). We observed six interactions which indicated that adult females were dominant over sub-adult males. For instance, the female Josh supplanted the male Doba, even though she was disabled at the time. The male made several 'squeak' vocalisations and moved out of the way when she brachiated in his direction.

4.7. ADULT FEMALE – ADOLESCENT INTERACTIONS

Adult females and adolescents, other than the female's own offspring, were observed together on 30 occasions. In general, adult females showed great tolerance towards adolescents, even during first encounters with experimentally introduced rehabilitants. Sometimes rehabilitants were allowed to touch a female's infant and play with it. The tolerance mainly expressed itself in the absence of agonistic elements of behaviour during the close proximity of the adult female and the adolescent (see also p. 295). Usually such contacts took place during temporary associations but four times we observed that adolescent females followed close behind female-infant units. We had the impression that adolescent females were especially strongly attracted by infants, and that the females trailed behind mother-infant units in order to attempt to make contact with the infants. The adolescent females Jet and Sin both followed the mother-infant unit Mif-Mug. However, only Sin was seen to make contact with Mug, she stroked, touched and tickled the infant who at that time was approximately 9 months old. Jet was also seen to follow behind the mother-juvenile unit Rim-Rom. As far as could be judged from our observations on family relations of the Ketambe population, these adolescents were not directly related to the female-infant units they followed. Not only adolescent females displayed interest in infants. The rehabilitant male Bobo approached the female Mif during an introduction-experiment and was also allowed to touch and play with her infant Mug.

4.8. SUB-ADULT MALE – ADOLESCENT INTERACTIONS

Sub-adult males and adolescents were observed together on 63 occasions, of which 32 times in a real social context. Group size varied from 2 to 5 individuals and such groups contained individuals of both sexes. Adolescents and sub-adult males were the age categories which most actively sought social contact and formed social groups that might last several days. Within social groups individuals foraged together and were engaged in frequent social interactions, especially play. It seemed that relationships ensuing from such social groups were long lasting.

In large fruit trees, attracting temporary associations of orang utans, individuals might supplant one another from particular feeding sites. Such behaviour was observed from all age categories, but was especially notable in the social groups of youngsters. The individuals in social groups frequently watched each other, and supplanting attempts were sometimes indistinguishable from play invitations. It is noteworthy that we rarely had the impression that the availability of fruits at the site of the supplanted partner was the incentive for such behaviour. In particular when older individuals in such groups supplanted others, we had the impression that it concerned the assertion of social status, rather than active competition for food. The trees where such supplanting was observed were often enormous in size, with plenty of food in almost every location. Similar forms of supplanting in large food trees has been observed in several other primate species, e.g. chimpanzees (see WRANGHAM, 1975). Rehabilitant orang utans sometimes attended social groups of their wild counterparts and often the wild adolescent female Jet played a role in the initiation of contacts between wild- and rehabilitant individuals leading to such groups. Since 1972, Jet became a regular visitor at the feeding place of the rehabilitation station. Though she was later given provisions, her visits were undoubtedly aimed at seeking contact with some rehabilitants with whom she built up a positive social relationship. During her visits she often initiated play with several rehabilitants and in the course of 1973 she engaged in a stable, long lasting affiliative bond with the female Bin. On several occasions she became engaged in short lasting sexual interactions with sub-adult male rehabilitants, usually such interactions resembled 'rapes' in the sense that they occurred mainly during the first hour of every other of her visits. However, the interactions usually lacked a violent character and at times Jet clearly cooperated.

Thus, young orang utans seem to have a sociable tendency and engage in long lasting affiliative relationships. Adult orang utans, however, seem to lack such character. Some behaviour characteristics, mainly observed in the younger (socially immature) age categories, seem to present a suggestion for the mechanism underlying the change in social attitude from sociability to limited gregariousness, so typical of the stage of adulthood.

For instance, the termination of the affiliative bond between the rehabilitant female Bin and the wild female Jet appeared to coincide with the sexual development of the former. When Bin became sexually attractive and was consorted by the wild sub-adult male Doba, she became aggressively intolerant towards other females in her immediate surrounding, including her former bond-partner Jet. On a number of occasions she attacked the rehabilitant female Yoko and we observed her chasing Jet three times. Possibly the physiological (and related psychological) changes associated with becoming sexually mature can decrease the ability to form or maintain an affiliative bond with potential rivals in female orang utans. It is noteworthy that such a change was not so obvious in the maturing process of males: bonds between sub-adult males might endure. It is clear, however, that our observations on this process are too incidental to allow conclusions and only a long term monitoring of the development of young orang utans can give firm insight in this complex matter.

Increasing intolerance, coinciding with sexual development, which may be the cause of a break up of affiliative relationships is possibly foreshadowed by the intolerance evident in some triadic interactions among juvenile and adolescent rehabilitants. Perhaps its precursor may even be found in the intolerance displayed by juvenile primates towards males who copulate with their mothers.

For instance, several juvenile rehabilitants, notably the partners who actively sought the proximity and contact of the other in an affiliative bond, were very intolerant towards other individuals who came near, touched or attempted to play with their partner. The female juvenile Puk used to attack every other individual, including humans, who tried to touch or play with her older bond-partner Djahé. Even if the latter initiated play with another individual, the juvenile interferred aggressively, irrespective of the other animal's size or status.

Similar aggressive actions directed at a third individual were shown by the adolescent female Tjali. She had an almost obsessive attachment to humans and did not engage in any bond with a peer. She displayed aggressive behaviour towards other orang utans who got attention from people. On one occasion we observed that she even repeatedly rushed at the adult male O.J. with apparently aggressive intentions. The male was at that moment the subject of observations and consequently all our attention was focussed on him. The adult male did not react offensively towards the rehabilitant female and once even backed away when she approached.

Also the provisioning of rehabilitants might elicit similar forms of aggressive intolerance. Giving extra attention to one particular individual, which inevitably is included in the act of giving food, could evoke an aggressive action from another rehabilitant aimed at the receiver of the food (or attention). On several occasions the individuals displaying such intolerance had already been fed and were satiated.

As in the case of intolerance with respect to potential sexual rivals we had the impression that the latter form of intolerance was again much more obvious a part of the female's than of the male's behaviour. The examples cited all have a female in the active role. Yet, the aggressiveness of adult males towards sub-adult males and even to humans in triadic interactions involving a female, may reflect a similar attitude which can be considered analogous to human 'jealousy'.

There is little data on adolescent and sub-adult male relationships given in the literature. MÜLLER has noted that immature orang utans may frequently be encountered in small groups of two to three individuals (SCHLEGEL and MÜLLER, 1839–44).

> 'Buiten de tijd der paring leven de oude mannetjes van den Orang-oetan meest alleen. De onvolwassenen daarentegen, en ook de oude wijfjes, vindt men dikwerf ten getalle van twee of drie bij elkander; onder deze laatste zijn er somwijlen zelfs, die jongen hebben, ofschoon de dragtigen zich veelal, tegen dat zij moeten werpen, van de anderen afzonderen en gedurende eenigen tijd met hare jongen alleen blijven'. (SCHLEGEL and MÜLLER, 1839–44; p. 13).

MÜLLER's observation is confirmed in WALLACE (1869) who has mentioned that 'at other times, three or four young ones were seen in company' (p. 46). SCHALLER (1961) observed two adolescent orang utans together and concludes that 'adolescents may at times form social groupings' (p. 82): MACKINNON (1974) observed adolescents together on three occasions and a combination of sub-adult males and adolescents only once, but he must have had the impression that these age categories engage in social groupings more regularly since he treats 'adolescent-adolescent' and 'adolescent-male' linkages (p. 52) as a general pattern of orang utan behaviour.

4.9. REACTION TO DEAD CONSPECIFICS

Although 4 dead orang utans were found during the present study, of which three were rehabilitants, the reaction of rehabilitants towards a dead fellow was observed only once.

We noticed several rehabilitant orang utans displaying at something on the ground, and found the dead female Djahe partly hidden under herb vegetation immediately beneath them. The adolescent female apparently had been killed by a clouded leopard, which subsequently caught more victims among the rehabilitants in the months following this incident. Her wound had probably been made by a sharp claw, which left a neat, sharp-edged cut penetrating her abdomen. It was not clear whether the rehabilitants were reacting towards the dead female or towards an invisible predator or scavenger. Yet, as the corpse showed rigor mortis, and no fleeing mammals were heard nor seen, it is likely that the apes in the trees were reacting towards the corpse. When I approached, two rehabilitants followed suit, i.e. the sub-adult male David, highest ranking male in the group, and the adolescent male Seamus, who had had an affiliative bond with the female. David gently touched the corpse with his extended hand, sniffed his finger, and then touched the body again, nearer the wound. After sniffing his finger again, he turned and left the corpse. Then Seamus came near, he sniffed persistently at the dead female's nose, in a gesture resembling the 'face to face smelling' (see p. 202), and then sat next to the body peering at the face. After two minutes he stood up and moved away, only to sit down again 5 meters away. He sat there for some minutes, occasionally looking at the body and then suddenly reared up, grabbing and shaking vegetation and dragging a branch as he went. He approached David and initiated a rather vigorous playbout with him. Two other rehabilitants who had initially participated in the display did not come near the corpse, but watched the sub-adult male closely and followed him when he left.

On another occasion, the adolescent male Pon was found dead under a tree. He had a broken neck due to a fall and must have died instantaneously. The accident and possible reactions of other orang utans were not observed. Yet it was peculiar that the next day two rehabilitants were seen to pause at the place were the corpse had lain; they bent down and sniffed the ground carefully before moving on.

The dead wild orang utan female Josh was found in the study area. No other orang utans were present at the site or in the near vicinity. This animal had been an invalid for two months prior to her death; the reactions of other orang utans to her invalid state are described on p. 290.

The data presented here are limited indeed and only concern rehabilitant orang utans. Nevertheless they supplement similar observations on wild chimpanzees (TELEKI, 1973). I got the impression that orang utans had some awareness of the finality of death.

5. DISTRIBUTION OF RELATIONSHIPS IN THE KETAMBE POPULATION

In order to get a very rough idea of the relationships between the individual animals of the Ketambe population, I have considered two main categories of behaviour as observed between actor- reactor combinations of orang utans. In fig. 138 a matrix is given, showing the distribution of these behaviour categories over the observed individuals. On the one hand, submissive behaviour is considered, including elements such as 'hesitant advance', 'avoid', 'hesitant avoid', 'flight', as well as the more subtle submissive signals such as 'silent-pout' facial expression and 'squeak' vocalisation. Moreover, I included 'being raped' in this category. When an individual advancing towards a particular fruit tree suddenly made an obvious detour or turned back, while another individual was feeding in the tree, such behaviour was considered as avoidance. Such avoidance is easily overlooked in the fieldsituation, especially as the observer's attention is usually focussed on the ape that is already present

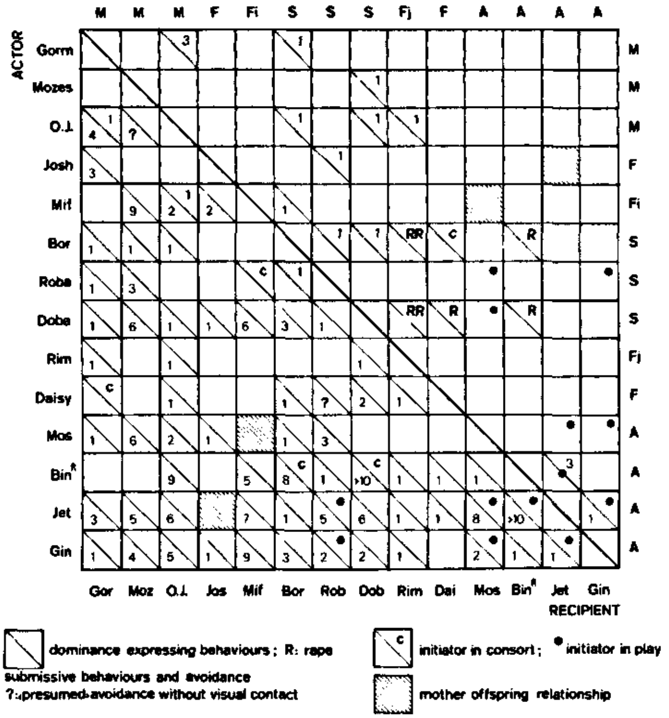

FIG. 138. The observed dominance and/or submission containing interactions between individuals of the Ketambe population in the period 1973–74. Some data concerning non-agonistic relationships is given in addition.

in the tree. Therefore, it is likely that this type of avoidance from some distance is much more common than the other, more obvious forms, and is under-represented in our data.

On the other hand I have considered dominance asserting behaviours, including complexes of behaviour such as 'bluffing', 'threatening' and 'attack'. Where dominance asserting behaviours were noticed, the submissive reactions of the partner have also been scored. Every instance in which an individual displayed behaviour which evoked a submissive reaction in the partner, such as for instance 'approach', is only scored as submission on behalf of that partner.

The picture emerging from these data only roughly illustrates the actual relationships situation. Important interactions in a socio-sexual context, affiliative interactions, play and even the lack of overt interactions between individuals in one another's close proximity (i.e. tolerance) undoubtedly play a role in the individual's relationships, not to mention the time-scale, during which social experience has been accumulated and the environmental context at any moment of interaction.

6. SUMMARY OF THE BEHAVIOUR PROFILES OF THE DIFFERENT AGE- SEX CLASSES

The obvious sexual dimorphism shown by orang utans as well as the clear changes in physical appearance during the successive life- stages suggest a clear differentiation of roles within the social organisation of this species.

The population studied consists of a fairly stable set of individuals whose interaction patterns gave the strong impression that they were familiar with one another. Individual homeranges overlapped to a large extent, or even entirely. Additions to the population were mainly through births. Experimental introduction of strangers (i.e. rehabilitant orang utans) indicated that in some cases such individuals can become accepted members of the deme. Adolescent orang utans may have a good chance to integrate themselves into an established unfamiliar population.

For convenience I have summarized the social development of the observed orang utans, referring to the life stages of adolescence-, sub-adulthood and adulthood, with some emphasis on the development of the male.

a. *adolescence*

After becoming independent of its mother, the adolescent individual spends several years before reaching sexual maturity. During this period the ape actively seeks contact with its peers and with sub-adult males to travel and play. Adolescents showed the highest percentage of engagement in groups; many of such groups may be considered as real social groups.

Adult individuals of both sexes are fairly tolerant of adolescents. This tolerance may make exploratory trips beyond the range of familiar individuals easier and could enable an adolescent to become acquainted with unfamiliar adults and gradually establish a suitable core area within a large homerange.

The frequent play interactions of adolescents and sub-adult males in the group setting may serve to establish (rank-)relationships with peers in a relatively non-violent manner.

We have no evidence that wild adolescent males showed particular sexual attention to females. Yet, rehabilitant males did, although they usually had no access to the somewhat older, sexually receptive females who rebuffed them.

The older, sexually receptive adolescent female on the other hand, employs considerable effort to arouse the sexual interest of older males, rather than that of her peers.

The ability to engage in affiliative bonds with peers appears to cease when the individual engages in sexual relationships. For females this is the period when they reach sexual maturity, in males it is during late sub-adulthood.

FIG. 139. The facial difference between (a) sub-adulthood (Sibujong) and (b) adulthood (O.J.).

b. *sub-adulthood* (fig. 139a).

Orang utans, especially males, require a further period to reach full social maturity which coincides with the dramatic development of their secondary sexual characteristics. During this stage, the sub-adult male continues to travel and play in peer-groups although his gregariousness gradually wanes. The sub-adult male has special attention for adult females with whom he establishes relationships, mainly by means of 'rape' behaviour. Adult male orang utans are usually intolerant of sub-adult males, especially in triadic interactions when a female is present; receptive adult females seem to avoid encounters with sub-adult males. The relationship of sub-adult males with adult females is complex, apparently reflecting a process of achieving a dominant position. Young sub-adult males were often subordinate to older females: older sub-adult males were usually dominant over most of the females they encountered (fig. 140).

c. *adulthood* (fig. 139.b)

At maturity, the male's appearance changes dramatically, and at the same time, his social attitude changes and he takes up the life style of limited gregariousness so typical of this species. Adult males become progressively less tolerant with respect to lower ranking males, both peers and sub-adult males, and they may even challenge the established males in the deme. The males ac-

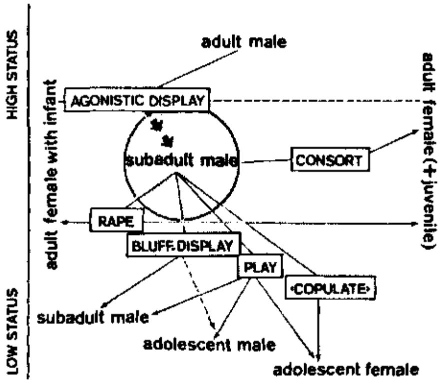

FIG. 140. The role of the sub-adult male orang utan.

tive interest in females apparently ceases; adult males were not seen to rape females. To assert his status he may direct impressive displays at other males and emit the typical adult male 'long call' vocalisation. The call gives information on the location and status of the caller, information which may be important in attracting receptive females and in spacing out adult males. Adult males are solitary only in that they do not join social groups. Adult males quite frequently engage in temporary associations with females and youngsters.

Similarly, adult females are rarely found in social groups outside the mother offspring unit. The adult female is occupied most of her life with rearing her offspring.

7. SOLITARY LIFE; SPECULATIONS ON THE EVOLUTION OF A PARTICULAR FORM OF SOCIAL ORGANISATION

Social organisation, whether of a low or a high degree of gregariousness may be seen as an adaptation to a certain niche in which the particular distribution of vital incentives in space, time and quantity in combination with predatory pressure are main determinants (EISENBERG, 1966; CROOK, 1970). Living in groups may have several adaptive effects such as the increase of food searching efficiency, of protection and defence, and it may facilitate reproduction and synchronization of reproduction. The adaptive effects are brought about in many cases by the transmission of information from one individual to another. Such information may concern for instance, the location of food resources (see RIPLEY, 1970) and sentry of predators (see KRUUK, 1964). Obviously, gregariousness may also be disadvantageous in as far as individuals with identical interests may compete for the same incentives (SCHOENER, 1971) and thus waste energy in conflict. Direct, active competition in general yields a dispersing force and thus, if gregariousness appears to benefit the animal most in an adaptive sense, an adequate balance between group-disruptive and group-cohesive forces will be reached by natural selection. The ethological litterature abounds with examples showing how adaptive compromises can be obtained and there are strong indications that almost every form of social behaviour bears aspects of agonistic tendencies between any two conspecific individuals. The relationship which is inevitable for reproduction between two sexual partners, as well as the parent-offspring bond, and eventually the peer-relationship can all have provided the basis for increasingly complex and graded qualities of behaviour that maintain the balance in both parties' interest.

In reproduction, it is obviously in the interest of each party to invest in the sexual partner that offers the best prospects of successfully developing that investment (see TRIVERS, 1972). Because of physiological differences in reproductive potential, this applies in particular to the part of the female, especially in mammals. Thus females have to follow a strategy, predominantly aimed at producing offspring of good quality, whereas males may follow a strategy, predominantly aimed at a large quantity of offspring. Such different interests lead to sexual selection, i.e. animals develop a preference for characteristics of the partner which can be indicative of its fitness.[22]

Perhaps the most primitive information sources of fitness are (a) an individual's physiognomy, which reflects his state of nourishment and health

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[22] As DARWIN (1871) has noted, not all characteristics resulting from sexual selection seem equally relevant. Sexual selection may lead to additional effects, which emphasise non-essential features or freakish characteristics, apparently permitted by the environment.

and (b) the quality of his range (see HARCOURT et al., 1976).[23] Both these parameters are affected by competition when vital resources are limited. Competition, which results in a dominance-submission relationship with reference to the time-factor, provides an important parameter for the relative fitness of mates at any one moment, as DARWIN (1871) has noted.

If ecological factors such as a particular distibution of resources and predatory pressure make gregariousness of vital importance for survival, the information about fitness should include measures of the gregariousness of mates as well. If sexual selection is governed by the need to increase transmission of information on the fitness of potential mates, a multi-male group structure is undoubtedly one of the forms which provide the most reliable information:[24] the female can form an almost continuous, cumulative picture of the fitness of her potential mates with whom she grows up in her group.

However, convening animals, especially males, with identical interests inevitably results in severe competition, unless the community accepts normative rules and values that set the pattern for interactions and relationships. In other words, the atmosphere in groups containing several mature individuals, – notably males – with identical reproductive interests, promotes the emergence of 'roles' (cf. BERNSTEIN, 1963). The mechanism by which such is achieved may be termed 'social selection' (cf. CROOK, 1972).[25] .

Thus, if the selection pressures of the ecosystem 'favour' the formation of groups, and sexual selection 'favours' the formation of multi-male groups, a new selective force, associated with the norms and values, set by a group of more than two reciprocally dependent individuals, can be brought about. In other words, natural selection is the ultimate pinciple: the ecological- and eventually the social niche provide derivate selection mechanisms as sexual- and social selection.

It then follows that animals develop a preference for characteristics of the partner which are indicative of its fitness in the context of the 'in-group', i.e. the quality of potential mates may become measured in terms of aspects of positive social relations, or in 'bond-servicing' abilities, as much as in the straightforward (agonistic) measures of dominance. For instance, the prestige[26]

[23] For birds, see VERNER and WILLSON, 1966; and VERNER and ENGELSEN, 1970.

[24] The multi-male group may be seen as an advanced and almost unique characteristic of the higher primates (CARPENTER, 1954; CROOK and GARTLAN, 1966). A similar trend for association in reproductive males, perhaps to increase the possibilities for females to chose a mate that displays maximal fitness relative to others, is the 'arena' or 'lek' system that evolved in some ungulate and some bird species. For, in addition to the location of the male's territory, his physical presence and competing skill relative to that of the others are almost continuously at display.

[25] In The Descent of Man, DARWIN (1871) discussed some of the important effects of this type of selection in groups of people.

[26] As a parameter correlated with reproductive succes.

of a chimpanzee individual seems to be determined more by the subtle ways he achieves a dominant position, and by his positive social relations with others,[27] rather than by physical strength and vigour (see VAN LAWICK-GOODALL, 1968, and BYGOTT, 1974).

On the basis of the stabilizing core of groups in different primate species, one can imagine the evolution of multi-male groups as follows:
(a) they may have derived from one male groups (EISENBERG et al., 1972), in which offspring, and eventually perhaps other relatives become tolerated for life; and
(b) they may have arisen from aggregations of one-male units.

One striking aspect of the chimpanzee's multi-male structure, namely the stability of the male community in time, as well as the exceptionally long mother offspring bond (see VAN LAWICK-GOODALL, 1968) suggests an evolution along the line (a) that I sketched first, namely the 'extended' one-male group. The hylobatids with their monogamous family structure in which offspring is tolerated until adulthood, and the gorilla with its social structure that consists of a dominant male with its females and subordinate sons[28] (see HARCOURT et al., 1976), may be seen as early stages in an evolutionary process which can ultimately lead to a multi male structure such as that of the chimpanzee.

On the other hand, the multi-male groups of the cercopithecoids are characterized by more fluidity and allow for changes especially in the male composition. Langur groups in particular are stable reproductive 'sisterhood' units, difficult for alien females to join (BLAFFER HRDY, 1974). It may be conjectured from the extensive studies of baboon social structure (e.g. WASHBURN and DE VORE, 1961; ROWELL, 1966; HAUSFATER, 1975) that the multi male group of cercopithecoids has evolved along the line of aggregating one-male units, much the same as the temporary formation of – nocturnal – aggregations of hamadryas baboons (see KUMMER, 1968).

In theory, the information concerning the fitness of potential mates in a structure that allows for a changing male composition may be less reliable, notably in the aspect of sociability, and hence the accent in e.g. the female's partner choice may be on competitive dominance and physical appearance.

However, such a theoretical trend towards reliability of information with respect to sociability of potential mates is apparently not the rule, even in chimpanzee communities. It has been observed that young primiparous chimpanzee females may transfer into other communities, apparently for reasons of reproduction (PUSEY, 1977) and perhaps make their choice of a sexual mate according to the 'primitive' parameters of physiognomy and dominance rank. Similar choice parameters seem to play an important role in adolescent females of the human race, despite an even more sophisticated information transmission system. Undoubtedly, such a mechanism guards against a too high degree of inbreeding in the group of related individuals. On the other

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[27] Ability to raise support in agonistic interactions.

[28] Which are perhaps tolerated until their – reproductive – interest clashes with that of their father.

hand, inbreeding in combination with active 'social selection' (e.g. infanticide (see DICKEMAN, 1975)), 'raiding' behaviour, and warfare) may allow for a comparatively rapid evolution of particular characteristics. It seems not impossible that the comparatively rapid development of the genus *Homo* has been achieved by means of these interacting processes (see also FOX, 1972).

I have given this rather extensive introduction in order to add some speculative thoughts to the hypothesis, put forward by JOLLY (1973), that the increase in neurophysiological organisation has evolved because of a more complex social life-style as a biological function of increasingly complex ecological survival. As said, the orang utan's social organisation of relatively great individual independance is highly exceptional among primates. It has even been characterized as a comparatively 'simple' lifestyle (see e.g. MACKINNON, 1974). On the other hand, the orang utan shows a remarkable similarity in intelligence with the gorilla and the chimpanzee (see RUMBAUGH, 1970; and RUMBAUGH and GILL, 1972). Following the above suggestion, this could indicate that sociability in the orang utan was at one time more strongly developed, than it is nowadays.

This raises the question which selective pressures have forced the social attitude of this species towards a less social lifestyle. In the following paragraphs I shall consider possible selection pressures which may have led to the presently acknowledged 'solitary' lifestyle or the limited gregariousness as I would like to name it.

The investigation is based on a comparison of some of the seemingly most relevant environmental variables of the three allopatric species *Pongo pygmaeus*, *Pan gorilla*, and *Pan troglodytes*; occasionally I shall include other close relatives in this comparison, such as the hylobatids and *Pan paniscus*. To this end, some of the variables concerned will be discussed in detail. First a few characteristics of the species (A) will be considered, namely

1) the social attitude, and
2) sexual dimorphism,

secondly, as the environment and the species' characteristics will influence and modify one another, I shall pay attention to the parameters that reflect the inter-relations of animal and environment (B). In addition to those specific parameters, such as biomass, home range size, distance travelled per day and the ratio between feeding and travelling time, which express aspects of food-availability and foraging efficiency, I discuss the degree of arboreality of the orang utan. Finally, the most relevant environmental variables and their influences (C) will receive attention, namely:

1) distribution of food resources, and
2) predatory pressure.

Some fifty percent of the larger mammal species (i.e. those exceeding 15 kilograms of adult weight) in the South-East Asian rainforest have a social organisation which is characterized by a relatively great individual independence. Thus, a so called solitary lifestyle is by no means an exceptional condition in this habitat. Yet, solitary life is highly exceptional for a higher primate and such a condition in orang utans, confirmed by all field studies since the pioneer study of MÜLLER in 1828–1836 (SCHLEGEL and MÜLLER, 1839–1944), generates a number of questions with respect to the functional aspects of this particular form of social organisation for a primate.

The orang utan distinguishes itself from other solitary forest species by its slow ontogenetic development and long mother-offspring bond, a characteristic which it shares with its more gregarious relatives. The only animals in the phylogenetic lineage of the orang utan which show similarities in the aspect of a great individual independence are to be found among the sub-order of the prosimians (see also RODMAN, 1973).

As both LEYHAUSEN (1965) and SCHALLER (1967) have stressed, solitary mammals often have a communal organisation, much the same as those that live in groups. The individuals living in a certain region are familiar with each other, may maintain a dominance hierarchy and, in general, may be well aware of each other's whereabouts. It thus appears that the differences between gregariousness and solitariness in mammals are mainly of degree.

From the descriptions of the orang utan's behavioural repertoire given in the present study and other references (e.g. MACKINNON, 1971; 1974; JANTSCHKE, 1972) it is clear that this ape displays nearly all the elements which are to be found in the chimpanzee (cf. VAN LAWICK-GOODALL, 1968, and VAN HOOFF, 1971).

Although a comparative analysis of the 'application' of these similar elements in both species has not yet been performed, I have the impression that several aspects of the behavioural repertoire of each ape differ mainly in quantitative degree, i.e. the occurrence of particular elements is less frequent, and the context in which such elements are displayed differ only in minor respects. Notably elements of behaviour with an appeasing- or reassuring function (i.e. 'mouth-to mouth', 'embrace', 'hold out hand', 'allogrooming', etc.) which are employed by chimpanzees in a variety of social contexts, were displayed by orang utans in particular, restricted contexts such as play (i.e. 'mouth to mouth') and occasional bonds (i.e. 'embrace' and 'allogrooming') only. Appeasement gestures have an important 'bond servicing' function in chimpanzees. It is remarkable that many of these behaviours were displayed almost exclusively by young orang utans, it may be significant that some behaviours such as e.g. allogrooming were most frequently observed of –, or in interactions with rehabilitant individuals, i.e. those apes who were forced in more or less continuous gregariousness because of the food provisioning and the lack of a relation with a mother.

Thus, notwithstanding an almost identical behaviour repertoire, the social organisation of the orang utan is strikingly different in many aspects to that of the chimpanzee. This is particularly expressed in the rigid maintenance of a large interindividual distance between adult males.

The social organisation can be seen as the consequence of the behavioural characteristics of a collection of individuals that compose a deme. These characteristics, of which the degree of tolerance towards potential competitors is a good example, will be determined by 'set points' or 'norm values', which undoubtedly show phenotypic variability, and probably are subject to phylogenetic constraints, modified by the various selection mechanisms that constitute natural selection. One could imagine that the striking difference in social organisation between the orang utan and the chimpanzee is determined by gradual differences in social attitude, which are not the result of different behavioural mechanisms, but of a different tuning of the 'norm values' of these mechanisms.

Although reports about serious experiments to convene two or more adult male orang utans are lacking, the general opinion in zoos is that adult male orang utans are incompatible (BRANDES, 1939: JANTSCHKE, 1972), even when the individuals have been raised together for a long time. This suggests that the social attitude of this ape species cannot easily be modified by experience and other learning processes. However, the rather anecdotal nature of the data with respect to this interesting issue make conclusions premature. The role of social experience in the ontogeny of orang utans certainly deserves more intensive attention. It would be worthwhile to know whether individuals that have had the opportunity to live in peer groups for longer periods of time, and thus, escaping from the natural and traditional situation of social deprivation in their ontogeny, could not develop into more gregariously oriented animals. Rehabilitant individuals may provide excellent subjects for such an experiment.

In a comparison of the social attitude of the great apes, a fruitfull approach may be to distinguish between individuals from their own group, usually relatives, and those outside the group. I shall refer to these as 'in-group', and 'out-group' conspecifies respectively (cf. SHERIF and SHERIF, 1953).

Orang utans maintain the largest inter-individual distance among the apes; tolerance on part of adult males towards other recognizable males, (i.e. subadult, and adult males) was virtually absent.

The male mountain gorilla tolerates certain males within his group, namely those who are almost certainly his offspring (HARCOURT et al., 1976), but he maintains a large inter-individual distance towards 'out-group' males. The tolerance within the group could perhaps better be characterized as indifference (SCHALLER, 1963).

Chimpanzee males maintain a strikingly high degree of tolerance towards other males within their group and show even coordinance and supportive male-male relations (VAN LAWICK-GOODALL, 1968; BYGOTT, 1974). Yet, despite such tolerance, a certain tension is apparent within a chimpanzee male-community, even under 'normal' circumstances (BYGOTT, 1974). Such tension may perhaps be related to status maintenance of the community members in close proximity. Towards 'out-group' males,[29] however, they may maintain a large inter-individual distance and even show active antagonism in the form of violence or mortal assault (GOODALL, 1976). [30] It is likely that such behaviour represents the precursor of 'raiding' behaviour (i.e. head-hunting, 'mob-violence', and warfare) in humans (RIJKSEN, in press).

Still, peaceful or indifferent interactions between male parties of different communities have also been reported (IZAWA, 1970; NISHIDA, 1970). Perhaps the degree of familiarity with individuals or parties of the out-group and/or, the numerical size of such parties determines the degree of inhibition of hostility in encounters.

In contrast to the male-male relations of orang utans and chimpanzees, those between females show considerably more resemblance. In both species, gregariousness among adult females seems rather poorly developed. Unless they are sexually receptive, their attendance to groupings or associations remains restricted or occasional.

With respect to the inter-individual relations in general, the most marked similarities are between the orang utan and the (mountain) gorilla. Several authors have stressed the paucity of social interactions between orang utans in associations. Similarly, SCHALLER (1963) was struck by the paucity of interactions within the gorilla groups he observed. The males 'ignored' each other most of the time and when interactions did occur, they generally concerned dominance assertion.

Hierarchical patterns in the relations are apparent in all three apes, and males may play a 'control-role' (cf. BERNSTEIN, 1966) towards subordinates. As I have described on p. 290, some observations suggest that orang utan females were more tolerant towards other females when an adult male was present in the temporary association (see also ANON., 1969). A similar phenomenon has been observed in chimpanzees, even with respect to 'stranger' (i.e. 'out-group') females. When such females from neighbouring communities transfer into a group, they usually stay closely to the resident males; when travelling on their own, they are liable to severe attacks by resident females. (PUSEY, pers.comm., 1975; see also NISHIDA and KAWANAKA, 1972).

This comparison of social attitudes already suggests that the tendency to expell 'out-group' conspecifics, particularly of the same sex, from their per-

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[29] It is interesting to notice that earlier accounts on the social organisation of chimpanzees suggested a pattern of continuously overlapping ranges of both males and females (VAN LAWICK-GOODALL, 1968). I have presented an identical model for the organisation of orang utans as observed in the Ketambe area. More recent studies on chimpanzee organisation, however, have revealed that, although the individuals are distributed in personal home-ranges, they are grouped in rather fixed communities or 'unit groups' of familiar individuals who share a communal range (NISHIDA, 1968; SUGIYAMA, 1968; SUZUKI, 1969; BYGOTT, 1974; WRANGHAM, 1975).

[30] Similar forms of infanticide and mortal assault have been observed in mountain gorillas (HARCOURT, pers. comm., 1975; FOSSEY, 1977).

sonal or the 'in-group's' sphere, is common to all apes. This phenomenon possibly finds its most conspicuous expression in the behaviour of the males.

In the hylobatids, the personal space is rather clearly defined in topographical terms, and can be called a territory (see CARPENTER, 1940; ELLEFSON, 1968); CHIVERS, 1972). The personal spaces of the other apes are less rigidly defined topographically,[31] but stretch as far around the individual(s) as visual and especially vocal signals carry. The three great apes all employ a long ranging, loud calling, which is exclusively, or almost exclusively emitted by the adult male individuals in the community. Such calls undoubtedly serve to advertise the location of the caller to both the familiar 'in-groups' members, as well as to strangers or 'out-group' conspecifics, and thus serve in regulating the distribution of individuals (cf. 'pant-hoot': chimpanzee; 'hoot series': gorilla; and 'long call': orang utan). Chimpanzee, and orang utan males emit such calls regularly during their ranging or patrolling through the home range, gorillas add visible cues to their calling by their conspicuously destructive foraging habits (FOSSEY, 1974; CARO, 1976).

Chimpanzee males of one community together maintain a 'community range' (BYGOTT, 1974) or 'unit group range' (SUZUKI, 1969), which is patrolled at regular intervals by small male groups. Similarly, young gorilla males may establish their own space before they form a group, mainly by immediate methods such as circuitous routing and trampling of the area (FOSSEY, 1974).

The three observed adult male orang utans in the Ketambe area had largely overlapping ranges, but the behaviour of a male to the calling of another in the overlap zones invariably suggested agonistic tendencies (see p. 234). This comparison of behaviours related to the intrusion of the personal space suggests that the orang utan male represents one extreme case of the scale of variation; after becoming adult and on the summit of his status, the male expells all other males from his range as far as he is able to perceive their presence. He regards all other males as 'out-group' conspecifics, so to speak. At the other extreme there is the adult male chimpanzee. He shares a communal space with some associates, but, like the other apes, expells all other males who do not belong to his community from that space, with the proviso that he is opportunistically able to do so, i.e. by acting cooperatively against a minority.

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[31] Obviously, territoriality is only feasible when the size and topography of the range is practicable in the owner's exclusive use. Certainly, the size of an orang utan's home-range in combination with the view obstructing structure of the rainforest make exclusive use of the area almost impossible. That is, unless they employed olfactory marking. It is noteworthy that orang utans, and in particular males, have a well developed sternal gland in their early youth (see also SCHULTZ, 1921). During adulthood this gland seems to become hypotrophied. No particular behaviour with respect to this gland was observed during the present study and its function remains obscure. Other primates which reportedly have a sternal gland are: *Tupuya*, *Galago*, *Mandrillus* and *Ateles*. Note that all these are rainforest species.

Sexual dimorphism

The orang utan shows a remarkable, strongly developed sexual dimorphism both in physiognomy as well as in size and weight. Males are about twice as heavy as females and posess impressive features in the form of lateral extensions of fatty tissue on the head and extra long hair on the arms and along the lateral sides of the back. Among the primates, the orang utan shows one of the most marked forms of sexual dimorphism, which is only matched by some baboon species and perhaps by the gorilla.

Marked sexual dimorphism in size is usually found in gregarious or temporarily gregarious, polygynous mammals. The most notable exception to this rule – at least in the South-East Asian region – is the orang utan.

General size of a species may have a function in the inter-specific relations. If predation is sufficiently intense to constitute a significant selective pressure, increase in size – 'outgrowing the predator' – may be one of the adaptive answers. For instance, the orang utan may be too large a prey for the clouded leopard. Another answer may be increased agility, as is so obviously displayed by the gibbons. In other words, predator selection, rather than sexual selection or social selection mechanisms, is responsible for such a phenomenon. However, if sexual selection in a species has resulted in extremely fierce males, the side effect of such differential size of males may again be advantageous in anti-predator behaviour, as has been described for baboons by WASHBURN and DE VORE (1961). It is not necessary to assume a group protective function of males, to account for the emergence of such size dimorphism, as was originally postulated by WASHBURN and DE VORE, (1961) (see STRUHSAKER, 1969; ALTMANN and ALTMANN, 1970).

Similarly, an 'important group-protective role of the adult male' of prehistoric, perhaps more gregarious orang utans does not implicitely follow from the alleged 'greater sexual dimorphism' of that ancient race, as postulated by MACKINNON (1974; p. 68). Before accepting such an explanation we should investigate whether the significance of the marked sexual size dimorphism cannot be found primarily in the intra-specific sphere.

The size, the obvious facial mask and the conspicuous tree swaying associated with the weight transfer during locomotion – and displays – of the adult male make him clearly recognizable from quite a distance. Our observations on the reactions of – even naive rehabilitant – orang utans to large adult males indicate that their size and 'weighty' demeanour inspires great awe in social partners; smaller individuals invariably showed clear signs of submission or outright avoidance in encounters with adult males. At the same time it seems to exert a strong attraction onto potentially receptive females. Although adult males cannot possibly control the reproductive behaviour of other orang utans within their range, and although there is as yet only weak evidence showing that receptive females mate primarily with adult males; no doubt, female preference is responsible for the sexual selection that perpetuates and strengthens the dimorphism. The adaptive significance of such preference is that it makes the female invests her reproductive effort in a contribution of a male that has proven its competence. The Sumatran rainforest ecosystem apparently 'allows' the adult male orang utan's 'handicap' (cf. ZAHAVI, 1975) of extraordinary weight and size.

It is evident that the ecological needs of the sexes can be different as a consequence of the size dimorphism; that size dimorphism separates the sexes ecologically holds for a large number of animals. However, the observations on feeding behaviour of orang utans (see p. 82) suggest that the special techniques, employed by this ape during food gathering do not lend support to the idea that males are significantly constrained through their extreme dimorphism. Terminal branches laden with fruits were as easily reached by adult male – as by female orang utans, usually by means of the bending-breaking technique.

The degree of sexual dimorphism in the apes appears to be related to the social attitude of adult males towards their 'in-groups' members. Only the hylobatids provide a special case. The gibbon family shows the least sexual dimorphism. This seems to accord with the general trend that monogamous animals,[32] where both partners contribute to rearing the offspring (see CHIVERS, 1974), are perhaps subjected to less severe sexual selection. Possibly the quality of the range of a young debutant male is among the main parameters in the mate choice of gibbon females.

7.2. INTER-RELATIONS OF ANIMAL AND ENVIRONMENT

In theory, individuals (or groups) have to find a balance between occupancy of the appropriate parts of the habitat and minimizing competition with others, that have identical or almost identical ecological needs. This in combination with the advantage of an established, familiar area, may result in a mosaic distribution of home ranges with contiguous or minimally overlapping boundaries. ALTMANN and ALTMANN (1970) have argued that the amount of home range overlap will depend primarily upon those essential resources that have the most restricted spatial distribution.

As I described on p. 307, both orang utan, and chimpanzee individuals of both sexes live in home ranges that overlap extensively with those of their fellows in the deme. On p. 69 I demonstrated that the availability of food in particular is perhaps as dispersed in space, in time and in quantity for the orang utan, as it is for the chimpanzee.

Several factors may determine the upper limit to the size of a home range in a patchy habitat; the lower limit to the size is undoubtedly determined by the sparcity of resources (see ALTMANN and ALTMANN, 1970).

Thus, a comparison of the smallest observed size of home range of related

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[32] DENHAM (1971) has argued that in the case where resources are dense, and their locations and seasons predictable and defendible, the optimum strategy for animals is 'double defence', i.e. a monogamous, territorial lifestyle. If this hypothesis fits the gibbon, and the siamang, it is difficult to understand why the orang utan with a strongly corresponding diet, in the same habitat lives a polygynous, solitary lifestyle.

species which utilize similar food resources, may give some indication of the relative sparcity of such resources within the respective habitats. According to presently available data, a chimpanzee female occupies a home range or year range of approximately 8 square kilometer (WRANGHAM, 1975), the smallest observed range of orang utan females amounts to 0.6 square kilometer (RODMAN, 1973): the smallest female range in the Ketambe area was approximately 2 square kilometer. The figures for the gibbon and siamang are 0.4, and 0.2 square kilometer respectively. The folivorous gorilla covers a year range of approximately 5 square kilometer (FOSSEY, 1974).

MCNAB (1963) has demonstrated for a large number of mammals that, given their mode of food gathering, namely 'hunting', or 'cropping', the size of the home range is linearly correlated with body weight. Among the apes, only the gorilla fits the definition of a 'cropper', the others are frugivorous 'hunters'. According to MCNAB (1963), the home range of a 'hunter' is four times as large as that of a 'cropper' of the same weight. As the orang utan and the chimpanzee have almost the same range of body weights, i.e. 30–70 kilograms, and almost identical feeding habits, the application of MCNABS's equation would result in an almost identical prediction of both species' home range size. This does not concur with the observed situation. ALTMANN and ALTMANN (1970) have pointed out that 'in making intra-specific comparisons within a small range, other factors may have an overriding influence' (p. 202). Evidently, the same applies to the inter-specific comparison of both ape species. If both species had a similar mode of life, the large discrepancy in range size might suggest that the S.-E. Asian rainforest is richer in terms of vital resources for orang utans, than the African woodland savanna habitat is for the chimpanzee.

Irrespective of the size and extent of overlap of home ranges, the carrying capacity of the area sets an upper limit to the biomass of individuals. A full comparison of the three great apes, with the aim of obtaining insight into the carrying capacity of the respective habitats, is difficult to make because of the considerable variation in data from different areas. As I noted in section 1.2, the figures given by different authors for the population density of orang utans in rainforest areas range from less than 0.1 individual per km sq., to 5 orang utans per km sq. Population density of chimpanzees in different types of habitat, ranges from 0.3 individuals per km sq. (Rio Muni; JONES and SABATER PI, 1971) to 7 chimpanzees per km sq. in Budongo forest (Uganda; SUGIYAMA, 1968; see also KORTLANDT, 1972). Thus, biomass in orang utans may be as high as 140 kg/km sq. When correcting the mean weight according to the age and sex composition of sub-groups, the biomass of chimpanzees may be as high as 200 kg/km sq. in African rainforest and as high as 72 kg/km sq. in the woodland savanna habitat (i.e. Gombe Stream National Park, where the population density amounts to 2.5 individual per km sq.; WRANGHAM, 1975). Obviously, figures for biomass should be interpreted with some caution, as small changes, or differences in the population composition contributing to the density figures, result in considerable changes in biomass figures.

Comparison of the biomasses of chimpanzees and orang utans results in the suggestion that, in approximate order of carrying capacity, the respective habitats can be ranked from high, i.e. African rainforest, for chimpanzee, to medium, i.e. Sumatran rainforest, for orang utan, to low, i.e. African woodland savanna for chimpanzee. It is important to realize that these figures represent the situation for the respective species, and does not represent the absolute carrying capacity of the respective habitats. No doubt the South-East Asian rainforest is richer in fruit productivity than the African forest, as may be inferred from the more numerous food competitors, both in species and in individuals in the orang utan's situation as compared with that of the chimpanzee. In other words, although the Sumatran rainforest offers a larger food-availability, the orang utan apparently has not been able to take a greater share, due to the competitive effects of other frugivores occupying an overlapping (or contiguous) niche.

One interesting aspect of the comparison given above is that differences in the carrying capacity of different African habitats have not affected the social organisation of the chimpanzee populations concerned, to a significant degree. The 'in-between' position of the Sumatran rainforest condition for the orang utan suggests that there is no direct relation between carrying capacity and social organisation in ape species.

Although the mean length of the day journey is influenced even more by social factors, it may serve as a measure for the relation of the animal with its environment. In theory, the mean length of the day journey depend upon those vital resources with the sparsest and most restricted distributions (ALTMANN and ALTMANN, 1970). When comparing species with an identical, or almost identical 'mode of life', such as certain macaque- or baboon species, it may be valid for acquiring information on the habitat. The parameter, however, is useless for a comparison of 'solitary' orang utans and 'gregarious' chimpanzees. Even though both apes have at times very similar patterns of social organisation with respect to feeding, i.e. temporary associations, their respective modes of foraging and travelling between food sources are too divergent to make such a comparison valid.

An individual that 'hunts' (cf. McNAB, 1963) in association with many others has to cover a distance which is longer, proportional to the number of associates, than an individual that hunts alone. That is, provided the food is equally distributed in both cases, and both have equal needs (see also PIANKA, 1974). Thus, the average day range of a chimpanzee, i.e. 3000 (WRANGHAM, 1975) – 4000 meters (JONES and SABATER PI, 1971), in comparison with the 500 (MACKINNON, 1971) – 650 meters (this study) covered by an orang utan, may reflect more of the 'mode of life' of the respective species than of their habitat and the food therein.

Yet another measure of the relation animal-environment is the ratio of feeding to travelling time, proposed as a valuable parameter by RODMAN (1971) and MACKINNON (1974) (see also WRANGHAM, 1975). I present a comparison of these ratios in table 20, as drawn from the literature.

TABLE 20. The daily activity budget concerning feeding and travelling.*

	Feeding	Travelling	Ratio: F/T
Sumatran orang utan:			
Ketambe area	49.3%	12.2%	4.0
Renun area (from MACKINNON, 1974)	54.1%	20.5%	2.6
Bornean orang utan:			
Kutai reserve (RODMAN, (1973)	45.9%	11.1%	4.1
Segama area (from MACKINNON, 1974)	38.7%	20.9%	1.9
Chimpanzees:			
in 'forest' (WRANGHAM, 1975)	55.3%	13.4%	4.1
in grass land (WRANGHAM, 1975)	56.1%	15.8%	3.5

* 'Feeding' in the present study includes instances of 'foraging', i.e. the searching activity employed to feed on small scattered food-items.

'Travelling' in the present study is defined as moving beyond the crown of one particular tree, and thus is distinguished from 'moving', which encompasses all changes of location by means of locomotor activity.

Notwithstanding the fact that the figures are very suggestive, great caution and reserve is required in their interpretation. Only small changes in the relative frequencies of feeding and travelling time, due to different criteria during observations, result in considerable changes of the ratio. One important drawback of this ratio is that it requires the use of very strictly defined terms to make it a valuable measure in a comparison. For instance, I noted on p. 53, that when recording 'foraging' under field conditions, it is almost impossible to distinguish between the time spent in the actual consumption, and the time spent in search for small scattered food items (e.g. insects) in the course of travel. In addition, the term 'travelling' may be interpreted as any locomotor activity, or as moving beyond the crown of a particular tree. It is relevant to note that those studies which made use of the ratio did not give strict enough definitions of these terms to allow reliable inter-study comparisons. However, the range of the data given in the comparison, perhaps permit the suggestion that both the orang utan and the chimpanzee spend almost equal proportions of their daily activity in feeding and travel. In combination with the data on day journeys, this may reflect the observation that ground walking is a much faster, and presumably more efficient way to cover a certain distance than arboreal travel. Perhaps this allows the speculation that animals, heavier than a certain weight class and concomittant degree of arboreal agility can simply not afford to be gregarious and arboreal at the same time, as arboreality does not allow the necessary degree of travelling efficiency.

Arboreality

Foods, especially fruits, are most abundantly available in the higher strata of a rainforest. All apes, including even the terrestrial gorilla and man, are excellent climbers.

The orang utan is the largest and heaviest truely arboreal primate; it shows remarkable anatomical adaptations to this arboreal lifestyle, such as curved phalanges and extraordinary long arms (SCHULTZ, 1968; NAPIER and NAPIER, 1967). These are adaptations which might indicate a long arboreal history.

As a rule, the heavier primate species, with a body weight exceeding 15–20 kilograms are more terrestrial. Examples are the pig tailed macaque, the baboons, including the drill and the mandrill, the chimpanzee, the gorilla and man. Only the gorilla and man exceed the orang utan in body weight and both are ground-dwelling primates. Chimpanzees are semi-terrestrial; when travelling and fleeing their locomotion takes place on the ground, but when foraging they may travel considerable distance through the arboreal strata of the forest (KORTLANDT, 1966; REYNOLDS and REYNOLDS, 1965). This also applies to the bonobo (*Pan paniscus*) (BADRIAN and BADRIAN, pers.comm., 1975; MACKINNON, 1976), although its smaller size and anatomy would seem to allow a more arboreal lifestyle.

By contrast, the orang utans in the Ketambe area rarely descended to the ground, and then usually to cross gaps in the vegetation, to feed from low growing food items or to flee from a conspecific pursuer. Quite remarkable, the incidents of groundwalking in orang utans, especially of the Bornean race, mainly concern adult males. MACKINNON (1974) has suggested that size and weight become constraints on the degree of arboreality of adult male orang utans. However, it should be considered that groundwalking may be part of an individual strategy to avoid encounters with conspecifics. Adult males especially may, by travelling along the ground, avoid the conspicuous tree-swaying associated with arboreal locomotion, which would betray their presence in an area occupied by a higher ranking fellow. There are observations from the present study as well as from other studies (i.e. MACKINNON, 1974; p. 54) which support this idea.

In most of the incidents of groundwalking observed in the Ketambe area, a clear incentive to do so could be identified. A need to travel as efficiently as possible in terms of energy expenditure, by avoiding the horizontal and vertical meandering of arboreal locomotion, hardly ever seemed to be a reason for ground locomotion under normal circumstances. Not even when individuals were apparently after some goal (see p. 173). However, it was remarkable that we could induce ground walking in some of the wild, artificially provisioned orang utans. When we carried bananas to the feeding place, thereby traversing some 500 meters of forest, both the adult male O.J. and the adolescent female Jet occasionally descended to the ground in order to keep pace with us.

Our experience with rehabilitant apes suggest that such orang utans may lead a semi-terrestrial life when arboreal locomotion is not actively promoted by experiental history. Arboreal locomotion in rehabilitants seemed strongly promoted by fear, i.e. individuals frightened by unfamiliar stimuli would immediately take to the trees. Such observations suggest that the degree of arboreality may be influenced by experience in the ontogeny of orang utans.

Obviously, only a detailed bio-mechanical and bio-energetical analysis of arboreal locomotion with reference to foraging can produce conclusive evidence on the degree of efficiency of this mode. That is, relative to ground-walking between food sources, and ascending towards the food, as appears to be the strategy of the African apes.

Perhaps the particular architectural structure of the Malesian rainforest, with its abundance of lianas that inter-connect the strata, is an important aspect favouring the efficiency of arboreal travelling. Of the rainforest ecosystems in the world, the South East Asian forest harbours the most abundant liana flora, both in species and in individuals (RICHARDS, 1952).

Although conclusive evidence is still scant, the exceptional position of the orang utan as nature's heaviest arboreal animal, with its inherent risks in terms of falling accidents (see p. 140), generates the idea that strong selective pressures have promoted the shift to almost total arboreality in this ape. As a consequence, arboreal life may have brought about a decrease in gregariousness, because it may not allow the degree of travelling efficiency necessary for such a large animal when feeding in a group. In addition, certain selective pressures may have promoted non-gregariousness and arboreality more directly.

7.3. THE ENVIRONMENT

The social attitude may directly reflect a species' strategy with respect to the exploitation of a certain niche. In the preceding section I stated that the orang utan's behaviour repertoire shows great similarities with that of the other apes, particularly that of the chimpanzee and the gorilla. However, differences in the application of these behaviours seem to account for striking differences in social organisation. I concluded that the differences in the social attitude of males towards conspecific appear to be of crucial importance within this framework. It has been noted for quite some time that many different animal species do not fit into one clearly defined social organisation but often are engaged in an alternating pattern of two or more social phases and sub phases. Thus, jungle fowl (*Gallus* spp.) for instance are organized in two distinct social phases (MCBRIDE et al., 1969) and many ungulate species show similar alternating organisation patterns. Certainly many, if not all these species, are subject to environmental regimes that influence the individual's endocrine system, mediating behaviour which leads to a particular social phase. Primates, however, have a short term menstrual cycle, which would presumably allow more stability in the social organisation (see BUTLER, 1974). Yet, it has been noted that several primate species (*Alouatta* spp., COELHO, 1975, *Colobus* spp.: DUNBAR & DUNBAR, 1975, *Presbytis* spp., JAY, 1965, this study) employ different social phases within a general framework of gregariousness. This phenomenon may indicate some plasticity of the relation between social strategy and ecological constraints as the sub-phases usually occur within the same habitat structure.

This chapter deals with the question to what extent the two main ecological factors, food-availability in space and time and predatory pressure offer suggestions to understand the rather exceptional social organisation of the orang utan. The manner in which ecological factors might influence the previously discussed variables of arboreality and social organisation of the orang utan will be investigated by comparing these with corresponding aspects of the ecology of chimpanzees and gorillas.

Distribution of food-resources

The apes are without exception – at least by origin – animals of the humid tropical rainforest. The orang utan's distribution is limited to rainforest regions on the islands of Borneo and Sumatra in South-East Asia; the gorilla is limited in distribution to the equatorial rainforests of West and Central Africa (SCHALLER, 1963), while the chimpanzee, which in some areas is sympatric with the gorilla (SABATER PI, 1960) has adapted to a wider range of habitat types including woodland savanna regions (for a review see KORTLANDT, 1972). Nevertheless the latter's distribution remains restricted to areas containing riverine gallery forest (KANO, 1971).

The tropical rainforests are amongst the most ancient stable eco-systems in the world. The S.-E. Asian rainforests at least, have a history in which a state of equilibrium was reached many thousands of years ago, probably without any major changes since the last glacial period (VERSTAPPEN, 1975). The diversity of species, the density of individual floristic components and the concomittant overall food-productivity in a tropical rainforest are far greater than that of the woodland savanna; the higher population densities of forest living primates may be indicative in this respect (CROOK, 1970). In comparison with the African rainforest, the lowland mixed rainforest associations of the Malesian region stands out as being the more divers (RICHARDS, 1952).

It is an acknowledged fact that various distribution patterns of food are one of the major determinants for the feeding strategy and consequently for aspects of the social organisation of a species (CROOK, 1970). Small amounts of food distributed randomly (e.g. insects) favour individual feeders.[33] When this condition is constant, it may favour a 'solitary' lifestyle in animals. On the other hand, temporarily available large amounts of food distributed discontinuously in space and time (e.g. fruits) may favour gregariousness. An illustrative example for this theory is the rainforest bird *Zosterops palpebrosa*, that 'roosts singly during one half of the year when it is feeding solitarily on insect-food, and forms communal roosts in the other half year when feeding in flocks on

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[33] An interesting exception to this rule may be the squirrel monkey (*Saimiri* spp.), that forages for small dispersed food items, notably insects, yet lives gregariously (see BALDWIN and BALDWIN, 1972). Perhaps gregariousness in this species is promoted by a high degree of predatory pressure by feline and, or, other animal predators.

fruits' (FOGDEN, 1970; cited in WARD & ZAHAVI, 1972, p. 519). Among the large forest dwelling mammals, the tiger may serve as another example of a solitary animal which is faced with the condition in which food is more or less randomly distributed in small quantities (SCHALLER, 1967).

One, – and perhaps the most important – adaptive advantage of gregariousness is the potential to increase feeding efficiency, as the individual can draw on the experience of others (see RIPLEY, 1970; EISENBERG et al., 1972). There are indications that the formation of parties by chimpanzees serve the same function. It has been observed in the wild, and in an experimental setting, that individuals without relevant information tend to follow the fellow(s) whose decisive behaviour expresses his good knowledge of a food source (see MENZEL, 1971). It has even been noticed that individual chimpanzees may deceive their companions in order to monopolize their knowledge of a food source (see WRANGHAM, 1975; and VAN LAWICK-GOODALL, 1971). This supports the idea that such information is generally used.

If the distribution of food sources were one of the important selective pressures acting upon the evolution of gregariousness in the chimpanzee, it is again hard to understand the difference in social organisation between orang utan and chimpanzee.[34] This is because the two species show strong resemblance in their diet composition as well as in their (at least) partial dependence on a few commonly available staple food items such as figs (see REYNOLDS and REYNOLDS, 1965; SUGIYAMA, 1968; etc.). Moreover, the descriptions of chimpanzee habitat (e.g. KORTLANDT, 1972: REYNOLDS and REYNOLDS, 1965; SUZUKI, 1969; KINGDON, 1971; WRANGHAM, 1975), as well as my personal impression of the chimpanzee habitat of the Gombe Stream National Park (Tanzania) suggest that its 'patchiness' corresponds closely with that of the orang utan's habitat: it may even contain less large food sources and offer a more dispersed availability of small quantities.

As I have shown in chapter II 2.4 (p. 69), the Ketambe habitat represents a true 'parchy' environment (cf. PIANKA, 1974) in which we find a proportion of fruit tree species that produce small quantities and which are well spaced, as well as species that offer very large quantities of food in one location. These two examples are extremes in a range of possibilities with respect to dispersal and quantity. Especially in the case of large localized amounts of food, the trees producing such loads are usually dispersed and fruit asynchronously. One could imagine that an efficient exploitation of these sources would lead to the formation of groups or sub-groups, as in chimpanzees. On the other hand, if only the small scattered quantities of food were available one could understand the'solitary' mode of life of individuals that live in more or less extensively overlapping home ranges. The orang utan has quite clearly choosen for the latter option. For one reason or another it has rejected the option of gregari-

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[34] Perhaps the indicator effect of the hornbills associated with ripe strangling fig trees make this information transmission model less relevant for the orang utan's condition.

ousness, although indeed a tendency to form aggregations in large fruit trees is still notable. Moreover, immature individuals have a more intense social lifestyle.

Since fruit trees are stationary incentives, the only aspect of uncertainty for an animal with good topographical knowledge of its home range is the time of availability of ripe, or edible fruits. Of course, an ape can have such knowledge by means of cumulated impressions of the reproductive state of known fruit trees in the course of regular wanderings through his range. This may be a rather difficult task for a large animal in a large homerange.

Thus, the orang utan's limited gregariousness stands out as the exceptional option against the essential gregariousness of sympatric and allopatric primate species. It seems highly doubtfull whether an explanation for the differences in social organisation of the great apes will come from mere 'examination of relations between orang utans and their food' as has been argued by RODMAN (1973; p. 166; also DESCAMPS, 1920), rather than from the complex of ecological factors in which predation and other mortality factors play an important role.

Predatory pressure and other mortality factors

RODMAN (1974) has stressed that predatory pressure on orang utans is not significant; MACKINNON (1974) has added the important remark 'except where hunted by man' (p. 38) to this statement.

The semi-arboreal monkey predator *Neofelis nebulosa* (clouded leopard) may prey upon young orang utans up to adolescent size, but because such youngsters usually remain under close guidance and perhaps under protection of their mothers, the net effect of this pressure is most likely to be negligible. The essential similarities in arboreality and social organisation of orang utans in Sumatra, where tigers occur, and in Borneo, where tigers do not – and have never occurred, also do not support the idea that feline predation is among the main causes for the ape's arboreality. It is known, however, that Sumatran apes may fall victim to tigers on occasion. On the other hand, the African apes are faced by the predatory pressure of the leopard (*Panthera pardus*) (SCHALLER, 1963; KINGDON, 1971) and in woodland savanna, possibly of the lion (*Panthera leo*). This fact does not seem to have had a significant influence on overall arboreality of both species.

One of the adaptations of animal species to predatory pressure by felids and canids, notably in the more open habitats, is to increase sociability and to congregate in groups. On the other hand, gregariousness may not be the most efficient strategy when one runs the risk of being exterminated 'en masse', as may be extracted from the descriptions by MERFIELD and MILLER (1956) of the native hunting practice on gorillas in Central Africa (see also SCHALLER, 1963; p. 306 and p. 320). Humans hunt in groups, use distance tools for killing and as said, tend to exterminate whole groups when they have the opportunity. The causes for hunting in humans may be many; I have argued that a basic cause may constitute aggression elicited within the 'in-group' of the hunter, that is subsequently redirected onto 'out-group' conspecifics or onto 'substitute' conspecifics (RIJKSEN, in press: in prep.). Such hunting may become institutionalized, and, especially when the victims, either real or 'substitute conspecifics, are in a clear (food) competitive relation with the aggressor, the persecution may become severe. Human history is full of such intolerance.

The comparable competitive factors on the ground level for the chimpanzee and for the orang utan in rainforest regions have been, and in some regions still are, the gorilla and man, respectively.

Mankind, i.e. *Homo erectus* and later forms, has been present in South East Asia for a very long time. His arrival in 'Sunda-land' dates back to the middle Pleistocene, according to fossil remains found in Java (DUBOIS, 1907). The historical picture of Africa is different. The presence of man (*Homo sapiens*) in the equatorial forests of West and Central Africa is of a much more recent date, perhaps some 12,000 years (CLARK, 1967; BROTHWELL and SHAW, 1971).

Where both African apes occur sympatrically they seem to segregate ecologically with regard to utilization and occupancy of the same habitat by means of temporal spatiation (JONES and SABATER PI, 1970). Thus, the agile chimpanzee and the large impressive gorilla have certainly influenced eachother's biology. Perhaps the gorilla's physical presence in combination with its destructive influence on the habitat were among the factors that forced the chimpanzee into the forest fringe habitat. Conversely, the influence of the more agile, and perhaps more selectively feeding chimpanzee may have forced the gorilla to adopt a less selective feeding technique, eventually resulting in herbivorous life. The analogy with the siamang-gibbon competition, in which the larger (and more offensive) siamang adopted a more foliovorous diet, is perhaps not coincidental.

In contrast to these immediate competition effects of the apes on one another's biology, man's competition, as said, takes much more the form of active and sometimes even institutionalized persecution. BECCARI (1904) has suggested, even in 1868, that mankind may have had a very important influence on the orang utan's biology (see p. 208). Of the recent authors, only MACKINNON (1972; 1974) has treated the sympatry of the orang utan and man in some detail by relating man's ancient and recent hunting pressure to the ape's present geographical distribution, to its body size and sexual dimorphism, and, incidentally, to some aspects of its social organisation (i.e. 'the animals' quiet solitary nature, and its habit of hiding' (p. 37)).

In supposing a vigorous competition between the two South East Asian anthropoids, namely man and orang utan, one must wonder whether both had a significant ecological inter-relationship. Speculating on the basis of archeological evidence and on ethnological and anthropo-ecological data of presently still extant, ancient ethnic groups in the South East Asian region (i.e. the Punan, and Orang Ot; Borneo: SCHWANER, 1853; LING ROTH, 1896; ELLIS, 1972: the Semang; Malaysia: WILLIAMS-HUNT, 1952; the Tsembaga, Papua-New Guinea: RAPPAPORT, 1968) one is inclined to confirm this ecological relationship. As I have noted on p. 139, the first hominids as well as the subsequent waves of human races that invaded the vast rainforest of the Pleistocene Sunda-land from the continent of Asia, probably kept to the large rivers. Most likely the riparian forest provided these peoples with the most suitable habitat for their predominantly gathering life style. Because of the constant degree of limited disturbance, which prevents the development of a climax plant community, riparian forest, like the Ketambe area, may in places be among the richest in terms of food productivity for apes, including man. Most likely, early man relied to a large extent on gathered fruits, leaves, insects and other items, for food. At any rate a diet which presumably rather closely resembled that which the orang utan has had to rely on up to present times. The similarity in preference for certain fruits in the human- and the orang utan's diet has been noted by several authors since WALLACE (1869). Even nowadays, when these fruits are only utilized as a supplement to people's daily diet, the resulting competition is known to lead to hostility on part of man towards the orang utan. An ape feeding in a wild fruit tree which is claimed as 'property' by indigenous people exposes itself to fatal risks. As orang utans have also been observed to feed on grasses and on low growing fruits (see BECCARI, 1904, p. 200; this study, p. 56; GALDIKAS-BRINDAMOUR, pers.comm. 1975), it is easily supposed that the ecological overlap in food of man and orang utan concerned the vegetation of all forest strata.

The preservation of food resources may have been vital, especially during the period that man had not yet developed the advanced technical applications that enabled him to shape the habitat in an agricultural fashion.

Clearly, the rainforest is a non-uniform plant community. It is a complex mosaic pattern of different habitat types, according to environmental conditions. On the basis of the preference for the same fruits it may be speculated that both man and the orang utan have had a preference for the same habitat type. Moreover, the habitat alterations caused by man, inducing certain types of secondary vegetation, may have attracted orang utans, similar to the attraction of modern plantations for chimpanzees and gorillas in Africa. Such conditions indeed induce severe competition and since man shows active intolerance with respect to his home range (like other apes), an acknowledged competitor may readily acquire the status of 'substitute' conspecific and be persecuted whenever the opportunity offers. It is an historical fact that earlier human inhabitants were likewise subjected to fatal persecution by later invaders (see NIEUWENHUIS, 1907).

It would be of particular interest to test these speculations with data on the autecology and synecology of the last, still extant gatherers (i.e. Punan) and orang utans in a large tract of undisturbed primary forest. Unfortunately such data are not available. In view of the large scale timber exploitation and rapid acculturation of the relics of gathering cultures by modern ideology, this question will most likely remain unsolved.

Following the speculations, it may be postulated that in the interspecific clash between orang utan and man, the subordinate species was forced into a niche for which it had the best adaptation potentials, relative to those of its competitor. Against man with his eminent ground walking adaptation of bipedalism, the option that was left open for the orang utan to withdraw itself as much as possible from human competition was arboreality. To withstand the hunting pressure of man it would be most advantageous for an animal, the size and weight of which does not allow it to outrun its predator, to live an arboreal life, as well as a solitary life.

In other words, it is quite imaginable that man's hunting pressure on a large and comparatively slow moving primate such as the orang utan, would have selected for the most inconspicuous, and hence for the more arboreal, as well as the more 'un-social' individuals in the course of the evolution. The architectoral structure of the Malesian rainforest as well as the enormous size of the area with its particular distribution, and overall availability, of food resources would be permissive factors with respect to such a development. The reported size reduction of the orang utan during the last 30,000 years (HOOYER, 1948; 1949; see also MACKINNON, 1974) may then be seen as a trend towards decreasing conspicuousness (i.e. the effect of interspecific selection), perhaps thwarted by sexual selection.

It is interesting to speculate what the combined influence of man and the leopard (*Panthera pardus*) has been on the orang utan's biology. The fact that orang utans became extinct in the regions where both predators occur, namely on the South East Asian continent (Vietnam, Birma, Laos, Malaysia) and Java, and still survive where leopards are absent may suggest that a possible tendency to congregate in response to feline predators (and other factors) is incompatible with the response to human predation. Hence the combination of these factors may have brought about the eradication of the prey-species.

Concerning other mortality factors such as parasites and diseases, no indication for a significant selection pressure could be ascertained in the present study. The presence of terrestrial leeches in the Malesian forest might have been a relevant factor, if they ever played a role in the transmission of serious diseases. However, no indication of such a vector function could be found with respect to the closely related humans. At any rate, it apparently did not affect the spread of terrestrial human races in South East Asia. Also rehabilitant orang utans never seemed to be affected. Parasitic infestation in orang utans seems similar to that found in the terrestrial African apes, both in the number of parasitic species and in the degree of infestation (see p. 196). The arboreal lifestyle of orang utans apparently does not safeguard them against becoming infested.

7.4. CONCLUDING SUMMARY

Although the orang utan's life style seems to be anomalous among the anthropoids, it shares many behavioural characteristics with the other apes. It is clear that, with respect to the social-spatial interrelations of individuals, which I termed the 'social attitude', all apes have a strong tendency to defend their personal sphere. However, the defensive mechanism discriminates with regard to certain classes of conspecifics, namely, 'in-group' and 'out-group' conspecifics. There is a trend in the apes to tolerate individuals that belong to the kinship lineage of established individuals, which ultimately resulted in the multi-male group structure of the chimpanzee. Others, i.e. 'out-group' conspecifics evoke a more or less strong degree of antagonism. It is remarkable that the orang utan with its high intelligence is classified at the lowest level of complexity in this trend: orang utan males consider every other recognizable male as an 'out-group' conspecific, so to speak.

Since the different forms of social organisation displayed by the anthropoids are undoubtedly based on a common phylogeny, one is tempted to speculate that both the forms of social organisation displayed by the chimpanzee on the one hand, and by the orang utan on the other hand are derivations in two opposite directions of a basic age graded male group pattern as is presently still displayed by the gorilla.

At the end of the last century, before evolutionary – and ecological theories had been established firmly, the Italian naturalist O. Beccari wondered what influence man has had on the biology of the orang utan. Of the recent students of the orang utan's biology, only MacKinnon followed this suggestion to some extent. The other authors questioned, or entirely ignored the influence of 'man the hunter'. In the present study, Beccari's suggestion is taken up again and elaborated further.

Two characteristics of *Pongo pygmaeus* stand out as being remarkable among the Anthropoidea. In the first place its non-sociability, in the second place its almost total arboreality.

Social organisation, i.e. the set of behavioural characteristics associated with temporal and spatial proximity of individuals, is an adaptation to environmental conditions, in which availability of vital resources and predatory pressure are determinant factors.

A comparison of the presently available information on the ecological variables relevant for the chimpanzee and the orang utan suggest that both species have to cope with very similar ecological conditions with respect to their food, i.e. with a decidedly discontinuous patchwork of irregularly sized food quantities. Such conditions *per se* certainly do not predict a solitary life as the adaptive strategy, but rather seem to favour some form of gregariousness. The overall availability of food resources, as reflected in the biomass may also not be notably different for both ape species: it certainly seems not less favourable for the orang utan in the South-East Asian rainforest.

The view presented in the present study sees arboreality, associated with the non-sociability of the orang utan as an adaptive characteristic to the complex of long term, more or less stable ecological factors in which the effects of long term persecution by man is an important determinant. Climbing ability may be regarded as an adaptation to locomotor efficiency with respect to food-gathering in a forest habitat. All apes have this ability to a higher or lesser degree. In the orang utan, this adaptation is forced to the extent of an almost entirely arboreal life style, effected by human persecution, and favoured by the architectoral structure of the South-East Asian rainforest. In addition, hunting pressure by man may have selected for inconspicuous, solitary animals.

PART IV

CONSERVATION

1. INTRODUCTION

The need to conserve 'nature' is intricately related to human influence on the environment, reflected especially in the human biomass. The concept of nature conservation is based on the insight that, being a fully dependent component of an eco-system, man cannot continue to destroy all fellow-components without fatal results.

Although so-called primitive societies might obey rules which served to conserve a number of natural resources, as illustrated in RUTTER's observation, that says: 'Among the Tambunan Dusuns there is a custom known as "*tegah*" (reserve) whereby a reach in which good fish are known to be is closed for a certain period to allow the fish to increase' (RUTTER, 1903; p. 109) large scale conservation of ancient ecosystems is a recent concept. It has emerged in societies where some people began to experience the deleterious effects of development and progress with its concomitant inevitable degradation of nature.

Most primitive societies fitted into the ecological environment. The people were subjected to all those ecological variables which kept the biomass within limits. Animistic religion assured these people of a balanced psychological integration in their natural environment, which was largely uncontrolled. By contrast, the technologically advanced societies have managed to control much of their environment, notably the immediate population regulating factors (i.e. diseases, etc.). The people have adopted an ideology which is ego- or anthropocentric, and which puts a premium on over-exploitation of natural resources.

One of the many problems of nature conservation in the so-called developing countries is that the western ideologies, which only recently displaced traditional cultures and religions, and introduced an attitude of neglect for nature, cannot easily be converted into an attitude of respect for the natural environment. Not only because the majority of expatriate people, who set the trend in such countries, are commercially oriented and continue to promote over-exploitation for their own sake (backed up by 'foreign aid' programs), but also because nature conservation and the measures to keep human biomass within certain limits (i.e. birth-control, etc.) may be rejected as conservative, or worse, as a political attempt to keep such societies in a backward and poor condition. Unfortunately, most people do not realize that an individual's happiness refers to his experience during his own life (i.e. accords to his own standards), and not to the standards set by the technologically advanced societies in another hemisphere.

I shall discuss in this chapter the main human actions which threaten the orang utan's existence in their approximate order of magnitude, namely hunting pressure as the least, and *ladang*-agriculture and timber-exploitation as the worst disruptive activities. The latter are the result of the world's largest problem, namely a vastly expanding, ever increasing human population.

Accounts on endangered animal species usually emphasize hunting pressure (often wrongly named 'poaching'), and although no doubt hunting pressure has played an important role in the biology of the orang utan (see section 2.8.2 and p. 318), it is certainly not the main cause of this ape's imminent eradication. Still, I will pay special attention to hunting, because this form of inter-specific aggression may be closely related to the intra-specific aggression (i.e. 'raiding' behaviour, mob-violence, head-hunting, etc.) which is so remarkable of man's condition.

In a discussion of the other, far more important threats, namely habitat destruction due to conversion of forest into agricultural fields and due to timber-exploitation, one inevitably touches a political issue. These sections are not meant to reproach any particular form of government. The problems are certainly not restricted to Indonesia and are virtually the same in all overpopulated countries with a desire for technological development (including the Netherlands). On the contrary, only when delineating the problems as clearly as possible, one can hope to find solutions before the situation has become irreversible. The destruction of a particular, complex ecosystem such as the rainforest is indeed irreversible, and as a rule the ultimate consequences are increased erosion and even desertification.

The present study also provided data concerning the management actions to be undertaken in order to improve the conservation situation of the Gunung Leuser reserve, but these have been published in a number of internal reports, mainly because measures of management are time and context dependent, and final decisions with respect to management are with the Indonesian authorities. As the conservation action dealing with rehabilitation of orang utans was one special aspect of the study, I have described the process in some detail and discuss its conservational and biological implications. Other, much more strenuous actions in the field of conservation are necessary, however, to ensure the survival of the Sumatran orang utan as a component of the tropical rainforest ecosystem.

2. PROTECTION OF THE ORANG UTAN AND HIS HABITAT

2.1. RESERVES

Orang utans are exclusively found in the islands of Borneo (Kalimantan) and Sumatra (fig. 141; and 33). Thus, almost 85% of the orang utan's range lies within the Republic of Indonesia, the remainder in Sarawak and Sabah, both of which incorporated in the Federation of East Malaysia. This particular distribution puts a heavy responsibility on these two states, notably on the government of Indonesia. The present policies of these states insufficiently support the preservation of the unique tropical rainforest ecosystem. on the undisturbed state of which the orang utan and numerous other biological phenomena are dependent for survival.

The present concession maps of Kalimantan and Sumatra show little space unoccupied by timber concessions, while so-called selective logging in reserved areas becomes increasingly sanctioned by the Indonesian government.

Almost one third of the distribution range of the Sumatran orang utan falls within the Gunung Leuser group of reserves, some 7500 square kilometers in extent (fig. 141; (1)). However, this reserve is very mountainous with large tracts over 2000 m in altitude, rendering it not uniformly suitable as orang

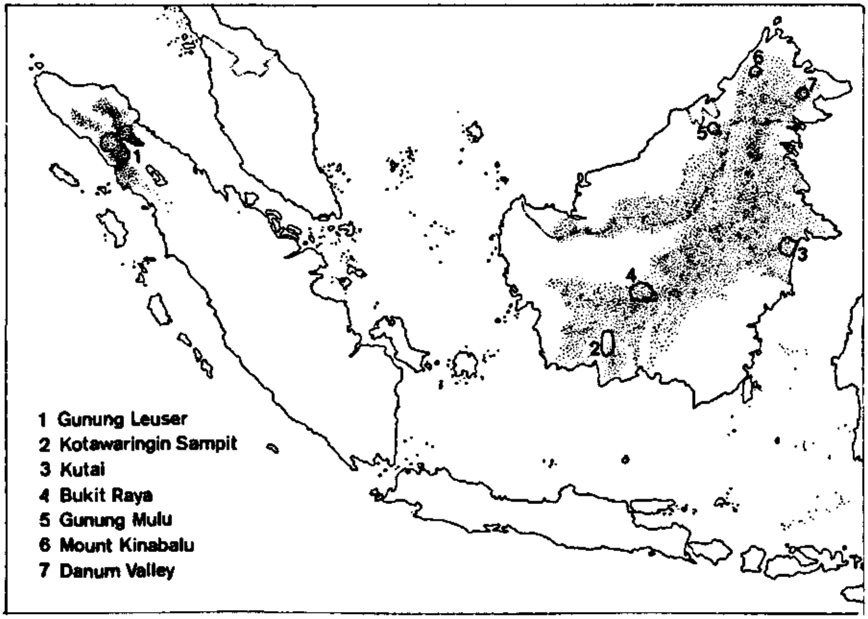

FIG. 141. Reserves within the distribution of the orang utan in Sumatra and Borneo.

utan habitat. Moreover, the reserve is divided into two separate regions, i.e. the Leuser reserve proper and the Langkat-Sikundur reserve, on both sides of the densely populated Alas valley (fig. 1); a situation which increases the danger of intrusions.

In Kalimantan, the situation is quite different. Significant reserves for the preservation of the orang utan are the two wildlife sanctuaries, namely Kotawaringin Sampit (3,050 km sq., swamp and mixed lowland forest), in South Kalimantan (fig. 141; (2)) and Kutai (3,060 km sq., mixed lowland forest) in East Kalimantan (fig. 141; (3)). Unfortunately, the location of these reserves, i.e. close to the sea, is such that the harvesting of timber is very profitable. Consequently, large sectors of both sanctuaries have been leased as timber concessions. More than thirty percent of the Kutai reserve has already been logged (REKSODIHARDJO, et al., 1974). Moreover, oil exploitation is in process in the region. The Kotawaringin Sampit reserve is threatened by commercial logging; concessions already having been granted. In addition, the proposed Bukit Raya reserve (2000 km sq., hill forest) in Central Kalimantan is an important area for the preservation of the orang utan and several other fauna- and flora- components, typical of the Borneon region south of the equator (fig. 141; (4)). Some sectors of this reserve may still be inhabited by small bands of gathering – hunting people, i.e. the *orang Ot* (see SCHWANER, 1853–1854, and SCHÄRER, 1946). The only sanctuaries presumably large enough to preserve representative parts of the various rainforest ecosystems to be found in Borneo are situated in the Indonesian sector (Kalimantan).

The state of Sarawak has no reserved areas large enough for the preservation of an ecosystem in which a viable orang utan population is to survive. All proposed conservation areas are smaller than 1000 km sq. For instance, Gunung Mulu (National) Park, which includes all the major vegetational types of Sarawak, and awaits ratification by the federal government, is only 528 km sq. in extent (fig. 141; (5)).

The state of Sabah at present has one medium sized sanctuary, namely Mount Kinabalu National Park (690 km sq.) (fig. 141; (6)). The Kabili-Sepilok forest reserve (only 40 km sq.), although still connected with large tracts of rainforest, cannot be considered to be of significance for orang utan conservation, unless the contiguous forest regions achieve legally protected status before they are logged. Even the proposed Danum valley reserve in the Segama catchment area, though excellent orang utan habitat (see MACKINNON, 1971) is a comparatively small sector (i.e. 620 km sq.: see fig. 141; (7)). It is rather small for a viable orang utan population, for, when estimating the population density at 0.5–1.5 individuals per km sq. (see p. 161), the region can only support a maximum population of 930 individuals.

Thus, at present some 25% of the orang utan's range on Sumatra is more or less safeguarded by nature reserves. This figure is considerably lower for Borneo where only approximately 2.6% of the range is protected (when adding the proposed areas: 3.5%). However, it is important to realize that these figures are on paper, and do not represent the actual situation. Legislative protection in this vast region is still insufficient; recent developments in timber exploitation and the concomitant government policies as regards timber export in for instance Indonesia, strongly decrease the survival of reserved forest regions. As I mentioned above, the Kutai reserve has to a large extent been logged, the Sumatran situation is not much better. The main lowland forest region of the Gunung Leuser group of reserves, namely the Sikundur area, is being logged to the extent of some 50 km sq., and even larger concessions in that reserve await ratification. It is hoped that conservation efforts can succeed in saving this unique part of North Sumatran lowland rainforest. This is vitally necessary as the only other remaining lowland forest in Sumatra north of Lake Toba, namely the huge watercatchment basin of the Jambu Aye river in East Aceh province, is also seriously threatened by commercial timber logging. Moreover, this – unfortunately – unprotected lowland forest is one of the two main concentration regions of the Sumatran orang utan's range. Destruction of this habitat range will probably halve the present orang utan population (see also RIJKSEN, 1974–75; p. 167).

2.2. LEGISLATIVE PROTECTION OF THE ORANG UTAN

Hunting or killing orang utans has been prohibited by Ordinance since 1925 in Indonesia, which was then the Netherlands East Indies (DAMMERMAN, 1937). Additions to this Ordinance came into effect in 1931 and 1932, which made it illegal to catch alive, to disturb, to trade alive or dead, or to hold orang utans in captivity.[35]

Despite this legal protection, the orang utan has been subjected to continuous illegal hunting pressure (fig. 142) (see VAN DER VALK, 1940; BRANDES, 1937; 1939; MILTON, 1964). Control and enforcement of the Ordinance has been lacking almost entirely (fig. 143). Apart from occasional confiscation of illegally traded orang utans, this situation continued until 1971, when the present study, and its parallel rehabilitation program started. Before that date, confiscated apes were usually placed in zoos, but this procedure was hardly a solution for the trade-problem as zoos in Indonesia play(ed) an important role in the orang utan export, both legal and illegal. The strict execution of the Fauna Protection Ordinance has not always been easy under the local conditions (see RIJKSEN and RIJKSEN-GRAATSMA, 1975). However, since the WWF aid program and the expatriates' attention to the problem became widely published, the situation has improved considerable. Still, effective prosecution of offenders, as stipulated in the Ordinance, has not yet been feasable to my knowledge.

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[35] See Fauna Protection Ordinance 1931: Stbl. 134; Stbl. 226, Fauna Protection Ordinance 1932: Stbl. 28, and Fauna Protection Ordinance 1935: Stbl. 513.

FIG. 142. Indonesian youth dealing in illegal orang utan infants (January 1972).

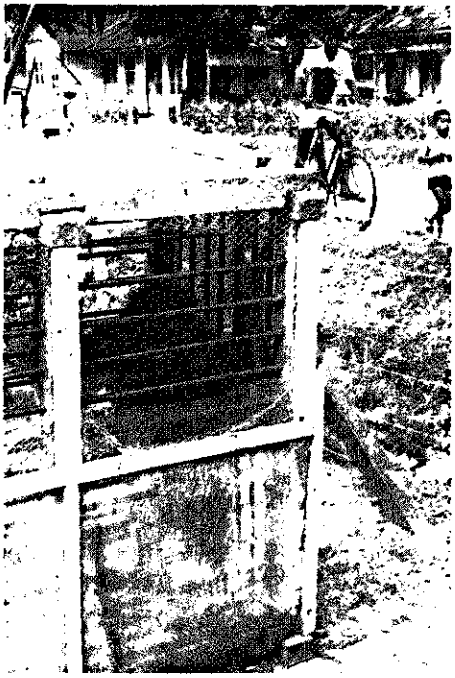

FIG. 143. An orang utan 'pet' kept in a typical condition of captivity.

2.3. LEGISLATIVE PROTECTION OF THE HABITAT

According to the Indonesian Constitutional Law (1945): 'Earth and water and natural resources situated therein and thereon, belong to the country and are used as much as possible for the welfare of the people' (Art. 33: par. 3). The Basic Agrarian Law of 1960, applying to the island of Sumatra, is based on 'common law', i.e. law according to the *adat*, and explicitly acknowledges the 'right of disposal' (*hak ulayat*) of the lower legislative communities. These communities (*desa* in Aceh, *huta* or *kuria* in North Sumatra) have jurisdiction over their entire area, and accordingly have the rights to give permits for *ladang* (i.e. slash and burn agriculture) and small scale logging operations for areas up to a maximum size of 100 ha. However, Art. 3 and Art. 5 of the Basic Agrarian Law explicitly state that the rights of disposal of the lower legislative communities may be effectuated only when they agree with the general interest of the State (etc.). The establishment of a nature or forest reserve affects this right of disposal by the lower legislative communities, and the Central Administration retains the right to propose and effectuate destinations for land-use (Constitution 1945: Art. 33, par. 3), such as the establishment of reserves.

On the other hand, the Central Administration may grant large scale timber concessions.

Two types of forests are recognized in Indonesia, (1) state-owned forest (*hutan negara*), and (2) communal forests (*hutan milik*). The state-owned forests are subdivided into four types:

a) *hutan lindung* or protected forests, water catchment areas;
b) *hutan produksi* or exploitable forests;
c) *hutan suaka alam* or conservation forests, which are further sub-divided into *Cagar alam*: strictly protected nature reserve, and *Suaka margasatwa*: wildlife sanctuary;
d) *hutan wisata* or recreational area, subdivided in true recreational parks and regions for 'sports hunting' (*Taman buru*).

The state-owned nature conservation forests (*hutan suaka alam*), fall under the authority of the Ministry of Agriculture. This authority delegates responsibility to the Directorate General of Forestry,[36] which for its part delegates responsibility to the Directorate of Nature Protection (P.P.A.).

In the Forestry Law of Indonesia, no emphasis is laid on the forests' important ecological functions (cf. for instance the Ecological Guidelines for the Development in the Tropical Forested Areas of South-East Asia Conference, Bandung, 1974; POORE, 1975). Yet, some principles concerning these functions may be found in some Forestry Regulations and Instructions, although these matters are nowhere stressed.

Both *Cagar alam* and *Suaka margasatwa* only fall under legislative jurisdiction when being marked in the field with proper boundaries. Consequently, local farmers may encroach the area without risk of being persecuted when such markings are inadequate or lacking.

According to Article 5, par. 2, of the Nature Protection Ordinance (1941; 1957): 'It is prohibited in a *Cagar alam* to act in any way that changes the condition of the soil, the vegetation, the flora and the fauna, or that changes or disturbs the structure and condition of the reserve.' A *Cagar alam* is closed to the public, unless special permits are given.

Although the Ordinance concerning the *Suaka margasatwa* has a very similar text, namely: 'It is prohibited... to act in any way that destroys the fauna, the flora and the forest structure, or to perform acts which result in the loss of the characteristics of the reserve' (Art. 5; par. 1) the protection of a *Suaka margasatwa* is less effective. It is open to the public unless otherwise decided by the local government. Moreover, it is allowed to collect firewood, to fell trees for private use, to herd cattle, and to catch fish in a *Suaka marga-*

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[36] This relic from colonial times, in which one government office has two entirely opposing functions, namely, on the one hand exploiting the rainforest wood-resources, while on the other hand preserving them, is quite dangerous with respect to the conservation. It can give rise to controversial actions (i.e. selective logging as so-called 'conservation management', etc.). It should strongly be recommended through the appropriate channels, that the Government of Indonesia establishes a Department for the Environment to deal with matters of nature conservation and management of reserved areas.

satwa. Even the exploitation of an industry (*perusahan*) is permitted (see Art. 8; par. 1). Unfortunately this paragraph is officially being interpreted in such a way that the legal operation of commercial timber felling is sanctioned (see PRIJONO, 1975). However, any commercial logging seriously disrupts the structure of the forest (BURGESS, 1971), resulting in a serious loss of the characteristics of the reserve, and thus contravenes the Ordinance. It affects the faunal and floral species composition, and thus alters the physiognomic aspect and the functions of a reserve. In other words, the interpretation of commercial logging activity as *perusahan*, results in activities which are contradictory[37] to the intent of the Ordinance as put down in Art. 5.

The Gunung Leuser reserves have the legal status of *Suaka margasatwa*. Whether this status offers sufficient protection to the ecosystem is highly questionable. In practice the protection of such an area is largely dependent on the policy of the local government(s) and other local factors. Moreover, legal protection leaves room for destructive activities which may be sanctioned by the Central Government. Since a severely disturbed and degraded habitat cannot support a viable orang utan population, the present status of this large reserve cannot sufficiently safeguard the future existence of this ape. Unless measures are taken to improve the present legislative status of the reserve, there is not much hope for the orang utan's survival.

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[37] Therefore, it is strongly recommended that Art. 8; par. 1 of the Nature Protection Ordinance (1941; 1957) should be altered to such an extent that it prohibits all commercial activity within reserves. Only in such a way can a proper conservation of ecosystems be guaranteed. An appropriate recommendation pertaining to this subject is to be found in the Proceedings of the Bandung Conference on Ecological Guidelines for the Development in the Tropical Forested areas of South East Asia (POORE, 1975).

3. THREATS

3.1. MAN VERSUS APE; HUNTING

In chapter II, I reviewed much of the anthropological evidence with respect to finds of prehistoric orang utans in the South-East Asian region (see also GROVES, 1971). Based on additional anthropological information I made some speculations regarding the extent of hunting of apes by hominids. Undoubtedly hunting has played an important role in the evolution of the hominids (SERVICE, 1966; DE VORE and LEE, 1968; TIGER and FOX, 1971); I suggested the hypothesis that the hunting of conspecifics or congenerics played a major role in the emergence of modern man. In the approximate order of evolutionary development, I speculated that hunting on other species of the superfamily hominoidea, other primates, and subsequently all other 'game' displaying some symbolically interpretable trait may be seen as derivate or redirected forms of the 'predatory' behaviour of man against man (RIJKSEN, in press). In other words, the hunting of apes by man is closely related to e.g. head-hunting, and cannibalism. Some of the observations and anecdotes that led to this hypothesis, shall be reviewed below.

Several authors have reported that certain ethnic groups from the interior of Borneo have both hunted and eaten orang utans (see SCHLEGEL and MÜLLER, 1839–1844; VROLIK, 1854; VAN HASSELT, 1860; DE SILVA, 1971; MEDWAY, 1976). PERELAER (1870) has noted that some Dayak tribes consumed '*apen*' because they were supposed to posess a human soul.[38] He thus suggested a cannibalistic motive behind the practise of hunting primates. Until now, some Batak people in North Sumatra still believe that eating the meat of orang utans makes one physically strong. Perhaps this belief is a relic of this ethnic group's cannibalism, which was abandoned quite recently (see VOLZ, 1912).

It is noteworthy that both SABATER PI and GROVES (1972) and FOSSEY (1974) mention truly cannibalistic practice on gorillas in West and Central Africa. The parts reportedly taken from the quarry are practically the same as those mentioned in cannibalistic rituals in Sumatra (a recent case of cannibalistic ritual by Batak people took place in Sumatra in 1973 (see also VON BRENNER, 1894)); SABATER PI and GROVES (1972) did indeed relate gorilla hunting by the Fang people in Rio Muni (West Africa) to the recently prohibited cannibalism of this ethnic group.

Although cannibalism and head-hunting may be regarded as different forms of behaviour, based on different philosophies, some observations on certain cases of head-hunting practice clearly suggest that there is a transitory stage: Some head-hunters ate parts of the hands (LING ROTH, 1896), or the

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[38] Note that the Dutch word '*aap*' means both monkey and ape.

liver (RUTTER, 1929); others might just taste their slain victim's blood (LING ROTH, 1896) or the brains[39] (RUTTER, 1929). This transition may also be reflected in the interesting case history of the Mentawai people (see SCHEFOLD, 1972; TILSON, 1975). These changed from (human) head-hunting into hunting and consuming the snub-nosed langur (*Siamas concolor*) and other primates. Apart from eating their quarry, these people keep (and venerate) the skulls of these animals, as they formerly kept and venerated the skulls of their human victims.

Such cases, in which human skulls were venerated together with those of other primate species have been reported for the Bornean region by ST. JOHN (1862) and by WHITEHEAD (1893).[40] Similarly, CARPENTER (1940) has noted that 'the natives of Doi Nangkas (Thailand) were said to have many gibbon skulls in their huts' (p. 177). As for the orang utan specifically, O. BECCARI, in the translation of his book 'Cenno di un viaggio a Borneo' mentioned in 1868:

> '...in the house I saw a Mayas Tjaping's skull, well smoked, and hanging up with numerous human skulls. I should like to know why these Dyaks placed the skull of an ape amongst their war trophies. Perhaps they, too, have an inkling of the relationship existent between Man and the Anthropoids, and in one of their war expeditions, having failed to secure human heads, brought back what they may have considered a substitute.' (BECCARI, 1904; p. 325–326).

Similar instances of veneration of orang utan skulls together with those of human victims have been reported by HORNADAY (1885; p. 485) and by DE SILVA (1971; p. 52).

Utilisation of orang utan organs, such as hair, skin and perhaps teeth, for decoration of war-paraphernalia may also reflect the relation between head-hunting and hunting on orang utans, particularly with respect to that aspect of hunting which concerns gaining prestige. It is noteworthy in this respect that the shields and other paraphernalia, most prized by e.g. the Kenyah (see HOSE, 1926), were those decorated with tufts of human hair taken from the heads of their slain enemies. In the museum collections of the Ethnographical Museum in Leyden, and the Ethnographical Museum in Cambridge, as well as in the collection of the K.I.T. in Amsterdam, I noted orang utan skin and hair used to decorate or made into, (a) war-caps, (b) shields, (c) *mandau* (i.e. head-hunting sword) handles and sheaths, and (d) war-masks. Another use of orang utan skin that we noticed was that it was made into the inner-sheath of the *sumpitan* (i.e. blow-pipe) dart-quiver (see also NIEUWENHUIS, 1907; p. 382). JAMES BROOKE, the first white radjah of Sarawak, described the dress of a

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[39] It is noteworthy that chimpanzees also seem to have a special zeal for the brains of their primate quarry (TELEKI, 1973). FOSSEY (1974) explicitely mentions the brains of the slain mountain gorillas as one of the organs prized by the hunters. It is interesting in this respect that the four orang utan skulls known to have been used in Dayak veneration that I examined, had their *foramen occipitale* enlarged by slashes from knives, perhaps to facilitate extraction of the brain (see fig. 60).

[40] Unfortunately, neither of the authors specified his observation. It is however very likely that orang utan skulls were among these collections.

coastal Melanau chief as including, 'a Maias skin jacket hung over his shoulders...' (BROOKE, 1866; see also HARRISSON, 1960, a). War-coats made of orang utan skin have also been reported for the Kenyah people of Sarawak (HARRISSON, 1960, b; also DE SILVA, 1971), although HOSE and MCDOUGALL (1923) explicitely mention that the Kenyah (and Kayan) entertained a strong respect for orang utans. It is interesting that some (Iban) tribes regarded the orang utan as being one of the representatives of their war-god '*Klieng*' (HOSE, 1926), in a series of several predatory animals. Perhaps the remarkable use of orang utan hair, reported by KÜKENTHAL (quoted in LING ROTH, 1896, p. 201) for the Kelabit-Kayan tribe, who had the custom of rubbing 'dirt and ape hair onto a newborn child's breast to insure its not being stolen by apes', referred to this war-god concept.

Apart from the artefacts which give evidence for man's hunting pressure on the orang utan, and which lend weight to the suggestion that head-hunting and ape-hunting have a common emotional basis, some of the many folk tales and legends in Borneo seem to reflect this relation even more directly. In one particular Sakaran legend, in which the origin of head-hunting is narrated, the orang utan is presented as an alternative for a human head. It states:

> '...the daughter of the great ancester who resides in heaven... refused to marry until her betrothed brought her a present worth her acceptance. The man went in the forest and killed a deer, which he presented to her; but she turned away in disdain. He went again and returned with a Mias, the great monkey that haunts the forest; but this present was not more to her taste. Then, ... the lover went abroad and killed the first man he then met, and throwing his victim's head at the maiden's feet ...., she smiled and said that now he had discovered the only gift worthy of herself...' (MCDOUGALL, p. 64; in LING ROTH, 1896, p. 163).

In addition to this tale, there are several legends among the Bornean peoples which suggest that the distinction between man and orang utan was regarded to be of a gradual quality. In the earliest accounts on this ape, both the physician DE BONT and the captain BEECKMAN mention that, according to the Malay people, orang utans are humans who refuse to speak (either for fear of blasphemy, or for fear of being set to work, i.e. being enslaved; BONTIUS, 1658; BEECKMAN, 1718). Rather detailed accounts of Dayak folklore with reference to orang utans have been given by BROOKE (1866), who notes:

> 'A stranger or visitor might, however, load a diary with anecdotes of Dyaks, who going to the woods, becoming orang utans and after several years, having borne many children, have returned and reverted to their former condition. Or he might hear that females have become pregnant by them, and borne twins, one as a human being, and another taking the form of its jungle parent.' BROOKE, (1866, p. 64) then adds: 'There are many other fables of a like kind; but there is no truth in them, and they themselves (the Dayak informants) are very far from believing them. They would be indescribably horrified if such an experiment were seriously proposed to them'.

Thus, while the Dayak informants in the middle of the last century allegedly disregarded the authenticity, they nevertheless entertained a number of legends in which the close kinship between orang utan and man, including inter-specific sexuality and reversion of one physiognomic form into the other, was emphasized. It is conceivable that in the atmosphere in which such legends evolved, head-hunting raids were applied to orang utans.

The hunting practice

Among the causes for the steady decline in numbers of orang utans in this century, hunting pressure has played an important role (see MILTON, 1964; HARRISSON, 1961; 1965). In the imminent eradication of this ape-species the emphasis has recently shifted towards large scale destruction of the rainforest habitat. Still orang utan hunting by people takes its yearly toll of the population.

The preceding section contained some indirect evidence for the hunting activity on orang utans by indigenous people of Borneo from accounts written in the last century, before large scale acculturation took place among these peoples. HAGEN (1890) and VAN DER VALK (1941) have presented evidence for similar hunting activity by indigenous people in Sumatra. Paraphernalia, adorned with orang utan skin or hair (as described on p. 336) may still occasionally be found in use in the Bornean (see DE SILVA, 1971; and RODMAN, 1974), and Sumatran region, perhaps mainly as decoration. In 1971 I saw a Batak youth in the Alas valley wearing a cap of orang utan skin. We recorded at least three instances in the course of the present study in which Batak people in the Alas valley had caught and butchered an orang utan. The apes had been encountered more or less accidentally during forest clearing activities and were subsequently slain.

Although nowadays people in North Sumatra seldom deliberately set out to hunt orang utans, the Batak people in particular are known to eat almost every vertebrate animal they can lay their hands on. To the contrary, the Gayo-, Alas- and Acehneese people profess the Islamitic religion and eating of orang utans and many other animals is stricly prohibited. Yet, these peoples may kill orang utans on occasion when they find one in a privately claimed, wild growing, fruit tree. Thus, in 1975 a sub-adult male orang utan was clubbed and speared to death in the Alas valley when people found it feeding in a durian tree (VAN STRIEN, pers.comm., 1975).

Since the beginning of this century, a commercial aspect has been introduced into the hunting practice, i.e. a steadily growing demand from European and North American zoos and institutions for live and dead orang utans set a trend for increased hunting pressure. For an extensive review of the effects of this commercially oriented aspect of hunting pressure on orang utans the reader is referred to T. HARRISSON (1960) and B. HARRISSON (1961; 1963; 1965); a comprehensive account of the situation in Sumatra can be found in MILTON (1964) and in RIJKSEN and RIJKSEN-GRAATSMA (1975).

In the periods when international trade in orang utans boomed, namely the thirties (see BRANDES, 1938; 1939) and the sixties (MILTON, 1964), the Gayo people were renowned orang utan hunters. According to demands they trapped orang utans alive, irrespective of age and size (see VAN DER VALK, 1941).

The method of capturing dependent infant, or juvenile orang utans by shooting the mothers is a more recent development. Until recently, orang utans were shot frequently by soldiers and other officials armed with firearms; sometimes orang utans were considered to be fair 'stand-ins' during field excercises. At other times, obtaining the dependent offspring was a main incentive for such behaviour. As late as 1970, soldiers reportedly shot at any orang utan or other primate they encountered along the forest-bordered road leading from Kutacane to Blangkedjeren. A lieutenant based in the Kluet region boasted that he had shot some 8 adult orang utans on a field excersise through a forested area in 1969 and thus obtained three orang utan infants from his trip.

The prohibiting effect of rehabilitation programs on hunting is described on p. 368.

3.2. LADANG AGRICULTURE

For a large part of man's history in the rainforest of the South-East Asian region, his influence consisted mainly of gathering forest products and hunting. The main forest products gathered by the – increasingly rare – gatherers of the Bornean and Sumatran forest are the pith of the sago-palm (*Metroxylon* spp.), several fruits (e.g. *Artocarpus* spp., *Nephelium* spp., *Mangifera* spp., *Ficus* spp. etc.), herbs, and other vegetable material (see e.g. ELLIS, 1972; for the Papuan region: RAPPAPORT, 1968).

Little is known about the beginning of agricultural practice in the South East Asian region. Some form of agriculture may have been practiced since 5000 years B.C. (BULMER and BULMER, 1964; POWELL, 1970). The earliest form of agriculture may well have been the burning of forest patches for promoting the growth of secondary succession (see LEWIS, 1972). Environmental manipulation by using fire, subsequently followed by the practice of actively propagating and planting certain plant species (e.g. *Colocasia* spp., *Musa* spp., *Saccharum* spp., *Dioscorea* spp., etc.) provided a basis for progressing beyond the limitations of seasonality and local distribution or wild food-crops. This more advanced technique became the 'swidden agriculture' which, in some remote places (e.g. Irian; see RAPPAPORT, 1968) has remained the same until recently. The technique consists of felling the vegetational stand of a plot, allowing the remains to dry, burning the dead and dried plant debris and subsequently planting cuttings in the ashes (fig. 144) (see also RAPPAPORT, 1971). After the plot has yielded one or two crops, it is abandoned and allowed to revert to its natural state (called '*belukar*' (fig. 145); for at least 10 years. An important point is that 'swidden agriculture' in its primitive form is subjected to several cultural restrictions based on the people's religious concepts. Interestingly, many of these restrictions appear to aim at conserving the delicate ecological balance in the clan's territory. Moreover, warfare and head-hunting hold clans within certain areas (cf. community ranges), in which the arable

FIG. 144. A 'ladang', much of the plant debris remains, the crop is planted between the fallen logs, which are used as pathways to reach the crops between the sprouting weeds.

land is divided among the clan members. Since the system is based on subsistence, only small fractions of the cultivable area are in use at any one time; some 90–95% of a clan's range is usually lying fallow (see RAPPAPORT, 1968; 1971).

The restrictions prescribed by '*adat*' might be to the extent that tree seedlings on the plot were spared and protected and that certain trees of saplings were not felled but merely stripped of their twigs and leaves.

In the Tsembaga language of Papua-New Guinea such trees were named 'mother of gardens' (RAPPAPORT, 1968). Consequently the recovering trees induced the people to abandon their forest plot before serious depletion of the soil occurred. Moreover, diverse randomly planted crops of different heights have a better soil conserving effect than a monoculture. The resulting stratified system makes maximal use of the available area, not unlike that which occurs in a forest eco-system (RAPPAPORT, 1968). After abandoning a plot, people prefer to clear old secondary forest (*belukar*) rather than primary forest, since *belukar* is easier to fell and burn.

FIG. 145. Several months old secondary vegetation ('*belukar*'); a stretch of forest, felled one year earlier, is allowed to revert to its natural state (Kappi area).

Primitive swidden agriculture is capable of maintaining a population density of at most 30–40 individuals per square kilometer (see VAN BEUKERING, 1947; CLARKE, 1966; RAPPAPORT, 1968) without evidence of serious deterioration of the habitat. The delicate balance between so-called primitive agriculture and the eco-system has lasted for a very long time, perhaps 5000 years (BULMER & BULMER, 1964). However, this balance is maintained only as long as human biomass is adequately regulated and limited by ecological and cultural factors. Primitive swidden agriculture has now become very rare in Borneo and Sumatra, due to the widespread and intensive impact of new, imported ideologies and subsequent acculturation processes. Unfortunately the enforcement of new ideologies and new religions induces people to shed the restrictions imposed by the '*adat*' on their daily life pattern. It is, therefore, appropriate to distinguish 'slash and burn' agriculture, which is simply 'swidden agriculture', stripped of all restrictive '*adat*' aspects that made the original ('primitive') form such an ecologically 'sound' method (fig. 146). At present, in most regions in North Sumatra the human biomass by far exceeds the carrying capacity of the system for any of these types of ('ladang') agriculture. Since most adjacent regions are also in use, people have nowhere to go and they abandon their 'ladang' only after soil exhaustion and serious erosion. Reversion of abandoned land to *belukar* under such conditions is impossible since there is no surrounding forest left to provide seeds. Moreover people

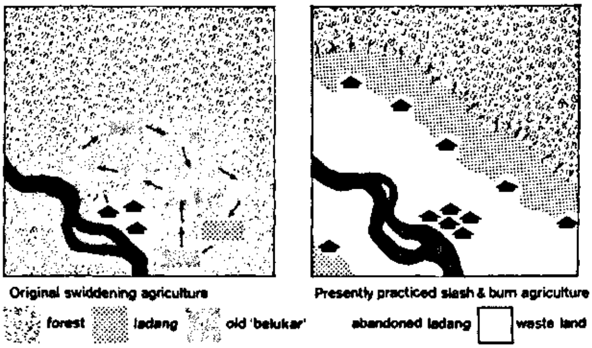


FIG. 146. Schematic representation of the difference between 'swidden agriculture' and 'slash and burn agriculture'.

actively create an impoverished habitat of coarse-sedged grasses (e.g. *Themeda gigantea, Andropogon* spp.) and ferns (e.g. *Pteridium aquilinum, Gleichenia linearis*), in such abandoned areas by frequently setting fires. Such fires even destroy the inaccessible remnants of gallery forests in ravines, i.e. the potential cores for future regeneration.

The agricultural activity found at present in the range of the orang utan in Sumatra can be sub-divided into four categories, following the scheme put forward by CHAPMAN (1973):

FIG. 147. Making 'ladangs' for growing cash crops; Sukarimbun within the Gunung Leuser reserve (September 1973).

(A) People subsisting of their 'ladang', who, because of relatively fertile soil conditions (i.e. river valleys) can stay in one place for a long period or who have to stay in one place because of lack of new areas suitable for cultivation. These occur e.g. in remote regions of the Alas valley, the Gayo highlands and along Aceh's west coast.

(B) The making of supplementary 'ladangs' on mountain slopes and in forested regions for growing cash crops (fig. 147 and 148). This type of agricultural activity is now widespread, and is found in large parts of the Alas valley, the Gayo highlands and Aceh, but particularly in Deli and the Karo highlands.

(C) Wide-ranging slash and burn agriculture by many people simultaneously invading an area. Such people often have moved massively, or have been 'transmigrated' from regions where all the land is used for cultivation and where living conditions have become poor. For example, regions in Tapanuli and Java have become so crowded with people that all arable land is rapidly becoming exhausted and people are forced to seek better living conditions. Such a human invasion at present threatens sectors of the Gunung Leuser reserve, particularly in the southern part of the Alas valley, where large numbers of Batak people from Tapanuli re-settle. The same is true for the region South of Bakongan where, according to a government plan, a large 'transmigration' project for Javanese people will be established.

FIG. 148. People penetrate deeper into forested regions along the water courses they have earlier explored during fishing trips; note the new 'ladang' at the left (Leumbang region, Kluet reserve).

(D) Clearance of large areas for plantation crops such as rubber, coffee, pine-trees and coconut palms. This type of slash and burn technique is to be found in North Sumatra mainly along the eastern boundaries of the Langkat reserves, in Deli, and along the western boundaries of the Gunung Leuser reserves, in West Aceh. Plantations of pine-trees cover extensive areas around Blangkejeren and Takengon in the Gayo highlands.

The 2nd and 3rd categories especially often follow legal, or illegal timber felling operations and often seem to be initiated by people who took part in these felling operations.

Increasing numbers of people who lived one generation ago on a subsistence basis, have rapidly developed a 'consumers' attitude. This was induced by improved means of communication which served the widespread advertisement of luxury articles (e.g. portable radios, cassette recorders, motor-bikes, air-guns). Such people at present attempt to abandon the subsistence mode of life and cultivate extra ladangs to grow cash crops in order to meet the recently created demands for such articles. Thus, for instance, people may clear forest in remote regions to grow illegal, but very profitable crops such as *Cannabis*

FIG. 149. An advertisement in the South East Asian edition of a widely read world magazine.

(for the marihuana trade). In the remote Kapi area, several such *ladangs* were observed.

Formerly, under Netherlands colonial rule, the Government in Sumatra encouraged local people to clear forested regions in an attempt to 'improve' their living conditions. Even equipment was provided for this purpose. The attitude that clearing forest is a sign of progress is still prevalent in South-East Asia (see also fig. 149); yet, at present a permit from the local Government (i.e. *Dinas Agraria* and *Camat*) is needed to clear an area and make a 'ladang'. Only small sums of money are involved in such a transaction. In 1973, a permit for one hectare costed approximately 5000 Rp. in administration fees. After having obtained the permit, one is proprietor of the plot. When such a 'ladang' can be converted into an irrigated ricefield (*sawah*), the price of such land increases by a factor of 80 to 100. Notwithstanding the small sums required for a ladang permit, it was common practice in the Alas valley to start felling before a permit had been granted.

In cases where local people, who consider all forest free for use (according to their '*adat*'; see also Constitution Art. 4.) had (accidentally) been granted permits to make their ladangs inside a reserve, it appeared extremely difficult to undo the action. Due to the fact that accurate maps of the region were usually lacking, and that control is insufficient to safeguard against errors, the

FIG. 150. Almost entirely denuded country along the Kabanjahe – Lao Balang road (Karo highlands).

authorities often appeared to be not very well informed about the exact location of areas requested for slash and burn practise, nor about the location of reserves.

In conclusion, the effect of a modernized, rapidly increasing human population, employing an ancient type of agricultural practice, stripped of *adat* restrictions, is that the remainder of the rainforest is being destroyed over a wide front, leaving behind vast areas of devastated grass-covered land exposed to erosion. Striking examples of this form of human influence can be observed in the region surrounding Lake Toba, and in the Karo highlands along the Kabanjahe – Lao Balang road (fig. 150).

3.3. HUMAN POPULATION GROWTH

As stated in the Introduction (p. 327), conservation of an ecosystem is closely related to the disturbing effect of biomass surpassing the limits set by the carrying capacity of that system. It is clear that the human population of the world, and in particular in some regions in Indonesia, has by far surpassed these limits. I will now discuss some aspects of population dynamics in humans, which are the ultimate cause of the increasing destruction of the ecosystem, and hence of the orang utan's imminent extinction.

More than 70% of Indonesia's human population subsists on agricultural activity. The 1971 population census revealed approximately 21 million inhabitants in Sumatra and approximately 5 million inhabitants in Kalimantan. Corresponding population density figures, calculated with reference to the total potentially arable land area are 44 individuals per km sq. and 10 individual per km sq., respectively. The comparable figures for Java are some 50 times as high.

The human population density along the forested edges of the orang utan's range in Sumatra (see fig. 151) amounts to:
a) 25–80 individuals per km sq. along the coasts of Aceh, west- and north-east of the range; (b) 250–300 individuals per km sq. in the southern sector of the Alas valley (see fig. 151). The cultivated, and densely populated Alas valley protrudes like a wedge into the main range of the Sumatran orang utan; (c) 10–50 individuals per km sq. in the forested regions and *blang* areas around Blangkejeren, south-east and north-west of the range, respectively; (d) 40–100 individuals per km sq. in the eastern region, bordered by the extensely cultivated lands of Langkat and the coastal Deli plains.

The annual population increase in North-Sumatra is on average 2.5‰. Still, it may be even higher in some regions where the conditions of development, i.e. education and medical care, are more advanced and where the local tradition is for numerous offspring (i.e. the Batak ethnic group). While the birth rate has remained stable since the nineteenth century at approximately 45 ‰, the mortality rate decreased drastically to less then 20‰. This decrease was certainly effected by the widespread introduction of western ideology

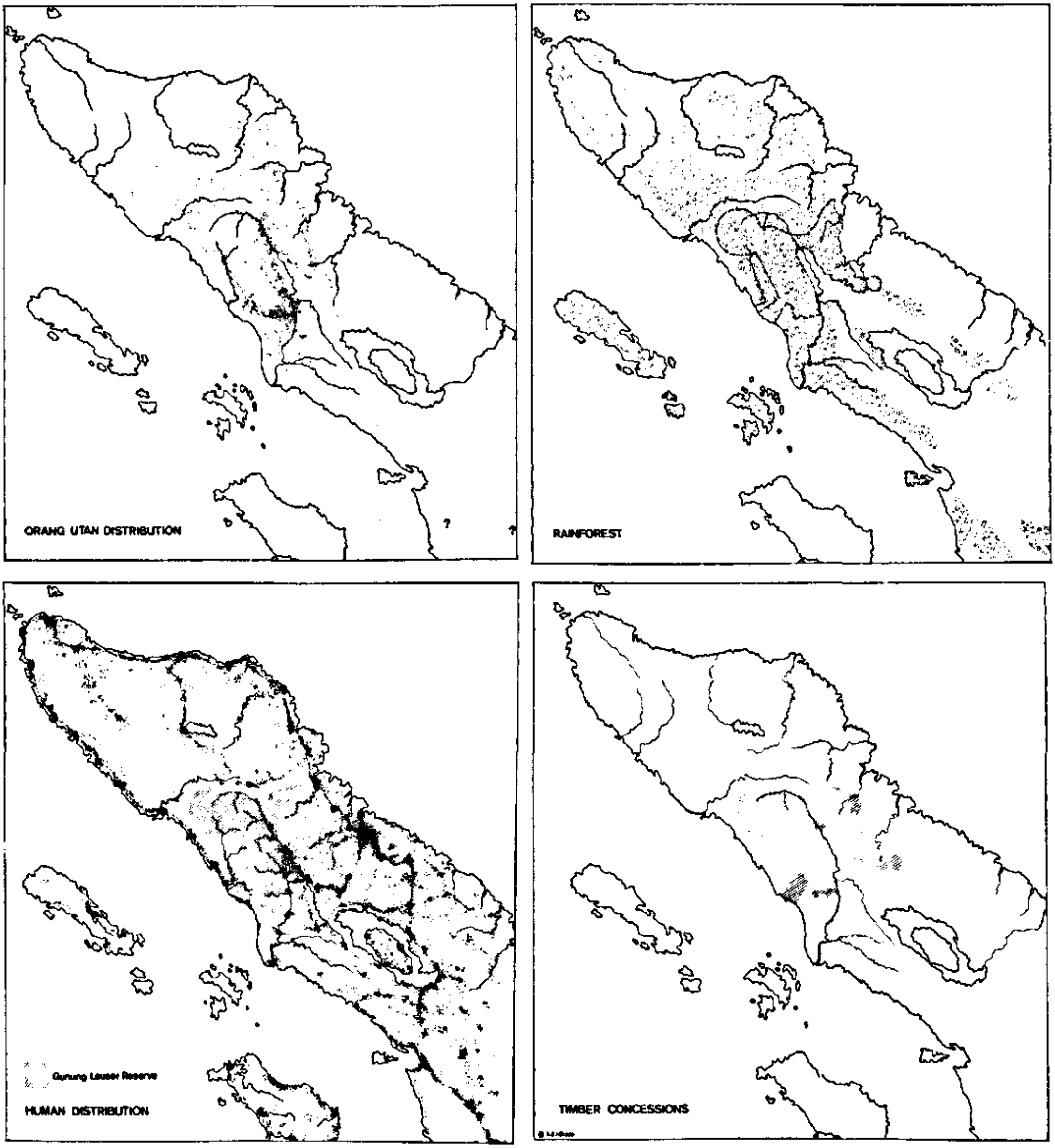


FIG. 151. The present conservation situation in North Sumatra; extent of forest, orang utan distribution, human distribution, timber concessions.

which shattered local religion and *adat*, and brought with it increasingly efficient medical care.

The traditional rules (*adat*) of many so-called primitive societies prescribed certain restrictions with respect to reproduction (see e.g. MARSHALL, 1961;

NEEL, 1970). For instance tradition prohibited copulation with nursing females in certain societies, thus introducing a spacing out between parturations which might last as many as 3–6 years. It also controlled the population by means of generally accepted abortion and certain forms of infanticide (see e.g. MARSHALL, 1961; CHAGNON, 1968; DICKEMAN, 1975). Similar population controlling mechanisms were also prevalent in early Europe, before the Christian religion put an end to it (BRØNDSTED, 1960). Yet, despite such regulations, it can be safely assumed that there was always a high premium on a large number of offspring, especially in peasant, stationary, tribes. However, the ecological mortality factors of disease, and perhaps animal predation, together with the even more important human behaviour of raiding and warfare, kept numbers of people low.

Thus, several cultural patterns, either within the group, such as birth- and neonate-control, or between groups, such as warfare and raids, resulted in a degree of population control, that kept human biomass in balance with the carrying capacity of the land. Technological tackling of the ecological mortality factors such as diseases, (and animal predation), and firm administrative control (which banned warfare, etc.) rapidly resulted in a steadily increasing, and subsequently expanding population. Because of this expansion the ecological balance became disturbed in a progressively serious way.

The only way left open by modern ideology to achieve a new ecological balance in countries such as Indonesia is to increase technology. In the first place this can be done by means of birth control and family planning, accompanied by efficient propaganda and perhaps enforced by strong governmental actions (cf. Singapore). In the second place it is attempted by education and improvement of local agricultural techniques (see e.g. GREENLAND, 1975).

Effective conservation of nature and natural resources can be achieved only by keeping the human biomass within limits. Not so much as to preserve certain peculiar plants or animals, but primarily to conserve the tropical ecosystem in which man has his place. 'Transmigrating' excess populations to areas with a low population density does not solve the problem, but merely shifts it in space and in time. Moreover, when such measures are not carried out concomittantly with very strict regulations to keep subsequent birth-numbers within limits, population increase in such newly invaded regions may be even stronger than in the area from where the people came, because of the favourable living conditions.

During our surveys we learned that several local informants with large families would have preferred smaller families, if they had had the opportunity to prevent conception. Their arguments centred around the theme that few children have a better chance to get educated and hence are assured of a better future, as the possibilities for agricultural subsistence are limited on account of the scarcity of arable land.

Birth control programmes sponsored by the government are in operation in several regions of Indonesia. Such programmes are not everywhere as effective as could be, and authorities, midwives and influential clergymen not always display a cooperative attitude. For instance, anti-conception devices were not easy to come by in the Alas valley, and people had far to travel for more elaborate treatment (i.e. vasectomy and placement of IUD's). One important aspect, noticed with respect to the problems encountered in birth-control is that suckling infants and toddlers add considerable prestige to a woman's social status. A mother with infant attracts much more social attention from adult males and females, than would be the case if the female was alone. This attention reinforces the mother's role. This was clearly discernible in several families in which the male partner had a positive attitude towards birth control, but the female partner opposed the idea of no longer having dependent infants.

3.4. COMMERCIAL FOREST-EXPLOITATION

There is a rapidly growing international demand for wood, due to a strong increase in the number of consumers as well as in the development of different uses for wood products (e.g. WADSWORTH, 1966). Apart from the enormous local consumption of wood for cooking (EKHOLM, 1976; WADSWORTH, 1966) many of the wood products may be classified as luxury goods. These include the fuel-wood and charcoal products exported to Arabian, American and European countries. Wood is made into, or used for: paper, plywood for packing material, fire-wood, charcoal, industrial wood (building material), veneer fór decoration and road-markers, and in many luxury products.

Foreign investment in forestry exploitation in Indonesia amounted to more than 500 million US dollar in 1970. The investment of such large sums in forestry projects usually makes reasoning for conservation of the rainforest sound futile in the ears of people obsessed with ideas of 'development' according to western standards. Similarly, the arguments of an ecological disaster (DASMANN, 1965; MEADOWS, 1972), easily forseeable for tropical countries without sufficient – hill and mountain – forest cover, usually meets with little sympathy. The expatriate technocrats, that set the trend in such tropical countries easily make utopian promises of western-type industrialisation, enveloped in terms of development, progress and modernisation. In such an atmosphere, it is easy to understand that the destruction of the forest ecosystem in order to exploit so-called free resources, i.e. timber, to be exported to technologically advanced western countries is often euphemistically claimed as beneficial to the country.

There is a general trend to underestimate the destructive influences of commercial logging operations, notably so-called selective logging. Consequently areas in Indonesia reserved for the protection of wildlife are increasingly being used for exploitation. Except for some reserved areas and remote regions where logistics as yet make economic exploitation non-feasible, virtually all forest habitat has been leased to timber concessions (for North Sumatra see fig. 151) (MEIJER, 1975). Large-scale logging programmes (10,000–1 million ha) are

FIG. 152. Local people, transforming logs into beams by hand.

invariably carried out by foreign companies, notably from the USA, Japan, the Philippines, Europe, Hongkong and Singapore.

Logging operations, size and organisation

Logging operations can be divided into two main categories, according to size and organisation; (a) local concessions and (b) multi- or bi-lateral concessions. The local concessions, recently restricted to 100 ha per concessionaire, are granted by the provincial government, but are subject to ratification by the Central Forestry Department. The large multi- of bilateral concessions are issued by the Central Forestry Department and ratified by Ministerial decree. These concessions range in size from some 1000 to 1 million hectares of forest (see also OVINGTON, 1974). Such consessions affect ecosystems, and often threaten the existence of local peasant people, for instance in Kalimantan, on the Mentawai islands, and in Irian.

Besides these State controlled logging schemes, a considerable number of local people operate privately (fig. 152), felling trees illegally and selling the logs to local saw-mills for processing and distribution. This illegal logging is insufficiently controlled by the local authorities.

Within the range of the Sumatran orang utan some 10 large-scale timber concessions are being operated, covering approximately 40–50% of the entire range (see fig. 151). In addition to these, numerous local concessions operate, affecting much of the remaining areas. Although the total area of local concessions may seem very unimpressive on a map, their actual logging operations cover a much wider area than the 100 hectares which have been granted. Proper control is often lacking, and some of the controlling authorities themselves are involved in the lucrative business of 'legalising' illegally extracted wood. The destructive influence of some 5 saw-mills in the northern part of the Alas valley, between Kutacane and Ketambe, was discernible in an area of some 16,000 ha (fig. 153). Officially this should have been merely 500 ha. This large area was selectively felled, i.e. only the most valuable Dipterocarps were extracted, whereas the legal concessions are practically clear felled, and subsequently converted into arable land or waste land.

The illegally harvested trees are often felled by local people who are not employed in the proper sense, but work on a more or less freelance basis. This situation is somewhat in-between 'private enterprise' logging and outright stealing of wood by legal concessionaires.

Local concessions are often worked on the basis of a privately owned saw-mill, where the logs are processed into boards, beams and rafters and sold to dealers in the larger cities and towns. In the Alas valley such saw-mills work with rather primitive equipment, consisting of one rotating saw driven by a car motor. The logs are supplied to these mills via floatation on the Alas river, and by being dragged in by water-buffaloes. A number of 5–10 trees is processed per day by the average sized saw-mill (i.e. Seldoq) in the Alas valley. Crude logs, some 5 meters in length, fetch 7000–8000 Rp per ton (4–5 such logs make 1 ton of wood) for the supplier. The price of processed wood brought between 18000 and 22000 Rp. per ton in 1974, depending on whether it was second or first quality wood.

Some of the local concessionaires relied almost entirely on the harvest of their illegally operating suppliers. For instance, the large saw-mill in Laklak, that had been established in 1974 processed only illegal wood supplies during its first year. In accordance with the Forestry Law, this mill was built for a 100 ha timber-concession. However, the concession area almost exclusively consisted of agricultural fields, lacking trees. Awaiting a larger concession, this saw-mill induced a boom in illegal timber extraction from the Gunung Leuser reserve. Within three months of completion, its influence was discernible in an area of some 3000 ha. The illegal suppliers of the Laklak saw-mill destroyed much of the scenic beauty of the roadside north of Aunan, that had great potential as a tourist attraction.

The usual order of events is that, as soon as a new saw-mill is established, local youth invade the upstream region and start to fell and extract all accessible, valuable timber trees. In hilly country this type of illegal felling may penetrate as far as 2–3 km from the rivers.

While local concessions often still work with rather primitive equipment,

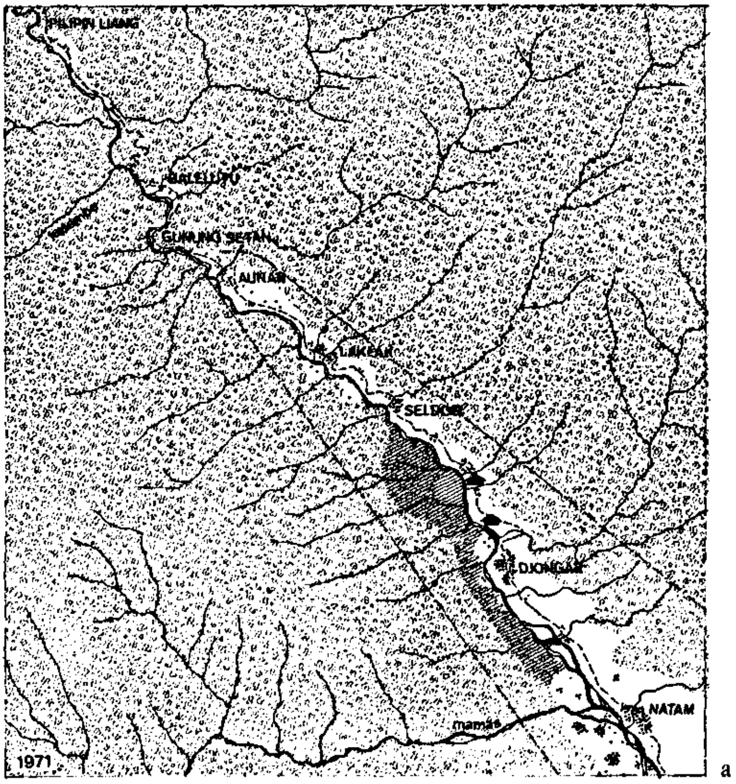


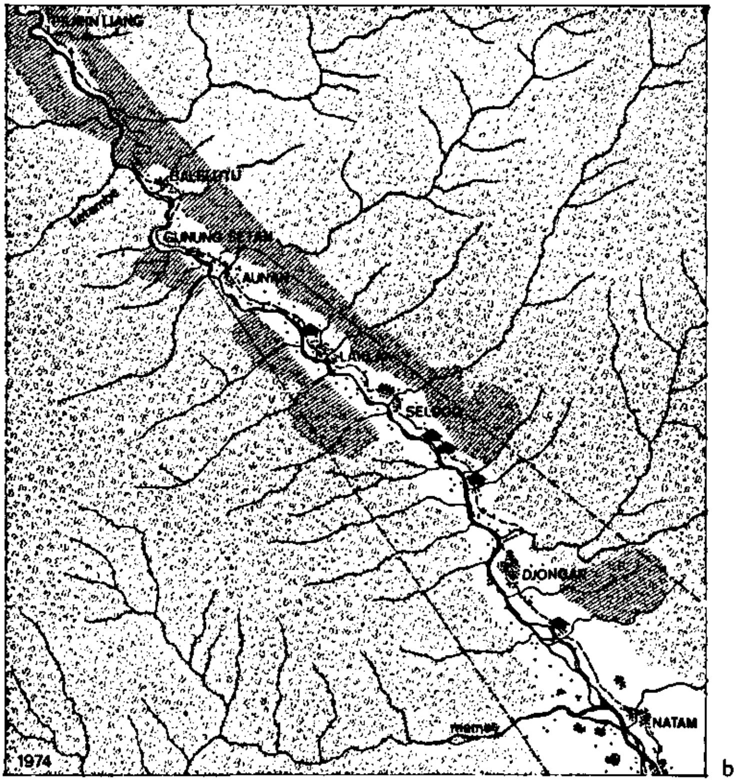
FIG. 153a, and b. The increasing destruction due to commercial timber exploitation and subsequent ladang activity in the northern part of the Alas valley since 1971.

using hand-axes to fell the trees and waterbuffaloes to extract the logs, larger concessions work with very sophisticated and heavy equipment such as motorised chain saws, tractors, bulldozers, etc. Most of the timber extracted from the large concessions is exported unprocessed as logs.

Logging technique; disturbance

Two extreme types of logging operations can be distinguished, namely (a) clear-felling, in which the entire wood stand is removed, and (b) selective logging, in which only some of the most valuable timber trees are extracted. Selective logging aims at sustained yield. The forestry regulations restrict the harvesting to trees with a girth larger than 90 cm and usually limit the number to some 8 trees per hectare. Under such regulations the forest is assumed to have sufficient potential left to regenerate.

Despite the regulations, the number of felled trees is often 12 or 15 per hectare (MEIJER, 1973; see also WILSON & WILSON, 1975) or, in rich stands of valuable trees, may reach as many as 75 trees per hectare (BURGESS, 1971), thus approaching clear-felling in ultimate effect.



In general it can be said that, due to the great investments and profits involved in the timber trade, and to inadequate and insufficient control (KARTAWIMATA *et al.*, 1974), regulations are violated whenever the opportunity offers. Concessionaires readily violate the regulations and restrictions, particularly when valuable timber trees are known to occur in adjacent areas, no matter if these are reserves. They 'accidentally' harvest such trees and destroy the region, often said to be due to inaccuracies in the concession maps if it ever comes to the light. Such an incident was witnessed by us during our visit to the Kluet reserve (fig. 155), where a timber company operating near the reserve intended to fell large stands of protected camphor trees[41] (*Dryobalanops aromatica*) within the reserve, some 8 km away from their official concession (fig. 151; 4).

In practice, forest management is in the hands of the, usually foreign, concession owner, who has to work on the basis of priorities dictated by fluctuating economic market requirements. Such priorities are too often contradictory

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[41] These represent probably the last remaining stand of this species in North Sumatra (RAPPARD, pers.comm. 1972).

FIG. 154. The shores of the inaccessible lake Bangko in Kluet reserve, still unaffected by human influence (February 1973); a rare sight in North Sumatra.

to those ensuring the long term productivity of the forest (Fraser; quote Aggarwala, 1975), let alone the conservational aspects of the eco-system.

Due to the present economic development and advanced processing techniques, modern logging schemes tend to increase the effectiveness and speed of their logging operations. This results in diminished discrimination between valuable and less valuable trees (Van Steenis, 1971; Wadsworth, 1975) and the harvesting of smaller trees (Meijer, 1975). The trend to increase efficiency thus induces greater harvests per hectare, resulting in doubling of the legally set limit, but often also aims at clear-felling (Wilson, 1976; pers.comm.). The ecological implications, and the impossibility of future yields of such clear-felling are often debated against with promises of reforestation. On the very rare occasions that logged-over areas are indeed re-planted, this is generally done with a mono-culture; in Sumatra notably *Pinus merkusii* or *Dacridium* spp. However, the unique complex rainforest community of plants and animals never returns. The complexity of such a planted forest is extremely poor in comparison with the rainforest.

The commercially most valuable trees in Sumatra are often members of the *Dipterocarpaceae* family (*'meranti'*), and the *Lauraceae* (*'medang'*), invariably those which contribute to the higher strata of the forest. The felling of such large trees creates a wide area of destroyed vegetation, measuring approximately 50 × 30 meters. In addition, surrounding trees are also pulled down by the inter-connecting lianas and creepers.

In general, the felling of 10% of the trees in a certain area results in an actual destruction of at least 55% of the other trees (Burgess, 1971). This means that after extraction of 10% of the timber trees, only 35% of the vegetation remains.

For the extraction of the logs by heavy caterpillar tractors, wide roads paved with logs of non-commercial trees are constructed. Notably the construction

FIG. 155. Felling of valuable timber inside Kluet reserve, several kilometers away from the official timber concession (February 1973).

and use of such roads add to the devastation of the area. In fact, it is considered even more detrimental for the regeneration of the forest ecosystem than the actual felling damage (see BURGESS, 1971; and MEIJER, 1974), as such roads are often the cause of erosion and facilitate later encroachment by migrant people.

3.5. INFLUENCE OF LOGGING ON THE ECOSYSTEM

Surveys

In the initial stages of this study, several surveys were carried out in the Alas valley, in order to find a suitable location for a study area and to get an idea of the status of different sectors of the Gunung Leuser reserve adjacent to the inhabited Alas valley. During many of these surveys I traversed undisturbed rainforest which, in subsequent years, became exposed to various degrees of human disturbance, due to selective logging by local people (see fig. 153). Some of these areas were re-visited, some time after the disturbance had taken place, in order to get an impression of possible changes in the occurrence of orang utans.

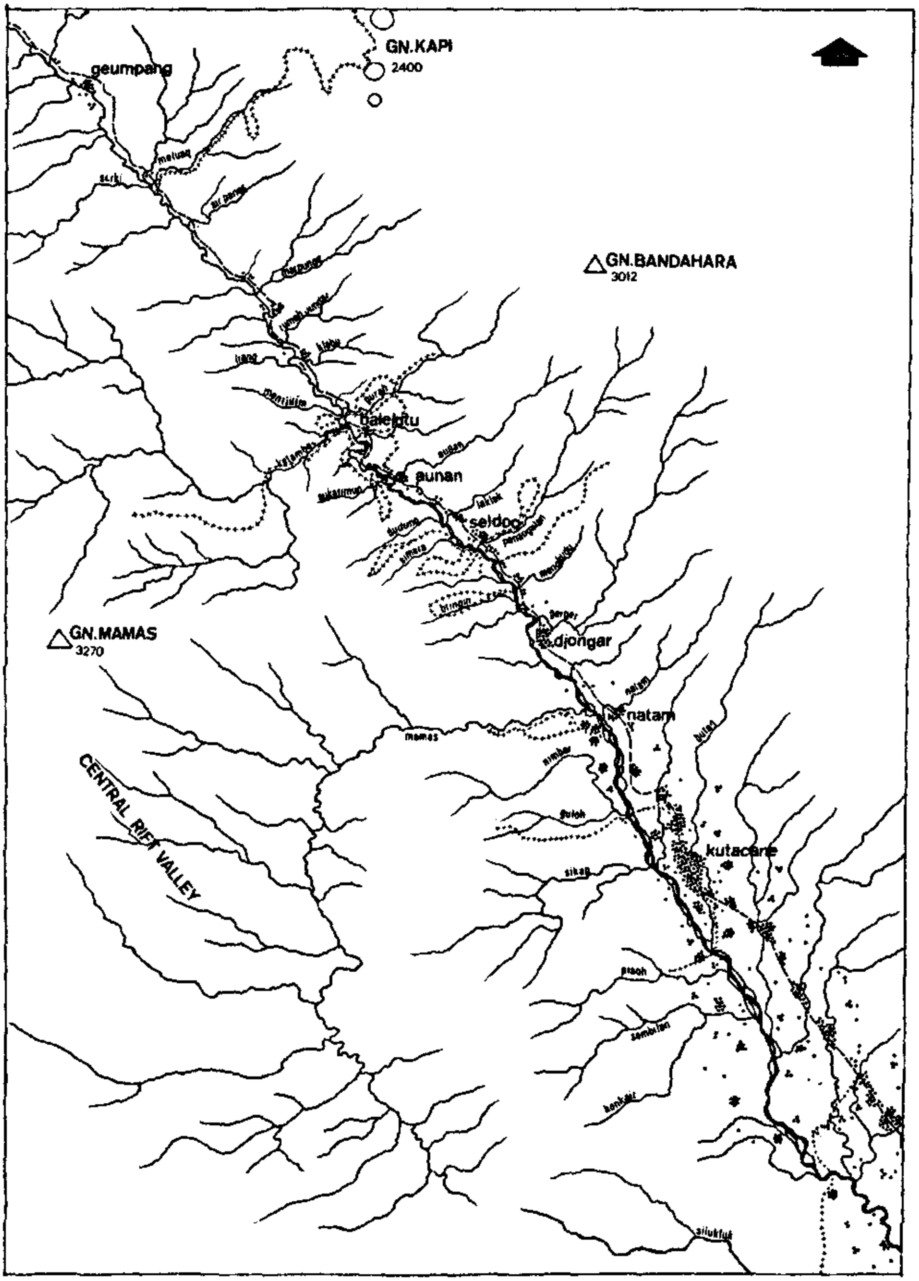

FIG. 156. Map showing the surveys in the Alas valley.

FIG. 157. The destructive influence of one felled tree in a lowland forest; an example of 'selective logging' (Sikundur reserve, 1971).

Usually such surveys lasted one day only. The distance covered was on average 6 kilometers (range 5–8) through forest. As in the search for orang utans in the Ketambe area, all sightings of other animal species were recorded, but particular attention was given to the counting of orang utan nests. On p. 39 I discussed the inaccuracy of nest counting as a means of estimating the density of orang utans. However, nest counting was the only way to get an impression in a short period of time. As I tried to match the surveys through the same areas as much as possible, the raw data, i.e. nests per covered kilometer, (see table 21) allow a fair comparison as to the effects of the disturbance.

The number of nests per kilometer, found during the initial surveys are consistently higher than those found in the surveys after disturbance had taken place. This is in spite of the fact that the search technique had almost certainly improved since then, as may be inferred from table 21, b. The data given in table 21, suggest that orang utans are less numerous, or may even be absent in areas affected by logging and ladang disturbance, especially when the disturbance has a permanent character.

In addition to the comparative surveys in the Alas valley, we made several other, general conservation surveys in different sectors of the Gunung Leuser reserves through undisturbed- and disturbed forest. The results of these surveys are shown in table 21,c; the distance covered in these conservation surveys was

Table 21a. Showing the number of orang utan nests per kilometre (n/km) gathered during comparative surveys before and after disturbance by logging and/or ladang activity. (–: no disturbance, + : local timber extraction and minor ladang activity, + + : commercial logging and large scale ladang activity.)

Survey	Habitat type altitude in m.	1971/1972 before disturbance n/km	1972/1973 after disturbance n/km	Degree of disturbance
Renun	hill forest (100 m)	1	0.6	+ (momentarily)
Seldoq	hill forest (300 m)	1.4.	0	+ + (permament)
Kompas	river valley (200 m)	2.3	0.3	+ (permanent)
Gulo/Mamas	hill forest (200 m)	0.8	0.4	+ (momentarily)
Gn. Setan	hill forest (300 m)	1.9	0.9	+ (momentarily)
Penangelan	river valley (200 m)	1.8	0	+ (permanent)

Table 21b. Comparative surveys through areas where no disturbance took place.

Gurah	hill forest (400 m)	2.1	(2.5)	–
Ketambe	hill forest (350 m)	1.2	(2.6)	– (study area)

Table 21c. Showing the number of orang utan nests per kilometre (n/km) gathered during general conservation surveys in the Gunung Leuser reserves in undisturbed (–) and disturbed (+) areas.

Survey	Habitat type altitude in m.	Number of nests per kilometre	Degree and type of disturbance
Kapi	hill forest (1200 m)	0.9	–
Meluaq	hill forest (1000 m)	1.3	–
Gn. Ketambe	mountain forest (1500–1700 m)	0.8	–
Bengkung	river valley (100 m)	1.6	–
Mukap	river valley (250 m)	2	–
Kluet	swamp forest (50 m)	0.7	–
Laot Bangko	river valley (50 m)	1	(+) old ladang
Leumbang	river valley (50 m)	0	+ + timber concession
Bukit Lawang	hill forest (100 m)	0.6	+ selective logged area

on average 7 kilometers (range 2–25). Two of these surveys, i.e. Leumbang river, and Sikundur, were either in or adjacent to commercial timber logging areas. The Sikundur survey, that lasted 10 days (November 1971), gives a picture which is in many aspects illustrative for the disturbance in a forest ecosystem, and is treated in more detail (see table 22).

Although conclusions from table 21c. have to be highly tentative, the results of the general conservation surveys support the suggestion drawn from table 21a., i.e. that areas without disturbance contain a larger number of orang utans than disturbed regions. Furthermore, in currently active places (i.e., timber felling: Seldoq, Penangelan, and Leumbang river), orang utans may be absent altogether. This picture is supported by the data from the Sikundur surveys.

The Sikundur area, although protected as '*suaka margasatwa*' has in part (i.e. 5000 ha) been leased as commercial timber concession by the Indonesian Forestry Department. Ironically, the concession has been granted to improve the conservation situation. The timber company was obliged to construct roads, to erect watch-towers and to clear areas in order to promote grass-growth for deer, so that the region would allegedly become 'more attractive' for tourists.

Our surveys covered (a) sectors where logging had already been accomplished some time ago and secondary vegetation had developed ('*belukar*') (5 km), (b) sectors where logging was in operation (4 km), (c) sectors of slightly disturbed forest, i.e. primary forest traversed by survey tracks and path, where the logging operations were audible from their source, 1–3 kilometres away (14 km), and (d) sectors of undisturbed primary lowland forest (7 km). Table 22 shows the direct observations on the fauna with reference to the surveyed sector, as well as the indirect observations on animal species, such as nests or tracks.

Local information revealed that for the last two years, orang utans had only rarely been seen in the concession, whereas these apes had been 'numerous' in the days when the logging operations started. Employees of the concession also stated that, although they used to hear orang utan 'long-calls' every time they felled a tree several years ago, they had not heard the sound since. No 'long-calls' were heard by us either during the logging operations that we witnessed.

Although there are some anecdotal observations of young orang utans moving through '*belukar*' (see STOTT and SELSOR, 1961; HAILE, 1963), even from the Sikundur area (WALMAN SINAGA, pers. comm., 1972), such indidental records do not permit conclusions such as that 'orang utans will re-occupy and subsequently thrive in logged-over forests' (STOTT and SELSOR, 1961; p. 41). Such statements seem strongly biased by an urge to obscure the disastrous effects of logging on the ecosystem.[42]

Table 22 shows that orang utans nests were only found in regions with little

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[42] It is noteworthy that a subsequent survey through a logged region (i.e. the Gomantong area in Sabah), reported as suitable orang utan habitat by STOTT & SELSOR (1961) only one year before, revealed that no orang utans nor nests could be found in the region any more (HARRISON, 1962).

TABLE 22a. Direct observations on the fauna of the Sikundur lowland forest with reference to human disturbance.

Species	'*Belukar*' secondary vegetation observ./km	Forest under logging observ./km	Slightly disturbed forest* observ./km	Undisturbed primary forest observ./km
Siamang	–	–	0.07	0.14
White handed gibbon	–	–	0.35	0.57
Long tailed macaque	–	–	0.14	0.14
Pig tailed macaque	–	–	0.07	0.14
Thomas' leafmonkey	–	0.25	0.07	0.29
Silvery leafmonkey	0.6	–	–	–
Elegans flying squirrel	–	0.25	–	–
Horse tailed squirrel	–	–	0.21	0.57
Tenuis squirrel	0.2	0.25	0.28	0.57
Tupaya	–	–	0.21	0.28
Flying lima	–	–	–	0.14
Pigs	–	–	0.14	0.14
Argus pheasant (call)	–	0.25	0.64	0.71
Helmeted hornbill (call)	–	–	0.14	0.86
Rhinoceros hornbill	–	–	–	0.42
Bushy crested hornbill	–	–	0.14	0.14
Total observations of species per kilometer	0.8	1.00	2.46	5.11

TABLE 22b. Indirect observations (i.e. nests and tracks) per km.

Orang utan nests	–	–	0.28	1.57
Elephant track	0.4	–	0.21	0.14
Deer track	0.4	0.25	0.28	0.28
Pig track	1.0	0.50	(0.86)	(0.57)
Total number of species	5	6	15	17

(*: forest traversed by survey tracks and pathes, logging action audible, 1–3 km away.)

or no disturbance, i.e. 11 of the 15 nests were found in entirely undisturbed forest. Though far from conclusive, these data are in accordance with the picture from tables 21a, b, and c.

Siamangs were rarely encountered in the Sikundur region. In the course of the ten days survey only one group was seen, and another one was heard calling. No siamangs were found in the *belukar* and action zones. The observed group was found in the sector adjacent to the logging operations some 600 meters away and it was very shy.

Gibbons were more numerous, a total of 9 groups were found during the surveys. Again, no groups were seen, nor heard in the *belukar* and action zones, and gibbons were only found in intact rainforest. As hylobatids are territorial apes, it is puzzling as to what happened to the groups that had been driven from their range by the logging actions. Such animals cannot possibly integrate into adjacent groups because of the aggressive reactions of neighbours with respect to intruders into their territories.

The only arboreal mammals encountered in the secondary vegetation zone of the Sikundur area were two groups of silvery leaf monkeys (*Presbytis obscura*) and a pigmy squirrel (*Sundasciurus tenuis*). In general, silvery leaf-monkeys were found to be even more numerous in secondary vegetation throughout North Sumatra [43] (see also WILSON and WILSON, 1975). In fact, the only group of silvery leaf monkeys observed in the Alas valley, lived in a mixed habitat of plantation and '*belukar*' near the village of Buluh Biang, some 8 km North of Kutacane.

Tracks of elephants, pigs and deer indicated that these species were present in the sector of secondary vegetation, presumably more abundantly than in the other sectors.

The paucity of observations of hornbills during the survey, particularly in the regions other than the undisturbed primary forest was remarkable.

In conclusion, the logged *belukar* sector was extremely poor in mammal species, and our impression that most of the characteristic animals of the rainforest were lacking altogether, is strongly reflected in the data. When entering into undisturbed forest areas, the numbers of species encountered increases relative to the distance from the sources of disturbance. It appears that most of the animals flee from the disturbance of logging operations; only pigs, deer and elephants may soon return when the vegetation regenerates. Most of the other animal species are pushed into the remaining undisturbed sectors. Such migration inevitably upsets the ecological balance of the sectors adjacent to the logging operations. The undisturbed lowland forest of Sikundur was as rich in animal species as other undisturbed rainforest regions visited during this study.

3.6. DISCUSSION

The tropical rainforest of the South-East Asian region is one of the most complex and diverse, ancient ecosystems in the world (VAN STEENIS, 1971). Most of the components are dependent on the intactness of the system; i.e. the evolutionary adaptations of most species are finely tuned to a comparatively narrow, but stable niche. Both MARGALEF (1968) and ODUM (1971) have even suggested that selection in a mature ecosystem is not merely a matter of competition between individuals or species that occupy the same level in a food chain, but that it favours those species that contribute positively to the stability and efficiency of the system.

[43] Some primate species, notably the leaf-eating Hunuman langur (*Presbytis entellus*) appear to have striking adjustability to new food-items forced upon them by dramatically changing habitat conditions (see POIRIER, 1969).

Since each organism affects its environment, the intactness of course incorporates continuous 'natural' disturbance. The biomass of any particular organism determines its degree of influence, but the system, by definition exerts counter-pressures which regulate this biomass. The occasional removal of trees by man for local use may be considered as such a 'natural' disturbance. However, as soon as the subsistence level of people is replaced by commerce, or when human biomass outgrows the carrying capacity of the system, the activities of man rapidly become detrimental to the rainforest. The disturbing influences of man are graded. They range from those which the system can overcome when given time, (e.g. the primitive swidden agriculture), to those which the system cannot overcome, such as the many forms of clear-felling and over-exploitation, which eventually result in erosion and desertification. The influences of commercial logging on the rainforest ecosystem can be grouped into two categories, (a) the short term disturbance, and (b) the long term effect of habitat change. In this section, only the effects concerning the fauna, and the orang utan's ecology are discussed.

Short term effects

The data in the foregoing section reveal that nearly all animal species flee from the sites of logging operations. They presumably become wanderers as the zone contiguous with the sites of disturbance seems less densely populated than the undisturbed forest. Several authors have stressed this repelling effect of actual felling operations (e.g. BURGESS, 1971; WILSON and WILSON, 1975). MACKINNON (1971) has reported on the migratory movements of orang utans, induced by timber logging operations, and he stated that this severe disturbance had caused a significant 'drop in birth rate' among the local orang utan population. Although such a statement would require a long term field study, it is certainly conceivable that reproduction is negatively affected under stress conditions (cf. AUTRUM and VON HOLST, 1968). We noticed that orang utans often react to the sound of a breaking branch; mothers always made reassuring 'squeak' vocalisations when breaking a branch for nest construction when their child was near. Adult male orang utans often gave a display, including a 'long-call' vocalisation, following the crashing sound of a falling (or felled) tree. It is not difficult to imagine that the repeated sound of crashing trees connected with other sounds of logging operations, result in serious arousal and stress in a local orang utan population. MACKINNON'S (1971) observations suggest that resident orang utans are driven out of their home range and start wandering over areas hitherto unfamiliar to them. Such wandering individuals remain under stress conditions because of decreased opportunities to find food in an unfamiliar area and because of unfamiliarity with the individuals of the local population. The latter situation increases the probability of agonistic encounters (cf. WILSON and WILSON, 1969, for chimpanzees). Similarly, the local population will experience an increased state of arousal because of unfamiliarity with the invaders, aggravated by increased food competition.

For certain animal species (e.g. tupayas: AUTRUM and VON HOLST, 1968) it is known that stress conditions can negatively affect reproduction. Moreover, stress may result in increased susceptibility for diseases and subsequently decreases the chances of survival. Consequently, the influences of logging operations not only upset the immediately affected population of animals, but also negatively affect adjacent populations. Since most animals live within a more or less clearly defined home range (EISENBERG, 1966), such deleterious effects apply for almost every forest animal.

Long term effects

Since some 70% of the South-East Asian mammals may be considered to be dependent upon undisturbed forest conditions (see MEDWAY, 1971), it is clear that the net result of forest reduction to some 35% after selective logging of 10% of the timber (BURGESS, 1971) is to reduce the original animal biomass to a fraction. Several studies confirm this hypothesis. STEVENS (1969) recorded that at least 48% of the mammal fauna disappeared from logged forest. A comparison of the mammal faunas of undisturbed and disturbed forest revealed that the latter contained less than half (40%) the number of species of the primary forest (see HARRISON, 1969). Similar findings have been reported for birds (e.g. HARRISON, 1965; WELLS, 1971; DIAMOND, 1973; 1975; SCHODDE, 1973); MCCLURE & HUSSEIN (1965) have demonstrated that these failed to establish themselves in adjacent areas when driven out of their range by timber felling operations. As can be expected, a similar impoverishing effect applies to invertebrates, notably insects (see ELTON, 1975).

Thus, the long term effects of logging concern a dramatic decrease in the number of species. Initially these are mainly the vegetational components, but this is followed by many animal components of the system as they experience a decrease in the quantity, and in especially the quality of their food. The impoverishment of the floral components is not only due to the removal of commercially valuable trees, but also due to side-effects resulting from felling, extraction, and other forestry activities (fig. 158). For instance, since commercial logging extracts the large, often emergent trees, it not only destroys the structure surrounding such trees, but also removes all potential hosts for (e.g.) the strangling *Ficus* spp. Moreover, strangling figs are often deliberately killed during logging operations or, when left undamaged, often die of exposure after neighbouring trees have been removed. The death of such trees may be caused by desiccation of the soil (see LEWIS, 1972), or, as is the case with the European beach, by direct sun radiation on the trunk. Left over strangling fig trees are exposed to wind and rain-storm damage and seem to have increased chances of being struck by lightning. Since strangling fig trees are of paramount importance in the ecology of many forest animals (e.g., orang utan, siamang, gibbon, and several hornbill species, to mention only the most conspicuous species), a decrease in the density of this plant genus severely affects the living conditions of these animals.

In at least two recent publications dealing with the conservation aspects of

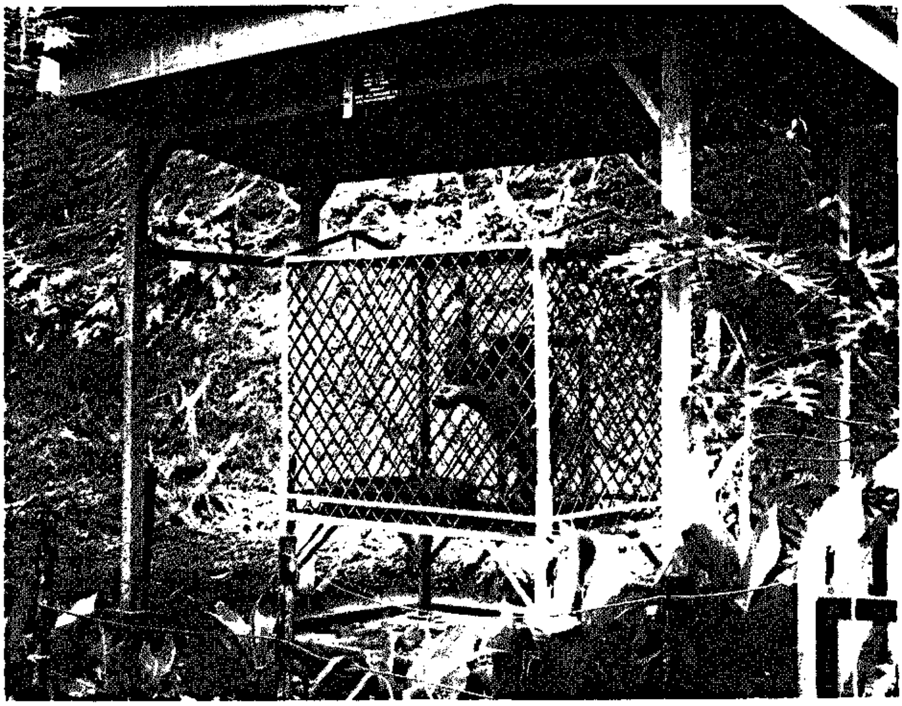

FIG. 158. The way orang utans are kept in some Indonesian zoos (Medan).

timber exploitation in rain forest areas, the statement has been made that 'important food trees such as figs (*Ficus* spp.) are more numerous in secondary forest' (see WILSON and WILSON, 1975, p. 246; CHIVERS, 1976, p. 107), suggesting a positive effect of tree extraction on the ecology of, for instance, primates. However, in their generalized statement, these authors do not distinguish between (a) the *Ficus* species that are predominantly utilized by primates, namely the strangling- and creeping figs, and (b) those species that are rarely, or not at all, eaten by primates, i.e. the cauliflorous and other, single fig tree species. From CORNER's statement that 'excepting the strangling figs, most of our wild (*Ficus*) species are small trees of secondary growth...' (CORNER, 1940, p. 666), it may be assumed that the latter category (b) can become more numerous as the result of felling operations. However, as I argued above, notably the important strangling *Ficus* spp. (a), which provide food for so many animal species are negatively affected by timber exploitation.

As for the orang utan, it is conceivable that the long term effects of commercial logging and forestry activities will be severe, if not detrimental. The most important foods of this ape are found in the higher and middle strata of the forest (see fig. 25), i.e. those affected most by logging operations. Since most of the floral food-components of the orang utan's diet may be classified as belonging to primary forest species, it is highly questionable whether these plants survive in the changed conditions of logged forest (see MEIJER, 1971; 1973). The category of creeping, climbing and liana-type plants, that constitute some 25% of the food plants of the orang utan, is also severely affected by logging operations (see FOX, 1969). It is noteworthy that lianas not only provide this heaviest of arboreal mammals with food, but, perhaps more importantly, with an efficient pathway structure that enables the ape to reach its food with a minimum in effort. Destruction of such means of travel may affect the orang utan's foraging efficiency to such extent that it endangers survival considerably.

4. MEASURES CONCERNING THE PROTECTION OF THE ORANG UTAN

In chapter 3, I described that three main human actions threaten the orang utan's existence, namely, hunting pressure, habitat destruction due to local agricultural expansion, and habitat destruction due to commercial timber exploitation. Although by far the most important threat, habitat destruction will not be treated in this section, mainly because this is more an issue of international politics which goes beyond the scope of this study. As I briefly delineated, it concerns matters of birth control, agricultural development, soil rehabilitation and transfer of local populations. As regards the measures which can improve the management of the Gunung Leuser reserves in particular, I circulated a number of internal reports.

Concerning the actions necessary to tackle the problem of hunting on, and trade in orang utans, I shall only discuss the aspect of rehabilitation in detail (see also RIJKSEN, 1974; and RIJKSEN and RIJKSEN-GRAATSMA, 1975).

4.1. REHABILITATION

Introduction

Being concerned about increasing numbers of illegally captured young orang utans in Sarawak, MRS. BARBARA HARRISSON initiated a program in 1961 to condition three young Bornean orang utan orphans to living in a natural environment. For this purpose she established a modest station in Bako National park (Sarawak). The park is covered with undisturbed primary forest but contains no wild orang utan population; at that time absence of orang utans was considered disadvantageous for such a program (HARRISSON, 1963). When this program, started in Bako National Park, was terminated for political reasons in 1964, the animals were transferred to a newly established rehabilitation station in the Sepilok forest reserve in Sabah. Since then this station has absorbed a considerable number of confiscated orang utans to be reintroduced into the wild (see DE SILVA, 1968; 1971).

As the result of a successful fundraising campaign by the Netherlands National Appeal of the WWF, and on recommendation of WWF/IUCN reconnaissance survey no. 596 (KURT, 1970), a rehabilitation centre was set up parallel to the research project in the Ketambe area in 1971 (RIJKSEN, 1974). Within the same year, a rehabilitation station for Bornean orang utans was established within a study on the behaviour of orang utans in the Kotawaringin-Sampit reserve (South Kalimantan) (GALDIKAS-BRINDAMOUR, 1975).

In 1973, because of its interest in the rehabilitation and conservation of the Sumatran orang utan, the Frankfurter Zoologische Gesellschaft sponsored a second rehabilitation project in Bohorok (North Sumatra), which was estab-

FIG. 159. A captive juvenile female; note her finger sucking behaviour (comfort behaviour).

lished near Bukit Lawang, some 100 km east of Ketambe. Apart from these programs, some private efforts are being made for the conservation of orang utans in Indonesia. Some zoos have quite large collections of orang utans, officially claiming to use them in 'breeding programs' but more often keeping them for trade with foreign zoos to augment their meagre income (fig. 158).

Altogether four rehabilitation programs are at present in operation. Unfortunately, the efforts are not efficiently distributed. The vast area of Kalimantan in particular, is imminently threatened by large scale habitat destruction but is poorly covered by the conservation action, in comparison to the much smaller area in Aceh and North Sumatra. This inefficient distribution appears to be mainly due to private initiatives. It would have been a considerable improvement in the conservation situation if World Wildlife Fund and IUCN, having close connections with both Sumatran projects had promoted rehabilitation in Kalimantan, instead of concentrating on Sumatra.

Aims of rehabilitating orang utans

For some animals which are on the verge of extinction, artificial breeding groups in carefully managed environments may provide possibilities to save them. For some bird species, e.g. the Nene goose and the peregrine falcon, such conservation programs have achieved spectacular successes. However, it is as yet unknown how temporary or partial domestication of mammal species will affect their re-introduction into the original habitat.

Originally, the main aim of orang utan rehabilitation was to withdraw young, orphaned apes from the animal trade. Rehabilitated animals were thought to support the existing population and to add to the breeding potential (see HARRISSON, 1961; 1963; DE SILVA, 1965; 1971). This idea was apparently mainly based on the assumption that the wild stock of orang utans was depleted to the extent of near extinction, as is also reported in the IUCN redbook (SIMON, 1966).

No doubt, the orang utan is a highly endangered animal species, but, in contrast to earlier assumptions, this is not solely due to the critically small numbers, but because of the imminent, almost total destruction of the tropical rainforest. Due to new insights into the numerical status of the still extant orang utan population in Sumatra (perhaps applying to Borneo as well, (see p. 45)), it seems no longer relevant to re-introduce ex-captive orang utans into areas still inhabited by a wild orang utan population. The negative effects of such an action may even outweigh the supposed supporting effect to the wild population. The functions of rehabilitation having most value for conservation are discussed below.

a. *Decrease of the trade*

The main aim of the Ketambe rehabilitation station is to provide a place where confiscated orang utans can be brought to, as laid down in Fauna Protection Ordinance 1931 and 1957 which state that 'live animals confiscated..... will be set free, unless.....' (Undang Perlindungan Binatang[2] Liar: Art. 6 (5).) It was hoped that the legal execution of the Ordinance (Art. 2), to confiscate all illegally caught and kept orang utans, could be enforced by providing such a station. Confiscation means the devaluation of the market value of these animals and consequently substantially diminishes the capturing and trade if firmly executed.

Confiscation is the responsibility of the Indonesian authorities. For a satisfactory execution of the confiscation program, a rather extensive investigation network has to be operated in order to find the illegally kept animals. Confiscation itself is not always easy since the high social status of some owners sometimes challenges the authority of those who attempt to enforce the law (see also RIJKSEN and RIJKSEN-GRAATSMA, 1975).

b. *Propaganda and Tourism*

Rehabilitation of orang utans is a project with strong public appeal. The care for orphaned young apes, with their attractive image (fig. 159) offers important propaganda potential for local and international nature conservation. A rehabilitation station, moreover, is one of the few places where local and foreign visitors can see orang utans in their rainforest environment. Local visitors can be educated the marvels of the ecosystem they have so close at hand; can be shown the touristic and economic potentials of rainforest; and can be introduced into the problems of preserving it for the future.

Nonetheless, a serious difficulty presents itself. Since the aim of a rehabilitation program is to reintroduce the apes to survive under wild conditions and independent of human attendance, the regular attention by visitors is in fact contradictory to this aim.

The animals are too regularly exposed to contact with friendly humans to become rehabilitated in a true sense. The attention of occasional visitors in the Ketambe station considerably delayed or even totally spoiled the efforts to rehabilitate several of the orang utans. Thus, the important function of educating people locally and of making full use of the propagandistic potentials of rehabilitation programs is offset by drawbacks in the actual rehabilitation process and by the hazards of creating tame orang utans.

c. *Research and education*

Thanks partly to rehabilitation attempts, a better knowledge of the behaviour of orang utans could be obtained (see e.g. HARRISSON, 1963; 1969). MACKINNON (1971; 1974), RODMAN (1974) and GALDIKAS-BRINDAMOUR (1975) also included observations on rehabilitants in their studies of wild orang utans.

In a wider context, an orang utan rehabilitation station may serve as a base for scientific studies in forest ecology and primatology; the Ketambe station

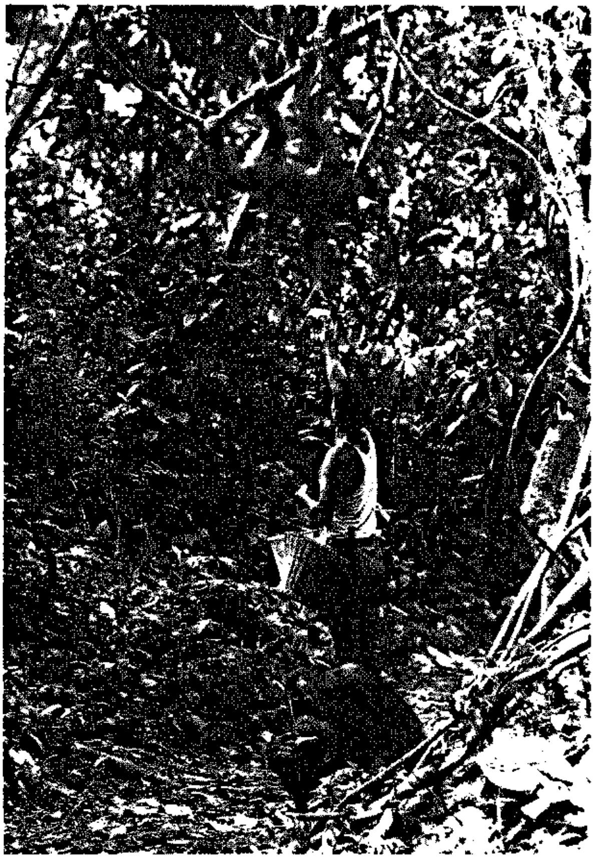

FIG. 160. A rehabilitant adolescent gets his share of cooked rice up in the trees; in the foreground the wild subadult male Doba, searching for scraps.

was established according to this outline. The tropical rainforest is one of the most poorly studied ecosystems, mainly because of its immense complexity and because of the comparative lack of comfort (i.e. all tracking has to be done by foot-safari, usually through remote inaccessible places) for the observer. Yet, despite the current lack of knowledge, the rainforest ecosystem is being destroyed at an alarming rate. Research into rainforest ecology is, therefore, urgently needed, not least for substantiating the conservation pleas for a more careful way of exploitation. A number of well established field centres, perhaps run on a bi-, or multi-lateral basis can give a good start to biological research and conservation studies concerning rainforest ecology and management. At present, the plans to improve the research station in the Ketambe area are in an advanced stage.

Methods

All confiscated or otherwise acquired orang utans entering the Ketambe rehabilitation project underwent medical examination, were cured for verminosis and were kept in quarantine for some time. The superficial clinical diagnosis of ailments relied mainly on my own diagnostic skill and clinical feeling. Accurate tests in order to detect possible concealed diseased were impractical as the nearest hospital with proper X-ray facilities was approx-

FIG. 161. The wild adult male O.J. visiting the feeding ground of the rehabilitation station. The feeding-cage for the juvenile rehabilitants is shown in the left hand corner; contacts between wild and rehabilitant orang utans are inevitable.

imately 9 hours driving away. Only occasionally, when for example tuberculosis was suspected on clinical grounds (e.g. coughing), was an individual transported to a hospital in order to examine it properly. As tuberculosis was of special concern, we thought of carrying out tuberculin tests on the rehabilitants, to be followed by prophylactic BCG vaccination. However, apart from the difficulties associated with the application (the test has to be applied in the lower eye-lid), the interpretation of the results in unrestrained animals is highly inaccurate (see SENCER, 1972; and TRIBE, 1976). In addition, routine vaccination in individuals, presumably free of tuberculosis, would not entirely prevent subsequent infection (SIEGMUND et al., 1967). Furthermore, vaccination in suspect or infected individuals would neither cure them, nor would it have diagnostic value under field conditions. The idea was abandoned. In its place, we hoped to detect such diseases in a prolonged period of quarantine. Dependent on the condition of the orang utan, quarantine lasted from a minimum of two weeks, to several months. The quarantine cages, 2 × 2 × 2 meters in size, were built near our field-station and assured separation from the feral and the wild orang utans.

After they were released the rehabilitant orang utans were provisioned daily with two portions of a monotonous food type. Cooked rice was, as a rule, provided in the early morning (i.e. 8.00 a.m.), and bananas were provided in the late afternoon (i.e. 4.00 p.m.) (fig. 160). By offering such a monotonous diet, the orang utans were encouraged to look for additional foods in the surrounding forest. Very young rehabilitants, and those in bad physical condition were provided with a qualitatively better and more varied diet containing e.g. fruits and milk. For more details on the methods of rehabilitation see also RIJKSEN and RIJKSEN-GRAATSMA (1975).

Results

By the end of the present field-study in August 1974, a total of 31 orang utans had been taken into the Ketambe rehabilitation station (p. 415). The presence of a rehabilitation project and the concomittant activity of the Indonesian Nature Conservation Service (Dinas PPA) to enforce the conservation acts by tracing illegally kept apes and confiscating them, have resulted in a decline in hunting pressure. In this respect, rehabilitation of orang utans in Sumatra is a successful conservation activity (RIJKSEN, 1974–75).

In the actual process of rehabilitation, two phases may be distinguished, namely (a) ecological rehabilitation, and (b) social integration. The adjustment of ex-captive orang utans to the rainforest environment proved to be a relatively rapid, and easily achieved process.

Undoubtedly as a consequence of their close contact with humans (whom they had come to consider as a social reference), newly introduced rehabilitants were largely, or entirely terrestrial. They even rested and slept on the ground (cf. HARRISSON, 1969). Infant and juvenile rehabilitants froze and 'ducked' (p. 217) on the ground if exposed to a frightening stimulus. By contrast, adolescent and sub-adult rehabilitants as a rule immediately ascended a nearby tree when exposed to a similar, fear-evoking situation. The loss of 8 juvenile rehabilitants due to predation, while some adolescent individuals were only wounded (see RIJKSEN and RIJKSEN-GRAATSMA, 1975) was perhaps a consequence of the 'inadequate' flight reaction of these younger apes.

A number of rehabilitants had not changed their semi-terrestrial habits, even after several months in forest surroundings. When travelling longer distances, they did so along the trails, on the ground. Yet, we noticed that most rehabilitants adopted a predominantly arboreal mode of locomotion when left unattended, or when individuals were brought into unfamiliar country. An aroused level of 'fear' was apparently an important condition for such animals, in order to lead a more arboreal lifestyle. We attempted to promote arboreality in reluctant rehabilitants by regularly chasing them up the trees and exclusively offering them their provisioned food in the trees.

Some ex-captive orang utans were unable to build a proper tree nest at arrival in the station. These individuals slept in various places, such as: In a sitting position on a large branch of a tree; in- or on top of a feeding cage; or they appropriated a nest of a fellow rehabilitant. However, these individuals also soon learned to build a proper tree nest, in some cases by imitating others during play sessions.

Rehabilitant orang utans learned to utilize most of the food items that were eaten by their wild counterparts in a short period of time (two to six months). The mode by which they learned to utilize only these specific foods (e.g. the leaves of *Acacia pennata*, and of *Erythrina subumbrans*) from amidst the wealth of vegetation remains obscure. On some occasions we did notice however that newly introduced individuals tasted food-items that were eaten by older rehabilitants (see also p. 180). A number of food plants eaten by rehabilitants (notably herbs such as *Asystasia* sp., *Peristrophe* sp., (*Acanth.*), *Crassocephalum* sp. (*Comp.*), and *Globba* sp. (*Zingib.*)) were not observed in the diet of the wild orang utans. It is noteworthy that *Crassocephalum* sp. is used as a vegetable by local people (B. SITOMPUL, pers.comm., 1972).

Despite the fact that the rehabilitants appeared to adjust rapidly to the forest environment (in the sense that they were familiar with most food types; were able to build a proper night nest; and had become skilled climbers). most of them stayed close to the feeding place of the rehabilitation station. Unfamiliarity with the surrounding forest, opportunism with respect to their food, and perhaps anticipating possible agonistic encounters with their wild counterparts, apparently made them restrict their feral activities to an area not larger than 30 ha around the feeding place. In order to induce rehabilitants to explore a larger area and become less dependent on the provisioned food, we carried out a number of experiments. Thus, we took individuals with us to the far ends of the study area; we reduced the amount of provisioned food, and even stopped provisioning some individuals altogether. The experiments were successful for some individuals, but for a few others, they were not. The latter stayed around the feeding place, and adopted the habit of raiding the houses in search of food.

Only two individuals wandered off on their own account, far from the feeding site. They usually returned after several days but sometimes stayed in the forest for months. As a rule such apes returned in excellent physical condition. Only these individuals are known to have integrated successfully into the wild population. Thus, the female Bin found her place in the wild orang utan population at Ketambe. She engaged in several consort relationships with various wild males and gave birth to a wild sired, healthy female infant in March 1975. At the time of writing this, she cares well for her infant, and in addition has 'adopted' a juvenile rehabilitant male, even allowing it to suckle (pers. observ.; SCHÜRMANN, pers.comm., 1976).

The other rehabilitant that integrated into the wild population is the male Usman. He disappeared in 1972, and was again seen by a reliable witness in 1974. This man, a former attendant of the rehabilitation station, had observed the male in association with two wild orang utans near Seldoq, some 15 km South of the Ketambe area. The orang utan had been seen, stealing a pan with cooked rice intended as lunch for a peasant farmer. The ape had eaten the rice before he vanished again into the forest. The account of this behaviour, which is highly exceptional for a wild primate, lends weight to the identification of this individual as a former rehabilitant. Apart from these two cases, only a small number of observations are available with respect to the social integration of rehabilitant orang utans into the wild population. In chapter 3.3 (Social behaviour) I have described the interactions of rehabilitants experimentally introduced into temporary associations of wild apes. In general, young individuals up to the adolescent stage were tolerated and might be engaged in positive social interactions, such a play. Individuals beyond the adolescent stage were more liable to experience agonistic actions following such encounters, although friendly interactions were also observed. Notably the encounter between the wild sub-adult male Roba and the rehabilitant sub-adult male Sibujong developed into a 'friendly' relationship. Rehabilitants who had been defeated in agonistic interactions tended to reduce their exploratory travels, and stayed at the feeding site of the rehabilitation station or close to the field station (i.e. close to their human attendants). In addition to the two cases mentioned above, and apart from 4 orang utans who were transferred to the area north of the Ketambe area, another 6 orang utans have disappeared. However, whether these apes have been successfully rehabilitated, became victims of a predator, or otherwise perished, remains obscure.

Individuals were considered fully rehabilitated if we observed encounters between rehabilitants and wild orang utans which included positive social contact, and if individuals stayed away from the provisioning regularly. Four orang utans, who we considered ecologically rehabilitated, but who eventually showed a decline in exploratory activity and even stayed near the houses all day, were transferred to the opposite bank of the Ketambe river and left unattended. These were the males David and Seamus, and the females Simi and Yoko, all mature orang utans, 7–10 years of age. No further accurate data on these individuals are available, apart possibly from a report made some months later by two fishermen, camping on the northern bank of the Ketambe river, who stated that two orang utans had approached them very closely one late afternoon, and had stayed near their camp until the next day.

The biological relevance of orang utan rehabilitation

The process of rehabilitating orang utans, notably the threats inherent in such a project stress the need for critical evaluation. The feelings of pity evoked by the considerable number of individual orang utan orphans who need our concern, should not divert our main attention from the preservation of the rainforest eco-system in which wild orang utans still have their place.

In the five years that the two rehabilitation projects have been operating in North Sumatra, less than 100 individuals have been reintroduced into the wild. This number may be assumed to represent less than 1% of the wild orang utan population in Sumatra. Such a small number of apes will certainly not contribute significantly to the breeding potential of the present population, even if all the animals concerned are mentally healthy, fit to reproduce and, more important, are capable of raising their offspring.

The introduction of rehabilitated orang utans into an established wild orang utan population (fig. 161), as has been the practice in all rehabilitation projects to date, bears several risks, which cannot be taken seriously enough. The present knowledge of the biology of the orang utan shows that he lives as a member of a local population, familiar with the other members. The particular relationships he maintains with the latter have been established over a long period of time. There is sufficient reason to believe that the population density of orang utans in areas where no serious disturbances have taken place is optimally balanced against the carrying capacity of the region.

Introducing strangers, (i.e. rehabilitants) into such a balanced population inevitably causes disturbances. These include not only social disturbance and stress, but also disruption of the ecological balance. Furthermore it includes the risk to introduce and transmit serious diseases. The great apes are highly susceptible to a number of human diseases (RUCH, 1959; SENCER et al., 1972), such as tuberculosis, poliomyelitis, meningo-encephalitis and hepatitis. Several of these are difficult to diagnose in a sub-clinical stage, particularly under the primitive conditions prevailing in remote areas. For instance, tuberculosis, which is the disease of greatest concern, can, as a rule, only be diagnosed clinically during certain advanced stages (SIEGMUND et al., 1967; TRIBE, 1976). Still, the majority of affected individuals have already become shedders before such an advanced stage is reached. Thus, notwithstanding a quarantine period and superficial medical examination, as is the practice in rehabilitation stations, the possibility remains that rehabilitants are carriers of a serious ailment. This may only become manifest when the individuals are exposed to social stress or to temporary shortage of food.

Apart from the possibility of introducing concealed diseases by means of rehabilitant orang utans, the day to day contact of such animals with their attendants and with visitors may also result in the transmission of serious ailments from local human sources on to the wild population. We noticed this means of transmission on three occasions (see p. 147). These cases clearly illustrate that the introduction of rehabilitant orang utans into an existing orang utan population bears a considerable risk of spreading an infectious disease with deleterious effects, despite the well-meaning efforts to prevent this.

Only speculations can be made as to the possible 'cultural' influence of rehabilitant orang utans, raised under various degrees of sociability, on the social organisation of the wild population. However, it is likely that such an influence will be of a limited and insignifincant nature.

In conclusion, rehabilitation of orang utans in areas with a wild orang utan population is hazardous to such extent that continuation of the present projects is not desirable. The alternative of transferring rehabilitation projects to protected rainforest areas where no wild orang utans occur, would confine the (health) risks to the rehabilitant group. This would be a considerable improvement over the present situation. Suitable regions in Sumatra are the South Langkat sector of the Gunung Leuser reserve, east of the Sungei Wampu, and perhaps other reserves in middle and south Sumatra (i.e. Sumatera Selatan I.). Another suggestion, put forward by MACKINNON (intern report; 1974) worth considering, is to (re-)populate certain suitable reserves in West Malaysia. A more detailed discussion on this subject has been laid down in a number of internal reports.

5. THE CONSERVATION PROBLEMS OF A RAINFOREST ECOSYSTEM: CONCLUDING DISCUSSION

In countries with relics of undisturbed ecosystems, nature conservation is usually considered by the public as some expatriate hobby with the aim of preserving a particularly exotic animal or plant for no other reason than what might be called 'ethics'. Unfortunately many conservation projects appear to strengthen this image. Only few enlighted people understand the biological, as well as economical meaning of nature conservation. Because of modern ideologies people have become reluctant to see man as an animal, as a component of an ecosystem which survives biologically or not at all, in spite of the impressive developments in technology. Man's biological survival, like that of all animals, requires the survival ot the other components which share the ecosystem on which he depends.

Tropical ecosystems are more labile than those in temperate regions. I am using the orang utans as an illustrative example, to demonstrate the vulnerability of the rainforest ecosystem and to identify the forces which are currently destroying that system. However, any other plant of animal component can be taken for the same purpose, including the relic populations of the gathering-hunting peoples of Central Sumatra and Central Kalimantan, the ethnic groups of Batak, Kenyah, etc., or, for that matter, the people of Indonesia. They are all equally affected by the destruction of the rainforest system, although they play one of the active roles in the process itself. Some plants and animals may perish earlier than others due to a lack of certain adaptive characteristics; the orang utan will certainly be among the first to disappear.

The present study attempts to demonstrate the intricate relationship of the orang utan with its environment. It is almost certain that man has played a role in that environment since the Pleistocene period, some 500,000 years ago. Obviously both orang utan and man have for a long time adapted themselves to that environment and to one another. This process is now coming to an end; the final stage probably began with the introduction of modern religions and Western ideology, some 300–500 years ago.

On the basis of ecological field data it is not difficult to show to what degree the orang utan is dependent on many of the components, plants in particular that exclusively belong to undisturbed rainforest ecosystems. Yet, time and again people argue that orang utans are capable of surviving in degraded habitats. Usually such arguments are based on incidental observations of an orang utan moving through secondary growth. It cannot be denied that orang utans, and in particular young individuals, may every now and then wander through areas not familiar to them, or perhaps explore secondary vegetation. However, it is inappropriate to give such incidental observations any weight and draw the conclusion that this ape can live in the badly degraded forests left after commercial logging, without sufficient long-term field observations to support such a thesis. Even in the hypothetical case that a particular individual might survive under such conditions, it is irrelevant to argue that all orang utans, i.e. the species as a whole can survive in a degraded habitat; it is also conservationally irrelevant to argue that orang utans sometimes breed in zoos. In the context of preserving this species one has to accept that orang utans are one inextricable component of the system; the species' value is within the system. It should not be seen as an isolated case.

It appears to be extraordinary difficult for most people to understand the implications of preserving an ecosystem. With proper propaganda people in general may readily become convinced of the need to protect or preserve one particular animal or plant species, especially when the measures do not directly affect their own business. The result is a tendency to over-emphasize that particular species; and conservation success is thought to be achieved when a census indicates that the numbers of the target species have increased, no matter if this has perhaps been achieved at the loss of other valuable components.

It may be assumed that the present number of wild orang utans in Sumatra is just sufficient to maintain a natural population. Or, to put it in biologically more meaningful terms, the amount of undisturbed rainforest habitat in Sumatra in 1973 may be regarded as a critical minimum to support a sufficiently diverse population of wild orang utans. This implies that within the range of this ape all large-scale destructive influences, notably commercial logging, must be banned, in order to give this species a chance to survive. Since several large-scale commercial logging concessions in this area were due to start their operations in 1973 and several more have requested new concessions after this, a heavy toll will be taken of the remaining population. It should be realized that these concessions do not only disturb and harm wildlife, they will also affect the green core of the northern part of Sumatra. The extant rainforest in Sumatra, north of Lake Toba is the water-catchment area for the east coast province of Deli, and the province of Aceh (including the Alas valley and the coastal regions). The Gunung Leuser reserves cover less than one third of this region and from the point of watershed management alone it would be wise to make a reserve of all remaining forests in the northern part of Sumatra.[44]

Another implication of the view that the orang utan is an inextricable component of an intact ecosystem is that activities aiming at increasing the orang utan population, i.e. breeding programs and reintroduction programs for captive-bred individuals, are not necessary and not favourable. If hunting of orang utans can be prevented, or diminished to the level of incidental predation, the actions for preserving this ape should concentrate on preserving

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[44] Recently, in 1977, the local Government of Aceh province took the wise decision to designate a particularly important watershed area, namely the Kapi region, as a reserved area, to be included in the Guning Leuser reserves. The Central Government of the Republic of Indonesia has ratified this decision (Surat keputusan Ment. Pertanian 697/Kpts/Um/12/1976).

the intact ecosystem. In practical terms, the conservation management should aim at getting local support to ban excessive hunting and fishing and to guard the edges of the reserved areas against commercial intrusions. Commercial harvesting of forest products is incompatible with the preservation of an intact forest ecosystem. Within this view rehabilitation of orang utans is justified only as a means for diminishing the hunting pressure and trade and to draw attention to the conservation problems of the tropical rainforest. Yet, the re-introduction of rehabilitant individuals into a stable eco-system containing wild orang utans, as has been practised, should be terminated. It would be more realistic to use rehabilitant orang utans to repopulate regions where this ape has become extinct and where the rainforest can be properly protected.

The greatest problem in the conservation of the orang utan as a characteristic component of the Indonesian rainforest ecosystem is the habitat destruction caused by a rapidly increasing human biomass, both locally and worldwide. Local people destroy the forest ecosystem for agricultural subsistence and, more recently, for cash-crop profits. The increasing world population induces a rapidly growing market for wood and wood products. The shrinking areas covered with rainforest in the South-East Asian region need a careful policy of sustained yield, protection of watershed areas and preservation of sufficiently large regions as a genetical reservoir for the many plant and animal species that one day might benefit future generations. Recently, several renowned scientists have made a plea to conserve the rainforest with arguments that should appeal to people concerned with the future of their country (VAN STEENIS, 1971; GOMEZ POMPA et al., 1972; MEIJER, 1973; 1975; WHITMORE, 1975; FURTADO, 1975; etc.). The Conference on Ecological Guidelines for the Development in Tropical Forested Areas, held in Bandung in 1974 reviewed these arguments (POORE, 1975), and sure enough, the theories are well-known in Indonesia and Malaysia. Unfortunately, the theories usually become corrupted in practice, and too often, at the instigation of foreign commerce, terms such as 'selective logging' are being used to soothe public awareness of the destruction and land devastation resulting from commercial timber exploitation. Even reserved areas are not free from such practices.

It is quite alarming that the trend to explain away the destructive influences of logging with the inappropriate argument that certain species may benefit from the operations, is reviving. Unfortunately this trend is supported by some biologists who are inclined to restrict their view to a limited set of variables. It is quite understandable that, since the profits from commercial logging of 'natural forest' add considerably to the national income, theories which explain away the ill effects are met with eager enthousiasm by authorities. In such an atmosphere, logging in reserves may ironically acquire the label of management and conservational limitations then fade away under the pressure of increasing demands.

In the present day situation in Europe and the USA, it seems a reasonable procedure that, in order to protect human life against the ill effects of ir-responsible commerce, laws demand scrutinous testing of materials, processes and activities, well before they can be introduced to the public (e.g., pharmaceutical drugs, toxicological pest-control, nuclear powerplants). Only the scientific proof that the effects are in no way harmful is ground for legal permission of their application. Yet, in the battle for the conservation of ecosystems against commerce, conservationists must prove that the effects of commercial exploitation are harmful for the system. Obviously, this proof can only be given when irreplaceable and unique species and ecosystem have been eradicated.

Only if people accept the idea that, by definition, large-scale intrusions into an ecosystem are detrimental, can there be some hope for a more responsible way of extracting sustained yield from nature. In order to achieve a better awareness of the problems, the responsible authorities should be taught the basic concepts of biology. Without these concepts, people cannot understand the implications of their present policies for the future. The rainforest cover determines the weather, assures an even flow of water for agriculture and fertilizes the land in the valleys of the tributary rivers. Obviously, the ongoing destruction of the tropical rainforest, for whatever reason, has implications beyond the imagination of present day authorities. When viewing the timber concession maps of Indonesia it is clear that foreign commerce is rapidly robbing this country's resources. This modern form of colonialism seems possible because of the desperate attempt of tropical societies to be accepted as civilized, developed and technologically advanced, according to the standards set by the rich, aggressive and powerful societies of temperate regions.

At present a number of scientists have become impressed by the sophisticated and highly effective biological adjustments laid down in the traditional rules and religion of so-called primitive peoples (see e.g. NEEL, 1970). They are realizing that modern, imported ideology has shattered these rules, and there is a growing concern that new ideologies may be outright disastrous for the labile ecosystems of tropical countries. RAPPAPORT (1974) has argued that:

> 'we are led to ask whether civilization, the elaborate stage of culture with which are associated money, ..., high energy technology, and social stratification and specialization, is not maladaptive. It is in civilized societies that we observe most clearly over-segregation, ... domination of higher by lower order systems, and the destruction of ecosystems. Civilized man has devised aberrant regulatory structures, and to the extent that their activities are freed from local ecosystemic limitations, they maintain their aberrant regulatory structures in the face of mounting difficulties.' (p. 387).

The incapacity of civilized countries to adjust to imminent energy shortage and to solve serious problems of self-pollution are other indications for the maladaptive nature of this form of social organization that seems the inevitable result of over-population. Unfortunately, the inhabitants of tropical countries will realize too late that such a civilization process, which they so badly attempt to copy at the instigation of- and with financial aid from- western technology, will only lead to ecological disasters in the form of desertification and famine. The present developmental aid from western societies and its concomitant ideological pressure on local governments usually strives after the welfare and well-being of all peoples and especially of the poor. However, these terms are ill defined, usually referring to the standards of western ideologies. Moreover, no consideration is made regarding the consequences of such a policy, notably with respect to the effect it will have on the inevitable population increase. As DICKEMAN (1975) has put it:

> 'The role of western ideology, now widely adopted by formerly colonial societies, seems to be to prevent a return to traditional methods, even when they are perceived on the local level as necessary, and to demand instead the use of less efficient means, eventually resulting in the totality of human suffering' (p. 133).

One of the adaptations that presumably led to the emergence of 'modern' man was the acquisition of a hunting trait, and concomitant means of communication. It may well be that this adaptation was governed by a 'tendency to gain social prestige', brought about by selection pressures within and between small groups. A precursor of such a tendency seems clearly discernible in the other great apes, notably the chimpanzee.

The first boom in improverishing the larger mammal fauna characterized the birth of the genus *Homo* during the late Pleistocene period (see MARTIN and WRIGHT, 1972). The second boom will probably usher in his final stage. Man's talent for ritualized competition, increasingly disguised in redirected forms, is currently eliminating and eradicating most other vertebrates and numerous other biological phenomena. Man's primate brain, although considered to be without limits as far as technology is concerned, appears to be incapable, or at most deficient in adjusting motivations and tendencies governing his behaviour, according to ecological necessities. The human case may well be the best example that social selection can lead to extinction, due to the non-adaptive effects it eventually has brought about.

SUMMARY

The results of a three year research project on the ecology, behaviour and conservation of the Sumatran orang utan are discussed. The 150 hectares Ketambe study area lie within the boundaries of the Gunung Leuser reserve in Aceh Tenggara, and consists of mixed rainforest typical of hilly regions.

The orang utan's food is irregularly distributed in quantity, space and time within this area. Although the orang utan is frugivorous he also eats leaves, insects, 'bark' and several other less important foods, such as bird's eggs. By far the largest part of the 114 food plants collected is typical primary rainforest growth. Figs make up an important part of the diet, particularly those known as the 'strangling' *Ficus* spp. As the fruiting seasons of the various strangling fig species are staggered over the whole year, and such trees are often enormous in size, they form particularly suitable food sources. Orang utans appear to have a good topographical knowledge of their 'home range'. There are indications that fig trees bearing ripe fruits are sometimes found by using the flight paths of flocks of hornbills, which also feed on figs. With respect to figs in particular, the orang utan must compete for its food with many other species, notably primates.

The study area was regularly used by 22 individually recognized orang utans. Both males and females live in homeranges which overlap considerably and are 2–10 km sq. in extent. The population density of the Ketambe area is considerably higher than that reported for other areas in Indonesia, being approximately 5 individuals per square kilometre. Orang utans live a 'limited gregarious' lifestyle, that is, adult males spend the largest part of their time alone, and avoid encounters with other adult males. The adult females and their offspring stay together for the first 4–5 years of life (the birth interval is at least 3 years.). Adolescent social groups form after the mother-offspring bond becomes weaker. This social phase continues for each individual until either (a) the sexual dimorphistic characteristics of males are clearly distinguishable (at approximately 15 years of age), or (b) the female's first young is born (approximately 10 years of age). Adults also have social moments in their lives. Several individuals in an area can come together to form a 'temporary association' in certain fruit trees. It may be seen from their behaviour that they know each other well and that a network of relationships exist which is partly based on competitive dominance. A peaceful co-existence between adult males however, has not been observed; meetings between adult males had invariably an agonistic character. The sexual behaviour of the orang utan is roughly divisable into: (a) 'raping' of some females by sub-adult males; and (b) co-operative matings, where females often take the intitiative by presenting themselves to, usually, adult males. It appears that only the latter makes an essential contribution to reproduction.

The social behaviour of the orang utan is considered and described in detail.

Comparison of the behavioural repertoire of this species with that of the (gregarious) chimpanzee shows that the two species are closely related. There are clear differences in social organisation, however, which appear to be mainly of degree, rather than of quality. The social organisation of an animal must be a factor that fits its situational (i.e. environmental) context, but is based on phylogenetic characteristics. Comparison of the habitats of these two apes reveals that they both live in a similar ecological condition with respect to food. The reasons for the exceptional life-style on the part of the orang utan are possibly to be found in the predation pressure the species is exposed to, particularly by man. Man has been present in regions of South-East Asia since the Pleistocene. It is plausible that the orang utan has been persecuted by man continuously from this time. A comparable influence on the chimpanzee is much more recent. The orang utan is the heaviest arboreal creature and has an exceptional social organisation for a primate. If it may be assumed that high intelligence is a biological outcome of complex group life then, on grounds of intelligence, and from the distinct social organisation and current arboreal life-style it may be postulated that the orang utan has evolved from a ground-living social ape. This original form was supplanted from its niche by a better adapted ground-living social ape, that is, man. It is possible that a stricly arboreal life style for an animal as heavy as an adult orang utan is not compatible with a social life-style. Moreover, it is likely that refraining from a high degree of sociability and inconspicuousness are the best strategies against human predation.

Since one possibility is that the hunting pressure in ancient (and current) times had a great influence on the biology of the orang utan, I have paid particular attention to hunting behaviour in hominids. At present, this form of threat is overshadowed by excessive habitat destruction. Cultivation in connection with the explosive population growth in Indonesia, together with the commercial timber concerns, affect the tropical rainforest ecosystem in such proportions that even reserves are threatened. Despite being protected since 1932, the orang utan is a severely endangered species. Rehabilitation of orang utans is a conservation action directed at reducing the still ongoing hunting pressure. This is despite the fact that there are clear risks in this to the wild population. These risks can be negated by confining rehabilitation projects to areas lacking a wild orang utan population.

The orang utan is a component of an intact ecosystem and it is of utmost importance that the emphasis of nature conservation schemes is placed on the totality and balance of the tropical rainforest ecosystem. Every form of commercial exploitation within this ecosystem is incompatible with the proposed goal of preserving the system. The removal of components (e.g. 'selective logging' or 'selective hunting') does real damage to the balance of the system.

An orang utan who lives in an exploited forest is in principle of equally small biological value as an orang utan in a zoo; it is a, debatably essential, biological solution that does not correspond to the set of conditions originally operating in its natural selection.

SAMENVATTING

Deze dissertatie geeft de resultaten van een driejarig veldonderzoek (1971–'74) naar de ecologie, het gedrag en de bescherming van de wilde Sumatraanse orang utan. Het 150 ha grote studiegebied Ketambe is gelegen binnen de grenzen van het Gunung Leuser reservaat in Aceh Tenggara.

Het habitat in Ketambe is gekarakteriseerd als een gemengd regenwoud van het heuvelland type. Voedsel voor orang utans is onregelmatig verspreid in hoeveelheid, ruimte en tijd. Orang utans zijn frugivoor; naast vruchten omvat hun dieet blad, insecten, bast en enkele minder belangrijke voedingsmiddelen zoals vogeleieren. Van de 114 verzamelde voedselplanten in het gebied behoort het grootste gedeelte tot soorten van het primaire bos. In het dieet nemen vijgen van de wurgvijgsoorten een zeer belangrijke plaats in. De verschillende soorten wurgvijgen hebben vruchtseizoenen die verspreid liggen over het gehele jaar zodat vijgen vaak beschikbaar zijn als voedsel. Orang utans hebben een goede topografische kennis van hun 'home range'; er zijn aanwijzingen dat ze informatie betrekken uit de vluchtrichting van groepen neushoornvogels voor het vinden van vijgebomen met rijpe vruchten. In het bijzonder voor wat betreft vijgen ondervindt de orang utan voedselconcurrentie van verschillende andere diersoorten, met name van primaten.

Tweeëntwintig orang utan individuen maakten regelmatig gebruik van het studiegebied. Zowel mannelijke als vrouwelijke orang utans leven in 'home ranges' die elkaar sterk overlappen en in de orde van grootte zijn van 2–10 km^2. De populatiedichtheid in het Ketambe gebied is hoog in vergelijking tot andere gebieden, en bedraagt ongeveer 5 individuen per vierkante kilometer. Orang utans zijn 'solitair' levende primaten; met name volwassen mannen brengen het grootste deel van hun tijd alleen door. Volwassen vrouwelijke orang utans zijn vergezeld van hun nakomelingen, die tot een leeftijd van 4–5 jaar in haar nabijheid verblijven. De spreiding tussen geboorten is minimaal 3 jaar. Zodra de band tussen de jonge orang utan en zijn moeder zwakker wordt, sluit het nog niet volwassen dier zich aan bij leeftijdgenoten en vormt met deze 'sociale groepen'. Deze sociale leeftijdsfase houdt op te bestaan (a) als bij mannen de kenmerken van sexuele dimorfie duidelijk aan de dag treden, op ongeveer 15-jarige leeftijd, en (b) als vrouwen hun eerste nakomeling hebben voortgebracht, op ongeveer 10-jarige leeftijd. Volwassenen kennen echter ook sociale momenten in hun leven. In bepaalde vruchtbomen kunnen meerdere individuen uit een gebied bijeen komen in 'tijdelijke groeperingen'. Uit het gedrag van de dieren onderling blijkt dat ze elkaar goed kennen en een netwerk van relaties onderhouden, dat voor een deel op competitieve dominantie is gebaseerd. Het vreedzaam samenzijn van volwassen mannelijke orang utans is niet waargenomen; ontmoetingen tussen zulke dieren waren zonder uitzondering agonistisch van aard. Het sexuele gedrag van orang utans is grofweg onder te verdelen in (a) 'verkrachtingen' van sub-adulte mannen tijdens ontmoetingen

met sommige vrouwen, en (b) 'coöperatieve paringen' waarbij vrouwen vaak het initiatief nemen door zich te presenteren aan – meestal volwassen – mannen. Het lijkt erop dat alleen deze laatste vorm wezenlijk bijdraagt aan de reproductie, terwijl de eerste vorm meer gezien kan worden als het forceren van een relatie.

Het sociale gedrag van de orang utan wordt nauwkeurig beschreven. Bij vergelijking van het gedragsrepertoire van de orang utan met dat van de chimpansee is de overeenkomst opvallend, hoewel beide nauw verwante soorten toch duidelijke verschillen in sociale organisatie laten zien en de een gekarakteriseerd is als een 'solitair', de ander als een 'sociaal' dier. De sociale organisatie van een diersoort is een aanpassing aan omgevingsfactoren. Bij een vergelijking van het habitat voor beide primaten lijken de orang utan en de chimsee te leven onder gelijkwaardige ecologische condities met betrekking tot voedsel. Aanwijzingen voor het ontstaan van de 'solitaire' leefwijze van de orang utan zijn wél te vinden in predatiedruk, met name van de mens. De mens komt voor in bepaalde delen van Zuidoost Azië sinds het Pleistoceen. Het is zeer aannemelijk dat de vervolging van de orang utan door de mens vrijwel continue is geweest. Een vergelijkbare invloed van de mens op de chimpansee is van veel recentere datum. De orang utan is het zwaarste boomlevende wezen en heeft een afwijkende sociale organisatie voor een primaat. Als men veronderstelt dat hoge intelligentie een biologische functie is van gecompliceerd groepsleven, zou, op grond van die intelligentie, van de afwijkende sociale organisatie en van het boomlevend bestaan geconcludeerd kunnen worden dat de orang utan afstamt van een grond-bewonende sociaal levende mensaap. Deze zou door selectieve invloed van een andere grondbewonende sociale mensaap (de mens) verdrongen zijn naar de niche waarvoor eerstgenoemde betere aanpassingsmogelijkheden bezat. Waarschijnlijk is een boombewonend bestaan voor een dier met het gewicht van een volwassen orang utan niet verenigbaar met een sociale levenswijze. Bovendien lijken onopvallendheid en alléén zijn de beste strategie tegen menselijke predatie.

Aangezien verondersteld wordt dat jachtdruk in het verleden van invloed is geweest op de biologie van de orang utan, wordt daaraan bijzondere aandacht besteed. Tegenwoordig is deze vorm van bedreiging nog overschaduwd door verregaande habitat-destructie. Ontginning voor de explosieve bevolkingsgroei en commerciële houtkap vernietigen het tropische regenwoudsysteem in zulke proporties dat zelfs reservaten bedreigd zijn. Hoewel wettelijk beschermd sinds 1932, is de orang utan een ernstig bedreigde diersoort. Rehabilitatie van orang utans is een beschermingsactie die ten doel heeft om de nog aanwezige jachtdruk op wilde orang utans te verminderen, hoewel er voor de wilde orang utan pupulatie duidelijke risico's aan rehabilitatie verbonden zijn. Deze risico's kunnen vermeden worden door rehabilitatie uitsluitend uit te voeren in gebieden waar geen wilde orang utans voorkomen.

De orang utan is een onderdeel van een intact ecosysteem, en het is van groot belang dat de nadruk van de natuurbescherming komt te liggen op het instandhouden van het evenwicht binnen het tropische regenwoudsysteem. Iedere vorm van commerciële exploitatie binnen dat systeem is onverenigbaar met de doelstellingen van de bescherming van het systeem. Het verwijderen van componenten (bijvoorbeeld door middel van 'selectieve houtkap' of 'selectieve jacht') doet wezenlijk schade aan het systeem.

Een orang utan die overleeft in uitgekapt bos, is in principe van even weinig biologische waarde als een orang utan in een dierentuin; het is een noodoplossing waarvoor het dier geen natuurlijke aanpassingen heeft.

KESIMPULAN

Disertasi ini menggambarkan hasil-hasil penelitian lapangan selama tiga tahun (1970–1974) di bidang ekologi kelakuan atau tabiat dan pengamanan orang utan liar Sumatera. Daerah penelitian tersebut mencakup lapangan seluas 150 ha di Ketambe dalam suaka margasatwa Gunung Leuser di Aceh Tenggara.

Habitat (ruang hidup alami tumbuh-tumbuhan dan binatang-binatang) terdiri dari hutan hujan campuran dari tipe tanah yang berbukit-bukit. Makanan untuk orang utan terdapat terpencar-pencar lagi tidak merata dalam jumlah, ruang dan waktunya. Orang utan adalah 'frugivoor'; disamping buah-buahan, makanannya terdiri dari daun-daunan, serangga, kulit kayu dan sedikit banyak juga telur burung. Dari 114 jenis tumbuhan makanan yang dikumpulkan didaerah tersebut sebagian besar termasuk jenis-jenis tumbuhan dari hutan primair. Buah berbagai jenis *Ficus* mengambil tempat yang amat penting dan memiliki musim buah sepanjang tahun sehingga buah/biji *Ficus* tersedia sewaktu-waktu. Orang utan mempunyai pengetahuan topografi dari deretan tempat tinggalnya (home-range). Ada tanda-tanda bahwa mereka memperoleh informasi dari arah terbang burung-burung enggang untuk mendapatkan pohon-pohon *Ficus* yang sedang masak buahnya. Dalam hal ini orang utan banyak mendapat saingan dari jenis-jenis kera lainnya.

Sebanyak dua puluh dua ekor orang utan menempati daerah penelitian tersebut diatas secara teratur. Baik orang utan jantan maupun betina hidup dalam 'home-ranges' yang banyak bertindih dengan tingkatan luas yang berkisar diantara 2–10 km^2. Kepadatan populasi di daerah Ketambe adalah tinggi jika dibandingkan dengan daerah lainnya, jumlahnya ± 5 individu setiap km^2. Orang utan adalah primat yang hidupnya 'solitair' (bersendirian); jantan-jantan yang dewasa berkeliaran sendirian sepanjang hari. Betina yang sudah dewasa diiringi oleh anak-anaknya, sampai pada umur 4–5 tahun mereka tetap berada disamping ibu mereka. Jarak kelahiran paling sedikit adalah tiga tahun. Begitu hubungan antara anak orang utan dan ibunya menjadi kurang mesra, anak-anak yang belum dewasa ini menggabungkan diri dengan anak-anak orang utan sebayanya dan bersama mereka membentuk 'gerombolan-gerombolan sosial'. Masa umur sosial ini akan berhenti (a) apabila pada orang utan jantan sudah kelihatan tanda-tanda seksuil yang sifatnya 'dimorf', yaitu pada umur 15 tahun dan (b) jika orang utan betina sudah melahirkan buat pertama kalinya, kurang lebih pada umur 10 tahun.

Orang-orang utan dewasa juga mengenal masa-masa sosial dalam hidup mereka. Pada pohon-pohon buah tertentu tidak jarang berdatangan individu-individu dari suatu daerah dan terbentuklah 'gerombolan-gerombolan sementara'. Dari kelakuan binatang ini terhadap sesamanya nyata, bahwa mereka saling mengenal dan memelihara satu jaringan relasi (hubungan) yang sebagian didasarkan pada dominasi persaingan. Hidup bersama dalam suasana damai dikalangan orang-orang utan jantan tidak kelihatan. Perjumpaan diantara satu dengan yang lain tanpa kekecualian adalah bersifat agonistis. Sifat seksuil dari pada orang utan secara dapat dibagi sebagai berikut: (a) 'perkosaan' dari pada jantan yang setengah umur waktu berjumpa dengan betina, dan (b) persetubuhan koperatif dimana kerap kali para betina mengambil initiatief terhadap jantan yang sudah dewasa. Ada indikasi, bahwa hubungan seks terakhirlah yang memberikan turunan sedang bentuk pertama boleh dianggap sebagai relasi paksaan.

Sifat sosial dari pada orang utan akan diuraikan secara teliti. Dibandingkan segala sifat-sifat yang dimiliki orang utan dengan apa yang dimiliki oleh chimpansee, maka persamaannya adalah nyata, namun kedua-dua jenis binatang tersebut yang biologis berdekatan satu sama lain menunjukkan perbedaan yang besar dalam organisasi sosial; yang satu adalah binatang 'solitair' dan yang lain binatang 'sosial'.

Organisasi sosial dari satu jenis binatang adalah satu penyesuaian diri terhadap faktor-faktor lingkungan. Dalam perbandingan habitat bagi kedua-dua primat maka baik orang utan maupun chimpansee kelihatan hidup dibawah kondisi-kondisi ekologi yang sama sepanjang mengenai bahan makanan. Indikasi dari pada cara hidup 'solitair' dari orang utan adalah tekanan predasi, yaitu dari pada manusia. Di beberapa bagian dari Asia-Tenggara menusia sudah muncul sejak jaman 'Pleistoceen'. Dapat diterima bahwa pengejaran orang utan oleh manusia sejak itu berlangsung secara terus-menerus. Suatu gambaran persamaan pengaruh manusia terhadap chimpansee adalah relatif baru saja. Orang utan adalah makhluk terberat yang hidup diatas pohon dan mempunyai organisasi sosial yang berbeda dari pada primat lainnya. Jika kita bayangkan bahwa inteligensi yang tinggi adalah satu fungsi biologis dari persekutuan hidup yang kompleks, maka berdasarkan inteligensi itu, organisasi sosial yang menyimpang dan kehidupan diatas pohon dapat ditarik kesimpulan bahwa orang utan itu berasal dari primat sosial yang hidup diatas tanah (manusia). Pada suatu ketika ia terdesak kesatu tempat dimana golongan yang pertama memiliki kemungkinan-kemungkinan penyesuaian diri yang lebih baik. Mungkin sekali kehidupan diatas pohon bagi seekor binatang dengan berat yang dimiliki orang utan tidak dapat disatukan /disesuaikan dengan satu cara hidup sosial. Lagi pula, tanpa adanya penonjolan dibarengi dengan sifat bersendirian adalah strategi yang terbaik terhadap tekanan-tekanan dari fihak manusia.

Oleh karena dapat dianggap bahwa pemburuan dimasa lampau adalah berpengaruh terhadap biologi orang utan, maka dewasa ini sangat besar perhatian yang ditujukan kepada orang utan.

Sekarang bentuk ancaman serupa itu diiringi pula dengan penghancuran habitatnya. Penebasan-penebasan hutan untuk menampung pertumbuhan penduduk yang sifatnya explosief dan tebangan-tebangan dengan tujuan komersil menghancurkan hutan-hutan hujan tropis sedemikian rupa sehingga suaka-suaka margasatwa turut terancam. Biarpun orang utan telah dilindungi oleh undang-undang sejak th. 1932 ia masih saja mengalami ancaman. Rehabilitasi orang utan adalah merupakan tindakan pengamanan yang bertujuan untuk mengurangi tekanan pemburuan.

Orang utan itu adalah sebagian dari satu 'ecosistem' yang sudah ada kian dan amatlah penting apabila perlindungan alam dititik beratkan kepada perimbangan sama dalam sistim hutan hujan tropis. Setiap bentuk exploitasi komersil dalam systim tersebut adalah bertentangan dengan tujuan mengamankan sistim itu. Menghilangkan komponen² (umpamanya dengan tebang pilih dan pemburuan terbatas) pada hakekatnya akan merusak sistim yang dimaksud.

Seekor orang utan yang dapat hidup terus dalam hutan yang sudah diusahai pada prinsipnya mempunyai nilai biologis tidak lebih dari yang dimiliki orang utan dalam kebon binatang, itu cuma penyelesaian darurat yang bertentangan dengan kodrat alami binatang itu sendiri.

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APPENDIX 1

LIST OF ORANG UTAN FOOD-PLANTS FROM THE KETAMBE AREA, SUMATRA (LISTING CF. KENG, 1969)

The specimens are stored at the Rijks Herbarium, Flora Malesiana Collection, Leyden, under the reference numbers; HR, (my own collection), and W, (collection W. J. J. O. DE WILDE and B. E. DE WILDE-DUYFJES).

If available, the latin names are followed by the vernacular name. The code (F), (L), (B), (S), (FL) refers to the parts utilized, namely, fruits, leaf-material, growth-layer, terminal shoots and flower, respectively. The identity of the plant is designated in parenthesis. The code R refers to utilization by rehabilitants only. For the +, and ++ code, see p.

ANNONACEAE					
HR113	*Cyathocalyx (cf) sumatranus* Scheff.		F	(tree)	++
HR153	*Mitrephora*	*(banitan keleton)*	F	(tree)	
HR140	*Monocarpia*	*(bebaulangit?)*	F	(tree)	+
HR192	*Orophea*		F	(tree)	
HR105	*Polyalthia*		F	(tree)	
	Polyalthia		F	(tree)	
MYRISTICACEAE					
HR174	*Knema conferta* (King) Warb.	*(pala hutan)*	F	(tree)	
MENISPERMACEAE					
HR109	*Tinomiscium phytocrenoides* Kurz. ex Thysm. and Binnend.	*(akar kambing susuh)*	F	(liana)	++
HR145	*Pycnarrhenia longifolia* (Decne ex Miq.) Becc.		F	(liana)	+
SAXIFRAGACEAE					
HR164	*Polysoma*		F	(tree)	
CONNARACEAE					
HR166	*Rourea minor* (Gaern.) Leenhouts		F	(liana)	+
LEGUMINOSAE					
HR112	*Acacia pennata* (L) Willd.	*(akar rambut galang)*	LS	(liana)	+
HR146	*Erythrina subumbrans* (Hasik) Merr.	*(dedap)*	L	(tree)	+
HR157	*Phylacium bracteosum* Benn.		F	(climb)	R
HR175	*Spatholobus ridleyi* King.		F	(liana)	+
CUCURBITACEAE					
HR156	*Melothria*		F	(climb)	
HR152	*(cf) Trichosanthes*		F	(climb)	
DILLENIACEAE					
	Dillenia indica L.		F	(tree)	
ACTINIDIACEAE					
HR188	*Saurauia*	*(rembele)*	F	(tree)	

GUTTIFERAE					
HR130	*Garcinia (cf) bancana* Miq.	*(kandis)*	F	(tree)	++
HR150	*Garcinia (cf) forbesii* King.	*(kandis)*	F	(tree)	+
HR133	*Garcinia parvifolia* (Miq.) Miq.	*(kandis)*	F	(tree)	++
PROTEACEAE					
HR189	*Helicia serrata* (R. Br.) Bl.		F	(shrub)	
PIPERACEAE					
HR158	*(cf) Piper*	*(sirih hutan)*	S	(creep)	
FAGACEAE					
	Castanopsis		F	(tree)	+
	Lithocarpus	*(geseng)*	F	(tree)	
ULMACEAE					
HR132	*Trema cannabina* Lour.		L	(treel)	+
URTICACEAE					
HR135	*Dendrocnide sinuata* (Bl.) Miq.	*(latong gadjah)*	S	(tree)	+
HR118	*Dendrocnide stimulans* (L.f.) Chew	*(latong rusa)*	F	(treel)	+
HR160	*Villebrunnea*		S	(tree)	
MORACEAE					
HR193	*Antiaris toxicaria* (Pers.) Lesch.	*(rahu, ipoh)*	F	(tree)	++
HR186	*Artocarpus elasticus* Reinw.	*(terap)*	F	(tree)	++
HR167	*Brousonnetia kurzii* (Hook f. Corner)		F	(liana)	
HR203	*Ficus annulata* Bl.		F	(str. F)	++
HR201	*Ficus benjamina* L.	*(rambung)*	F	(str. F)	++
HR200	*Ficus (cf) benjamina* L.	*(bungan)*	F	(str. F)	+
HR215	*Ficus drupacea* Thunb.	*(rambung)*	F	(str. F)	++
HR208	*Ficus elastica* Roxb.	*(rambung)*	F	(str. F)	++
HR202	*Ficus glaberrima* Bl.		FL	(cr. F)	+
HR207	*Ficus glandulifera* Wall.		L	(tree)	+
HR212	*Ficus obscura* Bl.		F	(cr. F)	
HR210	*Ficus obscura* Bl. var. *borneensis* Miq.	*(genipos)*	F	(cr. F)	+
HR211	*Ficus obscura* Bl. var. *scaberrima* (Bl.) Corner		F	(treel)	+
HR213	*Ficus parietalis* Bl.		F	(cr. F)	+
HR206	*Ficus pubinervus* Bl.		FB	(tree)	
HR214	*Ficus racemosa* L.	*(gala gala)*	FB	(tree)	+
HR216	*Ficus stupenda* Miq. var. *minor* Corner		F	(str. F)	++
HR209	*Ficus sundaica* Bl.	*(rambung)*	F	(str. F)	++
HR205	*Ficus subulata* Bl.	*(huah-huah)*	FL	(cr. F)	+
HR204	*Ficus virens* A.t. var. *glabella* (Bl.) Corner		F	(str. F)	+
HR190	*Maclura amboinensis* Bl.		F	(liana)	+
RHIZOPHORACEAE					
HR148	*Carallia brachiata* (Lour.) Merr.	*(kekuran)*	F	(tree)	+
COMBRETACEAE					
HR104	*Combretum latifolium* Bl.		F	(liana)	+

MYRTACEAE					
HR181	*Eugenia*	*(jambu seré)*	F	(tree)	
TILIACEAE					
HR154	*Microcos*	*(bebeloh)*	F	(tree)	+
BOMBACACEAE					
HR103	*Bombax valetonii* Hochr.	*(kekapok rimba)*	Fl	(tree)	+
W13458	*Durio oxleyanus* Griff.	*(durian hutan)*	F	(tree)	++
	Durio spec. nov. (near *Durio wyatt-smithii* Kosterm.)		F	(tree)	
STERCULIACEAE					
HR131	*Heritiera elata* Ridley		F	(tree)	++
HR171	*Scaphium javanicum* (Blanco) Kosterm.	*(buah gerupuk ?)*	F	(tree)	+
MALPIGHIACEAE					
HR168	*Aspidopterys*		L	(liana)	
MELIACEAE					
HR124	*Aglaia*		F	(tree)	
HR125	*Aglaia elliptica* Bl.		F	(tree)	
HR102	*Aglaia speciosa* Bl.	*(setur)*	F	(tree)	+
HR178	*Lansium* aff. *domesticum* Jack.	*(langsat hutan)*	F	(tree)	+
HR187	*(cf) Walsura*	*(kayu lasun)*	F	(tree)	
EUPHORBIACEAE					
HR169	*Baccaurea javanica* Muell. Arg.	*(kayu gading)*	F	(tree)	
W12781	*Baccaurea lanceolata* (Miq.) Muell. Arg.	*(duku)*	F	(tree)	+
W14042	*Baccaurea* cf. *maingayi* Hook f. var.	*(bergang)*	F	(tree)	+
HR115	*Baccaurea motleyana* (Muell. Arg.) Muell. Arg.	*(rambé)*	F	(tree)	+
HR184	*(cf) Excoecaria*		F	(tree)	
HR117	*Macaranga diepenhorstii* (Miq.) Muell. Arg.	*(tampu)*	FB	(tree)	+
HR114	*Mallotus oblongifolius* (Miq.) Muell. Arg.		F	(shrub)	
HR143	*Mallotus shaerocarpus* (Miq.) Muell. Arg.	*(pepuah)*	FB	(tree)	++
W12814	*Neoscortechinia forbesii* (Hook f.) Pax ex S. Moore		F	(tree)	+
CELASTRACEAE					
HR126	*Celastrus hindsii* Benth.		F	(liana)	+
HR149	*Salacia chinensis* L.		F	(liana)	+
HR141	*Siphonodon celastrineus* Griff.		F	(tree)	+
VITACEAE					
HR147	*Cissus*		F	(liana)	+
HR127	*Cissus*		F	(liana)	+
HR163	*Cissus*		F	(liana)	

Sapindaceae					
	Nephelium aff. lappaceum L.	*(rambutan)*	F	(tree)	++
HR179	*Paranephelium*		F	(tree)	+
	Pometia pinnata Forst.	*(pakam)*	F	(tree)	+
HR121	*Xerospermum*	*(krakah)*	F	(tree)	++
Staphyleaceae					
HR128	*Bisschofia javanica* Bl.	*(tjinkam)*	F	(tree)	+
HR110	*Turpinia laxiflora* Ridley	*(kayu memè)*	F	(tree)	+
HR176	*Turpinia sphaerocarpa* Ridley	*(kayu memè)*	F	(tree)	+
Icacinaceae					
HR101	*Iodes yatesii* Merr. var. *yatesii*		FLS	(liana)	+
Anacardiaceae					
W14435	*Mangifera foetida* Laur.	*(berhul)*	F	(tree)	+
Cornaceae					
HR111	*Alangium scandens* Bloemb.		FLB	(climb)	+
HR142	*Mastixia trichotoma* Bl. var. *trichotoma*	*(banitan?)*	F	(tree)	
Araliaceae					
HR129	*Schefflera*		F	(liana)	
Sapotaceae					
HR122	*Payena lucida* (G. Don.) Dc.	*(kayu majang)*	F	(tree)	+
Ebenaceae					
HR120	*Diospyros sumatrana* Miq.		F	(tree)	+
Loganiaceae					
HR151	*Strychnos ignatii* Berg.		F	(liana)	+
Asclepidiaceae					
HR139	*Dischidia*		L	(epi)	
HR161	*Hoya*		L	(epi)	+
HR119	*Hoya*		L	(epi)	
HR155	*Marsdenia*		F	(epi)	+
Compositae					
HR165	*Crassocephalum crepidioides* (Bth.) S. Moore		S	(herb)	R
Acanthaceae					
HR162	*Asystasia*		S	(herb)	R
HR163	*Peristrophe*		S	(herb)	R
Palmae					
HR173	*(cf) Calamus*	*(rotan)*	F	(rattan)	
Araceae					
HR137	*Pothos aff. rumphii* (Presl.) Schott.		L	(creep)	+
HR123	*Rhaphidophora foraminifera* (Engler) Engler		SF	(creep)	+

HR116	*Scindapsus hederaceus* Schott.		FS	(creep)	+
PANDANACEAE					
HR195	*Pandanus*		S	(climb)	
HR198	*Pandanus*		S	(herb)	R
ZINGIBERACEAE					
HR194	*Globba*		S	(herb)	
ORCHIDACEAE					
HR185	*Coelongyne asperata* Lindl.		Pb	(epi)	
HR159	*(cf) Eria*		Pb	(epi)	
HR177	*Liparis*		Pb	(epi)	
GRAMINEAE					
HR193	*Axonopus compressus* (Sw) Beauv.		SF	(grass)	
HR197	*Centhotheca latifolia* (SSb) Trin.		S	(grass)	
	(*cf*) *Dendrocalamus*	*(bambu)*	SL	(bamboo)	
FILICES					
HR136	*Davallia denticulata* (Burm.) Mett.		S	(epi-fern)	
HR138	*Drynaria quercifolia* (L.) J. Smith		S	(epi-fern)	

APPENDIX 2

PERCENTAGE OF ORANG UTAN FOOD-TREES IN THE TREE INVENTORY (FERNHOUT, 1974; UNPUBLISHED DATA)

‘banitan keleton’	*(Mitrephora spec. Annon.)*	0.09%
‘banitan’	*(Mastixia trichotoma.: Corn.)*	8.47%
‘bebaulangit’	*(Monocarpia spec.: Annon.)*	1.03%
‘bebeloh’	*(Microcos spec.: Tiliac.)*	0.75%
‘bergang’	*(Baccaurea* cf. *maingayi.: Euphorb.)*	1.31%
‘berhul’	*(Mangifera foetida: Anac.)*	0.01%
‘beringin’	*(Ficus spec.: Morac.)*	0.05%
‘djambu seré’	*(Eugenia spec.: Myrtac.)*	1.26%
‘duku’	*(Baccaurea lanceolata.: Euphor.)*	0.09%
‘durian’	*(Durio spec.: Bombac.)*	0.84%
‘geseng’	*(Lithocarpus spec.: Fagac.)*	3.14%
‘ipoh’	*(Antiaris toxicaria.: Morac.)*	0.14%
‘kandis’	*(Garcinia spp.: Guttif.)*	1.97%
‘kekapok rimba’	*(Bombax valetonii.: Bombac.)*	0.23%
‘kerakah’	*(Xerospermum spec.: Sapind.)*	4.77%
‘kepayang’	*(Scaphium javanicum: Stercul.)*	0.37%
‘kekuran’	*(Carallia brachiata.: Rhizoph.)*	0.28%
‘kuwal’	*(Trema cannabina.: Ulmac.)*	0.33%
‘langsat’	*(Lansium spec.: Meliac.)*	0.33%
‘k. lasun’	*(*cf. *Walsura spec.: Meliac.)*	4.21%
‘latong’	*(Dendrocnide spp.: Urtic.)*	1.45%
‘k. mayang’	*(Payena lucida: Sapot.)*	0.05%
‘pagar anak’	*(*e.g. *Castanopsis spec.: Fagac.)*	0.09%
‘pakam’	*(Pometia pinnata.: Sapind.)*	1.97%
‘pala hutan’	*(Knema conferta.: Myrist.)*	0.09%
‘pepuah’	*(Mallotus sphaerocarpus.: Euphor.)*	1.68%
‘rambe’	*(Baccaurea motleyana.: Euph.)*	0.37%
‘rambung’	*(*strangling figs: *Morac.)*	3.09%
‘rambutan hutan’	*(Nephelium spec.: Sapind.)*	1.64%
‘rembele’	*(Saurauia spec.: Actin.)*	0.47%
‘setur’	*(Aglaia spp.: Meliac.)*	11.47%
‘simpur’	*(Dillenia indica.: Dill.)*	0.42%
‘tampu’	*(Macaranga diepenhorstii: Euph.)*	2.25%
‘terap’	*(Artocarpus elasticus: Morac.)*	0.19%

APPENDIX 3

COLLECTED SPECIMENS OF HYMENOPTERID-FOOD OF THE ORANG UTANS IN THE KETAMBE AREA

HR11.	Nasutitermes matagensis	(in dead wood)
HR 4.	Coptotermes curvignathus	(in dead wood)
HR 8.	Myrmicaria brunnea	(nest on leaves)
HR 1.	Polyrhachis villipes	(nest in epiphytes)
HR 7.	Polyrhachis hector	(nest in epiphytes)
HR 6.	Crematogaster sp.	(nest between branches)
HR 2.	Oecophylla sp.	(nest between leaves)
HR 3.	Camponotus sp.	(nest in epiphytes)
HR 5.	Camponotus sp.	(nest in hollow tree)
HR12.	Camponotus sp.	(nest between tree roots)

APPENDIX 4

POTENTIAL PARASITES AND DISEASES OF ORANG UTANS

explanation of the signs and abbreviations:
(+) observed in the Ketambe orang utans
(...) in parenthesis: the affected organs
T: transmission mode of the parasite: **f** via faecal contamination
P: pathogenous; and the name of the ailment.
NP: non pathogenous
... in brackets: the primate species in which the parasite is commonly found
?: unknown whether orang utans are susceptible.

HEMOFLAGELLATES

Pentatrichomonas hominis (caecum, colon) T. **f** NP.
Chilomastix mesnili (caecum, colon) T. **f** NP.
Giardia lamblia [?] (anter. small intest.) T. **f** P: enteritis

SARCODINES

Entamoeba histolytica (caecum, colon) T. **f** P: diarrhoea
Entamoeba coli (caecum, colon) T. **f** NP

MALARIAL PARASITES

(+) *Plasmodium pitheci* (blood) T. unknown P: tertian malaria
P. cynomolgi [?: macaca and man] T. unknown
P. knowlesi [?: macaca, presbytis and man] T. unknown
P. inui [?: macaca and man] T. unknown
P. hylobati [?: gibbons] T. unknown

CILIATES

\+ *Balantidium coli* (caecum, colon) T. **f** NP.

PARAMPHISTOMIDS (Trematoda)

(+) *Gasterodiscoides hominis* (caecum, colon) T. **f** P. enteritis
Leipertrema rewelli (pancreas) T. **f** P. ?

CESTODA (Anoplocephalids)

Bertiella studeri (small intest.) T. mites P?

NEMATODA (Strongyloidids)

\+ *Strongyloides stercoralis* (lung, duodenum, jejunum) T. **f** P.: coughing, diarrhoea debilitation, pneumonia, death
Strongyloides fülleborni [?] (id.) T. **f**
Strongyloides papillosus [?] (id.) T. **f**
\+ *Ancylostoma brasiliense* (small intestine) T. **f** P: diarrhoea, anaemia
\+ *Oesophagostomum blanchardi* (colon) T. **f** P: diarrhoea
O. apiostomum [?: macaca and man] (colon) T. **f** P: enteritis
O. bifurcum [?: macaca and man] (id.) T. **f** P: diarrhoea
O. aculeatum [?: macaca and man] (id.) T. **f** P: diarrhoea
Ternidens deminutus [?: macaca, chimpanzee and man] (caecum, colon) T. **f** P: anaemia
(+) *Pithecostrongylus alatus* small intestine T. **f** P?
(+) *Trichostrongylus colubriformis* [?: chimpanzee and man] (id.) T. **f** P: diarrhoea

\+ *Ascaris lumbricoides* (small intestine) T. f P: diarrhoea, abces
\+ *Enterobius buckleyi* (large intestine) T. f P: restlessness, aggressiveness
Streptopharagus pigmentatus [?: gibbons] T. arthropods P?
\+ *Abbreviata caucasica* (oesophagus, stomach) T. arthropods P: gastritis, enteritis, ulcers
Dicrofilaria pongoi (muscles, blood, right ventricle heart) T. mosquito P: condition decline
\+ *Trichuris trichuria* (caecum, colon) T. f P: anorexia, colitis death
Brugia malayi [?: man] (blood lymphatics) T. mosquito P: condition decline
Capillaria hepatica [?: man] (liver) T. insects P: condition decline

ACANTHOCEPHALIDS
Prostenorchis elegans [?: macaca, gibbon] (ileum, caecum, colon) T. insects P: enteritis, anorexia, death
Prostenorchis spirula [?: macaca, chimpanzee] (id.) T. insects P: id.

LEECHES
\+ *(Dinobdella ferox)* (nasal cavity, pharinx) [rehabilitants] T. water. (own propulsion) P: weakness, epistaxis, death.
\+ *(Haemadipsa picta)* [rehabilitants] NP. (blood loss) (skin) T. ground, own prop.
\+ *(Haemadipsa zeylanica)* [rehabilitants] NP. (blood loss) (skin) T. ground, own prop.

MITES
\+ *Sarcoptes scabei* P: parakeratosis
\+ *Eutrobicula wichmanni* N.P.

TICKS
\+ *Haemaphysalis cornigera* P:?
(+) *(Dermacentor atrosignatus)* [rehabilitant] P:?

INSECTS
\+ Calliphorid flies:
Chrysomya bezziana P: primary myiasis
Lucilia sp. P: id.
Phormia sp. P: id.
Calliphora sp. P: id.
Phaenicia sp. P: id.
\+ Sarcophagid flies:
Wohlfahrtia sp. P: secondary myiasis
Sarcophaga sp. P: id.
\+ Muscid flies:
Musca sp. P: secondary myiasis, & mechanical vectors for enteric pathogenous organisms.
Fannia sp. P: id.
Muscina sp. P: id.

DISEASES REPORTED FOR ORANG UTANS
Tuberculosis (SAVOY, 1964; E. DIEHL, pers. comm., 1974) (lungs) [animal of P. Siantar Zoo]
Muco-purulent airsac infection (DIEHL, pers. comm., 1975 also GUILLOD & MCCLURE, 1969)
Appendicitis (VERVAT, 1961)
Abcesses (SCHULTZ, 1956)
Caries (SCHULTZ, 1956)
Osteoarthritis (SCHULTZ, 1969)

+ Ulcerated colitis (CRAGG & SCOTT, 1974) possibly similar to nodulous colitis.
+ Blastomycosis (BINKLEY, 1959)
Melioidosis (TAMMEMAGI, 1963; DE SILVA, 1965)
'Monkey pox' and 'Chicken pox' (varicella) (HEUSCHELE, 1960; PETERS, 1966)

APPENDIX 5

LIST OF ORANG UTANS TAKEN TO THE REHABILITATION STATION KETAMBE (JULY 1971–AUGUST 1974)

name	*sex*	*arrival in station*	*estimated age at arrival*	*remarks*
1. Kuifje	M	7-9-71	2 months	died 2-2-72, encephalitis
2. Seamus	M	23-11-71	4 years	in forest since december 1973
3. Djahe	F	2-12-71	5 years	died 16-4-72, clouded leopard
4. Pim	F	2-12-71	3 years	disappeared 16-4-72, (clouded leopard)
5. Puk	F	2-12-71	3 years	died 8-6-72, clouded leopard
6. Usman	M	23-1-72	7 years	in forest since October 1972
7. Bin	F	23-1-72	7 years	
8. Marga	F	25-1-72	2 years	
9. David	M	9-2-72	8 years	in forest since October 1973
10. Bobo	M	9-2-72	4 years	
11. Pon	M	16-2-72	4 years	died 7-7-73, fall from tree
12. Nikki	F	21-2-72	2 years	in forest since 14-4-72?
13. Simanis	M	13-3-72	3 years	
14. Barby	F	13-3-72	2 years	disappeared, July 1974
15. Sam	M	13-3-72	1 year	died 23-4-72, clouded leopard
16. Lotje	F	13-3-72	2 years	died 14-6-72, clouded leopard
17. Joanna	F	13-3-72	4 years	died 27-7-72, clouded leopard
18. Belia	F	13-3-72	2 years	
19. Max	M	13-3-72	3 years	died 27-7-72, clouded leopard
20. Gala gala	F	23-3-72	2 years	died 16-9-73, accident, choked
21. Yoko	F	26-3-72	7 years	in forest since February 1974
22. Peter	M	26-3-72	3 years	died 30-6-74, tiger
23. Sibujung	M	14-6-72	7 years	
24. Bas	M	12-7-72	1 year	died 3-9-73, orchitis/peritonitis
25. William	M	14-10-72	3 years	died 6-11-72, cachexy
26. Linda	F	6-2-73	4 years	died 4-10-73, encephalitis
27. Tjali	F	1-3-73	4 years	
28. Simi	F	13-3-73	9 years	in forest since May 1973
29. Koen	M	10-9-73	1$^1/_2$ year	disappeared August 1974
30. Luk luk	M	7-3-74	2 years	
31. Bumi	M	8-7-74	2 years	

APPENDIX 6

List of names of vertebrate animals observed in the Ketambe area.
(those species which were observed commonly are denoted with *)

AMPHIBIANS
(Toads) *Bufo cf. melanosticus**
(Toad-frogs) *Megophrys natusa*
(Frogs) *Rana spp.*
(Caecilians) *Ichtyophis cf. glutinosa*

REPTILIANS
(Mud turtles) *Trionyx cartilagineus*
(Land tortoises) *Testudo emys*
(Box tortoises) *Geomyda spinosa*
Cuora amboinensis
(Geckos) *Gymnodactylus marmoratus*
cf. Hemidactylus platyurus
(Agamid lizards) *Draco volans**
Draco cf. fimbriatus
cf. Aphianotis acutirostris
Gonyocephalus sumatranus
Gonyocephalus cf. liogaster
*Calotes cristatellus**
(Monitors) *Varanus salvator*
Varanus rudicollis
(Skinks) *Mabuya multifasciata**
(Lizards) *Lygosoma cf. anomalopus*
Lygosoma cf. sumatrense
(Snakes) *Typhlops lineatus*
Python reticulatus
Dendrophis pictus
*Zaocys fuscus**
Xenelaphus hexagonotus
Coluber melanurus
Coluber oxycephalus
Simotes purpurascens
Psammodynastes pictus
Dryophis prasinus
Chrysopelea ornata
Naja tripudians
Naja hannah
Agkistrodon rhodostoma
Trimeresurus cf. wagleri
Doliophis bivirgatus

BIRDS
(Herons) *Butorides striatus* (little green heron)
(Ducks) *Dendrocygna javanica* (whistling duck)
(Falcons) *Machaerhampus alcinus* (bat hawk)
Accipiter virgatus (asiatic sparrow hawk)
Spizaëtus cirrhatus (changeable hawk eagle)
Circaëtus gallicus (short toed eagle)

Spilornis cheela (serpent eagle)*
(Pheasants) *Rollulus roulroul* (green crested partridge)*
Lophura ignita (crested fire back pheasant)
Polyplectron malacensis (peacock pheasant)
Rheinartia ocellata (ocellated pheasant)
Argusianus argus (argus pheasant)*
(Plovers) *Tringa hypoleucos* (common sandpiper)
Capella gallinago (common snipe)
(Pigeons) *Columba argentina* (grey wood pigeon)
Ducula aenea (green imperial pigeon)
Macropygia ruficeps (little cuckoo dove)
Chalcohaps indica (green winged pigeon)*
Treron curvirostra (thick billed pigeon)
Treron sphenura (wedge tailed pigeon)
(Parrots) *Psittacula longicaudata* (long-tailed parakeet)
Loriculus galgulus (blue crowned hanging parrot)
(Cuckoos) *Phaenicophaeus chlorophaeus* (Raffles's malcoha)
Phaenicophaeus javanicus (red billed malkoha)
Phaenicophaeus sumatranus (chestnut bellied malkoha)
Centropus chinensis (greater coucal)*
Centropus bengalensis (lesser coucal)
(Owls) *Bubo sumatranus* (barred eagle owl)
Glaucidium brodiei (collared owlet)
Strix leptogrammica (brown wood owl)
(Frogmouths) *Batrachostomus cf. javensis* (javan frogmouth)
(Swifts) *Apus affinis* (house swift)
Hirundapus cochinchinensis (white vented needle tail swift)
Rhaphidura leucopygialis (silver rumped swift)*
(Treeswifts) *Hemiprocne comata* (whiskered treeswift)
(Trogons) *Harpactes kasumba* (red naped trogon)
Harpactes duvaucelii (scarlet rumped trogon)
(Kingfishers) *Laceda pulchella* (banded kingfisher)
Halcyon pileata (black-capped kingfisher)
Halcyon concreta (rufous-collared kingfisher)
Ceyx erithacus (black-backed kingfisher)
(Bee-eaters) *Nyctyornis amictus* (red-bearded bee-eater)
(Hornbills) *Berenicornis comatus* (white-crowned hornbill)
Anorrhinus galeritus (bushy crested hornbill)
Aceros corrugatus (wrinkled hornbill)
Aceros plicatus (blyth's hornbill)
Anthracoceros malayanus (black hornbill)
Anthracoceros convexus (pied hornbill)
Buceros rhinoceros (rhinoceros hornbill)
Buceros bicornis (great hornbill)
Rhinoplax vigil (helmeted hornbill)
(Barbets) *Megalaima chrysopogon* (gold-whiskered barbet)
Megalaima henricii (yellow-crowned barbet)
Megalaima australis (blue-eared barbet)
Megalaima haemacephala (coppersmith barbet)
Calorhampus fuliginosus (brown barbet)
(Honeyguides) *Indicator archipelagicus* (Malaysian honey guide)
(Woodpeckers) *Sasia abnormis* (rufous piculet)
Sasia abnormis (rufous piculet)
Dinopium rafflesii (olive-backed woodpecker)
Picus cf. miniaceus (banded woodpecker)

Blythipicus rubiginosus (maroon woodpecker)
Hemicircus concretus (grey-and-buff woodpecker)
Chrysocolaptes validus (orange backed woodpecker)
(Broadbills) *Calyptomena viridis* (green broadbill)
Cymbirhynchus macrorhynchus (black-and-red broadbill)
Eurilaimus javanicus (banded broadbill)
Corydon sumatranus (dusky broadbill)
(Pittas) *Pitta moluccensis* (blue-winged pitta)*
Pitta guajana (banded pitta)
(Swallows) *Hirundo tahitica* (pacific swallow)*
(Minivets) *Hemipus hirundinaceus* (black-winged flycatcher shrike)
Coracina striata (bar-bellied cuckoo-shrike)
(Bulbuls) *Pycnonotus atriceps* (black-headed bulbul)*
Pycnonotus zeylanicus (straw-headed bulbul)*
Pycnonotus erythrophtalmus (spectacled bulbul)
Criniger bres (grey-cheeked bulbul)
Criniger phaeocephalus (yellow-bellied bulbul)
(Leafbirds) *Aegithinia tiphia* (common iora)
Chloropsis cf. sonnerati (greater green leafbird)
Irena puella (fairy bluebird)
(Drongos) *Dicrurus leucophaeus* (ashy drongo)
Dicrurus aeneus (bronzed drongo)
Dicrurus paradisea (greater racket-tailed drongo)
(Orioles) *Oriolus xanthonotus* (Malaysian black-headed oriole)
(Jays) *Platylophus galericulatus* (crested jay)
Platysmurus leucopteris (black-crested magpie)
Corvus enca (slender billed crow)
(Babblers) *Malacopteron cinereum* (lesser red-headed tree-babbler)
Malacopteron affine (plain babbler)
Macronus gularis (striped tit-babbler)
Stachyris maculata (red-rumped tree-babbler)
Stachyris erythroptera (red-winged tree-babbler)
Napothera macrodactyla (large wren-babbler)
Pnoepyga pusilla (pygmy wren-babbler)
(Thrushes) *Copsychus malabaricus* (common shama)
Enicurus leschenaulti (white-crowned forktail)*
(Warblers) *Prinia flaviventris* (yellow bellied wren-warbler)
Orthotomus sutorius (common tailorbird)*
Orthotomus ruficeps (ashy tailorbird)
(Flycatchers) *Ficedula dimetoria* (rufous chested flycatcher)
Hypothymus azurea (black-naped monarch)
Terpsiphone paradisi (paradise flycatcher)
(Shrikes) *Lanius tigrinus* (thick billed shrike)
(Starlings) *Acridotherus fuscus* (jungle mynah)*
Gracula religiosa (hill mynah)*
(Sunbirds) *Hypogramma hypogrammicum* (purple naped sunbird)
Nectarinia sperata (purple throated sunbird)
Aethopyga siparaja (crimson sunbird)
Arachnothera longirostris (little spiderhunter)
Arachnothera affinis (grey breasted spiderhunter)
(Flowerpeckers) *Dicaeum cruentatum* (scarlet backed flowerpecker)
Dicaeum ignipectus (buff-bellied flowerpecker)
Zosterops palpebrosa (oriental white-eye)
(Sparrows) *Lonchura maja* (white headed munia)
Erythrura prasina (pin tailed parrotfinch)

MAMMALS

(Insectivores) *Echinosorex gymnurus* (moonrat)
Crocidura fulginosa (white toothed shrew)
Suncus etruscus (pygmy shrew)
(Flying lemur) *Cynocephalus variegatus* (colugo)
(Fruit-bats) *Pteropus vampyrus* (flying fox)*
Cynopterus brachyotis (malaysian fruit bat)
cf. *Megaerops ecaudatus* (tailless fruit bat)
(Horseshoe bats) *Hypposideros larvatus neglectus* (roundleaf horseshoe bat)
Hypposideros diadema (diadem roundleaf horseshoe bat)
(Common bats) *Myotis mystacinus* (whiskered bat)
Pipistrellus imbricatus (brown pipistrelle)*
(Treeshrews) *Tupaia glis* (common treeshrew)*
(Loris) *Nycticebus coucang* (slow loris)
(Monkeys) *Presbytis thomasi* (Thomas's leaf-monkey)*
Macaca fascicularis (long tailed macaque)*
Macaca nemestrina (pig tailed macaque)*
(Apes) *Hylobates lar vestitus* (white handed gibbon)*
Hylobates syndactylus (siamang)*
Pongo pygmaeus abelii (orang utan)*
Homo sapiens (man)
(Squirrels) *Ratufa bicolor* (black giant squirrel)*
Callosciurus notatus (plantain squirrel)
Sundasciurus hippurus (horse tailed squirrel)*
Sundasciurus tenuis (slender squirrel)*
Lariscus insignus (three striped ground squirrel)
Rhinosciurus laticaudatus (shrew faced ground squirrel)
(Flying squirrels) *Hylopetes* cf. *lepidus* (grey cheeked flying squirrel)
Petaurista elegans (spotted giant flying squirrel)
(Rats) *Mus musculus castaneus* (house mouse)
Rattus exulans (polynesian rat)*
cf. *Rattus cremoriventer* (dark tailed tree rat)
(Porcupines) *Hystrix brachyura* (malayan procupine)
(Dogs) *Cuon alpinus* (dhole)
(Bears) *Helarctos malayanus* (sun-bear)
(Otters) *Lutra sumatrana* (jairy nosed otter)
(Martens) *Martes flavigula* (yellow throated marten)
(Weasels) *Mustela nudipes* (malay weasel)
(Civets) *Viverra tangalunga* (common civet)
Pryonodon linsang (linsang)
Paguma larvata (masked palm civet)
Arctitis binturong (bear-cat)
Herpestes brachyurus (short-tailed mongoose)
(Cats) *Panthera tigris* (tiger)
Neofelis nebulosa (clouded leopard)
Felis bengalensis (leopard cat)
Felis temminckii (golden cat)
(Rhinoceros) *Dicerorhinus sumatraensis* (sumatran rhinoceros)
(Pigs) *Sus scrofa* (wild pig)*
(Deer) *Tragulus javanicus* (lesser mouse deer)*
Tragulus napu (large mouse deer)
Muntiacus muntjak (barking deer)
Cervus unicolor (sambar)
(Goats) *Capricornis sumatraensis* (serow)
(Badgers) *Arctonyx collaris* (sun badger)

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CURRICULUM VITAE

HERMAN DIRK RIJKSEN was born January 9, 1942, in Zeist, The Netherlands. After Highschool (F. C. de Munnik HBS-B, Utrecht), he commenced his study at the Agricultural University in Wageningen in 1961. In 1963 he changed over to the study in Veterinary Medicin at the University of Utrecht, where the degree of Doctor of Veterinary Medicin (D.V.M.) was obtained in January 1971. Under the supervision of Dr. J. H. KOEMAN, he assisted a toxicological-ecological fieldstudy in Nigeria to investigate the side effects of Dieldrin spraying – applied in a nation-wide Tse-tse fly eradication programme – on the wild fauna of a woodland savanna habitat, in 1969.

From June 1971 until August 1974 he worked together with his wife, Ir. A. G. RIJKSEN-GRAATSMA, in the Gunung Leuser Reserves in Aceh, Indonesia, in order to study the biology of wild Sumatran orang utans. The fieldstudy was supported by the Netherlands Foundation for the Advancement of Tropical Research (WOTRO), and was carried out under the supervision of Prof. Dr. M. F. MÖRZER BRUYNS, Nature Conservation Department of the Agricultural University, Wageningen.

In March 1976 he was appointed a research assistant at the Zoological Laboratory, Ethology Department of the University of Groningen.

Since 1974 he is a member of the Netherlands Committee of International Nature Conservation. the Netherlands Gunung Leuser Committee (World Wildlife Fund, Zeist) and the International Advisory Committee of WWF/IUCN on Nature Conservation in Indonesia.