SEXUAL BEHAVIOUR AND MATING PATTERNS IN A COMMUNITY OF WILD CHIMPANZEES (*PAN TROGLODYTES SCHWEINFURTHII*)

by

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SUMMARY

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The aim of the study is to gain an understanding of chimpanzee reproductive behaviour and through this to assess the role of sexual selection in the evolution of the species' social structure.

Chapter 2

The Gombe National Park, where the study was carried out, is described. The Kasakela community was the focus of the study, and over 1000 hours of observation was made of 11 females showing cycles of sexual swelling. Recording methods are outlined and discussed.

Chapter 3

Data from 15 years of observation of individual chimpanzees in the Gombe population are collated to assess the reproductive potentials of males and females. The interval between successive live births is long, and each female can produce a maximum of 5-6 offspring in a lifetime. Limited data on known individuals indicate that this maximum is rarely achieved and the average number of offspring produced by a single female which survive to adulthood is two. Females are sexually receptive for a very small proportion of their lives and the majority of cycles shown appear to be infertile.

Chapter 4

Cyclic phenomena in reproduction are described. Births are non-randomly distributed over the year with significantly more occurring in the dry season. Sexual behaviour is heavily concentrated in the female cycle phase of maximal tumescence. This phase lasts an average of 9.8 days and ovulation is believed to occur towards the end of the phase. Copulation frequency increases in the latter half of the phase when the mating pattern is promiscuity. Copulation rate shows a consistent circadian rhythm, with the peak occurring in the early morning. Diurnal rhythms in other female behaviours exist but are not directly correlated to the fluctuations in copulation rates. The possible influence of hormonal factors is discussed.

Chapter 5

Behavioural elements of copulation are described and the functions of courtship discussed. Individual differences in the form of adult male courtship are small and it is concluded that courtship serves to communicate the male's willingness to mate, but does not convey information used by females to discriminate between males. The ontogeny of sexual behaviour in males and females and their reactions to the copulations of others are described. Dyadic copulation rates in promiscuous mating vary, indicating that partner preferences exist. The strongest of these is the negative one shown by closely related individuals. Incest avoidance mechanisms in wild chimpanzees are described and compared to other primates.

Chapter 6

Possessive behaviour is described. It is shown that the alpha male of a community is able to monopolise receptive females by showing possessive behaviour and interrupting or inhibiting the copulation attempts of other males. For non-dominant males, possessive behaviour appears to serve as an intermediate step towards consort formation.

Chapter 7

Consorting behaviour between pairs of adult chimpanzees is described. One consortship was observed for 13 days and the relationship between the pair is described in detail. Female cooperation, in remaining silent and following the male, is essential for the maintenance of consortships. Limiting factors to consort formation are discussed and of these the most serious appear to be 1) the risk of inter-community encounters incurred while avoiding members of the consort pair's own community, and 2) the risk of attack on return to their community. Females' circumstances at the time of conception are examined and the data indicate that the majority of females conceive whilst in consort relationships.

Chapter 8

The adaptive significance of the flexible mating system of wild chimpanzees is discussed. Consort formation allows females to exercise choice, and the criteria for choice appear to be the relative frequencies of affiliative behaviours, with males who show high frequencies being preferred. Male-male competition results in the formation of a dominance order and the alpha male gains reproductive advantage through the ability to monopolise receptive females without incurring the risks associated with consorting. Social behaviour and structure are examined with respect to maximising individual reproductive success.

Chapter 1

INTRODUCTION

1. Aims

The aim of the study was to describe the reproductive biology of wild chimpanzees (Pan troglodytes schweinfurthi) and to relate this to aspects of their ecology and social organisation. Within this general framework the specific aims were:

(a) To determine the reproductive potential of female chimpanzees and to assess the limits this places on species' reproduction;

(b) To examine the adaptive significance of female reproductive physiology in terms of optimal reproductive success;

(c) To examine environmental constraints on reproduction;

(d) To describe copulatory behaviour and the nature of the three mating patterns shown by wild chimpanzees, and to assess the adaptive significance of the flexible mating system;

(e) To relate reproductive behaviour to social organisation in an attempt to assess the role of sexual selection in the evolution of chimpanzee social behaviour and structure.

2. Background

Many field studies of non-human primates have concentrated on the relationship between social structure and environmental factors. Social organisation is regarded as being adapted to the environment of the species, with natural selection acting to create a social system which maximises individual survival. Whilst this approach has proved useful when applied to a particular species or population (e.g. DeVore, 1963; Kummer, 1968; Struhsaker, 1969; Clutton-Brock, 1972), attempts to make general correlations across species have been less successful (Crook & Gartlan, 1966). It has been pointed out that simple correlations between types of social organisation and environmental variables should not be expected because species differ in their genetic backgrounds and may thus adapt differently to similar environmental pressures (Crook, 1970; Kummer, 1971). Another complicating factor which has until recently received little attention is that social behaviour may be shaped by sexual selection as well as by natural selection (Goss-Custard et al, 1972; Crook, 1972).

In The Descent of Man and Selection in Relation to Sex (1871), Darwin described sexual selection and its role in the evolution of both physical characters (secondary sexual characters) and behaviour. In comparing natural and sexual selection, he stated: "Sexual selection depends on the success of certain individuals over other individuals of the same sex, in relation to the propagation of the species; whilst natural selection depends on the success of both sexes, at all ages, in relation to the general conditions of life. The sexual struggle is of two kinds; in one it is between individuals of the same sex, generally the males, in order to drive away or kill their rivals, the females remaining passive; whilst in the other, the struggle is likewise between individuals of the same sex, in order to excite or charm those of the opposite sex, generally the females, which no longer remain passive, but select the more agreeable partners." (1871, p. 939). Huxley (1938) refined Darwin's concept of sexual selection, emphasising the two main principles of (1) intra-sexual selection, which results from advantages accrued from the possession of morphological or behavioural characters which increase reproductive success through competitive rivalry between members of the same sex; and (2) epigamic, or inter-sexual selection, which results from a reproductive advantage gained by individuals with stronger heterosexual stimuli.

The relationship and distinction between natural and sexual selection is not always clear. Fitness at the genetic level is measured in terms of the contribution an individual makes to the gene pool of the next generation. This definition, coined with respect to the relative selective advantages of individual genes, or combinations of genes, gives no indication as to whether the selective advantage was gained as a result of superior adaptation to the environment, or as a result of reproductive advantage that does not enhance the species' overall adaptiveness. However, the distinction between natural and sexual selection is useful when considering the whole organism and the selective forces which led to the evolution of particular morphological and behavioural characters.

The importance of natural selection is paramount, as an individual must survive in order to reproduce. Once this is assured, through the selection of morphological and behavioural adaptations to maximise survival in the species' environment, further adaptations which maximise an individual's reproductive success, will gain selective advantage. Inter-sexual selection has been invoked to explain the evolution of characters which have no apparent advantage, and in many cases apparent disadvantage, for individual survival. Examples of the most brightly coloured males of an avian species, or the stag with the largest antlers, being preferred by females are widespread (see Zahavi, 1975). If female discrimination is made on relative rather than absolute criteria then the preferred character will spread rapidly through the population and become exaggerated.

Why do females make such discriminations, selecting a male with a particular character, which in itself confers no advantage in terms of survival? This problem caused some to dismiss Darwin's theory of sexual selection by mate preference (e.g. Wallace, 1889). Others (e.g. Fisher, 19~~30~~29) argued that the characters preferred by females may initially have been correlated with gen etic quality in the male. The preference of females for males possessing the particular character itself creates an additional selective advantage. Thus the character will be maintained despite a subsequent decrease in its survival value as long as females continue to make similar discriminations. Zahavi (1975) presented an alternative explanation, arguing that females discriminate between males on the basis of characters with <u>negative</u> survival value. The reason for this is that males which can survive to reproductive age with morphological or behavioural "handicaps" demonstrate superior genetic fitness over males who survive without the handicap. Thus, the handicap, whether it be bright plumage that increases the risk of predation, large morphological adornments such as antlers that decrease mobility and hence feeding efficiency, or altruistic behaviour with an unfavourable cost/benefit outcome, advertises to the female that the male has a level of fitness sufficient to overcome the disadvantage incurred, As Zahavi states "It is possible to consider the handicap as a kind of test imposed on the individual. An individual with a well developed sexually selected character, is an individual which has survived a test. A female which could discriminate a male possessing a sexually selected character, from one without it, can discriminate between a male which has passed a test and one which has not been tested. The more developed the character the more severe the test. Females which select males with the most developed characters can be sure that they have selected from amongst the best genotypes of the male population." (1975, p. 207).

Natural selection will impose an upper limit only when the handicap is so great as to preclude survival to reproductive age. A male with a large handicap which reduces his lifespan through increased risk of predation, or decreased feeding efficiency, might still leave more offspring than a male with a smaller handicap, if the increase in reproductive success over the other male is sufficient to compensate for a reduced reproductive lifespan. However, this will depend on the mating system of the species. Maynard Smith (1958) pointed out that in species in which both sexes contribute parental investment, sexual selection will only have evolutionary consequences if the individuals with the characters which bring success in competition for mates are also better parents. Thus one would expect sexually dimorphic characters which increase male reproductive success but have negative survival value (i.e. handicaps), to evolve in species in which, (1) the female has the potential to choose a mate from a large number of males, and (2) the males make little or no parental investment. One might also predict that such handicaps would be more common among species in which association between the sexes was restricted to a brief period of hetereosexual activity, since in these species discriminations between potential mates must be made rapidly and with little information other than the physical appearance of the males. In other species female discriminations could be based on more subtle and comprehensive information about male fitness, gained through longer periods of association and interaction. If females are able to discriminate on subtle cues which do not entail a decrease in male fitness, one would not expect severe handicaps to evolve.

Non-human primates fall into the latter category; individuals are long-lived and the existence of social groupings with lifelong membership results in relatively permanent associations between males and females. In this situation one might predict that mate selection would be made on behavioural rather than morphological criteria, and that if handicaps did develop these too would be behavioural.

The potential for both inter- and intra-sexual selection depends on the form of social structure. As the non-human primate female makes such a large commitment in terms of parental investment in each offspring, one might expect social structures which permitted females to exercise choice to have evolved (Maynard Smith, 1958; Orians, 1969; Williams, 1966; Trivers, 1972). The importance of sexual selection as a factor in the evolution of avian social structure has been examined (Crook, 1965; Lack, 1968), but only recently has it been explicitly examined as a factor of significance in the evolution of primate social structure (Crook, 1972; Goss Custard _et al_, 1972).

Sexual selection is one cause of sexual dimorphism. Intra-sexual selection in primates seems to have led to increased male size and changes in pelage length and colour (Struhsaker, 1969; Crook, 1970, 1972). Inter-sexual selection has not given rise to any additional features comparable to the spectacular plumage of certain birds, but reasons for this have been discussed above.

Three types of primate social organisations are recognised and classified with respect to the sex ratio of the adults: One-male to one-female pairs, one-male/all-male groups, and multi-male groups. Crook (1972) related the degree of sexual dimorphism in body size amongst primates to the types of social organisation, and found that sexual dimorphism was greatest in the one-male/all-male sociotypes and least in monogamous pairings.

In the one-male/all-male sociotype a single adult male associates with a number of adult females and their offspring. The degree of spatial dispersion of these groups ranges from situations in which one-male groups occupy territiries from which solitary males are excluded, e.g. Cercopithecus mitis (Aldrick-Blake, 1970), to situations in which one-male groups associate in bands with peripheral non-reproductive males, as in Papio hamadryas (Kummer, 1968). Between these two extremes are species with some overlap of range between the one-male and all-male groups or solitary males, e.g. Erythrocebus patas (Hall, 1966), Presbytis entellus (Jay, 1965; Sugiyama, 1965) and Gorilla gorilla (Fossey, 1974). The potential for females to exercise choice in their selection of mates is severely limited in this form of social organisation as the identity of the one male in the group is decided by male-male competition.

Monogamy is rare among non-human primates, occurring only in a few species of Indridae (Petter, 1965; Pollock, 1975), Hylobatidae (Carpenter, 1940; Chivers, 1972; Ellefson, 1968; Tenaza, 1975) and Callithricidae (Mason, 1968). Little is known of pair formation in the wild in these monogamous species, and so the relative importance of male-male competition and female choice cannot be assessed.

In multi-male groups where a number of adult males associate with equal or greater numbers of adult females and their offspring, both male-male competition and female choice might be expected to play important parts in determining individual reproductive success. Male-male competition is well documented, with aggressive and other interactions leading to some form of dominance ordering amongst the males (see below). The role of female choice in primate reproduction is less well known. Theoretically one would expect it to be important, for reasons described above, but its expression may be subtle and hard to detect compared to the conspicuous behaviours of male-male competition. The potential for females to select a particular male exists in these multi-male groups, but to be effective there must be a mechanism to ensure impregnation by a selected male. Such a mechanism exists in temporary monogamous consortships formed between a single male and female at the time when conception can occur. Consort formation is common in species which have multi-male groups, e.g. *Papio anubis* (Ransom, 1971); *Papio cynocephalus* (Altmann & Altmann, 1970); *Papio ursinus* (Saayman, 1970); *Macaca ~~rhesus~~ mulatta* (Bernstein, 1963; Loy, 1970); *Macaca fuscata* (Tokuda, 1961); and *Pan troglodytes* (McGinnis, 1973; van Lawick-Goodall, 1974; Tutin, 1975); but is apparently absent in others, e.g. *Cercopithecus aethiops* (Struhsaker, 1967; Gartlan, 1969).

The basic unit of chimpanzee social structure is the community or unit-group (Itani & Suzuki, 1967; Nishida, 1970; Bygott, 1974; van Lawick-Goodall, 1974; Wrangham, 1975). The number of individuals within a community varies from 15 to 80 (Nishida & Kawanaka, 1972; Sugiyama, 1973; van Lawick-Goodall, 1974). The only permanent associations of individuals within the community are mothers and their dependent offspring. Other individuals form temporary associations in groups or parties which vary both in size and age-sex composition. Wrangham (1975) described the effects of food availability on group size, and also found a sex difference in ranging patterns. The adult males of a community jointly hold a large range within which females have small individual core areas. The distribution of female ranges with respect to the large male ranges remains unclear, so it is not possible to state whether all females 'belong' exclusively to one community, or whether some at least, associate regularly with the males of more than one community. Wrangham suggested that the adaptive value of this pattern of ranging lay in the fact that males, by acting cooperatively, gain access to more females than they would if they maintained individual ranges. Thus it is not possible to classify chimpanzee social structure exactly in terms of the proposed sociotypes, but it approximates to the multi-male sociotype described by Crook (1970; 1972).

Chimpanzees were initially thought to mate promiscuously (Kortlandt, 1962; Goodall, 1965; Nishida, 1968). However, like the early misconception about the absence of any permanent social structure, this view has been modified by continued observation (McGinnis, 1973, and in press; van Lawick-Goodall, 1974; Tutin, 1975). The mating system of the chimpanzee population of the Gombe National Park in north western Tanzania comprises three mating patterns; non-competitive group mating (called promiscuity for the sake of brevity), possessive behaviour, and the formation of temporary monogamous consortships. Long term observation of the chimpanzee population in the Mahali Mountains of western Tanzania has failed to reveal the existence of consortships (Nishida, in press, and pers. comm.), and so the possibility exists that cultural variation in mating systems occurs.

The existence of the non-promiscuous mating patterns is important because sexual selection can only operate under these restrictive patterns, where through female choice, male-male competition, or both, certain males can increase their reproductive success at the expense of others. The initial reports of chimpanzee promiscuity have persisted, causing consternation to those arguing for the importance of sexual selection in hominid evolution (e.g. Caspari, 1972; Fox, 1972). The questions to be answered in this study are aimed at assessing the relative importance of the three mating patterns, not merely in terms of their relative frequencies, but also with respect to the more pertinent evolutionary variable, the number of conceptions occurring as a result of each pattern.

Agonistic male-male competition is well documented amongst wild chimpanzees and a dominance order among adult males is recognisable (van Lawick-Goodall, 1968, 1974; Bygott, 1974). The validity of the concept of social dominance in non-human primates and its usefulness in understanding and interpreting behavioural data have been questioned (Rowell, 1974) and so justification of its use and meaning in wild chimpanzee communities is required. Bygott (1974) found that certain aggressive and submissive behaviours shown in dyadic interactions between adult male chimpanzees at Gombe occur in a consistent way allowing the ranking of individuals in a more or less linear order. This order was relatively stable over time, and changes in it were often characterised by intense agonistic interactions between the individuals concerned. Simpson (1973) found that for the same population of chimpanzees, frequencies and durations of social grooming sessions were related in a consistent~~ly~~ way to agonistic rank. Similar findings have come from other studies of wild chimpanzees (e.g. Nishida, 1970). This indicates that the dominance concept is useful and a salient feature in examining and understanding a variety of interactions between adult male chimpanzees.

Contradictory reports exist on the relationship between male dominance ~~and~~ rank and sexual behaviour in non-human primates. High ranking males have been reported to mate more frequently than lower ranking males in Papio anubis (DeVore, 1965), Macaca mulatta (Carpenter, 1942; Kaufman, 1965) and Macaca fuscata (Tokuda, 1961; Hanby et al, 1971). Other studies have failed to find a correlation between dominance rank and the frequency of sexual behaviour, e.g. in Papio ursinus (Saayman, 1970), Macaca mulatta (Koford, 1963), and Macaca fuscata (Eaton, 1974). Caution is needed in interpreting these data, as many of the studies were of captive groups in which dominance-subordinance relationships are often distorted (Rowell, 1974), and because the frequency of sexual behaviour is not the only factor important in determining reproductive success. The timing of copulations with respect to the time of ovulation probably has a greater effect on a male's reproductive success than does his overall frequency of copulation.

Nishida (in press) found a positive correlation between male dominance rank and frequency of copulation amongst the 5 adult male chimpanzees of the K unit-group in the Mahali Mountains. He reported that "Among 383 examples of copulation observed so far in the K-group, 177 (46.2%) cases were accomplished by the top-ranking male. Although the frequency of copulation among adult males was noticed to be in direct proportion to the status an adult male occupies in the dominance hierarchy, the top-ranking male excelled the others very conspicuously and had especially more opportunity to copulate young 'newcomer' females." Neither McGinnis (1973) nor Bygott (1974) found a correlation between the frequency of copulations or consortships and male dominance rank in the Gombe chimpanzees. Both related absolute frequencies of sexual behaviour to male dominance rank and did not distinguish between sexual behaviour which led to conception and that which did not.

Description and understanding of chimpanzee social structure has proved elusive, and only after 15 years of observation of the

Gombe chimpanzees is a picture beginning to emerge of the patterning of individual relationships, and how these combine into the larger unit of community structure (Bygott, 1974; van Lawick-Goodall, 1974; Wrangham, 1975). Wrangham described the relationship between chimpanzee ecology and social organisation and speculated as to the selective forces responsible for its evolution. Whilst much social behaviour may be explained as a result of natural selection acting to optimise individual survival, it also seems that sexual selection might have been an important factor in shaping the social structure. However, the existence of neither inter- nor intra-sexual selection is yet demonstrated. Male-male competition is an obvious and important aspect of chimpanzee social behaviour, and yet it does not appear to be related to individual reproductive success (McGinnis, 1973; Bygott, 1974). The flexible mating system offers the potential for females to exercise choice and to ensure impregnation by the chosen male, but the existence of such choice remains undemonstrated (McGinnis, 1973). The aim of the present study was to observe all aspects of chimpanzee reproductive biology accessible to the limited methods of field studies.

CHAPTER 2

STUDY AREA, POPULATION, AND METHODS

1. Study Area

i. The Gombe National Park

The Gombe National Park (4 40'S; 29 38'E) is on the eastern shore of Lake Tanganyika, 12 miles north of the town Kigoma. The approximate dimensions of the Park are 13.5 km by 1.5-3.0 km, the boundaries on the longer sides being Lake Tanganyika and the escarpment crest of the Western Rift Valley, see Figure 2.1. The Park is bisected by 13 major stream valleys, most of which support permanent streams, which run in parallel from the rift escarpment (approximately 5,000 ft. above sea level) to the lake (2534 ft. above sea level). The exact area of the Park is difficult to assess because of the rugged terrain. Teleki *et al* (in prep.) estimated the map area of the Park to be 32 km^2 but stated that the true surface area may be as much as 40% larger.

The Park was first gazetted as a Game Reserve in 1943, thanks to the foresight of G.G. Rushby, who recognised the need to protect the chimpanzee population. It became a National Park in 1968.

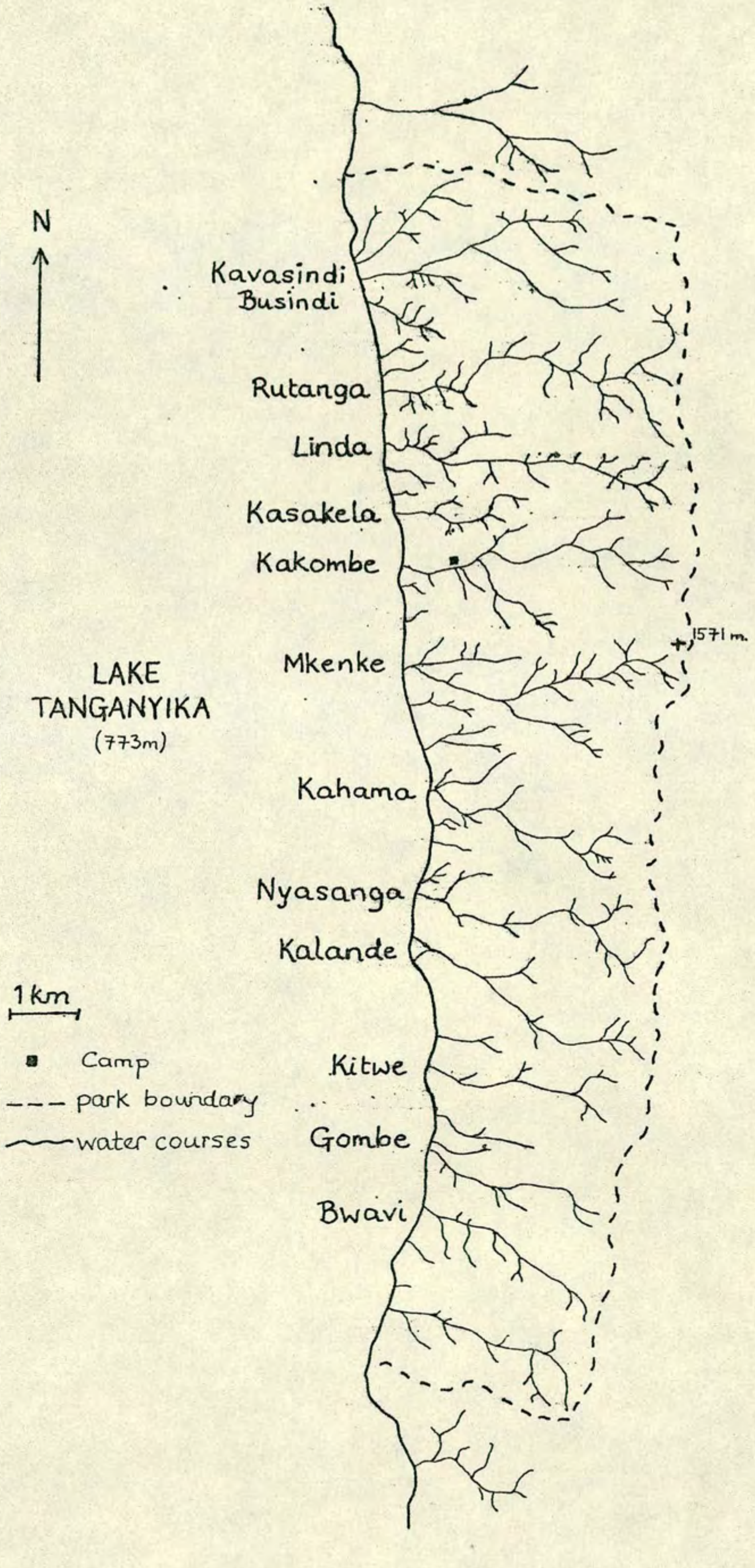
ii. Vegetation

The vegetation of the Park has been described in detail elsewhere (Thomas, 1961; van Lawick-Goodall, 1968; Clutton-Brock, 1972; Wrangham, 1975). In brief, it comprises a mosaic of evergreen forest, semi-deciduous forest, dry woodland and grassland, whose distribution is closely related to topography.

iii. Fauna

Seven species of nonhuman primates occur within the Park. Of these 5 - chimpanzees (*Pan troglodytes schweinfurthii*), olive baboons

Figure 2.1 The Gombe National Park.



(Papio anubis), red colobus (Colobus badius tephrosceles), blue monkeys (Cercopithecus mitis), and red-tail monkeys (Cercopithecus ascanius), are common. A small population of vervet monkeys (Cercopithecus aethiops) exists but range only on parts of the lake shore area and are rarely seen. Needle-nailed galago (Euoticus sp.) have also been recorded in the Park but observations are scarce as they are nocturnal and uncommon. Other mammals occurring in the Park are listed in Wrangham (1975, p. 4.22).

iv. Climate

Annual and circadian rhythms in climate have been described by Clutton-Brock (1972). There is a single wet season from November to May during which approximately 60" of rain falls. Temperature variations are slight, ranging from 19°C to 30°C. August and September are the hottest months, when daily maxima are regularly 30°C.

v. The Research Centre and Human Activities in the Park

There are two permanent human settlements within the Park boundaries, one is the Park Ranger Station in Nyasanga Valley and the other is the Research Centre in Kakombe Valley. In addition to these there are numerous fishing villages along the lakeshore which are inhabited for about 3 out of every 4 weeks. The movements of the fishermen and other transient humans in the Park are limited to the beach and to a number of major paths which run along ridge tops, connecting the beach to the villages on the east side of the rift escarpment. Prior to 1943 when the area became a Game Reserve there was more extensive human settlement in the Park which resulted in some modifications of the vegetation (see Wrangham, 1975, p.2.1).

Since 1962 the chimpanzees have been provisioned with bananas, which greatly facilitated their habituation to human presence (van Lawick-Goodall, 1968, p. 166). Wrangham (1974) described the methods of artificial provisioning and how they have changed over the years. During 1972-75 chimpanzees were fed only occasionally, each individual receiving 7-10 bananas once every 7 days, at maximum, and once every 10 days on average. All provisioning took place in Camp, a cleared area of approximately 1,500 sq. metres, about 500m from the lakeshore, in Kakombe valley, see Plate 2.1. Bananas were fed to the chimpanzees through hatch doors in a sunken trench, see Plate 2.2.

Standardised records were kept of the attendance and behaviour of chimpanzees visiting Camp, and with rare exceptions at least one observer was present from 07.00 to 18.00, each day. The frequency of visits by individual chimpanzees to Camp varied considerably and has declined substantially since the reduction in provisioning (see Wrangham, 1974). Some individuals still visited 2-4 times per week but others could not be depended on to visit Camp more than 2-4 times per month. Wrangham (1975, chapter 6) discussed the influence of Camp on the ranging patterns of the chimpanzees.

2. The Study Population

An accurate census of the total chimpanzee population of the Gombe National Park has yet to be carried out. Van Lawick-Goodall (1968) estimated there to be between 100-150 chimpanzees in the Park, divided into at least 4 communities. These communities can be spatially and socially distinguished although they are neither reproductively nor behaviourally isolated as females transfer between them (Pusey, in press) and behavioural interactions occur (Goodall *et al*, in press).

The habituated chimpanzee population comprised two neighbouring

Plate 2.1 A view of Camp, showing the banana trench and research buildings.

Plate 2.2 Mike receives bananas from the trench.

Table 2.1. The Kasakela Community, November 1972 - February 1975.

FEMALES

Name (Initials)	Age Class
*SPROUT (SP)	OLD
PASSION (PS)	ADULT
MELISSA (ML)	
NOPE (NP)	
ATHENA (AT)	
PALLAS (PL)	
*NOVA (NV)	
GIGI (GG)	
MIFF (MF)	
FIFI (FF)	
DOVE (DO)	
WINKLE (WK)	
SPARROW (SW)	
GILKA (GK)	
**LITTLE BEE (LB)	
PATTI (PI)	ADOLESCENT
HARMONY (HR)	
POM (PM) m. PS	
|	
SPRAY (SY) m. SP	JUVENILE
MOEZA (MZ) m. MF	
SKOSHA (SS) m. NV	
GREMLIN (GM) m. ML	
|	
DOMINIQUE (DM) m. DO	INFANT
APHRODITE (AP) m. AT	
LOLITA (LO) m. NP	
SWALLOW (SA) m. SW	
VILLA (VL) m. PL	

MALES

Name (Initials)	Age Class
HUGO (HG)	OLD
MIKE (MK)	
HUMPHREY (HM)	
|	
FABEN (FB)	ADULT
EVERED (EV)	
FIGAN (FG)	
JOMEO (JJ)	
SATAN (ST)	
|	
SHERRY (SH)	
GOBLIN (GB) m. ML	ADOLESCENT
|	
MUSTARD (MU m. NP	
ATLAS (AL) m. AT	JUVENILE
BEETHOVEN (BE)	
FREUD (FD) m. FF	
|	
PLATO (PT) m. PL	INFANT
PROF. (PF) m. PS	
WILKIE (WL) m. WK	
MICHAELMAS (MM) m. MF	
GANDALF (GD) m. GK	

| = Transitional age-stage

* = Peripheral female who probably associates with males of another community.

** = Little Bee is considered a member of the Kahama community but made temporary visits to the Kasakela community.

m. - Mother

communities, Kasakela (also referred to as Northern) and Kahama (Southern). During the 1960's these two intermingled peacefully and were not recognised as distinct communities, but after a gradual process of fission they separated (see Bygott, 1974) and by the beginning of the present study, November 1972, the division was complete. The focus of the present study was the Kasakela community but included females from other communities who associated with the Kasakela chimpanzees. All individuals who were members of the Kasakela community for all, or part, of the study period are listed in Table 2.1. The use of the age-class terms, infants, juveniles, adolescents, adults and old, corresponds to van Lawick-Goodall (1974) and roughly represents the ages 0-5 (birth to weaning), 6-9 (weaning to puberty), 9-14 (puberty to the attaining of full adult size), 14-30 (full adult size) and 30+ (obvious signs of aging - weight and hair loss etc.).

During the study period there were changes in the composition of the Kasakela community due to births, deaths, immigrations and emigrations, see Table 2.2.

Table 2.2 Changes in the study population during the period November 1972-February 1975.

Births:	Aphrodite	June 1973	Deaths:	Plato	April 1973
	Lolita	June 1973		Gandalf	June 1974
	Michaelmas	Oct. 1973		Hugo	Jan. 1975
	Swallow	Oct. 1973		Mike	Feb. 1975
	Villa	April 1974			
	Gandalf	June 1974	Immigrations:		
Emigrations:				Patti	Nov. 1973
				Harmony	Sept. 1974
	Gilka - Nov. 1972 - May 1973, with Kahama community.			Beethoven	Sept. 1974
				Little Bee - periodic visits.	

3. Observation Methods

16 months were spent collecting data at the Gombe Stream Research Centre, November 1972-July 1973; October 1973-February 1974 and December 1974-January 1975. During this time 1192.5 hours of observation was made on a total of 11 females. The degree of habituation of the majority of members of the Kasakela community allowed a human observer to follow and observe at close range, individual chimpanzees for prolonged periods. In this study a single individual was selected as a target and each period of observation was designated a follow. The aim of the study was to gain an understanding of the sexual behaviour and mating systems of wild chimpanzees and to maximise the chances of observing relevant behaviour, only females showing cycles of sexual swelling were selected as targets. Table 2.3 shows the community females, who, during the study period, showed cycles of sexual swelling and the observation hours for each one.

Table 2.3. Females who showed cyles of sexual swelling during the study period, Nov.'72-July'73; Oct.'73-Feb.'74 and Dec.'74-Jan.'75.

Female	Period during which swelling cycles shown	Observation Hours: at no swelling	Observation Hours: at maximal tumescence
NOPE	Nov. 1972	0	0
ATHENA	Nov.'72-Jan.'73	0	26.5
MIFF	Nov.'72-Mar.'73	8	57.5
SPARROW	Nov.'72-July'73 & Dec.'74	13	120.5
GIGI	Nov.'72-Jan.'75	58.5	243.5
LITTLE BEE	Nov.'72-Jan.'75 (periodic)	4	86
PALLAS	June '73-Nov.'73	190	147.5
GILKA	June '73 & Dec.'74	36.5	0
NOVA	Oct. '73	5	0
MELISSA	Oct. '73	13	55.5
SPROUT	Dec. '73	0	6.5
PATTI	Dec. '74-Jan. '75	38.5	82
	TOTAL	366.5	826

Total Observation Hours - 1192.5

Follows were initiated in one of 3 ways:

1) Individuals who visited Camp were followed when they left;

2) If the location of an individual's night nest was known, a follow could start by going to the nest at dawn (un-nesting);

3) Individuals could be found by searching within the range. Locating chimpanzees in this manner was facilitated by their loud vocalisations and by a knowledge of their movements on previous days.

Once initiated, a follow continued for as long as possible (until nesting or until the target individual was lost) or for a predetermined number of hours. As can be seen from Table 2.3 observation was heavily biased towards females in the maximal tumescent phase of their cycle.

Observations were tape recorded in the field and later transcribed onto two checksheets; the specialised copulatory behaviour checksheet and the more general activity and distance checksheet. Copulatory behaviour was recorded continuously using a glossary of 60 behaviour patterns, see Appendix 1. Data was collected and transcribed onto the checksheet in such a way as to preserve the sequence in which the behavioural elements occurred. A total of 1084 copulatory sequences were recorded in this way.

The activity of the target female was recorded on the minute every 5 minutes. The following activity categories were used:

Feed: Have food in mouth or be in the process of picking or transferring it to the mouth.

Travel: Locomotion along the ground or through the trees.

Rest: Immobile, sitting or lying on the ground or in a tree whilst not engaged in feeding or grooming.

Social grooming: Hand(s) and/or mouth manipulating the hair of another chimpanzee, or vice versa.

Self grooming: Hand(s) and/or mouth manipulating own hair.

Sexual behaviour: Involved in courtship or intromission.

Aggressive, submissive and reassurance behaviour (ASR): Performing behaviour patterns in these contexts, for definitions of individual behaviour patterns, see Bygott (1974, pp. 54-67).

The distance of all other individuals from the target female were also recorded on the minute every 5 minutes, using the following categories:

1 - in contact with the target female,
2 - within 1.5m of the target female, not in contact,
3 - between 1.5 and 5m from the target female,
4 - between 5 and 15m from the target female,
5 - greater than 15m from the target female but within sight.

As previously mentioned sexual behaviour was recorded continuously. Grooming, ASR and vocalisations involving the target female (including her response to all pant hoots given by others) were also recorded continuously. On all follows the observer was accompanied by a Tanzanian field assistant who collected standardised data on group composition, travel patterns and feeding behaviour, using a data sheet and map called the Travel and Group Chart.

4. Sampling Problems

Because the behaviour of interest to the study was concentrated at particular times. i.e. during the swelling cycle phase of maximal tumescence, sampling was biased. Collection of data was concentrated during this phase and subsequently it was impossible to control adequately for all the variables which may have been acting. The selection of target individuals was rarely a problem as it was uncommon for more than one female to be simultaneously maximally tumescent. When this situation did arise the female on whom least data had been collected was selected. Follow length and the decision on when to terminate an observation period, was another potential source of bias. A positive effort was made to reduce this but it was not possible to exclude such bias completely, as the observer's motivation to stay with a target chimpanzee was undeniably reduced by factors such as particularly inhospitable weather, terrain or vegetation. It was also true that observation would continue beyond the predetermined endpoint if something of special interest, e.g. consort formation, occurred. Consequently no effort will be made during data analysis to assess accurate frequencies of rare events such as consorting, as considerable effort was made to include as much observation on such events as was possible.

Table 2.4 shows the distribution of observation over the hours of the day. The low value at dawn and dusk represent variation in the times that the chimpanzees left and entered their night nests.

Table 2.4. Distribution of observation over the daylight hours

Hour	¼ hours of observation	% of total observation
06-07	43	1.8
07-08	142	5.9
08-09	179	7.5
09-10	217	9.1
10-11	242	10.1
11-12	265	11.1
12-13	239	10.0
13-14	210	8.8
14-15	219	9.2
15-16	215	9.0
16-17	177	7.4
17-18	136	5.7
18-19	91	3.8
19-20	13	.6
	2388 = 1192.5 hours	

Whilst the distribution is not completely even, variation is small and correction for differential observation hours is made when considering frequency of behaviours known to be affected by circadian rhythms.

5. Statistics

Non-parametric statistics (Siegal, 1956) are used throughout. All probabilities are two-tailed and only given at the .05, .01 and .001 levels.

6. Methodological Problems

i. Bias of data

The scope of the study meant that only a small proportion of the Kasakela community chimpanzees were observed as target individuals and these were all females showing cycles of sexual swelling. Observation was further restricted in that females were predominantly followed during their periods of maximal tumescence. All the other individuals were frequently encountered, but their behaviour was only recorded when they interacted with the target females. These biases in data collection mean that the picture of the behaviour of individual chimpanzees was, at best, composed from blocks of intensive observation, preceded and succeeded by gaps where little observation was made (cycling females), and at worst, sketchy and more or less limited to interactions with cycling females.

The dangers of interpreting behaviour from a limited sample of interactions have been pointed out by Hinde (in press). He stressed the need to understand relationships between individuals on a broad basis by observing the quality, quantity and patterning of interactions between individuals in order to gain a meaningful picture of a species' social behaviour. Such an approach is impossible from the limited data collected in a single study which concentrates on one aspect of behaviour, and consequently on a limited sample of the total types of interaction possible. Partial compensation for this shortcoming can be made in this case as other researchers were observing and collecting data on the Kasakela chimpanzees before, during and after the present study. This gives continuity over time and also adds considerable breadth as other researchers focused on different aspects of behaviour, and hence on other types of interaction.

In the relevant sections of analysis and interpretation, my own data are supplemented by those collected by other Gombe researchers. Much of the relevant data is as yet unpublished but has been made available to me in pre-publication form. Such data is gratefully acknowledged in the appropriate parts of the text.

ii. Interpretation of data

The behaviour of animals can be described in objective terms, but the 'coldness' of objectivity is difficult to maintain when one comes to know individual animals through long association. In parts of the text subjective, anthropomorphic, terms are used to complement objective description, not out of sentimentality but because the objective terms in isolation do not always suffice. As Hinde (1974, p.6) said - "Knowledge of human behaviour, if used with discipline, can sometimes give us increased understanding of that of animals. Students of animal behaviour are so aware of the horrors of anthropomorphism that they sometimes shy away from the most interesting aspects of their subject matter: the over-simple view they get could be corrected by a little disciplined indulgence." Care has been taken not to confuse the two levels of description, and the subjective content adds to rather than substitutes for quantitative data.

CHAPTER 3

LIFETIME REPRODUCTIVE PROFILES

1. Introduction

For a complete understanding of the sexual behaviour, mating system and reproductive biology of a species, it is important to place events in the perspective of individual reproductive life histories. No studies of wild nonhuman primates have continued long enough to follow known individuals through complete typical lifespans, and thus hypothetical reproductive life histories must be constructed by piecing together information on a number of different individuals of known or estimated ages. Data from groups of captive primates are of limited value as they are only rarely kept in social groups of composition approximating that of their wild counterparts. Even if this is achieved space is often very limited and behaviour is distorted by such practices as convenience feeding on un-natural diets. Infants are often removed from their mothers at birth, or before they would normally be weaned, thus affecting variables such as birth interval.

This chapter presents data from 15 years of observation of chimpanzees in the Gombe National Park. The data were collected by observers too numerous to acknowledge by name. Standard measures were used, and due to the considerable overlap between individual observers, reliability is considered high. Jane Goodall initiated and supervised the accumulation of long-term records, and Pat McGinnis systematised the regular and reliable recording of female swelling cycle states.

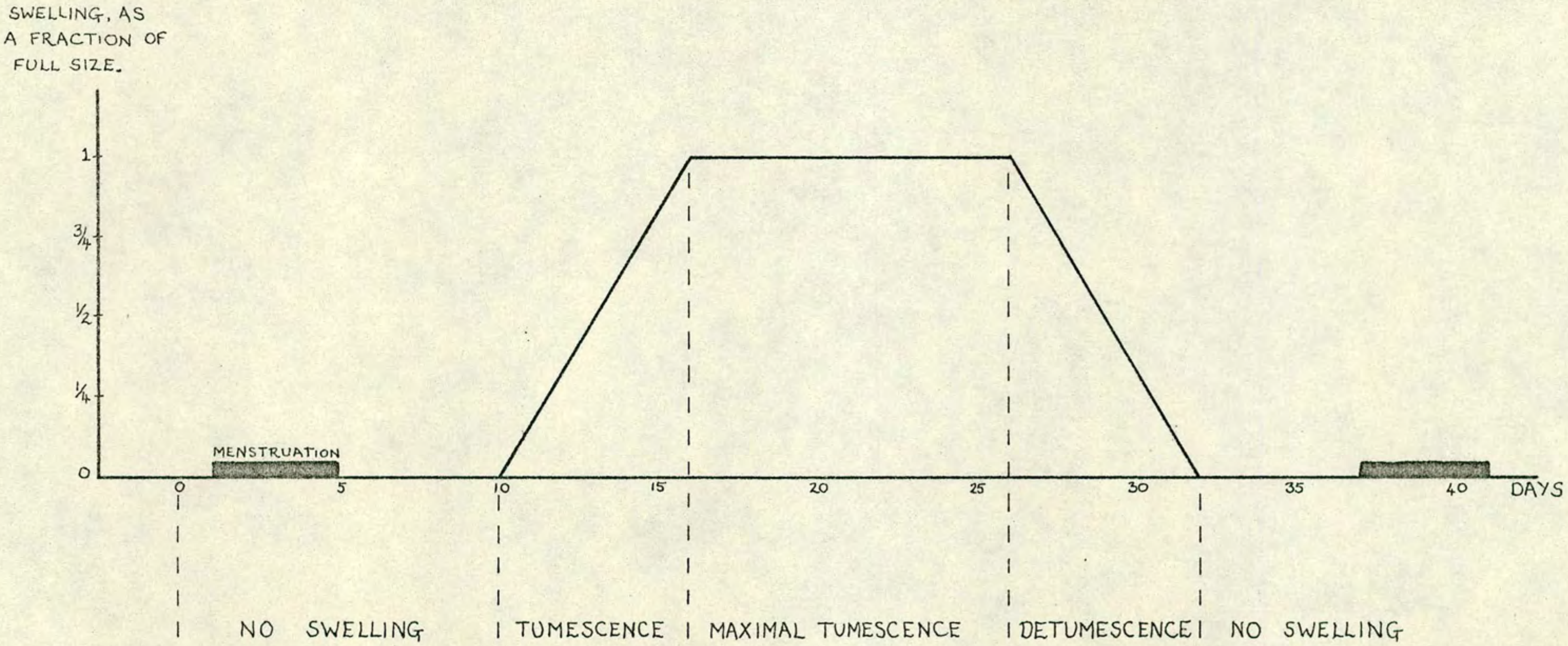
Even 15 years of continuous data do not give a complete picture and some of the conclusions may require modification as more data on known aged individuals become available. The basic data on the theoretical reproductive potentials of females and males and the realised reproductive contributions of individuals, give a better understanding of chimpanzee population dynamics. This allows better assessment of the evolutionary implications of the variable nature of the chimpanzee mating system and of the selective pressures operating to maintain the current situation.

2. Female Cycles

The cycle of sexual swelling of female chimpanzees has been described in detail for both captive individuals housed in cages (Tinklepaugh, 1933; Yerkes & Elder, 1936; Young & Yerkes, 1943; Erikson, 1963; Graham, 1970); captive individuals living in large outdoor enclosures (Tutin & McGrew, 1973); and wild chimpanzees (van Lawick-Goodall, 1968, 1969; McGinnis, 1973). The swelling cycle can be divided into 4 phases, no swelling (during which menstruation, if it occurs, is observable), tumescence, maximal tumescence and detumescence. Figure 3.1 shows a prototypical swelling cycle with the mean duration of the four phases (after Graham, 1970).

There is no evidence that captivity *per se* affects the time course of the swelling cycle. Young & Yerkes (1943) presented data from 653 complete cycles of 22 intact females ranging in age from 9 to 29 years. The mean length of the cycle was 37.3 days, the total range being 22 to 187 days. McGinnis (1973) found that the mean cycle length was 38.8 days (range 31 to 50 days) in a sample of 17 cycles of 3 wild nulliparous females. In both these studies cycle lengths were measured from one menstruation to the next. In the present study observation conditions were not ideal and menstruation could not be consistently recorded. It was only possible to estimate cycle lengths

Figure 3.1 Prototypical swelling cycle (after Graham, 1970).



with an accuracy of ± 2 days as females were not observed each day. For 29 non-pregnant cycles shown by 6 females, 3 young and 3 fully mature, the mean cycle length was 34.1 days with a range of 25-84 days, the median cycle length was 33 days.

Age is known to be an important variable affecting cycle length (Young & Yerkes, 1943), with young females showing longer cycles than older ones. This finding appeared to be substantiated by the present study but there were insufficient data for statistical confirmation.
Young and Yerkes (1943) found that during the first two years of cycling the no swelling, tumescent, and maximal tumescent phases became shorter while the detumescent phase increased in length, the overall result being a reduction in cycle length.

The swellings of all females show remarkable changes in size during the cycle although inter-individual variation can also be great. At full swelling the perineal area around both vagina and anus is distended and bright pink in colour. The volume of the swelling at maximal tumescence has been measured as 938 cc (Erikson, 1963) and 1400 cc (Yerkes & Elder, 1936). The perineum of a cycling female in the no swelling phase differs obviously from that of a non-cycling, lactating female. During the last stages of pregnancy and sometimes for a few months after parturition, the perineum has a flabby appearance, i.e. some pink skin is visible but there is no turgescence. During lactation little pink skin is visible and the perineum is tightly wrinkled and retracted. Whilst individual differences mean that the cycle phase of a female can only accurately be assessed by observers familiar with the whole cycle, it is usually possible to tell from only brief observation what a female's reproductive state is, because of the distinct appearances of the perineum of cycling females, females in late pregnancy and non-cycling, lactating females. There is no immediate change in the appearance of the perineum at conception, and females continue cycling for varying lengths of time into pregnancy (see below).

3. Endocrinology

The chimpanzee sexual swelling is probably the result of interstitial fluid accumulation, although the possibility that active tissue proliferation also takes place has not been excluded (Graham, 1970). The swelling appears to be under the control of ovarian hormones since the administration of estrogen to ovariectomised females induced swelling (Zuckerman & Fulton, 1934; Clark, 1947; Clark & Birch, 1948). More sophisticated hormone administration experiments by Graham *et al* (1972) indicated that tumescence of the swelling is associated with secretion or administration of estrogen while detumescence is associated with withdrawal of estrogen, and/or secretion or administration of progestin.

4. Time of Ovulation

Elder (1938) conducted a series of controlled mating experiments in which female chimpanzees were given access to a male on a single day of the cycle. He found that conception occurred only when the female had been mated during the last 6 days of the maximal tumescent swelling phase. He concluded therefore that ovulation occurs during the latter half of this phase. Young and Yerkes (1943) concluded from examination of chimpanzee ovaries that ovulation occurred just prior to the onset of sex skin detumescence.

In a study of the fluctuations in levels of serum FSH and LH during the menstrual cycle, Howland et al (1971) found that a surge of LH, which in humans would indicate ovulation, occurred 4-7 days before detumescence in a sample of 3 cycles. Graham (1973) reported a detailed study of changes in endometrial histology of chimpanzees during the menstrual cycle. He found that the earliest secretory changes detectable, i.e. the appearance of basal vacuolisation, usually occurred 24 hours after the beginning of detumescence. In women, secretory changes are thought to develop 36-48 hours after ovulation, due to the effect of progesterone on the estrogen-primed endometrium. If the interval is approximately the same in the two species, Graham concludes that ovulation in the chimpanzee occurs just prior to the onset of detumescence.

Thus, although the exact time of ovulation in relation to the sexual swelling may vary somewhat, the evidence suggests that ovulation occurs in the latter part of the phase of maximal tumescence, probably one or two days before detumescence begins.

5. Reproductive Development

i. Females

Accurate data on the time course of reproductive development in wild female chimpanzees is not yet available, as no female of known birth date has yet reached menarche. The oldest female whose birth date is known, Pom, began to show the first signs of sexual swelling in 1975, when she was almost 10 years old. Judging from the pattern of development observed in wild females of unknown birth date (McGinnis, 1973, p.23) it will be a further 2-3 years before Pom has full sized swellings and reaches menarche.

Chimpanzees born and reared in captivity seem to reach menarche earlier than their wild counterparts. Young & Yerkes (1943) found the mean age at menarche of 7 such females to be 8 years 11 months (range 7 years 4 months to 10 years 2 months). For 11 wildborn females raised in captivity from an early age, they estimated age at menarche to average 8 years and 3 months (range 7 years to 9 years 6 months). Smith et al (1975) estimated mean age at menarche for 6 wild born/captive raised females to be 8 years 9 months (range 7 years to 10 years 9 months). Pom's projected age at menarche would fall outside the range of all the captive females. Captive chimpanzees grow faster and weigh considerably more as adults than do wild chimpanzees, probably as a result of a relatively high protein diet in captivity. The weight difference does not result from obesity in the captive animals, as all body proportions are increased. The mean weight at maturity of chimpanzees at the Holloman Air Force Base consortium was 65.6 ± 5.9 kg. for males (N=11) and 56.8 ± 2.0 kg. for females (N=6) (Smith et al, 1975). At Gombe the mean weight for mature adult males (excluding aged males) was 42.3 ± 4.2 kg. (N=5), data from Wrangham (1975, p. 369). Data on adult females are harder to obtain as these females are almost always accompanied by a dependent offspring when weighed. However, an estimation of an average mature female weight would be between 32-37 kg.

A relationship between age at menarche, body weight and level of fatness has been demonstrated in humans (Frisch, 1974), and it seems likely that a similar relationship exists in chimpanzees. The mean weight at menarche for female chimpanzees in captivity is 29.1 ± 4.2 kg. (N=6) (Smith et al, 1975) corresponding to a mean age of 8 years 9 months. At 9 years 6 months Pom weighed only 20.9 kg. Although data are scarce it seems likely that wild chimpanzees at Gombe weigh approximately the same as the captive chimpanzees at menarche but because of slower growth rates this weight is not achieved by the Gombe chimpanzees until an age of 11-12 years.

The sexual swelling reaches full size some months prior to menarche (McGinnis, 1973, p.22) and once full swelling size is achieved the females are attractive and receptive to adult males. Before this young females are mated frequently by infant and juvenile males during their periods of swelling and are actively cooperative, often initiating sexual interactions by soliciting (van Lawick-Goodall, 1968; Pusey, pers. comm.).

The interval between menarche and the time when the female becomes capable of carrying the foetus to term has been designated the period of adolescent sterility (Hartman, 1931; Ashley-Montagu, 1939; Young & Yerkes, 1943). Young and Yerkes (1943) found that for chimpanzees in captivity the mean period of adolescent sterility lasted 11.3 months (N=7, range 4-17 months). The interval between menarche and the first conception leading to the birth of a live infant is known for 4 females at Gombe, see Table 3.1.

The pregnancies of the 4 females in Table 3.1 all resulted in the birth of a live infant, although Gilka's infant survived only 2-3 weeks. Of 4 other females who transferred into the Kasakela community after menarche one, Sparrow, conceived after 14 cycles of sexual swelling and gave birth to a live infant; the other three (Athena, Pallas and Nova) were each judged to have had one terminated pregnancy before giving birth to live young. Little Bee, a member of the neighbouring Kahama community, is believed to have had a pregnancy, but it is not known whether it resulted in the birth of a live infant who died

Table 3.1 Length of the period of adolescent sterility of 4 wild chimpanzee females

Female	Months between menarche and 1st conception leading to live birth	Number of cycles between menarche and 1st conception leading to live birth
MIFF	13	10
FIFI	34	27*
WINKLE	30	20
GILKA	28	18*
MEAN	26.25 months	18.75 cycles
MEDIAN	29 months	19 cycles

* Fifi and Gilka both transferred to other communities for part of this period and so cycle numbers are estimates.

shortly after birth or whether her pregnancy terminated before parturition. One female, Gigi, appears to be sterile. She reached menarche in 1965 and has shown regular cycles of sexual swelling for 10 years with no sign of conception.

Given a tentative estimate of age at menarche of 11-13 years, this means that a typical female at Gombe would not give birth until she was 13-15 years of age. Captive raised females give birth for the first time between 10 and 11 years of age (Young & Yerkes, 1943; Smith _et al_, 1975). Continued observations of the development of individuals of known birth data at Gombe should clarify the exact ages at which menarche and first birth occur in wild females.

During the period of adolescent sterility the females are attractive and receptive to adult males during their phases of maximal tumescence, and are mated frequently. The reason why they do not conceive seems therefore to be physiological. It appears likely that the onset of ovulation does not coincide with menarche and that the lag between these two developmental stages is responsible for the period of adolescent sterility. Corner (1923) demonstrated that menarche in female rhesus monkeys is followed by a period of relative infertility when many cycles are anovulatory. It is also known that the same phenomenon exists in humans, with menarche being followed by anovulatory cycles (Halewijn & de Waard, 1968; Doring, 1969). In well nourished human populations the period of adolescent sterility lasts about 3½ years but in undernourished populations the interval between menarche and conception resulting in live birth may be 4½-5 years (Frisch, 1974). There is no direct evidence from the chimpanzee that the cycles following menarche are anovulatory. The short duration of the period between onset of detumescence and menstruation which are common just after menarche (see Figure 3.2) may indicate anovulatory cycles. Young and Yerkes (1943, p. 128) found that if this phase of the cycle (which they named the postswelling phase) was longer than 6 days conception could occur, and surgery on one female revealed that ovulation had occurred in a cycle with a postswelling phase of 6 days.

Thus in chimpanzees, as in other primates studied, menarche does not mark the onset of fertility in females but is a developmental stage which precedes the ability to conceive and carry a foetus to term, by a period of 4-34 months. The intervening period of adolescent sterility is characterised by cycles of sexual swelling which are longer than those shown by fully mature females (Young & Yerkes, 1943; van Lawick-Goodall, 1968, p. 216). During the phases of maximal tumescence these young females are mated frequently by adult males but do not become pregnant. This is almost certainly due to the absence of ovulation. Of a sample of 9 young females at Gombe, 5 gave birth to live young at the end of their first pregnancies, while for the other 4, the first pregnancy was terminated by abortion or miscarriage.

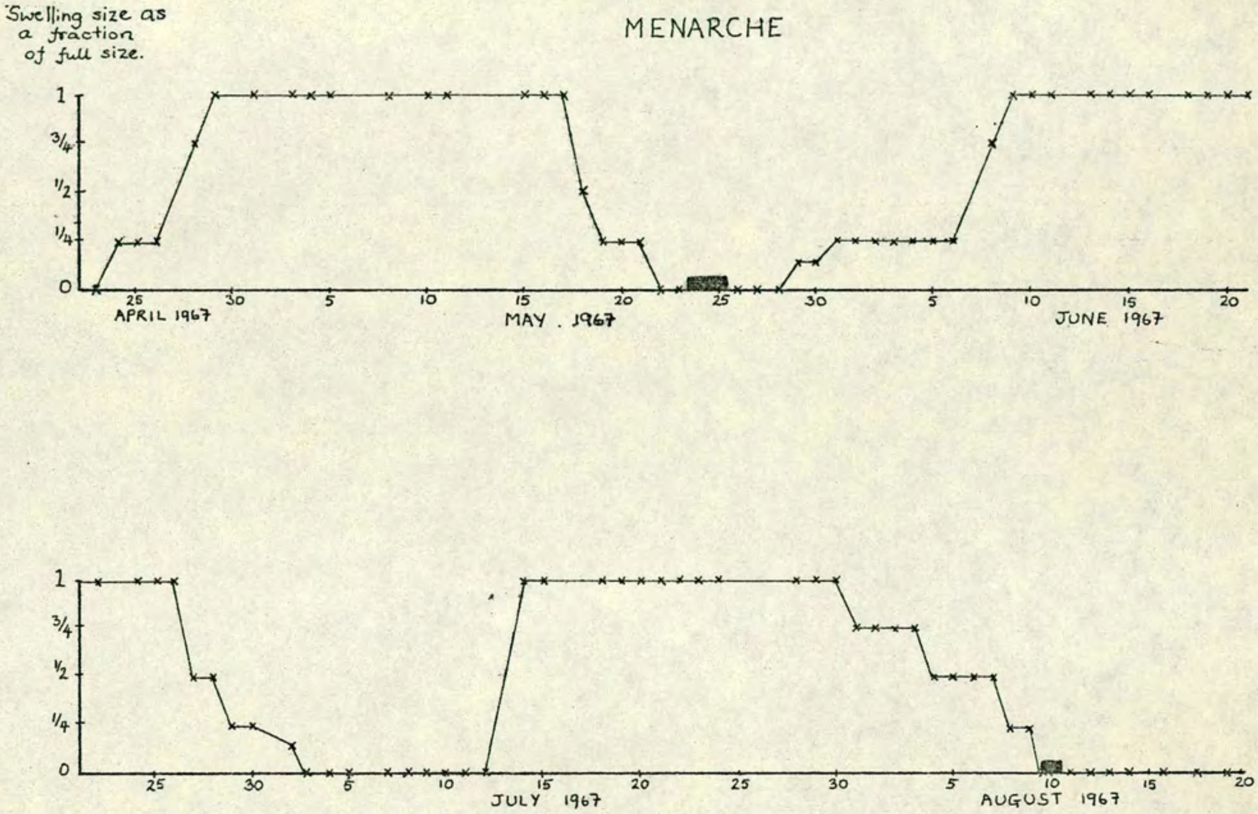
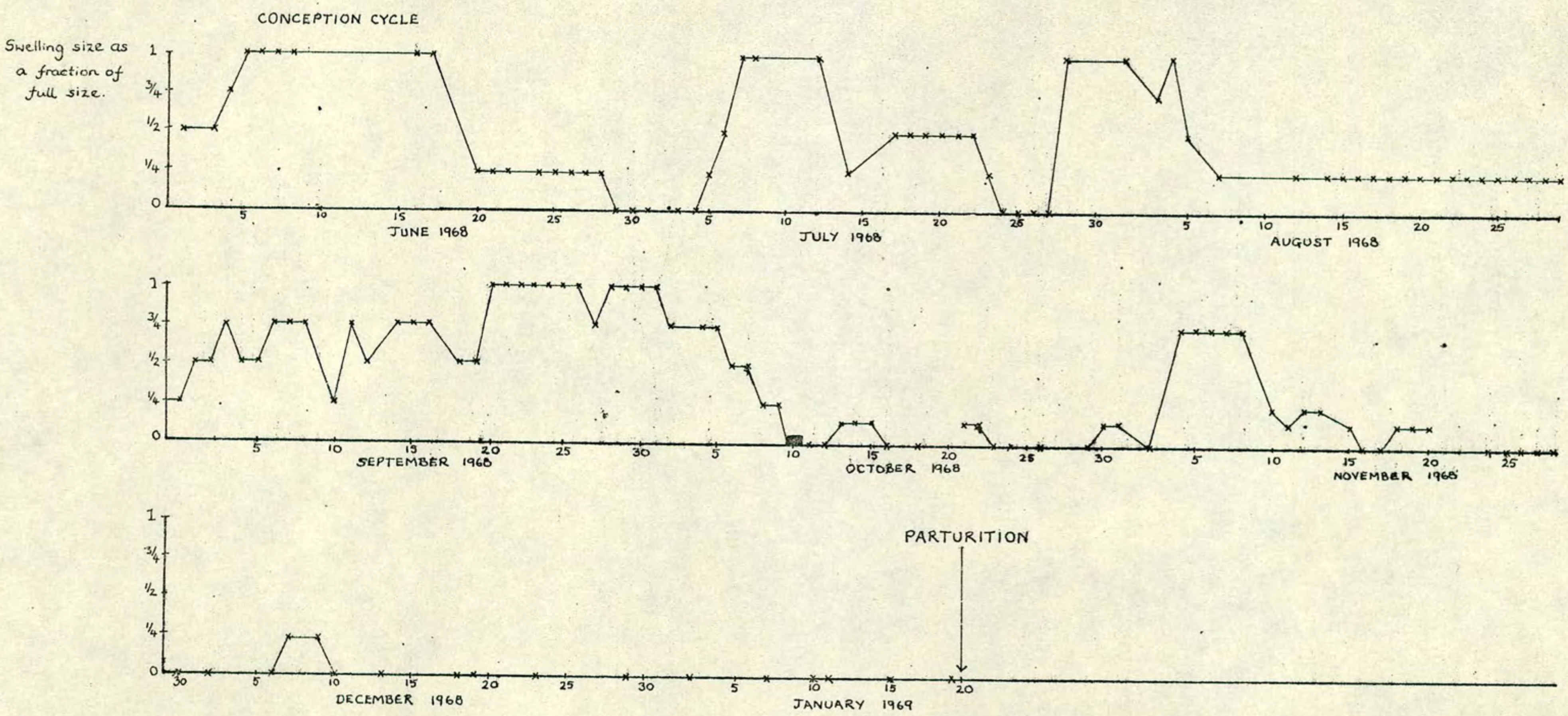


Figure 3.2 a) Miff's swelling cycles at, and just after menarche. Note long maximal tumescent phases and also that menstruation occurred very early in the no-swelling phase, possibly indicating anovulatory cycles.

Figure 3.2 b) Miff's conception and subsequent post-conception cycles. Bleeding occurred on October 10th, four months after conception.



Young and Yerkes (1943) reported that 7 of 13 females gave birth to live young at the end of their first pregnancies, while for the other 6, first pregnancies terminated in abortion or stillbirth. It is possible that some females at Gombe became pregnant earlier than the first recorded pregnancy. There is no obvious external indicator of conception and normal cycling can continue during pregnancy, so a pregnancy terminated in the first few months might go undetected.

ii. Male Reproductive Development

Male chimpanzees born and/or raised in captivity reach puberty at an age of 7 years 2 months ± 11 months (Smith et al, 1975) when they weigh 27.8 ± 5.8 kg. Goblin is the only known aged male at Gombe to have reached puberty. His testes descended during late 1972 - early 1973 and he was first observed to ejaculate in November 1973, at an age of 9 years 2 months when he weighed 21 kg.

6. Sexual Cycles during pregnancy

The mean length of gestation (conception to parturition) in the chimpanzee is 228 days (N=47, range 202-248 days) (Nissen & Yerkes, 1943). In some species of primates external indicators of pregnancy exist, for example in olive baboons (Papio anubis) the female's perineum turns a characteristic dark red soon after conception (Altmann, 1973) and in female patas monkeys (Erythrocebus patas) facial colouration changes during pregnancy (Loy, 1974). During 18 pregnancies at Gombe all 10 females continued to show some sexual swelling after conception. In all but one case (Gilka) this included at least one complete cycle, i.e. a cycle in which maximal tumescence was reached and maintained for several days, although many cycles showed atypical time courses. The mean number of complete cycles shown was 1.5 (N=18, range 0-6), and all females also showed irregular fluctuations of the sexual swelling which could not be described in terms of normal cycles (see Figure 3.2). In most cases the sex skin ceased fluctuations and remained nonswollen during the 2-4 months before birth, but one female (Sparrow) showed a complete cycle only one month prior to parturition. Nissen and Yerkes (1943) found a mean of 1.3 post conception cycles in 29 pregnancies of captive chimpanzees, with a range of 0-4 complete cycles. The hormonal basis of these post-conception swelling cycles is poorly understood (Graham, 1970). Hormonal changes during pregnancy in the chimpanzee have been described (Boorman, *et al*, 1974; Reyes *et al*, 1975) but have not been related to sexual swelling.

In some females the abdomen becomes obviously distended during the final months of pregnancy but in others there is little or no visible change. In the final weeks before parturition the breasts become somewhat enlarged and this is particularly noticeable in the first pregnancy. Menstruation ceases after conception, but poor observation conditions preclude the absence of menstruation as a useful indicator of pregnancy in wild chimpanzees. Very rarely bleeding is observed during pregnancy (see Figure 3.2) but the cause of this is unknown.

During phases of maximal tumescence occurring immediately after conception females are attractive and receptive to adult males. However during phases of maximal tumescence late in pregnancy, attractiveness decreases and copulations with adult males become rare. A similar low level of attractiveness was observed during initial post-partum cycles occurring when the female was still lactating (see below).

7. Frequency of incomplete pregnancies

The problems of accurately diagnosing pregnancy at an early stage preclude a completely reliable assessment of the proportion of conceptions which result in live birth. However the cycle features described above: irregularity, reduced attractiveness and, in the later stages, cessation of swelling, provide sufficient clues that a familiar observer usually suspects pregnancy in the first two months and is certain by the fourth. Direct evidence of abortion or miscarriage is rare. In most cases termination of pregnancy was inferred from the indirect evidence of a female, believed to have been pregnant, resuming normal cycles. During the 10 year period 1965-1974 there were 32 known pregnancies of which 23 (72%) resulted in the birth of a live infant. The 9 incomplete pregnancies almost certainly are an underestimate, because of the problems already discussed in early recognition of pregnancy. Of the 9 females whose first pregnancies were observed, 5 gave birth to live young while 4 did not. This suggests a higher probability of failure with first pregnancies than with subsequent ones.

8. Lactational amenorrhoea.

In humans there is usually an interval of some weeks between parturition and the reappearance of menstruation, and this interval is longer in lactating than non-lactating women. The period of amenorrhoea in wild chimpanzees is difficult to assess accurately since menstruation cannot be reliably scored as present or absent. If the infant survives, its mother's swelling cycles are suppressed for a considerable period and although not exactly equivalent, the interval between parturition and the next occurrence of maximal tumescence approximates to the period of lactational amenorrhoea.

For 9 females at Gombe the mean latency to maximal tumescence after a birth was 40.4 months (N=10, range 11-81 months). Only one female became pregnant in the first post-partum cycle, indicating that like humans, the first cycles following parturition are frequently anovulatory (Sharman, 1951).

Women who do not breastfeed their infants usually remain amenorrheic for a period of 8-12 weeks after parturition (Sharman, 1951). The duration of amenorrhoea in lactating women appears to be dependent on the length of time the infant suckles, the level of nutrition of the mother and possibly other social factors. For urban, well nourished women, lactational amenorrhoea persists for 5-6 months (Peckham, 1934; Stix, 1940). In rural, under nourished women, the interval can last for 10-14 months (Baxi, 1957; Dandekar, 1959). Bonte et al (1974) found striking differences in the intervals between parturition and the next conception of rural and urban lactating women in Rwanda. They found that in amenorrheic, lactating women a new pregnancy typically occurred 16 months earlier in the urban living women than in those living in rural areas. The median interval between parturition and conception being 5 months in the former and 21 months in the latter. There was no significant difference in this interval between rural and urban non-lactating women and the authors concluded from this that nutritional factors were not the critical factor. Differences in maternal behaviour existed: the rural mothers gave their infants free access to the breast and carried them on their backs all the time, whilst the urban women had less contact with their infants and fed them on a more-or-less regular time schedule. Whilst it is possible that differences in lactational behaviour contribute to the delay in conception of the rural women, nutritional factors cannot be discounted as the added nutritional load of lactation may have been sufficient to delay the return of menstrual cycles in the poorly nourished rural women. Lactational amenorrhoea appears to be responsible for the 4 year birth interval among women of the !Kung hunter-gatherers of the Kalahari Desert (Howell, cited in Kolata, 1974).

No detailed information is available on the duration of lactational amenorrhoea in chimpanzee females living on high-protein diets in captivity, as in the majority of cases, infants are removed from their mothers soon after birth. However, there is some indication that the interval between parturition and the first phase of maximal tumescence is reduced in some cases. A female at the Edinburgh Zoo reached maximal tumescence only 3 months after parturition but two other females in the Zoo have not yet resumed swelling cycles at 6 and 13 months post-partum. Nissen and Yerkes (1943) reported that a female who was allowed to nurse her infant for 12 months resumed sexual cycling 6 months after parturition.

9. Number of non-pregnant cycles between successive conceptions

The median number of complete cycles occurring in the interval between parturition, or earlier termination of pregnancy, and the succeeding conception was 3.6 (N=14, range 1-11) - see Table 3.2. There appeared to be a difference between the number of cycles occurring between the 1st and 2nd pregnancies and the number between subsequent pregnancies. A median of 5.0 nonpregnant cycles occurred between the first and second pregnancies of seven females (range 3-11) while between subsequent pregnancies the median was 2.0 (N=7, range 1-7). This difference is statistically significant: Mann Whitney U=5, $n_1=7$, $n_2=7$, $p<.01$). The difference might be a result of maternal age or of "pregnancy experience".

It seems likely that early post-partum cycles are anovulatory in

Table 3.2 Number of non-pregnant cycles shown by chimpanzee females between successive conceptions

1st to 2nd conception	2nd to 3rd conception	3rd to 4th conception	4th to 5th conception
5 (Miff)	3 (Pallas)	7 (Athena)*	2 (Athena)
11 (Pallas)	1 (Athena)*		1 (Flo)
3 (Athena)	2 (Melissa)		
10 (Melissa)*	3 (Passion)		
8 (Nova)			
3 (Gilka)			
4 (Nope)			
MEAN: 6.3 (N=7)	2.3 (N=4)		

COMBINED MEAN: 4.5 (N=14)

* Pregnancies ending in miscarriage or stillbirth.

in chimpanzees, as is the case for humans (Sharman, 1951). Sharman found that the proportion of anovulatory cycles decreased progressively after the first post-partum cycle, the percentages of anovulatory cycles being 64% for the first, 29% for the second and 19% for the third post partum cycle. He also found that first cycles occurring soon after parturition were more likely to be anovulatory than first cycles occurring later. The data from the Gombe chimpanzees would seem to indicate that patterns of post partum ovulation are similar. There is a trend towards an inverse relationship between the length of lactational supression of cycles and the number of complete cycles before the next conception (Spearman Rank Correlation Test, $r_s = -.77$, N=6, n.s.).

10. Birth Interval

Eight females have given birth to two successive live infants whose birth dates are known (in all cases the first infant was alive when the second was born). The mean interval between the birth dates of the sibling pairs is 5 years and 10 months (range 4 years 4 months-7 years 6 months), see Table 3.3. Melissa and Athena had additional pregnancies between the live births which did not result in the birth of live offspring. Melissa first conceived 4.2 years (4years 2months) after Goblin's birth and Athena conceived twice, first 2.2 years after Atlas's birth and again 4.3 years after Atlas' birth, but neither pregnancy resulted in live offspring. There does not appear to be any consistent

Table 3.3 Interval between successive live births of 8 females

Mother	1st infant	2nd infant	Birth interval
Flo	Flint - March 1964	Flame - August 1968	4 years 4 months
Melissa*	Goblin - Sept. 1964	Gremlin - Nov. 1970	6 years
Madam Bee	Honey Bee - Dec. 1964	Bee Hinde - May 1971	6 years 4 months
Passion	Pom - July 1965	Prof - Oct. 1971	6 years 2 months
Nope	Mustard - Nov. 1965	Lolita - June 1973	7 years 6 months
Mandy	Midge - June 1966	Mantis - July 1972	6 years
Athena*	Atlas - Sept. 1967	Aphrodite - June 1973	5 years 7 months
Miff	Moeza - Jan. 1969	Michaelmas - Oct. 1973	4 years 8 months
		MEAN:	5 years 10 months

*Melissa had one incomplete pregnancy and Athena two, between their two live infants listed.

relationship between maternal age and birth interval, the two shortest intervals were shown by Flo (4 years 4 months), the oldest female in the sample (estimated age: 35 years) and Miff (4 years 8 months) the youngest female (estimated age: 17-18 years).

11. Conception following infant death

Sexual cycling resume 1-2 months after the death of a suckling infant (van Lawick-Goodall, 1968, p. 217). Conception occurred 4-8 months after the death in 5 cases, resulting in the birth of another infant 12-16 months after the death of the first. The 5 deaths involved infants aged between 2 weeks and 2½ years. This indicates that lactation, possibly combined with the mechanics of suckling behaviour is a major factor in the suppression of post partum sex cycles and conception.

12. Sex of infant

Of the 23 infants born between 1965 and 1974, 14 were female and 9 male, the difference is not signficant (X^2=1.8, df=1, n.s.). Examination of the sexes of sibling pairs (i.e. siblings adjacent in the birth order) suggests that the sex of the second born of the pair may be dependent on the sex of its predecessor. Of 28 sibling pairs 8 are the same sex while 20 are different sex pairs. This difference is statistically significant (X^2=5.14, df=1, $p<.05$). The reason for the preponderance of alternating sexes of successive infants born to one female is not understood, but there is a possibility that it is related to the development of sibling incest avoidance, see Chapter 5.

13. Suppression of sexual cycles

Van Lawick-Goodall (1968, p.217) reported that illness or injury to cycling females may interrupt normal cycling for a few days, or in one case of serious injury, result in the cessation of sexual cycles for a period of 6½ months. She also suggests that social factors can influence swelling cycles. Van Lawick-Goodall (1971, p.121) reported a case of apparent social facilitation of sexual swelling, when an old female, Flo, developed a small swelling the day after reacting 'jealously' to the attention given by a group of males towards a maximally tumescent female.

Although few data are available, it is possible that the transfer of young females into a new community has a temporary effect on sexual swelling cycles. Patti had been observed periodically since 1971 but did not join the Kasekela community until November 1973. It is not possible to construct a detailed picture of her sexual development as observations were scanty, but she was observed to have a full-sized swelling and was mated by adult males in February 1973. In November 1973 when Patti first began to travel daily with the Kasakela community, she had a small swelling but did not reach maximal tumescence and was not mated. She was observed regularly over the next few months and showed slight fluctuations in swelling size but no complete cycles. It was not until June 1974 that she was first observed to reach maximal tumescence, and during this oestrus period she was mated frequently by all the adult males. From June Patti showed regular cycles. The above account indicates that normal cycles were suppressed during Patti's first 7 months of residence in the Kasakela community. Pusey (1975) showed that some females transfer between communities before they have reached the age at which full-sized swellings are shown. There are inadequate data to know whether Patti's case of suppressed cycles is typical but a possible functional explanation is presented below (see Discussion).

14. Lifetime Reproductive potential of females

From the information presented above, one can compute the potential reproductive output of an individual female in her lifetime. Life expectancy data is not yet available for wild chimpanzees and would be difficult to obtain even from Gombe as much observed mortality there can be linked to human carried diseases (e.g. the 1966 polio epidemic) and so patterns of mortality in the Gombe population may not be typical but influenced by the increased close contact with humans. For the purpose of this section, the maximum life span will be considered to be 40-45 years, with death occurring from 'natural' causes in old age.

The reproductive life of a female lasts from the end of the period of adolescent sterility (13-15 years) until death. This gives 25-32 reproductively useful years during which a maximum of 5-6 offspring who survive to weaning can be produced. If death occurs before old age suitable adjustments to the following computations can be made. Given that almost 30% of pregnancies do not result in live birth, one might expect that a typical female might in her reproductive life have 7 pregnancies, 5 resulting in the birth of live offspring.

Tables 3.1 and 3.2 show the number of non-pregnant cycles shown by females at Gombe. On the basis of this data an estimate can be made of the number of cycles of sexual swelling a female would experience during a full reproductive life. Between menarche and the first conception there are an average of 19 cycles, and between subsequent conceptions, of which there might be 6, a mean of 4.5 cycles. This would give a total of 46 non-pregnant cycles in a reproductive life beginning at menarche and ending with death from old age. In addition there might be 10-11 cycles during the 7 pregnancies. Thus a female shows non-pregnant cycles for only 15% of her reproductive life and is sexually receptive (i.e. at maximal tumescence) for just 3.8% (414 days out of 30 years).

Observations at Gombe have not been in progress long enough to follow individual females right through their reproductive lives. However, several females have died at an advanced age leaving a number of known and suspected offspring. Since ties between mothers and their offspring persist into the latter's adulthood, it has been possible to recognise relationships between old females and subadult chimpanzees, which strongly suggest mother-offspring bonds. Based on these presumed, and other known relationships, one can estimate the number of offspring of a single female who survive to adulthood. There are eight females for whom this is possible, 7 are dead and one is an aging female who is not expected to produce more than one further offspring. The mean number of births for the 8 females is 3.1, and the mean number surviving to reproductive age is only 2.0. This is a conservative estimate, as other older offspring could exist who no longer have close bonds with their mother, or, more probably, older female offspring might exist who have transferred to other communities.

15. Lifetime Reproductive potential of males

Although it is possible in some cases to assign paternity of an infant with accuracy (see Chapter 7) it is not yet possible to assess an individual male's lifetime reproductive success. Sperm production appears to be continuous from puberty to death. A male therefore, has a reproductive lifespan of 30 years, if he survives to old age. In a community the size of Kasakela there are about 12 reproductively active females at any time, each of whom would be capable of 7 pregnancies in 30 years (see above). This means that during the male's reproductive life 84 conceptions might occur (pre-natal mortality would reduce this to about 60 live births). Each male would hypothetically have the potential to impregnate females on 84 occasions. However, given approximately equal numbers of males and females, the mean number of impregnations would be 7, and any increase on this could only be achieved at the expense of other males in the community.

16. Discussion

Considerable and crucial differences exist between males and females in their reproductive potentials. Females have a very limited and small reproductive potential, the limits being determined by physiological factors, and females invest a considerable amount of energy, both pre- and post-natally in the production of offspring, spending almost the whole of their adult lives either pregnant or lactating. Males, on the other hand, have a very variable reproductive potential and invest relatively small amounts of energy directly to reproductive ends. The energy that males do invest directly in reproduction is spent attempting to impregnate females. There is no evidence of direct paternal investment among male chimpanzees and interactions between adult males and infants are rare. Some adult male behaviour will result in indirect benefits to infants, but their energy expenditure is minimal compared to that which a female invests in her infant. In general adult males do little which might directly increase the probability of survival of individual infants.

Females are limited physiologically and whilst differences in behaviour can probably effect small modifications, such as timing of weaning and encouragement of independence, their maximum reproductive potential is set within fairly rigid limits. Males, on the other hand, have little or no physiological limitations to their maximum reproductive potential, but differences in factors such as the quality and quantity of sperm produced might be important if it were competing with the sperm of other males in promiscuous mating. Assuming that all male chimpanzees surviving to adulthood in the wild are capable of the basic behaviour patterns of courtship and copulation (a possible exception to this is discussed elsewhere, see Chapter 5), then small differences in behaviour are probably very important in determining the actual reproductive achievements of each male.

In this situation where females make a very high investment in a small number of offspring, one would expect them to be discriminating in the identity of their impregnators and to exercise choice, selecting the best available male. One would also expect competition between males to be an important factor in determining their reproductive success. There are no permanent bonds between unrelated adults of the opposite sex, and so each member of one sex is a potential partner for every member of the other.

While mate selection is probably made largely on behavioural criteria, there are certain female physiological factors which might function to maximise the female's potential to exercise choice. While individual females only show sexual cycles for a small proportion of their adult lives, a relatively high percentage of the cycles shown are infertile. The period of adolescent sterility gives young females experience with the available adult males, such that with the onset of ovulatory cycles the females possess the knowledge needed to exercise choice. This is not to say that the period of adolescent sterility gained selective advantage for this reason alone. An interval between menarche and the ability to conceive and carry a foetus to term is widespread among primates and appears to be a standard stage in female reproductive development. However, this interval might, in species with multi-male groups, have an important secondary function of allowing females to become familiar with the available males. An important assumption in this argument is that the female is aware of the transition from anovulatory cycles and adjusts her behaviour accordingly. It remains to be shown that females become more selective, either gradually or suddenly, prior to their first conception. It appears that nulliparous females are more likely to solicit copulations from males than are older females (van Lawick-Goodall, 1968) but this behaviour is uncommon in most females and quantitative data are lacking.

The anovulatory post-partum cycles could serve in a similar fashion to re-familiarise the female with the community adult males, whose composition may have changed since the female was last receptive. Receptive females receive much more intensive attention from adult males than do non-receptive females. Differences are quantitative rather than qualitative except for sexual behaviour which is directed exclusively towards females currently showing cycles of sexual swelling. Thus, the experience gained in even one or two anovulatory post-partum cycles may provide useful additional information for these females.

The oestrous period of chimpanzee females lasts an average of 9.8 days with ovulation occurring at, or near, the end. The length of time spermatozoa are able to survive inside the female genital tract is not known for chimpanzees but data from other mammalian species (Chang, 1965) suggest that it would not be more than about 2 days. This means that only copulations occurring in the latter half, or even third, of oestrus could be expected to result in conception. It could be argued that the long period of oestrus is necessary because of the open nature of chimpanzee society. Females are not always in the presence of males and the 10 day oestrus increases the likelihood that the female will meet males and be mated at the appropriate time. However, copulations occur at frequencies of 1-4 per hour from the first day of maximal tumescence (Chapter 4). It appears that the long oestrus might serve a more subtle function of allowing females the time to exercise choice. The behavioural aspects of female choice are discussed in Chapter 7.

Transfer of females between communities has been observed regularly at Gombe (Pusey, 1975) and in the Mahali Mountains (Nishida & Kawanaka, 1972). At Gombe, such transfer appears to be restricted to juvenile and adolescent females, while in Mahali older females have also been known to transfer. No confirmed case of adult male transfer has been observed. Pusey (1975) found that many females transfer prior to menarche and the onset of full-sized swellings; these females go through the period of adolescent sterility in their new community. Other females may transfer when slightly older, although they may have been observed associating temporarily with the transfer community before joining it permanently. Patti fell into this category. She had been recognised since 1971 and was seen occasionally (10-12 times per year) during 1971-73. In November 1973 she began associating permanently with the Kasakela community and since then has been seen almost daily. As mentioned above, Patti did not show a complete cycle of sexual swelling until 7 months after her transfer. She is known to have showed full-sized cycles during early 1973 and was observed to be mated by adult males in February 1973, and so it appears that her cycles were suppressed during the interval November 1973-June 1974. Suppression of cycles among humans in situations of stress and social change is well documented (Matsumoto et al, 1968; Dean, 1949). A similar proximal mechanism could have functioned in Patti's case as she was certainly subjected to stress in the form of repeated and intense aggression shown to her by the community females (Pusey, in prep.). However, the period of suppressed cycles allowed time for Patti to become acquainted with the males of a community which she had only had brief contact with previously, giving her information which would allow future discrimination between the adult males.

Thus it seems that various physiological features of female reproduction could function to give the female knowledge of the potential progenitors in the community prior to the female's first pregnancy. Whether this in fact happens and to what extent females are able to be selective in their choice of mates will be discussed below.

While chimpanzee births are not randomly distributed over the year (see p. 54) there is not an intense concentration in any particular month. This, combined with the long birth interval, means that few females are showing cycles of sexual swelling at any one time. There is no evidence of cycle synchrony amongst Gombe chimpanzees. Thus a situation exists in which a single male could achieve a high proportion of impregnations, and each female would usually have the potential to choose from all the males in the community. This contrasts to species such as the rhesus monkey in which the pronounced birth season means that all available females cycle during the same, limited breeding season, making it difficult for a single male to consort and impregnate all, or even a high proportion, of the females.

CHAPTER 4

REPRODUCTIVE CYCLES AND PERIODICITY

1. Seasonality

Many species of nonhuman primates show annual cycles of reproduction which result in a non-random distribution of births over the year (Lancaster & Lee, 1965). Sometimes births are completely restricted to a certain portion of the year, producing a birth season as in Japanese and rhesus macaques (Kawai, 1962, cited in Lancaster and Lee; Drickamer, 1974), or they may occur at low frequencies for most of the year but show a peak of births at a particular time as in hamadryas baboons (Kummer, 1968, p. 176).

Birth dates are known for 28 chimpanzee infants born at Gombe between 1964 and 1974. Figure 4.1 shows the distribution of births over the months of the year. Births occurred in all months except December and February, at frequencies ranging from 1 (April and May) to 5 (October). There is a concentration of births in the dry season (June-October) which just reaches statistical significance (X^2=4.1, df=1, p<.05). However, one cannot dismiss the possibility that this may be an artifact of small sample size, as for example, all 5 October births occurred between 1971 and 1973.

However, the available data indicate that a seasonal effect may be acting to create a non-random distribution of births, and one would expect to find a correspondingly non-random annual distribution of female cycles. Figure 4.2 shows the mean number of cycles observed in each month during the period 1972-4. A division is apparent between the months April-August when monthly means range from 1.3 - 2.7 cycles, and the months September to March when means range from 3.0 - 4.3 cycles

Figure 4.1 Annual distribution of births.

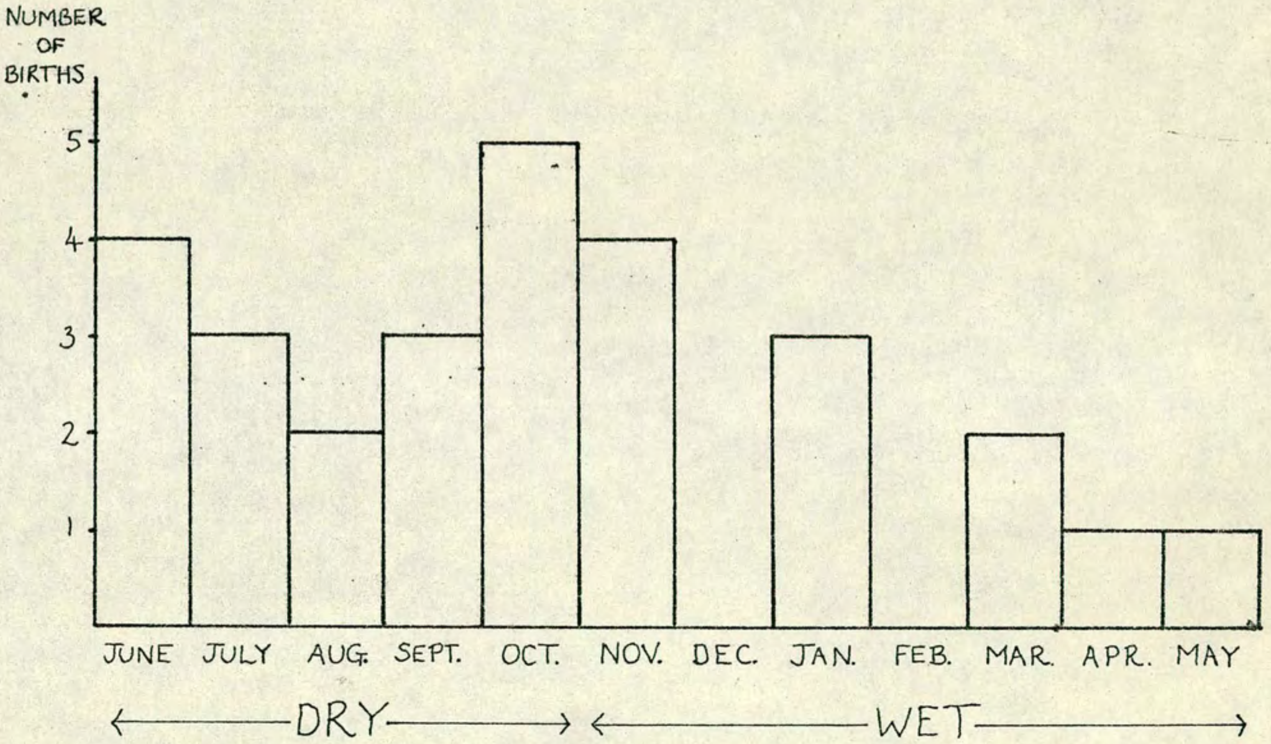
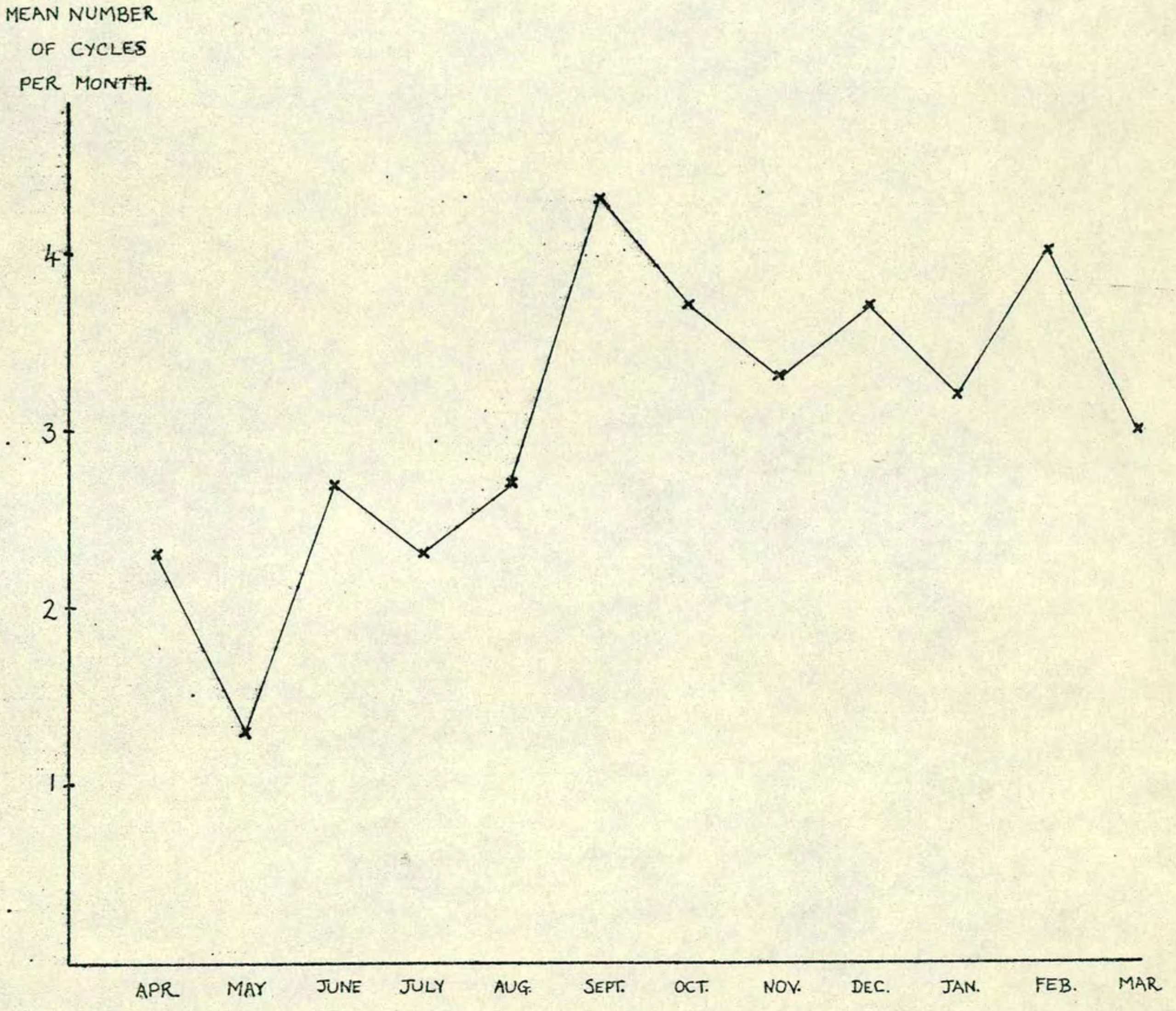


Figure 4.2 Annual distribution of female swelling cycles.



per month. The division between these two blocks of months does not itself reflect the wet-dry seasonal cycle but it fits with the data on birth distributions, giving a reduced probability of births occurring between December and April. As the cycle data are not related directly to the seasons, it is difficult to postulate an ecological mechanism which would control the observed distribution. It is somewhat surprising that a birth peak should exist in the chimpanzee, as the infantile period of total dependency lasts for several years. Thus, even if food availability showed seasonal variation, periods of food shortage could not be avoided by a non-random seasonal distribution of births. However, there is some evidence from Gombe to suggest that the latter part of the wet season, January-March, is a high-risk time for diseases which result in mortality. In January 1968 many chimpanzees suffered from a flu-type disease (van Lawick-Goodall, 1968, p. 170). Four adults and two infants died as a direct result or indirect result (both infants survived the disease but died soon after being orphaned). A similar disease affected the chimpanzees in early 1975: three adults and one infant died and a juvenile female whose mother died still lives at the time of writing. Mortality at Gombe is generally low, and the two incidents described were unique, and both occurred in the early months of the year. If this is a time of relatively high mortality then a mechanism to avoid giving birth during this period could have evolved through natural selection. Chimpanzee infants orphaned when less than three years old could not expect to survive so the advantage gained by avoiding births in high-risk months will not be overwhelming as vulnerability persists for 2-3 years. This may explain why selection has not acted to produce a more pronounced birth season.

2. Distribution of copulations over the menstrual cycle

Primates show no consistent temporal pattern of copulation frequency with respect to the female ovarian cycle, variation being found both within and between species (Rowell, 1972). In the majority of species an oestrus period is found but in others such as the vervet monkey (Rowell, 1970) copulation appears to occur throughout the ovarian cycle. In species where the female develops a large genital swelling, oestrous periods usually coincide with maximal genital tumescence, (Rowell, 1967, *Papio anubis*; Chalmers, 1968, *Cercoebus albigena*; Saayman, 1970, *Papio ursinus*; van Lawick-Goodall, 1968, McGinnis, 1973, Tutin and McGrew, 1973 - *Pan troglodytes*). Data from this study confirm that for wild chimpanzees copulations are not randomly distributed with respect to the phase of the swelling cycle , see Table 4.1. A few copulations occur just before and just after the peak of swelling and prepubescent males are responsible for 70% of these, as compared to 36% of copulations occurring during maximum swelling. For all 7 females on whom sufficient data were available copulations occurred significantly more frequently at maximum tumescence than at other phases of the cycle.

Although the general rule for chimpanzees is that copulations are more-or-less restricted to the period of maximum tumescence, one interesting exception emerged. In April 1973 Plato, the 2½-year-old son of Pallas died, and whilst Pallas had remained completely anoestrus since his birth she began to show a small sexual swelling two months after his death. Her tumescent phase was protracted and during the 10 days prior to her first maximum tumescence she was mated frequently by all the males. This was not an example of an individual difference as in subsequent cycles Pallas was only mated during maximal tumescence. Nor was it simply a reaction to the novely of Pallas' first swelling for almost 3 years, as when Melissa showed her first post-partum swelling for 3 years, in October 1973, she was mated infrequently even during maximum tumescence. The difference in attractiveness in these two cases may have to do with whether or not the female is still lactating. Pallas presumably ceased to lactate following the death of her son, whilst Melissa was still producing milk for her 3 year old daughter.

Table 4.1. Distribution of copulations with respect to the female swelling cycle.

	Swelling size, as a fraction of full-size				
Female	0	¼ - ½	¾	1	Total copulations
ATHENA	0	2	7	32	41
PALLAS	0	11	26	171	208
MIFF	0	2	9	124	135
GIGI	2	10	7	272	291
SPARROW	2	0	11	177	190
PATTI	1	0	2	142	145
LITTLE BEE	0	0	7	84	91
TOTAL COPS.	5	25	69	1002	1101
TOTAL MALE CONTACT HOURS:	390.5	162	176	1936	2664.5

3. Distribution of copulations during the maximum tumescent phase of the cycle

As shown above, copulations are almost entirely restricted to the female cycle phase of maximum genital tumescence, and this phase can thus be called the oestrous period, in accordance with the strictly behavioural definition proposed by Rowell (1972). The mean length of oestrus was found to be 9.8 days (N=37, from 7 females, range 7-17 days) in this study. This contrasts with the figure of 6.5 days (N=20, from 10 females) given by van Lawick-Goodall (1968, p.216) and 16.3 days (N=11, from 3 females) given by McGinnis (1973). The discrepancies are almost certainly due to individual differences apparently related to age, with young females showing much longer oestrous periods than mature females (Young and Yerkes, 1943; van Lawick-Goodall, 1968, p. 216; Chapter 3, section 2). McGinnis' data came from three young nulliparous females; data from this study were from three young nulliparous, one mature nulliparous and three mature parous females. Van Lawick-Goodall did not individually identify the females in her data but they almost certainly included some old females.

The time of ovulation in chimpanzees has not been determined with complete certainty but it probably occurs during the latter half of maximum tumescence, 3 days prior to detumescence (Elder, 1938; Chapter 3, section 4). The timing of copulations within the oestrous period would therefore seem important, as copulations occurring close to the time of ovulation are more likely to result in conception than those occurring during the preceding and succeeding days. One might predict that copulation rates would be higher close to the time of ovulation than at other times, as natural selection would favour males who concentrated their sexual efforts at times when conception is most likely to occur.

To examine this question two oestrous periods were selected during which intensive observation was made. One was the 10 day oestrus period of Pallas between November 12-22, 1973. 73 hours of data were available for the period November 11-24. The second set of data were 60 hours of observation on Patti between December 11-19, 1974. Patti reached maximum tumescence on December 8th and detumescence began on

December 18th. Figures 4.3 and 4.4 show the data expressed as copulations per male-hour (one male present for 10 hours = 10 male hours = 10 males present for one hour) for each day of maximum tumescence when data were collected. Copulation frequencies in the first and second halves of maximum tumescence were compared and as

indicated by the shapes of the graphs the change in copulation frequencies occurred in different directions. For Pallas copulation rate is higher during the latter phase of maximum tumescence, while for Patti, the opposite is true, with copulation rate being reduced during the latter half.

The explanation of this contradiction is that different mating patterns were operating in the two cycles. Pallas was mated promiscuously throughout maximum tumescence and although an old male, Hugo, acted possessively towards her, he made no response to other males mating (see Chapter 6). During Patti's cycle promiscuous mating was observed from December 11-13 but on December 14th the dominant male, Figan, began acting possessively and he reacted aggressively when other males attempted to copulate with her. As the alpha male, he was almost completely successful in preventing other males from copulating, and so from December 14-17 the copulation rate remained low. In both cases the copulation rate dropped as soon as detumescence began, falling to zero on the first day of Patti's detumescence and the second day of Pallas'.

Mating patterns tend to show a constant temporal relationship within the days of maximum tumescence with the more restrictive mating systems dominating the latter half of oestrus. This fact, which will

Figure 4.3 Daily fluctuations in copulation rate during Pallas' maximal tumescent phase in November 1973.

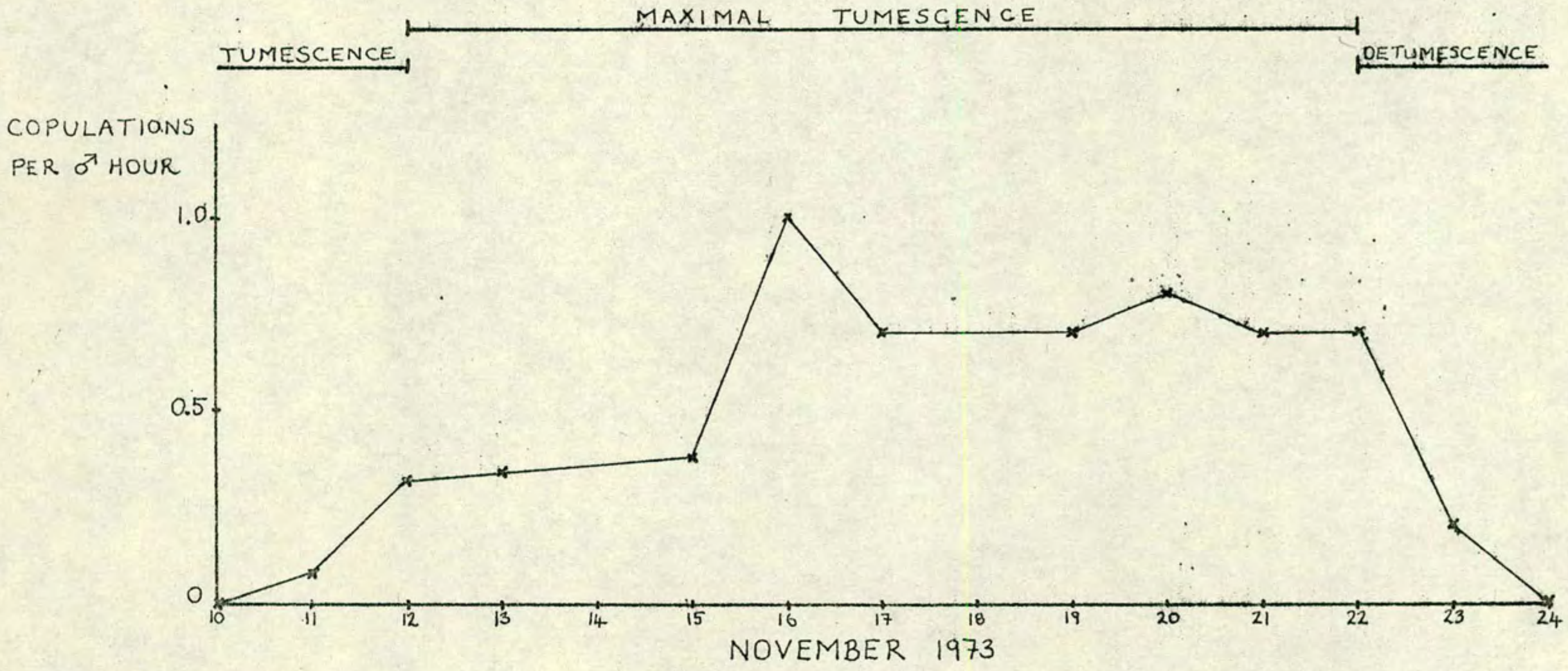
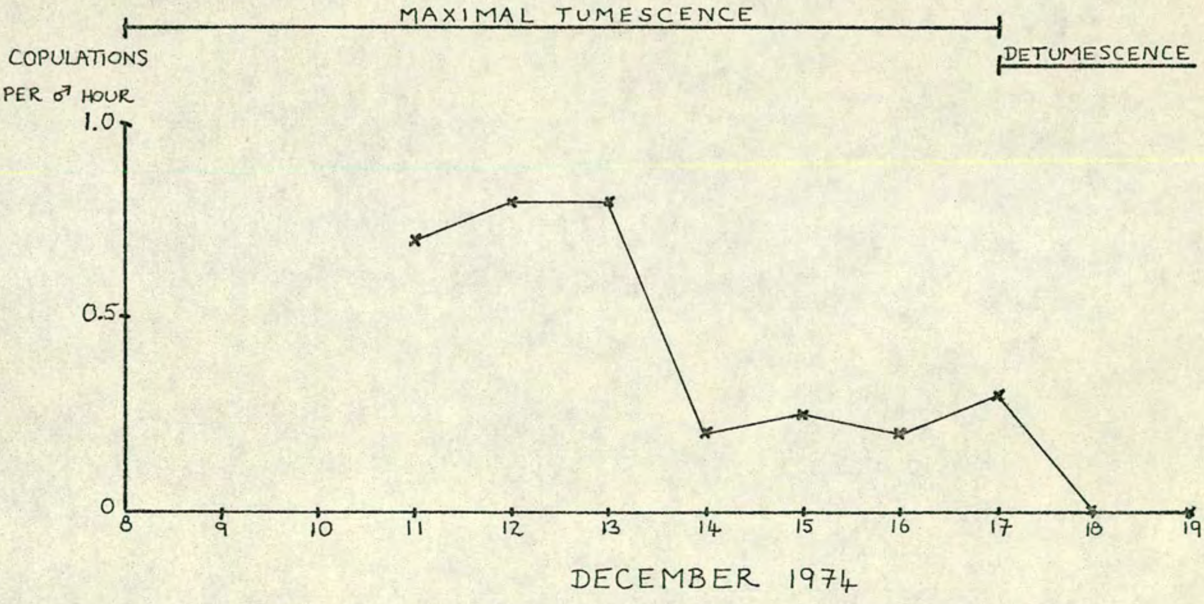


Figure 4.4 Daily fluctuations in copulation rate during Patti's maximal tumescent phase in December 1974.



be returned to in Chapter 6, indicates that males respond differently to females within the phase of maximal tumescence. In Pallas' November cycle when promiscuous mating occurred throughout oestrus, copulation rates per male hour did indeed rise significantly during the latter half of maximum tumescence. This would seem to indicate that males are more highly motivated sexually, or that females are more attractive, at the time in the cycle when ovulation is presumed to occur. It is possible that males are responding to pheromonal cues which change during maximal tumescence, making females more attractive and/or receptive during the days when ovulation is most likely to occur. It is of obvious adaptive value for males to concentrate their sexual activity, particularly the expression of the restrictive mating patterns, possessiveness and consort relationships, at times when conception can occur.

4. Nychthemeral periodicity

i. Introduction

No attempt has previously been made to investigate whether the sexual behaviour of wild chimpanzees is distributed randomly over the daylight hours or whether any consistent daily rhythm exists. Although systematic nocturnal observations have not been made, incidental observations of nested groups of chimpanzees suggest that little or no copulatory activity occurs in the hours of darkness. Van Lawick-Goodall (1968) indicated that copulations of Gombe chimpanzees occurred more frequently in the morning than in the afternoon but was not able to quantify any fluctuations. Tutin and McGrew (1973) found a similar morning concentration of copulations in a captive group of adolescent chimpanzees.

Many aspects of both the behaviour and physiology of nonhuman primates shows circadian periodicity (Altmann & Altmann, 1970; Clutton-Brock, 1974; Winget et al., 1969). The aim of this section is to quantify diurnal fluctuations in the occurrence of sexual behaviour and to determine what, if any, other aspects of chimpanzee behaviour relate to any such fluctuations.

ii. Results

The number of copulations occurring during the mornings (06.00-11.59) and afternoons (12.00-20.00) were compared for the 4 females on whom at least 6 long observation periods were available to permit the use of the Wilcoxon matched-pairs signed-rank test. Table 4.2 shows that all 4 females mated significantly more often in the mornings.

Table 4.2 Daily periodicity in the occurrence of copulations.

	Copulations occurring in matched periods of observation			Copulations occurring in matched periods of observation	
	a.m.	p.m.		a.m.	p.m.
PALLAS:	15	12	PATTI:	16	12
	18	7		21	14
	14	5		20	11
	23	14		13	6
	11	6		17	13
	29	13		11	5
$N=6, T=0, p<.05$			$N=6, T=0, p<.05$		
SPARROW:	17	13	GIGI:	11	6
	12	10		12	5
	14	7		20	13
	5	3		18	12
	12	10		11	6
	24	11		15	6
	13	9		11	9
$N=7, T=0, p<.02$			$N=7, T=0, p<.02$		

This method gives only a crude indication that diurnal periodicity exists and to investigate this in more detail copulation rates were calculated for each female for each hour period of the day from 06.00 to 20.00. This was done by dividing the number of incomplete and complete copulatory sequences observed in each period by the number of observation hours accumulated for each hourly period. Complete and incomplete copulatory sequences were considered together in this section. Only two females, Gigi and Pallas, were involved in enough incomplete sequences to make separate analysis possible. The hourly rates of incomplete and complete sequences were computed separately for these two females. The rankings of rates of complete sequences and rates of incomplete sequences were compared using a Spearman Rank Correlation (r_s) test and in both cases there was a statistically significant similarity (Gigi: r_s=.84, N+13, p<0.01; Pallas: r_s=.66, N=13, p<.05) indicating that rates of complete and incomplete copulatory sequences show a similar periodicity. Based on this finding it was decided that for all females incomplete and complete sequences would be lumped in computing the hourly rates used in this section.

Hourly copulation rates were calculated for each of the 6 females on whom sufficient data were available. As it was not possible to balance observation equally over the daylight hours the rates are based on different observation hours. In general the least data are available for the periods 06.00-07.00 and 19.00-20.00. This is because the chimpanzees usually un-nest and nest, respectively, during these periods, and it is rarely possible to collect a full hour of behavioural data. For two females, Miff and Sparrow, there is less than 2 hours of data for the 06.00-07.00 period and in Figures 4.7 and 4.9 a single data point is produced for the 06.00-08.00 period.

Figures 4.5-4.10 show the daily fluctuations in copulation rates for Gigi, Pallas, Sparrow, Little Bee, Miff and Patti. The magnitude of the rates differs between females and this is discussed elsewhere (see Chapter 5, section 11). The focus here is on the hour-to-hour fluctuations in rates and the general daily pattern. Figures 4.5-4.9 all show the highest rates in the first hour of the morning. Figure 4.10 (Patti), shows a different pattern, and the reasons for this will be discussed later. In the following section the data for Patti are excluded. The ranks of the hourly rates for the 5 females were compared using a Friedman 2-way analysis of variance test. The test confirmed the similarity, giving a highly significant result, $X_r^2=624$, df=4, $p<.001$. Based on this statistical confirmation of similarity the individual data were pooled to produce the graph in Figure 4.11. Figure 4.11 shows the pattern of daily periodicity which is consistent for 5 out of the 6 females in the present study. The rate is very high in the early morning, falling to a dip in the mid-morning (10.00-11.00), rising slightly in the early afternoon (12.00-13.00) and then gradually tailing off in the late afternoon. However, the method used in computing hourly copulation rates involved scoring only the number of copulatory sequences observed in a particular observation time and took no account of the party size, or more specifically, of the number of males available to copulate with the female at any time. Therefore, before any attempt is made to discuss the causes of the apparent periodicity in copulation rates, it must be determined whether these fluctuating ones can simply be explained by fluctuations in the number of available males.

iii. Periodicity in the number of males associating with maximally tumescent females

It is not easy to adequately define a chimpanzee group (Wrangham, Figures 4.5 - 4.10 Circadian rhythm in copulation rates with individual females.

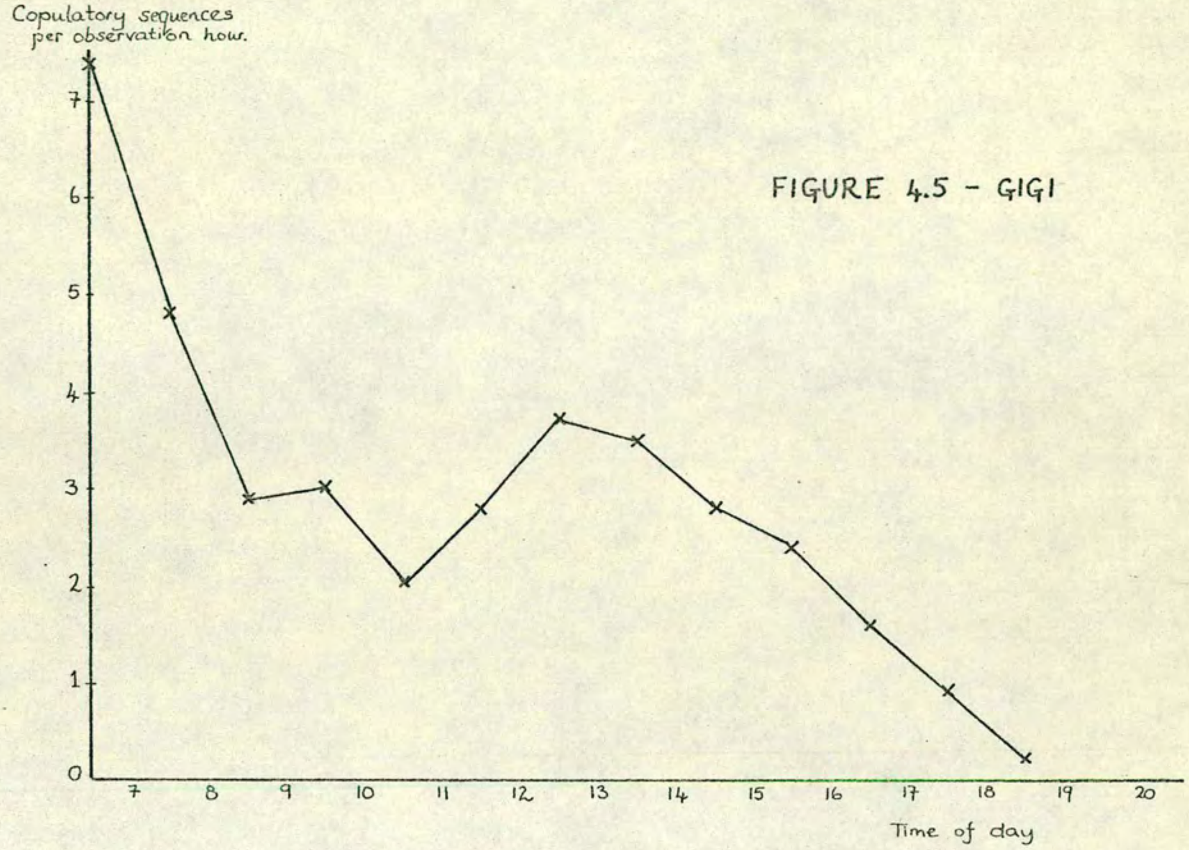


FIGURE 4.5 - GIGI

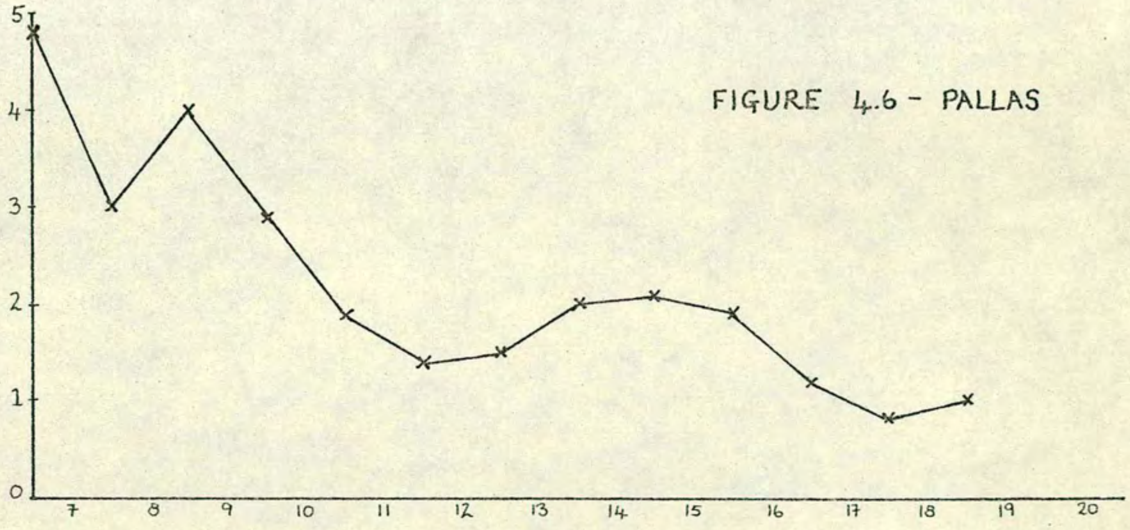


FIGURE 4.6 - PALLAS

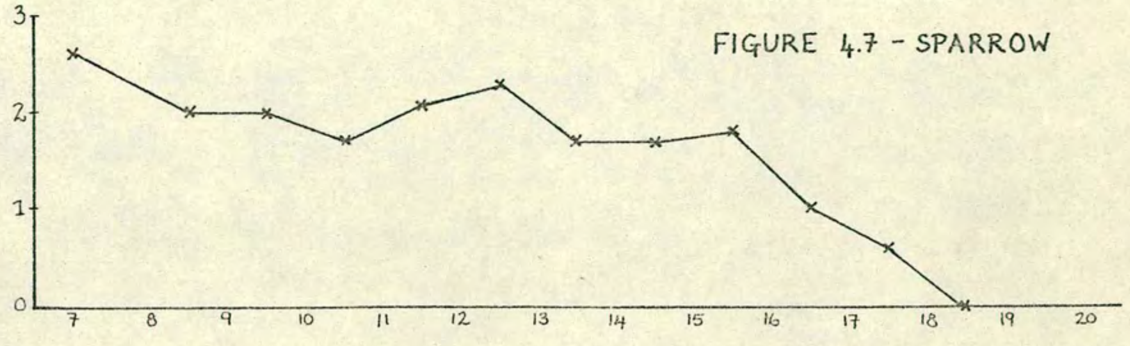


FIGURE 4.7 - SPARROW

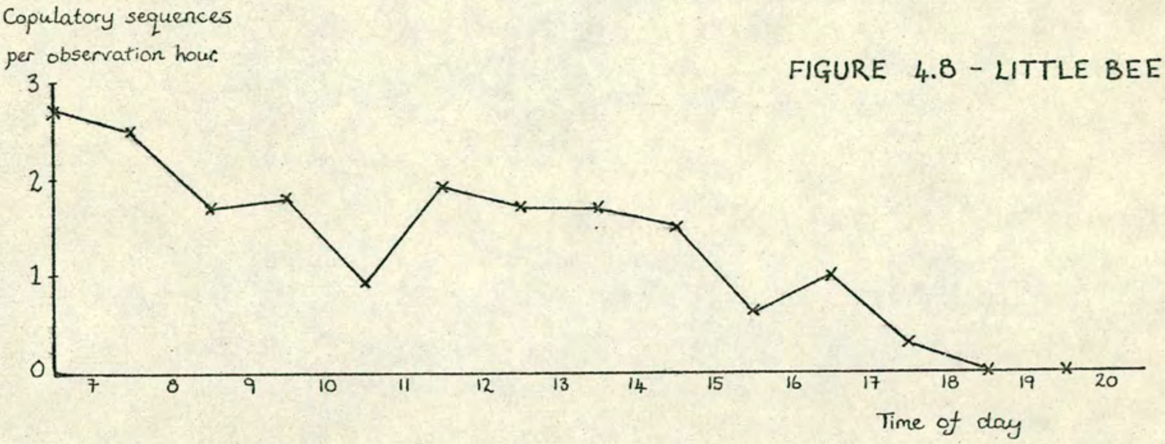


FIGURE 4.8 - LITTLE BEE

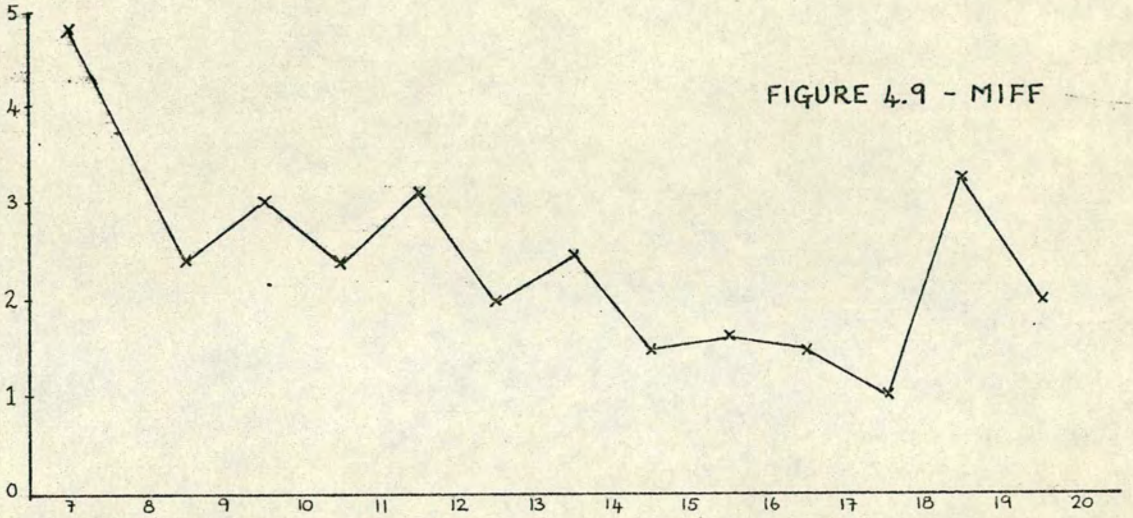


FIGURE 4.9 - MIFF

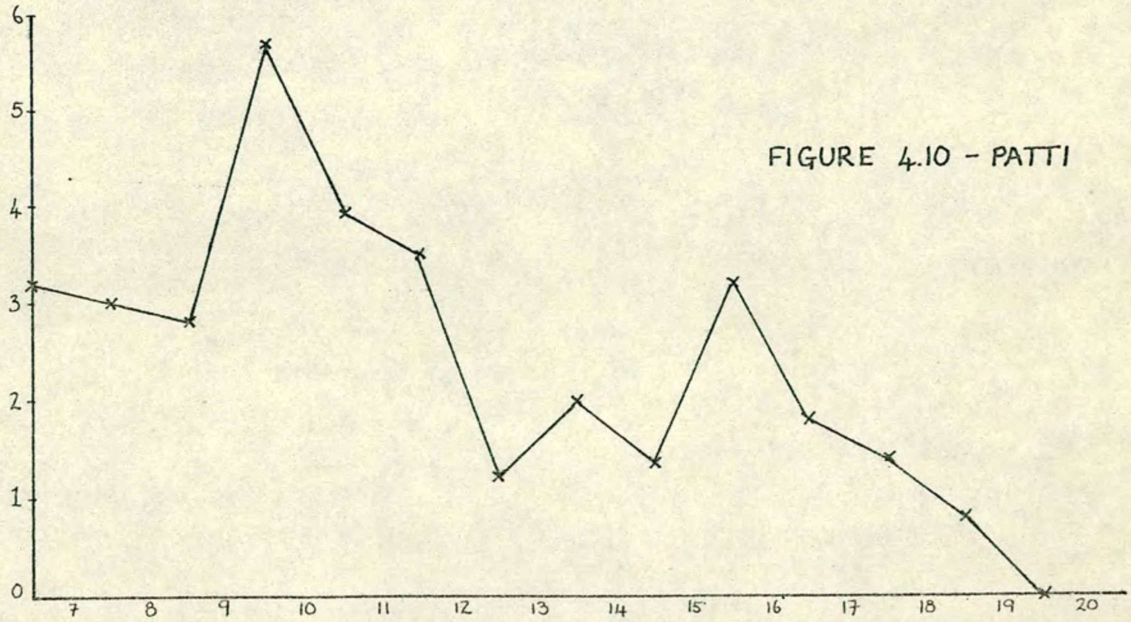


FIGURE 4.10 - PATTI

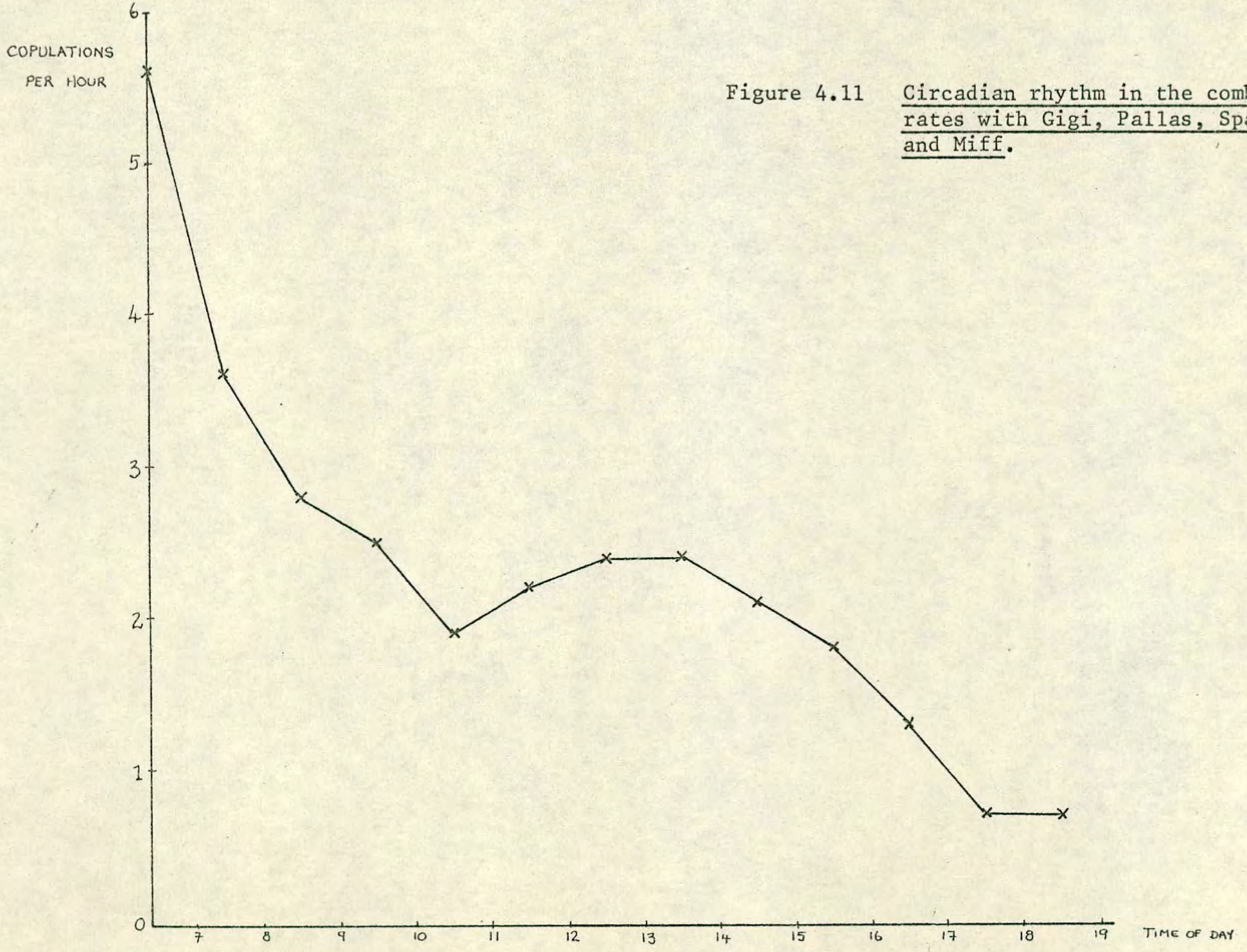
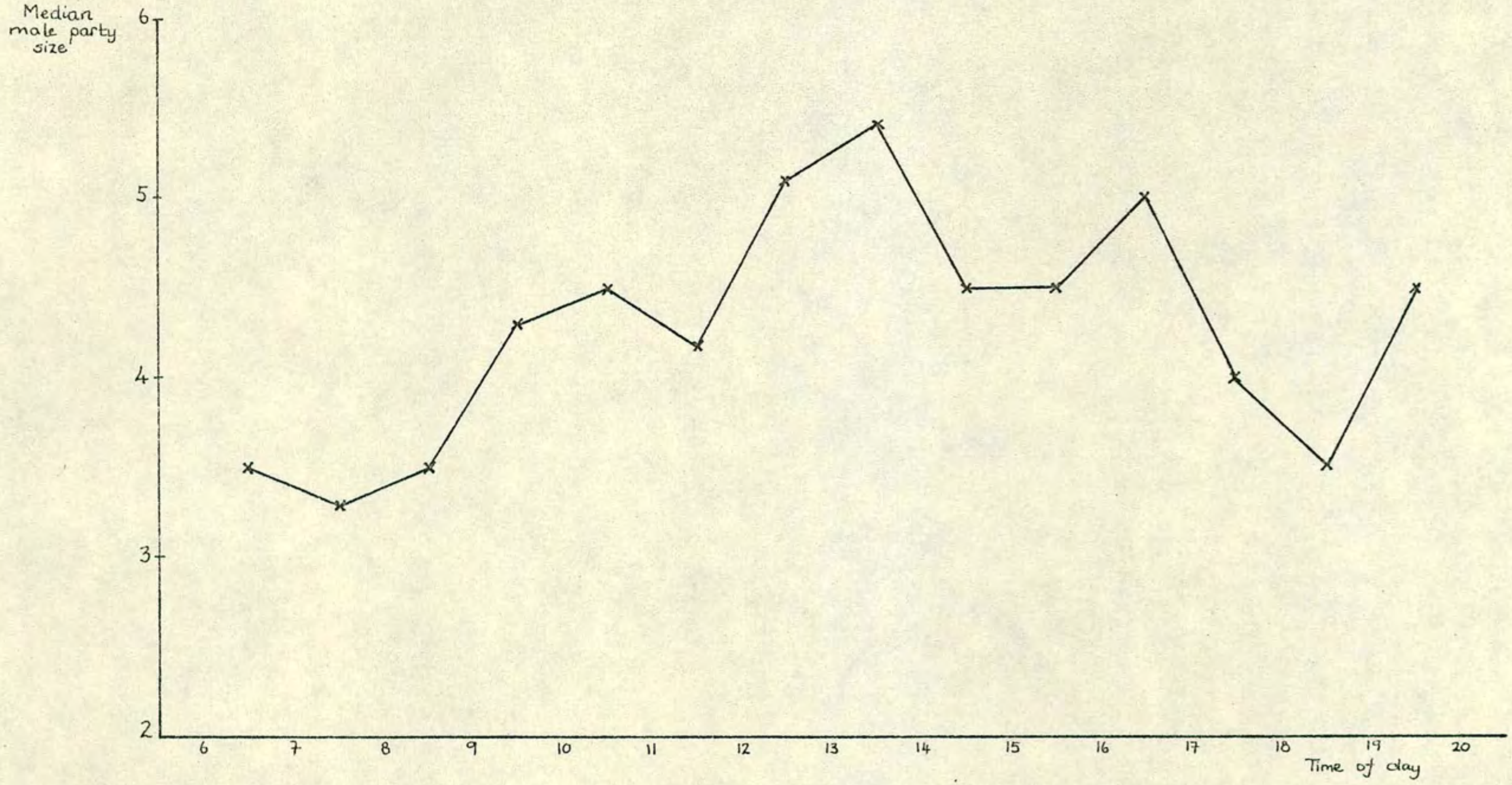


Figure 4.11 <u>Circadian rhythm in the combined copulation rates with Gigi, Pallas, Sparrow, Little Bee and Miff</u>.

1975). For the purposes of this section a group is defined as: the number of chimpanzees visible to the observer during a brief search in the vicinity of the target chimpanzee which covered a circular area of approximately 100m diameter. This is not an ideal definition as visibility varied tremendously depending on the season and the vegetation type (Wrangham, 1975). However, it was necessary to have an operational definition which would permit fairly consistent recording without detracting seriously from the observability of the target individual. Only 'independent' individuals were recorded. Independent individuals were those who have been observed travelling separately from their mothers for at least 24 hours. There were 12 independent males in the Kasakela community for most of the study period; Atlas was the youngest, and he achieved independent status in June 1973.

Figure 4.12 shows the diurnal fluctuation in the median number of independent males (hereafter, male party size) associating with a maximally tumescent female (pooled data for the 6 females). Values fluctuate from a nadir at 07.00-08.00 (3.3 males) to a zenith at 13.00-14.00 (5.4 males) but changes over the daylight hours are not dramatic. It is obvious from comparing Figures 4.11 and 4.12 that no consistent relationship exists between copulation rate and male party size. In the morning there appears to be an almost inverse relationship while in the afternoon there is an appearance of concordance. It is difficult to know what could cause the relationship to change from negative to positive at mid-day and so it is doubtful whether these are meaningful relationships. Intuitively one would expect a positive relationship between the number of available males and the number of copulations observed, and it might be that there are factors

Figure 4.12 Diurnal fluctuations in male party size.



affecting morning copulation rates which outweight the effects of male party size, but that the positive relationship in the afternoon is genuine.

Measures of male party size take no account of group dynamics and this might be an important variable as van Lawick-Goodall (1968, p.219) reported that copulations were most frequent when groups are socially stimulated, e.g. "as when two groups meet". The composition of parties is rarely stable for more than 1-2 hours since individuals constantly join and leave. In the following section only the arrival of males will be considered as departures would not be expected to have an effect on copulation rate. If increases in group size are not evenly distributed over the day but show periodicity then this might be a causal factor in the observed diurnal periodicity of copulation rates. Figure 4.13 shows the mean number of increases in male party size per hour of observation, for each hourly period of the day. The mean number of increases for all hours of the day is 1.2/observation hour, and values range from 0.4/obs. hour (06.00-07.00) to 1.8/obs. hour (07.00-08.00). Again there is no consistent relationship between the fluctuations in Figure 4.13 and those in Figure 4.11. Thus, while increases in party size are often immediately followed by copulatory activity, both by the newly arrived males and those already in the group (see Chapter 6, section 3.i.), the diurnal fluctuation in the frequency of increases in male party size are minimal and do not determine diurnal changes in copulation rate.

iv. Diurnal periodicity of female behaviour other than copulatory activity

If chimpanzees are more likely to copulate whilst engaged in some activities rather than others then any circadian rhythms in such

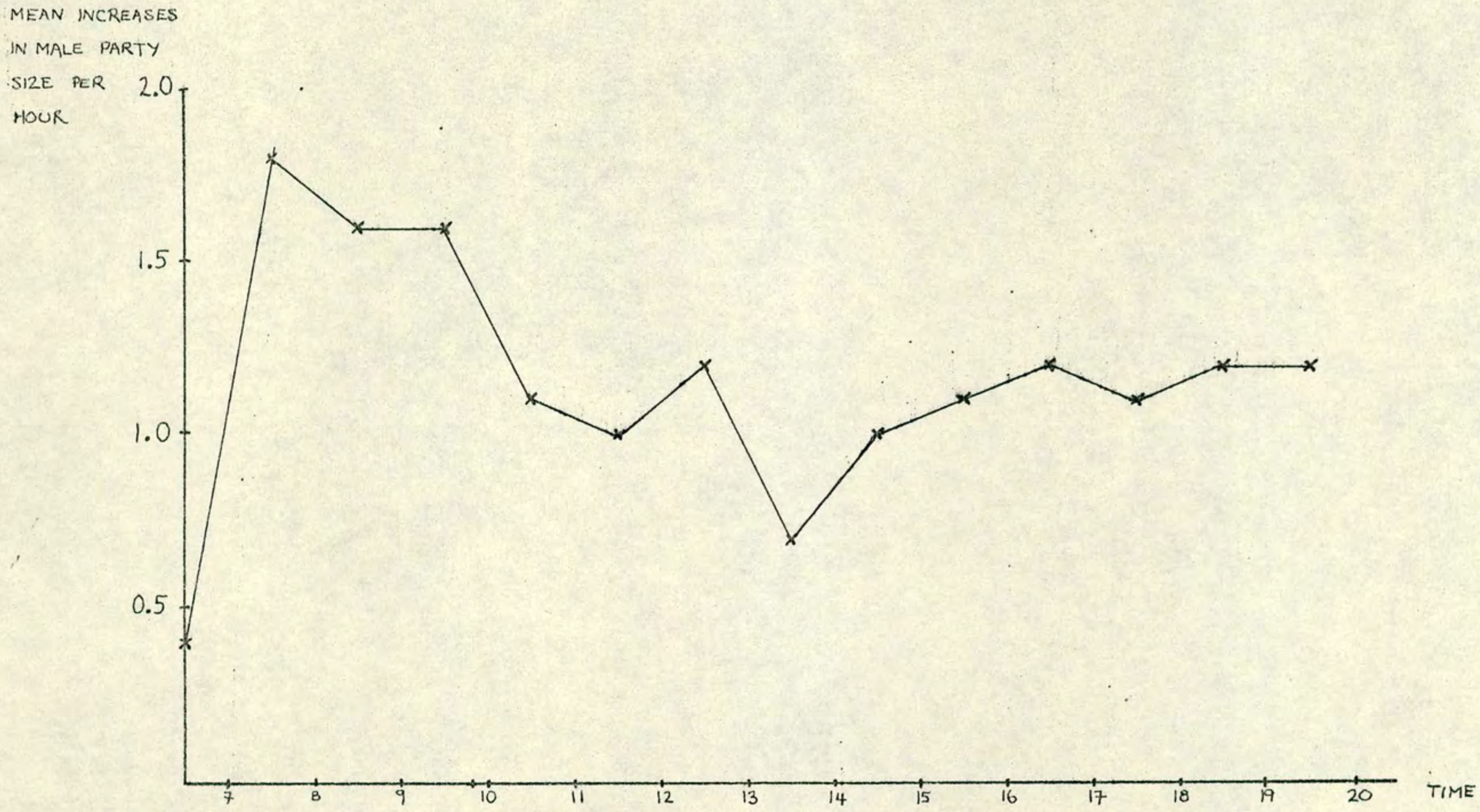


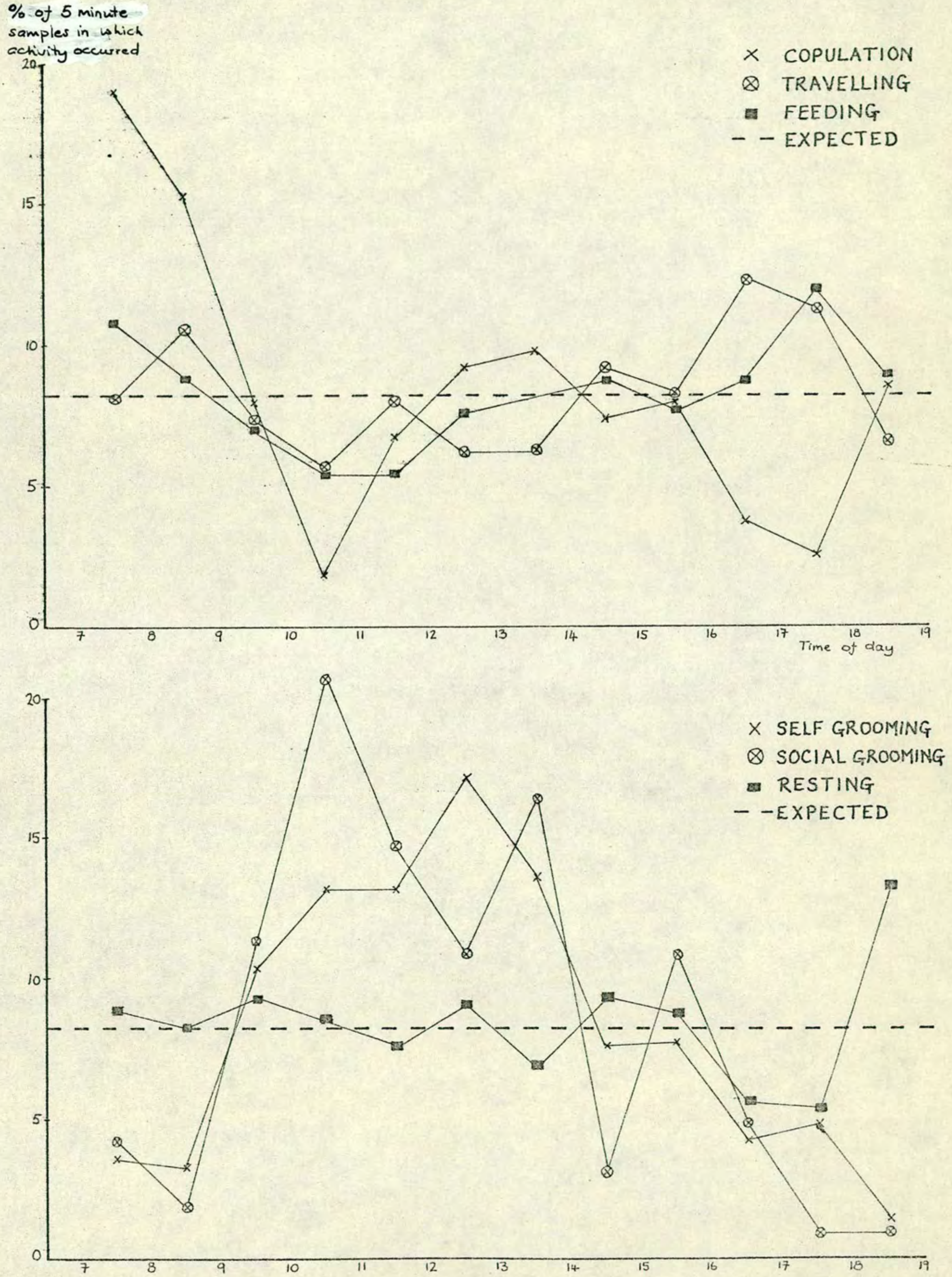
Figure 4.13 Diurnal fluctuations in the number of increases in male party size.

activities might be partially responsible for the rhythmicity in copulation rates. To investigate this possibility the periodicity of the following activities: feeding, resting, travelling, self grooming, and social grooming, were computed for each of the target females (N=5) on whom sufficient data were available.

The hourly frequencies of each behaviour shown by the 5 females were tested by the Kolmogorov-Smirnov one sample test to establish whether deviations from randomness were statistically significant. The results for feeding, resting and travelling were non-significant, indicating that there was no marked circadian periodicity for these activities. The distributions of self grooming, social grooming and copulations over the hours of the day showed significant non-randomness, with $p<.01$, in all 3 cases. Figure 4.14 shows this graphically; feeding, resting and travelling show small fluctuations about the expected level, whilst self grooming, social grooming and copulations show much larger fluctuations above and below the expected level of performance. Copulations occur at the highest frequency in the early morning whilst grooming, both self and social, peak later in the morning. Each activity was tested against copulation rate using a Spearman Rank correlation test (N=12) to establish whether or not the frequency of any of the recorded activities covaried, either negatively or positively, with it. None of the coefficients were significant; feeding ($r_s=-0.2$) and travelling ($r_s=-0.1$) both gave small negative coefficients; resting ($r_s=0.2$), self grooming ($r_s=0.2$) and social grooming ($r_s=0.3$) all gave small positive coefficients.

It appears that the distinct circadian rhythm apparent in copulation rates is neither a result, nor a cause of the circadian periodicity in other gross behaviour categories of female chimpanzees.

Figures 4.14 a) & b) Diurnal fluctuations in female activities.



It is possible that male chimpanzees show different patterns of behaviour and that these patterns have a direct relationship to the circadian periodicity of copulations. As male activities which were unrelated to copulations were not recorded in this study, this possibility could not be ruled out although no obvious sex differences in the distribution of activities were apparent. None of the variables so far considered showed any direct relationship to copulation rates, but it remains possible that some of these variables were interacting and affecting the frequency of copulations in some more complex fashion.

v. Hormonal Factors

Males The exact nature and extent of hormonal control of sexual behaviour in nonhuman primates remains unclear. Ford and Beach (1951) hypothesised that the human males' sexual behaviour is less dependent on gonadal hormones than that of male nonhuman primates and that the latter are in turn, "somewhat freer of hormonal control than are the lower mammals" (p. 249). Experimental studies by Phoenix *et al* (1973) and Wilson & Vessey (1968) compared the sexual behaviour of adult male rhesus monkeys before and after castration. While their results show tremendous individual variation in the monkeys' response to castration, the general conclusion of both studies is that while castration causes a definite, if slow, decline in the mean frequency of sexual behaviour of adult male rhesus monkeys. The effect is not however, as drastic or quick acting as that shown by some rodents and lagomorphs after castration (Beach & Pauker, 1949; Davidson, 1966). However, another study of the effects of castration on adult male rhesus monkeys (Wilson, Plant and Michael, 1972) concludes that sexual behaviour in the male primate is highly dependent on gonadal hormones and that the loss of the ejaculatory response occurs as quickly as in the rat. Despite the contradictory results and the apparently great individual differences in response to castration, it seems safe to conclude that gonadal hormones do influence male nonhuman primate sexual behaviour though other genetic and experiential factors are certainly involved.

It is certainly possible that the diurnal rhythm observed in chimpanzee copulation rates is related to diurnal rhythms in levels of testosterone. It has been established for a number of species from rats (Kinson & Liu, 1973; Bartke et al, 1973) to humans (Rose et al, 1972) that distinct diurnal rhythms exist in levels of circulating plasma testosterone. The rhythm in man is characterised by an early morning peak, levels being highest between 04.00 and 12.00 which then falls off to the lowest level at about 20.00 (Nieschlag & Ismail, 1970). Plasma cortisol also shows a marked diurnal rhythm with the highest levels again being found in the early morning (Rose et al, 1972; Ismail et al, 1972). Precise information on the relationship between these two hormones and male libido is not available for humans, although Fox et al (1972) suggest that a positive relationship might exist in humans between male libido and high levels of plasma testosterone. However, it is doubtful whether behavioural data on humans will illuminate any relationship as the timing of the expression of human sexual behaviour is under considerable cultural influence. In rhesus monkey males there are considerable individual differences in levels of circulating testosterone, and it appears that these are not correlated with different levels of sexual performance (Resko and Phoenix, 1972; Phoenix, 1975). Gordon et al (1973) found rhesus males to have significantly higher levels of plasma testosterone during the mating season than during the sexually quiescent phases of the year. This data indicates that a relationship, although not necessarily a causal one, exists between plasma testosterone and male libido. It seems therefore, that changes in levels of testosterone within individuals might be a more important variable than differences between males in trying to unravel the relationship between hormones and behaviour.

The circadian rhythm of circulating gonadal hormones, with an early morning peak, seems a widespread pattern among male mammals, and it seems likely that it also exists in male chimpanzees. The similarity of pattern of the endocrine and behavioural rhythms is striking, and it is tempting to speculate that the high early morning levels of sexual activity may result from the peak levels of circulating gonadal hormones.

Females Circadian periodicity of two ovarian hormones (progesterone and estradiol) has been reported during the luteal phase of the rhesus monkey menstrual cycle (Spies et al, 1974), but no diurnal variations in levels of progesterone, estradiol or LH were found during the follicular phase. The lack of evidence concerning diurnal rhythms of ovarian hormones combined with the available behavioural data suggest that this is not a significant factor in determining periodicity of sexual behaviour.

The rates of complete and incomplete copulatory sequences showed similar diurnal fluctuations. In the majority of cases, it is the females' active avoidance or passive nonresponse that terminates copulatory sequences prior to intromission (see Chapter 5, Section 12). As the data indicate that the proportion of copulatory sequences that remain incomplete shows no diurnal periodicity, we can conclude that female receptivity shows no circadian periodicity. Michael (1968) showed that female attractiveness in rhesus monkeys is dependent on a vaginal pheromone whose production is under oestrogen control. The vaginal opening of female chimpanzees is frequently inspected by other individuals, and this behaviour suggests that pheromones are also produced by chimpanzees. As no diurnal fluctuations in levels of oestrogens are known, it seems likely that chimpanzee female attractiveness, like female receptivity shows no diurnal fluctuations.

The circadian periodicity found in copulation rates is not related in a simple manner to any of the variables investigated. Other gross behavioural categories show diurnal periodicity, but these do not relate to the fluctuations in copulation rates. Physiological rhythms have been reported for nonhuman primates, but few data are available for the chimpanzee. Male gonadal hormones show marked diurnal fluctuations in some species, and the pattern of circadian periodicity matches the pattern of fluctuating copulation rates. However, as the relationship between male libido and hormone levels remains unclear, conclusions about causality must remain tentative.

Chimpanzees are generally inactive during the night and although systematic observations of nocturnal behaviour are lacking it is unlikely that any sexual behaviour occurs during the hours of darkness. As male chimpanzees, like humans, show a latency period between successive ejaculations, the period of nocturnal abstinences would result in all males being simultaneously capable of copulation. While this probably has some effect on early morning copulation rates, particularly the very high rate in the first hour of the day, it alone cannot account for all the observed fluctuations.

The observed periodicity is almost certainly a result of a number of interacting variables and the nature of the study makes it impossible to assign, or even accurately assess, the relative contributions of the individual factors. In this section of analysis, the data were presented without regard to mating pattern - an important variable which will be considered in detail in Chapter 6. The nature of the mating pattern has a tremendous effect on copulation rate, but as the different mating patterns show no consistent relationship to time of day, it was felt that the effect of this variable would cancel out over females, so that the data could safely be combined in considering circadian periodicity.

5. Discussion

Seasonality of breeding and consequently births is a widespread phenomenon in the animal kingdom and is generally considered to be a result of the selective advantage incurred by producing offspring at times when their survival is optimal. For species where the period of infant dependency exceeds a year one would expect a reduced selective advantage for seasonal breeding. However, if the foetus or infant were particularly vulnerable at certain stages in development, such as early in pregnancy (McClure, 1967) or at birth, annual cycles of breeding might result in the timing of these vulnerable phases to avoid periods when food was scarce or disease frequent. The annual pattern of chimpanzee births indicates a non-random distribution which results in a concentration of births in the dry season and a tendency to avoid births during the wet season. The small sample size dictates cautious interpretation but some indications exist that the wet season is a high-risk time for disease. The annual distribution of chimpanzee births while being non-random, does not show a well defined peak or season, so it is difficult even to attempt to determine what environmental cues are responsible. However, as the frequency of female cycles also shows a non-random annual distribution, we can tentatively conclude that the observed distribution of births results from a seasonally atuned physiological mechanism and not simply from seasonal differences in foetal mortality.

The ovarian cycle is a fundamental mammalian pattern which in most species places constraints on sexual behaviour. Continuous female receptivity is uncommon, and the general pattern is of periods of receptivity interspersed with non-receptive periods in the non-pregnant female. In spontaneously ovulating species the periods of receptivity coincide with the time of ovulation. The active life of sperm, in the female reproductive tract, is short in most of these species and copulation must occur at, or around, the time of ovulation if conception is to occur. Towards this end, females have evolved patterns of behavioural and physiological communication which transmit information about their reproductive state to the male.

In chimpanzees the most obvious of these signals is the ano-genital swelling, the size of which changes dramatically during the course of the female cycle. The phase of maximum tumescence of the ano-genital swelling, which coincides with the period of female receptivity, i.e. oestrus, lasts an average of 9.8 days, and ovulation is thought to occur towards the end of this phase. The swelling at maximum tumescence almost certainly acts as a powerful long-range visual signal, being visible at distances up to 300m. The shiny pink surface of the swelling also greatly enhances its visibility in dim light at dusk and dawn. There is also some indication that a tumescent swelling facilitates the mechanics of copulation. Dixson (1975) found that male celebes apes (*Macaca nigra*) achieved intromission more frequently and with greater speed and ease after mounting females with maximally tumescent swellings than after mounting females at other times. The female ano-genital swelling plus more subtle olfactory cues from the vagina and aspects of female behaviour serve to attract and maintain large groups of males with the female during the time when conception can occur.

Copulations occur at high frequencies throughout maximum tumescence and at low-to-negligible frequencies at other swelling states. A maximally tumescent female with a large party of males may be mated 30-50 times in a 12 hour day, so that there is little possibility of a female not becoming pregnant if ovulation occurs. It might appear that a shorter receptive phase of 2-3 days at the time of ovulation would suffice, so that impregnation may not be the sole function of the receptive phase. Adaptively, it is important for the female not only to conceive but also to be impregnated by the fittest available male. The period of receptivity prior to ovulation allows the female to associate with all the available males and to enjoy the benefits of these associations, such as increased social grooming, and food sharing and the potential, at least, to form consort relationships. The female's level of attractiveness during oestrus, by bringing together large groups of males, allows the female to exercise some choice in the idntity of her impregnator. Gorilla females, who because of the one-male group social structure, have no choice as to the identity of their impregnator, have an oestrous period of only 1-4 days (Nadler, 1975).

There is marked circadian periodicity of chimpanzee copulation rates. The early morning peak of copulatory activity may be a behavioural response to the zenith of levels of circulating testosterone within each male, combined with the period of nocturnal abstinence. Evidence exists of a circadian rhythm in the time of ovulation in women, with it occurring more frequently during the night (Malek, 1962). If this were also the case in chimpanzees, males who concentrate their copulations early in the morning might have an adaptive advantage. Because of the period of nocturnal abstinence and the short lifespan of sperm, competition between sperm of different males within the female's vagina, might be reduced in the early morning. It seems likely that if ovulation occurs during the night, an advantage will be gained by the sperm of the first male to copulate with the female the next morning. However, this alone seems insufficient to account for the early morning peak in copulatory activity, since rates remain high for the first two hours of the day.

CHAPTER 5

Copulatory Behaviour Patterns and Promiscuous Mating

1. Introduction

The mating system of a species is usually easy to recognise if long-term observations are made in the natural habitat, and it can be categorised into one of the main types, promiscuity, polygamy (more specifically polygyny or polyandry) or monogamy. In non-promiscuous mating systems, bonding between individuals of the two sexes exists, although the duration and intensity of the bonding may vary enormously. It was probably this fact, the species-specificity of one of these main types of mating system, which led early field workers to prematurely describe the chimpanzee as having a promiscuous mating system (Goodall, 1965; Kordlandt, 1962; Nishida, 1968). Whilst the data now available indicate that no long-term, exclusive sexual bonds exist between adult chimpanzees of the opposite sex, it has become apparent that promiscuity is not the only, or even the predominant, mating pattern shown by wild chimpanzees (McGinnis, 1973; van Lawick-Goodall, 1975; Tutin, 1975).

Because of the chimpanzee's complex situation certain terms require definition. Following standard usage mating system will be used to denote the total reproductive behaviour of the species, i.e. the chimpanzee mating system is variable and not classifiable in terms of a single main type. Similarly, mating pattern will be used to denote the different sub-systems of the mating system. Three such patterns have been identified in the wild chimpanzee population at Gombe. The first is promiscuity, following common usage to mean that two or more males copulate with a single female without overt signs of competition. Selander (1972) pointed out that this term has been used inappropriately as synonomous with "random mating", which seldom or never actually occurs. The second mating pattern is possessiveness, in which a single male, or more rarely two closely related males, maintain spatial proximity with a maximally tumescent female and may prevent other males from copulating with her (see Chapter 6). The third mating pattern involves the formation of temporary, monogamous consortships, in which an adult male and female avoid other members of their community, often moving to the edge or outside of the normal community range (see Chapter 7).

There are other examples of species which show variability in mating patterns. Some avian species pair either monogamously or polygynously, e.g. red winged blackbirds (Orians, 1969). The potential for variety and its expressed form may result from the relative environmental qualities of the territories held by individual males. A female's reproductive success may be greater if she joins an already paired male who holds a high quality territory, than if she joins an unmated male with an inferior territory. The variability in chimpanzee mating patterns does not relate in any obvious way to environmental factors. A female may participate in different patterns during a single sexual cylce, and all adult males have the potential to show each type of mating pattern.

Van Lawick-Goodall (1968, p. 219) briefly described each type of mating pattern but did not elaborate on their relative frequencies or inter-relationships. McGinnis (1973) described consortship formation and discussed some of the variables which appeared to affect its expression. In the next 3 chapters I shall describe first the basic patterns of chimpanzee sexual behaviour which are common to all the mating patterns, and then each mating pattern in detail, in an attempt to elucidate the structure of the mating system of wild chimpanzees. Finally, I shall attempt to assess the relative importance of the mating systems in terms of impregnating females.

2 Copulatory Behaviour Elements

i. Introduction

A copulation was defined as an interaction between a male and a female which included at least one intromission. Some copulations included multiple intromissions, and to be classified as separate copulations, intromissions had to be separated by at least 10 minutes of non-interaction between the two individuals. Copulatory behaviour patterns were those shown in interactions which included intromission. Few of the patterns were unique to the copulatory context but the way in which they were combined allowed unequivocable recording, in most cases. Behaviour patterns shown in the combinations typical of copulatory sequences but observed in interactions which did not lead to intromission were also recorded, as incomplete copulatory sequences (see below).

The elements of copulatory behaviour recorded during this study coincided almost exactly with the units of description used by van Lawick-Goodall (1968; and unpublished glossary) and McGinnis (1973). Definitions of all the behaviour patterns appear in Appendix 1, Plates 1-10 illustrate selected patterns. Table 1 lists the behavioural elements recorded, divided by sex (whether exhibited by the male, the female, or both) and by time (whether shown before or after intromission, or both).

The distribution of the elements of copulatory behaviour by time and sex indicates the nature of the interaction. There were few female-specific patterns, whilst there were 12 patterns exclusive to

Table 5.1. Behavioural elements exhibited in copulatory sequences

	Male	Female	Both
Pre-intromission:	bipedal	scream	advance
	branch shake	present	approach
	branch jerk	fend	avoid
	hair erect		follow
	hunch		gaze
	male invitation		glance
	penis erect		look away
	penis adduct		scratch
	rock		
	stamp		
	arm stretch		
	contact		
* Post-intromisson:	thrusting	grin	end intromission
	copulatory pants	squeal	self inspect
	wipe	dab	
	ejaculation	hit away	
Both:	whimper		self groom
	inspect		social groom
	penis manipulate		kiss
	hand-on-branch		extend hand
			touch
			play
			turn towards
			turn away
			leave

* In this category are behaviours which occurred after intromission had been initially achieved, some of which occurred during intromission.

Plate 5.1 Satan tactilely inspects Miff after she has presented to him.

Plate 5.2 Atlas visually inspects Sparrow's perineum during travel.

Plate 5.3 Satan, with penis erect, branch shakes and gazes during courtship.

Plate 5.4 Mike, with hair out, arm stretches as he approaches Gigi, who ignores his courtship.

Plate 5.5 Goblin sits in the male invitation posture as Pallas approaches to present to him.

Plate 5.6 Jomeo arm stretches to Winkle, who approaches him. This is a greeting interaction, note that Jomeo does not have a penile erection.

Plate 5.7 Goblin copulates with Pallas. Goblin is in the leanback posture. Pallas crouches and has a full open grin.

Plate 5.8 Mustard copulates with Patti.

Plate 5.9 Satan copulates with Little Bee. Satan is in the mount posture and Little Bee in a low crouch.

Plate 5.10 Goblin self inspects as Pallas leaves, ending intromission.

the male which were performed prior to intromission. These behaviours constitute a complex of courtship behaviour. The elements which were shown by either sex prior to intromission are mainly to do with spacing and visual orientation with respect to the other interactant. The exception, scratching, is considered a displacement activity and was predominantly shown by males, interspersed with courtship patterns, when a female did not approach in response to courtship gestures.

The group of 10 non-sex-specific elements which were shown either before or after intromission are spacing and orientation patterns plus grooming, play and reassurance patterns. Grooming occurred most frequently in the social form of the male grooming the female after intromission. Both self and male-to-female inspection usually occurred after intromission when, in both cases, attention was focused on coagulated semen. Male-to-female inspection occasionally occurred before intromission.

ii. Courtship

Bastock (1967) discussed the problems of adequately defining courtship. She pointed out that although there is usually no difficulty in recognising courtship (meaning the displays shown by the males of many species to their female partners immediately prior to mating), some species have several distinct displays and types of interaction which although temporally separated from copulation do influence sexual behaviour. Morris (1956) defined courtship as "the heterosexual reproductive communication system leading up to the consummatory sexual act". This broad definition is useful as it emphasises that many different types of interaction between males and females can influence their sexual behaviour even if far in advance of copulation. This applies to chimpanzees and other primates in which memories of previous experiences and interactions with group members undoubtedly affect sexual behaviour. For instance the 'adoption' of young, pre-pubescent female Papio hamadryas by subadult males (Kummer, 1968) must be considered as courtship in terms of Morris' definition, as this behaviour selects the female's sexual partner, even though the consummatory sexual act will not take place for up to 2 years.

While agreeing in principle with the wisdom of Morris' broad definition, I propose here to limit the term courtship to the male-female interactions which immediately precede copulation. I do this for practical reasons for it is difficult to religate any type of male-female interaction in chimpanzees as being unimportant in determining the two participants in any copulation. In this situation, Morris' broad definition renders the term too all-inclusive to be of value. This is not, however, to dismiss the salience of the other types of interaction, and their relevance will be described later.

Chimpanzee courtship constitutes a distinct and easily recognisable complex of behaviours. Whilst many of the individual patterns occur in other contexts, the form and combination leading to intromission is unique. When directed to a receptive (i.e. maximally tumescent) female male courtship usually lasts less than one minute before intromission. The mean number of behavioural elements in a sample of 200 courtship sequences was 4.6 and the overall range in the 1084 courtships observed was 2-87 elements. (Each element was counted each time it occurred.) Table 5.2 lists the frequency of each behavioural element in a sample of 200 courtship sequences. (Every fifth courtship up to the thousandth was selected from the total data.)

Figure 5.1 shows a flow chart of the behavioural elements

Table 5.2 Occurrence of behavioural elements in 200 courtship sequences

Element	Times observed	Element (contd.)	Times observed(contd.)
penis erect	200	male glance	19
female glance	164	bipedal	15
male invite	126	arm stretch	14
male gaze	82	rock	13
hand-on-branch	69	hunch	5
hair erect	63	female gaze	5
branch shake	60	stamp	2
penis adduct	28	branch jerk	2

observed in 32 copulatory sequences involving Faben and Gigi (the adult male-adult female dyad on whom the most data were available). The 3 type sizes indicate 3 degrees of frequency of the behavioural elements. The smallest type denotes elements occurring in 25-33% of interactions, the middle type, those occurring in 34-67% of interactions and the largest type, those occurring in over 68% of interactions. The lines between the elements represent transitions from one element to another in the direction indicated by the arrows. The 4 line ticknesses, from narrowest to widest, represent 10-25, 26-50, 51-75 and 76-100% of cases, respectively. These percentages were calculated from the proportion of the total occurrences of element A which were immediately followed by element B. Elements which occurred in fewer than 25% of interactions, and transitions comprising less than 10% of the total for each element, were omitted for the sake of diagrammatic clarity.

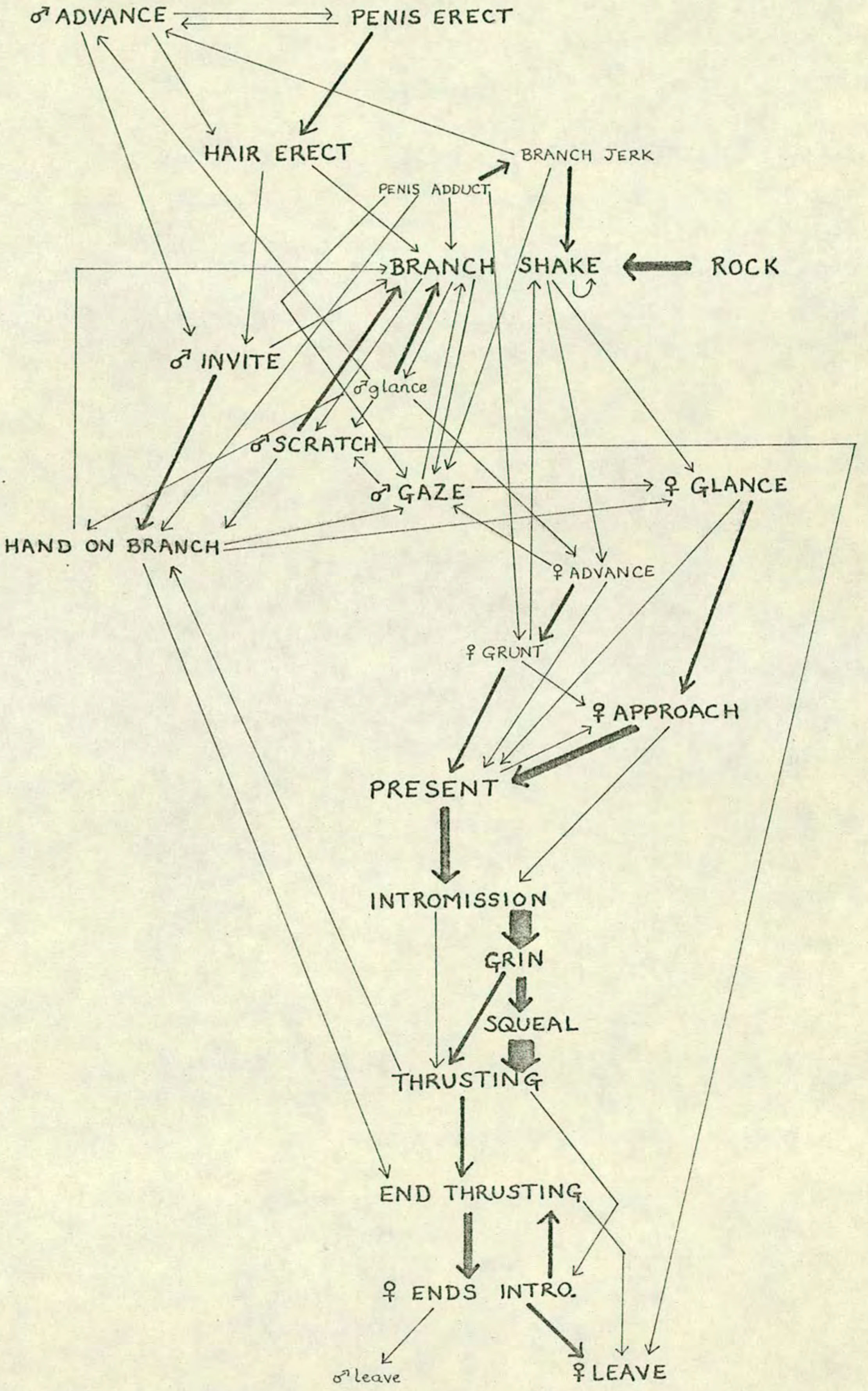
The copulation can be divided into the pre- and post intromission phases. The lack of a consistent sequence of events during courtship (i.e. the pre-intromission phase) is immediately striking. Only 7 (19%) of the 37 transitions between courtship elements comprise more

KEY TO FLOW CHARTS (FIGURES 5.1, 5.2 + 5.3).

ELEMENT	occurring in > 68% of total sequences
ELEMENT	occurring in 34-67% of total sequences
element	occurring in 25-33% of total sequences

→	10-25% of total transitions
→	26-50% of total transitions
⇨	51-75% of total transitions
➡	76-100% of total transitions

Figure 5.1 Sequences of behavioural elements shown in 32 copulations between Faben and Gigi.



than 25% of the total transitions for the individual elements. There is less variation in the behavioural elements shown. Eight of the 12 courtship elements shown in Figure 5.1 occurred in at least 68% of the total interactions. The typical general sequence of events began when the male, with penis erect, advanced to within sight of the female (if he had not previously be so). He then directed a variety of courtship elements towards the female, the commonest being branch shake, hair erect, male invite, gaze and hand-on-branch. These continued until the female responded, normally by glancing, approaching, and presenting to the male. The male rarely showed courtship elements after the female had begun to move towards him. Once the female presented to the male he effected intromission and made 3-30 pelvic thrusts (the mean was 9 for Faben and Gigi), before intromission was terminated by the female moving away. Faben and Gigi interacted little after intromissions and although grooming and inspection occurred occasionally, it was in less than 25% of the total interactions and so does not appear in Figure 5.1.

McGinnis (1973) discussed reasons why most male courtship occurs when the pair are further than 1.5 meters (arms' reach) from each other. He concluded that because several patterns shown during courtship, especially the autonomic pattern, hair erect, also occur in male aggressive displays, the female may be placed in an approach-avoidance conflict. This will be minimised if the male remains some distance from the female, allowing her to approach him.

Figure 5.1 illustrates the copulatory interactions of one dyad, and although minor variations existed across adult male-adult female dyads, these were limited to small differences in the relative frequencies of courtship elements and some variability in the frequency of post-intromission elements. Scanning the flow charts of interactions of other dyads (see examples in Appendix II) indicated that the inter-dyadic differences were too slight to warrant elaboration. The pattern of considerable intra-dyadic variability in the sequencing of courtship elements held true for all adult dyads, and this made inter-dyadic comparison difficult. Diversity in the copulatory behaviour of different age classes of males was much greater, and this is described below.

iii. Function of courtship

Courtship displays are widespread amongst both vertebrates and invertebrates. Its general function was long considered to be the facilitation of, first, recognition of the species, and second, identification of the sex of others. A less obvious function of courtship which has recently received considerable attention is the opportunity that it may provide for females to *select* a mate from among the available males. In some species the criteria used for selection by the females have been established. For example, in *Drosophila melanogaster* wing movements are an important part of male courtship, and various mutants have been found to show relatively ineffective courtship (Bastock, 1956). She found that the courtship of mutants with vestigial wings was slow to arouse females and that of a yellow-eyed mutant with reduced general vigour, was dramatically less successful in inducing females to allow copulation. The implication is that females have evolved the ability to discriminate between males based on the quality of their courtship displays, and that the male mutants' performances do not excite the female to a level where she will allow copulation. In avian species in which reproduction is linked to male-held territories, females of some species, such as the ruff (*Philomachus pugnax*), select a male on the basis of his territory size (Hogan-Warburg, 1966). In Some species territory size can often be related directly to productivity, and so the male's ability to maintain a large territory in competition with other males will directly benefit his offspring by increasing their chances of survival (Lack, 1968).

In some animal species the female makes a higher pre-conception investment in reproduction than the male, due to the dimorphism in gamete size, although in other species this may be balanced by the male producing vast numbers of gametes. In almost all warm-blooded species there is disproportionate investment by the female after conception and throughout the period of infant dependency. Thus females which can recognise differential genetic quality amongst the available males will gain a selective advantage. Similarly, males who possess a superior genotype and are able to advertise it in a way comprehensible to the females will gain a selective advantage. Darwin (1871) recognised the importance of this sexual selection, which does not concern individual survival per se, but the maximisation of an individual's reproductive achievement. Two types of sexual selection are recognised; The first is inter-sexual or epigamic selection; the second is intra-sexual selection, which operates on characters used in competition amo g members of the same sex, usually males, when the result of such competition affects reproductive success, see Chapter 1, section 2i. Courtship falls into the first category, as only interactions between members of the opposite sex can sensibly be considered as courtship.

Problems arise in attempting to assess the function of chimpanzee courtship in terms of either of the two general explanations described above. That courtship should function to allow correct species and/or sex identification is untenable; ample evidence exists to show that chimpanzees are capable of far more complex discriminations without the aid of specialised behavioural interactions. The second explanation also appears of little value, as in the previous section it was found that only minor differences exist in the courtship behaviour of individual males and that intra-individual differences are great. Whilst it remains possible either that the small difference detected in the form and sequencing of male courtship patterns are used by females to discriminate between males, or that more subtle differences exist but were not detected by the recording method seems unlikely. A more cogent explanation of the function of chimpanzee courtship exists.

My limitation of the term courtship was done for convenience and not out of disregard for the importance other types of social interaction may have on sexual behaviour. It seems unlikely that an intelligent, long-lived, social species would use only the brief interaction preceding copulation to determine a female's choice of mate. A more plausible explanation is that a female's discriminations and choices are based on previous experiences with the adult males and that courtship merely serves to attract her attention to the fact that at that particular moment, the male is motivated to copulate with her. No primates have pre-copulatory courtship displays to rival those of many bird and insect species in their elaborateness or duration, and this can be explained by the differential opportunities and/or capacities that these species have to gain and store information about the qualities of their potential mates.

Many of the elements observed in chimpanzee courtship have auditory and visual components which serve to attract the female's attention and to direct it to the male's erect penis. Branch shaking creates a distinctive sound not heard in other contexts. Once the observer had become attuned to this sound, it frequently served as the first cue directing attention to a courting male. Branch jerking, rocking and stamping also have an auditory component and patterns such as hair erect and hunch make a male appear larger in size. The male invitation posture and penile adduction served to direct the female's attention to the male's erect penis.

iv. Copulations without courtship

The presence of a penile erection does not in itself constitute courtship as penile erections do occur in non-sexual contexts of high arousal. Only 3 copulations involving adult males were observed in which the male had a penile erection but showed no other courtship elements prior to the female approaching and presenting. On 12 other occasions maximally tumescent females approached and presented, sometimes repeatedly, to males who had penile erections, but intromission did not occur. Such behaviour, when a female approaches and presents to a male who shows no courtship is referred to as female solicitation. An example was observed on November 19, 1973; Pallas was maximally tumescent and was accompanied by 4-7 adult males throughout the day. Between 15.00 and 15.17, she approached and presented to Sherry 5 times. Sherry had a penile erection throughout, but he showed no courtship gestures and ignored or avoided Pallas each time she presented. Finally Pallas left Sherry and groomed with another male. At 15.20 Sherry, still with an erect penis, gazed at Pallas and shook branches; Pallas glanced up and immediately approached and presented to Sherry, who mated her.

This observation, combined with the rarity of female solicitation, suggests that a penile erection does not in itself indicate a male's willingness to copulate. This reinforces the earlier conclusion that it is courtship which serves this purpose.

v. Courtship without copulation

I saw 209 courtship sequences which did not lead to intromission. In the vast majority (86%) the avoidance or non-response of the female terminated the interaction. In 10% of cases the interaction was terminated by extraneous events such as group aggression, inter-community encounters or predations, which distracted one or both members of the dyad, terminating the interaction. In the remaining 9 cases (4%) the male ended the interaction after courting the female but then no responding when she approached and presented. Twice females responded aggressively to the male: Gigi hit out, striking Satan across the face, and Patti attacked the infant male Freud.

Courtship behaviour patterns commonly occurred during possessive and consorting behaviour unaccompanied by penile erection. The patterns functioned in these contexts to induce the female to follow the male and were referred to as leading behaviour (see Chapters 6 & 7).

5.3 Reaction of other individuals to copulations

i. Adult males

Situations in which an individual adult male acted possessively to a receptive female and interrupted to other males' matings and mating attempts are discussed in Chapter 6. In promiscuous situations overt signs of competition between adult males for access to receptive females rarely emerged. Adult males normally showed no response to a copulation even if it occurred less than 5 metres away.

Several examples of apparent social facilitation occurred when a nearby male developed a penile erection during another's copulation and then courted and mated with the female immediately afterwards. This seemed to be especially true of the 2 pairs of adult male brothers, Faben and Figan and Jomeo and Sherry, and on numerous occasions they mated the same female, one brother immediately after the other.

I saw a few instances of 2 or more males simultaneously courting the same female. In most cases the female presented to the closer of the 2 males, and the other male showed no aggressive response but resumed his courtship once the first copulation finished. Pallas was once simultaneously courted by Satan, Hugo and Goblin as she descended from her nest early in the morning. After hesitating for a moment Pallas approached and presented to Hugo, who was closest to her, but before Hugo could intromit Satan charged towards them with his hair erect and Pallas avoided him, screaming. Hugo turned and attacked Goblin and Satan joined him, kicking and dragging the screaming Goblin downhill. After the attack, Satan and then Hugo mated Pallas. This, however, was the only case in which aggression was observed in a competitive mating situation. The data were insufficient to establish whether or not females showed any consistent preferences for particular males in such situations.

In promiscuous mating groups adult males typically show little or no overt competition for access to receptive females, and in some cases they seemed 'polite' in their approaches. Figan, the alpha male, twice approached with penis erect a receptive female who was being groomed by another adult male. In both cases Figan sat and groomed the male for several minutes before moving away slightly to court the female.

ii. Adult females

Only 2 cases were observed of adult females responding to copulations. On May 21, 1973, when Satan mated Sparrow, Miff (who was pregnant but had a $\frac{3}{4}$-full swelling) approached to about 3 metres and presented in parallel to Sparrow during intromission. While Satan thrust on Sparrow, Miff gave the typical copulatory squeal, and as intromission ended both Miff and Sparrow leapt away. During the copulation Miff behaved as if she were copulating, and she mirrored Sparrow's behaviour with perfect synchrony.

The other copulatory interaction which provoked a response from an adult female was between the juvenile male Mustard and Patti on January 28, 1975. Patti was one of 3 maximally tumescent females present in a large group, the other two being Gigi and Little Bee. Mustard courted Patti, and she responded quickly by approaching and presenting. Before Mustard could achieve intromission, Gigi charged towards them with her hair erect. Both Patti and Mustard avoided her, screaming as she charged up into the tree. Gigi pursued, approached and presented to Mustard, and he mated her.

While adult females' responses to others' copulations were rare during the present study, van Lawick-Goodall (1968, p. 242) reported that an old female (Flo) and her adolescent daughter (Fifi) frequently approached each other's matings and made physical contact, interfering in a way typical of infants and juveniles (see below). No similar mother-daughter dyad has been observed, so no conclusions can be drawn about the typicality of such incidents. It appears that adult females may occasionally react to the copulations of others in a way that could be considered competitive.

iii. Immature individuals

The commonest response to copulations by immature individuals was interference which was observed 340 times during the study. As mentioned earlier, some male courtship elements have visual and auditory components which attract the female's attention to the courting male. These same patterns also appear, in many cases, to alert youngsters, who respond by advancing to the male, often following the female. Interfering youngsters were never seen to make contact with either the male or female before intromission, but usually did so immediately intromission began. In the 340 interferences, the interferer made contact with the copulating male in 72%, and the female in 28%, of cases. In 91% of the cases where contact was made with the copulating female, the male was also contacted. In these cases the contact with the female appeared to be incidental and an intermediate step (often literally) towards contacting the male, see Plate 5.11. Orientation was towards the male in over 90% of cases, and the interfering individual most often touched his head. Two typical cases were:

1) March 2, 1973; copulation between Miff and Satan: Moeza (Miff's 4 year old daughter) runs up, approaching Miff and Satan just as they achieve intromission. She climbs onto Miff's back and looks towards Satan. Moeza extends her hand to Satan's mouth, and Satan bites her hand gently while giving copulatory pants. Moeza has a full closed grin and squeaks softly. As Satan stops thrusting, both Miff and Moeza leave him, running 5 metres and then turning to face him. Satan approaches and grooms Miff, and a few seconds later Moeza joins them and also grooms Miff.

2) May 26, 1973; copulation between Gigi and Jomeo: Gigi and Jomeo are on the ground, and as intromission begins Atlas (5½ year old, unrelated juvenile male) hangs from a small tree above them and extends his hand, putting it into Jomeo's open mouth. Atlas then jumps from the tree and contacts both Jomeo and Gigi, keeping his hand in Jomeo's mouth. Jomeo has a full open grin and Atlas also grins briefly.

Plate 5.11 Goblin interferes in a copulation between Satan and Little Bee, lying across Little Bee's back and leaning towards Satan.

Plate 5.12 Goblin moves away from Satan as intromission ends but gazes back as Satan self inspects.

As thrusting ends, Gigi leaves. Atlas breaks contact with Jomeo but remains close to him and watches his penis.

Goblin, an adolescent male, interfered frequently but showed much ambivalent behaviour, rarely making contact with the copulating pair. For example, on December 12, 1974, during a mating between Satan and Patti: Goblin advances, running towards Satan and Patti as intromission begins. He pant grunts and stops 4 metres away from them. Goblin extends a hand towards them but is too far away to make contact. He has a full open grin and gazes at Satan's face. As intromission ends Goblin moves 7 metres away and sits watching as Satan grooms Patti.

In most cases the interferer left as intromission ended and did not interact further with the copulating pair, see Plate 5.12. More rarely the interferer stayed close to the male watching his penis or on two occasions, presenting to him, see Plate 5.13. Thus, interference is limited almost completely to the duration of intromission and is directed towards the copulating male. The interferer's behavioural elements are submissive and fearful, aggressive patterns are absent. Van Lawick-Goodall (1968, p. 220) described interference patterns shown by young chimpanzees and reported that the sex of the youngster and the identity of the copulating female, specifically whether or not she is the mother of the interferer, affected the form and frequency of the behaviour.

The data collected during the present study support van Lawick-Goodall's conclusions on these two variables and also indicate that the age of the youngster is another salient factor. Table 5.3 lists the 17 immature individuals (by sex and in decreasing age order) whose reactions to copulations were seen at least 10 times.

Plate 5.13 Freud presents to Satan immediately after interfering in a copulation. Satan touches Freud's back.

Table 5.3. Response of immature chimpanzees to copulations of others

		Response to Copulation		
	Age-class	Interference	No response	Total
MALES(N=8):				
GOBLIN	juv.-adol.	203(40%)	302(60%)	505
MUSTARD	juv.	11(15%)	61(85%)	72
*ATLAS	juvenile	49(36%)	87(64%)	136
BEETHOVEN	juvenile	17(81%)	4(19%)	21
FREUD	infant	11(11%)	87(89%)	98
PROF	infant	1(2%)	40(98%)	41
WILKIE	infant	1(1%)	114(99%)	115
MICHAELMAS	infant	0	17(100%)	17
TOTAL		293(29.2%)	712(70.8%)	1005
FEMALES(N=9):				
POM	juvenile	0	50(100%)	50
*SPRAY	juvenile	9(53%)	8(47%)	17
*MOEZA	juvenile	29(18%)	132(82%)	161
GREMLIN	infant	8(7%)	106(93%)	114
DOMINIQUE	infant	0	23(100%)	23
APHRODITE	infant	0	13(100%)	13
LOLITA	infant	1(3%)	35(97%)	36
SWALLOW	infant	0	18(100%)	18
VILLA	infant	0	16(100%)	16
TOTAL		47(10.5%)	401(89.5%)	448

* Individuals whose mother's copulations accounted for at least 25% of the total copulations at which they were present.

[redacted]

The mothers of 6 of the individuals in Table 5.3 showed cycles of sexual swelling during the study period, affording an opportunity of observing a youngster's reaction to copulations involving the mother. Sufficient data were available only on Atlas, Moeza and Spray, as Goblin, Gremlin and Swallow were observed only rarely when their mothers were being mated. Sufficient data are available to allow individual comparison of Atlas's and Moeza's responses to copulations involving their mothers and to those involving other females. Both interfered significantly more often in copulations involving their mothers, see Table 5.4. [redacted]

5.4 Development of Interference

Very young infants did not show interference. Only the oldest two (Freud and Gremlin) of the 10 infants observed showed more than isolated cases of interference, see Table 5.3. Gremlin was only seen to interfere in copulations involving either her mother or her elder brother, Goblin. On 3 occasions she approached and contacted Goblin while he was copulating. Although these were recorded as interference, Gremlin showed no signs of the distress and arousal typical of intereference but appeared to be motivated by curiousity. Each time she sat on the female's back watching closely as Goblin made pelvic

Table 5.4 Comparison of interference responses shown to copulations involving the mother and to those involving other females.

	Copulations of mother			Copulations of other females		
	Interfere	No response	Total	Interfere	No response	Total
ATLAS	29	6	35	20	81	101
($X^2=28.7$, df=1, $p<.001$)						
MOEZA	29	90	119	0	42	42
($X^2=10.3$, df=1, $p<.01$)						
SPRAY	10	1	11	0	7	7
(Binomial test: $x=0$, $p<.001$)						
TOTAL	68	97	165	20	130	150

thrusts. Twice after the copulation ended Gremlin inspected both the female's perineum and Goblin's penis. In October 1973, Gremlin's mother, Melissa, showed her first cycle of sexual swelling since Gremlin's birth in November, 1970. Melissa was only observed to mate 6 times, and on 5 of these occasions Gremlin interfered, with high intensity patterns, such as screaming, grinning and grabbing or pushing at the male.

Freud was first observed to interfere in December, 1974, at the age of 3 years and 7 months. At that time his mother, Fifi, had not yet shown any postpartum swelling cycles. Freud interfered in a very gentle way and showed no distress. He usually approached and peered at or embraced the male, remaining in contact until intromission ended. In February, 1975, Fifi began to show cycles of sexual swelling, and Freud interfered in most of her copulations, showing high intensity patterns similar to those described for Gremlin (Pusey, pers. comm.).

Sparrow resumed sexual cycles when her daughter Swallow was only 11 months old. They were observed infrequently in December 1974 when Sparrow was maximally tumescent and Swallow's reactions to 3 copulations involving her mother were observed. Swallow, aged 14 months, stayed ventral on her mother during all 3 matings and made no observable response. This agrees with van Lawick-Goodall's report (1968, p.248) that Goblin, at the same age, made no attempt to interfere when males copulated with his mother. The 7 other infants, aged between 9 and 39 months, interfered rarely or never in copulations involving other females, but none of their mothers' had yet resumed cycles of sexual swelling.

The emergence of interference is apparently not merely a developmental stage governed by social or physical maturation, since the age at which it first appears is variable. Locomotor independence of a degree sufficient to permit interference is present by the age of 2 years, and yet the behaviour does not appear until much later in some individuals. The mother's first post-partum swellings seems a significant point, as this was when two infants first showed intense interference. However, in males, at least, the patterns once established towards the mother's copulations generalise to include copulations involving unrelated females. Weaning is a traumatic event for chimpanzee infants and often coincides with the mother's first post-partum swelling cycles. Both Freud and Gremlin experienced this, as did other individuals cited in van Lawick-Goodall (1968, p.248). Swallow was an exception, as Sparrow's post-partum cycles started long before weaning.

Fewer data are available on the cessation of interference but 3 adolescent females (Sparrow, Patti and Little Bee) never showed it during the study, nor did any adults. While adult males were usually very tolerant of interfering youngsters, two notable exceptions occurred. One of these, the responses to interference by the juvenile male Beethoven, is described below, and the other was in the increasingly aggressive responses shown towards interference by Goblin from late in 1973.

As can be seen from Table 5.3, Goblin was present at almost half of the copulations observed during the study. He responded to 40% of these by interfering. During the first 6 months of the study Goblin's interference was tolerated by all the adult males, but changes emerged during 1973. No observation was made during August-September, but from October onwards Goblin's interference elicited aggressive responses from the copulating male more and more frequently. The males showed considerable individual differences, as some consistently threatened him while others continued to tolerate his interference. Goblin soon stopped interfering in the copulations of the males who threatened or attacked him, but he continued to interfere often in the copulations of males who remained tolerant. Table 5.5 shows the frequency of interference for copulations involving the 9 adult males from October 1973 - January 1975. Hugo and Faben showed the highest frequency of aggressive responses to Goblin's interference, and during December 1974

Table 5.5 Goblin's pattern of interference, October 1973-January 1975

Male	No. of copulations at which Goblin was present	No. of times Goblin interferes	No. of aggressive responses shown by male
HUGO	16	4	3
MIKE	5	1	0
HUMPHREY	26	5	2
FABEN	19	6	5
EVERED	4	2	0
FIGAN	37	17	3
JOMEO	23	16	1
SATAN	22	16	2
SHERRY	25	14	6

and January 1975, Goblin was never seen to interfere in their copulations. He continued to interfere in the copulations of Figan, Satan, Jomeo and Sherry, but showed increasing ambivalence, approaching but rarely making contact with either of the pair, and squeaking, grinning and extending his hand towards them. Goblin may have been atypical in continuing to interfere in copulations as an adolescent. Van Lawick-Goodall (1968, p. 220) reported that interference by juveniles was uncommon and that she had never observed a juvenile male interfering. It is not yet possible to draw any definite conclusions about the degree of individual difference existing in the ontogeny of interference, but it seems to be a pattern of behaviour which decreases in frequency with age and is probably usually extinguished by adolescence.

Discussion

5.5. Motivation and Function of interference

Although interference in copulations by immature individuals has been described for a number of nonhuman primate species, e.g. Macaca iris (de Benedictus, 1973), Macaca arctoides (Gouzoules, 1974), Cercopithecus aethiops (Struhsaker, 1967) and Presbytis entellus (Jay, 1963), few authors have attempted to assess the motivational state of the interferers or the function of the behaviour. What effect does interference have on copulation? Struhsaker (1967) reported that harrassment by juvenile males "sometimes" terminated copulations, and Poirier (1970) reported one instance of a mating in Presbytis johnii being terminated by the interference of the copulating female's young offspring. In chimpanzees, the copulating pair generally tolerated interference and it made little or no difference to the act of copulation. Even when 3 juvenile males simultaneously interfered, literally engulfing the copulating pair, the copulation continued.

Ejaculation could only be recorded with certainty in 30% of observed copulations during the study. The proportion of copulations with interference, in which ejaculation was recorded was slightly less, but not significantly different from those in which interference was absent (X^2=2.01, df=1, n.s.). Similarly, harassment by young individuals was not observed to terminate matings in either Macaca iris or Macaca arctoides (de Benedictus, 1973; Gouzoules, 1974).

The behaviour of young chimpanzees during interference indicates that they are excited but submissive and ambivalent in their approach to the copulating pair. There is no indication of aggressiveness. In 14% of the observed cases of interference, the copulating male directed reassurance gestures to the interferers, usually by kissing or patting. This was commonest when the interferer expressed intense submission by grinning and screaming. However, Beethoven was atypical in this respect as he showed intense and persistent interference which evoked aggression in 10 of 17 observed interactions. Beethoven was assumed to be an orphan of 4-5 years of age. He immigrated into the Kasakela community during 1974 accompanying his presumed sibling, the an adolescent female, Harmony. His interference was the most frequent of all the youngsters observed, and he behaved in a distinct way. A typical case occurred on December 12, 1974, when, during a copulation between Patti and Satan, Beethoven approached, climbed onto Patti's back and grabbed Satan's cheek hair with both hands. During intromission Beethoven stayed in this position, screaming into Satan's face. When Patti left, Beethoven remained clinging to Satan's cheek hair, which now supported his whole weight. Satan then grabbed Beethoven and attacked him, biting his back, before flinging him away. Beethoven is thought to have been orphaned at approximately 3 years of age. He behaved atypically for his age, and was never observed to copulate. During interference his attention was always completely focussed on the male, and he continued to show the behaviour despite the high frequency of attacks that resulted.

De Benedictus (1973) found that the young iris macaques in the captive group she observed responded with excitement to copulations, rushing around an adult male as he "stalked" females prior to intromission, often mounting each other. During intromission they watched closely and sometimes touched the male. She concluded that the excitement aroused in the youngsters served to focus their attention on the act of copulation and that close observation "might contribute as much to sexual development in primates as do mother-infant ties and peer-group interactions". If observation learning does play an important role in the development of sexual competence, then behaviour which leads to repeated close contact with copulating adults would gain selective advantage. This explanation seems somewhat unlikely for two reasons. Firstly, other species of macaque, such as Macaca mulatta, do not show interference or harassment of adult copulations. Secondly, in a captive group of chimpanzees raised with only peer experience, competent copulatory behaviour appeared at adolescence (Tutin and McGrew, 1973b). Interference may provide opportunities for observation learning and may contribute to the development of sexual behaviour in the young of species in which it occurs. However, de Benedictus' conclusion that the opportunities provided for observation learning are of primary importance in understanding the function of interference, seems unlikely.

Gouzoules (1974) postulated a functional explanation of interference performed by adults and youngsters in copulations of Macaca arctoides. In this species the male has been observed to bite the female on the neck or arms during copulation, sometimes inflicting noticeable wounds (Blurton-Jones & Trollope, 1968). Gouzoules suggested that the close proximity of other animals during intromission and the subsequent copulatory tie, serves to re-direct the copulating male's aggression to the harassers and away from the mounted female. The main weakness in this argument is that male aggression towards females in the copulatory situation may be atypical, as it has principally been observed in restricted pair matings of relatively unfamiliar animals. The behaviour was rare in Gouzoules' group-living subjects and has not been observed in another colony of stumptail macaques who live in large group cages (Chamove, pers. comm.). Even if Gouzoules' argument were correct, it is difficult to envision a way in which such altruistic behaviour could have evolved amongst unrelated individuals.

Temerlin (1975) described the responses of Lucy, a home-raised chimpanzee, to the sexual behaviour of her human 'parents'. Lucy showed no responses until she was 2½ years old, but from that age "intercourse has disturbed her and she always tries to stop it. Curiously, she seemed to make the same interpretation of it that human children make when they witness parental intercourse: Daddy is hurting Mother, or at least an aggressive and dangerous act is taking place. I say this because Lucy tries to stop it with the same appeasement behaviors which she uses to stop or minimise non-sexual kinds of inter-personal aggression." (p.130) Lucy's behaviour in this situation resembled that of Gombe chimpanzees, and she always directed her attention to her 'father'. Temerlin's interpretation of Lucy's response to sexual behaviour is plausible if one considers that young chimpanzees view copulation as a mild form of aggression. In a threatening-aggressive situation, such as high levels of group excitement, a wild infant seeks protection and reassurance in contact with its mother. However, in a high intensity aggressive situation, such as an adult male physically attacking a female, her infant is less likely to approach, and a juvenile almost always avoids such an encounter, rather than seek to make contact with its mother or her aggressor. A young chimpanzee is even less likely to approach an aggressive encounter between an adult male and an unrelated female. The double overlap of: 1) behavioural elements shown in courtship and aggression; and 2) behavioural elements shown by the female in sexual and submissive contexts, e.g. presenting, squealing/squeaking, could lead to confusion in the infants' interpretation of the motivational state of the courting male. This explanation would not account for the sex difference in the frequency of interference, and it also seems far-fetched to apply such a simplistic 'confusion' explanation to the behaviour of 7-9 year old juveniles, who have themselves been courting and copulating with females for several years.

Another possible explanation is that interference when directed to copulations involving the youngster's mother is an expression of the parent-offspring conflict over birth-spacing (Trivers, 1974). As resumption of the mother's sexual swelling cycles, and hence the commencement of copulations with her, coincides with the weaning of the infant and that weaning is not usually completed until the ensuing pregnancy (Clark, in press), it would be in the interests of the infant to do all possible to delay its mother's impregnation.[1] While this explanation is attractive in offering an obvious selective advantage to the behaviour, the data do not support it. First, as we have seen,

1. I am indebted to Gordon Jensen who first suggested this interpretation of interference to me.

the occurrence of interference does not significantly reduce the frequency of ejaculation. Second, this explanation cannot account for either the sex-difference in the frequency of interference, or the occurrence of interference in copulations of unrelated females.

The ontogeny of interference suggests clues as to motivation and the function of the behaviour. Its onset varies between individuals, with the commonest starting point being at about the time of the mother's first post-partum swelling cycles. Exceptions to this were the two infants (Goblin, in 1965 and Swallow, in 1974), who were less than 18 months old when their mothers resumed swelling cycles. Weaning is a prolonged and traumatic period for young chimpanzees, as they incur their first experience of maternal rejection. Normally the weaning process begins somewhat before the resumption of the mother's sexual swellings, and terminates around the time the mother next conceives. During this time many infants show a greater dependency on their mothers than they had in previous months and are liable to throw temper tantrums if rejected by their mothers (van Lawick-Goodall, 1968). It seems possible that during this time of emotional disturbance, the sight of copulations, particularly those involving the infant's mother, is very distressing. The conflict of wanting to approach the mother for comfort, but wanting also to avoid the male due to fear, could result in the distressed and submissive behaviours shown in interference. This explanation accounts for the fact that Beethoven, who presumably suffered greater trauma than most youngsters do at weaning, through the loss of his mother, shows more intense interference behaviour. However, like the previous explanations, this one does not account for <u>all</u> the data. It does explain the interference shown by all infants to copulations involving their mothers which occur during the weaning process. It does not however, account for the extension of interference to females other than the mother, except if one postulated an extension by association, to all copulations. However, this does not explain why male juveniles interfere more frequently than females.

During possessive incidents, adult males interrupt the copulations of other males (see Chapter 6, section 7). Such behaviour can have great adaptive value, but its expression and success is determined by social factors, especially social rank relative to other adult males. A link between the interference of young males and this later behaviour cannot be ruled out. It does not seem unreasonable to propose that interference by juvenile and in some cases, adolescent, males is based on the same motivational system - of attempting to monopolise receptive females. There are some agonistic patterns, particularly components of display, such as slap-stamping, which are shown by very young males in non-social situations, but which only appear in the full social setting when the male has reached a level of maturity and social status which permit such expression. A similar situation might exist with respect to interference. It was apparent that the decreasing frequency and increasing ambivalence of Goblin's interference during adolescence was a result of the increase in aggressive response from the copulating males, and not of any maturational change. This increase in aggressive response seems to result in interference being suppressed during adolescence.

Females rarely, if ever, interfere in copulations not involving their mothers, and the data indicate that the behaviour is only shown by female infants during their mothers' initial post-partum swelling cycles, i.e. at the time when these infants are being weaned.
Van Lawick-Goodall (1968, p. 248) reported that Fifi, when an adolescent, interfered in her mother's copulations. At the time Fifi

herself, was also sexually receptive and "she invariably solicited the male concerned as soon as he had finished copulating with her mother". Fifi's behaviour must be considered as competitive rather than as interference.

No single explanation of the motivation or function of interference accounts for all the facts. The facts are: 1) that all infants interfere in a proportion of their mothers' copulations; 2) females more or less restrict their interference to copulations involving their mothers, but males do not; 3) interference stops during adolescence, not as a result of a maturational change but as a result of a change in the response of copulating adult males to the interferer; and 4) patterns similar to juvenile interference reappear in high status adult males when they effectively terminate copulations of other males, [this behaviour is called interruption, see Chapter 6, section 7.] What I propose, is that there are two categories of interference, the first is shown by 3-5 year old infants of both sexes towards the copulations of their mothers; the second is shown by older male juveniles towards copulations involving other females. The exact motivation behind the first category is difficult to assess. Infants find their mothers' copulations disturbing, but this may be due to the trauma of weaning, a confusion of sexual and aggressive behaviour, or a combination of both.* The motivation of the second category appears to be the same as that behind adult male interruption of copulations, i.e. the desire to prevent other males from copulating with the female. It is only during adolescence that the young male becomes fully socialised in this respect, having acquired the knowledge of which are appropriate social contexts in which this interference/ interruption behaviour can be shown.

5.6 Development of male sexual behaviour

i. Introduction

Male nonhuman primates show precocious sexual behaviour, the full patterns of courtship and copulation appearing long before puberty. The development of male sexual behaviour appears to be dependent on an adequate social environment, and interruption of the mother-infant relationship, or social deprivation results in inadequate sexual behaviour in later life (Harlow & Harlow, 1969; Mason, 1965; Riesen, 1971). Some behaviour patterns occur in both sexual and other social contexts and these are referred to as socio-sexual behaviours (Hanby, in prep.). During early development patterns such as mounting and thrusting are shown in play, directed to both peers and inanimate objects, whilst in adult chimpanzees these patterns are almost completely restricted to sexual contexts.

The data collected on male sexual development during the present study are incomplete. Females showing cycles of sexual swelling were the target of all observations, and so the majority of data presented here pertain to the interactions of young males with these females. Other types of interaction do affect sexual development and these will be referred to, although quantitative data are not available. Detailed studies on infant development (Plooij, in prep.) and socialisation of older infants (McGrew, in prep.) will yield more relevant data on other aspects of the development of sexual behaviour. What is presented below is a brief outline of the ontogeny of male sexual behaviour, largely qualitative in nature, but supported by quantitative data whenever possible.

ii. Sexual interactions between male infants and adult females

Male infants show an interest in females' sexual swellings from a very early age. Van Lawick-Goodall (1968, p. 221) reported that two male infants began to touch and smell the sexual swellings of adult females at 6 and 9 months of age, and that both had successfully mounted and thrust on adult females by the time they were one year old. Van Lawick-Goodall does not specifically mention whether these two infants achieved intromission. The three youngest males observed during the present study were first observed to successfully achieve intromission at 20 months (Prof) and 15 months (Wilkie and Michaelmas). Following its first appearance, the behaviour was repeated at almost every opportunity the infant had to interact with a receptive female. Male infants showed a fascination with the swellings of maximally tumescent females, frequently inspecting, touching and licking them, see Plates 5.14 & 5.15.

Although observation was biased it did seem that even these very young males concentrated their sexual behaviour on adult females showing cycles of sexual swelling, although, unlike adult males, their behaviour was not restricted to the phase of maximal tumescence. The association patterns of these young males were determined by their mothers, who were infrequently seen with maximally tumescent females, see Table 5.5.

Table 5.5 Mean number of hours that males of each age-group were observed associating with maximally tumescent females.

Age-class		Hours with maximally tumescent females
OLD	(N = 2)	141
MATURE	(N = 7)	180
ADOLESCENT	(N = 1)	299
JUVENILE	(N = 2)	50.5
INFANT	(N = 4)	30.6

Plate 5.14 Wilkie (at 16 months) inspects Gigi while sitting on her back. Winkle, Wilkie's mother, grooms Gigi.

Plate 5.15 Michaelmas (at 15 months) inspects Gigi while retaining contact with his mother. (Gigi is licking salt from the ground.)

Male infants and juveniles had considerably fewer opportunities to interact with maximally tumescent females than did older males. The increased association of juvenile males compared to infants reflects their greater ability to influence the behaviour of their mothers' (Pusey, in prep.). While opportunities to observe young males with receptive females were limited due to the rarity of association, additional observations were made in Camp, of infants interacting with cycling females during all phases of the swelling cycles.

In early mountings (15-36 months), achieving intromission was not an essential pre-requisite for pelvic thrusting to occur, and young males often thrust against the side of a female's swelling, see Plate 5.16. No courtship was shown prior to the approach and the female often did nothing to cooperate, merely continuing the activity she was engaged in before the infants approached. Sexual elements often occurred mixed with other social behaviour, principally play and maternal patterns, which were initiated by the female and often served to distract the infant from his mounting attempts. Females differed markedly in their responses to male infants, Gigi and Little Bee were very tolerant of the sexual advances of infants and both showed high frequencies of play and maternal-type contact behaviours, such as ventro-ventral embracing, and dorsal and ventral carrying. Sparrow, Patti and Pallas, were less tolerant of infant advances and frequently rebuffed them (see Plates 5.17 and 5.18), or evaded their mounting attempts. These three females were rarely observed to play with infants and they directed no maternal behaviour towards non-related infants during the study period.

An example of a mixed sexual-play-maternal interaction occurred

Plate 5.16 Michaelmas (at 15 months) makes unintromitted thrusts against the side of Gigi's swelling. (Gigi is licking salt.)

Plate 5.17 Freud, with penis erect, approaches Patti who is maximally tumescent, as she arrives in Camp.

Plate 5.18 Patti rebuffs Freud's approach, pushing him gently away.

on January 29, 1975, between Michaelmas (aged 16 months) and Little Bee, who was maximally tumescent. Little Bee was feeding in the same tree as Figan, and Miff and her two offspring, juvenile daughter Moeza, and infant son Michaelmas. At 15.25 Michaelmas moved 15 metres away from his mother to approach Little Bee, he inspected her, and during the next 10 minutes made a series of mounts, with pelvic thrusts. Some of the thrust were intromitted, but the majority were against the side of Little Bee's swelling. At 15.35 Miff moved into an adjacent vine tower but Michaelmas remained with Little Bee, and the two of them played, with Michaelmas mixing mounts and thrusting within the play sequences. Moeza joined Little Bee and Michaelmas for a few minutes of triadic play but then she too moved away, joining her mother some 30 metres away and out of sight of Michaelmas, Little Bee and Figan. For the next 30 minutes Little Bee and Michaelmas stayed together, playing, grooming and interacting sexually. At 16.17 Michaelmas left Little Bee and approached Figan who had been feeding 10 metres away throughout. Figan looked up, and Michaelmas suddenly whimpered loudly and rushed back to Little Bee, who took him in a ventro-ventral embrace. Miff and Moeza both returned rapidly in response to Michaelmas' whimpers and Miff retrieved her son from Little Bee.

Infants are still very dependent on their mothers at the time when male sexual behaviour first emerges, and are often spatially close to their sons' first mating attempts. Occasionally a mother actively retrieves her infant son but they usually remain impassive, see Plate 5.19.

Courtship patterns emerge gradually during late infancy and the juvenile period. Figure 5.2 shows the behavioural elements and

Plate 5.19 Wilkie (at 16 months) copulates with Gigi, who lies on her side being groomed by Wilkie's mother, Winkle.

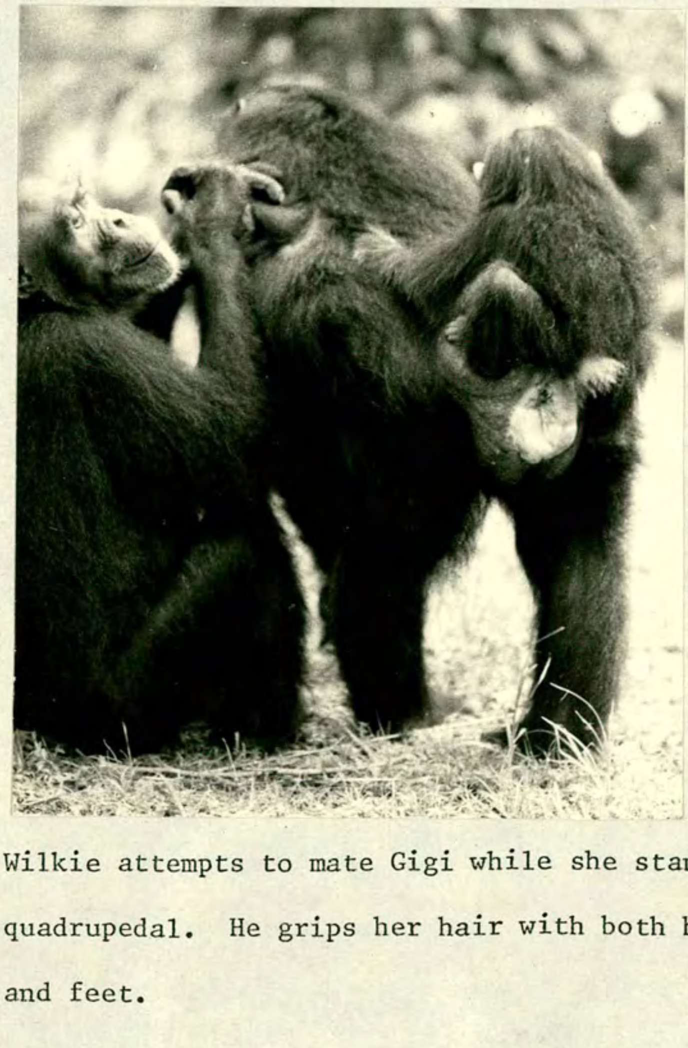
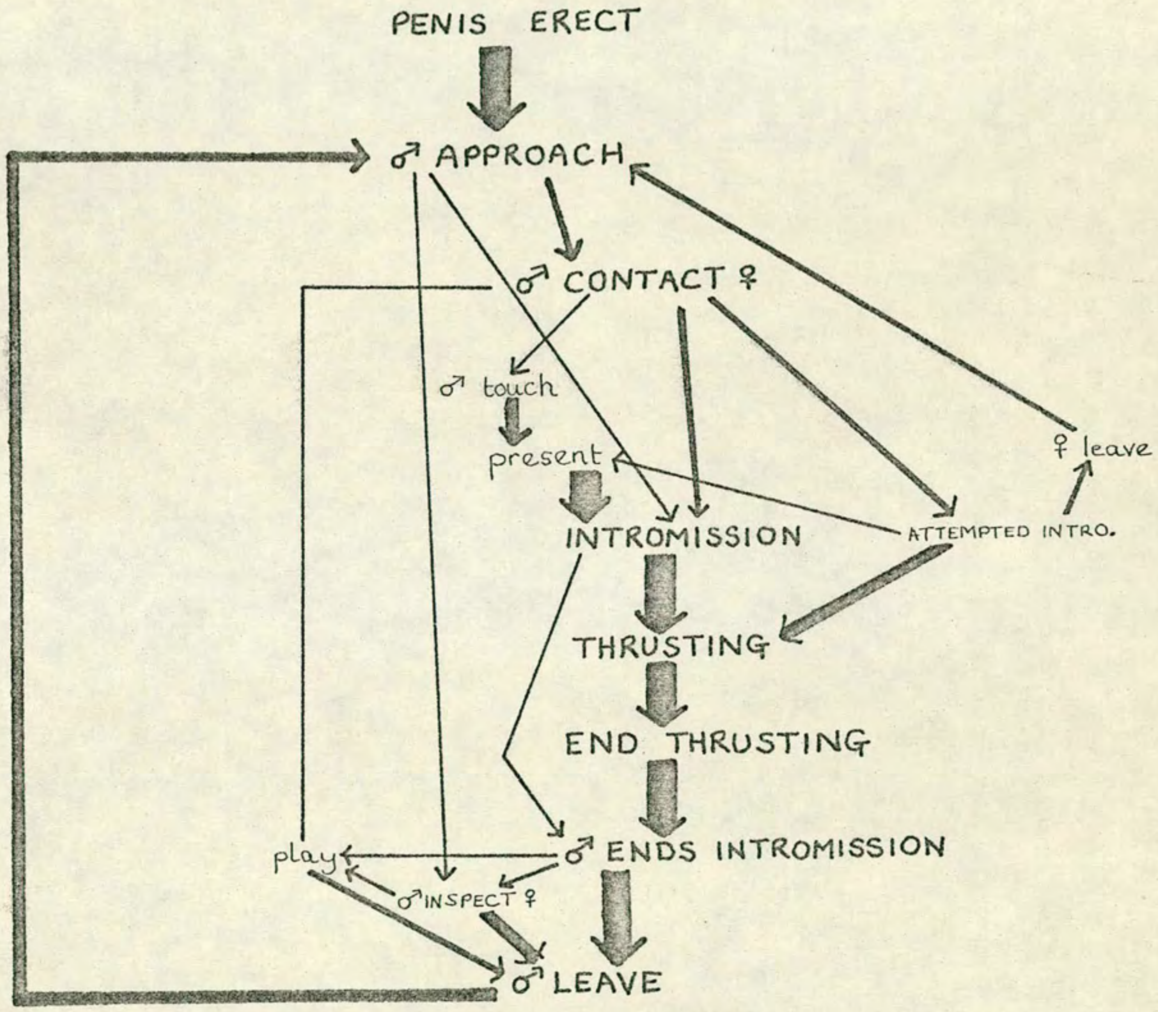


Plate 5.20 Wilkie attempts to mate Gigi while she stands quadrupedal. He grips her hair with both his hands and feet.

Figure 5.2 Sequences of behavioural elements shown in 15 copulations between Freud and Gigi.

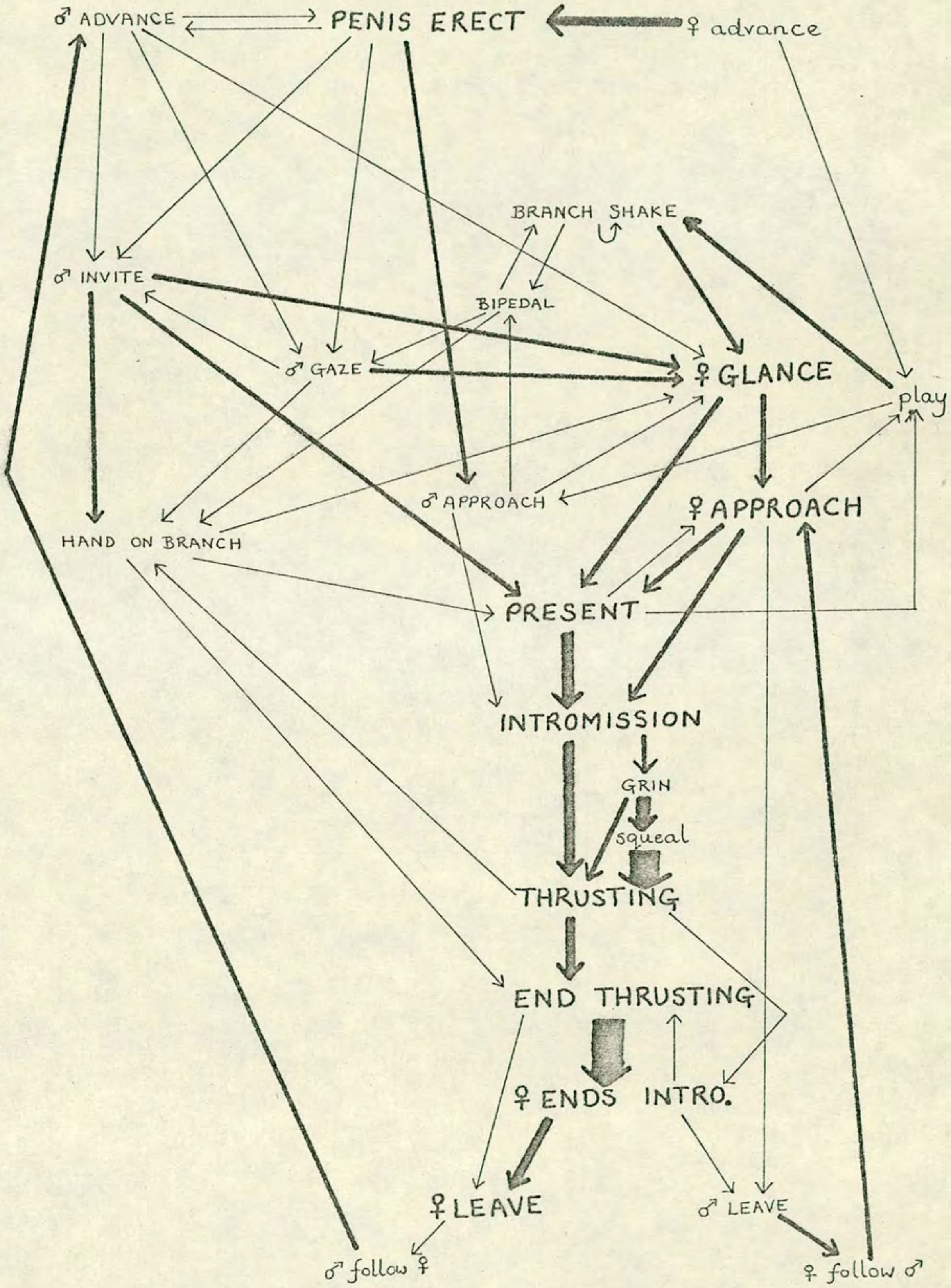


transition frequencies in the 15 copulations involving Freud and Gigi between April 1973 and February 1974 (Freud was born in May 1971). Courtship elements are absent, and sequences were initiated by Freud approaching with a penile erection and making direct contact with Gigi. (Freud did show courtship elements prior to some intromission (see Plate 5.21), but none were shown in more than 25% of copulatory sequences and so do not appear in Figure 5.2). Gigi only rarely presented, and when she did it was after Freud had contacted her, either by touching her or by attempting to intromit. Male infants commonly achieved intromission while females were lying on the ground (Plate 5.19), standing quadrupedal (Plate 5.20), or sitting on a branch. Multiple intromissions and combined sequences of attempted and successful intromissions were common.

Juvenile males showed courtship in almost all their copulatory sequences, which were characterised by long, variable and erratic performances of a series of courtship elements, often interspersed with play, locomotion and sometimes aggression. Figure 5.3 shows the patterns of behaviour shown by Mustard (born November 1965) in 32 copulations observed between January 1973 and January 1975. There were insufficient data on copulatory sequences between Mustard and any single female and so the data of 4 females have been combined. The single element of adult courtship never shown by Mustard was the shoulder hunch posture. This appears to be the last courtship pattern to develop, and was never shown by infant or juvenile males. Goblin was first observed to incorporate shoulder hunch in his courtship in December 1974, at the age of 10 years 3 months. Mustard's courtship involved a considerable amount of locomotion and if a female approached him in response to courtship gestures, he sometimes moved away, and she might follow him a distance of 15-20 metres

Plate 5.21 Freud (at 3 years 7 months) arm stretches and makes contact with Patti's back in an attempt to mate her.

Figure 5.3 Sequences of behavioural elements shown in 32 copulations involving Mustard with Gigi, Patti, Pallas and Little Bee.



before he stopped and indicated with further courtship, that he was ready to intromit. This locomotion often served to take the female some distance from adult males and reflects the growing awareness of older juveniles to the possible dangers of copulating in close proximity to adult males.

Goblin was the only male who reached puberty during the study period. He was first observed to ejaculate in November 1973. Changes in Goblin's patterns of interference following puberty have been described (see Section 4) and changes in his sexual behaviour were also noticed. The changes in Goblin's sexual behaviour were of similar origin to the changes in his interference, i.e. the result of a change in the way other individuals interacted with him. Sufficient data were available to compare Goblin's copulation rate with Gigi before and after puberty. In 37 contact hours between December 1972 and October 1973, Goblin copulated with Gigi 21 times, giving an hourly rate of 0.56. In 40.5 contact hours between November 1973 and February 1974, there were 10 copulations between Goblin and Gigi, giving an hourly rate of 0.25. The difference between these two periods is statistically significant ($X^2=4.97$, df=1, $p<.05$).

Goblin's reduced copulation rate after puberty appeared to be a result of the increasing aggression shown by Gigi as a response to his courtship. The change in her behaviour was dramatic, as before November 1973, she had not been seen to threaten or attack Goblin in sexual interactions. During November and December, Gigi was somewhat erratic in her response to Goblin, threatening him every time be approached her on some days, whilst readily presenting to him on other days. By January her aggressive responses to Goblin's approaches were consistent. During the period November 1973 to February 1974, Goblin was beginning to direct aggressive behaviour towards adult females and was successful in eliciting submissive responses from the younger ones, such as Gilka and Sparrow. Observations of the sexual behaviour of a group of adolescent chimpanzees in captivity (Tutin and McGrew, 1973) suggested that the aggressive component of male courtship creates difficulties for an adolescent male wishing to mate females with whom he is actively competing for dominance status. In the captive group, Shadow, an adolescent male, developed idiosyncratic behavioural elements which he used in all his courtship towards two females who outranked him. When Shadow became dominant to these females he immediately began to show courtship elements typical of wild-living adult males and abandoned his idiosyncracies. An explanation of the change in Shadow's behaviour was that the aggressive component in a typical male courtship rendered it too threatening to use to females whom the male was attempting to dominate. Shadow's ingenious solution to this problem was to 'invent' the idiosyncratic patterns lip-flip and bipedal display, which were specific to the courtship context and had no aggressive component. Goblin found no such solution to his problem with Gigi, but for much of the time alternative sexual partners, such as Patti and Little Bee, were available, and these females never reacted aggressively to his courtship.

iii. Sexual behaviour in non-sexual situations

During infancy and the juvenile period some sexual behaviour patterns, especially mounting and thrusting, occur in peer play. No quantitative data are available but such patterns appear frequently enough in peer interactions to have significance in the development of male sexual behaviour. Mounting and unintromitted thrusting were directed to younger individuals of both sexes and were made either dorso-ventrally (Plate 5.22) or ventro-ventrally (Plate 5.23). This behaviour was shown commonly by Freud, Atlas and especially Mustard.

Plate 5.22 Mustard mounts and thrusts against 19 month old Aphrodite during play.

Plate 5.23 Atlas holds Prof in a ventro-ventral embrace and thrusts against him during play.

Goblin never mounted and thrust on a younger individual during the study period. Adult males occasionally mounted and thrust on other adult males in reassurance, and on non-receptive females during greeting.

5.7 Development of female sexual behaviour

The ontogeny of female sexual behaviour is closely linked to the changes which occur at, and just before puberty. Female infants show little sexual behaviour and do not engage in intercourse until they begin to develop sexual swellings. No female was observed to go through this developmental stage during the present study. Female infants were observed to present in the adult manner both to other (male) infants (Plate 5.24) and to adult males (Plates 5.25 & 5.26) from the age of 4 years. Gremlin showed a fascination with her own genitals during her fourth year, manipulating them directly with her hand and also rubbing objects, such as stones and leaves, against them.

5.8 Inter-specific sexual interactions

Van Lawick-Goodall (1974) reported that two juvenile male chimpanzees (Flint and Mustard) occasionally mounted and thrust, with intromission, on adolescent female baboons. During the study period Mustard was once observed to copulate with a tumescent female baboon (Riss, pers. comm.). This behaviour was uncommon and in all cases the baboons involved were young adolescent females, in whom the males of their own species showed little interest. Mounting and thrusting were also observed in inter-specific play, when an adolescent male baboon mounted and thrust against a juvenile male chimpanzee (Plate 5.27). The same male mounted a juvenile female chimpanzee during play and for a while these two individuals (Copper and Pom) seemed to form a special relationship, and contact play with occasional mounting was common whenever the two met. Van Lawick-Goodall (1974, p. 94) described a

Plate 5.24 Gremlin presents to Wilkie during play.

Plate 5.25 Humphrey mounts and thrusts against Scotia (aged 4 years 3 months) who has presented to him in greeting.

Plate 5.26 Nova, Scotia's mother, attempts to retrieve Scotia.

Plate 5.27 Copper, a subadult male baboon, mounts Mustard during play.

similar relationship that was formed between Fifi, at about the same age as Pom, and another adolescent male baboon.

An adolescent female baboon with a small swelling presented to Goblin, but he showed no interest (Plate 5.28). Baboons occasionally showed interest in the sexual swellings of female chimpanzees (Plate 5.29), but no mounting was directed to older adolescent or adult females.

5.9 Beethoven

Beethoven's atypical behaviour during the copulations of others has already been described (see Section 5). It was noteable that during the two months that he was observed (December 1974 - January 1975) he never showed any sexual interest in receptive females, despite ample opportunities to do so. Beethoven's exact age was not known, but he was believed to be at least 4 years of age. (He was first recognised in December 1973, and at that time was with his presumed older sister, Harmony, not his mother. Previous observations (van Lawick-Goodall, 1968), indicated that an infant under 3 years of age could not survive as an orphan.) Males of 4 years and older typically approach, inspect and copulate with receptive females whenever an opportunity to do so arises. Beethoven showed none of these behaviours during the 18 hours he was observed with maximally tumescent females. Either Beethoven showed sexual behaviour at an atypically low frequency, or it was completely absent. His atypical behaviour might be a result of extreme emotional disturbance resulting from being orphaned at an early age.

5.10 Incest avoidance

i. Introduction

Among human societies there is almost complete universality of

Plate 5.28 An adolescent female baboon presents to Goblin who ignores her.

Plate 5.29 An adolescent baboon inspects Sparrow's full swelling.

incest avoidance, formalised by cultural or legal prohibitions, labelled incest taboos. The origin of these taboos has concerned sociologists and anthropologists who see them as a phenomenon of central importance in social and cultural evolution: "Incest prohibitions constitute the passage from nature to culture, from animal to human life" (Levi-Strauss, 1956, p. 278). Incest taboos are seen as uniquely human, and the existence of systematic incest avoidance in other animals is denied by many (e.g. Livingstone, 1969). Anthropologists tend to play down or completely dismiss any biological basis for the origin of incest prohibitions, preferring to explain them in social terms, of exchanging women between groups to increase the size of social units, or reducing stress due to role-conflict within nuclear families.

Inbreeding results in a decline of fitness through concentrating homozygotes. If a trait possesses a degree of heritability, and if some loci display either dominance or superior heterozygote performance, or both, inbreeding will cause a decline in the trait within the population. The decline will affect not only the trait averaged over the population as a whole, but also the performance of an increasing number of individuals, if inbreeding persists (Crow & Kimura, 1970; Cavalli-Sforza & Bodmer, 1971). Studies of inbred human populations have shown that both physical and mental abilities are negatively affected (Schull & Neel, 1965; Cavalli-Sforza & Bodmer, 1971). A particularly dramatic demonstration of the rapid deleterious effects of human inbreeding comes from a Czechoslovakian study of children of incestuous relationships. Of a sample of 161 children resulting from father-daughter, mother-son, or brother-sister sexual relationships, 15 were stillborn or died within the first year of life, and more than 40% suffered from various physical and mental defects, including severe mental retardation, heart and brain deformities and deaf-mutism. In a control group of 95 children born to the same women through non-incestuous relationships, 5 died during the first year of life, none had serious mental deficiencies and 4.5% had physical deformities. This control group conformed to the population norms (Seemanova, cited in Wilson, 1975, p. 78-79). The other, more general effect of inbreeding is to reduce genetic variability within the breeding population, making them less adaptable to social or environmental changes.

Many animal populations show behaviours which reduce inbreeding. The pre-requisite for specific incest avoidance is some kind of family grouping which enables individuals to 'recognise' their primary kin, through specific relationships built up during socialisation. A general kind of incest avoidance can be achieved without this pre-requisite, by migration of young from the social groups in which they were raised, before they reach reproductive age. Evidence suggests that individuals who are cosocialised are unlikely to engage in heterosexual intercourse. Hill (1974) found that pairs of prairie deer mice (Peromyscus maniculatus bairdi) raised together, whether true siblings or unrelated individuals, exhibited delayed breeding compared to sibling and unrelated pairs introduced to each other after they had reached sexual maturity. Shepher (1971) studied children raised in peer groups in an Israeli kibbutz, and found that not one of the 2,769 marriages which occurred, was between individuals from the same peer group. Individuals cosocialised in the kibbutz formed close friendships but were not sexually attracted to one another. There was no form of social pressure exerted against peer group marriages, the absence of any such unions was solely a result of individual choice.

Itani (1972) described how various types of social organisation found in nonhuman primates lead to either partial or complete incest avoidance. Young adult male baboons and those of several macaque species leave their natal troop and transfer into another, usually a neighbouring troop. Packer (1975) showed that for at least one population of olive baboons (Papio anubis) all males transferred between troops before becoming full mature, and many transferred several times during their lifetime. In species with one-male-group social structures such as langurs (Sugiyama, 1965; Rudran, 1973) and patas monkeys, the male is periodically replaced by another male, and a male will seldom remain in the same group long enough for his daughters to reach sexual maturity. Transfer of adolescent females has been reported in chimpanzees (Nishida & Kawanaka, 1972; Pusey, in press) and also occurs in gorillas. In monogamous primates such as indri, gibbons and callicebus, the young of both sexes either leave, or are expelled from the group before puberty (Pollock, 1975; Carpenter, 1940; Tenaza, 1975). There is also evidence that males who remain in their natal group after puberty either refrain from mating their mothers, as in chimpanzees (van Lawick-Goodall, 1968) or mate them very infrequently (Sade, 1968; Missakian, 1973).

ii. Incest avoidance in the Gombe chimpanzees

The transfer of females between communities both temporarily and permanently is common at Gombe (Pusey, in press). To date such transfer has been restricted to juvenile and adolescent females, but in the Mahali Mountains, Nishida and Kawanaka (1972) reported that transfer of older females also occurred. No reliable reports of the transfer of males between communities exist. If all females emigrate from their natal community at, or before puberty, and do not return, brother-sister and father-daughter matings are precluded, even though the identity of the father is unknown. In this situation the only incestuous mating possible amongst primary kin would be between mothers and their sons. In fact all females do not emigrate permanently, some return to their natal community once they have become pregnant and remain during subsequent periods of receptivity, being impregnated by males of their natal community. Data are still too few to understand which variables are responsible for determining whether or not a female remains in the new community. Van Lawick-Goodall (1968, p.220) reported that within the Kasakela community no matings between mothers and mature sons were observed. Two mature males were observed to mate their younger sister (p. 256).

During the present study none of the receptive females observed had a male sibling. Three receptive females were observed in the presence of their sons, one adult (Satan with Sprout), one adolescent (Goblin with Melissa), and one juvenile (Atlas with Athena). The only mother-son copulation observed was between Satan and Sprout. Only sporadic observation of Sprout was possible as she was shy and unhabituated to human presence. During December 1973, Sprout was receptive for several days and was accompanied by all the adult males of the Kasakela community. She mated frequently with the adult males, and Satan was observed to court her on three occasions. Twice, she avoided Satan when he approached her with a penile erection. On the third occasion Sprout avoided Satan but he followed her to the top of a tall tree, from which there was no escape route. Sprout screamed loudly and did not present to Satan, but he approached her and achieved intromission. Ejaculation was not recorded and almost certainly did not occur, as Sprout leapt away, ending intromission before Satan had finished thrusting. Data were too scarce to compute an expected frequency of Satan mating Sprout and so no definite statement can be made with respect to the rarity of copulations between this pair. However, Sprout's response to Satan's courtship differed markedly from that to the other males, to whose courtship she responded quickly by presenting.

During Melissa's isolated post-partum swelling cycle in October

1973, Goblin was her constant companion but he never directed any courtship gestures to his mother and no copulations occurred. Goblin showed great interest in his mother's swelling, inspecting it frequently, and they spent much time grooming. Goblin mated all other receptive females at high frequencies at this time, and so his behaviour towards Melissa was uncharacteristic.

Atlas and Athena were observed together for 25 hours whilst Athena was maximally tumescent. During this time Atlas never courted or mated Athena, although he mated all other receptive females at high frequences, see Table 5.6. Athena did present to her son on one occasion when Atlas had been courting Sparrow (both females were maximally tumescent) for 3 minutes without receiving any response. He began to whimper and Athena, who fed nearby, approached to within one metre of Atlas and presented to him. Atlas watched his mother but made no further response. After a few seconds Athena resumed feeding.

Van Lawick-Goodall (1968, p. 220) reported that frequent copulations were observed between two mothers and their infant sons (Flint with Flo, and Goblin with Melissa). Atlas and Mustard had also been observed to copulate with their mothers during the latter's initial post-partum swelling cycles. These early mother-son matings may not be directly comparable to other copulations. The time at which they occur suggests that mothers may present to their infant sons as a reassurance gesture, in which case these copulations should be regarded as primarily reassurance rather than sexual. This is speculation, as detailed descriptions of such matings are not available, and none occurred during the study period. No reports could be found, and no observers could recall, seeing an infant court his mother. This might be due to the general lack of courtship prior to infant copulations, but might also be explained if the copulations followed the mother presenting in reassurance. The observation described above, of Athena presenting to her son when he whimpered, supports this speculation, as does the fact that these matings occur at the time the infant son is being weaned.

iii. Discussion

Two separate mechanisms operate to reduce the probability of incestuous matings occurring in wild chimpanzees. The first is the general avoidance by the female of all male members of her natal community, achieved by emigrating to another community prior to the age at which conception can occur. The second is a specific avoidance of mother-son matings within the community. All females appear to leave their natal community for a certain amount of time, usually during adolescence. Some remain permanently in the new community, others remain for periods up to six months but then return, and still others move repeatedly, remaining for relatively brief periods of one week to two months, and returning to their natal community between moves. It is not known whether these young females visit more than one community during their travels.

Pusey (in press) has pointed out differences between the patterns on immigration and emigration in the Kasakela community. During the period 1965-1974, more females permanently joined the community than left, and those that joined moved at an earlier age than those who left. Pusey suggested that this difference could be due to chance variation in the demographies of neighbouring communities and possibly also an indirect result of the changes in community structure and behaviour caused by the intensive artificial provisioning during the period 1965-1968. It is clear that relationships between chimpanzee communities cannot be completely understood until two or more, habituated and preferably unprovisioned, communities are available for study.

If all females transferred between communities before reaching reproductive age and did not return, matings between siblings and father-daughter pairs could not occur. However, although all the females born in the Kasakela community visited other communities during adolescence, not all remained in their new communities even until their first conception. Fifi and Gilka did conceive for the first time while with another community, but Miff was impregnated by a male of the Kasakela community. Miff and Gilka have both conceived for a second time, both as a result of copulations with males of the Kasakela community, see Table 7.9. In the Mahali Mountains female transfer appears to be more common and to involve females of different ages. Nishida (in press) reported that 6 of the 9 females in K-group, moved into another unit-group at least once during their 7 year study period. Five of the females moved "when their dependent young attained the developmental stage from early juvenility to early adolescence", which in most cases corresponded to the mothers' post-partum resumption of sexual swelling cycles. Mother-son matings are extremely rare, if the matings of infant sons are omitted from consideration. Avoidance of matings between mothers and their post-pubertal sons appears to be achieved by a mutual lack of sexual attraction between such pairs. The hypothesis that a high degree of familiarity, such as exists between mothers and their offspring, especially when the period of infant dependency is protracted, is associated with lack of sexual attraction, has been put forward by a number of authors (Parsons, 1954; Shepher, 1971; Hill, 1974). There is strong evidence from studies on a number of different species, to suggest that the types of relationships formed during socialisation; between mothers and their sons, siblings (especially those of the same age) and, when the father is involved in socialisation, between father and daughter, block the later formation of sexual relationships. That it is the relationships which are important, rather than the degree of relatedness *per se*, is shown by the experiments of Hill on *Peromyscus*, and the observations of Shepher and also Wolf (1968, 1970) on humans. Hill found that mating was delayed in pairs of *Peromyscus* formed at weaning age compared to pairs formed at sexual maturity. This effect held for both sibling and unrelated pairs although the sibling pairs also showed inbreeding depression, indicated by reduced fertility and low survival rates of offspring. Shepher (1971) and Wolf (1970) both found that unrelated human children who had been cosocialised from birth or an early age, did not readily form heterosexual relationships when adult. In Shepher's study of children in an Israeli kibbutz, the extent of cosocialisation was greater than it would be in normal family group rearing. In Wolf's study of Sim-pua marriages in Taiwan, the prospective bride was adopted by the prospective bridegroom's family at a very young age. The two were raised as siblings and married when mature. Wolf found that Sim-pua couples were reluctant to consummate their marriages, and when compared to couples married to partners of their own choice, Sim-pua couples had more extra-marital sexual relationships, a higher divorce rate and produced fewer children.

Hill's conclusion from his experiments with *Peromyscus* was that the "delay in breeding apparently results because a nonsexual relationship formed before puberty interferes with the later establishment of a sexual relationship." (1974, p. 1042). Shepher sees this process as a kind of imprinting which occurs during a sensitive period when children are between 0-6 years of age. He concludes "The established imprinted model prevents sexual attraction towards subjects who were imprinted in early childhood and forms part of a neuronal model with which the erotic attraction is incompatable." (1971, p. 302). The data on nonhuman primate incest avoidance fit well with this concept of the incompatability of different kinds of relationship.

During socialisation a nonhuman primate's closest relationship is with the mother. In chimpanzees the next closest relationship is with siblings immediately adjacent in the birth order. It is doubtful whether a special relationship exists between siblings not adjacent in the birth order. The long birth interval means a gap of about 12 years between, for example, a first and third born, and by the age of 12 both males and females are associating relatively infrequently with their mothers. Incest avoidance is most marked between mothers and sons, as would be predicted by the 'familiarity' hypothesis. Data on sibling matings (van Lawick-Goodall, 1968, p. 256) also lend support to the hypothesis. During Fifi's early sexual cycles van Lawick-Goodall reported that she allowed her eldest brother, Faben, to mate her but tried to avoid the sexual advances of Figan, the brother immediately above her in birth order. When Fifi resumed sexual cycling in February 1975 she allowed both Figan and Faben to mate her without protest (Pusey, pers. comm.). This observation combined with the observation of Satan courting and mating his mother, Sprout, suggest that the inhibition against sexual relationships with a very familiar member of the opposite sex, becomes reduced if the degree of association with that individual declines. The close relationship formed between adjacent siblings during early life does not persist into adulthood. The mother-son relationship is more enduring but in the case of Sprout, whose range is peripheral to that of the Kasakela community, association with her son was much reduced when he became independent.

A process whereby a high degree of familiarity with an individual of the opposite sex reduces, or eliminates, sexual responses to that individual, would reduce the frequency of copulations between recognised primary kin. For a chimpanzee female such a process would gain selective advantage, as any loss of fitness (due to inbreeding depression) in her offspring would reduce her already small reproductive potential. For males, a selective advantage would only be gained if incestuous copulations occurred at the expense of non-incestuous ones. This is unlikely in chimpanzees, as only a few females are receptive at any one time. Thus, one might expect females to be more aversive to incestuous matings than males and this does appear to be the case. There are many records of adult males courting their adult or adolescent sisters, where copulation did not occur due to the females avoidance of the male. Evered, for example, has been observed courting his sister Gilka, but no copulations between them have been seen as Gilka always managed to avoid Evered (Gombe long-term records).

Many conceptions occur during consort relationships (see Chapter 7, section 12), and this means that females remaining in their natal community have another way of avoiding being impregnated by their brothers. No record exists of a consort relationship between primary kin, neither mother-son, nor brother-sister. The possibility of father-daughter consorts remains, but older adult males pay relatively little sexual attention to young females, and it is unlikely that a male would survive beyond his daughter's first impregnation.

In conclusion, it seems that mechanisms exist in wild chimpanzee groups to ensure exogamy - permanent movement of pre-reproductive age females away from their natal community, combined with behavioural avoidance of mother-son matings achieved by mutual disinterest. The advantage of ensuring outbreeding is the avoidance of homozygote recessive genes which appear to be mainly deleterious, and the maintenance of genetic variability within the population. A possible proximal mechanism is the incompatability of two types of relationship - a close nonsexual one formed during socialisation, and a sexual one later in life, the former apparently precluding the latter. If one postulates a positive, graded correlation between the level of familiarity, as measured by frequency of association, in the early relationship, with the degree of avoidance of later sexual relationships, the same proximal mechanism can be invoked to explain all incest avoidance. A female is more familiar with all the males of her natal community than she is with any males in the neighbouring communities, making the latter more attractive for sexual relationships. This might explain why a young female voluntarily leaves the familiar natal community and enters an unfamiliar one, where she is likely to meet aggression from the resident females (Pusey, in press). Observations of the Gombe chimpanzees over the past 15 years suggest that these mechanisms are not employed to best advantage, as females often return to their natal community after their first conception. There is some indication that the Kasakela community may be atypical, and the possibility remains that artificial provisioning has affected patterns of female migration.

In many nonhuman primates it is the young males who move between troops (e.g. Macaca rhesus, Boelkins & Wilson, 1972; Papio anubis, Packer, 1975; Presbytis senex, Rudran 1973; Macaca fuscata, Nishida 1966). Transfer of females gives the potential for complete exogamy, as it precludes father-daughter matings even though the father's identity is unknown. Behavioural avoidance of incest, such as occurs in chimpanzees between mothers and sons, can only be achieved if the relationship is recognised by both individuals. The combination of female migration and behavioural avoidance of matings between the remaining primary kin (i.e. mothers and sons), is the only way to ensure complete exogamy.

5.11 Dyadic copulation rates in promiscuous mating

The dictionary definition of promiscuity is "indulging indiscriminately in sexual intercourse". The term has been used rather more loosely in the literature, to refer to mating systems where no overt competition is shown by males for copulatory access to receptive females, as is sometimes the case for chimpanzees (van Lawick-Goodall, 1968; McGinnis, 1973). However, it remains to be shown that these situations which lack overt competition do indeed result in truely promiscuous mating, or whether discriminations are being made on more subtle levels. If mating was truely promiscuous one would expect each male to copulate at similar frequencies with every female, and *vice versa*.

Table 5.6 shows the hourly copulation rates of complete copulatory sequences (i.e. sequences which included at least one intromission) for 106 male-female dyads. Males are listed in descending age order and females in order of decreasing age from left to right. The rates were computed by dividing the number of observed copulations by the number of contact hours for each dyad. Contact hours were the hours that the dyad were simultaneously present in a group while the female was a target individual (see Methods). Twenty-five dyads had fewer than 5 contact hours, these are marked with an asterisk in

Table 5.6. Dyadic rates of completed copulatory sequences

	FEMALES							
MALES	Athena	Pallas	Gigi	Miff	Sparrow	Patti	Little Bee	MEAN
Hugo	1.45*	.43	.07	.59	.24	0*	0	.26
Mike	0*	.49	.35	.49	.26	.25*	.11	.33
Humphrey	0*	.51	.61	.43	0	.87	.35	.53
Faben	1.14*	.66	.46	.90	.55	.53	.25	.54
Evered	1.23*	.58	.69	.78	.34	-	.15	.54
Figan	.29*	.47	.35	.48	.20	.39	.19	.36
Jomeo	1.50*	.52	.50	.42	1.18	1.02	.37	.64
Satan	1.33*	.49	.69	.47	.53	.72	.44	.56
Sherry	1.71	.46	.70	.28	1.36	1.22	.37	.72
Goblin	.50	.78	.38	.63	2.18	.43	.45	.67
Mustard	0*	1.85*	.91	.24	2.29	.84	.57	.89
Atlas	0	1.00*	1.56	.89*	1.30	.27	.69	1.13
Beethoven	-	-	-	-	-	0	0*	0
Plato	1.14*	-	1.14	0*	0*	-	-	1.14
Freud	0*	1.12*	1.23	0	.34	1.22	2.00	.74
Prof.	-	0*	1.50	-	-	0*	1.00*	.56
Wilkie	-	0	0	-	-	0	.12	.03
Michaelmas	-	-	-	-	-	0	.27*	.10
MEAN	.99	.56	.52	.53	.77	.54	.31	

- No contact hours

* Less than 5 contact hours

Table 5.6. Copulatory rates for these dyads are considered unreliable as the data come from such a small time sample. Mean copulatory rates for each male with all females and each female with all males are also shown in Table 5.6.

Mean male copulation rates range from .03 per hour to 1.14 per hour. There was no overall correlation between these rates and male age ($r_s = -.12$, N=18, n.s.), but if infants (Plato - Michaelmas) are excluded a statistically significant negative correlation exists ($r_s = -.94$, N=12, $p<.001$). The highest hourly rates are shown by juvenile and adolescents, adult males show lower rates and the lowest rates are shown by the two aging males, Mike and Hugo. The mean hourly rates of the 7 females show less variation, ranging from a low value of .31 (Little Bee) to a high of .99 (Athena). There is no correlation between female age and mean hourly copulation rates.

The hourly rates are small in all cases and so there is a possibility that the inter-dyadic variation is due to chance. To test whether this was the case, a split-half reliability test was performed on the data for each female. The observation time for each female was divided into two approximately equal groups by allocating consecutive follows to alternate groups - i.e. the first follow on each female was placed in group 1, the second in group 2, the third in group 1, and so on. The hourly copulation rate was computed for each dyad using the two pools of data, giving two frequencies. These two frequencies were then ranked, and the ranks compared using a Spearman Rank Correlation test. The results are shown in Table 5.7. Insufficient data were available to apply a split-half test to the males' copulation rates with Athena.

For all the females except Pallas, there is a significant positive

Table 5.7. Spearman Rank Correlation Coefficients (r_s) of male copulation rates with females, comparing the two pools of data (see text).

Female	r_s	N *	p
PALLAS	+.03	11	n.s.
GIGI	+.76	11	$<.01$
MIFF	+.90	11	$<.01$
SPARROW	+.95	12	$<.01$
PATTI	+.86	9	$<.01$
LITTLE BEE	+.82	7	$<.05$

*Males with less than 5 contact hours in either pool of data are omitted.

correlation between the hourly copulation rates of each male computed from the two pools of data. This means that although, in some cases, the variations in hourly rates are small, they are consistent and can thus be considered reliable indicators of true differences. The non-correlation of the rates with Pallas may be because the males show very similar copulatory rates with her, varying from a high value of .78 (Goblin) to a low value of .43 (Hugo). Relatively small differences in the hourly frequencies computed from the two pools of data therefore alter the ranks considerably.

5.12 Partner preferences

The data in Table 5.6 indicate that some males copulate at variable rates with different females and *vice versa*. To investigate this an arbitrary index of partner preference was arrived at by comparing dyadic copulation rates with the mean copulation rates of the male and female involved. A positive index was established if

$$\frac{\text{dyadic rate}}{\text{mean male rate}} > 2, \text{ or } \qquad \frac{\text{dyadic rate}}{\text{mean female rate}} > 2.$$

Similarly, a negative index was established if

$$\frac{\text{dyadic rate}}{\text{mean male rate}} < .5, \text{ or } \frac{\text{dyadic rate}}{\text{mean female rate}} < .5 .$$

A negative index was also inferred if a dyad had 5 or more contact hours but was never seen to copulate. The indices of partner preference are calculated from dependent variables as each dyadic rate contributes to the mean rate of the male and female concerned. However, the bias is a conservative one, and is thus permissable.

Figure 5.4 shows the indices of partner preference which emerged. Of the 81 dyads with 5 or more contact hours 34 show indices of preference, 14 positive and 20 negative. Eight of the negative indices come from dyads who were observed together for 5 or more hours but who were never seen to copulate. Of the remaining 26 indices, 10 are reciprocal, i.e. an index of preference emerged from comparing the dyadic rate with the mean rate of both members of the dyad, and 16 are unidirectional, emerging when the dyadic rate was compared to the mean rate of one member of the pair but not the other. Although only a minority (38%) of the indices of partner preference are reciprocal, in most of the unidirectional cases the index of the other member of the dyad, was in the same direction, although it did not reach the chosen levels of significance at 2 and 0.5.

The distribution of the indices of partner preference suggests that the negative correlation between male age and copulation rates is an important factor. In Figure 5.4 the males are listed in descending age order and the females in order of decreasing age from left to right. In the 63 dyads involving adult and old males, negative indices outnumber positive, 11 to 3. In the 22 dyads

KEY TO FIGURE 5.4 :

✚	RECIPROCAL POSITIVE INDEX
▬	RECIPROCAL NEGATIVE INDEX
✙	UNI-DIRECTIONAL POSITIVE INDEX
▭	UNI-DIRECTIONAL NEGATIVE INDEX, OR, ONE INDICATED BY 5 OR MORE CONTACT HOURS WITHOUT COPULATION
╳	DYAD NEVER OBSERVED IN CONTACT

FIGURE 5.4. Indices of partner preference

	FEMALES							
	ATHENA	PALLAS	GIGI	MIFF	SPARROW	PATTI	LITTLE BEE	
HG			▬	+	▭		▭	HUGO
MK					▭		▬	MIKE
HM					▭			HUMPHREY
FB							▭	FABEN
EV					▭	✕	▬	EVERED
FG					▭			FIGAN
JJ								JOMEO
ST								SATAN
SH	+			▭		+		SHERRY
GB					✚			GOBLIN
MU				▬	✚			MUSTARD
AL	▭		+			▬	+	ATLAS
BE	✕	✕	✕	✕	✕	▭		BEETHOVEN
PT		✕	+			✕	✕	PLATO
FD			+	▭	▬	+	✚	FREUD
PF	✕		✚	✕	✕		+	PROF.
WL	✕	▭	▭	✕	✕	▭	+	WILKIE
MM	✕	✕	✕	✕	✕	▭	+	MICHAELMAS

involving adolescent and juvenile males (Goblin - Beethoven) there are four negative and four positive indices. In the 20 dyads involving infant males (Plato - Michaelmas) there are six negative and seven positive indices. Thus although the general age-related trend in male copulation rates may be partially responsible for some of the indices of partner preference, there are others that it cannot explain.

The data presented in Table 5.6 and Figure 5.4 give no indication of whether the low rates shown by some dyads are due to a low rate of male courtship or a high rate of female avoidance of the male's courtship, as only rates of complete copulatory sequences are involved. Table 5.8 shows the dyadic rates of incomplete copulatory sequences per contact hour. A sequence of behaviour was recorded as an incomplete copulatory sequence when an interaction between a male and a female indicated that one or both members of the pair was desirous of intromission, but that for one of a variety of reasons this goal was not achieved. In operational terms two definitions were used, depending on the sex of the initiator of the sequence. If a male had a penile erection and directed two or more additional elements of courtship behaviour towards a female, without intromission resulting, it was recorded as an incomplete copulatory sequence. If a female approached a male and presented in a non-submissive situation (i.e. one where no aggressive patterns had been shown previously by the male, and the female showed no submissive behaviour patterns, prior to or simultaneously to presenting), and the male made no response or avoided her, it was also recorded as an incomplete copulatory sequence.

During the study 222 incomplete copulatory sequences were observed and only 13 (6%) of these fell into the latter category of unsuccessful female solicitation. The other 94% of the incomplete sequences were

Table 5.8. Dyadic rates of incomplete copulatory sequences

	FEMALES							
MALES	Athena	Pallas	Gigi	Miff	Sparrow	Patti	Little Bee	MEAN
Hugo	0*	.02	.12	0	0	.33	0	.05
Mike	0*	0	.16	0	0	.25	0	.08
Humphrey	0*	0	.07	0	0	.08	0	.04
Faben	0*	.21	.37	.07	.07	.24	0	.21
Evered	0*	.32	.10	0	.05	-	0	.08
Figan	0*	.03	0	0	0	.01	.03	.01
Jomeo	0*	0	.05	.25	0	.08	0	.05
Satan	.27*	.03	.08	.06	.02	.11	.08	.06
Sherry	0	.20	.15	.07	.09	.25	.21	.15
Goblin	.13	.12	.22	.11	.16	.18	.06	.16
Mustard	0*	.62*	.09	.24	0	.46	0	.26
Atlas	0	0*	.15	.44*	.09	0	.11	.12
Beethoven	-	-	-	-	-	0	0*	0
Plato	.29	-	0*	0*	0*	-	-	.19
Freud	3.00*	0*	.90	0	.26	.18	0	.43
Prof.	-	2.00*	.67	-	1	0*	.33*	.64
Wilkie	-	0	.26	-	-	.53	.22	.23
Michaelmas	-	-	-	-	-	0	.53*	.20
MEAN	.14	.10	.17	.05	.06	.14	.05	

- No contact hours

* Less than 5 contact hours

initiated by males. A distinction must be made between incomplete sequences involving males under the age of three years, and those involving older males. Males under three years of age do not show completely proficient sexual behaviour. Although infant males may first achieve intromission during their second year of life, their sexual behaviour remains erratic and incompletely integrated until their fourth year. Dyads involving the four young males, Freud, Prof, Wilkie and Michaelmas, accounted for 36 of the 222 incomplete sequences observed. Copulatory sequences terminated prior to intromission in dyads involving males older than three years, because of female avoidance or non-response in 97% of the 168 male-initiated sequences. In the remaining 3% the pair were distracted by 'extraneous' events, such as aggression within the group, causing avoidance of one or both members of the pair, although they were not directly involved; predations made by other group members; or inter-community interactions. Thus, most incomplete copulatory sequences (90.3%), were initiated by males and failed to reach intromission because of the females' non-cooperation.

The predominance of female termination of incomplete copulatory sequences allows some assessment of the relative role of the male and female in determining partner preferences. If a male is not attracted to a particular female one might expect a low rate of courtship, giving a negative index in Figure 5.4; but not a high rate of incomplete sequences in Table 5.8. On the other hand, if a female is not attracted to a particular male, but the male is attracted to her, one would expect a high rate of courtship combined with a high rate of female avoidance, giving a negative index in Figure 5.4 and a high rate of incomplete sequences in Table 5.8.

Comparison of the indices of partner preference with the rates of incomplete sequences does little to clarify the situation. No consistent relationship between the data in Figure 5.4 and that in Table 5.8 exists. On reflection this is not a surprising result, as the preferences shown by individuals are built on their particular relationships with others, which have developed over a number of years. For example, if a female disliked a particular male and consistently avoided his courtship, one would not expect him to persist in the face of continual negative reinforcement, but to turn his attention to other, more cooperative, females. Observations of individuals for a small part of their lifetimes can only reveal that preferences, both negative and positive, exist between particular dyads. The explanations of such preferences are more elusive, and lie buried in the past history of individual relationships.

On 38 occasions an opportunity arose to directly test a male's choice of copulatory partner. These were times when two females were simultaneously maximally tumescent, and members of the same group. The conditions for an interaction to be included as a direct male choice were: 1) that both females were maximally tumescent; 2) that the rejected female was at least as close to the male as the chosen female, and 3) that the rejected female was not interacting with another chimpanzee at the time the choice was made. Data were insufficient to look at individual preferences, but it was striking that on 30 of the 38 occasions the older female was selected. If only choices made by adult males are considered, then 27 out of 30 were for the older female. This preference of adult males for the older of two available females is statistically significant (X^2=19.2, df=1, $p<.001$). Although few data are available, it seems that young males did not show a preference. In the eight incidents of choice involving juvenile males, the older of the two females was chosen on three occasions, and the younger on five.

The data indicate that truely promiscuous, i.e. random, mating does not occur among wild chimpanzees. Individual differences in overall copulation rates suggest that females differ in their attractiveness to males, and that males differ in their levels of copulatory activity. Amongst juvenile, adolescent and adult males, a negative correlation exists between copulation rate and age. Copulation rates were highest in the period between achieving complete copulatory competence (at the age of 4-5 years) and puberty (at about 10 years). For these males the normal culminative event of ejaculation is absent and it is possible that the lack of such a terminating stimulus results in a higher rate of copulatory interactions. Copulations involving males of this age group commonly had multiple intromissions, while amongst post-pubertal males, a single intromission is the rule. The longest copulatory interaction recorded was between Sparrow and Goblin (before he reached puberty); it lasted for 19 minutes and included 12 intromissions. Whilst these prolonged copulatory interactions do not increase copulation rates (intromissions separated by less than 10 minutes, are recorded as a single copulation) they do suggest that in the absence of ejaculation there is no natural point of termination to a copulatory sequence. It was not possible during the present study to collect accurate data on the length of time between successive ejaculations in adult males, as the occurrence or non-occurrence of ejaculations was only observable in 30% of copulations. However, adult male copulations are normally separated by 30-60 minutes and this interval is at least partly enforced physiologically by the refractory period, a restraint which does not operate on pre-pubescent males.

Another factor which might contribute to the high copulation rates shown by young males is their immunity from social constraints. Goblin's copulation rate with Gigi dropped to a lower level after he reached puberty, the decrease resulting from Gigi's increasingly aggressive responses to Goblin's courtship, see Section 6. In addition to the change in the reaction of females, there is also a change in the attitude of adult males to adolescent males. Adults who have previously tolerated juvenile males and allowed them complete freedom in their expression of sexual and other types of behaviour, cease to do so (Nishida, in press). An example of this was described with respect to interference in Section 4. Van Lawick-Goodall (1968) reported that adolescent males appeared to be inhibited from copulating with females when in close proximity to adult males. In promiscuous mating aggression was not shown to adolescent males, but it is possible that the adolescent's increasing awareness and fear of adult males does act to inhibit or reduce their attempts to copulate when close to adult males.

5.13 Synposis

In tracing the development and expression of copulatory behaviour in wild chimpanzees a number of points become apparent:

1) Variation both in individual behaviour and in individual male-female relationships is great, and makes both generalisations and interpretation difficult.

2) Behaviour patterns may emerge early in life but their expression may be modified, or they may be suppressed, by social factors. These changes appear to be concentrated during adolescence.

3) Truely promiscuous mating does not occur. Partner preferences are shown and the most extreme of these are the negative ones shown by primary kin.

The basic behavioural elements of copulation, i.e. mounting, intromission and pelvic thrusting, appear during the first two years of a male's life but do not become properly coordinated and integrated until the fourth year of life. Although observation was biased, it appears that infant males direct copulatory behaviour predominantly towards females showing cycles of sexual swelling, but they do not limit their behaviour to the cycle phase of maximal genital tumescence. Isolated copulatory elements are shown by young males during play when they are directed to both male and female peers. Courtship elements are not typically shown by infant males, but during the juvenile period courtship emerges, first erratically and later developing into long and intricate sequences of behaviour in 6-9 year olds. Copulation rates peak during the late juvenile period then fall off during adolescence, probably as a result of physiological (onset of ejaculation) and social (increase in aggressive responses of females to courtship) factors.

Courtship serves to attract the female's attention and to communicate the male's motivation to copulate. Some of the behavioural elements shown in courtship are common to aggressive interactions, and it appears to be the female's perception of this aggressive component that makes courtship difficult for adolescent males who are competing for social status with adult females. For adult males the aggressive component of courtship may aid in obtaining a prompt and appropriate response from the female. However, for the female the aggressive component introduces an element of conflict, and this approach (in response to the sexual invitation) - avoid (in response to the aggressive component) conflict may explain why the majority of male courtship occurs when the pair are separated by a distance of 10-15 metres. The male's erect penis is probably an important cue in alleviating the female's conflict. Penile erections are not typically shown in aggressive interactions, and the distance maintained by the male during courtship allows the female time to assess the male's intention. If the male were to approach the female directly she might first react to the aggressive component and avoid the male.

Forced matings or rapes, such as have been reported in orang-utans (MacKinnon, in press) do not occur in chimpanzees and females were able to avoid or ignore a male's courtship. During the study period males were never seen to attack females who did not respond to their courtship. It is of interest that two high ranking males, Humphrey and Figan, were involved in very few incomplete sequences (see Table 5.8). As females do not risk being attacked by males whose courtship they avoid, it seems that both Figan and Humphrey were attractive sexual partners. However, it is not possible to assess whether this was because of their high social status or other factors. Female solicitation is rare, and even when it occurs it seldom leads to copulation. The normal course of events in a copulatory sequence is for the male to take the initiative by courting the female, who then has the choice of whether to continue the sequence, by approaching and presenting, or whether to terminate it by avoiding or ignoring the male.

Immature individuals reacted to others' copulations in promiscuous situations by interfering. It was argued that this behaviour is motivated by two different factors depending on the age of the individual. Interference by infants of both sexes in their mothers' copulations was considered as a distress reaction, the distress apparently being a result of the trauma of weaning. Interference by juvenile and adolescent males was considered to have the same motivation as the interruption of copulations during possessive behaviour (see

Chapter 6). Interference in copulations has been observed in a number of other species of nonhuman primates. The only detailed reports of interference patterns come from captive groups of *Macaca iris* (de Benedictus, 1973) and *Macaca arctoides* (Gouzoules, 1974). Behaviour shown during interference differs between species but there appear to be some general similarities: the behaviour is more-or-less limited to the duration of intromission, and the attention of the interferers is directed to the copulating male. In *Macaca iris* infants and juveniles interfered most frequently in copulations involving their mothers and field reports suggest that the same is true of *Cercopithecus aethiops* (Struhsaker, 1967; Gartlan, 1969) and *Presbytis entellus* (Jay, 1965). In the *Macaca arctoides* group studied by Gouzoules, interference was not restricted to immature individuals, and no age or sex differences existed. Thus it seems, that although there may be some generality in the explanations presented of chimpanzee interference, they do not account for the behaviour of all species. *Macaca arctoides* is unique amongst primates in having a copulatory tie, which extends the duration of intromission, this could be an important difference, but more detailed data, especially from field studies, are required before more definite conclusions can be reached.

Chimpanzees, like many other species of nonhuman primate, show a general behavioural mechanism which reduces inbreeding, in the emigration of individuals from their natal group before reproductive age. However, in chimpanzees it is only females who migrate. The advantage of female, as opposed to male, migration is two-fold. First it allows for more complete exogamy as father-daughter matings are precluded despite this relationship not being recognised by the individuals concerned. Secondly, because males do not move, very close bonds can be established between the individual males within a community, through life-long association. Wrangham (1975) found that chimpanzee males gained access to more females, and hence increased their reproductive success, by acting together to maintain a group range, than they would by maintaining individual ranges. To defend a group range requires cooperation and for this, strong relationships between the adult males are important. The absence of male migration results in a higher degree of genetic relationship between the community males than if males migrated. This would be expected not only to increase the probability of cooperative and altruistic behaviour evolving through kin selection, but also to decrease the probability of male-male competition over females (Popp & Devore, in press).

Mothers and their sons remain members of the same community, at least in the Gombe population where migration is apparently restricted to nulliparous females. Matings have been observed between mothers and their infant sons, but it was argued in Section 10, ii., that these copulations should be considered as reassurance behaviour. Matings between juvenile and adolescent males and their mothers do not occur. In 15 years of observation at Gombe only one copulation between an adult male and his mother has been observed. This copulation (between Satan and Sprout) was atypical in that the female tried unsuccessfully to avoid the male's approach, and broke off intromission before he had finished thrusting. Sibling matings do occur, but females often avoid their brothers' courtship, especially that of a brother immediately adjacent in the birth order. The mechanism for the avoidance of these matings appears to be the incompatability of a close relationship formed during socialisation with later sexual relationships. The avoidance appears to increase proportionally to the degree of closeness of the intial relationship, such that it is greatest between mothers and sons, then siblings adjacent in the birth order, and is less in siblings not adjacent in the birth order. This suggests a possible selective advantage to the phenomenon described in Chapter 3, section 12, of the preponderance of alternating sexes of infants born to the same female.

Although mechanisms to ensure exogamy exist, they are not always utilised to maximum advantage. Females return to their natal community after, or occasionally even before, their first conception and do not leave again. It is impossible to assess to what extent, inbreeding does occur in wild chimpanzees. The behavioural avoidance of copulations with primary kin is complemented by the absence of consort relationships between known primary kin. (Father-daughter copulations and consort relationships may occur but they cannot be detected.) Even if consort relationships are utilised by females to avoid breeding with their brothers or sons, the probability of other males in the natal community being genetically related to them to some degree, e.g. half siblings or cousins, is high. The data from the Mahali Mountains (Nishida & Kawanaka, 1972; Kawanaka & Nishida, 1975; Nishida, in press) indicate that the patterns of female migration observed at Gombe may be atypical, but further data are required to clarify this.

CHAPTER 6

POSSESSIVE BEHAVIOUR

1. Introduction

Possessive behaviour is not a clear-cut category of behaviour but rather, a useful blanket term to cover a variety of behaviour patterns shown by a male to a female who is currently showing cycles of sexual swelling. In the majority of cases possessive behaviour is shown by an individual male towards an oestrus female; more rarely the female will not be in the receptive phase of her cycle and on two occasions during the study period two males acted cooperatively, being jointly possessive of a single female. A male is described as acting possessively towards a female if he shows persistent special attention to her beyond the bounds of normal courtship for a period of time longer than one hour. This involves the male making an active attempt to maintain close proximity with the female, achieved by following, leading, or repeatedly gazing at and waiting for her. Another complex of behaviours commonly, but not always, shown by possessive males is interruption of matings between 'his' female and other males. This can be achieved either actively, by charging aggressively at the offending male, or passively, by intimidating other males merely by remaining spatially close to the female. The occurrence and success of possessive behaviour is intimately linked with male dominance status. The patterns of behaviour shown by males both in the maintenance of proximity and in interruptions of copulations, differ widely and I shall discuss later the possibility that lumping these behaviours under one term, possessive behaviour, is artificial and masks differences in underlying motivation.

Table 6.1 lists the 33 incidents of possessive behaviour

Table 6.1 Possessive incidents observed during the 18 month study period

	Dyad	Date(s)	Observation Hours	Female's Swelling	Leading?	Interruption of other males' mating?
1)	Faben/Miff	20/12/72	6	1	No	Yes - FG,JJ,GB,MU
2)	Satan/Miff	20/12/72	2	1	No	Yes - GB
3)	Faben/Miff	27/12/72	10	1	No	Yes - MK
4)	Satan/Miff	5/3/73	2¼	1	Yes	Yes - GB
5)	Evered/Miff	13/3/73	5¼	¾	Yes	Yes - HG
6)	Hugo/Gigi	25/4/73	4¾	1	Yes	Yes - SH
7)	Satan/Sparrow	7/5/73	4	1	No	No
8)	Hugo/Gigi	27-8/5/73	10	1	Yes	Yes - SH,GB
9)	Faben/Gigi	28/5/73	5	1	No	Yes - SH
10)	Faben/Pallas	16/6/73	1¾	1	Yes	Yes - HG,GB,MU
11)	Humphrey/Gigi	23/6/73	4	1	Yes	No - no males
12)	Satan/Pallas	16/7/73	7	½	Yes	No
13)	Faben/Pallas	17/7/73	3½	¾	Yes	No
14)	Goblin/Pallas	19/7/73	3	1	Attempt	No- no males
15)	Figan/Pallas/ Faben	19-22/7/73	12	1	Yes	Yes - SH,GB
16)	Hugo/Pallas	14/10/73	1	0	Yes	No - no cops
17)	Faben/Pallas	14/10/73	1½	0	Yes	No - no cops
18)	Hugo/Pallas	11/11/73	3	¾	Yes	No - no cops
19)	Hugo/Pallas	12/11/73	1	1	Yes	No

/contd..

Table 6.1 contd.

Dyad	Date(s)	Observation Hours	Female's Swelling	Leading?	Interruption of other males' mating?
20) Hugo/Pallas	15-6/11/73	6½	1	Yes	No
21) Goblin/Pallas	16/11/73	2½	1	Attempt	No - no males
22) Hugo/Pallas	17/11/73	4	1	Yes	No
23) Satan/Patti	18/11/73	1	½	Yes	No - no cops
24) Hugo/Pallas	19-22/11/73	24	1	Yes	Yes - GB
25) Satan/Patti	1-2/12/73	5	0	Yes	No - no cops
26) Faben/Sprout	21-22/12/73	8	1	Yes	Yes - JJ, SH
27) Figan/Gigi	5-8/1/74	7½	1	No	Yes - SH,GB,AL
28) Figan/Gigi	6/2/74	2	1	Yes	No
29) Figan/Gigi/ Faben	9-12/2/74	12½	1	Yes	Yes - EV,MK,SH,GB,AL
30) Figan/Patti	13-17/12/74	38½	1	Yes	Yes - HM,HG,GB,MU,AL
31) Satan/Patti	30-31/1/75	11	1	Yes	Yes - JJ,SH,GB
32) Figan/Patti	2-3/2/75	4	1	Yes	Yes - JJ
33) Satan/Patti	3/2/75	1	1	Yes	Yes - SH

INVOLVEMENT: Males - Faben 10, Satan 8, Hugo 8, Figan ~~5~~ 6, Goblin 2, Evered 1, Humphrey 1

Females - Pallas 13, Gigi 7, Patti 6, Miff 5, Sparrow 1, Sprout 1 observed during the 18 month study period. Not all incidents were observed from beginning to end but those that were (N = 17) ranged in length from one hour to 5 days. Incidents involving a single dyad had to be separated by a minimum period of 24 hours during which no possessive behaviour occurred, to be classified as separate incidents. Six of the 9 females who showed cycles of sexual swelling, and 7 of the 10 adult and adolescent males, were involved in possessive incidents in 16 different dyadic combinations. In the majority (76%) of incidents the female was in the maximally tumescent phase of her swelling cycle (i.e. in oestrus).

2. Initiation of possessive behaviour

Initiation of possessive behaviour was observed on 22 occasions and in 19 of these it was the male who made the first move. In 11 incidents the first sign of possessive behaviour developing was the male's obvious attempt to maintain spatial proximity to the female; initially by following her closely, often with his hair erect. In 3 incidents (nos. 5, 7 & 30, in Table 6.1) the male behaved in this manner from the time he left his nest in the morning and in 3 other cases (11, 15 & 16) the male began following the female immediately upon joining the party of which she was a member. In the remaining 5 cases (6, 9, 12, 17 & 29), following behaviour emerged for no obvious reason after the male and female had been in the same group for some time. In 6 incidents (10, 13, 18, 24, 31 & 33) the male's vigilance became apparent following a copulation between himself and the female; in these cases the copulation was often followed by a protracted grooming session after which the male led, or followed the female closely. In two cases (19 & 21) the first indication of possessive behaviour came when the male suddenly attempted to lead the female with vigorous branch shaking.

In the other 3 observed initiations (7, 23 & 27), the female was responsible for the onset of possessive behaviour. Sparrow (no. 7), waited, gazing back at Satan as the 5 other males in the group left a feeding site. As Satan began to travel Sparrow followed him closely and he occasionally glanced back at her. Twenty minutes later they reached the crest of a valley and Satan charged off, displaying down to the stream bed. Sparrow followed at a more decorous pace and during this 500m of travel, Satan was lost from sight. As Sparrow reached the stream bed, Satan sat waiting and travelled on again as soon as she got to within 10m of him and she followed.

Pallas and Hugo (no. 23) had been present in the same group for 4 hours and no possessive behaviour had been observed. During a rest period Pallas approached Hugo and presented for grooming. Hugo, who was grooming with another male, ignored Pallas and after standing watching for two minutes Pallas moved away grunting, and headed towards Goblin, an adolescent male. Goblin began courting Pallas and she approached him, glancing back at Hugo. Hugo stopped grooming and, with his hair erect, hurried after Pallas, who presented for grooming as he arrived. Hugo groomed Pallas for 30 minutes and showed possessive behaviour towards her for the rest of the observation period.

Gigi (no. 27) had been travelling in a large party for 1½ hours when Sherry advanced towards her and began to court her. Gigi turned away from Sherry and gazed at Figan, the dominant male, who sat 10m away. Gigi faced Figan barking and squeaking and Figan gazed at Sherry. Sherry, after gazing at Figan for 15 seconds, left. Gigi approached Figan, squeaking with a full-closed-grin and then followed him as he initiated travel, during which he frequently glanced back at her. Figan remained possessive of Gigi until the start of her detumescence 3 days later.

In these 3 incidents the female is described as the initiator because she made the first move in a sequence of events that led to possessive behaviour being established. However, it need not have been the female's intention to initiate possessive behaviour. In each case the female could have had a more immediate intention, of gaining a travelling companion, or grooming partner, or of avoiding being mated by a particular male. Towards this end she might direct certain behaviour at an individual male, who might respond in such a way as to establish possessive behaviour.

3. Grooming during possessive incidents

Table 6.2 shows the percentage of observation time that females performed and received grooming during possessive incidents by four males. Comparable data on grooming in promiscuous group situations are included for comparison.

Table 6.2 Social grooming during possessive incidents and in promiscuous groups.

Male	Percentage of contact time male groomed female:		Percentage of contact time female groomed male:	
	Possessive	Groups (max. tum. only)	Possessive	Groups (max. tum. only)
SATAN	5.4	7.2	1.1	4.3
HUGO	5.3	1.0	1.1	0.7
FIGAN	3.3	0.8	0.7	0.8
FABEN	1.8	0.7	0.06	0.4

Males spent more time grooming females than females spent grooming males during both possessive incidents and in non-possessive group situations. Individual differences exist among the four males, both in the amount of time spent grooming and in the amount of time being groomed by females during possessive incidents. Three of the 4 males groomed females more often during possessive incidents than in promiscuous group situations. Satan, the exception, groomed females less often during possessive incidents, but despite this decrease he groomed females more frequently than did the other 3 males. Females groomed Satan and Faben less during possessive incidents, though Figan received only slightly less grooming and Hugo more.

During possessive incidents females frequently presented for grooming and males usually responded promptly. On a number of occasions when a male was slow to respond to a female's groom present she left him and approached another male for grooming. The possessive male in such cases, reacted by following the female and grooming her, often displacing the other male. The impression gained was that social grooming is, to the female, one of the benefits of possessive behaviour. It is something she expects from the male and if he is slow to respond to her groom presents she is able to exert stronger pressure by moving towards an alternative male partner. If the possessive male does groom the female she will respond only by grooming him in such a way as to prolong grooming sessions, e.g. by grooming him if he stops grooming her but only until he resumes. Females involved in possessive incidents were seldom groomed by other males. Possessive males often responded aggressively to males of lower dominance status who approached their females and this combined with the relatively high frequency of grooming by the possessive male, limited the female's seeking and finding alternative grooming partners.

4. Maintenance of Possessive Behaviour

Because the behaviour shown during possessive incidents was so variable it would be misleading to describe an average or typical incident. Possessive behaviour was not characterised by any unique behaviour patterns but comprised a special combination of patterns seen in other contexts. Table 6.3 lists the number of possessive incidents in which various behaviour patterns were observed.

Table 6.3 Behaviour patterns observed in 33 incidents of possessive behaviour.

Behaviour Pattern	Male/Female	No. of possessive incidents in which the pattern was observed
Gaze	Male	28
Wait	Male	26
Pilo-erection	Male	24
Branch shake	Male	19
Display	Male	12
Scream/squeak	Female	9
Bipedal search	Male	6
Dab	Female	4
Arm wave	Female	3
Attack	Male	3
Attack	Female	2
Arm stretch	Male	2
Rock	Male	1

In each case included in Table 6.3 the behaviour pattern was judged to have been directed towards the other member of the dyad in the context of maintaining possessive behaviour. Or, as in the case of much of the female behaviour, it occurred as an immediate response to a male's gesture made in this context. A number of the behaviour patterns listed occur frequently in male courtship. To exclude behaviour occurring in this context, the presence or absence of penile erection was used as an indicator of the male's motivational state. If behaviours such as gaze, branch shake or hair erection occurred while the male showed penile erection they were classified as courtship; if the male showed no penile erection then they were assumed to be directed towards maintaining possessive behaviour. While this distinction aids in the clarification and understanding of possessive behaviour it is not without problems. Firstly, it is known that penile erection is not limited to courtship but may also occur in situations of high arousal, such as the discovery of food sources and in some agonistic encounters. Secondly, it seems probable that courtship by the possessive male may be an integral part of maintenance of possessive behaviour. However, it was felt necessary to make this distinction when examining possessive behaviour although the problems must be borne in mind when interpreting the resultant analysis.

5. Individual Differences

Four males (Figan, Faben, Satan and Hugo) and four females (Gigi, Pallas, Miff and Patti) were involved in sufficient incidents to permit analysis of individual differences. A comparison of the frequency of behaviour patterns shown by each male to all females, and all males to each female will establish whether significant individual differences in the form of possessive behaviour exist.

Table 6.4 Comparison of frequencies of behaviour patterns shown during possessive incidents involving four males and four females.

Behaviour Pattern	Incidents involving each of the 4 males, lumped across females.		Incidents involving each of the 4 females, lumped across males.	
	X^2	p	X^2	p
Gaze	8.59	$<.05$	32.2	$<.001$
Wait	23.4	$<.001$	26.1	$<.001$
Branch shake	177.6	$<.001$	63.1	$<.001$
Pilo-erection	52.1	$<.001$	49.3	$<.001$
Display	8.8	$<.05$	1.4	n.s.

The data used in calculating the X^2 values in Table 6.4 involve differential observation hours on each individual and so do not indicate whether inter-dyadic variation in behaviour is due to the male, female or both. To investigate this the behaviour of pairs of dyads in same-male-different-female (e.g. Figan/Gigi & Figan/Pallas), and different-male-same-female (e.g. Figan/Gigi & Faben/Gigi) combinations were compared. If same-male-different-female dyads are more similar than different-male-same-female dyads then the individual differences observed are attributable largely to the male, and *vice versa*. If no consistent pattern emerges then individual differences in both male and female behaviour contribute to the observed differences in behaviour.

Table 6.5 shows the results obtained from comparing the frequencies of five behaviour patterns shown by all 9 combinations of dyads involving three males (Figan, Faben and Hugo) and two females (Gigi and Pallas). The X^2 one sample test was used in all cases where expected values were greater than five. Of the 11 tests comparing frequencies of behaviour patterns between same-male-different

Table 6.5 X^2 values from a comparison of frequencies of behaviour patterns shown by same-male-different-female and different-male-same-female pairs of dyads during possessive incidents

Behaviour Pattern	Same-male-different-female dyads			Different-male-same-female dyads					
	FB & PL vs FB & GG	HG & PL vs HG & GG	FG & PL vs FG & GG	FB & PL vs HG & PL	FB & PL vs FG & PL	FG & PL vs HG & PL	FB & GG vs HG & GG	FB & GG vs FG & GG	FG & GG vs HG & GG
GAZE	1.1	0.7	0.7	0.5	0.01	5.2*	5.3*	4.8*	5.6*
WAIT	3.5	0	3.6	2.8	2.1	1.5	0.2	5.6*	0
HAIR ERECT	1.1	0.6	0	1.3	7.1**	9.3**	0.3	4.5*	7.9**
BRANCH SHAKE	-	3.3	-	28.9**	-	24.2**	16.7**	-	25.0**
DISPLAY	-	0.3	-	3.6	-	1.7	-	-	-

* $p < .05$

** $p < .01$

\- Expected values less than 5, X^2 test not applicable female pairs of dyads (N = 3), none reached statistical significance. Of the 24 tests comparing frequencies of behaviour patterns shown by pairs of different-male-same-female dyads (N = 6), 13 reached statistical significance while 11 did not. These results indicate that it is largely individual differences in male behaviour which lead to the inter-dyadic variation observed in possessive incidents.

Table 6.6 *Frequencies of behaviour patterns in possessive incidents involving 4 males (no. of behaviour patterns/ 50 obs. hours)*

	Gaze	Wait	Hair erect	Branch shake	Display
HUGO (N=8;54.5 hours)	21	12	56	82	12
FABEN (N=9;54.5 hours)	24	42	65	11	6
SATAN (N=7;33 hours)	21	17	18	11	9
FIGAN (N=5;74.5 hours)	8	18	17	0	3

Table 6.6 lists the frequencies of behaviour patterns for the possessive incidents involving four males. The most commonly occurring pattern is different for each male but for all four *display* occurs at the lowest frequency. *Gaze* and *wait* are passive behaviour patterns while *branch shake* and *display* are active; *hair erection* is an autonomic pattern associated with high arousal. Hugo appears to rely heavily on active leading patterns whilst the other three males depend mainly on passive ones to maintain possessive behaviour. Hair erection occurs at relatively high frequencies in all males but is most common in incidents involving Faben and Hugo. In general,

Figan shows all the behaviour patterns at low frequencies, Hugo and Faben show high frequencies and Satan falls between these two extremes.

The data in Table 6.6 gives an impression of the magnitude of the individual differences in behaviour. These help to explain why, in Table 6.5, the differences between different-male-same-female dyadic pairs are greatest and more often significant when the two males compared are Hugo and Figan, greater when Figan and Faben are compared, and least when the males compared are Faben and Hugo.

6. Qualitative impressions

The above quantification of the data concerning individual differences in male behaviour during possessive incidents, gives results that conform to the qualitative, subjective impressions formed during observation. Hugo and Faben tended to be impatient during possessive incidents, reacting whenever the female delayed during travel, remained feeding after they had finished, or left a feeding site before they were ready. During one possessive incident with Pallas, Hugo repeatedly shook branches at her in an attempt to maintain close proximity as they fed. When this failed he resorted to breaking off large fruiting branches which he carried across his back as he moved to stay within 5m of Pallas. Another characteristic interaction occurred during this same possessive incident; Pallas was resting in a day nest in a tree 5m above the ground. Hugo sat below the tree 10m from a group of four adult males who were grooming. For two minutes Hugo showed great ambivalence, first moving towards the grooming males but then rushing back to the base of Pallas' tree, apparently torn between the desire to join the grooming session and the desire to stay close to Pallas. He sat below the tree and shook branches several times but Pallas remained in her nest. Finally, after a further six minutes of glancing repeatedly between Pallas and the grooming males, and scratching furiously, Hugo joined the grooming group but kept a watchful eye on Pallas.

Figan and Satan, on the other hand seemed much calmer and relaxed during possessive incidents. They rarely used branch shaking as a signal for the female to follow them but were content to wait quietly until the female was ready to travel. If the female moved off ahead of them, they would follow and regain the lead by overtaking. In December 1974, at the height of the termite fishing season, Figan was acting possessively to Patti. Time after time Patti continued to fish for termites after Figan had finished. On each occasion Figan would sit inactive and waited for periods sometimes as long as 40 minutes, until Patti was ready to move on. Satan's behaviour was similar to Figan's, but if a female was very slow to follow, or kept him waiting for periods greater than 10-15 minutes, then he resorted to branch shaking to encourage her progress.

7. Interruption of copulations or copulation attempts by other males

Active interruption by the possessive male of copulations or copulation attempts by other males was observed in 18 of the 33 possessive incidents (see Table 6.1). In eight cases no opportunity to interrupt matings existed, either because other males present showed no sexual interest in the female (cases 16, 17, 18, 22 & 25), or because no other males were encountered during the possessive incident (cases 11, 14 & 21). In the five incidents where other males were present but showed no sexual interest, the female was not maximally tumescent. In the remaining seven cases (7, 12, 13, 19, 20, 23 & 28), copulations involving other males occurred, but the possessive male made no attempt to interrupt them.

Table 6.7 Responses of possessive males to copulations and copulation attempts of other males

Male	Interruption	No Interruption	No Sexual Interest	No Other Males	Total
FABEN	7	2	1	0	10
SATAN	4	2	2	0	8
HUGO	3	3	2	0	8
FIGAN	5	0	0	0	5
GOBLIN	0	0	0	2	2
EVERED	1	0	0	0	1
HUMPHREY	0	0	0	1	1
TOTAL	20	7	5	3	35

Table 6.7 shows how each possessive male responded to copulations and copulation attempts made by other males. Individual differences may exist but the data are too scarce to draw any firm conclusions. It is however of interest to note that Figan, the alpha male, actively interrupted copulations and copulation attempts during all five possessive incidents in which he was involved. Scoring of interruption in Table 6.7 does not mean that the possessive male interrupted all copulations and copulation attempts, but merely that he did so at least once.

Figure 6.1 shows the number of times each male interrupted every other male's copulations or copulation attempts during possessive incidents. The males are listed in descending order of dominance status. Attempts at interruption that were unsuccessful, i.e. when the possessive male was not able to terminate a copulation are also noted. Of the 70 successful cases of interruption only one involved a possessive male interrupting the mating of a more

Figure 6.1 Interruption of copulations and copulation attempts during possessive incidents (row male interrupts column males mating).

	FG	EV	HM	ST	FB	JJ	HG	SH	MK	GB	MU	AL
FIGAN		1	1			1	1	2	1	9	1	4
EVERED							1	1				
HUMPHREY							1	1				
SATAN					1+A	1	2	3		7	1	
FABEN	1	3A	A			2	2	6	2	9	2	
JOMEO												
HUGO			A		A			2		2		
SHERRY										1		
MIKE												
GOBLIN											1	
MUSTARD												
ATLAS												

A = Unsuccessful attempt to interrupt.

dominant male; in the remaining 69 cases the possessive male was of higher dominance status than the male whose copulation or copulation attempt was terminated. Of the ~~6~~7 unsuccessful attempts, 6 involved males of higher dominance status than the possessive male. 7 ??

The single exception, where the possessive male was of lower dominance rank than the copulating male, involved the brothers, Figan and Faben. Faben had been acting possessively towards Miff for three hours when the group they were in moved through Plum Tree Thicket, an area of dense and tangled vegetation. Miff began to termite and Faben fed 10m away in a tangle of vines, completely out of sight (at least to the observer). Figan approached and courted Miff and as intromission began Miff vocalised, giving the typical copulatory squeal. Faben, with his hair out crashed through the vines and landed right on top of Miff and Figan. The copulation terminated as Miff avoided Faben, screaming. Faben glanced briefly at Figan, (who did nothing, but looked slightly surprised) and then turned and attacked Mike who was termite fishing nearby. It seemed as though Faben had not known the identity of the copulating male until after the interruption but reacted to Miff's squeal - a vocalisation specific to the copulatory context. Faben's attack on Mike, an innocent bystander, seemed pure redirected aggression, prompted perhaps by his surprise at interrupting the copulation of his more dominant brother.

In all active interruptions of copulations and copulation attempts, the possessive male directed aggressive behaviour patterns towards the male and female involved. Table 6.8 lists the behaviour patterns occurring in 63 cases of interruption in which details of the interaction were observed. In 61 cases the possessive male

Table 6.8 Behaviour patterns shown during interruption of copulations and copulation attempts made during possessive incidents.

Behaviour patterns shown by the possessive male	Percent. of total interactions in which pattern was shown
Hair erect	92
Advance	51
Charge	37
Approach	22
Gaze	19
Chase copulating male	6
Attack copulating male	6
Branch shake	6
Chase copulating female	5
Rock	3
Hunch	3
Response of copulating male	
Avoid	64
Scream	18
No response - copulation continues	13
Pant grunt	6
Crouch	6
No response - copulation terminated by female	6
Gaze	5
Approach possessive male	3
Response of copulating female	
No response - copulation terminated by male	40
Avoid	38
Scream	14
No response - copulation continues	13
Squeak	3

initiated the sequence of behaviour leading to the interruption. In the two exceptions the female, Gigi, initiated the interaction by squeaking loudly and gazing at the possessive male when another male began to court her. As can be seen from Table 6.8, the most common sequence of events was for the possessive male to move with his hair erect towards the offending pair, and for the interloper to avoid quickly, terminating the copulation or copulation attempt. The female often reacted by avoiding of the possessive male. Attacks were rare, being observed only six times in the 63 interactions. Four times the possessive male attacked the offending male, once the female, and once (as described above) an uninvolved male. In 3 of the 8 cases where the possessive male's behaviour failed to terminate a copulation, the possessive male showed no aggressive patterns but merely gazed towards and shook branches at, the offending pair. In the other 5 cases the aggressive behaviour patterns shown by the possessive male elicited no avoidance response from either of the copulating pair. Three times the possessive male stood only 2m from the copulating pair, bouncing up and down with his hair erect, rocking and shaking branches, but still the copulation continued in a normal manner. Passive interruption or inhibition of copulations also seemed to occur, but an objective definition of this phenomenon was impossible to reach as no recordable behaviour was involved. However, the reduction in copulation rate that followed the establishing of some possessive incidents (see Figure 4.4, p. 63 , for the best documented example) was striking. In these cases active interruption of copulations and copulation attempts occurred but not frequently enough to explain the general decline in copulation rates. While other factors, e.g. female attractiveness or receptivity, could have been responsible, this seemed unlikely. An alternative and more probable explanation was that the mere presence of the possessive male, combined with earlier active interruptions, inhibited other males from even attempting to copulate with the female.

To summarise, the relative dominance ranks of the possessive male and the copulating male are of great significance in the occurrence and success of interruptions of copulations and copulation attempts. Possessive males rarely attempt to interrupt copulations involving males of higher dominance rank than themselves and only once in 7 occasions did a lower ranking male succeed in this. Conversely, all 64 interruptions were successful when the possessive male was of higher dominance rank than the copulating male. In all cases of interruption the possessive male was fully adult and dominant to the female involved. Thus, it seems that a female's response to the behaviour of a possessive male during interruption must be mediated by the response of the copulating male. If this were not the case any adult male would be capable of terminating any copulation merely by aggressing against the female.

8. Response of possessive males to copulations involving males of higher dominance status than themselves

The dependence of the ability to interrupt copulations on the relative dominance ranks of the two males means that theoretically only the highest ranking male has the capacity to completely monopolise a female whilst in the presence of other males. Table 6.9 shows the responses made by possessive males to copulations by more dominant males.

Table 6.9 Response of possessive males to copulations by more dominant males

	Percentage of times seen (N=174)
No discernable response:	76%
Agonistic interaction with another male:	9%
Watches copulation:	8%
Attempts to interrupt copulation:	3%
Advances or approaches the copulating pair:	2%
Avoids copulating pair:	2%

It can be seen from Table 6.9 that in the majority of cases when a more dominant male copulates with a female during a possessive incident, the possessive male made no discernable response to the mating. It was sometimes difficult to make an objective judgement as to whether or not the possessive male was aware of the copulation if he made no obvious response. However, in the majority of cases the possessive male's proximity to the female made it unlikely that he remained in ignorance of the copulation. In 19 cases when the possessive male made no obvious response to the copulation he was engaged in some other activity which may have diverted his attention. These activities were, agonistic interactions not involving the copulating pair (10 cases), social grooming (4 cases), active hunting of mammalian prey or eating meat (4 cases) and vocal interaction with chimpanzees of another community (1 case). In all the other cases (N = 15) the possessive male was not involved in an activity which would distract him to any great extent.

Possessive males responded noticeably to 24% (40 cases) of copulations between 'their' female and a male of higher dominance rank than themselves. The commonest response seen was an agonistic interaction between the possessive male and a male of lower dominance rank. Such an interaction was recorded as a response to the copulation if it occurred either immediately after the courtship of the more dominant male or simultaneously with the copulation. On five occasions the possessive male directed agonistic patterns to another male who was totally uninvolved in the copulatory interaction, and in the other ten cases the victim was an adolescent male who approached the copulation and attempted to interfere. In all cases the possessive male's aggression seemed directly triggered by the occurrence of a copulation he was powerless to prevent. It can thus possibly be regarded as a re-direction of aggression, which, if the copulating male had been of lower dominance status would have been channeled into interruption of the copulation.

In 14 cases the possessive male watched the copulating pair but made no other response. In 5 cases he attempted unsuccessfully to interrupt the copulation. In 3 cases the possessive male advanced or approached to the copulating pair, and on one of these occasions he groomed the copulating male during intromission. In the final 3 cases the possessive male avoided the copulating pair and returned to his female only after the copulating male had left.

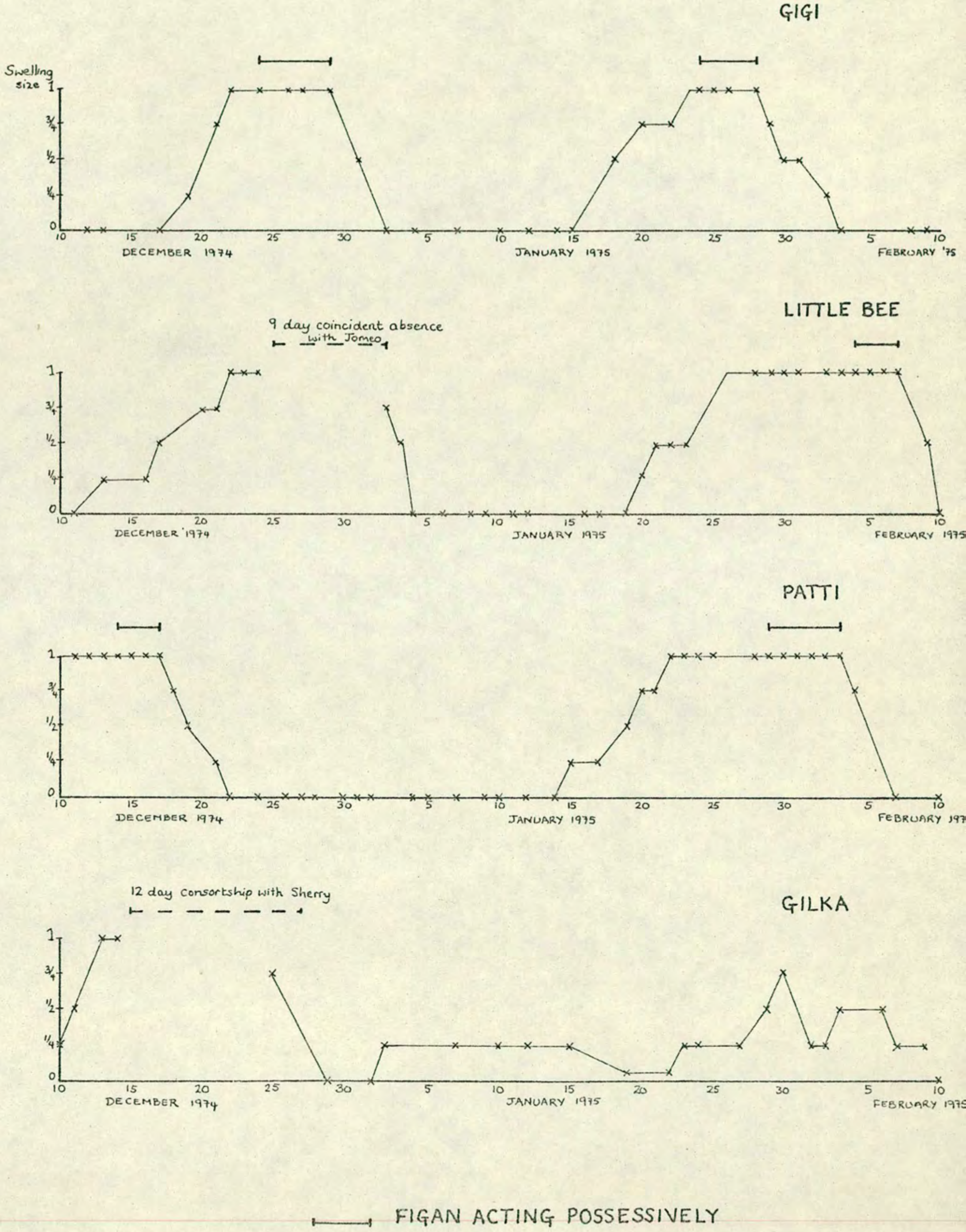
9. <u>Possessive behaviour shown by the dominant male</u>

Figan was recognised as the dominant male of the Kasakela community from June 1973 (Riss, in prep.). He was not observed acting possessively in the seven months prior to achieving his alpha status, but in July 1973 he cooperated with his brother Faben to show possessiveness of Pallas. From January 1974 he was frequently involved in possessive incidents. Four such cases were observed during this study (in Jan. & Feb. 1974 & Dec. 1974 - Feb. 1975), but throughout 1974 Figan was regularly involved in possessive incidents with all females who showed cycles of sexual swelling (Riss and Busse, pers. comm.). The pattern of behaviour established by Figan in January 1974 persisted until observations at Gombe ceased in May 1975 (Pusey, pers. comm.). Typically Figan established his possessiveness about mid-way through the female's maximally tumescent phase and maintained it until the onset of detumescence.

Figure 6.2 shows the swelling cycle records of the 4 females who were sexually receptive during the 2½ month period from December 1974 to mid February 1975. The 4 females collectively showed 7 cycles during this period and in 5 of these Figan acted possessively towards the female during part of her oestrus phase. The two oestrus phases during which Figan did not act possessively were coincident with another female's oestrus phase, such that he had a choice of one of the two females. In early December he acted possessively towards Patti, and Gilka who was simultaneously receptive was involved in a consort relationship with Sherry. In late December Gigi and Little Bee were in oestrus simultaneously. Figan initiated possessive behaviour with Gigi on December 24. From December 25 to January 3, Little Bee was not seen and Jomeo was also then absent. As all the other male chimpanzees were seen during this period, it was assumed that Jomeo and Little Bee were in consort.

Figan, as the dominant male, had the potential when acting possessively, to prevent all other males from copulating with his female. However, observation shows that in practice this was not

Figure 6.2 Swelling cycles of four females from December 1974 - February 1975, showing Figan's pattern of possessive behaviour.



an easy thing to achieve. Whilst he was successful every time he attempted to interrupt copulation attempts by other males, he was not able to eliminate these totally. Despite Figan's possessive behaviour, copulations with other males occurred in two general types of situation. The first were situations where Figan's attention was temporarily distracted by events such as predations, agonistic interactions, excitement associated with arrivals of males at groups and inter-community encounters. The second kind of situation occurred when, during feeding or especially travel in dense vegetation, the female was temporarily out of Figan's sight. During possessive incidents Figan usually led in travel and thus could not keep a continuous watch on his female. Goblin, an adolescent male, was particularly sensitive to this type of situation, being quick to surreptitiously court and copulate with a female during travel, while keeping his gaze fixed on Figan's back in case he should glance back and see them.

July 22, 1973, was the third day of a possessive incident involving Figan and Faben with Pallas. During the previous two days they had successfully monopolised Pallas, allowing only infant males to mate her with impunity. Observation on 22 July began at 07.15, and at 07.25 the chimps heard the bleat of a young bushbuck close to where they were feeding and became tremendously excited. Figan, Faben and Humphrey descended from the trees squeaking and embracing each other. They stood in a tight group gazing towards the bushbuck. Pallas remained in the tree and during the next five minutes was mated by Mike, Hugo and Goblin, while Figan and Faben, only 10m away, totally focused their attention on the prospective prey. Hugo descended, caught and killed the bushbuck and was immediately surrounded by Figan, Faben, Evered, Humphrey and Mike. Tremendous excitement followed as the males repeatedly displayed and grabbed at the prey which remained in Hugo's tight grip. Pallas and Goblin watched from the trees and were joined by Satan. Satan mated Pallas and 5 minutes later the threesome left the predation site and travelled rapidly north. After 3 minutes of travel Goblin pant hooted as he, Satan and Pallas crossed a stream. On hearing this pant hoot Figan and Faben began screaming (Mkukwe, pers. comm.), and 2 minutes later they left the predation site and travelled north (neither had obtained any meat). Only 90 minutes later did Figan and Faben catch up with Pallas, Satan and Goblin, and in this period there had been 3 further copulations. Figan and Faben copulated with Pallas on reunion and immediately re-established their possessiveness. They monopolised Pallas for the next five hours, interrupting a copulation attempt by Goblin. At 14.30 Humphrey joined the party of Figan, Faben, Satan, Mike, Sherry, Goblin and Pallas, who were feeding quietly on fruit. Pandemonium erupted as Figan and Faben charged at Humphrey and rapidly dispossessed him of the part of the bushbuck carcass that he carried. Immediately Figan and Faben charged at Humphrey, 3 other males, Goblin, Satan and Mike ran towards Pallas. Goblin arrived first, but before he could mate her he was displaced by Satan, who copulated with Pallas. Mike followed Satan and also mated Pallas. Faben, having obtained some meat, turned to see Mike mating Pallas, he charged towards them but arrived too late to interrupt.

In this 10½ hour observation period there were 16 copulations with Pallas; Faben 5, Figan 3, Satan 3, Mike 2, Goblin 2, Hugo 1. This indicates that even a relatively brief distraction of possessive males may enable a number of other males to copulate with the unguarded female. It also emphasises the awareness that adult males have of a more dominant possessive male. No adult male attempted to copulate with Pallas while Figan and Faben were being actively possessive, but within one minute of them being distracted by the arrival of Humphrey carrying meat, three males had penile erections and queued up to mate Pallas.

Another striking example of the problems that the dominant male has in effectively monopolising a female by possessive behaviour, comes from observations of Figan and Patti on December 15, 1974. Observations began at 08.10 when Figan and Patti were found feeding in oil palm trees on the south side of Kakombe stream. Camp, 200m distant on the other side of the stream, was clearly visible from their feeding site. At 08.45 Humphrey, Mike, Satan and Goblin arrived in Camp and began displaying repeatedly and noisily. Figan watched from the top of his palm tree and after a few minutes with his hair erect, he started to whimper. At 09.00 with the displays from Camp still in progress Figan descended from the palm. His hair was still erect and he whimpered with a full-closed-grin. He stopped at the base of the tree and gazed up at Patti who still fed. A minute later she too descended and Figan led travel down the main path towards Kakombe stream and Camp. After travelling about 75m Figan, still whimpering, turned to Patti; she approached him and he put his arm across her back, in a brief embrace. He then looked up the path towards Camp and after standing briefly bipedal, grasping his scrotum (Figan's unique way of registering his unease, see Bygott, 1974 p.63), Figan charged off displaying towards Camp. Satan, Humphrey and Goblin must have been just out of sight, for they appeared only seconds after Figan vanished round a bend in the path. Figan displayed into Camp and then threw a tantrum, screaming and whimpering for several minutes before settling down to groom with Mike (McGrew, pers. comm.). Meanwhile Humphrey, Satan and Goblin copulated one after the other with Patti. On this occasion Figan did not reassert his possessive behaviour for almost 2½ hours, during which time there were 16 copulations by 4 males. However, once Figan re-established possessiveness, he monopolised Patti for the remainder of that day and for the next two days prior to the onset of her detumescence.

These examples clearly indicate that whilst the dominant male has the theoretical potential to monopolise a female, by interrupting any copulation attempts by other males, in practice it is a difficult task. Constant vigilance is necessary and distractions must be ignored if the male is to be completely successful. Observations indicate that a male is unlikely to achieve total success in possessive incidents lasting for several days. However, it is important to maintain perspective. Possessive behaviour by the dominant male dramatically reduces the number of copulations achieved by other males. It is striking that Figan showed the same pattern of behaviour, i.e. establishing possessive behaviour approximately mid-way through oestrus and maintaining it until the onset of detumescence, thus reducing competition on the days when ovulation is likely to occur.

10. Function of possessive behaviour

Possessive incidents where the male interrupts matings reduce competition for the female and hence increase the possessive male's chances of impregnating the female. The dominant male is the only one who, by showing possessive behaviour, is theoretically able to monopolise the female while remaining in groups with other males.

Although in practice he rarely achieves a monopoly, he significantly reduces competition and may be responsible for up to 90% of copulations taking place around the time of ovulation. This unique ability of the dominant male gives him a considerable advantage over other males who cannot reduce competition over the female while remaining in groups with higher ranking males. A non-dominant male can only monopolise a female by forming a consort relationship and taking her away from the other males.

What are the causes and functions of possessive behaviour? Both individual differences in male behaviour and the tremendous effect of dominance rank on the form and result of the behaviour suggest that causal factors may not be the same in all possessive incidents. For the dominant male, possessive behaviour is a valuable reproductive strategy, as he is able to significantly reduce competition with other males by interrupting or inhibiting their matings. For the other, non-dominant males, possessive behaviour sometimes appears to be an intermediate strategy, the ultimate end being the formation of a consort relationship. Evidence for this comes from two sources. First, one possessive incident (no. 4) was observed to lead to the formation of a consort relationship and in several other cases there were indications that the male's ultimate intention was to form a consort relationship although he was unable to do so. For example, Satan tried several times to lead Patti away from other males in the group, but each time she returned to it. Secondly, it is difficult to explain most of the possessive incidents involving anoestrus females except as an intermediate step in consort formation, although none of the four observed cases actually led to a consort relationship being formed.

Exceptions to the above generalisation about possessive incidents involving anoestrus females, were two incidents between Satan and Patti (nos. 23 & 25 in Table 6.1). Patti originally belonged to another community but in mid-November 1973 she transferred, becoming a permanent member of the Kasakela community (Pusey, 1975). Her arrival elicited considerable aggression from the resident females of the Kasakela community who chased and attacked her whenever opportunity arose. Patti found protection from these attacks by associating closely with adult males, who interceded on her behalf in aggressive encounters with the resident females. During her first six weeks in the Kasakela community Patti had a series of adult male 'escorts', but in the majority of cases proximity was maintained purely by her initiative. During the first two weeks she spent the majority of her time with Satan, and on occasion he actively led her and showed agonistic patterns if she strayed too far from him. Patti was not receptive during this time, and Satan was not observed to make any attempt to form a consort relationship. This situation, of a new female joining the community, appears to be a different and quite separate context for possessive behaviour. Here, the ultimate aim of the behaviour could be to increase the probability that the female will stay to become a permanent member of the community rather than return to ner natal community.

The oldest male of the Kasakela community, Hugo, showed frequent possessiveness. He was not observed to form consort relationships during the study period and none of his behaviour suggested that his possessiveness was directed to this ultimate aim. He was singularly ineffective at preventing other males from copulating with 'his' female, partly because of his low dominance status and partly because he was inconsistent, often not attempting to interrupt even those matings he would have been able to prevent. The females were often uncooperative with Hugo, ignoring his attempts to lead them. Gigi and Pallas both directed aggressive behaviour towards Hugo during possessive incidents and although Hugo was still considered to hold a higher social status than these females he was unable to impose his will on them. Gigi once ended a possessive incident with Hugo by attacking him (the only attack by a female on an adult male observed in the study) after he had repeatedly tried to direct her travel. Thus, whilst it was difficult to assess the ultimate motivation behind Hugo's frequent possessive behaviour, it could be that he intended to form consort relationships but that his inability to direct the female's movements made this impossible.

Goblin, an adolescent male, was involved in two possessive incidents with Pallas. In both cases he was the only male to follow her when she left a group. After following Pallas for some time, Goblin made several attempts to lead her by branch shaking, most of which she completely ignored. He made a brave show of leadership, but it was always Pallas who determined the timing and direction of travel. Goblin would keep about 5m in front of her and glance back so frequently that sometimes he was almost walking backwards. Each time she changed direction he would adjust his own travel, often with brief bursts of running, in order to maintain the leading position. On the one occasion that he made a serious attempt to lead her from her chosen direction, by shaking branches and displaying, she promptly attacked him. After this he allowed her to lead and followed doggedly at her heels. Goblin was in the transitional period of adolescence and while he was able to dominate some of the young adult females, many of the older females still outranked him. His possessive behaviour seemed to comprise incipient consort behaviour but his subordinate rank to Pallas seemed to invalidate his efforts to lead her in directions that she did not wish to go.

Possessive behaviour appears to be an efficient reproductive strategy for the dominant male in the community. As it is a behaviour which results in increasing the male's chances of impregnating females, it gives a selective advantage to him. Possessive behaviour shown by other males can not be considered a useful reproductive strategy in itself, for although competition can be somewhat reduced by interruption of copulations and copulation attempts, the impact made is not large. However, if possessive behaviour is used by non-dominant males as an intermediate step, leading, if all goes well, to the formation of a consort relationship, then it could be expected to confer a selective advantage on such male individuals. By encouraging newly transferred females to remain permanently in the community, through protecting them from the aggressive behaviour of the resident females, possessive behaviour may be a valuable long-term, reproductive strategy. If the female is anoestrus at the time of her transfer, possessive behaviour will convey no immediate benefit, but behaviour that increases the probability of the female's staying will give long-term benefits to the males of the community. It is possible that possessive behaviour shown at this early stage creates a special relationship between the 'escort' male and the female which will facilitate future consort formation.

The evolutionary implications of possessive behaviour will be discussed more fully at the end of the next chapter.

Chapter 7

CONSORT BEHAVIOUR

1. Introduction

Consort behaviour is characterised by many of the behaviour patterns shown during possessive incidents and is also directed only to females showing cycles of sexual swelling at the time. The male maintains close proximity with the females but extends the leading behaviour, typical of possessiveness, to remove the female from the group. Once alone, the pair, plus any dependent offspring of the female, cease all loud vocalisations and actively avoid encounters with other chimpanzees. This avoidance often results in the pair moving to the edge, or even outside, the normal range of the community. The initiation and maintenance of consort behaviour depends on the female's cooperation; if this is forthcoming a consort relationship will last for several days.

2. Occurrence of consorts during the study period

Table 7.1 lists the 15 consorts and 4 consort attempts which occurred during the 18 month study period. Nine of the 15 were directly observed for all (3 cases) or part (6 cases) of their duration. The remaining six consorts were assumed to exist on the basis of the strong circumstantial evidence of prolonged, coincident absence from all observation records of a single male and female. McGinnis (1973) devised a method for determining the frequency of consort relationships in the Gombe chimpanzees by comparing absences of individuals from Camp. During the period 1972-74, Camp attendance had fallen to a level where McGinnis' method was no longer applicable in its original form, but out of Camp observation time had substantially increased (to an average of 400 hours per

Table 7.1 Consort relationships and attempted consorts occurring during the 18 month study period

Dyad	Date	Duration days	Female's Swelling State	Comments
1) Jomeo/Nope	Nov 27-Dec 14 1972	18	?	Coincident absence
2) Humphrey/Miff	Feb 2-19 1973	18	1	Coincident absence
3) Satan/Sparrow	Feb 12-14 1973	3	1	Observed
4) Satan/Little Bee	Feb 19-23 1973	5	1	Observed
5) Satan/Miff	March 5-12 1973	7	1	Observed
6) Satan/Sparrow	March 17-20 1973	4	1	Observed
7) Satan/Pallas	June 16-23 1973	7	1	Coincident absence
8) Faben/Pallas	June 26-July 8 1973	13	0	Observed
9) Humphrey/Pallas	July 23-August 19 1973	28	1	Coincident absence
10) Humphrey/Pallas	Aug 23-Sept 19 1973	20	1	Coincident absence
11) Satan/Melissa	October 15 1973	4 hrs	1	Observed
12) Faben/Melissa	November 15 1973	3 hrs	0	Observed
13) Sherry/Gilka	December 13-26 1974	14	1	Observed
14) Satan/Little Bee	December 22-23 1974	1	1	Observed
15) Jomeo/Little Bee	Dec 26-Jan 1	7	1	Coincident absence
16) Sniff/Little Bee (from Kahama community)	May 21-23 1974	2½	¾	Observed by D C Riss
Attempts				
17) Satan/Melissa	November 17 1973	½ hr	0	
18) Sherry/Pallas	November 19 1973	½ hr	1	
19) Satan/Little Bee	February 16 1974	½ hr	1	
20) Satan/Patti	December 12 1974	1 hr	1	

month). By combining all observation records it was possible to draw some conclusions about prolonged simultaneous absences of a single adult male and a female currently showing cycles of sexual swelling.

The 6 periods of coincident absence which occurred during the study period, and which were taken as indicating a consort relationship between the absent male and female ranged in length from 7 to 28 days. In 5 of the 6 cases the male and female were either seen together on the last sighting prior to the absence or on the first sighting after the absence, providing supportitive evidence for the existence of a consort relationship. Whilst absences of 7 days are not uncommon for females, who tend to be much more solitary than males, it is unusual for females to be alone during their periods of maximum tumescence. Both females involved in the 7 day absences were maximally tumescent at the time, and in each case the absence was perfectly coincident with that of a single adult male, and all the other adult males were seen during the period. On June 16th 1973 Pallas and Satan are known to have left a large travelling group at about the same time although their actual departure was not witnessed. Thus, in all 6 cases where the existence of a consort relationship was deduced from the coincident absence of a male and female the evidence, although circumstantial, is strong, either because of the length of the absence or because some additional evidence is available.

The mean length of the 15 consorts was 9.7 days (range 3 hours to 28 days). This is probably somewhat inflated as there was no method of recording brief consorts which were not directly observed. The mean length of the 9 consorts which were directly observed is 5.3 days (range 3 hours to 14 days). The female was maximally tumescent for at least part of 13 of the 15 consort relationships and for 3 of the 4 attempted consorts.

A total of 172.5 hours of observation were made on consort relationships. Three (nos. 8, 11 & 12) were observed from beginning to end, although only one of these (no. 8) lasted for longer than a day. Some observation was made on 6 other consorts and the 4 consort attempts were observed from beginning to end. Rugema Bambaganya, Stella Brewer, William McGrew and David Riss are gratefully acknowledged for their assistance in collecting data on the 13 day Pallas-Faben consort. Data on a 2½ day consort relationship in the neighbouring Kahama community have kindly been made available by David Riss.

3. Consort Initiations

The start of 7 consort relationships were observed, as were the 4 attempts to initiate consorts which were unsuccessful. In 6 of the 7 consort initiations observed the male and female were seen leaving a group in which other adult males were present, in 5 of these 6 cases the female was maximally tumescent at the time. The seventh initiation (no. 8) involved the pair meeting when no other chimpanzees were present, the female's swelling was only ¼-full and was detumescing.

The strategy used in all the observed consort initiations from group situations was an opportunistic one. The pair took advantage of times when the adult males in the group moved off in travel. The consorting male then either immediately led the female away in a different direction, or remained close to her, grooming or feeding, for a while and then left in a different direction to that taken by the other males.

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5) Satan/Miff	March 5-12 1973	7	1	Observed
6) Satan/Sparrow	March 17-20 1973	4	1	Observed
7) Satan/Pallas	June 16-23 1973	7	1	Coincident absence
8) Faben/Pallas	June 26-July 8 1973	13	0	Observed
9) Humphrey/Pallas	July 23-August 19 1973	28	1	Coincident absence
10) Humphrey/Pallas	Aug 23-Sept 19 1973	20	1	Coincident absence
11) Satan/Melissa	October 15 1973	4 hrs	1	Observed
12) Faben/Melissa	November 15 1973	3 hrs	0	Observed
13) Sherry/Gilka	December 13-26 1974	14	1	Observed
14) Satan/Little Bee	December 22-23 1974	1	1	Observed
15) Jomeo/Little Bee	Dec 26-Jan 1	7	1	Coincident absence
16) Sniff/Little Bee (from Kahama community)	May 21-23 1974	2½	¾	Observed by D C Riss
Attempts				
17) Satan/Melissa	November 17 1973	½ hr	0	
18) Sherry/Pallas	November 19 1973	½ hr	1	
19) Satan/Little Bee	February 16 1974	½ hr	1	
20) Satan/Patti	December 12 1974	1 hr	1	

month). By combining all observation records it was possible to draw some conclusions about prolonged simultaneous absences of a single adult male and a female currently showing cycles of sexual swelling.

The 6 periods of coincident absence which occurred during the study period, and which were taken as indicating a consort relationship between the absent male and female ranged in length from 7 to 28 days. In 5 of the 6 cases the male and female were either seen together on the last sighting prior to the absence or on the first sighting after the absence, providing supportitive evidence for the existence of a consort relationship. Whilst absences of 7 days are not uncommon for females, who tend to be much more solitary than males, it is unusual for females to be alone during their periods of maximum tumescence. Both females involved in the 7 day absences were maximally tumescent at the time, and in each case the absence was perfectly coincident with that of a single adult male, and all the other adult males were seen during the period. On June 16th 1973 Pallas and Satan are known to have left a large travelling group at about the same time although their actual departure was not witnessed. Thus, in all 6 cases where the existence of a consort relationship was deduced from the coincident absence of a male and female the evidence, although circumstantial, is strong, either because of the length of the absence or because some additional evidence is available.

The mean length of the 15 consorts was 9.7 days (range 3 hours to 28 days). This is probably somewhat inflated as there was no method of recording brief consorts which were not directly observed. The mean length of the 9 consorts which were directly observed is 5.3 days (range 3 hours to 14 days). The female was maximally tumescent for at least part of 13 of the 15 consort relationships and for 3 of the 4 attempted consorts.

A total of 172.5 hours of observation were made on consort relationships. Three (nos. 8, 11 & 12) were observed from beginning to end, although only one of these (no. 8) lasted for longer than a day. Some observation was made on 6 other consorts and the 4 consort attempts were observed from beginning to end. Rugema Bambaganya, Stella Brewer, William McGrew and David Riss are gratefully acknowledged for their assistance in collecting data on the 13 day Pallas-Faben consort. Data on a 2½ day consort relationship in the neighbouring Kahama community have kindly been made available by David Riss.

3. Consort Initiations

The start of 7 consort relationships were observed, as were the 4 attempts to initiate consorts which were unsuccessful. In 6 of the 7 consort initiations observed the male and female were seen leaving a group in which other adult males were present, in 5 of these 6 cases the female was maximally tumescent at the time. The seventh initiation (no. 8) involved the pair meeting when no other chimpanzees were present, the female's swelling was only ¼-full and was detumescing.

The strategy used in all the observed consort initiations from group situations was an opportunistic one. The pair took advantage of times when the adult males in the group moved off in travel. The consorting male then either immediately led the female away in a different direction, or remained close to her, grooming or feeding, for a while and then left in a different direction to that taken by the other males.

For example, on March 5th 1973, Miff and Satan had been members of a large group for 6 hours. Satan had been acting possessively towards Miff for $2\frac{1}{4}$ hours when, at 15.10, the group began to travel slowly to the west. Prior to this movement the group had been very sedentary, feeding, resting and grooming in the same location for almost 4 hours. Travel was initiated by several adult males and by 15.20 when Miff began to travel, the only chimpanzees visible were Satan, Goblin and two females accompanied by their juvenile male offspring. Miff headed west, taking the same path that the other group members had used. Satan moved in front of her and travel continued. They crossed an open space 5 minutes later and two adult males were seen travelling 25m ahead. Their path then went through dense vegetation and Satan continued to lead Miff while Goblin and the two other females also follow. At 15.35 they reached a small stream and after pausing to drink Satan mated Miff. Travel continued with Satan leading, now in a northerly direction. During this travel Satan frequently glanced back at Miff and she travelled steadily behind him. At 15.48 a loud chorus of pant hoots was heard from the other males, not ahead but some 500m to the west. Miff turned abruptly and oriented to the calls. She then gazed at Satan, who sat 5m away shaking branches. Miff approached Satan; he left, still heading north, away from the calls of the other males, Miff followed him and neither vocalised in response to the other males' pant hoots. During the next 10 minutes of rapid travel Miff and Moeza (Miff's juvenile daughter) followed Satan as he led them over the ridge and into the next valley, leaving Goblin and the other two females behind. This consort relationship lasted for 7 days, ending when Miff's swelling began to detumesce.

Three consort relationships were initiated through opportunities presented by group behaviour at nesting in the evening or un-nesting in the morning. Nesting times of individuals within a group can vary by as much as an hour and once in their nests, individuals whilst technically still members of the group, rarely interact with others. Maximally tumescent females frequently nested later than other individuals (Wrangham, 1975) and thus situations arise in which all adult males are in nests while the female remains feeding. Satan twice utilised this situation by leading a maximally tumescent female away from a nesting group late in the evening when all the other adult males were resting or sleeping in their nests (cases 11 & 14). Each time the pair travelled only 200-300m away from the other group members, before constructing their own nests. On each of the following mornings Satan left his nest early and sat close to the female shaking branches. She left her nest in response to this, and he then led her rapidly away, in the opposite direction from the other males' nests. In one case (no. 11) the pair reached the next valley without hearing any vocalisations. (The ridges between valleys form effective barriers to sound.) In the other case (no. 14) vocalisations were heard from the other males when, after 30 minutes of travel, the pair were almost 1km away. The female (Little Bee) gave a single pant hoot but then followed Satan as he continued to travel away from the other males. Little Bee's pant hoot attracted no other males to them, but at the time another older, maximally tumescent female was with the other males. This is a complicating variable which will be considered in detail later.

The initiation of the Miff-Satan consort relationship was typical, and in all the examples observed the crucial point during the initiation came when vocalisations from the other males were first heard. If at this point the female remained silent and continued to follow the male then the consort relationship continued. Observation of the 4 unsuccessful attempts to initiate consort relationships strengthen this belief. In 3 of the 4 cases of unsuccessful consort initiation, the female responded to vocalisations from other males heard 15-20 minutes after the consort male had initiated leading behaviour and was taking the female away from the other males. The female responded either by vocalising herself (1 case) or by travelling rapidly towards the vocalising males (2 cases). In the case when the female vocalised (Pallas, case 18) 4 adult males arrived within 10 minutes of her vocalisations, and Sherry, the consort male, made no further attempt to lead Pallas away. In two other cases the females (Patti and Little Bee) responded identically to consort initiation attempts made by Satan. Satan was successfully leading the females away from a group and all was going well until vocalisations were heard from the other group members. In both cases the females, on hearing the pant hoots, turned and began travelling rapidly towards the callers, although they did not, themselves, vocalise. Satan followed and made no attempt to prevent forcibly their return to the group. Once the females had returned to the other group males, Satan neither acted possessively nor made any further attempt to lead them away.

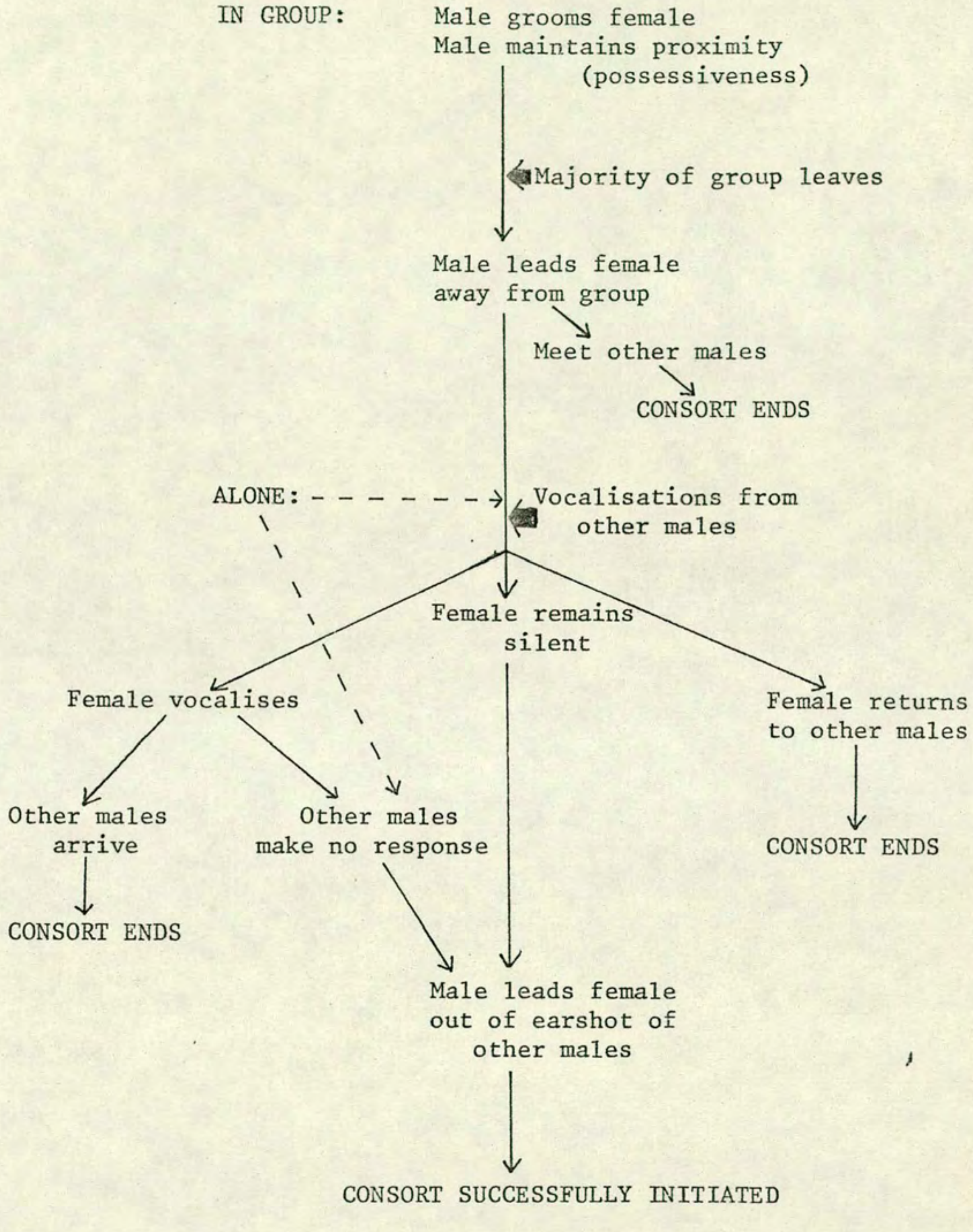
The fourth unsuccessful consort initiation involved Satan and Melissa, who was non-swollen (McGrew, pers. comm.). They met in Camp and left after a period of social grooming during which Satan groomed both Melissa and her 3 year old daughter, Gremlin. Satan led travel and frequently glanced back at Melissa and Gremlin, waiting if they lagged behind. After 10 minutes of travel they met Fifi, Freud and Mike who were coming from the opposite direction.

Gremlin and Freud began to play while the adults rested. Satan left 3 minutes later, and Melissa remained with Fifi, Freud and Mike.

Figure 7.1 summarises the events and contingencies of consort initiation. Caution must be exercised in making generalisations as sample size is small. The behaviour involved in consort initiation is inconspicuous and is only noticed by observers if they are following one of the pair. Observers following other members of a group from which a consort starts are unaware (as are their target chimpanzees) of the consort pair's actual departure, as it is exceptional in a large travelling group for all the members to be visible at any one time. The pair's absence only becomes apparent to such an observer (and the other group members?) when the group stops travelling and becomes more spatially compact.

It is of interest to consider the question - at what point in the sequence of events does the female become aware that the male's intention is to initiate a consort relationship? If the pair hear vocalisations of males, who were in the group which they left, and the male remains silent and persists in leading away from the calls, it must be clear to the female what he intends. (This certainly, is the point at which the observer realises what is happening.) It is possible that the female is aware of being led away from the other males before their vocalisations are heard, but the data argue against this. In each consort initiation the point when vocalisations were heard from other males was crucial. In each case the female made a response: Stopping and turning to face the direction from whence came the calls; responding vocally, or travelling towards the calls. It seems likely that had the females been aware of the males' intentions before the calls, then the

Figure 7.1 Events and contingencies of consort initiation



vocalisations of the other males would not have provoked responses from the females in such a consistent way.

The data indicate that during the early stages of consort initiation a female is able to end the relationship either by vocalising or by leaving the male and returning to a group containing other males. No male was seen to prevent forcibly a female, from leaving him. Thus it appears that, at least in the early stages of consort formation, the female has the choice of whether or not to continue the relationship and that the male cannot form a consort relationship with an uncooperative female.

4. Location and Range

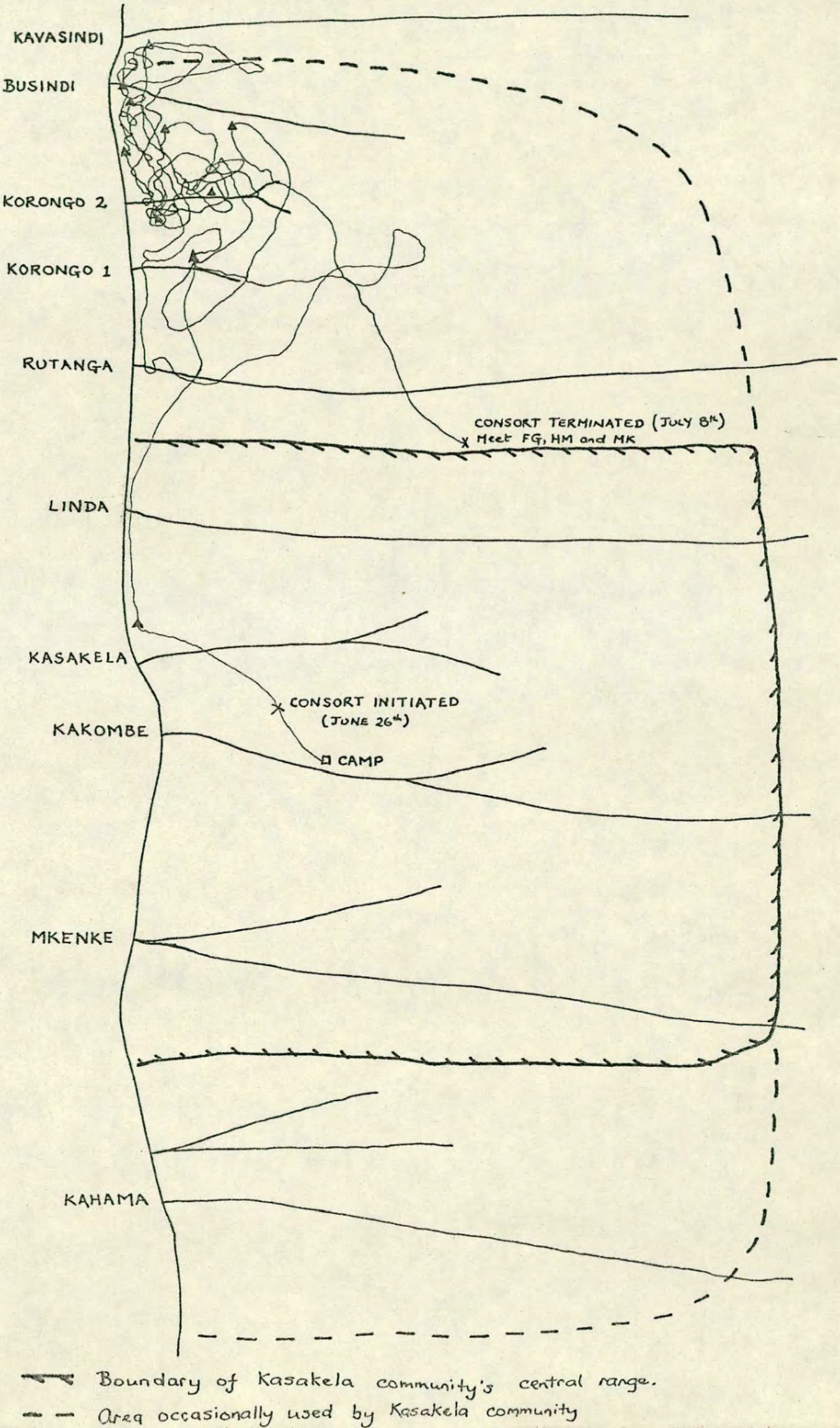
Wrangham (1975, Chapter 5) described ranging behaviour of the Gombe chimpanzees and found that large sex differences exist in the patterns of ranging. He found that the adult males of a community had a large range and that within this, females appeared to occupy smaller, overlapping ranges. He found that males travelled significantly further than anoestrus females, with median day ranges being 4.2km and 2.8km, respectively. Consort pairs behaved in a distinct manner, occupying small temporary ranges on the edge, or even outside, the normal range of the community males. Daily travel of consort pairs was relatively short, the median daily distance travelled being 3.2km.

Only two consort pairs have been followed for long periods of time during the 15 years of research at Gombe. One was a 27 day consort between Figan and Gigi which was followed for its first 11 days, from January 23 to February 2, 1972. The other was the 13 day consort between Pallas and Faben which was followed from beginning to end, June 26 to July 8, 1973. Bauer organised the data collected on Figan and Gigi. No other long consorts have been observed for sufficient periods to establish the pair's ranging behaviour.

In both the Figan-Gigi and the Faben-Pallas consorts the range occupied was small and located to the north of the community's range. Although the areas occupied by these two consort pairs were similar, Faben and Pallas spent their time further north (being south of Rutanga stream only on the first and last days of the consort, see Figure 7.2), than Figan and Gigi who ranged in Rutanga valley on both sides of the stream. Wrangham (1975, p. 5.45) reported that during the 1973 dry season the males of the Kasakela community made more frequent use of the northerly part of their range (Linda and Rutanga valleys) that they had during 1972. Thus, to avoid members of their own community, Pallas and Faben, in mid 1973 had to go further north than did Gigi and Figan in early 1972. The area used by Pallas and Faben although outside the normal range of the Kasakela community males, was visited very occasionally. During the study period, in almost 1000 hours of observation of oestrus females travelling with groups of males, only 9 hours of observation (in 3 follows) was on groups north of Rutanga stream. On these 3 journeys the males in the group showed behaviour typical of that shown at the periphery of their range (see Wrangham, 1975, p. 5.36-5.45 and Goodall et al, in press, for description of behaviour shown in this context) they twice made contact with chimpanzees of other communities. These occasional visits to the periphery of the range may serve to give the males of the community a limited knowledge of the ranges of neighbouring communities and of the potential of the peripheral areas for consort locations.

Brief observations of other consort pairs also indicate that

Figure 7.2 Map showing the location of the consortship between Pallas and Faben relative to the Kasakela community range.



locations outside the normal community range are preferred. Wrangham (pers. comm.) observed two consort pairs in upper Kakombe valley, east of the normal community range. One consort pair were observed crossing over the top of the rift escarpment, heading back to Kakombe valley after a long period of absence. This high point marks the boundary of the Gombe National Park and no group of chimpanzees has ever been observed to cross it. It seems that this consort pair (Faben and Passion) had been completely outside the usual limits of the Kasakela community's range. All the successful consort initiations observed during this study involved periods of rapid travel away from the centre of the community range. Unfortunately no pair other than Faben and Pallas were observed for long enough to establish the eventual location of the consortship.

Although the evidence is sparse it all seems to indicate that consort pairs move to at least the periphery of the normal community range. Once the chosen location is reached, daily travel distances are small and the small temporary range is intensively used.

Apart from the Gombe Stream Research Centre in Kakombe valley and the Park Headquarters in Nyasanga valley, no permanent human settlements lie within the Park boundaries. There are a number of semi-permanent fishing villages along the lake shore and several public footpaths run through the Park. The area used by Pallas and Faben was close to a large fishing village on Rutanga beach, and there were two much used paths, one running just above the beach and one on the ridge between Rutanga valley and Korongo 1 (see Figure 7.2). During the consortship they encountered unfamiliar humans several times daily and Pallas showed considerable alarm while Faben largely ignored them. It is possible that the relatively frequent contact with humans in this area made it undesirable to the community of chimpanzees in the north who are not used to human presence and thus an ideal consort location for the Kasakela community who are habituated to the presence of human observers.

5. Pallas-Faben Consortship

i Introduction

The 13 day consort between Pallas and Faben provided the bulk of the direct observational data on consort relationships. The long period of continuous observation gave a unique chance to look in detail at the structure of the relationship and at the various changes occurring during the 13 days. Caution should be exercised in generalising from a single consortship, as there are indications that it was not a typical relationship. However, as it is a unique record (the Figan-Gigi consort in 1972 was followed by field assistants who, at that time, took only unsophisticated and probably unreliable behaviour records) the data are presented in some detail, followed by the data from the other consorts.

ii Initiation

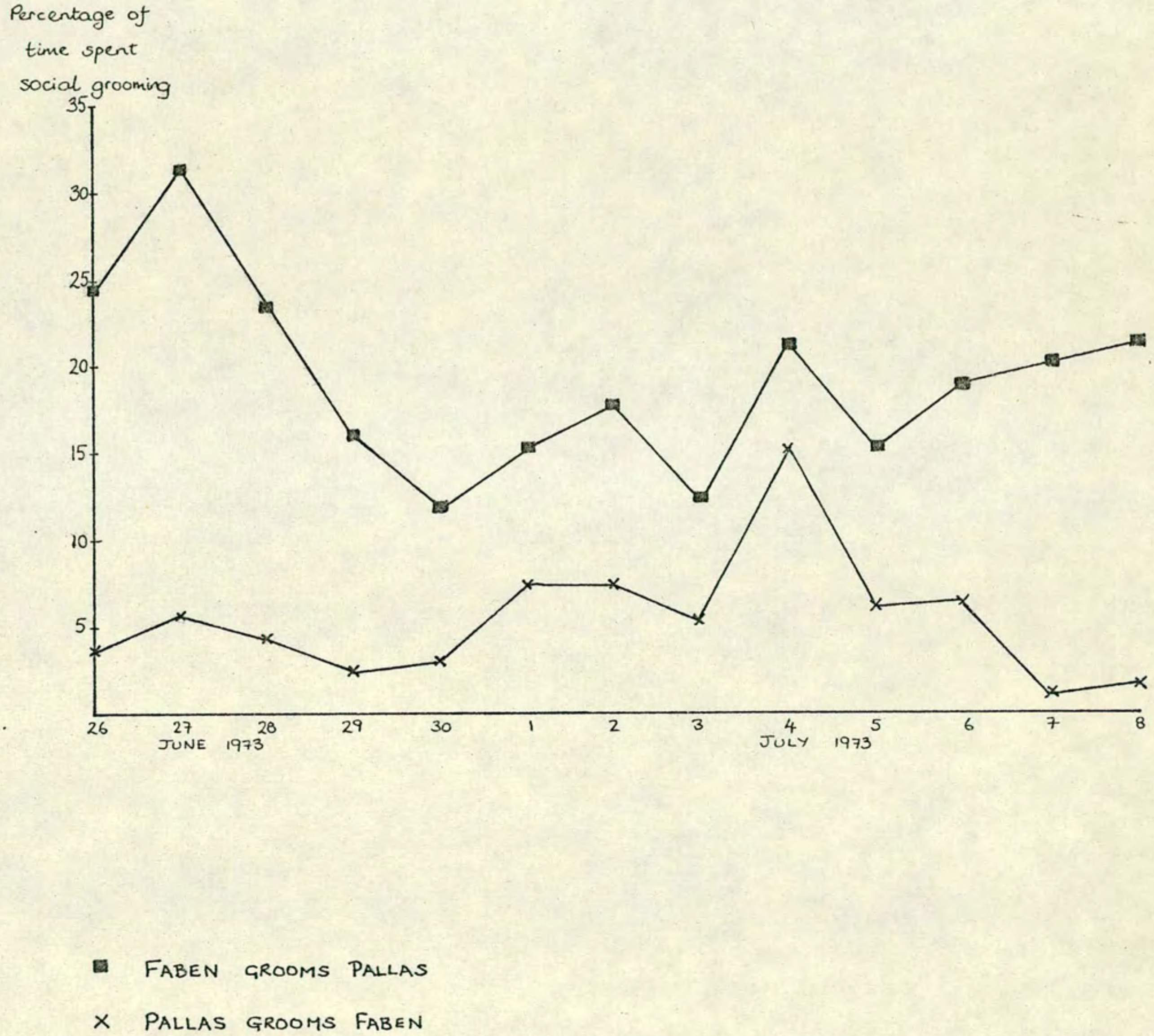
On June 26 1973, Pallas was alone in camp eating bananas; Faben arrived at 16.00. He approached her, she presented and after inspecting her swelling (it was $\frac{1}{4}$ full and detumescing) he began to groom her, making no attempt to dispossess her of the bananas she still held. The grooming lasted for 25 minutes and for the last five minutes Pallas, having finished her bananas, groomed Faben. At 16.25 Faben left Pallas and travelled out of Camp by the north-west path, Pallas followed 5m behind. During this travel Faben glanced back at Pallas frequently and waited while she stopped to urinate. It was not until 16.45, after they had fed near one another for 10 minutes, that Faben first showed overt leading behaviour in the form of branch shaking. Faben led Pallas into the next valley and they nested close together on the edge of the beach. No vocalisations were heard during this time and Faben and Pallas were both completely silent.

iii Grooming

Faben spent an average of 19% of his waking time grooming Pallas during the 13 day consort, with daily values ranging from 32% (on Day 2) to 12% (on Day 5), see Figure 7.3 and Plates 7.1 and 7.2. Pallas spent an average of 6% of her waking hours grooming Faben, with levels ranging from a high point of 15% (on Day 9) to a low of 1% (on Day 12). Figure 7.3 shows that Faben consistently groomed Pallas more than she groomed him. Faben groomed Pallas for less than 2% of the time that they were observed as members of the same group on other occasions.

Only bouts of grooming lasting longer than two minutes are included in the above analysis. Those shorter than two minutes were recorded as <u>brief grooming</u>, and are considered separately, in Figure 7.4. The frequency of brief grooming showed considerable day-to-day variation with hourly frequencies ranging from 0 to 3.3. With the exception of Days 1, 2 and 13, Pallas directed more brief grooming to Faben than he did to her. Brief grooming was seen in two contexts: The first was reassurance, when it was immediately preceded by a submissive gesture; the second context was in social grooming sessions. The first context accounted for 78% of the brief grooming shown by Faben to Pallas but none of the brief grooming shown by Pallas to Faben. Brief grooming was shown by Pallas to Faben during grooming sessions when Faben stopped grooming her. She would groom him briefly, stopping as soon as he

Figure 7.3 Percentage of waking hours spent in social grooming during the 13 day Pallas - Faben consortship.



Plates 7.1 & 7.2. Faben grooms Pallas during their 13 day consortship.

resumed his grooming of her. A typical grooming session during the consort would involve several long bouts of Faben grooming Pallas, with Pallas grooming Faben for shorter bouts, many of which would be brief.

Figure 7.5 shows the hourly frequencies of groom presents made by Pallas and Faben during the consort. On Days 1-7 Pallas presented for grooming to Faben more frequently than vice versa; while on Days 8-13 the situation was reversed. This change indicates a transition in the grooming relationship that occurred mid-way through the consort. At the beginning Faben appeared content with the imbalance in the grooming and he made few attempts to solicit grooming from Pallas. During the latter part of the consort Faben made more and more attempts to induce Pallas to groom him and these were often combined with agonistic behaviour (see below). Faben continued to groom Pallas at high frequencies and met with little success in his attempts to solicit grooming from Pallas. During the last two days of the consort Faben's attempts to solicit grooming became very intense and were probably a major contributory factor in the breakdown of their consort relationship. As the intensity of Faben's demands increased so did Pallas' reluctance to comply and she groomed Faben for only 1.2% and 1.8% of her waking hours on the last two days of the consort.

Grooming was the commonest form of social interaction between the consort pair and it occurred at frequencies far higher than would have been predicted from their interactions (or those of other male-female pairs) in groups. Pallas received the majority of the grooming, and her main motivation in reciprocating appeared to be the maintenance of grooming sessions. The function of social grooming is not a single, easily ascribed entity. It serves to

Figure 7.4 Frequencies of brief grooming during the 13 day Pallas - Faben consortship.

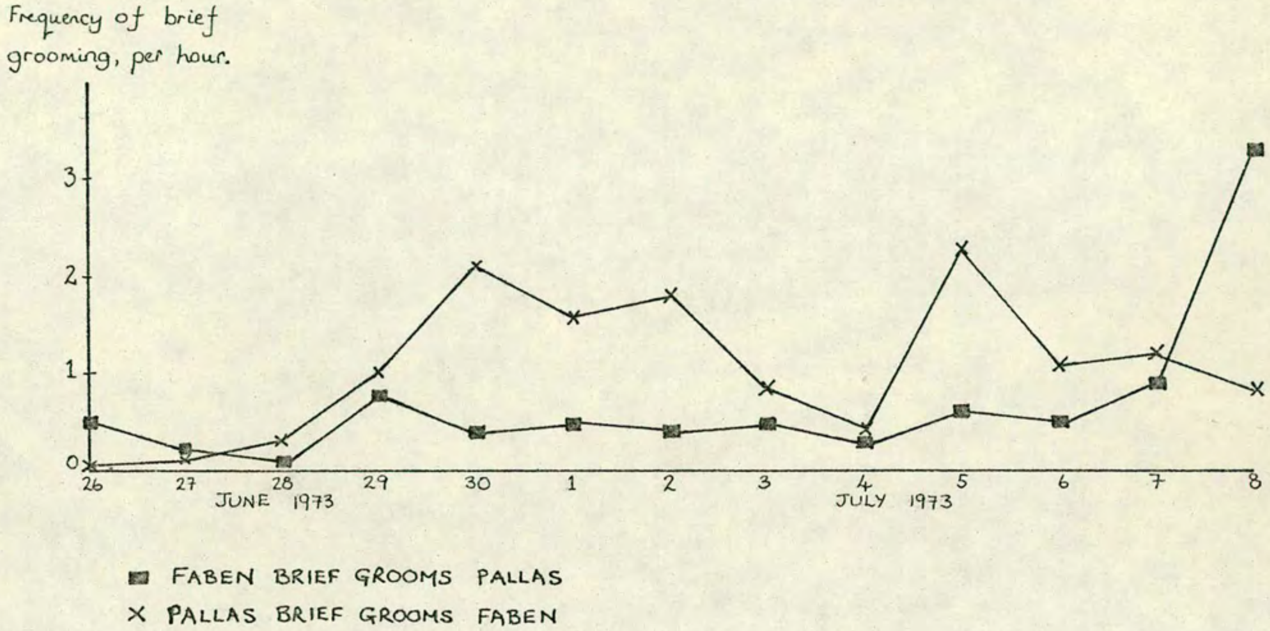
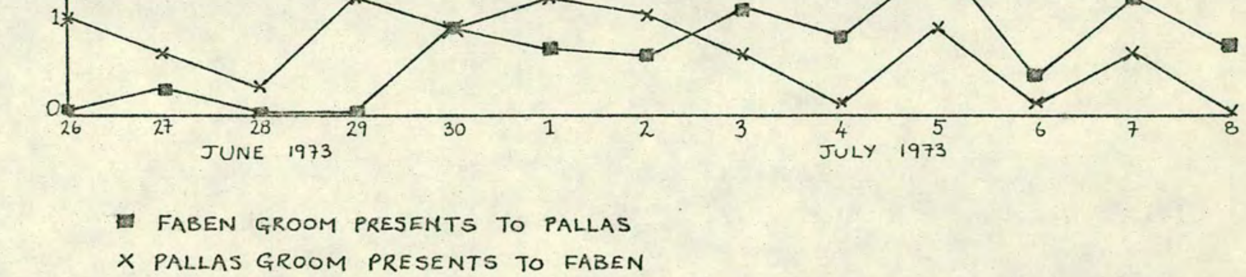


Figure 7.5 Frequencies of groom presents during the 13 day Pallas - Faben consortship.



reduce high levels of arousal in both groomer and groomee (Mason, 1965), but also more generally, it serves to establish and maintain close relationships, especially between adult males (Simpson, 1973) and between mothers and their offspring (van Lawick-Goodall, 1968). The high frequency of social grooming in consorts may function to first establish and subsequently maintain the close, if temporary, bond between the male and female. The imbalance of grooming in the Pallas-Faben consort, together with other aspects of their behaviour (see below) may indicate an imbalance of motivations, with Faben being more highly motivated to continue the relationship than Pallas. If however, the predominance of male to female grooming is a general feature of consort behaviour it could have wider implications (see Discussion, Section 7).

iv Leading and Agonistic Behaviour

Leading and agonistic behaviours (as defined in Bygott, 1974, p. 54) occurred at high frequencies throughout the consort. Forty separate patterns were recorded and these were grouped into 4 principal categories of functional context: Leading, aggressive, submissive and reassurance, (See Table 7.2). The grouping by context is not entirely satisfactory, as some behaviour patterns were observed in more than one. However, decisions for each pattern were easy to reach and agree with the contextual groupings used by van Lawick-Goodall (1968). There is some overlap between categories, especially aggressive and leading, as aggressive patterns, particularly hair-erection, were frequently combined with leading behaviours to elicit following and also submissive behaviours from the female.

Four behaviour patterns seen during the consort were new to the observer. These are defined below; definitions of other patterns can be found in Appendix 1. Scrotum bounce occurred commonly

Table 7.2 Leading and agonistic behaviour patterns observed during the Pallas-Faben consort, grouped into commonest context groups

LEADING (male patterns) N = 4

branch shake (13)*
gaze (13)
hand-on-branch (10)
mount embrace walk (1)

AGGRESSIVE (male patterns) N = 10

hair-erection (13)
charge (10)
hunch (9)
throw (8)
rock (8)
stamp (7)
chase (6)
attack (5)
bipedal swagger (3)
slap (2)

SUBMISSIVE (female patterns) N = 15

staccato grunt (13)
full grin (13)
present (12)
extend hand (12)
touch (11)
squeak (10)
pant (8)
scream (8)
avoid (8)
crouch (7)
whimper (7)
half embrace (6)
bend away (4)
glottal cramps (2)
kiss (2)

REASSURANCE N = 11

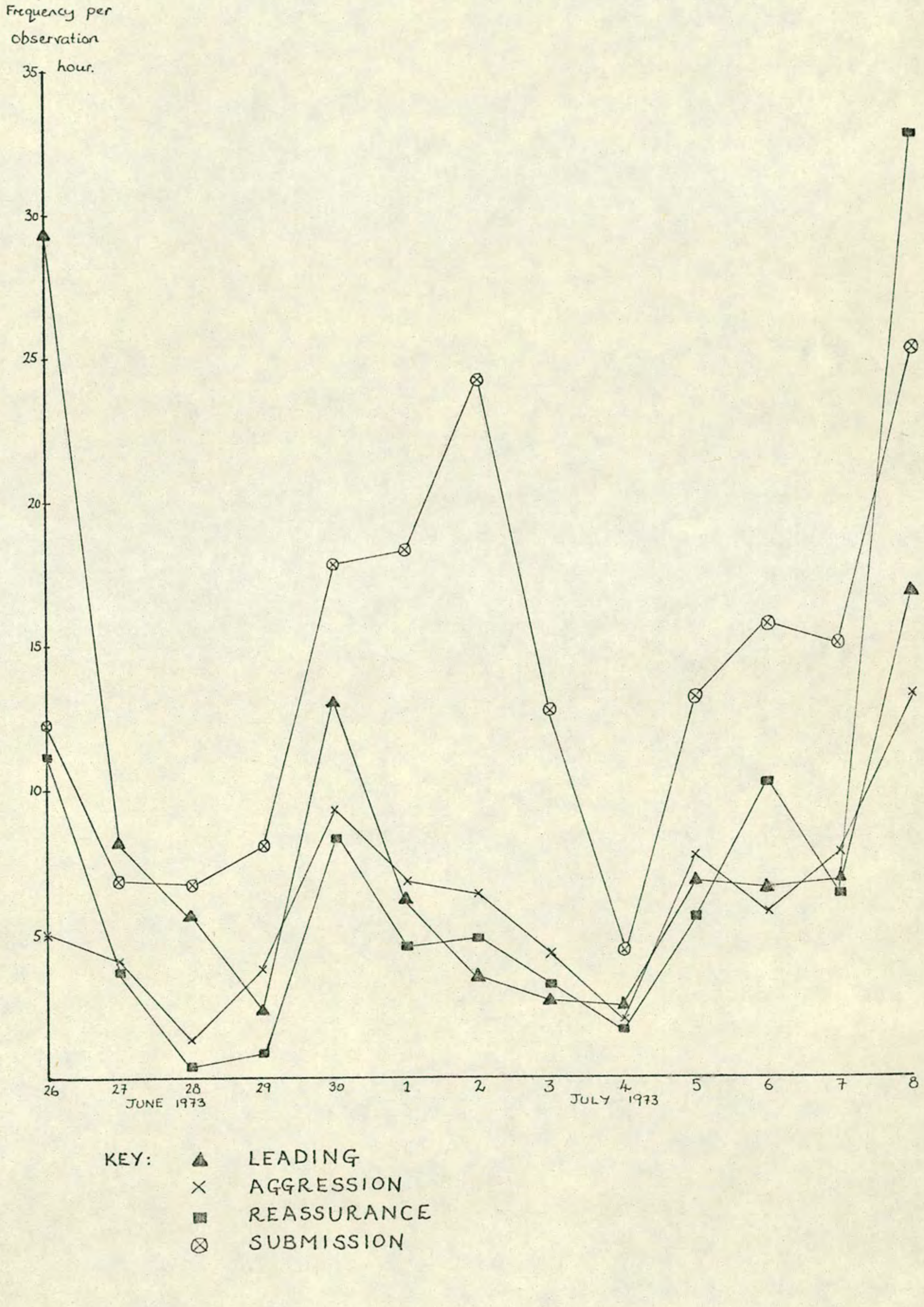
scrotum bounce (13)
male present (13)
inspect (12)
male extend hand (10)
male touch (10)
swelling bounce (8)
male mount (5)
male thrust (5)
male kiss (5)
male half embrace (3)
male mount embrace (2)

* Number of days (of 13) on which the pattern occurred.

throughout the consort. As Pallas approaches Faben, he presents to her while standing tripedally (his right arm is paralysed). She extends her hand, palm up, and places it below and in contact with, his scrotum. He then bounces up and down by flexing and extending his limbs. This pattern has previously been observed in reassurance contexts between Faben and other adult males (Bygott, 1974, p. 63) and appears to be an idiosyncracy of Faben's. Swelling bounce occurred occasionally from Day 5 of the consort. Pallas presents to Faben, he extends his hand, palmar surface up, making contact with the base of her ano-genital swelling. He then bounces her swelling with rapid up and down chucking movements of his lower arm and hand. Staccato grunts were uttered commonly throughout the consort. A rapid series of brief, breathy grunts. Pallas made this vocalisation frequently during the consort and whilst similar in form and context to pant grunts, all observers agreed them to be a distinct vocalisation, not previously heard. Mount embrace walk occurred at high frequency on last day of the consort. Faben ventrally embraces Pallas with his left arm under her stomach and then walks bipedally in the mount position; she walks quadrupedally. In this position Faben directs Pallas' walking by pushing from behind.

Figure 7.6 shows the day-to-day fluctuations in frequencies of the behaviour patterns in the 4 general functional categories. Reassurance and leading behaviours show similar daily fluctuations, with the two highest frequencies occurring on the first and last days of the consort. Aggressive behaviours fluctuate in a similar fashion but were not observed at high frequencies on Day 1 of the consort. Submissive behaviours show a different pattern, with a distinct peak between Day 5 and Day 8 of the consort; however,

Figure 7.6 Daily fluctuations in the frequencies of leading and agonistic behaviours during the 13 day Pallas-Faben consortship.



submissive behaviour like reassurance and aggressive behaviour is most frequent on Day 13.

v Stimuli provoking leading and agonistic behaviour

Faben's impatience shown in possessive behaviour (see p.186) extended in an extreme form to this consort. He insisted on maintained close proximity, not by his keeping close to Pallas but by branch shaking constantly to bring her close to him (Plates 7.3 & 7.4). For 96.6% of their waking hours during the consort, Pallas and Faben were within 5m of each other. This degree of proximity required constant vigilance from Faben and accounts for the high frequency of leading behaviours. Pallas was often slow or reluctant to respond to Faben's demands and this brought swift reprimand in the form of aggressive patterns such as hair-erection, charging, throwing rocks or sticks, from Faben (Plates 7.5 & 7.6). These aggressive patterns elicited submissive responses from Pallas which in turn brought reassurance from Faben. Faben was especially quick to reassure Pallas by approaching and making contact if she vocalised, and such reassurance acted to quieten her.

This chain-like pattern was established early in the consort but became more common and intense in the latter half. Aggressive patterns such as attack, chase and bipedal swagger, were not seen until Day 5 of the consort. Neither made loud vocalisations until Day 5 when Pallas screamed while being attacked by Faben. Her first screams were soft and brief but by the end of the consort she screamed loudly and more often in response to various aggressive patterns from Faben. The suppression of loud vocalisations is a characteristic of consort relationships that was not completely adhered to during this one. Faben, however, remained totally silent for the duration of the consort, and neither chimpanzee pant hooted

Plate 7.3 Faben branch shakes and gazes at Pallas who feeds.

Plate 7.4 Pallas stops feeding and follows Faben.

Plate 7.5 Typical travel during the consortship. Faben leads and Pallas follows close behind.

Plate 7.6 As Pallas moves into the lead Faben's hair becomes erect prior to an aggressive display.

until the final day.

Most of the leading and agonistic behaviour observed seemed to result from a conflict of desires or personalities of the two individuals. Some leading and agonistic behaviour was generated as a response to 'external' stimuli which included, the presence of humans unfamiliar to the chimpanzees, paths which were commonly used by these humans, distant chimpanzee vocalisations and a variety of noises, including baboons travelling ghrough dead vegetation, boat engines on the lake and loud human voices. The most commonly encountered of these were humans, who were seen 29 times in the 13 days. If the humans were at a distance of 100m or more the chimpanzees did not respond to them. On 10 of the 12 occasions however, when unfamiliar humans advanced to within 50m of the pair, one or both showed fearful and avoidance responses. It should be noted that the chimpanzees distinguished between familiar humans (i.e. members of the Gombe Stream Research Centre) and unfamiliar ones. During the consortship 12 different observers from the G.S.R.C. were present during observations of Faben and Pallas (each day two people followed one of whom was usually a Tanzanian field assistant responsible for the Travel and Group chart, see Methods). The chimpanzees never behaved fearfully to any of the observers. In the two incidents when the presence of unfamiliar humans did not elicit fear or avoidance, the people approached quietly and engaged in conversation with one of the observers. Thus while both Pallas and Faben are considered fully habituated to human presence it seems that their habituation is to a certain extent context specific and that some human behaviour outside that context cannot be tolerated.

Pallas was always more alarmed by humans than was Faben. Twice Faben chased and attacked Pallas after she had moved away from him during avoidance of humans walking along a path. However Faben avoided humans on 6 of the 10 occasions. The most extreme case happened on July 2. At 9.25 Pallas and Faben fed in a tree 20m downslope of a public footpath; both observers were seated in long grass and could not be seen from the path. Suddenly loud shouts were heard from the path and a man was seen standing 25m away, waving both arms in the air. His behaviour was directed to the chimpanzees and ceased as soon as he saw the observers. Faben and Pallas both leapt out of the tree, an 8m drop to the ground, and hid in the long grass. They were so well hidden as to be completely invisible to the observer from 5m. They remained in this position, motionless and silent, for 14 minutes after the offending human had left. At 9.40 Faben emerged from the grass and moved slowly back to the tree where they had been feeding; he ascended slowly and after watching the path for a minute he began to feed. Pallas then emerged and approached the tree whimpering softly; she sat on the ground beneath the tree, and Faben shook branches at her. She did not move and continued to whimper. Faben approached her at 9.43 and presented for scrotum bouncing; he then led her back into the feeding tree. Faben resumed feeding but for 3 minutes Pallas sat 2m from Faben, watching the path. No more humans were seen and she began to feed at 9.47, 22 minutes after the initial interruption.

Apparently as an extension of this fear of humans, Pallas became extremely reluctant to approach, cross, or feed close to the public footpaths, even when no humans were in the area. For instance, in the 4 hours following the incident described above, Pallas made 8 attempts to initiate travel away from the vicinity of the path. Each attempt was thwarted by Faben showing aggressive patterns and leading her back. Pallas' aversion generalised to all paths and it required intense leading, usually combined with aggressive patterns, to persuade her to cross or stay close to any path.

Distant chimpanzee vocalisations were heard 7 times in 4 days during the consort: Days 9, 10 (twice), 11 and 13 (three times). On all but the last day the vocalisations came from the north and were almost certainly from members of another community. The first time Pallas and Faben heard distant vocalisations they were on the south side of Kavisindi valley, close to the beach. The calls came from high on the north side of the valley. Faben and Pallas responded with only a 10 second visual orientation in the direction of the calls. The second, third and fourth calls, all came from Busindi valley and were heard while the pair fed on the south ridge of that valley. In all 3 cases the calls were relatively close, estimated distance of 500-750m. In each case Pallas and Faben resonded with rapid and silent travel to the south, i.e. away from the calls. They showed reassurance touching and embracing and both chimpanzees seemed equally alarmed.

The distant calls heard on Day 13 came from the south. The first calls (pant hoots) came from the ridge between Linda and Rutanga valleys at 14.03 when Faben and Pallas were on the north side of Rutanga. Immediately prior to this Faben had attacked Pallas, beating her across the back with a large stick. She had screamed loudly and the distant pant hoots seemed to be a response to her screams. Pallas reached to the distant calls by screaming again and then she pant hooted. Faben remained silent, mounted, and thrust on Pallas. Pant hoots were heard again at 14.07, and Faben immediately attacked Pallas and she screamed loudly. The next pant hoots came at 14.26 when Figan, Humphrey and Mike arrived, all displaying, and the consort ended. Pallas and Faben made no attempt to avoid the calling chimpanzees, and between the calls at 14.03 and the arrival of the other males at 14.26, Faben and Pallas travelled a short distance toward them. Individual pant hoots become recognisable to experienced observers and they seem to be easily identified by the chimpanzees (Marler & 1975). When pant hoots from unfamiliar chimpanzees were heard Pallas and Faben avoided them silently and rapidly. Their response to the pant hoots from males of their own community was very different; this incident is described in greater detail below (see Termination).

A fearful response similar to that shown to unfamiliar humans occurred on July 5 when Pallas and Faben heard something moving through the undergrowth. The pair had been grooming for 20 minutes when, on hearing the noise, they both ran 40m to a dry stream bed. In the stream bed they crouched behind a palm tree and peered in the direction from which the noise had come. They remained frozen in this position for 3½ minutes, until an adult male baboon came into sight. Upon seeing it, Faben and Pallas left the stream bed and resumed grooming.

An unusual natural event occurred on June 30th when, from 16.10-16.20, the sun was partially eclipsed. Despite much prior speculation about whether this might lead to early nesting or possibly to primal religious ceremony, the results were disappointing. There was no noticeable change in light intensity, and Pallas and Faben fed without interruption.

Leading and agonistic behaviours occurred at high frequencies throughout the consortship largely as a result of conflict between Pallas and Faben. Faben was a demanding leader who insisted on

Pallas staying close by him, whilst she was stubbornly self willed. This conflict led to a repeating chain of events: Faben's leading behaviours were ignored or disobeyed by Pallas; Faben then censured her with aggressive behaviour; this elicited submissive behaviour from Pallas, which, in turn led to reassurance from Faben.

Day-to-day fluctuations largely resulted from changes in the scale of the conflict. After the first day, they became more settled for 3 days (June 27-29) while Faben groomed Pallas at high frequencies and demanded little reciprocation. Pallas only rarely procrastinated in following Faben, and his frequencies of leading and agonistic behaviour were relatively low. Day 5 (June 30) was a harrowing day for all concerned and brought changes, as much of the day was spent near a well used footpath. (Being a Saturday, pedestrian traffic eas heavy, as there was a market and a football match in the village to which the path led.) Pallas' reluctance to approach and stay close to this path provoked the most severe aggression to date being shown by Faben. The first two attacks of the consortship occurred and Pallas screamed loudly and was very submissive. During the next four days (July 1-4) events were relatively more settled and peaceful, but Pallas continued to be extremely submissive. Conflict and tension between the pair built up on Days 10-13 (July 5-8), and Faben became more demanding in his desire to maintain proximity, and in his increasingly persistent demands that Pallas groom him. By the last day, Pallas became increasingly unwilling to move in <u>any</u> direction, and Faben initiated much of the travel by Faben literally pushing Pallas along using the mount embrace walk.

vi Termination

The consortship ended at 14.26 on July 8th when Figan, Mike and

Humphrey arrived following the vocal exchanges described above. However, there are some indications that Faben and Pallas 'gave up' prior to this. On Days 12 and 13 the pair moved further south than on previous days and moved into an area (lower Rutanga valley) where the probability of meeting or hearing chimpanzees from the Kasakela community was increased. Pallas screamed loudly and frequently during these two days, and although Faben's reassurance behaviour continued at high frequencies it was no longer directed so specifically at keeping Pallas quiet.

When the distant pant hoots of Figan, Mike and Humphrey, were first heard they were still a considerable distance away (about ¾-1km) yet neither Faben nor Pallas made any attempt to avoid them. Upon meeting the 3 arriving males charged downslope displaying towards Pallas and Faben, who avoided them. An excited greeting between Figan and Faben followed and Pallas was inspected by all three males. The 5 chimpanzees spent the rest of the day together. During travel Faben continued to keep a close watch on Pallas and frequently waited for her, but he did not branch shake or attempt to lead her away from the other males.

6. Other Consortships

i General Activity Budget

Table 7.3 shows the activity budgets for females during consort relationships and for maximally tumescent females in groups of males (excluding possessive incidents). Data from the long Pallas-Faben consort are shown separately. Wrangham (1975, p. 3.4) found that while some seasonal differences in the activity budgets of adult males existed, none proved to be statistically significant. Diurnal periodicity affects all activities (see Chapter 4), but

Table 7.3 ACTIVITY BUDGETS of Females:

(% 5 min samples spent in each activity)

	Rest	Travel	Feed	♂Grooms ♀	♀Grooms ♂	Self groom	Copulation	Agonistic	Play
Pallas-Faben 13-day consort (N = 1583)	11.7	12.5	44.2	18.8	5.8	1.8	0	5.1	0
Pooled data from all other consorts (N = 502	13.2	18.3	40.0	14.9	6.3	4.8	0.9	1.7	0
Promiscuous group (max. tum. 's only) (N = 1734)	21.1	20.0	39.3	5.3	3.9	5.7	3.4	0.7	0.8

N = no. of 5 min samples

insufficient data were available to control for the variable here.

The amount of time spent feeding is consistent but differences exist in the other activities. Consorting females spent less time travelling and resting, and more time engaged in social grooming, than did maximally tumescent females in groups. Consort females were involved in more agonistic behaviour but spent less time copulating and self grooming than females in groups. The Pallas-Faben consort and the other consorts differed in some ways, Pallas rested and travelled less, and spent more time in social grooming and in agonistic behaviour. These differences may be partially due to discrepancies in the sampling of observations. While the Pallas-Faben consortship was followed from beginning to end, the majority of data from the other consortships came from the initiation and early stages. Movement away from the centre of the community range involves more travel than the small daily distances covered once the consorting pair have reached their temporary range. Thus, it is not surprising that the overall percentage of time spent travelling is less for the Pallas-Faben consort.

ii Grooming

Table 7.4 Percentage of time spent in social grooming during consorts

Consort pair	Male grooms female	Female grooms male	♂grooms / ♀ grooms
3) Satan/Sparrow	24.3%	26.4%	.92
5) Satan/Miff	17.8%	4.2%	4.4
6) Satan/Sparrow	8.6%	5.0%	1.7
11) Satan/Melissa	11.6%	2.5%	4.7
12) Faben/Melissa	6.6%	4.4%	1.5
14) Satan/Little Bee	9.7%	1.0%	9.7
16) Sniff/Little Bee	21.7%	2.8%	7.8
MEAN	14.9%	6.3%	2.4
8) Faben/Pallas	18.8%	5.9%	3.2

Table 7.4 lists the percentage of observation time in which the consorting pair engaged in social grooming. In 6 of the 7 cases the male spent more time grooming the female than vice versa, and in 4 cases the male groomed the female more than 4 times as much as she groomed him. There was no consistent relationship between the female's age or parity and the amount of grooming given or received. There was also no relationship between the female's swelling state and grooming; all except Melissa (with Faben) and Little Bee (with Sniff), were maximally tumescent.

These data, combined with that from the Pallas-Faben consortship, suggest that a high frequency of male to female grooming is a consistent feature of consorting behaviour. Wrangham (1975, p. 3.4) reported that adult males spent an average of 6.2% of their time in social grooming. The percentage of time consort males were engaged in this activity averages 21.2% and even allowing for the time that the adult males in Wrangham's sample were alone (27.7% of observation time) this difference is still considerable. Correcting for the time spent without grooming partners by non-consorting males gives a magnitude of difference of 2.5. Consorting males of other primate species spend much of their time grooming their females (e.g. <u>Papio anubis</u>, Collins, in prep.). The function of consort grooming appears to be in cementing the temporary social bond between the male and female. The imbalance of grooming, with the male giving on average, 2.4 times as much as he receives, may indicate that the male is more highly motivated to maintain the bond than is the female.

iii Leading and agonistic behaviour

The hourly frequencies of leading and agonistic behaviours in the 7 consorts are shown in Table 7.5.

Table 7.5 Hourly Frequencies of leading and agonistic behaviour patterns

Consort	Leading	Aggressive	Reassurance	Submissive
3) Satan/Sparrow	1.1	0	0	.9
5) Satan/Miff	.3	0	0	0
6) Satan/Sparrow	2.0	.7	.2	1.6
11) Satan/Melissa	5.8	0	0	.3
12) Faben/Melissa	2.0	.5	.9	1.0
14) Satan/Little Bee	1.1	.5	.2	.3
16) Sniff/Little Bee	1.2	.6	.4	.8
MEAN	1.4	.4	.3	.8
8) Faben/Pallas	7.1	6.1	6.7	12.7

Neither leading nor any of the agonistic behaviour patterns occurred at such high frequencies in other consortships as they did during the Pallas-Faben one. In the other 7 consortships, both leading and agonistic behaviours occurred only sporadically and not in the near continuous fashion of the Pallas-Faben consort. Leading commonly occurred during consort initiation, but once the pair had left the immediate vicinity of other chimpanzees, it was uncommon and only appeared if the female showed prolonged reluctance to follow the male. Agonistic behaviours were also restricted to such occasions. In most cases the female was cooperative, and none showed the persistent resistance to leading that characterised Pallas' behaviour during her consortship with Faben.

Faben was a persistent leader in his brief consort with Melissa, insisting that she follow closely behind him. She was attentive to him and on 3 occasions left productive termite mounds to follow him immediately he stopped feeding. This consort lasted only 3 hours, ending when other chimpanzees arrived. Satan was much more 'permissive' than Faben in his leadership, and he frequently allowed the female to determine the timing and direction of travel, although once travel was initiated he generally moved into the lead. In his consortship with Melissa, all went smoothly until Satan began travelling north from Kasakela, heading towards Linda valley. Melissa had followed him closely during the early part of the morning when, after leaving their nests on the south side of Kasakela, they had crossed to the north side of the valley and had fed for 90 minutes. Satan waited for Melissa to finish feeding and then groomed her for 16 minutes before initiating travel. Melissa followed Satan slowly but then stopped after moving only 30m. Satan sat for the next hour trying to encourage Melissa to follow by branch shaking, but she remained immobile, and even after 60 minutes of deadlock, Satan did not resort to force. Thus, even in a consort with a relatively high frequency of leading behaviour, Satan showed no aggression.

The other male observed in consortship was Sniff, a young adult male from the Kahama community. His consort, Little Bee, is also a member of the Kahama community, but since 1972 she has made frequent visits to the Kasakela community. Little Bee's swelling was detumescing during their 2½ day consort, and she showed periodic reluctance to follow Sniff. Sniff responded to this with intense leading behaviour and some aggression. He succeeded in overcoming her reluctance, but she made several escape attempts and finally succeeded.

Although the data are limited, it seems likely that males show consistent individual differences in consorting behaviour. The differences are similar to those in possessive behaviour, with Faben being an impatient, demanding leader, but Satan being more relaxed and permissive. Leading and agonistic behaviours are used to take the female from the group, but once this is accomplished they appear only when the female is slow or reluctant to follow.

iv Responses to distant vocalisations

The responses of 3 consorting pairs to distant vocalisations were observed. Miff and Satan (Case 5) returned to Kakombe valley on the third day of their consortship and passed through Camp. They left Camp to the north but whilst still in Kakombe valley, vocalisations were heard from a large group of Kasakela chimpanzees on the opposite side of the valley. Miff remained silent but stopped and looked in the direction of the calls; Satan branch shook once and she immediately followed him.

The other two observations were of responses to calls from other communities. In both cases (nos. 6 and 12) the calling chimpanzees were at least 1km from the consort pair. Both pairs visually oriented to the calls briefly, but made no other response.

v Terminations

Six consort terminations were observed, including that of the Pallas-Faben consort, already described. Three other consortships (nos. 5, 11 and 12) ended in a similar way, when other males arrived and 'discovered' the consorting pair. Twice as in the case of Pallas and Faben, there was an intense period of agonistic behaviour as the other males arrived, and in one case the female was attacked. In none of the 3 cases did either of the consort pair vocalise before the males arrived and so it appeared that the other males located them either visually or by chance.

One consortship (no. 3) ended after 3 days when Sparrow approached and joined a group of males. Her arrival elicited considerable excitement, and the 4 males in the group mated her within 10 minutes. The group had been vocalising, and she headed straight towards them, leaving Satan, who moved off alone. The consort between Sniff and Little Bee ended when Little Bee successfully escaped. She had shown reluctance to follow him in the day prior to the termination. While Sniff was feeding in a tree Little Bee left hurriedly. Sniff did not notice her departure for 30 seconds by which time she was out of sight. Sniff then rapidly descended and looked around, smelling the ground. He rushed around smelling the vegetation and ground for 5 minutes before returning to feed.

It seems useful to distinguish between 'natural' terminations of consortships, when the relationship is abandoned by mutual consent, and 'premature' endings caused either by an unavoidable meeting with other chimpanzees, or by the female escaping. Three of the observed terminations (Cases 3, 5 and 8) fall into the first category. The behaviour of all 3 pairs changed before the end, in a way which gave the strong, subjective impression that they had given up. In two of the other 3 cases (nos. 11 and 12), termination coincided with the arrival of other males. In these cases the male showed leading behaviour up to the time when the other males arrived and was still leading the female away from the centre of the Kasakela community's range. In Case 16, there was no doubt that Little Bee's escape brought a premature end to the relationship from Sniff's point of view, but possibly from her own point of view it was long overdue!

In the 3 endings when meeting other chimpanzees was responsible, much agonistic behaviour was directed to the consorting pair by the arriving males. Humphrey attacked Melissa at the end of her consortship with Faben, and in two other cases, both of the pair fled charging displays of the arriving males. In the case of Pallas and Faben, they received more agonistic behaviour on subsequent days when they met other community members for the first time in at least 14 days. While the loose nature of chimpanzee social organisation means that individuals need not see each other daily, long separations are unusual and reunion behaviour after long periods of absence is intense and largely agonistic (Bauer, 1975).

7. How typical was the Pallas-Faben consort?

The general activity budget data (Table 7.3) indicate that the most atypical feature of the Pallas-Faben consortship was the large amount of time spent in leading and agonistic behaviours. In other respects, it resembled the other consortships observed during the study period. Social grooming occurred often, little time was spent travelling as daily ranges were small, and until the last day the consorts avoided encounters with other chimpanzees. The proximal reason for the high frequencies of leading and agonistic behaviours have been described, and data from Faben's other observed consortship indicate that his demanding leadership is characteristic. Unfortunately no other consort involving Pallas was observed, but data from group situations and possessive incidents suggest that her behaviour during the consortships was typical. Two facts, however, may have contributed to her stubborness: She was not swollen during the consort, and only two days previously she had returned from a consortship with another male. McGinnis (1973) described a consort relationship involving a non-swollen female, who had just returned from another consortship and she behaved in a similarly stubborn fashion.

Pallas was slow to concur with Faben's demands and consequently bore the brunt of his aggression. Why did the consort continue for as long as it did? It appears that in its early stages a female is able to terminate the consort either by vocalising or by travelling towards other males. During the initiation of the Pallas-Faben consortship no other chimpanzees were heard and Pallas did not call. By the second day Faben had led her out of earshot of calls originating in the normal range of the Kasakela community. Pallas made no escape attempts during the 13 day consort, possibly because she was unfamiliar with the area. The location of the only observed escape from a consortship (Little Bee/Sniff, Case 16) was Nyasanga valley, with which Little Bee is familiar.

Wrangham (1975) found that female chimpanzees had localised ranges of relatively small areas within the larger, group-range of the community's males. This seems to result in males being familiar with a larger area than females. There are indications that females are sometimes reluctant to be led to unfamiliar areas during consort formation. For instance Melissa, whose range is to the south, was reluctant to follow Satan north (Case 11), but willingly followed Faben south (Case 12). In December 1974 Satan attempted to lead Little Bee (whose range is with the southern, Kahama community) north, but she refused to follow him (Case 14). He then turned south and she followed him willingly. Miff, whose range is to the north, was willing to follow Satan as he led to the north during their consort in March 1973 (Case 5). If a consort pair move to the edge or outside of the normal community range, then by definition they will be an area relatively unfamiliar to both. However, it appears that females prefer a consorting location on the periphery that is the most familiar to them and this may be because a degree of familiarity allows them an increased possibility of escape from the male.

Pallas, having been led to the northern periphery of the community range was far from her normal range which centres on southern Kakombe valley. There was no way of judging just how familiar, if at all, the area of the consort was to Pallas, but in the 200+ hours of observation of her excluding the consort, she was only once observed north of Linda stream, and even this was considerably to the south of the consort locale. Her relative unfamiliarity with the area and its distance from her normal range probably made escape unfeasible. In the majority of cases it seems that the female has a choice as to whether or not to participate in a particular consort relationship. However, the Pallas-Faben consort indicates that situations can arise in which a female finds herself in an undesirable consort relationship. Once the pair has moved to a temporary range which is unfamiliar to the female, her ability to terminate the relationship is limited.

8. Consort formation and female swelling cycle states

In the majority (12 of 15, one unknown) of the consortships which occurred during the study period the female was maximally tumescent for at least part of the time. In two (Cases 8 & 16) of the 3 exceptions, the female showed reluctance in following the male. In the third (Case 12), the female followed the male willingly but the consortship lasted only 3 hours. Both Pallas (8) and Little Bee (16) were detumescing when their consortships began. Pallas next reached maximum tumescence on July 19, 24 days after the consort began and 11 days after it ended. If the male is to impregnate the female during the consort, she must be maximally tumescent for part of the time. The probability of this is enhanced if the consortship begins while the female is in either the maximum tumescent or tumescent phase of her cycle, as consortships may end unexpectedly for several reasons (see above).

On the other hand, tumescing and especially maximally tumescent females are more likely to be in large groups of males than are non-swollen females (McGinnis, 1973, p. 41). This means that consort initiation will be easier with non-swollen females, both because the male is less likely to face the problem of taking a female from a group, and because if she vocalises during consort initiation, her calls are less likely to attract other males.

However, the advantages of easier consort initiation with a detumescing or non-swollen female must be weighed against the disadvantages of the protracted consort relationship that would be necessary if the female is to reach maximal tumescence during it. In addition to the energy required to maintain the relationship, other risks associated with consort relationships arise.

9. Problems associated with consort relationships

i Inter-community encounters

Probably the greatest potential danger to a consort pair is the increased risk if inter-community contact, which comes from moving to the edge of their own community range. There is a certain amount of overlap of community ranges and it is in these overlap zones that consort pairs often establish their small temporary ranges. While this decreases the probability of encounters with members of their own community, it means that the consort pair are more likely to meet members of the neighbouring community.

Three inter-community encounters observed at Gombe resulted in the death of an adult male (Goodall, *et al*, in press). These encounters were similar: Each time, a group of males from the Kasakela community met a single adult male of the Kahama community in the area of community range overlap. The lone Kahama male was savagely attacked by several of the Kasakela males who inflicted fatal injuries on their victim. Inter-community aggression reaches a level of severity not witnessed in intra-community interactions. Three incidents of chimpanzee cannabalism have been observed, one at Gombe (Bygott, 1972), one in the Budongo Forest (Suzuki, 1971) and one in the Mahali Mountains (Itani, pers. comm.). In each case the victim was an infant who was killed and partially eaten by adult males who belonged to another community. Thus, it seems that an inter-community encounter might have very serious consequences for a consorting pair, especially if the female is accompanied by a dependent infant.

Consort pairs reacted aversively to vocalisations from chimpanzees of other communities especially when the calls were relatively close. Although no inter-community encounters involving consorting pairs have been observed, the evidence suggests that such encounters might have very serious consequences. When not consorting males only travel to the edge of their range in large parties (Goodall, et al, in press). Consort relationships are possibly the only time that a single adult male would move so close to the range of another community.

ii Reunions with members of the community after consorting

Riss (in prep.) discussed some of the signifcant dominance changes among the males of the Kasakela community and found that 4 severe attacks which caused changes in males' status occurred when they returned to the community after a prolonged absence. Two of the returning males were known to have been consorting females, and in each case the male who had been absent suffered a severe defeat resulting in a fall in dominance status.

Aggressive behaviour was directed to 3 of the 5 consort pairs whose relationship was terminated by the arrival of other males. Although empirical evidence is lacking, it appears that a relationship exists between length of separation and the intensity of reunion, with the aggressivity of reunion increasing proportional to the length of separation (Bauer, in prep.). If this is true, the probability of an aggressive reunion might discourage certain males from forming consort relationships. One might expect males with an unstable dominance position, for instance a male who was being actively challenged or one was was actively challenging another, to be most vulnerable to the prospect of an aggressive reunion.

The reason why community members respond aggressively to individuals who have been absent for prolonged periods may be linked to the fierce hostility shown to males of other communities. The 3 adult males of the Kahama community killed in encounters with the Kasakela community were not total strangers to their attackers. The two communities only became fully separate in 1972 and one of the males killed, Goliath, had been observed feeding with Kasakela males only two months before the attack. It appears, therefore, that the severe aggression is a response to relative unfamiliarity. Consort formation is probably the commonest cause of male absence from the community, and when the consort is prolonged, the risk that the pair will encounter aggression on their return to the community is increased. Both male and female are vulnerable to such aggression but its consequences are potentially more damaging to the male if it results in a loss of dominance status.

iii Risk of reduced food availability, quality and quantity

The evidence indicates that preferred consortship locations are areas on the edge of the normal community range which are visited infrequently by other chimpanzees. While such locations are desirable for the maintenance of the consort relationship, they may have drawbacks, e.g. reduced food availability. If the consort location is outside the normal ranges of the pair, they may have limited knowledge of the location and condition of food sources.

During the Pallas-Faben consortship there were some obvious differences in feeding behaviour. A major food being eaten by the Kasakela chimpanzees at the time, Monanthotaxis poggei, did not occur within the small temporary range of the consort pair. The number of different plant foods eaten per day by the consort pair avaraged 7.8 (range 5-11). Wrangham (1975, p. 3.18) found that the average number of plant foods eaten per day by adult males averaged 13.3 (range 7-21). The number of foods eaten daily during the consort may have been under-estimated, as feeding behaviour was not the major focus of the observers, who were less skilled than Wrangham in the identification of food plants. The amount of consortship time spent feeding was similar to that of non-consorting, but it appears that the variety of available foods was less than that of individuals within their normal ranges.

10. Male dominance rank and consort formation

McGinnis (1973, p. 83) found no correlation between male dominance rank and the frequency of consortships inferred from coincident absence data. His data however, indicated a possible relationship between male dominance rank and the stage of the female's cycle during which consorts began. Three males with mean dominance ranks above the median began consorts significantly more often with tumescing and maximally tumescent females than with detumescing or non-swollen females. In making this correlation he used the mean dominance rank, calculated from each male's rank in four periods from July 1966 - December 1970. Changes in dominance rank of some males during this 4½ year period were considerable, e.g. Figan rose from being ranked 13 of 23 to 4 of 15, while Goliath fell from 3 of 23 to 15 of 15. Lumping the data over such a long period may have obscured possible correlations.

During the present study 5 of the 9 adult males in the community were responsible for all 15 consortships and the 4 consorting attempts. The 4 adult males not involved were Mike and Hugo, the two eldest males, and Figan and Evered, the two highest ranking males. All 4 of these males had participated in consort relationships occurring before the present study.

For the first 7 months of this study Figan and Evered actively competed for the alpha male position, having deposed Humphrey, the previous alpha male in October 1972 (Halperin, in prep.). The reason for their abstinence from consorting may have been that their unstable dominance rankings made any absence from the community unwise, because of the risk of aggression on their return. Figan became the dominant male in mid-June 1973, when, with the help of his older brother Faben, he defeated Evered in a major agonistic encounter (Riss, in prep.). A week later Faben consorted with Pallas and during Faben's 13 day absence from the community, Figan was less assertive and appeared to avoid Evered (Riss, pers. comm.). Figan managed to maintain his alpha status without the help of Faben, and from mid-June to the present the dominance order of these males has remained constant.

From early 1974 Figan established the pattern of possessive behaviour described earlier (Chapter 6, Section 9). In this way he was virtually able to monopolise many oestrus females while remaining in the group. Given this ability unique to the dominant male, it seems that Figan achieved the benefits associated with consorting behaviour without incurring the risks that arise from leaving the group.

Evered became increasingly peripheral to the Kasakela community during 1974. He frequently was not seen for periods of 20-30 days and none of his absences coincided with those of any female. His present position in the community is poorly understood, as where he goes or what he does during his absences remains unknown. On his brief returns to the Kasakela community he is often severely attacked by Figan to whom he is very submissive, but his dominance rank exceeds that of the other community males. During observation in December 1974 - February 1975, Evered was not seen in the same group as oestrus females. Even when present in the community range, he tended to avoid Figan and, as Figan associated almost constantly with oestrus females, this avoidance appeared to be responsible for Evered's non-association with oestrus females. Because of this Evered had reduced opportunities to form consort relationships, at least with tumescent females. It is possible that Evered associated with other chimpanzees during his absence, but his reproductive opportunities within the Kasakela community have become negligible during this phase of peripheralisation.

The 5 males who were responsible for all the consorts and consort attempts are middle (Humphrey, Satan and Faben) to low (Jomeo and Sherry) ranking males. Sherry, the youngest of the 5 attained adult status in June 1974, 6 months before his first known successful consort.

Whilst there are yet insufficient data to give a completely clear picture of the relationship between male dominance rank and consort formation, it appears that consorting is most common amongst middle to low ranking males. The two eldest males, Mike and Hugo, were very low ranking, but their abstinence from consorting might be due to their low rank, old age, or both. Figan's non-participation in consorts may have initially resulted from being actively engaged in dominance competition, and later having gained the ability to monopolise females in groups, consorting became redundant. Although no unequivocal evidence is available, it appears that Humphrey formed some consortships (inferred from coincident absences), whilst he as the alpha male of the community. Thus, although Figan has not been involved in consorts while being the alpha male, no generalisations can be made to the behaviour of all dominant males.

11. Differential participation in non-promiscuous mating patterns

i Introduction

It was apparent that the individual male and female chimpanzees participate in consort relationships and possessive interactions at different frequencies. Possible reasons for the non-involvement of certain males in consort relationships were discussed in the previous section. Insufficient data were available to consider consorts and possessive incidents separately in this section, and so in the following analysis, the data are combined to enable examination of correlations of frequency of involvement in non-promiscuous mating patterns with other forms of social behaviour and individual physical attributes.

ii Females

Table 7.6 shows the frequency of female participation in non-promiscuous mating systems per hour of observation. No frequency can be calculated for Sprout as she is an unhabituated female on whom only sporadic observation was possible.

Table 7.6 Differential participation of females in consortships and possessive incidents

Female	No of consorts and possessive incidents	Hours observation at maximal tumescence	Frequency involvement/ observation hour
PALLAS	18	141.5	.13
MIFF	7	60	.12
PATTI	7	109	.06
LITTLE BEE	3	61.5	.05
GIGI	7	188	.04
MELISSA	2	61.5	.03
SPARROW	3	124.5	.02
SPROUT	1	sporadic	-

Pallas and Miff had similarly high frequencies of involvement, while the other 5 females had frequencies ranging from ½ to 1/6 of the highest value. Pallas and Miff were the only parous females observed over a number of cycles. (Pallas had no living offspring as her son Plato, died in April 1973). Melissa is also parous, but she was only observed during one isolated postpartum cycle, when she was still lactating. No other cycling females had infants. Gigi's low frequency shows that the phenomenon is not merely a function of age. Gigi is older than Miff but is apparently sterile, having shows cycles of sexual swelling for 10 years without signs of conception. Gigi is none the less attractive to males, as indicated by the high frequency at which she mates in group situations (see Chapter 5).

Nulliparous females have an average of 18.75 cycles (N = 4, range 10-27) before their first pregnancy. (Data from Gigi are excluded as she is apparently sterile.) Parous females average only 4.5 cycles (N = 14, range 1-11) between pregnancies, see Chapter 3. The probability of impregnation in any one cycle, is therefore greater for parous than for nulliparous females. This may supply the ultimate explanation for the greater involvement of parous females in non-promiscuous mating patterns. Males who select parous female partners for consort relationships or possessive incidents are more likely to achieve impregnation, and they thus gain selective advantage over those males who are non-selective or who select nullipares.

However, the immediate cause of the parous females being involved in possessive incidents and consortships at higher frequencies could be related to differential pheromonal cues, or to a novelty effect of the parous females' relatively infrequent cycles. The latter possibility is unlikely, as early post-partum swellings of parous females attract little attention from the males. At maximal tumescence females cycling during either pregnancy or lactation are not as attractive to males as are non-pregnant, non-lactating females. This suggests that pheromonal cues under oestrogen control (as in Macaca mulatta, Herbert, 1968) may determine the levels of female attractiveness. It is possible that consistent age-related pheromonal differences exist that make parous females more attractive to males than nullipares.

iii Males

Table 7.7 shows the differential frequencies of involvement of males in consorts and possessive incidents.

Table 7.7 Differential participation of males in non-promiscuous mating patterns

Male	No of consorts and possessive incidents	Hours observed with maximally tumescent females	Frequency of involvement/ observation hour
SATAN	18	243	.07
FABEN	12	246	.05
HUGO	8	199	.04
HUMPHREY	4	161	.03
FIGAN	5	284	.02
JOMEO	2	154	.01
SHERRY	2	212	.009
EVERED	1	160	.006
GOBLIN	2	346	.006
MIKE	0	132	0

The frequencies cannot be taken as indicating any constant differences between the males, as the period covered is only 18 months. As discussed above, factors such as dominance instability appear to affect the likelihood of a male being involved in non-promiscuous mating patterns. These influences probably affect each male for only a small portion of his total reproductive life and hence they might even out if life-time records were available. Evered was the most affected male during the study period, as he was actively competing for alpha status for the first 7 months and then, having been defeated by Figan, moved into a peripheral position (see section 7.10). Other males were affected for parts of the study period to a lesser extent. For this reason, Evered is omitted from the following analysis as his very low frequency of involvement in the non-promiscuous mating patterns was felt to have been a direct result of his unstable position within the community during the study period.

The frequency of male involvement in non-promiscuous mating patterns was found not to be statistically correlated with age (Spearman Rank Correlation coefficient, $r_s = .08$, $N = 9$, n.s.); dominance rank ($r_s = .53$, $N = 9$, n.s.), or the amount of agonistic behaviour directed to females in groups ($r_s = .31$, $N = 9$, n.s.). Significant, positive correlations emerged between the frequency of non-promiscuous mating patterns and, (1) the amount of time spent associating with maximally tumescent females in group situations ($r_s = .72$, $N = 9$, $p < .05$); (2) the amount of time males groomed maximally tumescent females in groups ($r_s = .80$, $N = 9$, $p < .01$); and (3) the frequency with which males shared bananas with females ($r_s = .68$, $N = 9$, $p < .05$). (See Table 7.8.)

Table 7.8 Spearman Rank correlations, comparing aspects of adult male behaviour with their frequency of involvement in non-promiscuous mating patterns (N = 9)

	r_s	p value
Age	+ .08	n.s.
Agonistic behaviour to females	+ .31	n.s.
Dominance rank	+ .53	n.s.
Banana sharing with females	+ .68	.05
Association with maximally tumescent females	+ .72	.05
Time grooming maximally tumescent females	+ .80	.01

iv Discussion

The positive relationships shown in Table 7.8 could indicate either male or female selectivity, or both.

In the majority of cases (30 of 33) where the initiation of consorting or possessive behaviours was observed the male made the first move. Whilst females probably have little choice as to which males direct these behaviours towards them, they have a choice as to whether or not a consort relationship develops. The observed differential participation of males in the non-promiscuous mating patterns is probably a result of differences in male inclination, mediated by female discrimination. For instance, while Satan and Hugo were both highly inclined to exhibit non-promiscuous mating patterns, as indicated by their high frequencies of possessive behaviour, females showed a preference for Satan but not for Hugo. This led to Satan being involved in many consort relationships while Hugo was involved in none. Faben fell between these two extremes.

Hugo, like Satan, spent much time grooming females and was generous to them in sharing food. The females may have discriminated against Hugo because of his advanced age. Whilst survival to old age may indicate genetic fitness, the disadvantages of physical deterioration may be of more immediate relevance. Hugo's old age probably reduced his ability to provide protection for the female in situations such as inter-community encounters, making consorting with him undesirable.

If females exercise choice one would expect them to select the fittest available male, in order to maximise their reproductive potential. Wild adult male chimpanzees interact rarely with infants (McGrew, unpublished data), but if the female chooses to consort with males with whom they have affiliative bonds then it is possible that their infants will gain future indirect advantages. Males who share food with females sometimes also give food to the females' offspring (McGrew, 1975), but even if no direct donation occurs a suckling infant will obtain indirect benefits through its mother's milk. Males who associate frequently with females may provide more protection for a female and her offspring in inter-community encounters. A male associate may also communicate his knowledge of food sources to the female (Wrangham, 1975, p. 3130; Menzel & Halperin, 1975), which will benefit both her and her dependents. Besides physical fitness, a female seems to favour males whose high rates of affiliative behaviours are likely to provide some parental investment, which though indirect, may increase the chances of survival of her offspring. This may help to explain the apparent discrimination against Hugo, as his advanced age made it unlikely that he would live long enough to contribute sufficient investment. (Hugo died, apparently of natural causes, in January 1975.)

Food pant hoots are sometimes given by adult males arriving at a food source. They attract other individuals to the food, increasing the competition for it (Wrangham, 1975, p. 3.34). Wrangham suggested that these calls might have important consequences on relationships within the community in terms of intra-sexual selection, as females will be attracted to the feeding male. He suggested that an individual male's ability to find food and his willingness to share it might be a valuable measure of his physical and psychological condition and thus provide females with information useful in mate selection. Although data were scarce, Wrangham (p. 3.36) found that individual differences in the frequency of food calling existed. Evered was the most frequent giver of food calls, and Hugo the least; Faben, Figan and Satan and Jomeo were intermediate. Data on Mike and Humphrey were inadequate.

No relationship between the frequency of food pant hoots and involvement in non-promiscuous mating patterns is apparent. Food pant hoots, like the sharing of food, is a behaviour which might convey benefits to an infant, if its mother was aided in locating food. Thus, it is somewhat surprising that no relationship exists, although that the paucity of data may obscure it.

It is of interest to note that various aspects of Evered's behaviour suggest that he has the characteristics of a male with high involvement in non-promiscuous mating patterns. He ranks second (after Satan) amongst the males in the amount of time spent grooming females and is the most generous of the adult males in food sharing. His frequency of association with maximally tumescent females is low, but this is at least partly due to his avoidance of Figan.

More definite statements require more data, as an 18 month period is not sufficient for a full understanding of lifetime mating patterns and their expression with respect to social variables. It is difficult to assess whether the individual differences observed in the present study are the result of constant differences in male behaviour or whether it is factors such as age and social status which cause the differences. It seems that no consistent age-differences in behaviour exist. Jomeo and Satan are approximately the same age, as are Hugo and Mike, who are probably 15 years older than the former pair. Yet Hugo and Satan behaved in ways more similar to each other than to their peers. The data suggest that individual differences in male inclination to be involved in non-promiscuous mating patterns exist. These differences can be modified by female discrimination (as in Hugo's case), social factors, related to male-male competition (as in Evered's case) and probably by certain other social and physical factors not isolated during this study. The result is differential male involvement, but the magnitude of the differences would not be expected to remain constant.

12. Conceptions and mating patterns

i Introduction

During the study period 7 known conceptions occurred, involving 6 females, one of whom (Gilka) conceived twice. In addition, data of 9 other conceptions were extracted from the long-term records of the Gombe Stream Research Centre, making a total of 16 conceptions during the period November 1966-February 1975. It is usually possible to establish the date of parturition with reasonable accuracy. The mean interval between the last observation of a female without an infant and the first observation of a mother and newborn, is 5.3 days (N = 13, range 0-14 days). Nissen and Yerkes (1943) reported that the mean gestation length (i.e. conception to parturition) in captive chimpanzees is 228 days (N = 47, range 202-248 days). The exact date of ovulation is not known for chimpanzees but available data suggest that it falls in the latter half of the maximal tumescent phase of the swelling cycle, probably 3 days prior to the start of detumescence (see Chapter 3). Using this information it was possible to establish the cycle during which the female conceived.

Once the time of conception has been established, the Camp attendance charts and travel and group charts can be consulted to determine whether the female was observed during the conception cycle. If the records indicate that during the conception cycle the female was observed with groups of adult males then no conclusions about the paternity of her infant can be made, unless the alpha male exhibited possessive behaviour. Absence of the female from these records indicates one of two possibilities: Either she was involved in a consort relationship; or she was associating with males of another community. If she consorted throughout the maximal tumescence phase of the conception cycle, then the consorting male was her infant's father. If she was absent from the community, no conclusions can be drawn regarding paternity of the infant.

ii Females' circumstances at the time of conception

Table 7.9 lists the 16 pregnancies which occurred in the Kasakela community between November 1966 and February 1975 and which resulted in the birth of a live infant. Five of the infants subsequently died; Flame (2), at 6 months, Plato (5), at 2½ years, Villa (14), at 11 months, Gandalf (15) at 2-3 weeks and Otter, (16), at 3 weeks. Wilkie (9) is the only infant whose small size and slow early development suggested premature birth.

In two of the 16 cases listed in Table 7.9 it was impossible to draw any conclusions about the mothers' circumstances at the time

Table 7.9 Conception of Kasakela Community Infants

Female	Infant	Date of birth	Conception date	Mother's circumstances	Conclusion
1) Athena	Atlas (AL)	25/9/67	10/2/67	max. tum. Feb. 2-8, in Camp daily	Group, father unknown
2) Flo	Flame (FM)	25/8/68	11/1/68	max. tum. Jan 8-11, in Camp daily	Group, father unknown
3) Miff	Moeza (MZ)	20/1/69	7/6/68	max. tum. June 5-16, coinc. abs. with Figan, June 8-15.	Consortship, father FIGAN
4) Nova	Scotia (SS)	26/3/70	13/8/69	abs. from Camp July 23-Aug 16, no coinc. abs., but records very patchy	Unknown
5) Pallas	Plato (PT)	7/9/70	25/1/70	max. tum. Jan 18-29, coinc. abs. with Faben Jan 22-28.	Consortship, father, FABEN
6) Melissa	Gremlin (GM)	18/11/70	5/4/70	coinc. abs. with Evered Mar 23-Apr 11, ML ¾ detum. on return	Consortship, father EVERED
7) Fifi	Freud (FD)	22/5/71	5/10/70	abs. from all records Aug 10-Oct 8, returns ¼ detumescing.	Associating with another community
8) Passion	Professor (PF) Hamburg	27/10/71	14/3/71	max. tum. Mar 3-12, stayed in group.	Group, father unknown

Table 7.9 contd.

Female	Infant	Date of birth	Conception date	Mother's circumstances	Conclusion
9) Winkle	Wilkie (WL)	21/10/72	8/3/72	max. tum. Mar 13-20, coinc. abs. with Evered, Mar 14-19.	Consortship, father EVERED
10) Athena	Aphrodite (AP)	22/6/73	7/11/72	max. tum. Nov 9-24, stayed in group.	Group, father unknown
11) Nope	Lolita (LO)	27/6/73	12/11/72	no obvious max. tum. NP abs. Nov 6-14, but no males coinc. abs. and 0 swelling before and after???	Unknown
12) Miff	Michaelmas (MM)	1/10/73	15/2/73	coinc. abs. with Humphrey Feb 2-19, MF returns ¼ detum.	Consortship, father, HUMPHREY
13) Sparrow	Swallow (SA)	26/10/73	12/3/73	max. tum. Mar 12-21, observed consort with Satan Mar 17-21	Consortship, father, SATAN
14) Pallas	Villa (VL)	20/4/74	6/9/73	coinc. abs. with HM, Aug 23-Sep 6, Pallas returns 0	Consortship, father HUMPHREY
15) Gilka	Gandalf (GD)	4/6/74	19/10/73	abs. Sep 30-Oct 14, presumed with Kahama community	Associating with another community
16) Gilka	Otter (OT)	19/7/75	3/12/74	max. tum. Nov 18-23, Figan possessive, Consort with Sherry Dec 13-26.	Either Figan or or Sherry father

of conception. Nova (4) conceived during a period when, for a fortnight, Camp attendance was not recorded. Nope (11) is a mystery, as she showed no complete cycles of sexual swelling during the conception period. She was absent from all records from November 6-14 and from November 27-December 14, 1972; no male was coincidentally absent during the first absence, but Jomeo was coincidentally absent during the second. Conception is more likely to have occurred during the first period of absence, giving a gestation length of 230 ± 4 days, rather than in the second, which would give a gestation period of 202 ± 8 days, as Nope's infant, Lolita, showed no signs of prematurity.

Of the remaining 14 cases, 4 females were seen with groups of males during their maximum tumescent phases when conception occurred, and 9 were absent from all records for part or all of the conception period. In the final case (16), the apparent conception data fell mid-way between two phases of maximal tumescence. During the first, in November 1974, Gilka was observed in the Kasakela community and Figan acted possessively towards her throughout the latter half of her maximal tumescence (Pusey, pers. comm.). During the second phase of maximal tumescence, in December 1974, Gilka was consorted by Sherry. One of the two males was almost certainly responsible for impregnating Gilka, but no additional evidence exists to indicate which one it was.

It was found that an adult male was coincidentally absent with 7 of the 9 females who were not observed during their conception cycles, and it is assumed that these 7 females were in consort relationships. The periods of absence of these 7, range from 5-19 days (X = 11 days), 5 different adult males were involved, 3 in one consort each and two in two consorts each. Behavioural observations were available for 4 of the 7 absences (6, 12, 13 & 14), providing definite evidence that, a consort relationship was formed and was the reason for the coincident absence of the male and female. In the two cases (7 & 15) where no male was coincidentally absent with the female, the females were probably associating with other communities. Both females had been absent previously, and Gilka was observed with males of the neighbouring Kahama community, during two of her previous absences. For these two females, the periods of absence during which conception occurred were 59 days (Fifi) and 15 days (Gilka).

Of the 13 females whose circumstances at the time of conception can be definitely established, two were associating with other communities, 4 were associating with groups of males in the Kasakela community, and 7 were consorting.

iii Discussion

These data indicate that the majority of chimpanzee females become pregnant whilst consorting with a single adult male. However a note of caution must be added, both because the conclusions in some of the cases depend on circumstantial evidence, and because the sample size is relatively small. Bearing this in mind, we can consider the interesting implications of these data and the significance of the flexible nature of the chimpanzee mating system.

It is difficult, if not impossible, to calculate the relative frequencies of the different mating patterns in a meaningful way, as it is not obvious what to compare. Should it be the proportion of days whilst maximally tumescent, the proportion of presumed ovulations, or some other measure? If we look at the cycle previous to the conception cycle for the 15 females in Table 7.9 (Gilka, case 16, has to be omitted as the conception cycle was undetermined), we find that 8 females stayed with groups of males, 3 consorted, one associated with another community and 3 showed no cycle of sexual swelling in the preceding two months. This contrasts dramatically with the females' circumstances during the conception cycle, and strengthens a subjective impression that the number of conceptions occurring during consort relationships is higher than one would predict from a knowledge of the number of consorts. If this is the case, there are two alternative explanations: Either the chimpanzees are able to detect in which cycles ovulation is likely to occur, and form more consort relationships during these cycles than in anovulatory cycles; or, female chimpanzees are more likely to conceive and implant successfully when on consort than when in a group. I favour the latter explanation as there appears to be no mechanism for the former.

A successful consort relationship is a peaceful affair, with little aggression or excitement and contrasts to the intense excitement often found in large groups associating with a receptive female. It is possible that the calmer social setting of consorts is more conducive to successful conception than the rather hectic milieu of the large group. The frequency of copulations during a consortship will be less than when a female is in a group situation, and this may affect the probability of successful conception and implantation. The effects of factors such as sperm competition are not understood in primates, but this and the purely mechanical difference between 30-50 copulations daily in groups and 5-10 daily whilst consorting may affect conception and/or implantation. Experiments with rats have shown that if females received genital stimulation soon after their first male partner had ejaculated, sperm transport and subsequent pregnancy were inhibited (Adler and Zoloth, 1970). Adler and Zoloth also showed that if a female rat were mated by two males in succession, a higher percentage of the resulting offspring were sired by the second male. This effect depended on the second copulation occurring relatively soon after the first, with the maximum effect after an interval of 15 minutes. They concluded that "in a competitive situation, therefore, it appears a male can cancel the effects of a previous male's copulation if the second male begins intromitting soon enough". (p. 1482). If a similar effect operates in chimpanzees it might explain the low proportion of conceptions resulting from group matings, when it is common for males to copulate in quick succession.

The important functional aspect of these results is that, although wild chimpanzees show a variety of mating patterns, it is the temporary monogamous consortships which account for most conceptions. This is the mating pattern which allows both males and females to exercise choice.

CHAPTER 8

OVERVIEW OF MATING PATTERNS AND REPRODUCTIVE STRATEGIES

1. Introduction

"Sex is an antisocial force in evolution. Bonds are formed between individuals in spite of sex and not because of it." (Wilson, 1975,p. 314) The advantage of sexual rather than asexual reproduction is that genetic variability is increased as every act of reproduction between unrelated adults results in genetically unique offspring. This diversity gives adaptability to species, allowing them to create new genetic combinations, the better adapted of which, will gain selective advantage and spread through the population faster by sexual than asexual reproduction (Crow & Kimura, 1965). However, the genetic diversity created by sexual reproduction automatically produces antagonism and conflict among the individuals of the population, a condition not present in asexually reproducing organisms.

Anisogamy, a condition common amongst sexually reproducing organisms, creates a basic conflict between the sexes. Females produce larger gametes than males, although in some species the much greater number of gametes produced by the male may balance the energy invested in the pre-conception phase of reproduction. In the vast majority of mammalian species there is differential investment in the post-conception phase of reproduction, as the female is responsible for parturition and contributes much, if not all, of the parental care neccessary for the infant's survival during the period of dependency. In this situation the reproductive potential of females is limited because of the high investment required for each offspring. The male, on the other hand has no such limitations, unless the environment is so harsh that considerable investment must be made by both parents in order for the offspring to survive. This is one of the conditions which would lead to the evolution of monogamous mating systems, a point which is returned to below. Conflict arises when the chances of an offspring's surviving would be increased if the male contributed post-natal parental investment, but the difference in probabilities of survival with and without this paternal investment do not compensate for the reduction in reproductive success which the male incurs by forsaking opportunities to impregnate other females. In this situation one would expect females to select males who are prepared to make the post-natal investment, and that through this female preference a greater degree of male investment would evolve. However, as Trivers (1972) pointed out, there will be counter selective pressures. Since the female already invests more energy than the male in gamete production, breeding failure for lack of additional investment selects more strongly against the female than the male. The female's larger initial investment commits her to continue with more additional investment than does the male's smaller initial investment.

A particular species' mating system evolves as a compromise between the basic male-female conflict in reproductive strategies, and the prevailing environmental conditions. Much social behaviour between unrelated adults, and the rituals of courtship and bonding patterns, have evolved as devices to over-ride the antagonism which inevitably results from both genetic variation, and sex differences in optimal reproductive strategies.

2. The chimpanzee mating system

The striking feature of the chimpanzee mating system when compared to other nonhuman primates is its flexibility. Two explanations for this situation exist; either the mating system observed is a transitional stage, a result of recent changes in the selection pressures operating on wild chimpanzees; or, the observed situation is static, and the counter selective pressures are stabilised to produce the evolutionary optimal mating system, which in this case is flexible.

The first alternative, that the mating system is in a dynamic state of evolution, is unlikely because of the very low probability of observing such a state. If for instance, one postulated that male consorting behaviour arose suddenly through mutation, then individuals with this behaviour would immediately gain tremendous selective advantage as they could impregnate all the females. The behaviour would thus spread very quickly, and the probability of the observed system being a transitional state between promiscuity and temporary monogamy is very low. In addition, the data argue against this explanation as all adult males have the potential to form consort relationships. A transitional situation might also arise as a result of recent changes in selection pressures brought about by environmental change. This seems unlikely as the habitat occupied by chimpanzees (open canopy woodland associated with evergreen forest) has changed little since the Miocene (Wrangham, 1975, p. 1.8). Although there have been recent changes in the environment associated with human encroachment, there is no evidence that this would effect the selective forces which effect the expression of consorting behaviour.

In balance it appears more likely that the present system is not transitional but is a result of stabilising selection, a compromise between the selective advantages gained by consorting, and the pressures against consorting which were described in Chapter 7, section 9. What results, is a situation where each male has the potential to express each mating pattern. Variables affecting the actual expression will be different for each male and will also change within an individual male during his adult life. Figure 8.1 summarises the advantages (in terms of male reproductive success), and the disadvantages, of the three mating patterns.

A female chimpanzee has a very limited reproductive potential and high parental investment in each offspring. It was shown in Chapter 3 that the hypothetical maximum number of offspring a female is capable of producing during her lifespan is 5-6, while the actual number varies between one and three, with a mean of two. One would thus predict that females would not mate randomly with males, but would be selective, choosing males whose phenotype indicates genetic fitness, and whose behaviour indicates that some contribution towards the survival of her offspring might be forthcoming. Figure 8.2 summarises the four reproductive strategies open to females, listing the advantages (in terms of the potential for choice) and the disadvantages of each one. The ability to transfer between communities appears to be limited to young females in the Gombe population. Once transfer is achieved, the three mating patterns are available just as they are in the female's natal community.

It appears from Figures 8.1 and 8.2 that the formation of consortships is the optimal reproductive strategy for both sexes in terms of benefits. An exception to this exists for the alpha male of the community and this point is returned to below. In Chapter 7, section 12, it was shown that the majority of females conceived whilst in consortships. However, not all females did so, and this indicates that either the disadvantages associated with consorting are sometimes so great as to preclude their formation, or that circumstances exist in which the advantages of another mating pattern equal or outweigh those of consort formation. The data suggest that both these contingencies do occur. It seemed (Chapter 7, section 10)

Figure 8.1 Male Reproductive Strategies.

- CONSORT
  - Benefit - Probability of reproductive success high
  - Cost - 1) Risk of inter-community encounters.
    2) Risk of intra-community aggression on return - variable risk, dependent on stability of social status and length of absence.
    3) Possibility of reduced variety, quality and quantity of food.
    4) Energy expended on vigilance and grooming female.
- POSSESSIVENESS
  - Benefit - Probability of reproductive success variable. High if alpha male, proportionately reduced if not, but increases probability of progressing to consort relationship.
  - Cost - 1) Energy expended in vigilance and in interrupting copulation attempts by other males.
    2) Possibility of reduced feeding efficiency because of vigilance.
- OPPORTUNISTIC (PROMISCUOUS)
  - Benefit - Probability of reproductive success low.
  - Cost - 1) None.

Figure 8.2 Female Reproductive Strategies.

TRANSFER
- Benefit - Ensures exogamy.
- Cost - 1) Aggression from females of new community.
  - 2) Loss of kinship benefits.
  - 3) Loss of familiar range.

CONSORT
- Benefit - 1) Choice of mate.
  - 2) High frequency of grooming from male.
- Cost - 1) Risk of inter-community encounters, higher if accompanied by dependent offspring.
  - 2) Possibility of reduced variety, quality and quantity of food.

POSSESSIVENESS
- Benefit - 1) If alpha male is possessive, and female prefers alpha male then benefits equal those of consorting.
  - 2) Protection from unwanted suitors.
- Cost - 1) Little choice about who acts possessively, and only the alpha male can be effective in preventing all others from copulating.
  - 2) Some risk of attack from possessive male if other males attempt to mate her.

PROMISCUOUS
- Benefit - Exposure to all the adult males in the community provides information on which future choices can be made.
- Cost - 1) No choice or control over who is responsible for impregnation.
  - 2) Reduced feeding efficiency when accompanied by large groups of males.

that males refrain from consorting when their social status is unstable. In this situation the risk of intra-community aggression, which might cause a decrease in the male's social status, might be too great to compensate for the advantage gained by consorting. In Chapter 6, section 9, the data indicated that whilst Figan was alpha male he could virtually monopolise a receptive female by exhibiting possessive behaviour. Thus, he gained almost as great a benefit from possessive behaviour as he would have from forming a consortship. The risks associated with consort behaviour far outweigh those of possessive behaviour and so in this case the latter provides the optimal reproductive strategy for the male. Indeed, in the period December 1974 - February 1975, when a number of females were showing cycles of sexual swelling, possessive behaviour was a superior strategy for Figan as it allowed him to monopolise each female as her swelling phase reached the latter half of maximal tumescence, see Figure 6.2. The precise timing involved in switching from one female to the next, made the formation of a series of consortships difficult, if not impossible, due to the problems of first locating the female and subsequently taking her away from the group.

From the female point of view choice is maximised in consort relationships. It was shown (Chapter 7, section 3) that in all but exceptional circumstances a female is able to terminate a consortship by either vocalising and attracting other males, or by joining a group containing adult males. Males were responsible for all the observed consort initiations, and so a female is dependent on her chosen male making the first move. When the community has a stable alpha male, such as Figan was from January 1974, the female can obtain the benefits of a consort relationship by staying in the community, if the alpha male directs possessive behaviour towards her. The benefits of ensuring impregnation by a single male will only ensue if the alpha male is the male that the female would have chosen as a consort partner. Once an alpha male directs possessive behaviour to a female it is doubtful whether she has a choice of whether or not to continue the relationship. A female can certainly make it more difficult for a male to maintain his monopoly over her, but it is unlikely that she could form a consort relationship with another male once the alpha male has established a possessive relationship.

This brings up the important issue of timing with respect to the expression of the different mating patterns. Possessive behaviour is only shown towards females during the maximal tumescent phase of their cycles, with the exception of newly arrived immigrant females. Consort formation is not as limited, and it appears that initiation of consortships is easier during the non-receptive phases of the females' cycles when they are less likely to be in the company of large groups of males. Although it is easier to initiate consortships prior to the onset of maximal tumescence, they must be continued throughout this phase of the cycle if the male is to have a chance of impregnating the female. Thus, the earlier the relationship starts, the longer it must be continued if the benefit is to be obtained. It is reasonable to assume that the risks associated with consorting increase proportionally to the length of the relationship. A balance must therefore be struck such that optimally, the relationship begins as late as is possible to ensure conception. This becomes difficult if the alpha male in the community is likely to form a possessive relationship with maximally tumescent females. In this situation a consort relationship must begin before the female reaches maximum tumescence, and the increased risks of a long consortship may discourage their formation, especially if the alpha male is attractive to the female.

Figures 8.1 and 8.2 indicate that there is little benefit associated with promiscuous mating for either male or female: Why then does it occur? The answer may lie with female reproductive physiology. In Chapter 3 it was shown that a relatively high proportion of female cycles are infertile. This is particularly true during adolescence and in the initial post-partum swelling cycles, but also applies to the cycles shown during pregnancy. There is evidence to suggest that females are less attractive to males during some of these infertile cycles. If female attractiveness is governed by oestrogen-dependent pheromones, as it is in rhesus monkeys, then attractiveness may be reduced in pregnant and post-partum cycles which occur while the female is still lactating, because of the reduced levels of oestrogen, or the presence of other hormones at levels atypical of cycles shown by non-pregnant, non-lactating females. In these cycles where conception cannot occur it would be maladaptive to repeatedly form consort relationships, as the risks would not decrease and yet there could be no benefit. It would therefore be adaptive if both males and females could distinguish between cycles in which there is no possibility of ovulation and those in which it might occur. There is some indication that males are capable of some degree of discrimination, as parous females are more frequently involved in the non-promiscuous mating patterns than are nullipares (Chapter 7, section 11, ii).

Why do females show such a high proportion of infertile cycles? It was argued in Chapter 3 that these cycles might function to give females experience of all the available males while there is no risk of pregnancy. The knowledge gained during these cycles enables females in their later, fertile cycles, to participate in a consort or possessive relationship with a male with whom through earlier experiences, they have formed a particular type of relationship. This provides a functional explanation of the period of adolescent sterility when, if a female transfers to a new community, she must form new relationships. It also explains why most females resume post-partum sexual cycles prior to the resumption of ovulation, as the long birth interval means that the available males might differ from those present when the female was last receptive. It is more difficult to explain why females continue to show cycles of sexual swelling during pregnancy.

The development of male sexual behaviour is a long process and opportunities to copulate with adult females during infancy, juvenility and adolescence seem to be essential for the development of sexual competence in adulthood, see Chapter 5, section 6, ii. If adult females only showed fertile cycles then opportunities for copulation would be severely limited. Cycles in which promiscuous mating occur are especially important as they allow all males free opportunity to copulate. The data indicate that chimpanzees engage in sexual behaviour to a greater extent than is essential for reproductive purposes alone, and it appears that copulation is a pleasant, positively reinforcing experience. Chimpanzee copulations are very brief, with intromission lasting for an average of only 7 seconds (McGinnis, 1973, p.49). In this time males ejaculate and reach orgasm but it is not clear whether female chimpanzees experience orgasm. Chevallier-Skolnikoff (1974) reported that female stumptail macaques (Macaca arctoides) achieve orgasm in homosexual mounting but do not show similar behaviour (a typical facial expression, vocalisation and muscular spasms) in heterosexual mountings. Behaviour indicative of orgasm has been observed in female chimpanzees as a result of masturbation (Pomeroy, 1972; Temerlin, 1975). Masturbation appears to be confined to chimpanzees in captivity and is rarely observed in the wild. There are no behavioural indications that chimpanzee females achieve orgasm in heterosexual copulation.

In summary, the chimpanzee mating system observed in the Gombe population can be regarded as an adaptive complex of behaviour patterns which act to maximise female reproductive success by permitting females to select a particular male as a mate. Infertile cycles occur prior to fertile ones both during adolescence and between successive conceptions. During these infertile cycles females often associate with large groups of adult males who mate the female with no signs of overt competition. The restrictive mating patterns, possessiveness and consorting, allow the female to ensure that a single male will impregnate her.

3. Criteria for female choice

Nothing definite can be said about the criteria used by females to discriminate between males. Insufficient data were available to consider consorting and possessiveness separately, let alone to allow examination of the selection criteria important to individual females. It was shown in Chapter 7, section 11,iii, that adult males were differentially involved in the non-promiscuous mating patterns. The frequency of male involvement was significantly, positively correlated with the amount of time males associated with maximally tumescent females; the proportion of that time that the males groomed the females; and the males generousity to females in sharing food. These data show which male characteristics co-vary with involvement in non-promiscuous mating patterns and hence give some indication of the criteria important in female choice. The correlations reveal nothing about individual male-female relationships, but they do suggest that affiliative types of male-female interaction (i.e. grooming and sharing food) may affect reproductive behaviour.

If all females showed a consistent preference for males who showed the most affiliative behaviour then these males would enjoy increased reproductive success at the expense of males who showed lower frequencies of affiliative behaviours. If, in addition, the affiliative behaviours increased the probability of offspring surviving then the frequencies of male-to-female affiliative behaviours would be expected to rise in the population as a result of sexual selection. However, this would only occur if there were no counter-selective pressures operating, i.e. if the increase in affiliative behaviours to females did nothing to decrease the male's chances of survival. Another factor which might counter the spread of a character through inter-sexual selection would be the ability to 'cheat'. If it were possible to over-ride a female's choice, then males who did not show the characters preferred by females would none-the-less continue to reproduce. Such a mechanism may exist in the form of possessiveness shown by a strong alpha male. A male's dominance rank is determined through male-male competition and, as was shown in Chapter 6, section 9, the alpha male is able to monopolise females by showing possessive behaviour. It appears that there is little or no potential for female selectivity in possessive behaviour, and so an alpha male may achieve considerable reproductive success without showing the characters preferred by females.

If females were able to completely determine which males were responsible for conceptions, and if all females chose males with similar characteristics, the frequency of those characters would increase in the population. If females slected on relative, rather than absolute criteria, then the characters would continue to spread and would become more extreme in form. Sexual selection provides a mechanism for rapid evolution, allowing the spread of characters which are concerned with increasing reproductive success, rather than with survival per se.

4. Male-male competition and reproductive success

Male-male competition in chimpanzees results in the formation of a dominance order. The order is not necessarily a linear hierarchy, and Bygott (1974) preferred to refer to males as high, middle, or low ranking, rather than by numerical linear rank order. However, in stable situations and alpha male can be recognised. Male rank was found to be correlated with age, typically increasing proportionate to age during prime adulthood and then decreasing during old age (Bygott, 1974).

The data in Chapter 6, section 9, indicated that Figan when he became alpha male utilised his position to successfully monopolise a number of females as they reached the latter half of their maximal tumescent cycle phase. Such behaviour must lead to increased reproductive success and is even more striking when compared to the behaviour of Evered (who was defeated by Figan in the contest for the alpha position (Riss, in prep.)). During December 1974 and January 1975, Figan directed possessive behaviour to 3 females during 5 of the 6 cycles they showed (see Figure 6.2). During this same period Evered was never observed even associating with maximally tumescent females and was not involved in any consortships.

When considering male reproductive success it is necessary to take a life-long perspective. If every male holds the alpha position for part of his life then the advantage gained from such status will not result in any absolute increase in reproductive success. Although insufficient data are available, it does appear that not all males do attain alpha status, and those that do, maintain it for varying lengths of time. Only two alpha males have been observed at Gombe throughout their 'reigns'. Mike held the alpha position for 6 years and Humphrey for two years (van Lawick-Goodall, 1975).

In summary, the relationship between male dominance rank and reproductive behaviour is not straightforward. Copulation rates in non-competitive matings are not correlated with dominance rank (Chapter 5, section 11). A positive, but not significant, correlation exists between dominance rank and frequency of involvement in the non-promiscuous mating patterns (Chapter 7, section 11, iii). Figan as alpha male, was not involved in any consortships, but was involved in a number of possessive incidents. It appears that the alpha status does confer advantage in terms of increased reproductive success, but for other males there seems to be no consistent relationship between dominance rank and reproductive success.

The failure to find any correlation between copulation rate and male dominance rank does not mean, at least for chimpanzees, that there is no relationship between male dominance and reproductive behaviour. This could shed light on the conflicting reports that exist (see Chapter 1, section 2) concerning the relationship between male dominance and reproductive success in nonhuman primates. Copulation rate per se does not necessarily reflect reproductive success, and this is especially true of species such as chimpanzees, baboons and macaques, in which the female is receptive for several days prior to ovulating. In these species, the frequency of consort formation, especially those occurring in the latter part of the receptive phase would be a more pertinent measure of male reproductive success.

5. Ranging patterns, social structure and reproduction

Wrangham (1975) described ranging patterns of the Gombe chimpanzee population. He found a consistent sex difference in individual ranging patterns, and also seasonal effects on ranging and association patterns which were related to differential food abundance. A community range was recognisable and all individuals appeared to have preferred areas within this, which Wrangham called 'core areas' (p. 5.52). He found that anoestrus females have smaller core areas than males or oestrus females. The larger core areas of the individual males were dispersed within the community range, although during times when food was abundant, males associated in large groups and utilised the whole of the community range. The dispersion of female ranges with respect to the community range remains unclear. Wrangham proposed two alternative hypotheses: 1) That female ranges conform to the boundaries of community ranges such that communities can be regarded as integrated, bisexual units of social structure; or, 2) that female ranges are continuous, and while some fall completely within the boundaries of a single male community range, others overlap two different male community ranges.

When food was scarce males travelled less and behaved in a fashion similar to females. This suggested that intensive utilisation of a small core area was the pattern of ranging which maximised feeding efficiency, and thus, at times of food abundance males sacrifice feeding efficiency in order to cover a larger range. The distribution of female core areas means that by cooperating to maintain the community range, males gain access to more females. This gives the potential for individual males to increase their reproductive success, although this can only be achieved at the expense of other community males. The community males cooperate to defend their range against neighbouring males (Wrangham, 1975; Goodall _et al_, in press). Territoriality is rare amongst mammals (Brown & Orians, 1970), and Wrangham (p. 5.63) concluded that chimpanzee males maintained a joint territory in order to gain exclusive access to the females whose core areas lay within the community range.

Whilst the maintenance of a joint range gives the males, as a group, access to more females, its effect on individual reproductive success must be known to understand how such a system evolved. Increased reproductive success can only be achieved at the expense of other group members, and yet it is difficult to postulate how cooperation in maintaining the group range arose, if only a minority of the males obtain benefits from the system. We have seen that the relationship between male-male competition (as expressed in the formation of a dominance order) and reproductive success is not straightforward. The alpha male achieves an advantage over all the others, but beyond this, dominance rank does not appear to influence individual reproductive success.

As the majority of conceptions occur during consortships, male participation in consort relationships gives an indication of individual reproductive success. Consorting frequency was determined by the male's inclination to initiate the behaviour, mediated by the female's choice as to whether or not to cooperate. Females, as a whole, preferred to consort with males with whom they had strong affiliative relationships, and male dominance rank did not appear to be important. Cooperative maintenance of the community range brings all the adult males into contact with all the females whose core areas are within the community range, allowing the formation of affiliative relationships with these females. The additional benefits reaped by the alpha male are transitory, as a single male maintains the status for only a small part of his life. However, more longitudinal data are required before conclusions as to the importance of the reproductive benefit gained by the alpha male can be assessed in absolute terms.

If individual male reproductive success is largely determined by male-female interactions rather than by male-male competition, it is easier to understand the evolution of the cooperative male territory. We have seen that male chimpanzees do not migrate, and therefore the males of a community are likely to be genetically related. This allows the evolution of cooperative behaviour through kin selection.

Wrangham (1975, p. 5.63) discussed functional aspects of chimpanzee ranging patterns in terms of individual survival. He concluded that the unpredictable food sources of chimpanzees may require each individual to retain access to a larger area than is needed at any particular time of year. This suggests a way in which the ranging behaviour of males confers advantages to females. Females are by no means restricted entirely to their core areas, and they do sometimes travel throughout the community range. Although quantitative data are lacking, it appears that females (both oestrus and anoestrus) are more likely to move far out of their core areas when accompanied by adult males. Whilst it cannot be stated with certainty that females are dependent on male escorts for these forays which often take them to food sources, it appears that adult male company facilitates such forays and provides benefits to females and their offspring through access to feeding sites outwith their core areas. Detailed studies of female ranging and association patterns, and how they are affected by the female's reproductive state are required to clarify the exact nature and extent of such benefits.

Inter-sexual selection provides a mechanism for the evolution of male behaviours which do not directly contribute to individual survival. Altruistic behaviour, such as sharing food, either through direct donation. or through the giving of food pant hoots, may gain selective advantage through inter-sexual selection. If all females chose to consort only with males who showed such behaviours then these males would gain a reproductive advantage and the behaviours would spread through the population. It is possible to consider altruistic behaviours as handicaps - after Zahavi's (1975) usage, see Chapter 1, section 2. These behaviours have negative survival value as they reduce the feeding efficiency of the actor.

From the female viewpoint the form of social structure shown by wild chimpanzees provides opportunity for the successful operation of mate selection. The ranging pattern, of intensively using small core areas within the larger community range, operates to maximise female feeding efficiency, and the sex difference in ranging patterns reduces male-female competition for food. Maximisation of feeding efficiency is essential for females, as for the majority of their lifetimes they bear the extra nutritional load of either pregnancy or lactation, which can demand an extra 1000 calories per day (Gunther, 1971). The system of small female core areas within a larger cooperatively maintained male range, gives females the benefits of having a free choice of mate, without the disadvantage of continuously competing with males for food.

6. Is the flexible mating system observed in the Gombe chimpanzee population typical?

The only long-term study other than that at Gombe has been of the chimpanzee population in the Mahali Mountains in western Tanzania. Despite 7 years of observation no consortships have been observed or suspected (Nishida & Itani, pers. comm.). Whilst the possibility of cultural variation exists, so too does a possible explanation of the absence of consortships in the Mahali chimpanzees. The K unit-group (community) is the most studied group in the Mahali Mountains and it comprises only 5 adult males, of whom one, Kasonta, has been the alpha male since 1969. Nishida (in press) reported that Kasonta was responsible for 46% of all the observed copulations. This suggests that Kasonta either showed possessive behaviour, or that his presence alone inhibited the other adult males from copulating for at least some of the time. If the alpha male of a community consistently shows possessive behaviour, then the frequency of consortships would be low. It was shown in Chapter 6, section 9, that in the two months of observation when Figan consistently acted possessively to receptive females, consortships only occurred when two or more females were simultaneously maximally tumescent.

If a comparable situation exists in the K unit-group observed by Nishida, the rarity of consortships combined with their low observability (see Chapter 7, section 3) might explain why consort pairs have not been observed in the Mahali Mountains. No other studies of wild chimpanzees have reported the occurrence of consortships. Most of the studies have been of relatively brief duration, and the probability of observing consort behaviour in such studies is very low. Reynolds (1963) reported that during his observations of chimpanzees in the Budongo Forest, Uganda, he never saw an oestrus female mated by more than one male during any single observation period. However he could draw no conclusions as only 4 copulations were observed. Stephenson (1973) described cultural differences in the form of sexual behavioural elements between 3 geographically distinct troops of Japanese macaques, but no examples of cultural variation in mating systems have been reported for non-human primates.

Additional data from long-term studies of other chimpanzee populations are required before any firm conclusions can be reached regarding the typicality of the flexible mating system observed in the Gombe population.

7. Other species.

On the basis of the arguments presented above, generalisations can be attempted regarding the interplay of sexual and natural selection as forces in the evolution of primate social structure. One might predict that whenever environmental conditions are sufficiently favourable to permit permanent associations of a number of adults, these would exist as they permit females to maximise their reproductive success by exercising choice; and for males the potential to increase their reproductive success increases proportionate to the number of available females. Additional constraints would operate on species for whom predation was a threat, or where parental investment from both parents was essential for the successful rearing of offspring, or greatly improved the chances of offspring survival.

The Gombe chimpanzees do not appear to be exposed to any risk of predation. Leopards do occur in the Park but they are uncommon and no evidence to suggest that they ever prey on chimpanzees exists. Female chimpanzees are capable of providing for all the needs of their growing offspring, in the absence of any direct paternal investment. It is difficult to assess what difference direct paternal investment would make, but it is possible that if it included regular provision of protein, in the form of mammalian prey, female reproductive success might be increased, due to a reduction in the birth interval and an increase in the rate of physical maturation of offspring (see Chapter 3 for a comparison of chimpanzee development in captivity and the wild). Whatever benefits accrued have to be balanced against the disadvantages of reduced reproductive potential (for the male), and of permanent competition for food with another adult (for the female). Thus, whilst for chimpanzees, social structure can be regarded as having evolved through interaction between the two principal necessities of optimising feeding efficiency and maximising reproductive success, the same cannot be assumed for other species.

The major difficulty in assessing the relative contributions of different factors in the evolution of social structure is accurate measurement of the factors. Difficulties in assessing food availability, both quantity and quality, have been encountered in all ecological studies (e.g. Wrangham, 1975), and the same is true of factors such as predation pressure. If one accepts a simplistic view that multi-male social structures will evolve whenever other factors permit, then restraints can be saught in species with different types of social structure. For instance, the evolution of monogamy is commonly linked to environmental pressures, the hypothesis being that territory formation and defence by an adult male is essential to provide the environmental resources necessary for a female to successfully produce and rear offspring. While this may be true for some monogamous species, other factors may be of over-riding importance in others.

Female primates typically produce a single young at parturition and this is assumed to be a result of physiological and/or nutritional limitations. One way to increase reproductive potential is for females to have multiple births, although this will only gain selective advantage if the offspring survive, and if the pre-natal energy demands on the female do not endanger her survival. Twin births are common in marmosets and tamarins, and in both of these species males invest considerable parental investment, often carrying the infants throughout the period of dependency. In these species it appears that paternal investment may be essential for offspring survival, as the energy burden of both feeding and transporting twin infants may be too great for the female to bear alone. It seems possible that a similar need for paternal investment arose in hominid evolution. The human neonate is considerably more dependent than its nonhuman primate counterpart. The hairless body of the mother precludes clinging, meaning that the mother has always to use one or both hands to support her child. The mother's mobility and hence feeding efficiency are thus greatly reduced during the long period of infant dependency, making paternal investment essential for the survival of offspring and mother. One would expect that paternal care would only be forthcoming if it benefitted the female either by reducing the birth interval or by allowing multiple births.

In summary, paternal care and permanent monogamous bonding has both advantages and disadvantages and will only gain selective advantage when the survival of infants and/or their mothers depend on paternal investment, whether it be direct energy investment, e.g. infant transport, or indirect investment by defending a feeding territory or donating food. Long-term studies such as that on the Gombe chimpanzee population are essential for an understanding of the factors involved in the evolution of social structure and mating systems. Speculation can be made, but accurate data on individual reproductive success under different mating systems, and in different forms of social structure are required from a variety of species before constructive models or theories on the roles of sexual and natural selection in primate evolution can be constructed.

Appendix I: Definitions of behavioural elements observed in copulatory interactions

Advance: Individual moves towards another but stops at a distance greater than 1.5m (arms' reach).

Approach: Individual moves to within 1.5m of another.

Arm stretch: The arm, or arms, of a male are extended towards a female. The palmar surface of the hand is directed downwards and towards the body. Sometimes the arm is raised in sweeping upward gesture. (Plates 5.4 & 5.6.)

Avoid: Individual moves away at the approach of another.

Bipedal: Individual stands with weight supported entirely by the legs.

Branch jerk: Individual holds onto rooted vegetation with one or both hands and jerks it with brief, unrepeated movement of the arm(s).

Branch shake: Individual holds onto rooted vegetation with one or both hands, and shakes it with repeated upwards and downwards movements of the arm(s). (Plate 5.3.)

Contact: Individual makes physical contact with the body of another.

Copulatory pants: Series of hoarse breathy inhalations, only made by certain males and occurring during pelvic thrusting.

Dab: Rapid hitting movements made with arm extended and back of hand towards the other individual. Usually directed towards the face, but no contact made.

Ejaculation: Semen expelled from the penis.

End intromission: Individual responsible for male's penis leaving female's vagina.

Extend hand: Individual holds its hand towards another but does not make contact. Wrist and fingers are extended; palm either up or down.

Female posture: Female may adopt the following postures during intromission;
crouch: Body supported on all four partially flexed limbs. (Plates 5.7, 5.8 & 5.9.).
upright quadrupedal: Body supported on all four extended limbs. (Plate 5.20.)
side: Body supported on either side, leg and arm positions variable, (Plate 5.19.)

Fend: Individual pushes another away, breaking physical contact. (Plate 5.18.)

Follow: Individual orients locomotion and travels behind another moving individual.

Gaze: Individual stares at another for two or more seconds.

Glance: Individual looks at another for less than two seconds.

Grin: Individual exhibits full-closed or full-open grin face: mouth corners retracted, upper and lower teeth together (full-closed) or apart (full-open) and exposed. (Plate 5.7.)

Groom: Hand(s) and/or mouth manipulating the hair of another or vice versa. (social grooming); or of self (self grooming).

Hair erect: Individual's hair is abducted from the skin. (Plate 5.4.)

Hand-on-branch: Individual holds onto rooted vegetation with hand.

Hit away: Individual extends arm horizontally toward another in a sudden movement, sometimes making glancing contact.

Hunch: Individual draws both shoulders up towards the head.

Inspect: Face and/or hands are brought close (within 20cm), or into contact with the genital area of self or another. The female's vaginal opening is socially inspected. The inspecting individual parts the lips of the vagina and uses fingers, mouth or nose to poke, lick or sniff. (Plates 5.1, 5.2 & 5.10.)

Intromission: Penis enters vaginal canal.

Kiss: Individual contacts body of another with lips.

Leanback: Male squats behind female during intromission with at least one hand on the ground, the other hand may rest gently on the female's back. (Plate 5.7.)

Leave: Individual moves beyond arms' reach (1.5m) of another.

Look away: Individual turns head away from another with horizontal turn of approximately 90°, and holds in this position for two or more seconds.

Male invite: Male sits with legs partially flexed and spread apart to reveal erect penis. (Plate 5.5.)

Mount: Part of the mounter's ventral surface contacts part of the other's back, and the mounter appears to rest weight on the other. (Plate 5.9.)

Penis adduct: Erect penis spasmodically jerks.

Penis erect: Penis fully distended.

Penis manipulate: Male briefly fingers or strokes his erect penis without looking at it.

Present: Female crouches with variable arm and leg flexion, in front of the male with her swelling oriented towards him.

Play: Vigorous non-agonistic interaction in which two or more individuals exhibit a similar set of behavioural elements (see van Hooff, 1971; van Lawick-Goodall, 1968; Loizos, 1969).

Rock: Individual oscillates torso forward and backward from hips in slow, rhythmical motion.

Scratch: Individual draws nails across skin often in rapid, repeated sweeping movement.

Scream: Series of high-pitched rasping vocalisations.

Squeal: Clear high-pitched sound of variable length, only made by females during intromission.

Stamp: Individual raises foot and then lowers it with rapid extension of the leg, striking the substrate hard and thus creating a noise.

Thrusting: Rhythmical back and forward movements of male's pelvis.

Touch: Individual contacts another by extending arm and fingers.

Turn away: Individual re-orients body to face away from another.

Turn towards: Individual re-orients body to face another.

Whimper: Series of soft single syllable vocalisations accompanied by extension of lips.

Wipe: Individual uses artifact, usually leaves, to wipe genital or body hair.

KEY TO FLOW CHARTS

ELEMENT	occurring in > 68% of total sequences
ELEMENT	occurring in 34-67% of total sequences
element	occurring in 25-33% of total sequences

→	10-25% of total transitions
➔	26-50% of total transitions
➡	51-75% of total transitions
🡺	76-100% of total transitions

Figure A. 1. Sequences of behavioural elements shown in 21 copulations between Figan and Patti.

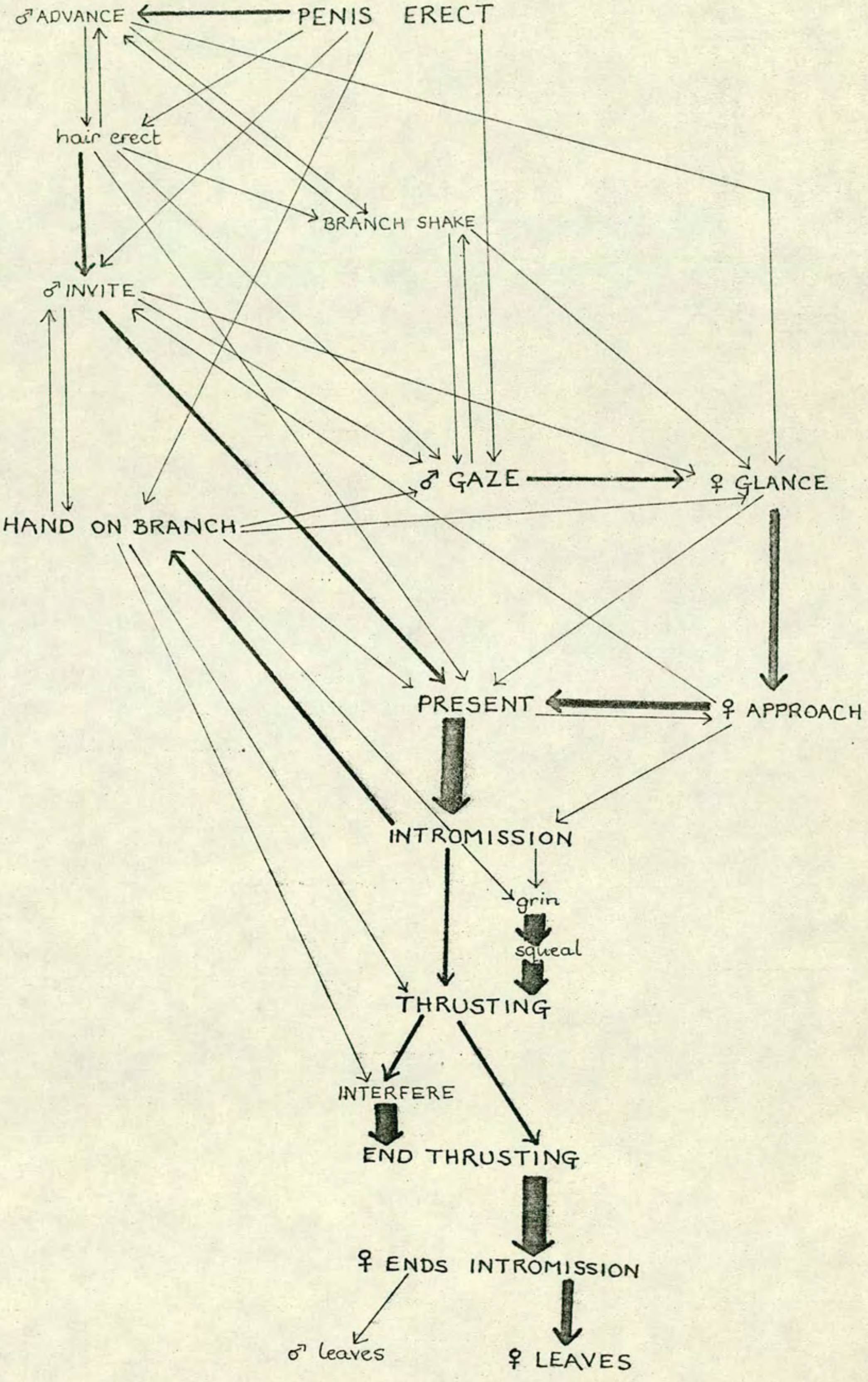


Figure A.2. Sequences of behavioural elements shown in 15 copulations between Satan and Pallas.

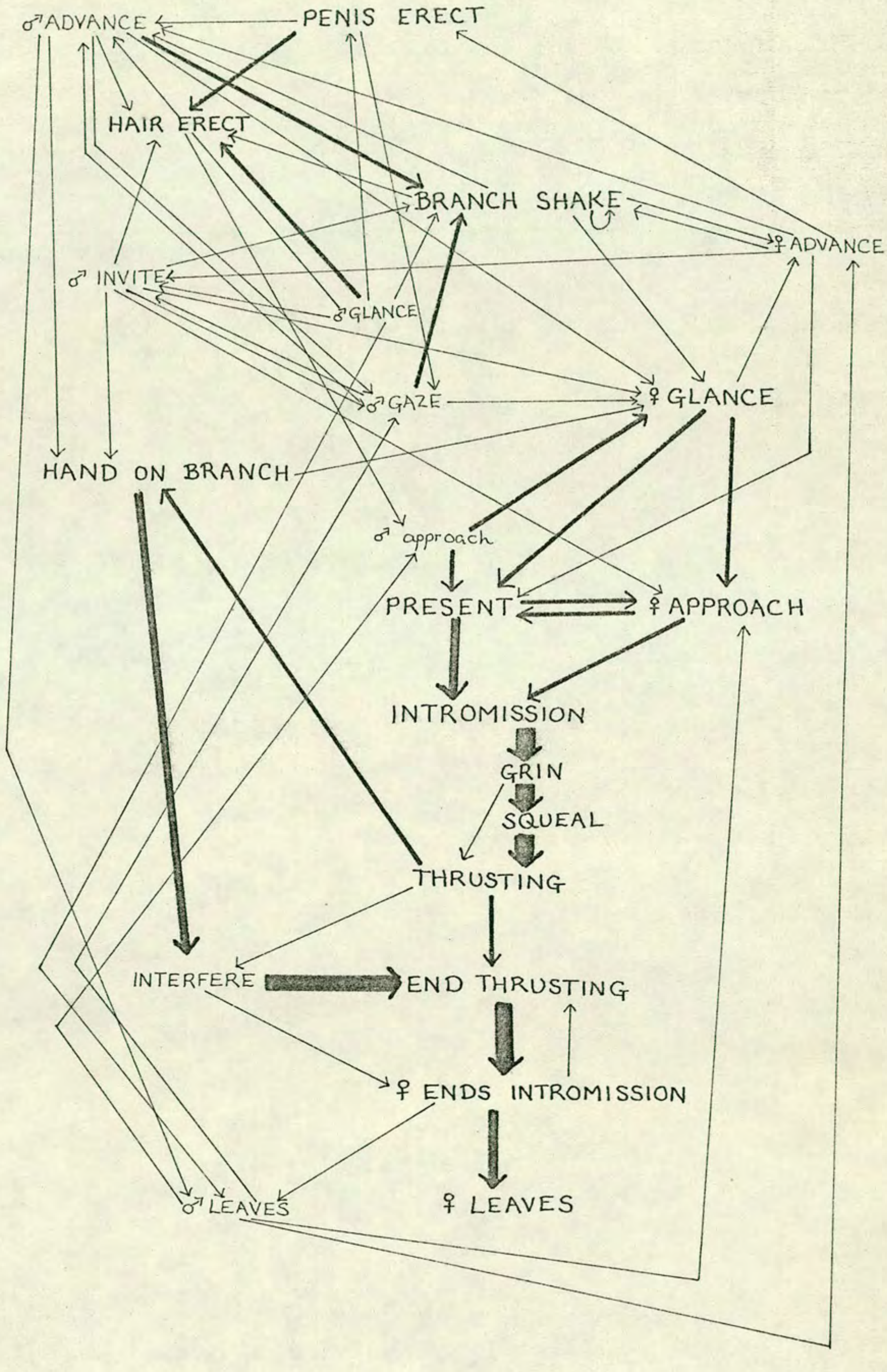
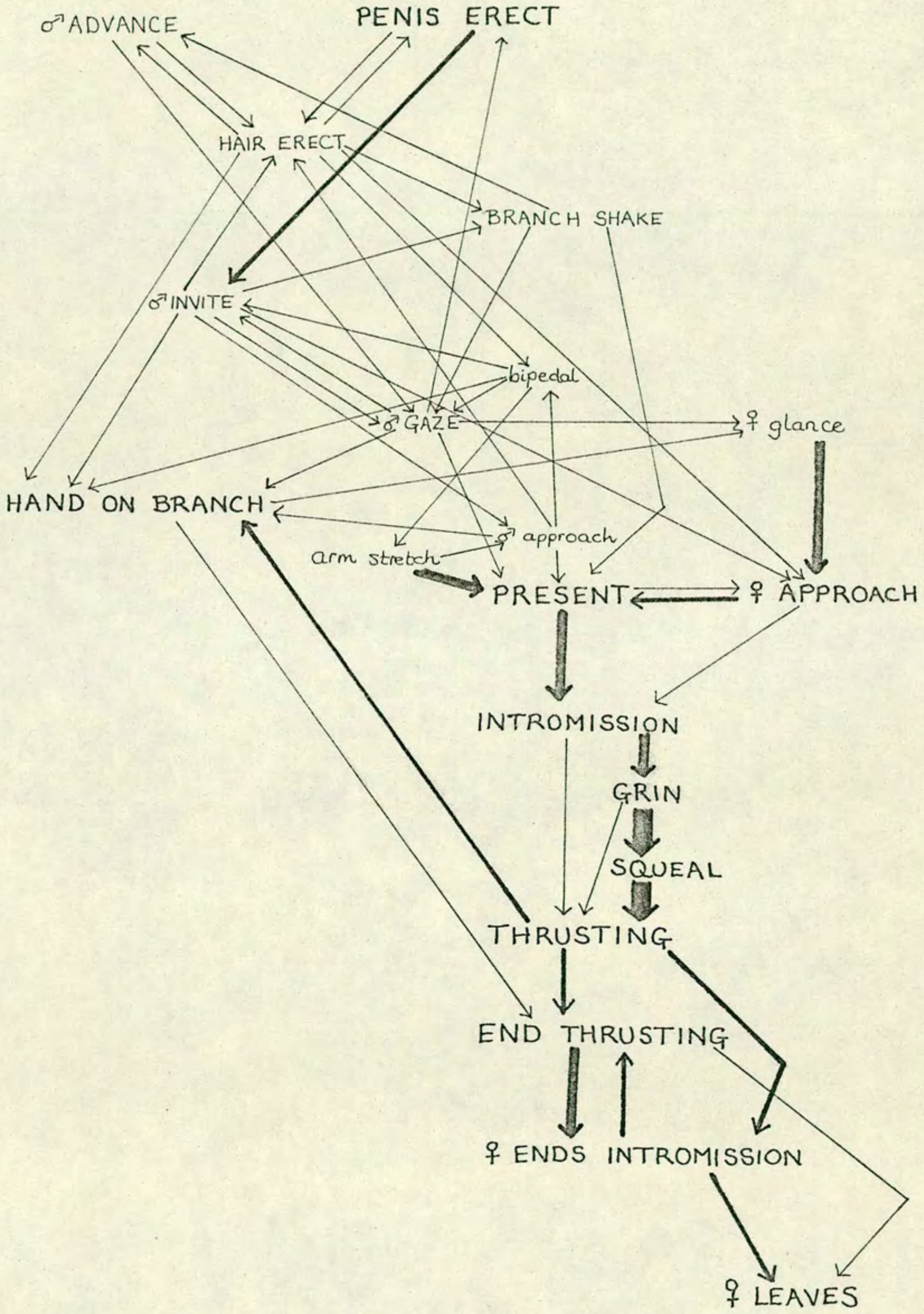


Figure A.3. Sequences of behavioural elements shown in 15 copulations between Mike and Gigi.



REFERENCES

Adler, N.T. & Zoloth, S.R. (1970) Copulatory behavior can inhibit pregnancy in female rats. Science 168: 1480-1482.

Aldrich-Blake, F.P.G. (1970) Problems of social structure in forest monkeys. Pp. 79-101, in Social behaviour in birds and mammals, J.H. Crook (ed.), Academic Press, London.

Altmann, S.A. (1973) The pregnancy sign in savannah baboons. J. Zoo. Anim. Med. 4: 8-12.

Altmann, S.A. and Altmann, J. (1970) Baboon ecology. Bibliotheca primatol. 12: 1-220.

Ashley-Montagu, M.F. (1939) Adolescent sterility. Quart. Rev. Biol. 14: 192-219.

Bartke, A., Stiele, R.E., Musto, N. & Caldwell, B.U. (1973) Fluctuations in plasma testosterone levels in adult male rats and mice. Endocrinology 92(4): 1223-1228.

Bastock, M. (1956) A gene mutation which changes a behaviour pattern. Evolution 10: 421-439.

Bastock, M. (1967) Courtship: A zoological study, Heinemann, London.

Bauer, H. (1975) Behavioral changes about the time of reunion in subgroups of chimpanzees in the Gombe Stream National Park. In Contemporary Primatology, S. Kondo, M. Kawai & A. Ehara (eds.), Karger, Basel.

Baxi, P.G. (1957) A natural history of child-bearing in the hospital class of women in Bombay. J. Obstet. and Gynecol. of India 8: 26-51.

Beach, F.A. & Pauker, R. (1949) Effects of castration and subsequent androgen administration upon mating in the male hamster (Cricetus auratus). Endocrinology 45: 211-221.

Benedictus, T. de (1973) The behavior of young primates during adult copulation: Observations of a Macaca iris colony. Amer. Anthrop. 75: 1469-1484.

Bernstein, I.S. (1963) Social activities related to rhesus monkey consort behaviour. Psychol. Rep. 13: 375-379.

Blurton Jones, N.G. & Trollope, J. (1968) Social behavior of stump-tailed macaques in captivity. Primates 9: 365-394.

Boelkins, R.G. & Wilson, A.P. (1972) Intergroup social dynamics of the Cayo Santiago rhesus (Macaca mulatta) with special reference to changes in group membership by males. Primates 13: 125-140.

Boorman, G.A., Speltie, T.M. & Fitzgerald, G.H. (1974) Urinary chorionic gonadotrophin excretion during pregnancy in the chimpanzee. J. med. Prim. 3: 269-275.

Bonte, M., Akingeneye, E., Gashakamba, M., Mbarutso, E. & Nolens, M. (1974) Influence of the socio-economic level on the conception rate during lactation. Int. J. Fertil. 19: 97-102.

Brown, J.L. & Orians, G.H. (1970) Spacing patterns in mobile animals. Ann. Rev. Ecol. Systemat. 1: 239-262.

Bygott, D. (1972) Cannibalism among wild chimpanzees. Nature 238: 410-411.

Bygott, D. (1974) Agonistic behaviour and dominance in wild chimpanzees. PhD. thesis, University of Cambridge.

Carpenter, C.R. (1940) A field study in Siam of the behavior and social relations of the gibbon (Hylobates lar). Comp. Psychol. Monogr. 16: 1-212.

Caspari, E. (1972) Sexual selection in human evolution. Pp. 332-356, in Sexual Selection and the descent of man, B. Campbell (ed.), Aldine, Chicago.

Cavalli-Sforza, L.L. & Bodmer, W.F. (1971) The Genetics of Human Populations. W.H. Freeman, San Francisco.

Chalmers, N.R. (1968) The social behaviour of free-living mangabeys in Uganda. Folia primatol. 8: 263-281.

Chang, M.C. (1965) Fertilising life of ferret sperm in the female tract. J. exp. Zool. 158: 87-100.

Chevallier-Skolnikoff, S. (1974) Male-female, female-female, and male-male sexual behavior in the stumptail monkey, with special attention to the female orgasm. Archives of Sex. Behav. 3: 95-116.

Clark, C.B. (in press) A preliminary report on weaning among chimpanzees of the Gombe National Park, Tanzania. In Primate Socialisation, vol. 2, F.E. Poirier & Chevallier-Skolnikoff (eds.), Aldine, Chicago.

Clark, G. (1947) Threshold bleeding and sex skin in the castrate female chimpanzee. Endocrinology 41: 327-329.

Clark, G. & Birch, H.G. (1948) Observations on the sex skin and sex cycle in the chimpanzee. Endocrinology 43: 218-231.

Clutton-Brock, T.H. (1972) Feeding and ranging beh aviour of the red colobus monkey. PhD. thesis, University of Cambridge.

Clutton-Brock, T.H. (1974) Activity patterns of red colobus (Colobus badius tephosceles). Folia primatol. 21: 161-187.

Collins, D.A. (in prep.) Consort behaviour in Papio anubis, PhD. thesis, University of Edinburgh.

Corner, G.W. (1923) Ovulation and menstruation in Macacus rhesus. Contrib. Embryol. Carneg. Inst. 15: 73-102.

Crook, J.H. (1965) The adaptive significance of avian social organisations. Symp. zool. Soc. Lond. 14: 181-218.

Crook, J.H. (1970) The socio-ecology of primates. Pp. 103-166, in Social behaviour in birds and mammals, J.H. Crook (ed.), Academic Press, London.

Crook, J.H. (1972) Sexual selection, dimorphism, and social organisation in the primates. Pp. 231-281, in Sexual selection and the descent of man, B. Campbell (ed.), Heinemann, London.

Crook, J.H. & Gartlan, J.S. (1966) Evolution of primate societies. Nature 210: 1200-1204.

Crow, J.F. & Kimura, M. (1965) Evolution in sexual and asexual populations. Amer. Nat. 99: 439-450.

Crow, J.F. & Kimura, M. (1970) An Introduction to Population Genetics Theory, Harper & Row, New York.

Dandekar, K. (1959) Demographic survey of six rural communities. Gokhale Institute of Politics and Economics, p. 62

Darwin, C. (1871) The Descent of Man and Selection in Relation to Sex. John Murray, London.

Dean, R.F.A. (1949) Women war captives in Russia. British Medical Journal 1: 691-695.

DeVore, I. (1963) A comparison of the ecology and behavior of monkeys and apes. In Classification and Human Evolution, S.L. Washburn (ed.), Aldine, Chicago.

Dixson, A.F. (1975) Notes on sexual and other behaviour in captive celebes 'black apes' (Macaca nigra). Primate Eye 4: 14-16.

Doring, G.K. (1969) The incidence of anovulatory cycles in women. J. Reprod. Fertil. (suppl.) 6: 77-81.

Drickamer, L.C. (1974) A ten-year summary of reproductive data for free-ranging Macaca mulatta. Folia primatol. 21: 61-80.

Elder, J.H. (1938) The time of ovulation in chimpanzees. Yale J. Biol. Med. 10: 347-364.

Ellefson, J.O. (1968) Territorial behavior in the common white-handed gibbon, Hylobates lar Linn. Pp 180-199, in Primates: Studies in adaptation and variability, P.C. Jay (ed.), Holt, Rinehart & Winston, New York.

Erikson, L.B. (1963) Sex skin turgescence, vaginal smear changes, and determination of the period of ovulation in the chimpanzee. Fertil. Steril. 14: 273-283.

Ford, C.S. & Beach, F.A. (1951) Patterns of Sexual Behaviour, Methuen, London.

Fossey, D. (1974) Observations on the home range of one group of mountain gorillas (Gorilla gorilla beringei). Anim. Behav. 22: 568-581.

Fox, C.A., Ismail, A.A.A., Love, D.N., Kirkham, K.E. & Loraine, J.A. (1972) Studies on the relationship between plasma testosterone levels and human sexual activity. J. Endocr. 52:

Fox, R. (1972) Alliance and constraint: Sexual selection and the evolution of human kinship systems. Pp. 282-331, in Sexual selection and the descent of man, B. Campbell (ed.), Aldine, Chicago.

Frisch, R.E. (1974) Demographic implications of the biological determinants of female fecundity. Paper presented at the annual meeting of the Population Association of America.

Gartlan, J.S. (1969) Sexual and maternal behavior of the vervet monkey, Cercopithecus aethiops. J. Reprod. Fert. Suppl. 6: 137-150.

Goodall, J. (1965) Chimpanzees of the Gombe Stream Reserve. Pp . 425-473, in Primate Behavior, I. DeVore (ed.), Holt, Rinehart & Winston, New York.

Goodall, J., Bandura, A., Bergmann, E., Busse, C., Matama, H., Mpongo, E., Pierce, A. & Riss, D. (in press). Intercommunity interactions in the chimpanzee population of the Gombe National Park. In Behavior of Great Apes, perspectives on human evolution, 4, D.A. Hamburg & J. Goodall (eds.), Holt, Rinehart & Winston, New York.

Gordon, T.P., Bernstein, I.S. & Rose, R.M. (1973) Seasonal changes in sexual behavior and plasma testosterone levels of group living monkeys. Amer. Zool. 13: 1267.

Goss-Custard, J.D., Dunbar, R.I.M. & Aldrich-Blake, F.P.G. (1972) Survival, mating and rearing strategies in the evolution of primate social structure. Folia primatol. 17: 1-19.

Gouzoules, H. (1974) Harassment of sexual behavior in the stumptail macaque, Macaca arctoides. Folia primatol. 22: 208-217.

Graham, C.E. (1970) Reproductive physiology of the chimpanzee. The Chimpanzee, vol 3: 183-220, Karger, Basel.

Graham, C.E. (1973) Chimpanzee endometrium and sexual swelling during menstrual cycle or hormone administration. Folia primatol. 19: 458-468.

Graham, C.E., Collins, D.C., Robinson, H. & Preedy, J.R.K. (1972) Urinary levels of estrogens and pregnanediol and plasma levels of progesterone during the menstrual cycle of the chimpanzee: Relationship to the sexual swelling. Endocrinology 91: 13-24.

Gunther, M. (1971) Infant feeding. Penguin, Harmondsworth.

Halewijn, E.A.B.V. & De Waard, F. (1968) Menstrual cycles shortly after menarche in European and Bantu girls. Human Biology 40: 314-330.

Halperin, S.D. (in prep.) Agonistic and other relationships of male chimpanzees. PhD. thesis, University of Washington, St. Louis.

Hanby, J. (in prep.) Socio-sexual Development in primates.

Harlow, H.F. & Harlow, M.K. (1969) Effects of various mother-infant relationships on rhesus monkey behaviors. In Determinants of Infant Behavior, 4, B.M. Foss (ed.), Methuen, London.

Hartman, C.G. (1931) Relative sterility of the adolescent organism. Science 74: 226-227.

Hill, J.L. (1974) Peromyscus: Effects of early pairing on reproduction. Science 186: 1042-1044.

Hinde, R.A. (1974) Biological bases of human social behaviour, McGraw Hill, New York.

Hinde, R.A. (in press) Relationships and the structure of non-human primate groups. In Behavior of Great Apes, Perspectives in Human Evolution, 4, D.A. Hamburg & J. Goodall (eds.), Holt, Rinehart & Winston, New York.

Howland, B.E., Faiman, C. & Butler, T.M. (1971) Serum levels of FSH and LH during the menstrual cycle of the chimpanzee. Biology of Reproduction 4: 101-105.

→ Itani, J. (1972) A preliminary essay on the relationship between social organisation and incest avoidance in non-human primates. Pp. 165-171, In Primate Socialisation, F.E. Poirier (ed.), Random House, Inc.

Itani, J. & Suzuki, A. (1967) The social unit of chimpanzees. Primates 8: 355-381.

Ismail, A.A.A., Davidson, D.W. & Loraine, J.A. (1972) Relationship between plasma cortisol and human sexual activity. Nature 237: 288-289.

Jay, P.C. (1965) The common langur of North India. Pp. 197-249, in Primate Behavior, I. DeVore (ed.), Holt, Rinehart & Winston, New York.

Hogan-Warburg, A.J. (1966) Social behavior of the ruff, Philomachus pugnax (L.). Ardea 54: 109-229.

Kawanaka, K. & Nishida, T. (1975) Recent advances in the study of inter-unit-group relationships and social structure of wild chimpanzees of the Mahali Mountains. Pp. 173-186, in Symp. 5th Cong. Int'l. Primat. Soc., (1974).

Kinson, G.A. & Liu, C.C. (1973) Diurnal variation in plasma testosterone of the male laboratory rat. Horm. Metab. Res. 5: 233-234.

Kolata, G.B. (1974) !Kung hunter-gathers: Feminism, diet, and birth control. Science 185: 932-934.

Kortlandt, A. (1962) Chimpanzees in the wild. Scientific American 206: 128-138.

Kummer, H. (1968) Social organisation of hamadryas baboons. Bibliotheca primatol. 6: 1-189.

Kummer, H. (1971) Primate societies: Group techniques of ecological adaptation. Aldine Atherton, Chicago.

Lack, D. (1968) Ecological adaptations for breeding in birds. Methuen, London.

Lancaster, J.B. & Lee, R.B. (1965) The annual reproductive cycle in monkeys and apes. Pp. 486-513 in Primate Behavior, I. DeVore (ed.), Holt, Rinehart & Winston, New York.

Lawick-Goodall, J. van (1968) The behaviour of free-living chimpanzees in the Gombe Stream Reserve. Anim. Behav. Monogr. 1(3): 161-311.

Lawick-Goodall, J. van (1969) Some aspects of reproductive behaviour in a group of wild chimpanzees, Pan troglodytes schweinfurthi, at the Gombe Stream Chimpanzee Reserve, Tanzania, East Africa. J. Reprod. Fert., Suppl. 6: 353-355.

Lawick-Goodall, J. van (1971) In the Shadow of Man. Collins, London.

Lawick-Goodall, J. van (1975) The behaviour of the chimpanzee. Pp. 56-100, in Hominisation und Verhalten, I. Eibl-Eibesfeldt (ed.), Gustav Fischer Verlag, Stuttgart.

Levi-Strauss, C. (1956) The family. In Man, culture and society, H.L. Shapiro (ed.), Oxford University Press.

Livingstone, F.B. (1969) Genetics, ecology and the origins of incest and exogamy. Current Anthrop. 10(1): 45-62.

Loy, J. (1970) Perimenstrual sexual behavior among rhesus monkeys. Folia primatol. 13: 286-297.

Loy, J. (1974) Changes in facial color associated with pregnancy in patas monkeys. Folia primatol. 22: 251-257.

MacKinnon, J. (in press) Reproductive behaviour in wild orang-utan populations. In The Behavior of Great Apes, Perspectives in Human Evolution 4, D.A. Hamburg & J. Goodall (eds.), Holt, Rinehart & Winston, New York.

Malek, J. (1962) Rep. 7th Conf. of the Soc. for Biol. Rhythm, Siena, 1960. Pp. 97-103. Edizione Panminerva Medica Turin.

Mason, W.A. (1965) The social development of monkeys and apes. Pp. 514-543, in Primate Behavior, I. DeVore (ed.), Holt, Rinehart & Winston, New York.

Mason, W.A. (1968) Use of space by Callicebus groups. Pp. 200-216, in Primates: Studies in adaptation and variability, P.C. Jay (ed.), Holt, Rinehart & Winston, New York.

Matsumoto, S., Igarsahi, M. & Nagaoka, Y. (1968) Environmental anovulatory cycles. Internat. J. Fert. 13: 15-23.

→ Mayr, E. (1972) Sexual selection and natural selection. Pp. 87-104, in Sexual selection and the descent of man, B. Campbell (ed.), Aldine, Chicago.

McClure, T.J. (1967) Infertility in mice caused by fasting at about the time of mating. II. Pathological changes. J. Reprod. Fertil. 13: 387-394.

McGinnis, P.R. (1973) Patterns of sexual behaviour in a community of free living chimpanzees. PhD. thesis, University of Cambridge.

McGinnis, P.R. (in press). Sexual behavior in free-living chimpanzees: Consort relationships. In Behavior of Great Apes, Perspectives in human evolution, vol 4, D.A. Hamburg & J. Goodall (eds.), Holt, Rinehart & Winston, New York.

McGrew, W.C. (1975) Patterns of plant food sharing by wild chimpanzees. Pp. 304-309, in Contemporary Primatology, S. Kondo, M. Kawai & A. Ehara (eds.), Karger, Basel.

Michael, R.P. (1968) Gonadal hormones and the control of primate behaviour. In Endocrinology and Human Behaviour, R.P. Michael (ed.), O.U.P., London.

Missakian, E.A. (1973) Genealogical mating activity in free-ranging groups of rhesus monkeys (Macaca mulatta) on Cayo Santiago. Behaviour 45: 225-241.

Morris, D.J. (1956) The function and causation of courtship ceremonies. Pp. 261-287, in L'Instinct dans le Comportement des Animaux et de L'Homme, P.P. Grass (ed.), Masson & Cie, Paris.

Nadler, R.D. (1975) Cyclicity in tumescence of the perineal labia of female lowland gorillas. Anat. Rec. 181: 791-797.

Nieschlag, E. & Ismail, A.A.A. (1970) Dirunal variations of plasma testosterone in normal and pathological conditions as measured by the technique of competitive protein binding. J. Endocr. 46: 3-4.

Nishida, T. (1966) A sociological study of solitary male monkeys. Primates 7: 141-204.

Nishida, T. (1968) The social group of wild chimpanzees in the Mahali Mountains. Primates 9: 167-224.

Nishida, T. (1970) Social behaviour and relationships among wild chimpanzees of the Mahali Mountains. Primates 11: 47-87.

Nishida, T. (in press). The social structure of chimpanzees of the Mahali Mountains. In The Behavior of Great Apes, Perspectives on Human Evolution 4, D.A. Hamburg & J. Goodall (eds.), Holt, Rinehart & Winston, New York.

Nishida, T. & Kawanaka, K. (1972) Inter-unit-group relationships among wild chimpanzees of the Mahali Mountains. Kyoto Univ. Afr. Stud. 7: 131-169.

Nissen, H.W. & Yerkes, R.M. (1943) Reproduction in the chimpanzee: Report on forty-nine births. Anatomical Record 86: 567-578.

Orians, G.H. (1969) On the evolution of mating systems in birds and mammals. Amer. Nat. 103: 589-603.

Packer, C. (1975) Male transfer of olive baboons. Nature 255: 219-220.

Parsons, T. (1954) The incest taboo in relation to social structure and the socialisation of the child. British Journal of Sociology : 102-115.

Peckham, C.H. (1934) An investigation of some effects of pregnancy noted six weeks and one year after delivery. Bull. Johns Hopkins Hospital 54: 186-207.

Petter, J. (1965) The lemurs of Madagascar. Pp. 292-319, in Primate behavior, I. DeVore (ed.), Holt, Rinehart & Winston, New York.

Phoenix, C.H. (1975) The role of androgens in the sexual behavior of adult male rhesus monkeys. Pp. 249-258 in Reproductive Behavior, W. Montagna and W.A. Sadler (eds.), Plenum Publishing Corp., New York.

Phoenix, C.H., Slob, A.K. & Goy, R.W. (1973) Effects of castration and replacement therapy on the sexual behavior of adult male rhesuses. J. comp. & physiol. Psychol. 84: 472-481.

Pianka, E.R. & Parker, W.S. (1975) Age-specific reproductive tactics. Amer. Nat. 109: 453-464.

Plooij, F.X. (in prep.) Early behavioural development of chimpanzee infants. PhD. thesis, University of Groningen.

Poirier, F.E. (1970) The Nilgiri langur (Presbytis johnii) of South India. Pp. 254-383 in Primate Behavior. Developments in field and laboratory research. L. Rosenblum (ed.), Academic Press, New York.

Pollock, J.I. (1975) Social behaviour and ecology of *Indri indri*. PhD. thesis, University of London.

Pomeroy, W.D. (1972) *Dr Kinsey and the Institute for Sex Research*, Signet, New York.

Popp, J.L. & DeVore, I. (in press) Aggressive competition and social dominance theory. In *Behavior of Great Apes, perspectives on human evolution 4*, D.A. Hamburg & J. Goodall (eds), Holt, Rinehart & Winston, New York.

Pusey, A. (in press) Inter-community transfer of Chimpanzees in Gombe National Park. In *The Behavior of Great Apes, Perspectives on Human Evolution 4*, D.A. Hamburg & J Goodall (eds.), Holt, Rinehart & Winston, New York.

Ransom, T.W. (1971) Ecology and social behavior of baboons in the Gombe Stream National Park. PhD. dissertation, University of California, Berkeley.

Resko, J.A. & Phoenix, C.H. (1972) Sexual behavior and testosterone concentrations in the plasma of rhesus monkey before and after castration. *Endocrinology 91*: 499-503.

Reyes, F.I., Winter, J.S.D., Faiman, C. & Hobson, W.C. (1975) Serial serum levels of gonadotrophins, prolactin and sex steroids in the non-pregnant and pregnant chimpanzee. *Endocrinology 96*: 1447-1455.

Reynolds, V. (1963) An outline of the behaviour and social organisation of forest-living chimpanzees. *Folia primatol 1*: 95-102.

Riesen, A.H. (1971) Nissen's observations on the development of sexual behavior in captive-born, nursery-reared chimpanzees. Pp. 1-18, in *The Chimpanzee*, vol *4*, Karger, Basel.

Riss, D.C. (in press.) Figan: The rise of an alpha male.

Rose, R.M., Kreuz, L.E., Holaday, J.W., Sulak, K.J. & Johnson, C.E. (1972) Diurnal variation of plasma testosterone and cortisol. *J. Endocr. 54*: 177-178.

Rowell, T.E. (1967) Female reproductive cycles and the behaviour of baboons and rhesus macaques. Pp. 15-32 in *Social communication in primates*, S.A. Altmann (ed.), *Univ. of Chicago Press*, Chicago, Illinois.

Rowell, T.E. (1970) Reproductive cycles of two Cercopithecus monkeys. *J. Reprod. Fert. 22*: 321-338.

Rowell, T.E. (1972) Female reproduction cycles and social behavior in primates. *Adv. in the Study of Behav. 4*: 69-105.

Rudran, R. (1973) Adult male replacemnt in one-male troops of purple-faced langurs (*Presbytis senex senex*) and its effect on population structure. *Folia primatol. 19*: 166-192.

Saayman, G.S. (1970) The menstrual cycle and sexual behaviour in a troop of free ranging chacma baboons. Folia primatol. 12: 81-110.

Sade, D.S. (1968) Inhibition of son-mother mating among free ranging rhesus monkeys. Sci. Psychoanal. 12: 18-38.

Schull, W.J. & Neel, J.V. (1965) The Effects of Inbreeding on Japanese Children. Harper & Row, New York.

Selander, R.K. (1972) Sexual selection and dimorphism in birds. Pp. 180-230, in Sexual selection and the descent of man, B. Campbell (ed.), Aldine Publ. Company, Chicago.

Sharman, A. (1951) Ovulation after pregnancy. Fertil. Steril. 2: 371-393.

Shepher, J. (1971) Mate selection among second generation Kibbutz adolescents and adults: Incest avoidance and negative imprinting. Archives sex. Behav. 1: 293-307.

Siegel, Sl (1956) Nonparametric Statistics for the behavioral Sciences. McGraw-Hill, New York.

Simpson, M.J.A. (1973) The social grooming of male chimpanzees. Pp. 411-506, in Comparative Ecology and Behaviour of Primates, R.P. Michael and J.H. Crook (eds.), Academic Press, London.

Spies, H.G., Mahoney, C.J., Norman, R.L., Clifton, D.K. & Resko, J.A. (1974) Evidence for a diurnal rhythm in ovarian steroid secretion in the rhesus monkey. J. of Clinical Endocrinology and Metabolism 39: 347-351.

Smith, A.H., Butler, T.M. & Pace, N. (1975) Weight growth of colony-reared chimpanzees. Folia primatol. 24: 29-59.

Stephenson, G.R. (1973) Testing for group-specific communication patterns in Japanese macaques. Pp. 51-75 in Precultural Primate Behavior, E. Menzel (ed.), Karger, Basel.

Stix, R.K. (1940) Factors underlying individual and group differences in uncontrolled fertility. Millbank Memorial Fund Quarterly 18: 239-256.

Struhsaker, T.T. (1967) Behavior of vervet monkeys (Cercopithecus aethiops). University of California Publications in Zoology 82: 1-64.

Sugiyama, Y. (1965) Home range, mating season, male group and inter-troop relations in Hanuman langurs (Presbytis entellus). Primates 6: 73-106.

Sugiyama, Y. (1973) The social structure of wild chimpanzees: A review of field studies. Pp. 375-410, in Comparative ecology and behaviour of primates, R.P. Michael & J.H. Crook (eds.), Academic Press, London.

Suzuki, A. (1971) Canivority and cannibalism observed among forest-living chimpanzees. J. Anthrop. Soc. Nippon 79: 30-48.

Teleki, G., Hunt, E.E. & Pfifferling, J.H. (in prep.) Demographic observations (1963-1973) on the chimpanzees of Gombe National Park, Tanzania.

Temerlin, M.K. (1975) Lucy: Growing up Human, Science and Behavior Books, Inc. Palo Alto, California.

Tenaza, R.R. (1975) Territory and monogamy among Kloss' gibbons (Hylobates klossii) in Siberut Island, Indonesia. Folia primatol. 24: 60-80.

Thomas, D.K. (1961) The Gombe Stream Game Reserve. Tanganyika Notes Rec. 56: 35-39.

Tinklepaugh, O.L. (1933) Sex cycles and other cyclic phenomena in a chimpanzee during adolescence, maturity, and pregnancy. J. Morphol. 54: 521-547.

Tokuda, K. (1961) A study on the sexual behavior in the Japanese monkey troop. Primates 3(2): 1-40.

Trivers, R.L. (1972) Parental investment and sexual selection. Pp. 136-179, in Sexual selection and the descent of man, B. Campbell (ed.), Aldine, Chicago.

Trivers, R.L. (1974) Parent-offspring conflict. Amer. Zool. 14: 249-264.

Tutin, C.E.G. (1975) Exceptions to promiscuity in a feral chimpanzee community. Pp. 445-449, in Contemporary Primatology, S. Kondo, M. Kawai & A Ehara (eds.), Karger, Basel.

Tutin, C.E.G. & McGrew, W.C. (1973) Chimpanzee copulatory behaviour. Folia primatol. 19: 237-256.

Tutin, C.E.G. & McGrew, W.C. (1973) Sexual behaviour of group-living adolescent chimpanzees. Amer. J. phys. Anthrop. 38: 195-199.

Wallace, A.R. (1889) Darwinism: An Exposition of the Theory of Natural Selection with Some of its Applications. MacMillan & Co, London.

Williams, G.C. (1966) Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought. Princeton Univ. Press, Princeton.

Wilson, E.O. (1975) Sociobiology, The New Synthesis, The Belknap Press of Harvard University Press, Cambridge, Mass.

Winget, C.M., Rahlmann, D.F. & Pace, N. (1969) Phase relationship between circadian rhythms and photoperiodism in the monkey. Pp. 64-74 in Circadian Rhythms in Nonhuman Primates, E.H. Rohles (ed.), Bibliotheca primatol. 9.

Wolf, A.P. (1968) Adopt a daughter-in-law, marry a sister: A Chinese solution to the problem of the incest taboo. Amer. Anthrop. 70: 864-874.

Wolf, A.P. (1970) Childhood association and sexual attraction: A further test of the Westermarck hypothesis. Amer. Anthropol. 72: 503-515.

Wrangham, R.W. (1974) Artificial feeding of chimpanzees and baboons in their natural habitat. Anim. Behav. 22: 83-93.

Wrangham, R.W. (1975) Behavioural ecology of chimpanzees in Gombe National Park, Tanzania. PhD. thesis, University of Cambridge.

Yerkes, R.M. & Elder, J.H. (1936) Oestrus, receptivity and mating in chimpanzees. Comp. Psychol. Monogr. 13(5): 1-39.

Young, W.C. & Yerkes, R.M. (1943) Factors influencing the reproductive cycle in the chimpanzee: the period of adolescent sterility and related problems. Endocrinology 33: 121-154.

Zahavi, A. (1975) Mate selection - A selection for a handicap. J. theor. Biol. 53: 205-214.

Zuckerman, S. & Fulton, J.F. (1934) The menstrual cycle of the primates. VII. The sexual skin of the chimpanzee. J. Anat., Lond. 69: 38-46.

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Sexual Behaviour of Group-living Adolescent Chimpanzees

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ABSTRACT This paper reports a study of the heterosexual behavior of three male and four female captive adolescent chimpanzees living a semi-natural life style in a large field enclosure. Observations made with binoculars from an overhead deck were balanced over the daylight hours and the seven weekdays. We recorded 213 copulations in 741.25 hours of observation between February 14 and July 21, 1972. Analysis of the observations suggests that group-living chimpanzees in a large field enclosure behave more like free-living chimpanzees than like other captive chimpanzees paired in small cages. In this group, copulations were non-randomly distributed throughout the day, a finding in agreement with results on wild-living chimpanzees but not previously reported for captive chimpanzees. In this group, moreover, copulations were highly concentrated within each female's period of maximum tumescence, as are those of free-living chimpanzees; and individual differences in sexual attractiveness among females were apparently based on a maturational threshold of swelling size, a phenomenon that has also been reported for wild chimpanzees.

This paper reports a study of the heterosexual behaviour of captive adolescent chimpanzees living a semi-natural life style. The most complete previous reports of chimpanzee sexual behaviour were based on captive animals housed in pairs in small cages (e.g., Yerkes and Elder, '36) or, more recently, on wild populations (van Lawick-Goodall, '68). Previous studies of chimpanzee sex in group situations in captivity are largely non-quantitative and generally descriptive (e.g., Kollar et al., '68). By studying in detail group-living chimpanzees in a large field enclosure, we hoped to achieve an ideal compromise between the types of studies cited. We hoped to remove the artificial and sometimes distorting limitations of the bare cell and limited companionship situation, while at the same time retaining the advantages of uninterrupted, unimpeded observation not available in the wild. Results of a detailed ethological study of the elements of sexual interaction and their frequencies and sequences will be presented elsewhere.

MATERIAL AND METHOD

Three male and four female wild-born chimpanzees (*Pan troglodytes*) at the Delta Regional Primate Research Center, Covington, Louisiana, participated in the study. Five individuals formed the basis for the findings presented here: the male *Shadow* (age 9), and the four females *Gigi* (10), *Polly* (9), *Belle* (8) and *Bido* (8). A female infant was born to Gigi in the enclosure on May 1, 1972, and is being reared in the group. The chimpanzees arrived at Delta when between one to four years of age and have lived in a group or as subgroups since then.

From September, 1969, to September, 1972, the chimpanzees were housed together (except for temporary absences) in a 30 x 120 m outdoor enclosure. It was open overhead, had walls 5 m high of sheet metal above and chainlink fence below, and was surrounded by pine forest. The enclosure was carpeted with natural vegetation and contained three elevated platforms, numerous upright and fallen poles and tree trunks, and a plentiful supply of small movable objects. Fresh woody foliage for roughage and nest building was supplied weekly. By captive standards it was a spacious and stimulating environment.

For one hour daily the chimpanzees were locked into a smaller, closed cage adjacent to the enclosure while cleaning and maintenance took place. Otherwise they were left to their own devices to move and interact freely. Thus, all our observations were made on a group living in continuous mutual access, minimally interfered with by man. Observations were made from an overhead deck using 7 x 35 binoculars. These were balanced over the daylight hours (from 06.30–18.30) and the seven weekdays.

RESULTS

We recorded 213 chimpanzee copulations in 741.25 hours of observation between February 14 and July 21, 1972. A copulation was defined as an interaction between a male and a female which included at least one intromission. Some copulations included multiple intromissions; to be classified as separate copulations, two intromissions had to be separated in time by more than five minutes of non-interaction between the two individuals.

Table 1 gives the distribution of the copulations over the four females listed at the left in order of sexual development. (Shadow was the male in all but one of the copulations). Up to four cycles of sexual swelling for each female are given in chronological order across the top (I-IV). Day 1 of a cycle was the day when the first tumescence occurred after a period of no swelling. The total number of copulations divided by the total hours of observation gives the overall rate of copulations for each female. Individual differences are obvious. Even discounting the partial inflation of Gigi's total, the difference between Gigi's overall frequency and Bido's is many-fold; Polly and Belle are equally intermediate.

Although we did not know it at the time, Gigi was pregnant when observations commenced. Consequently, we only saw most of her last full cycle and after that one isolated copulation before she ceased swelling altogether. Her copulation rate during that cycle was the highest we observed and more than double that of any other. A gap of ten days ensued during which Gigi remained unswollen before the last odd copulation. She gave birth to her first infant 41 days later. The assumption that it was a full-term infant means that Gigi engaged in coitus during more than 80% of the pregnancy. Some pregnant chimpanzees in the wild show cyclic sexual swellings and periods of receptivity up to 75% of the course of pregnancy (van Lawick-Goodall, '68: 217).

We observed Polly's sexual behaviour through four complete sexual cycles. Three of them (I, III, IV) showed a fairly regular rate of copulation, but in II it was low, possibly because it coincided with Belle's first adult swelling, which provided Shadow with a novel sexual alternative. Preliminary results from Cycle V indicate that her frequency is increasing and will

TABLE 1

Distribution of copulations of four female adolescent chimpanzees through up to four cycles of sexual swelling. Cycle begins on the first day of swelling in each new cycle

	Cycle				Total copulations recorded	Total hours observed	Total frequency
	I	II	III	IV			
Gigi	30 [1] (0.4)	1			31	68.5	0.5 [2]
Polly	18 (0.2)	7 (0.04)	10 (0.1)	38 (0.1)	73	658.75	0.1
Belle	1 (0.01)	20 (0.1)	31 (0.2)	46 (0.1)	98	919.5	0.1
Bido	0	0	11 (0.1)	0	11	520.0	0.02

[1] Number of copulations
(Frequency/observation hour).

[2] Recording of cycle began in mid-tumescence, so frequency is an over-estimate.

likely soon approach that of the experienced Gigi. Although Belle had shown cycles of sexual swelling for over four months prior to the study, she was first observed to copulate during her Cycle I. It was an isolated copulation, but 27 days later in Cycle II, her participation increased to its current frequency. The raw totals have increased with each cycle, so that Belle's transition from virginity to experience has been very rapid. Like Polly and Belle, Bido was observed through four complete sexual cycles. However, she was seen to copulate during only one of these (III). Her rate during that cycle (0.1/hour) resembled those of the more experienced Polly and Belle, although her initial copulation in this cycle was probably also her first one. The absence of copulations during Bido's other cycles considerably depressed her overall frequency relative to the other females. (One additional copulation occurred between Bido and Shadow, during her Cycle V).

The rise and fall of each female's sex skin is shown graphically in figure 1. Initially we only interpolated between significant turning points, such as when the swelling reached a plateau or when swelling decreased to a minimal flatness for several days running. Thus, the early results on the left side of the figure were schematic and rather crude. After two months, we felt confident enough to substitute the more refined interval system of fractional assessment: zero, one-fourth, one-half, three-fourths, one. This resulted in more accurate but less smooth vicissitudes in the right half of the figure. The four records coincide, so that instances in which two animals were simultaneously maximally tumescent can be derived.

The females' different stages of sexual development are indicated by their cycling patterns in figure 1. In her only cycle, the experienced Gigi showed both the typical swelling pattern and time course for the mature female chimpanzee. Polly also

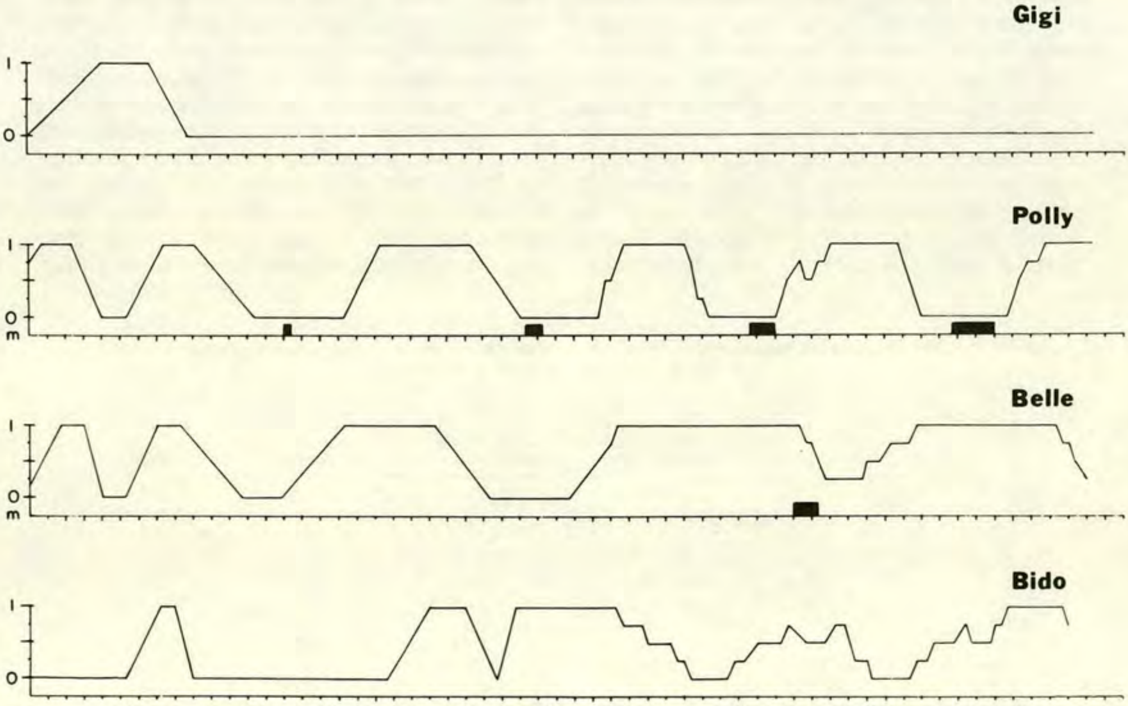

Fig. 1 Sexual swelling cycles of the four chimpanzee females. Ordinate gives the standard gradient of sexual swelling from "0" (no swelling) to "1" (maximum tumescence). Abscissa measures time in three-day intervals chronologically from left to right. The five instances of observed menstruation are indicated by solid horizontal bars beneath each group.

showed the typical pattern, although there was still some variability in the lengths of her cycles (29–42 days). Physically, both Gigi's and Polly's swellings resembled those described for adult female chimpanzees in size and shape. Polly's periods of menstrual bleeding increased in length with each swelling cycle. Belle's pattern of cycling was more irregular: two short cycles (24 days) followed by three long ones (as long as 48 days). Her only observed menstrual bleeding (probably her menarche) occurred during detumescence of one of these prolonged cycles, and her swelling never disappeared completely between that cycle and the next. Menstrual bleeding while at least partially swollen is rare but has been recorded previously (Graham, '70: 187). Belle's swelling size blossomed over the observation period from small swellings restricted to the vulvar lips (typically adolescent) to full swellings of the entire perineum. At the younger end of the spectrum, Bido's sexual cycling was that of a young adolescent. Her cycles showed the greatest variability in length (18–43 days) and the greatest irregularity from day-to-day. It was not always easy to delineate her swelling into cycles, e.g., the one-day drop to no swelling between Cycles II and III. Bido has not been seen to menstruate, and her swellings remain adolescent in size and shape. It should be noted that the only cycles in which she copulated were those during part of which both Polly and Belle were non-swollen. At other times her maximum tumescence overlapped with one or both of them, but during parts of her Cycles III and V she represented Shadow's only heterosexual outlet.

Table 2 gives the distribution of the observed copulations for the four phases of the females' swelling cycles. For each individual, copulations were markedly concentrated in maximum tumescence. Copulations occurred in the three other phases of the cycle but less frequently. Belle restricted her copulations almost entirely (96%) to maximum tumescence. Gigi and Polly exhibited more copulations outside this phase: 39% and 26% respectively. Their copulations occurred with approximately equal frequency during tumescence and detumescence but only rarely during the no swelling phase. This dispersion may have been related to their greater sexual experience and cooperativeness. Also, Belle may have been relatively less attractive to Shadow when not maximally swollen since her swellings were fairly small. Bido's position in this ranking was intermediate (82% of copulations during maximum tumescence), but she only participated in 11 copulations overall. The concentration of copulations during maximum tumescence agrees with both van Lawick-Goodall's ('68: 216) findings on free-living chimpanzees and Yerkes and Elder's ('36: 22) on captive ones. However, our high overall concentration during maximum tumescence (83%) and

TABLE 2

Distribution of copulations of four adolescent female chimpanzees through four phases of the sexual swelling cycle

	Phases				
	Tumescence	Maximum tumescence	Detumescence	No-swelling	Total
Gigi	2[1] (0.2)[2]	19 (0.6)	9 (0.3)	1 [2]	31 (0.5)[2]
Polly	6 (0.1)	54 (0.3)	11 (0.1)	2 (0.01)	73 (0.1)
Belle	3 (0.02)	94 (0.2)	0 (0.0)	1 (0.01)	98 (0.1)
Bido	2 (0.02)	9 (0.1)	0 (0.0)	0 (0.0)	11 (0.02)
Total	13 (0.03)[2]	176 (0.25)	20 (0.05)	4 (0.05)	213 (0.1)[2]

[1] Number of copulations
(Frequency/observation hour).

[2] Observations of Gigi began *during* tumescence, thus the frequency in this phase is exaggerated. Due to pregnancy Gigi showed no further swelling, and thus a no-swelling phase could not be delimited in this cycle. These factors combine to exaggerate Gigi's overall frequency.

TABLE 3

Daily periodicity in occurrence of copulations by four female adolescent chimpanzees. Chi-square one-sample test, df = *1*

	Occurrence of copulations				
	Morning	Afternoon	Total	χ^2	p
Gigi	23[1] (17)	8 (14)	31	4.69	< 0.05
Polly	43 (41)	30 (32)	73	0.23	< 0.70
Belle	65 (55)	33 (43)	98	4.18	< 0.05
Bido	8 (6)	3 (5)	11	1.47	< 0.30
Total	139 (119)	74 (94)	213	7.62	< 0.01

[1] Observed. (Expected)

virtual absence during no swelling (2%) resembled the former's findings (87% and 1%) more than the latter's (60% and 9%). The latter divergence occurred probably because Yerkes's chimpanzees were housed in pairs in small cages. Thus, the male had no alternative sexual partners available, and the female had insufficient space to escape his advances. The wild-living animals and ours faced neither of these abnormal restrictions.

Table 3 presents a preliminary analysis of daily periodicity in copulatory behaviour. All four females copulated more frequently than expected by chance in the mornings rather than the afternoons. This reached statistical significance for Gigi and Belle and for the pooled group. Van Lawick-Goodall ('68: 219) found similar periodicity in free-living chimpanzees in Tanzania: over two-thirds of copulations over a two and one half year period occurred in the mornings.

DISCUSSION

The results suggest that group-living chimpanzees in a large field enclosure behave more like free-living chimpanzees than like other captive chimpanzees paired in small cages. In this group copulations were non-randomly distributed through the day, a finding in agreement with results on wild-living chimpanzees. This observation has not previously been reported for captive chimpanzees, probably because short-term cohabitation schedules and rotating sex partners effectively prevent stable adjustments to long-term stimuli. In this group copulations were highly concentrated within each female's period of maximum tumescence, as are those of free-living chimpanzees. The similar but far less clear pattern reported for chimpanzee pairs in small cages probably reflects an opportunistic attitude forced upon the male by the limited access schedule to only one sexual partner. In this group, individual differences in sexual attractiveness existed among females, and these were apparently based on a maturational threshold of swelling size. A similar phenomenon has been reported for wild chimpanzees (van Lawick-Goodall, '68: 216).

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LITERATURE CITED

Graham, C. E. 1970 Reproductive physiology of the chimpanzee. In: The Chimpanzee. G. H. Bourne, ed. Karger, Basel, *3:* 183–220.

Kollar, E. J., W. C. Beckwith and R. B. Edgerton 1968 Sexual behaviour of the ARL colony chimpanzees. J. Nerv. Ment. Dis., *147:* 444–459.

van Lawick-Goodall, J. 1968 The behaviour of free-living chimpanzees in the Gombe Stream Reserve. Anim. Behav. Monogr., *1:* 161–311.

Yerkes, R. M., and J. H. Elder 1936 Oestrus, receptivity and mating in chimpanzee. Comp. Psychol. Monogr., *13:* 1–39.

Contemporary Primatology
Editors: S. KONDO, M. KAWAI and A. EHARA, Inuyama
Publishers: S. KARGER AG, Basel
SEPARATUM (Printed in Switzerland)

Contemporary Primatology
5th Int. Congr. Primat., Nagoya 1974, pp. 445–449 (Karger, Basel 1975)

Exceptions to Promiscuity in a Feral Chimpanzee Community

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Introduction

It has become clear in recent years that the sexual behaviour of feral chimpanzees is more complex than the freely promiscuous (i.e. random mating) system described by early field workers. VAN LAWICK-GOODALL [1968] and MCGINNIS [1973] have reported the formation of temporary consort relationships between pairs of chimpanzees in the Gombe National Park, Tanzania. This paper reports on data collected during 15 months of observation at the Gombe Stream Research Centre and describes consort behaviour and other examples of non-promiscuous sexual behaviour shown by a community of feral chimpanzees. It attempts to assess the relative frequencies of the different types of mating systems and to determine what factors are responsible for maintaining the observed proportions. The mating systems observed in the study community ranged from promiscuity at one extreme to the formation of temporary monogamous consortships at the other. Consistent dyadic differences in the frequencies of copulations, indicating partner preferences, and the exhibition of possessive behaviour in group situations fall between the two extremes.

Methods

The Kasakela community (the unit group whose range centres on the artificial feeding station, Camp) numbers 38 individuals of whom 8 females and 17 males contributed to the data. In addition, 3 females from other communities were observed during temporary visits to the Kasakela community. In the 15-month period from November, 1972, to February, 1974, 1,000 h of data was collected on females showing cycles of sexual swelling. Observations were tape-recorded in the field and subsequently transcribed onto checksheets and supplemented with written notes.

Results

Over 1,000 copulations were observed during the study. From these it was possible to compute copulation rates per hour for the 61 dyads who were observed in contact (i.e. simultaneously present in a group) for at least 5 h. Mean copulation rates for each male with all females, and vice versa, were also calculated [this data is presented elsewhere, TUTIN, in preparation]. Dyadic copulation rates ranged from 2.18 per contact hour to O, and the observed variability indicates that sexual partner preferences exist. An arbitary index of partner preference was arrived at by comparing dyadic copulation rates with the mean copulation rates for the male and female involved. A positive index was established if

$$\frac{\text{dyadic rate}}{\text{mean male rate}} \geq 2, \text{ or } \frac{\text{dyadic rate}}{\text{mean female rate}} \geq 2.$$

Similarly a negative index was established if

$$\frac{\text{dyadic rate}}{\text{mean male rate}} \leq 0.5, \text{ or } \frac{\text{dyadic rate}}{\text{mean female rate}} \leq 0.5.$$

A negative preference was also inferred if a dyad had 5 or more contact hours but was never seen to copulate.

Eight positive and 16 negative indices emerge. Only one male (of 14) and one female (of 6) show no indices of partner preference. This indicates that while promiscuous mating does occur in the chimpanzee it is the exception rather than the rule. It is not possible here to discuss in detail the diverse factors which contribute to partner preferences, but age, degree of relatedness and a number of personality factors all appear to be important.

The existence of partner preferences emerges during *post hoc* analysis, and as no characteristic behaviour patterns were involved they are not identified in the field at the time of observation. On the other hand, possessive behaviour was categorised during observation on the basis of behaviour shown by males to females. A male is described as acting possessively towards a female if he shows persistent special attention to her beyond the bounds of normal courtship. The male initiates possessive behaviour by maintaining close proximity to a female by either leading or following her over a minimum period of 2 h. In addition to maintaining proximity, a possessive male may interfere in copulations between 'his' female and other males.

During the 15 months of the study 30 incidents of possessive behaviour were observed. In 22 of these the female was maximally tumescent. Seven females were involved, 2 of whom were not resident members of the Kasakela community. Six of the 8 adult males showed possessive behaviour on at least one occasion as did the 2 adolescent males. In 11 of the 32 records of possessiveness (30 incidents, 2 of which involved joint possessiveness by 2 brothers) the male made no attempt to interfere in copulations between the female and other males. In 7 other cases no opportunity to interfere arose, either because no other males were encountered or because males made no attempt to mate the female as she was not tumescent. In 14 cases, effective interference was seen and in one of these cases the male also made ineffective attempts to interfere. An interfering male was always of higher dominance status than the male whose mating he terminated. In the one case where interference was ineffective the mating males were of higher dominance status than the possessive, interfering male.

There is nothing a possessive male can do to prevent more dominant males from copulating with 'his' female whilst in a group. Faced with this situation the possessive male may do one of 3 things: (1) remain inactive; (2) 'redirect' his interference by chasing or attacking an uninvolved lower ranking male; or (3) take the female away from the group and once alone avoid further contact with other chimpanzees, i.e. form a consort relationship. While consorting, the pair cease all loud vocalisations and if they hear other chimpanzees vocalising, the consort pair appear to take avoiding action. This avoidance often results in the pair's moving to the edge or even outside the normal range of the community. The maintenance of both possessive and consort behaviour depends on the female's cooperation. With female cooperation, a consortship will last for several days; possessive behaviour is more transient, only rarely persisting for more than a day.

13 consortships occurred during the study period, their lengths ranged from 3 h to 28 days with a mean length of 9.5 days. In the majority (9 of 12; 1 unknown) of cases the female was maximally tumescent for at least part of the consortship. Six of the 8 females who were regularly observable were involved in consorts. All consorting males were fully adult and 4 of the 8 adult males in the community were responsible for the 13 consorts.

Discussion

Both males and females are involved in possessive and consort behaviour at different frequencies. Parous females are involved at higher frequencies than are nulliparous females. Nulliparous females cycle for several years ($\bar{x} = 26$ months, $N = 4$) before conceiving whilst parous females usually conceive within a few months of resuming cycling. Thus, the probability of impregnating a parous female will be greater than that of impregnating a nullipare, in any one cycle. However, the immediate cause of parous females being involved in possessive incidents and consortships at higher frequencies than nullipares could be related to differential pheromonal cues or to a novelty effect of the parous females' relatively infrequent cycles. The frequencies of male involvement in possessive and consort behaviour do not correlate with age, dominance or the amount of agonistic behaviour males directed at females. However, the amount of time males spent grooming tumescent females in group situations does correlate positively with the frequencies of possessive and consort behaviour ($r_s = 0.63$, $N = 10$, $p < 0.05$). There is also a positive relationship between the amount of time males spent grooming females and their generousity to females in food-sharing situations [McGREW, personal commun.].

Both possessive and consort behaviour would seem to have obvious selective advantage to male chimpanzees in that they increase chances of impregnating females and hence passing on genes to the next generation. As previously mentioned, female cooperation is essential for the maintenance of these special relationships and they thus present an opportunity for females to exercise choice. If female choice is involved, it is of interest to note that the selection criteria appear to be social and caretaking abilities of the males and not their dominance status.

Consort relationships maximise the advantages outlined above as it is virtually impossible for even the dominant male to monopolise a female in a group situation. However, although in consort situations the male does not have the problem of other males, he does have to contend with the dangers encountered while avoiding other members of the community. Probably the greatest of these dangers is the increased risk of intercommunity encounters. Such encounters often involve extremely severe attacks and when a number of males of one community meet an isolated member of another community the attacks can result in fatal injuries [BYGOTT, 1972]. To minimise the possibility of both intra- and intercommunity encounters, the consort pair may be forced to move into an undesirable area where there may be less food available or where they are in relatively close proximity to humans. Despite these risks, consortships do occur and during the study period 3 females were impregnated whilst consorting.

Consort behaviour and other exceptions to promiscuity have rarely been reported for wild chimpanzees in other localities. REYNOLDS [1963] indicated that similar phenomena might exist in the Budongo Forest chimpanzee population, but he saw only 4 copulations. The possibility remains that cultural variations in sexual behaviour exist in different isolated populations of chimpanzees, such as the one in the Gombe National Park. STEPHENSON [1973] has described similar troop-to-troop differences in sexual behaviour of relic populations of Japanese macaques.

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References

BYGOTT, J. D.: Cannibalism among wild chimpanzees. Nature, Lond. *238:* 410–411 (1972).

LAWICK-GOODALL, J. VAN: The behaviour of free-living chimpanzees in the Gombe Stream Reserve. Anim. Behav. Monogr. *1:* 161–311 (1968).

MCGINNIS, P. R.: Patterns of sexual behaviour in a community of free-living chimpanzees; Ph.D. thesis, Cambridge (1973).

REYNOLDS, V.: An outline of the behaviour and social organisation of forest-living chimpanzees. Folia primat. *1:* 95–102 (1963).

STEPHENSON, G. R.: Testing for group-specific communication patterns in Japanese macaques; in MENZEL Precultural primate behavior (Karger, Basel 1973).

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Folia primat. *19:* 237–256 (1973)

Chimpanzee Copulatory Behaviour

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Key Words
Pan troglodytes
Sexual behaviour
Adolescence
Ontogeny of behaviour

Abstract. Observations were made of a group of adolescent chimpanzees *(Pan troglodytes)* living in one-acre field enclosure. In 1,200 h of observation, we observed 341 copulations involving six individuals. 34 elements of copulatory behaviour were described and recorded, including facial expressions, vocalisations, gestures, postures and locomotion. Frequencies, combinations and sequences of the elements were extracted in analysis. The results emphasise individual differences and the rapid ontogeny of copulatory behaviour elements.

Introduction

This paper reports an ethological study of the copulatory behaviour of adolescent chimpanzees living a semi-natural life style. Previous reports of chimpanzee sexual behaviour were based on captive animals housed in pairs in small cages [YERKES and ELDER, 1936; RIESEN, 1971) or, more recently, on wild populations [VAN LAWICK-GOODALL, 1968]. A few exceptions to these extremes exist in which chimpanzee sexual behaviour was studied in group situations in captivity [KOLLAR *et al.*, 1968; ROGERS and DAVENPORT, 1969], but these papers include only general descriptions of the behaviour. By studying group-living chimpanzees in a large field enclosure, we hoped to achieve an ideal compromise between the previously cited types of studies. We hoped to remove the artificial and sometimes distorting limitations of the bare cell and limited companionship situation, while at the same time retaining the advantages of uninterrupted, unimpeded observation not available in the wild.

The *development* of sexual behaviour in individual chimpanzees of both sexes has been previously reported only anecdotally [BINGHAM, 1928] or briefly [VAN LAWICK-GOODALL, 1968]. Yet sexual behaviour in higher primates is an extremely sensitive and complicated phenomenon, and knowledge of its ontogeny is crucial for its full understanding. Adolescence is a time of rapid physical and behavioural growth with great individual variation, so a careful longitudinal approach is preferable to a cross-sectional one.

Material and Method

Three male and four female wild-born chimpanzees *(Pan troglodytes)* at the Delta Regional Primate Research Center, Covington, La., participated in this study. The oldest male, age 11, was in the group for only 24 days during the observation period and was seen to copulate once. The youngest male, age 7, showed no interest in social sex throughout the study, although his behaviour was otherwise typical. The remaining male, *Shadow* (age 9), and the four females, *Gigi* (10), *Polly* (9), *Belle* (8), *Bido* (8), formed the basis for the findings given here. A female infant was born in the enclosure on May 1, 1972, to *Gigi*, and is being reared in the group. The chimpanzees arrived at Delta when between 1–4 years of age and have lived in a group or as subgroups since then.

From September, 1969, to September, 1972, the chimpanzees were housed together (except for temporary absences) in a 30 × 120-m outdoor enclosure. It was open overhead, had walls 5-m high of sheet metal above chain-link fence, and was surrounded by pine forest. The enclosure was carpeted with natural vegetation and contained three elevated platforms, numerous upright and fallen poles and tree trunks, and many small moveable objects. Fresh woody foliage for roughage and nest building was supplied weekly. By captive standards, it was a spacious and stimulating environment.

For one hour daily the chimpanzees were locked into a smaller closed cage adjacent to the enclosure while cleaning and maintenance took place. Otherwise they were left to their own devices to move and interact freely. All findings are based on a group living in continuous mutual access, minimally interfered with by man. Observations were made from an overhead deck using 7 × 35 binoculars and a 35-mm camera with a 300-mm telephoto lens.

Initially we took longhand descriptive notes on the chimpanzees' behaviour. Later, we devised a checksheet of behavioural elements from which frequencies, combinations, and sequences of these elements could be extracted. Observations were balanced over the daylight hours (from 06.30 to 18.30) and the seven weekdays.

Results

We recorded 341 chimpanzee copulations in 1,200 h of observation between February 14 and September 6, 1972. A copulation was defined as an interaction between a male and a female which included at least one intromission. Some copulations included multiple intromissions, and to be classified as separate copulations, two intromissions had to be separated by more than five minutes of non-interaction between the two individuals.

Table I gives the distribution of the copulations over the four females, listed at the left in descending order of sexual development. (*Shadow* was the male in all but one of the copulations.) Up to six cycles of sexual swelling for each female are given chronologically across the top (I–VI). Individual differences in the rate of copulations are apparent: the greater the sexual experience, the higher the copulation rate.

Gigi was in her sixth month of pregnancy when observations commenced. We saw most of her last full cycle before she ceased swelling altogether. We observed *Polly's* sexual behaviour through six cycles. Her copulation rate dropped during cycle II, possibly because this cycle coincided with *Belle's* first adult swelling, which provided *Shadow* with a novel sexual alternative. Although *Belle* had shown cycles of sexual swelling for at least four months prior to the study, she was first observed to copulate during her cycle I. It was an isolated copulation, but 27 days later in cycle II, she began to copulate regularly. The low rate in *Belle's* cycle V is probably partially due

Table I. Distribution of copulations of four adolescent female chimpanzees through up to six cycles of sexual swelling. Cycle begins on the first day of swelling in each new cycle

	Cycle						Total copulations recorded	Total hours observed	Total frequency
	I	II	III	IV	V	VI			
Gigi	30[1]	1					31	68.5	0.5[2]
	(0.4)								
Polly	18	7	10	38	66	44	183	1,198	0.15
	(0.2)	(0.04)	(0.1)	(0.1)	(0.2)	(0.2)			
Belle	1	20	31	46	17[3]		115	1,230	0.10
	(0.01)	(0.1)	(0.2)	(0.1)	(0.06)				
Bido	0	0	11	0	1		12	1,000	0.01
			(0.1)		(0.002)				

[1] Number of copulations (frequency/observation hour).

[2] Recording of cycle began in mid-tumescence, so frequency is an over-estimate.

[3] Animals anaesthetised during maximum tumescence of this cycle, no observations on one day and effects probably lasted 2–3 days.

to the animals being anaesthetised for a medical check-up. This occurred during her maximum tumescence; one day's observation was lost and several days elapsed before the chimpanzees' behaviour returned completely to normal. *Bido* only copulated in two of the five cycles observed. She had never been seen to copulate prior to cycle III, and the absence of copulations in three of her cycles considerably depressed her total frequency relative to the other females.

The rise and fall of the sex skins is given graphically in figure 1. Initially, we interpolated between significant turning points, such as when swelling reached a plateau, or when swelling decreased to a minimum flatness for several days consecutively. Thus, the left side of the figure is schematic and rather crude. Later, we substituted the more refined interval system of fractional assessment: $0, {}^{1}/_{4}, {}^{1}/_{2}, {}^{3}/_{4}, 1$. This resulted in the more accurate but less smooth vicissitudes in the right half of the figure. The four records coincide, so that occasions on which animals were simultaneously maximally tumescent can be derived.

The females' cycling patterns indicate their differing stages of sexual development. The normal sexual cycle of a mature female chimpanzee lasts 37 days [YERKES and ELDER, 1936] and in her only cycle, the experienced *Gigi* showed the typical swelling pattern and time course. *Polly's* swellings

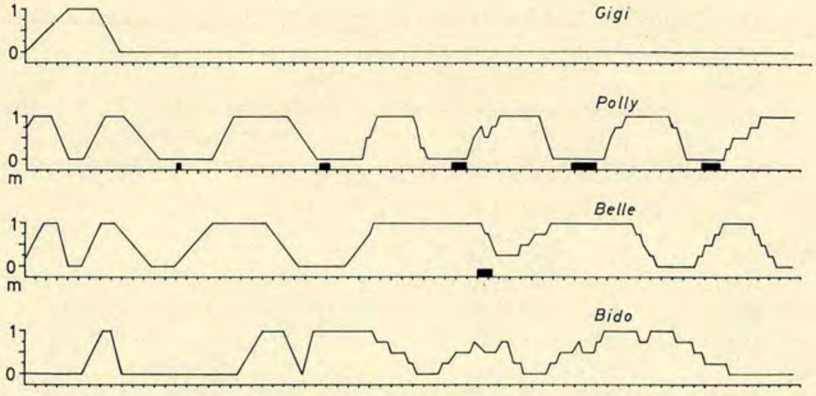


Fig. 1. Sexual swelling cycles of the four chimpanzee females. Ordinate gives the standard gradient of sexual swelling from 0 (no swelling) to 1 (maximum tumescence). Abscissa measures time in three-day intervals chronologically from left to right. The six instances of observed menstruation are indicated by solid horizontal bars beneath each graph.

were similar but varied more in length (29–42 days). Menstrual bleeding occurred regularly between each of *Polly's* cycles. *Belle's* cycles varied irregularly in length, her cycle V being the only one typical of the mature chimpanzee female. We observed menstrual bleeding only once (almost certainly her menarche), during detumescence of cycle III. *Belle's* swelling size blossomed dramatically over the observation period from small swellings restricted to the vulvar lips (typically adolescent) to full swellings of the entire perineum. At the younger end of the spectrum, *Bido's* sexual cycling typified young adolescence: small swellings showing irregular fluctuations from day to day. We never saw *Bido* menstruate. She only copulated when both *Polly* and *Belle* were non-swollen, i.e. when she was the only heterosexual outlet available to *Shadow*. All four females showed a high concentration of copulations during maximum tumescence and tended to copulate more frequently in the mornings than in the afternoons [TUTIN and MCGREW, 1973].

Table II. Behavioural elements exhibited in copulatory behaviour of adolescent chimpanzees

	Male	Female	Either
Pre-intromission	bipedal display 'branch' shake gaze glance hair erect lip-flip male invite manhandle nest build penis erect penis manipulate quadrupedal bounce rock sex display stick wave	female posture present	advance approach
Post-intromission	leanback mount number of thrusts	grin hit out squeal	end intromission
Either	bumprump inspect male 'frustration'		follow groom leave play self-inspect

Table III. Definitions of copulatory behaviour elements

Advance: Individual moves toward another but stops outside of arm's reach.

Approach: Individual moves toward another and stops within arm's reach.

Bipedal display: Male stands, walks or runs bipedally. Usually incorporates slight hair erection and side to side swaying.

'*Branch*' *shake:* Male repeatedly jerks a tree branch (or substitute) back and forth.

Bumprump: Rubbing of the perineal areas of two individuals. The active participant (male or female) backs toward the passive, usually prone recipient (always a somewhat swollen female), crouches quadrupedally, then repeatedly moves its perineum vertically against the other's, making contact on both upward and downward motions.

End intromission: Animal responsible for male's penis leaving female's vagina.

Female posture: Female may adopt the following postures during copulation:

- flat prone: lies on venter, arms usually at side of body, legs either straight back or pulled forward and flexed at knee, grasshopper-style;
- flat supine: lies on back, legs flexed at knee and jack-knifed against body;
- crouch: 'normal' copulatory posture. Body supported on all four partially flexed limbs;
- upright quadrupedal: body supported on all four extended limbs;
- side: body supported on either side, leg and arm positions variable;
- kneel: body primarily supported on knees and shins with arms partially flexed.

Follow: Individual orients locomotion and trails behind another moving animal.

Gaze: Male stares at female for two or more seconds.

Glance: Male looks at female for less than two seconds.

Grin: Individual exhibits full closed grin face: mouth corners retracted, upper and lower teeth together and exposed.

Groom: Manipulatory movements of fingers and/or lips directed to body surface (except for perineum) of self or others, characterised by:

(a) focus of attention on spot being groomed;

(b) often accompanying vocalisations, for example lip-smacking, teeth-clapping, or spluttering;

(c) transfer between site of grooming and mouth;

(d) relative immobility and passivity of groomee.

Hair erect: Male's hair is abducted from his skin.

Hit out: Female extends arm horizontally toward male in sudden movement, sometimes striking him with forearm or hand.

Inspect: Face and/or hands are brought close (usually within 20 cm) or into contact with perineum of self or others. The female's vaginal opening is socially inspected. The inspecting individual parts the lips of the vagina and uses fingers, mouth or nose to poke, lick or sniff. The self inspecting individual inserts a finger (female) or dabs with a finger (male).

Intromission: Penis enters vaginal canal.

Leanback: Male squats behind female during intromission with both hands on the ground and leans back slightly.

Lipflip: Male manually everts his lower lip and hooks it below his chin.

Leave: Individual moves beyond arm's reach of another.

Table III. (continued)

Male 'frustration': Combination of elements: full open grin, whimper, hand extended toward female without touching her.
Male invite: Male sits with legs partially flexed and spread apart, feet close together, revealing his erect penis.
Manhandle: Male pulls, pushes, or otherwise manipulates female into a posture permitting copulation.
Mount: Part of the mounter's ventral surface contacts part of the other's back, and mounter appears to rest weight on the other.
Nest build: Animal manipulates and interlaces sticks, grass, twigs, etc. in area next to and around his body.
Number of thrusts: Number of rhythmical back and forth pelvic movements.
Penis erect: Male's penis is fully distended.
Penis manipulate: Male briefly fingers or strokes his erect penis without looking at it.
Play: Vigourous non-agonistic interaction in which two or more participants exhibit a similar set of behaviour patterns [VAN HOOFF, 1971; VAN LAWICK-GOODALL, 1968; LOIZOS, 1969].
Present: Female crouches in front of male with her swelling oriented toward him.
Quadrupedal bounce: Male stands with rounded back and head lowered, repeatedly pushes his body up and down by flexing and extending limbs but not leaving ground.
Rock: Male oscillates torso forward and backward from hips in slow, rhythmic motion.
Sex display: Male stands bipedally with penis erect and hair down, often with flip-lip. He raised one or both arms vertically overhead while leaning slightly backward, thus maximally exposing his erect penis.
Squeal: Clear, high-pitched sound of variable length accompanying grin.
Stick wave: Male swings stick or branch to and from in low, looping horizontal motions while standing bipedally.

Table II lists the behavioural elements recorded in the study. They are divided by *sex* (whether exhibited by male or female or either) and *time* (whether before or after intromission or either). Table III lists brief definitions of the categories. Many of the definitions correspond to those in the unpublished glossaries of VAN LAWICK-GOODALL and MCGINNIS. Figures 2–8 illustrate selected elements.

The distribution of the elements of copulatory behaviour by time and sex in table II indicates the nature of the interaction. Almost half the patterns are performed by the male before intromission and constitute a complex of courtship behaviour. The female performs few exclusively sex-specific behaviours at any point in the interaction. The elements in table II exhibited by either sex are mostly general behaviours related to the participants' spacing or incorporated secondarily from other types of behaviour.

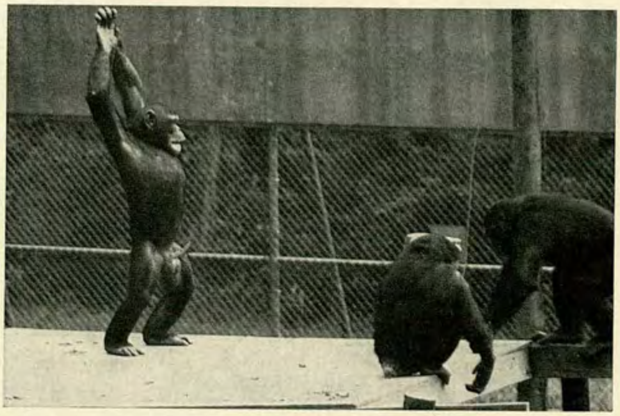


Fig. 2. Shadow gives sex display (note erect penis and lipflip to females *Belle* (left) and *Bido* (right).

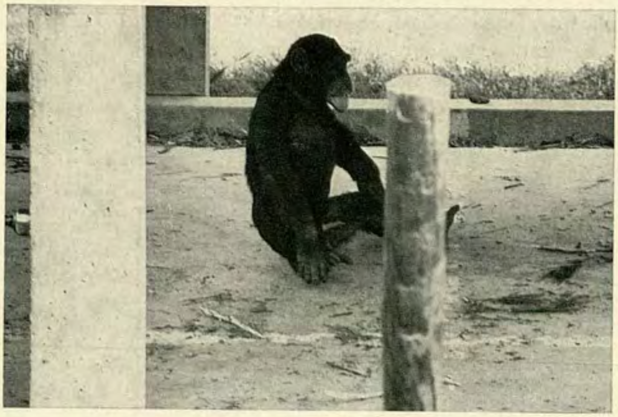


Fig. 3. Shadow sits in male invite posture with erect penis and lipflip.

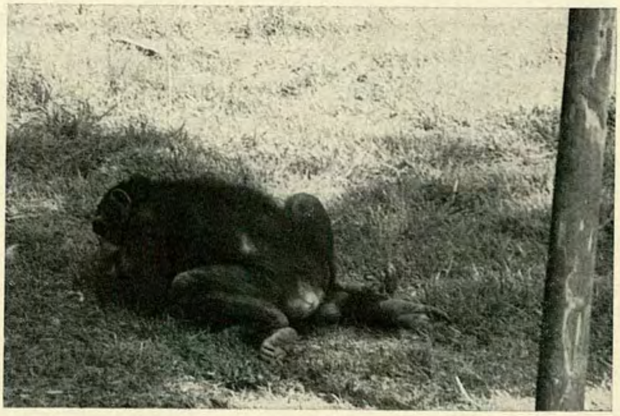
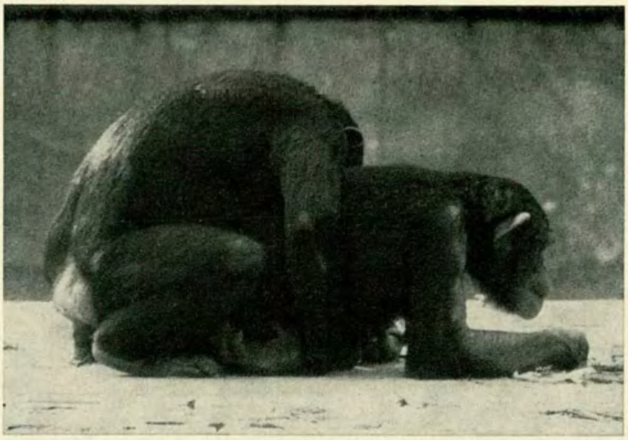


Fig. 4. Shadow and *Belle* copulate during her cycle II. *Belle* is in flat prone posture with legs extended; *Shadow* almost completely covers her body.



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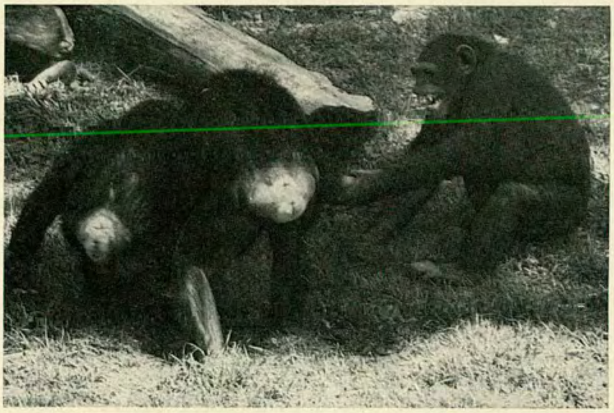

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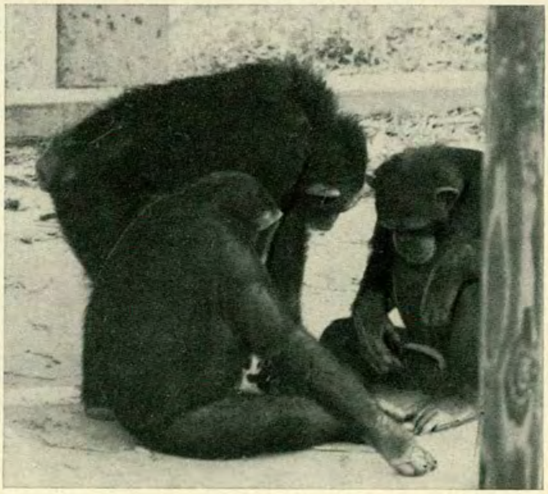

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Legends see p. 246.

Fig. 8. Belle ends intromission after copulation with *Shadow* during her cycle III. *Shadow* self-inspects.

Ontogenetic Changes

A pair of animals showed significant changes in copulatory behaviour from cycle to cycle. Figures 9 and 10 illustrate this by comparing *Shadow* and *Polly's* copulatory behaviour in her cycles I and IV. Behavioural sequences are summarised in flow chart form. In the figures, the three type sizes indicate three degrees of frequency of the behavioural elements. (The number of intromissions rather than the number of copulations represents 100%.) The smallest type size gives elements occurring in 11–33% of cases, the middle type those occurring in 34–67% of cases, and the largest type those occurring in over 68% of cases. The lines between the elements represent transitions from one element to another in the direction indicated. The four line thicknesses from the narrowest to widest represent 6–25, 26–50, 51–75, and 76–100% of cases, respectively. These percentages were cal-

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Fig. 5. Shadow and *Belle* copulate during her cycle III. *Belle's* posture more closely approximates the normal crouch with legs flexed beneath her.

Fig. 6. Shadow shows male 'frustration' (full open grin face) and holds onto *Belle* as *Polly* (centre) interrupts a *Shadow–Belle* copulation.

Fig. 7. Bido (sitting) and *Polly* (standing) watch *Shadow* self-inspect after a copulation with *Bido*.

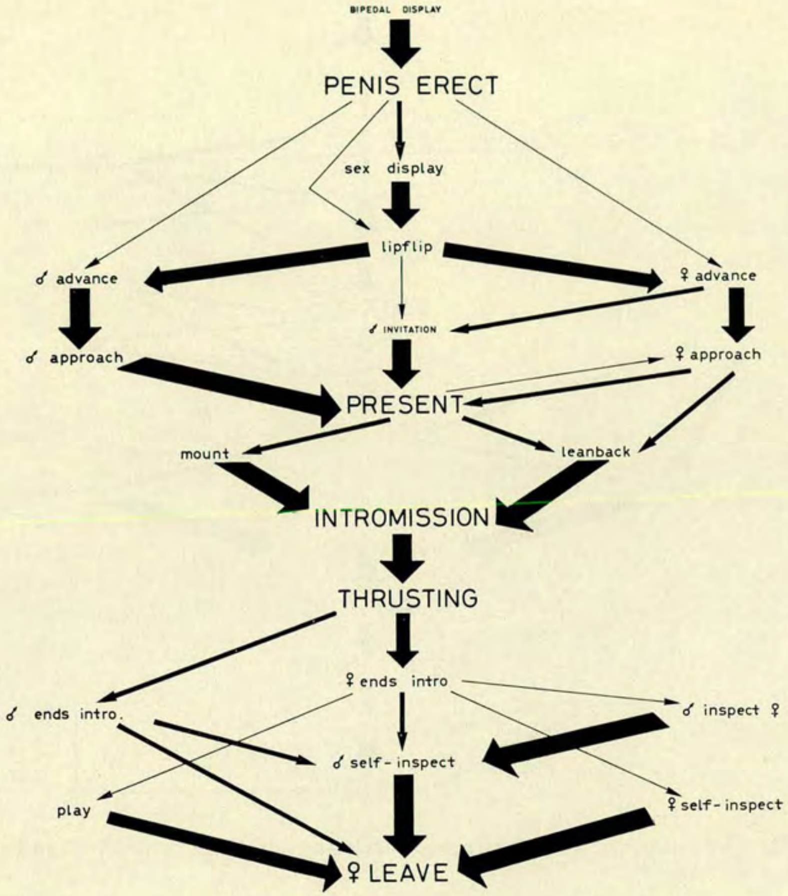

Fig. 9. Sequence of copulatory behaviour elements exhibited by *Shadow* and *Polly*, during her cycle I.

culated from the proportion of the total occurrences of element A which were immediately followed by element B. If element A occurred 20 times and was immediately followed by element B on 15 occasions the percentage for the transition from A to B was 75 %. Elements occurring in 10 % or less of cases and transitions occurring in 5 % or less of cases were omitted. Also omitted for the sake of diagrammatic clarity were cases in which transitions occurred only once but the relative rarity of the first element produced a transition occurrence of more than 5 %.

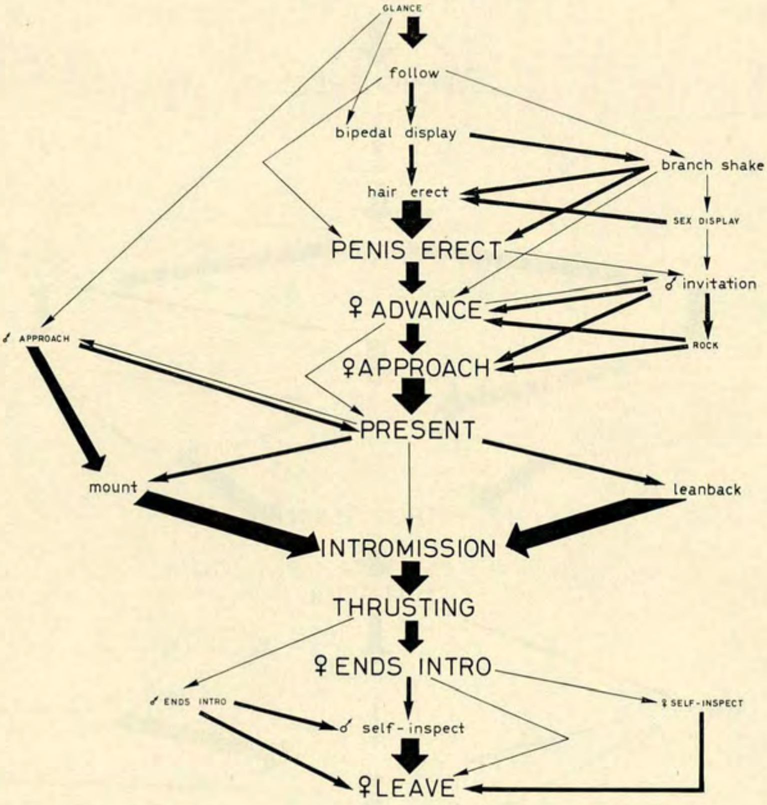

Fig. 10. Sequence of copulatory behaviour elements exhibited by *Shadow* and *Polly* during her cycle IV.

The flow chart in figure 9 is based on the 18 copulations of *Polly's* cycle I (all had a single intromission). The typical sequence began when *Shadow*, with penis erect, showed a sex display accompanied with the lipflip (fig. 2). *Polly* responded to this by moving to *Shadow* and presenting; alternatively, *Shadow* approached her and she responded by presenting. *Shadow* then effected intromission from a mount or leanback posture and commenced pelvic thrusting. The mean number of pelvic thrusts per intromission was 11.3 (n = 13, range 2–35). Either animal might end intromission but usually it was *Polly*. Genital inspection, self or social, often followed intromission. *Polly* usually ended the interaction by leaving, but sometimes they played before parting. The behavioural sequence was relatively consistent: *Shadow* showed much idiosyncratic behaviour before intromission, and *Polly* responded like a mature female chimpanzee.

Figure 10 is a flow chart for *Shadow* and *Polly* based on 37 intromissions in 35 copulations of her cycle IV. The typical copulatory sequence is depicted down the centre of the figure. *Shadow* usually glanced repeatedly at *Polly*, who then followed him as he walked away. He then performed a bipedal display accompanied by hair erection, sometimes incorporating other displays such as sex display, male invite, or rock. When *Shadow* had an erect penis, *Polly* advanced, approached and presented to him, and he effected intromission from a mount or leanback posture. During intromission he averaged 9.3 pelvic thrusts ($n = 35$, range 2–20). *Polly* commonly ended intromission, then either or both chimpanzees inspected their genitals and she left.

Four months separated *Polly's* cycles I and IV (mid-February to mid-June) and striking differences existed between the pair's behaviour in the two cycles. Table IV lists the behaviour patterns seen predominantly in one cycle or the other.

Lipflip and sex display, both significantly more frequent in cycle I than in cycle IV, were idiosyncratic patterns not previously reported for the chimpanzee. Branch shake, follow, glance, hair erect and bipedal display were all significantly more common in cycle IV than in cycle I, and these patterns have previously been described for adult male chimpanzee courtship. It appears that *Shadow's* courtship developed over these four months from idiosyncratic, adolescent to more typical adult male courtship.

During this time *Shadow* showed no marked physical development. He gained some weight and his upper canines lengthened but these happened gradually. Onset of spermatogenesis had occurred earlier; *Shadow* impregnated *Gigi* in August, 1971. However, a dramatic change occurred in the social relations of the group which was probably linked to his changed sexual behaviour. At the beginning of the study, *Shadow* was clearly subordinate to *Polly* and *Gigi*. (Dominance–subordinance was judged on three criteria: object possession, displacement from specific locations, and outcome of agonistic encounters. *Gigi* and *Polly* were very close and often acted in concert against *Shadow*.) Then followed a turbulant period during which the adult male *Rock* re-entered the group and, although clearly subordinate to *Rock*, *Shadow's* dominance relations to *Gigi* and *Polly* were difficult to assess. From early May when *Rock* left the group, *Shadow* gradually became more assertive over the others, including *Gigi* and *Polly*. By early June he was unquestionably the dominant animal in the group.

Table IV. Frequencies of behaviour patterns seen in *Shadow–Polly* copulations, differences between *Polly's* cycles I and IV

Behaviour pattern	I n = 18	IV n = 37	Total	χ^2	p[1]
Lipflip	12	0	12		< 0.001
Male advance	8	0	8		< 0.001
Sex display	9	5	14		< 0.02
Male approach	8	7	15	2.7	n. s.
Leanback	9	13	22	1.1	n. s.
Penis erect	18	31	49	0.3	n. s.
Male ends intromission	6	9	15	0.3	n. s.
Female self-inspect	3	5	8		n. s.
Intromission	18	37	55	0	n. s.
Thrusting	18	37	55	0	n. s.
Female leaves	17	36	53	0	n. s.
Present	17	37	54	0.1	n. s.
Female ends intromission	12	28	40	0.2	n. s.
Male self-inspect	9	22	31	0.2	n. s.
Mount	9	23	32	0.4	n. s.
Male invite	4	14	18	0.9	n. s.
Female approach	6	31	37	4.7	< 0.05
Bipedal display	3	22	25	5.1	< 0.05
Female advance	6	34	40	5.9	< 0.02
Glance	0	12	12		< 0.01
Follow	0	13	13		< 0.01
Branch shake	0	17	17	8.4	< 0.01
Hair erect	0	21	21	10.3	< 0.01

[1] When the total $\geqslant 15$, χ^2 test is used; when the total < 15, binomial test is used.

Some behaviour patterns are common to adult male courtship and agonistic interaction, for example bipedal display, hair erect, branch shake and rock. It is possible that while *Shadow* was competing for dominance with the females, his use of these behaviour patterns in courtship may have elicited an aggressive response. This may explain why *Shadow* showed idiosyncratic behaviour in this context during cycle I. The patterns lipflip and sex display have apparently not been reported previously for the chimpanzee in any context. They appear to be arbitrary signals devised by *Shadow* to obtain a goal unobtainable by conventional methods. A similar interpretation may explain the appearance of patterns such as glance and follow in the later cycle. Although these patterns have no agonistic connotations it seems likely that they require dominant, or at least equal, status to be effective. It is unlikely that a subordinate animal could induce a dominant one to follow him, sometimes for distances of several hundred feet, merely by glancing or gazing.

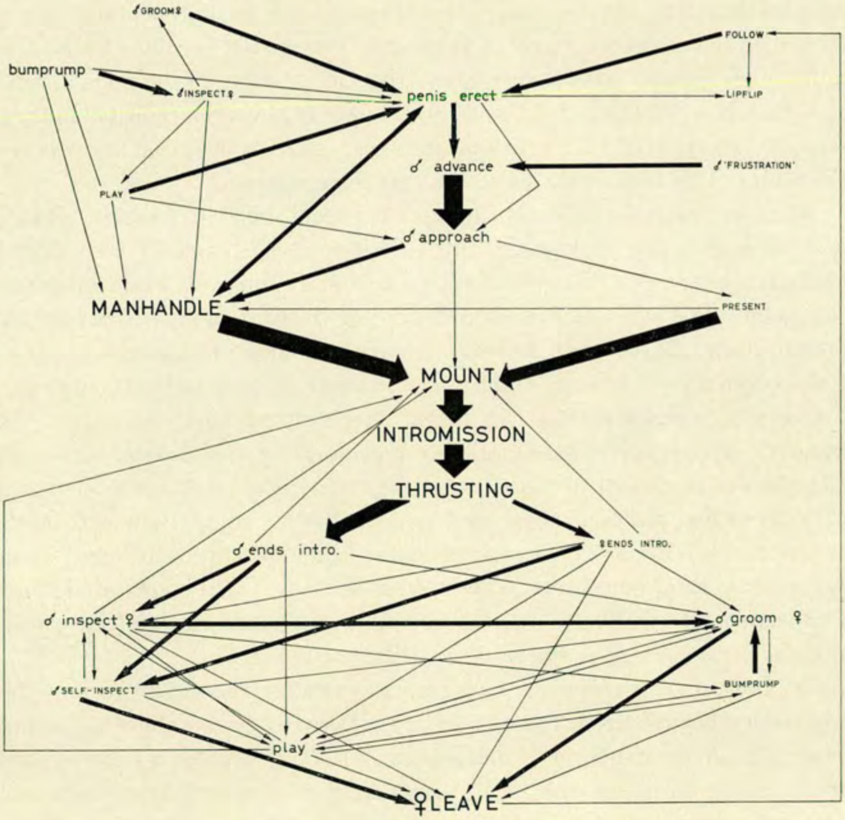

Fig. 11. Sequence of copulatory behaviour elements exhibited by *Shadow* and *Belle* during her cycle IV.

We conclude that *Shadow* was initially inhibited from displaying the behaviour patterns of an adult male chimpanzee because of his subordinate status relative to the available females. With his newly acquired dominance he was able to adopt more typical behaviour patterns and to abandon his early idiosyncracies.

Individual Differences

Figure 11 is the flow chart for *Shadow* and *Belle* based on the 63 intromissions in 46 copulations in her cycle IV. The overall pattern was less consistent than either of *Shadow's* or *Polly's* and no single typical sequence of copulatory behaviour emerged. Initially *Shadow* frequently engaged *Belle* in a non-sexual activity, for example play, grooming, and gradually manhandled her into intromission. He always used a mount posture during intromission with her, apparently in order to prevent her breaking away. The number of pelvic thrusts resembled that in *Shadow–Polly* copulations; $x = 10.9$, $n = 61$, range 2–25. After intromission they often returned to their pre-copulatory activity or exhibited some other non-sexual associative behaviour. This frequently led to another intromission.

Shadow's tactics obviously differed between the two females. *Belle's* cycle IV was in late June-early July, just after *Polly's* cycle IV. But *Belle's* level of experience in this cycle was closer to *Polly's* in cycle I (although not equivalent, as *Polly* had been copulating for over six months prior to the present study). *Shadow* and *Belle* exhibited four elements not seen in *Shadow–Polly* copulations: groom, bumprump, manhandle and male 'frustration'. Conversely, bipedal display, sex display, male invite, rock, hair erect and leanback were never or rarely seen in *Shadow–Belle* copulations. Although *Shadow* was dominant to *Belle*, he showed no typical adult male courtship patterns to her, although these were common in his copulations with *Polly* at this time. With *Belle*, *Shadow* probably had to incorporate many non-agonistic, general behaviour patterns since she was a non-cooperative, passive partner. The usual adult male courtship would have been ineffective with *Belle* as it requires an active response from the female.

At least, two alternative explanations exist for the differences in the copulatory behaviour of the two females. Perhaps *Belle* exhibited an unpracticed, adolescent form of behaviour while *Polly* showed a more typical adult female form because of differing degrees of sexual experience and physical maturation, with *Belle* lagging behind. Or, perhaps individual differences based on personality and past experiences existed, and *Belle's* behaviour may never come to resemble *Polly's*. Only continued observations to maturity will provide an answer. That the two females are at different stages of sexual development in physiological terms was shown earlier, but they also experienced different rearing conditions in early life. *Belle* arrived at Delta at approximately 12 months of age and was always housed with at least two males of a similar age. She always lived in large enclosures and was cared for by one person for five years. *Polly* was probably between 18 and 24 months of age upon arrival at Delta and lived alone for her first 2 ½ years, having only limited contacts with a series of similarly aged males and females. She lived in a small cage and was cared for by a series of human attendants. Thus, *Belle* had a more socially stimulating early upbringing, but her younger age at capture and the formation of a strong emotional relationship with a single human caretaker may have detrimentally affected the development of her sexual behaviour [ROGERS and DAVENPORT, 1969].

Belle was probably a virgin at the study's beginning. In her first cycle during our observations (when she still exhibited small adolescent swellings), we saw her copulate once with *Shadow*. In her next cycle, her swelling was noticably bigger and *Shadow* showed great sexual interest in her, and at least 19 copulations resulted. She behaved similarly in both cycles, appearing totally passive and allowing *Shadow* free license in his actions. She appeared oblivious to his activities and sometimes lay and self-groomed during intromission. In her cycle II, 40 % of copulations occurred with *Belle* lying prone or supine. In her cycle III, only 8 % of copulations involved lying either prone or supine, while 74 % occurred with *Belle* crouched in the normal position or standing quadrupedally with legs extended. By cycle IV *Belle* crouched in the normal posture for 80 % of copulations and only 5 % occurred with her lying prone or supine. *Belle* became no more actively involved in copulations, but she gradually made it easier for *Shadow*.

Gigi copulated for over a year before the study began. In the 31 copulations we observed, she was cooperative and efficient. The copulations averaged less than five minutes in length. *Shadow–Gigi* copulations were almost behaviourally identical to *Shadow–Polly* ones in *Polly's* cycle I, although *Gigi* was the only female who regularly vocalised and grimaced during intromission. *Gigi* and *Shadow* rarely indulged in non-sexual associative interaction, except for his occasionally grooming her.

Bido was probably also a virgin before her 11 copulations in her cycle III. Contact play preceded all her copulations and they all involved manhandling. She was more active than *Belle* but not cooperative; she frequently attempted to restart play during intromission. The duration of copulations were not systematically recorded, but *Shadow* and *Bido* had long copulations with bouts of non-sexual associative behaviour, such as play, grooming or nest building, interspersed with sexual interaction. Their longest copulatory sequence lasted 47 minutes and included two intromissions.

Thus, the four females represented a spectrum of sexual experience: *Gigi*, now a mother; *Polly*, experienced and cooperative; *Belle*, relatively experienced but still passive; and *Bido*, behaviourally inexperienced and physically immature.

Discussion

The results suggest that group-living chimpanzees in a large field enclosure behave more like free-living chimpanzees than like other captive chimpanzees paired in small cages. This is not surprising, but it illuminates some of the distortions of the typical captive chimpanzee's incarceration. Several behaviour patterns recorded in this study could not have occurred in the usual caged situation. Lack of space would preclude elements involving long distance locomotion, such as prolonged following by the female or glancing-and-leading by the male. Lack of suitable or even moveable objects would preclude other elements such as branch shaking, stick waving or nest building. In addition to being significant in this group, such behaviour patterns are commonly shown by free-living chimpanzees [VAN LAWICK-GOODALL, 1968].

In general, our group's sexual behaviour resembled descriptions given for free-living populations. However, *Shadow's* copulatory repertoire showed more variability and eccentricity than those of his wild-living counterparts. This may have resulted from *Shadow's* being reared exclusively in a peer group lacking adults on whom to model 'normal' copulatory behaviour. Or, because this group was not forced to spend long periods daily foraging for food, its members had ample time for experimentation and innovation. When *Gigi* and later *Polly* became sexually receptive *Shadow* was subordinate to them both. One can imagine the usefulness of a signal pattern such as lip-flip, being visually obvious from a distance and having no intrinsic agonistic meaning. A long range, sex-specific behaviour pattern would be useful to a young subordinate male temporarily faced with only more dominant females available for copulation. Later, after achieving dominance, he could abandon the idiosyncratic elements and adopt the more normals chimpanzee courtship patterns.

The greatest difference between this group's constituence and wild chimpanzee populations is its abnormally uniform age structure. This seems to have affected the males more than the females. In a wild mixed-age-sex population, the development of male sexual behaviour is long and probably intimately tied with male-male dominance. *Shadow's* development seems to have been accelerated and diversified by the lack of this. The females' behaviour was closer to that of their wild-living counterparts. Because their sexual development was closely linked to physiological events such as the first adult swelling, it appeared less susceptible to effects of the social and physical environment.

Chimpanzees brought up artificially, either in nurseries or under deprivation conditions, commonly show abnormal or inadequate sexual behaviour [RIESEN, 1971; ROGERS and DAVENPORT, 1969]. Effects are more pronounced in males, at least partly, because a copulation does not require compliance by the female. Competent male sexual behaviour appears to develop more as a response to the presence of a receptive female than to physiological maturation. The appearance of male sexual behaviour precedes the onset of spermatogenesis. In the wild, male infants fron five months onwards show interest in swollen females and are able to mount and show pelvic thrusting with intromission by one year of age [VAN LAWICK-GOODALL, 1968]. However. it seems that without the stimulus of a receptive female before maturity, male sexual behaviour may never develop. In the Holloman Air Force Base consortium, all adolescent and juvenile males introduced into the group showed normal sexual behaviour, but only two of the five adult introduced did so (one of the adequate males is reported to have had experience with a receptive female while adolescent) [KOLLAR *et al.*, 1968]. LEMMON [1971] reports that if artificially raised chimpanzees are given an adequate surrogate mother, i. e. they are home raised with full-time attention from at least one human, sexual behaviour will appear normally when they have access to a receptive female. (In all cases the access has been provided prior to maturity.) It seems that the crucial factors for producing sexually competent males is to give them an adequate social environment in early life and, equally important, access to a receptive female before they are fully mature. None of our females had any prior sexual experience, and LEMMON [1971] also reports that a receptive inexperienced female can elicit sexual behaviour from an inexperienced male. Most males on whom data are available were wild-born, but most were only a year old or less when captured. It is possible that some sexual behaviour was learned at this tender age. However, the evidence suggests that learning by imitation is not crucial to sexual development but that the important factors are an adequate social environment and exposure to a sexually receptive female before maturity.

Summary

Observations of the copulatory behaviour of group-living, adolescent chimpanzees *(Pan troglodytes)* in a large field enclosure revealed large individual differences in behaviour, and the rapid ontogeny of some behavioural elements. Each female elicited different courtship patterns from the same male. These differences apparently stemmed from differing levels of experience and influences of personality differences. The male changed his courtship of the females over the study period, probably in relation to his rise to dominance within the group.

Acknowledgements

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References

BINGHAM, H. C.: Sex development in apes. Comp. Psychol. Monogr. *5:* 1–165 (1928).

KOLLAR, E. J.; BECKWITH, W. C., and EDGERTON, R. B.: Sexual behavior of the ARL Colony chimpanzees. J. nerv. ment. Dis. *147:* 444–459 (1968).

LEMMON, W. B.: Experiential factors and sexual behavior in male chimpanzees. Medical Primatology 1970. Proc. 2nd Conf. exp. Med. Surg. Primates, New York 1969, pp. 432–440 (Karger, Basel 1971).

LOIZOS, C.: An ethological study of chimpanzee play. Proc. 2nd. Int. Congr. Primat., Atlanta 1968, vol. 1, pp. 87–93 (Karger, Basel 1969).

RIESEN, A. H.: Nissen's observations of the development of sexual behavior in captive-born, nursery-reared chimpanzees; in BOURNE The chimpanzee, vol. 4, pp. 1–18 (Karger, Basel 1971).

ROGERS, C. M. and DAVENPORT, R. K.: Effects of restricted rearing on sexual behavior of chimpanzees. Develop. Psychol. *1:* 200–204 (1969).

TUTIN, C. E. G. and MCGREW, W. C.: Sexual behaviour of group-living adolescent chimpanzees. Amer. J. phys. Anthrop. (in press, 1973).

VAN HOOFF, J. A. R. A. M.: A structural analysis of the social behaviour of a semi-captive group of chimpanzees; in VON CRANACH and VINE Expressive movements in non-verbal communication (Academic Press, London 1971).

VAN LAWICK-GOODALL, J.: The behaviour of free-living chimpanzees in the Gombe Stream Reserve. Anim. Behav. Monogr. *1:* 161–311 (1968).

YERKES, R. M. and ELDER, J. H.: Oestrus, receptivity and mating in chimpanzee. Comp. Psychol. Monogr. *13:* 1–39 (1936).

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