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CONCLUDING DISCUSSION: ECOLOGICAL FACTORS AND SPECIFIC BEHAVIOURAL PATTERNS DETERMINING PRIMATE DIET

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INTRODUCTION

Primatologists are arriving slowly at the same conclusions contained in the basic principles developed several decades ago by ecologists working on invertebrate and lower vertebrate populations. Only now, as sample sizes for particular habitats become adequate, can concepts such as the 'pyramid of production' and 'biomass' (Odum and Odum, 1959) be applied to primates. While the ecological approach in primatology has been overshadowed until recently by the work of psychologists and anthropologists, the main factor delaying progress has been that primate habitats in tropical regions are probably the most complex ecosystems in which one can work - the data return per man-hour of work has been very low in efforts to reconstruct the puzzle of forest ecology.

Most of the field studies described in this symposium represent the co-operation of several scientists, who have combined their efforts to elucidate behavioural problems against an ecological framework, realising that it is the ecosystem rather than the primate species which holds the key to answering so many problems. The variety of methods used in these field studies causes pessimists to claim that comparisons between areas are not possible. Nevertheless, material presented in this symposium, and subsequent discussion, has shown how similar are conditions throughout the tropical world from an ecological viewpoint. The various field studies not only permit comparison, but allow us to detail the numerous systems for sharing natural resources that have been developed among primates (and other living organisms) and to compare corresponding levels in the pyramid of production.

The first aim of this symposium is to consider these basic features of production and food availability for primates in different habitats in the light of data from the various field studies discussed. The second aim is to consider the composition of foods in relation to feeding behaviour. Although our knowledge in this area is currently very limited, many of the problems raised in this symposium appear to be related directly to food composition. The central question is: What makes food choice so different among primate species, and what mechanisms maintain them? The answers involve functional morphology as well as the evolution of feeding strategies, which tend to increase the inter-specific differences and give rise to the unique

human socio-cultural patterns; these problems can only be resolved once the ecological background is clarified.

FOOD PRODUCTION AND AVAILABILITY

Primary production

The primary production determines the level at which animal populations can be stabilized in a given habitat; at least it determines the maximum level which, if exceeded, would result in the destruction of the environment.

It is noteworthy that, in all the tropical forests where there have been long-term studies of productivity, the figures obtained for primary production are very similar. For instance, leaf production (calculated from litter production) in the rain forest of Gabon is 7 tons dry weight per hectare per year (A. Hladik, 1977); a similar level of production (6 tons) was found in Panama (Leigh, 1977), as well as in the evergreen forest of Japan (Iwamoto, this volume). Even in deciduous forests leaf production is of the same order of magnitude (3-4 tons/ha./yr/)/ These facts help to explain why the folivorous primates show a similar biomass in different parts of the world (exceptions observed would be populations below the saturation level). The diets of various species are obviously more complex, however, and further analysis of food production is necessary.
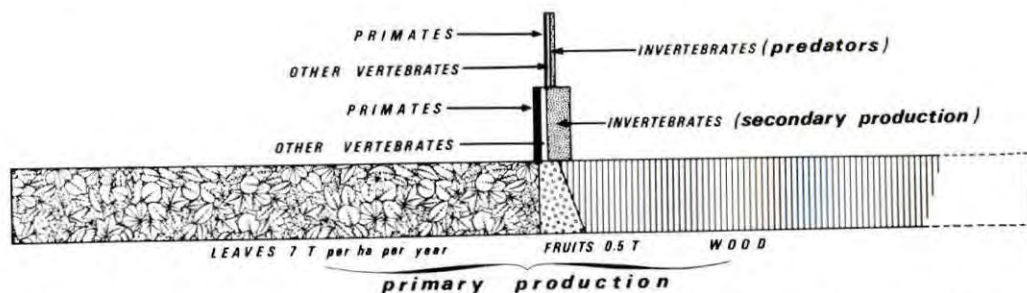

Figure 1. *Simplified pyramid of production in a rain forest, based on data of primary production from Gabon (A. Hladik, 1977). Our representation of invertebrate and vertebrate production, although small with regard to primary production, is considerably in excess of what is predictable in the absence of accurate data (see text).*

Trophic levels

Consider the pyramid of production in a rain forest as generally represented by ecologists (Fig. 1). Primary production includes wood as a major component, leaves (7 tons dry weight/ha./yr.) and fruits, including seeds (about 0.5 tons/ha./yr.). Secondary production includes all animals feeding on the primary production; very little is known about its exact size, but it is believed to be about one-hundredth of the primary production. There is only one record for insect production, in leaf litter in Gabon (23 kg./ha./yr., A. Hladik, 1977); other invertebrates might increase this value considerably - at a savanna site (Gillon and Gillon, 1974) the production of non-flying invertebrates reached 18 kg./ha./yr.

Primates are usually only a small fraction of the vertebrates in the secondary production, which includes all folivorous and frugivorous animals. The top of the pyramid (the tertiary production of predators) includes a very small part of the primate production, those species feeding on insects as well as other insectivorous animals and all carnivores. Again, the size of this level of the pyramid is about one-hundredth of the level below (secondary production).

These three trophic levels of production, presented in simplified form, can be measured in terms of energy; the primate component would be the total energy expenditure required for the maintenance of all primate species, including their share of the primary production (leaves and fruit) and the small part of the secondary production (insects and other invertebrates) used as food.

Grades of primate diet

The biomass of the folivorous and frugivorous primates maintained by this flow of energy would obviously be much higher than that of the insectivorous species. Because the diets of all primate species include insects, fruit and leaves to some extent, they can be classified into three grades (Hladik, 1975) according to a limited number of combinations. In each of these grades, the ecological significance of which is discussed by Petter (this volume), one can find any intermediate type of diet including, for instance, different proportions of insects and fruit, that can be considered as an 'intermediate' level in the pyramid of production. The biomass of primates at these 'intermediate levels' will be proportional to the energy taken from primary and secondary production.

This principle is illustrated by data from the various field studies contained in this symposium, compared with data from Panama and Sri Lanka (Hladik and Hladik, 1969, 1972). For each study area (horizontal axis) each primate species is located on a vertical scale of biomass, kg. fresh weight/hectare (Fig. 2). The smallest biomasses are those of insectivorous species, the highest are those of folivores. From bottom to top the three grades of diet are:-

Grade 1 species obtaining the bulk of their energy from insects and other prey, complemented by fruit or gums, with a biomass of about 0.01 - 0.1 kg./ha. (fresh weight).

Grade 2 intermediate types using fruit as a major source of energy, but including insects and/or other prey, seeds and young leaves to cover protein requirements, with specific biomasses of about 0.1 - 1 kg./ha. (exceptionally a little higher).

Grade 3 species relying exclusively on primary production, with diets including varying proportions of fruit and leaves, and biomasses of 1 - 10 kg./ha.

Maximum primate biomass

At any level the primary and secondary production can have only a limiting effect on the biomass of a species. Thus the figures presented in Fig. 2 have been selected from records of maximum biomass; similar maximum scores can be predicted when comparing species with similar diets living in similar habitats. Contrary to popular belief these maximum biomasses vary very little in undisturbed homogeneous habitats (Charles-Dominique and Hladik, 1971);
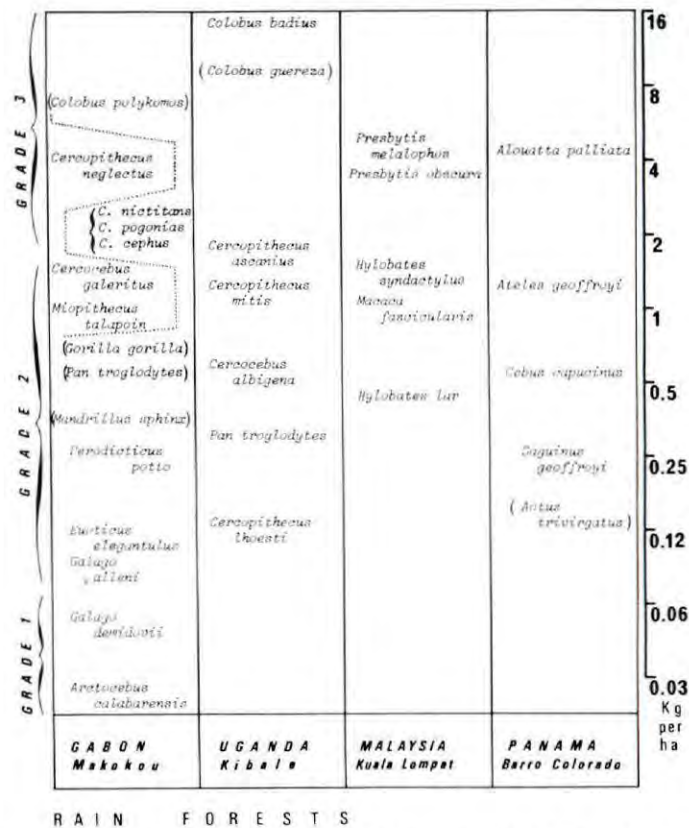
RAIN   FORESTS

Figure 2. Sympatric primate species in different field stations, classified
by biomass (kg. fresh weight/hectare) and, consequently, by diet.
The three ecological dietary grades (see text) are determined
mainly by three major foods - insects, fruits and leaves.

(a) GABON (Makokou area, near Ipassa or N'passa). The dotted line parti-
tions species living in flooded areas from those inhabiting the
rest of the primary forest. No data are available for species in
parentheses: they have been placed according to biomasses observed
in other areas. The three species of Cercopithecus living in
polyspecific groups have been plotted according to their total
biomass, which varied from 1.16 (in 1972) to 2.21 (in 1976). Data
from Gautier-Hion (this volume) and Charles-Dominique, (1976).

(b) UGANDA (Kanyawara area of Kibale Forest). The biomasses are from Struh-
saker (this volume, 1975) except for Colobus guereza, whose mean
biomass there is only 0.6 kg./ha.; it has been plotted according
to its maximum biomass in localized areas.

(c) MALAYSIA (Kuala Lompat area of Krau Game Reserve, Pahang). Data from Cur-
tin and Chivers (1977) and MacKinnon and MacKinnon (this volume).

(d) PANAMA (Barro Colorado Island). Data from Hladik and Hladik (1969) and
Moynihan (1976).
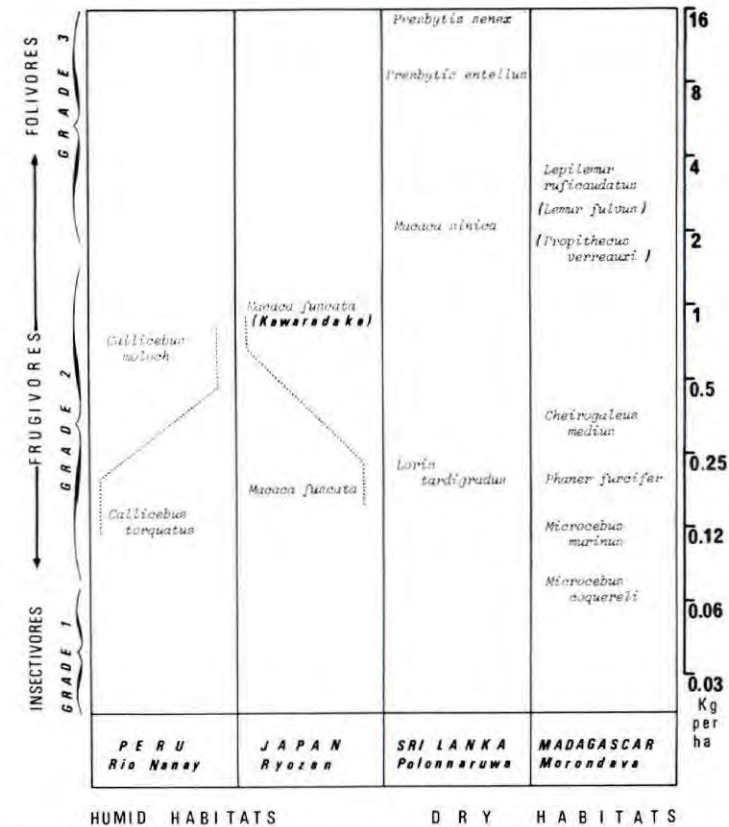
HUMID HABITATS   DRY   HABITATS

(e) PERU (Rio Nanay). Data from Kinzey (this volume); the dotted line
indicates the use of riverine lowland by the more folivorous
species.

(f) JAPAN (Ryozen, central Honshu, and Kawaradake, northern Kyushu). Two
allopatric non-provisioned populations of Japanese macaques have
been plotted according to the data of Iwamoto (this volume).

(g) SRI LANKA (Polonnaruwa). High biomasses in this dry deciduous forest
result partly from the lack of competitors (data from Hladik and
Hladik, 1972).

(h) MADAGASCAR (Morondava area, at Analabe). The biomasses of nocturnal
prosimians are from collective data presented by Petter (this
volume); diurnal species (in parentheses) have been observed
briefly in this area by Charles-Dominique (pers. comm.).

this means that any species will use the maximum capacity of the environment
which, in fact, is determined by the lowest level of production where there
are seasonal variations (see below).

Furthermore, the maximum biomass of a primate population (or of a social
group of a particular species) is related to the 'supplying area' (Hladik
and Hladik, 1972; Hladik, 1977a) to take into account the overlap of home
ranges and the way a population of a given species shares food resources.

The different primates represented in Fig. 2 have been placed at different trophic levels according to their biomass, which is also influenced partly by the way the same resources can be shared by different species. The relationship between food availability and biomass when several primate species cohabit is illustrated by *Cercopithecus mitis*, studied by Rudran (see Struhsaker, this volume): in the absence of competitors and in a fairly similar environment, this species can achieve a biomass five times higher than at Kibale. Other mammals can, of course, use some of these trophic levels by eating foods not used by primates or by competing partly for fruits and young leaves. For example, there is no leaf monkey in Panama and the corresponding folivore is *Bradypus* (Eisenberg *et al.*, 1972); in Gabon it is *Dendrohyrax* (Hladik, 1977); and in Malaysia large species of squirrel and hornbill are frugivorous (Chivers, 1974).

Following these general correlations between biomass and diet in terms of primary and secondary production, with data presented by Clutton-Brock and Harvey (this volume) affording corroboration for these ecological views, habitat use must be considered more fully to explain several aspects of primate diets described in this symposium.

SPATIAL AND TEMPORAL VARIATION IN FOOD RESOURCES

Among the various field stations compared in Fig. 2, one can find different systems of sharing food production between species of primate (and other mammals and birds competing for similar food resources):- (1) horizontal, macro- and micro-, (2) vertical, and (3) temporal distributions.

Horizontal distribution

(1) in a discontinuous environment. The first case is equivalent to allopatry; in the same field station species use different areas. For example, in Peru *Callicebus moloch* inhabits lowlands by rivers and streams, while *C. torquatus* is found on hilltops and ridges (Kinzey, this volume). The food production in these two areas should be calculated separately, so that the biomass of each *Callicebus* species depends on this local production and, of course, on its level in the pyramid of production. Since *C. moloch* feeds partly on leaves, its biomass is four times higher than that of *C. torquatus*, which feeds partly on insects. Thus in Fig. 2 these two 'allopatric' species are separated by a dotted line.

A comparable situation exists in Gabon (Gautier-Hion, this volume) where the biomasses of species such as *Miopithecus talapoin*, *Cercopithecus neglectus* and *Cercocebus galeritus* have to be related to food production only in the riverine habitat, while the other *Cercopithecus* species, living in polyspecific groups, use mainly the resources of the rest of primary rain forest.

In Uganda the distributions of *Colobus guereza* and *C. badius* (Struhsaker, this volume) also relate to habitats differing in climate and vegetation structure. The situation is more complex in Malaysia: while *Macaca fascicularis* and *M. nemestrina* are largely 'allopatric', favouring riverine and hill forest respectively (Chivers 1973, 1974), the separation of hylobatids and colobines is more subtle (Aldrich-Blake, and MacKinnon and MacKinnon, this volume).

(2) in mosaics. The second general pattern for sharing food resources differs only from the previous examples by the small size of areas used by the

species concerned. Among the prosimians of Gabon (Fig. 2), *Arctocebus calabarensis* is found only in natural 'clearing' in primary rain-forest, in very dense vegetation with many small vines and rapid tree growth (Charles-Dominique, 1976). These small areas of forest regeneration, usually following a tree fall, are part of a permanent cycle characteristic of the mosaic structure of the rain-forest (Whitmore, 1975). The biomass of such species should be calculated in relation to the food availability in these patches of forest only. This is not currently possible since food production is usually measured along transects, which include all stages of forest growth. It is more convenient, therefore, to consider *Arctocebus* with regard to the whole forest, so that its biomass and proportion of use of the total production appear very small.

There are many other examples of inter-specific differences in horizontal distribution, generally considered as ecological separation within the same habitat, that is best considered possibly as patchy distribution in 'subhabitats'. The study of variograms (A. Hladik, this volume) allows further analysis of irregular distributions of plants and phenology, which can be correlated with the horizontal distribution of primates. It is because the traditional botanical approach aims only at describing the composition, structure and phenology of a given area of forest, that transect investigation in Malaysia has been augmented by a regular grid of ¼-ha. plots to elucidate such local variations in floral activity and primate behaviour within the area.

Vertical distribution

The vertical distribution of primates at different heights in the forest canopy has often been referred to as a mechanism of niche separation (Chivers, 1973, 1974; Struhsaker, Gautier-Hion, Fleagle, MacKinnon and MacKinnon, this volume). This situation does not really differ from the horizontal pattern of localised 'sub-habitats'. One clear example relating to the prosimians of Gabon concerns *Galago alleni*, which uses exclusively the lower part of the primary rain-forest, wherein it moves by successive leaps between vertical small trunks and lianas; in contrast, *G. demidovii* only moves among the small twigs of the canopy (Charles-Dominique, 1976). Fleagle (this volume) describes how Malaysian primates are separated ecologically by their use of different kinds and sizes of support.

To a lesser extent there are differences in the heights generally used by cercopithecid species; these can be considered as a complementary system of niche separation, which allows (or follows) the use of partly differing food resources. Parallel situations, in terms of vertical distribution, were observed for *Cercopithecus ascanius* and *C. mitis* (Struhsaker, this volume) and for *C. cephus* and *C. nictitans* (A. Gautier-Hion, this volume) in East and West Africa respectively.

In any of these cases one must obviously consider the maximum biomass of primate species in the whole habitat, and refer to it in terms of primary and secondary production, and trophic level of the primates in the pyramid of production. The three cercopithecine species in Gabon have been grouped under their total biomass, because of the large overlap in feeding niches (now defined precisely by Gautier-Hion, this volume); this total biomass is at the same level approximately (Fig. 2) as that of *Macaca fuscata*, which eats the same kinds of food in the evergreen forests of Japan (Iwamoto, this volume).

Temporal use of food resources

Considering the primary and secondary production in a given habitat as a whole, the consequences of a temporal pattern of sharing food resources do not differ greatly from the spatial patterns. In spatial avoidance, however, an ecological concept, two species cannot share the same resource, whereas in temporal avoidance, a behavioural concept, they do share the resource, albeit at different times.

(1) *Daily rhythms*. Nocturnal *versus* diurnal activity cycles is a common pattern of niche separation preventing direct effects of competition between species with similar diets. It should be remembered, however, that alternative explanations are available in certain cases; it provides a way of avoiding predators, and food sources may not actually be shared where nocturnal and diurnal insectivores, for example, can be shown to consume different foods. Nevertheless, this system of sharing food resources is common among mammals and birds, and it has played an important part in the evolution of prosimians (Charles-Dominique, 1975).

Biomasses of the nocturnal species of Madagascar and Gabon have been presented along with those for diurnal species (Fig. 2), since trophic levels are not affected by this important pattern. In localities where diurnal and nocturnal forms cohabit, the total biomass of each must be considered; for example, *Lepilemur* (nocturnal) and *Propithecus* (diurnal) share a large proportion of leaves in their diet and the biomass of each species can reach 5-10 kg./ha., which is very high considering their dry habitat and the resulting low expectation for primary production.

Food resources can also be shared by more subtle differences in the activity patterns of diurnal species. In Malaysia, for example, hylobatids feed throughout the morning and retire to their sleeping trees in mid-afternoon, whereas the colobines feed more intensively, often on the same foods, at dawn and dusk with a long rest period in the middle of the day (Chivers, 1973). Similarly, asynchronous feeding by different members of a large troop of lion-tailed macaques (Green, this volume) also helps to reduce the direct effects of competition.

(2) *Seasonal rhythms*. The temporal patterns described by Petter (this volume), relating to peculiar physiological adaptations of the Cheirogaleinae, are more important. Generally, primate field studies show that diets change according to seasonal cycles (MacKinnon and MacKinnon, Oppenheimer, Milton, Iwamoto, Gatinot, this volume; Chivers, 1974, 1977; Chivers *et al.*, 1975). Consequently, biomasses are determined by the minimum level of food production. Because such variations are generally relatively small and are not meaningful when biomasses are plotted on a logarithmic scale (Fig. 2), they have not been considered in the preceding paragraphs.

In Madagascar, however, in the deciduous forests of Morondava, the drastic seasonal change in food availability strictly limits some of the species (Petter, this volume). The Cheirogaleinae, especially *Cheirogaleus medius*, which can hibernate for periods up to 9 months, use only foods that are periodically available in large quantities. These food resources are useless for other species because they are not available for long enough. The specialised physiology of the Cheirogaleinae is unique among primates, but there are numerous other physiological traits that should be considered when trying to explain the mechanisms of adaptation to different niches.

DIETARY VARIATIONS IN RELATION TO FIXED BEHAVIOURAL PATTERNS

The seasonal changes in the diet of a primate species are often more marked than many of the inter-specific differences at any given time (Hladik and Hladik, 1972; Chivers *et al.*, 1975; Struhsaker, Gautier-Hion, MacKinnon and MacKinnon, Iwamoto, this volume). These variations are obviously due to local and temporal changes in food production.

Constancy of food choice

It is important to note, however, the constancy of feeding behaviour in general terms (Curtin, 1976; Curtin and Chivers, 1977; Hladik, 1977a; Gautier-Hion, this volume; Raemaekers, in prep.). Whatever the seasonal fluctuations in supply, the most insectivorous of sympatric primate species will always eat more insects than the others. Similarly, the most folivorous primate will always eat more leaves than the others, even when its fruit intake is increased at times of abundance.

The central question of this symposium has been posed as: What makes each species maintain their characteristic feeding tendency? A complete answer would also explain how each species fits into the various ecological categories in the pyramid of production. The answer is not simple and will necessarily include hypotheses that can be resolved only in the laboratory.

Seasonal changes in food composition

From results obtained recently in Sri Lanka from biochemical analysis of all natural foods used by primates, the seasonal variations in food availability have not had the same effect on the food constituents ingested by the different primate species (Hladik, 1977a). While both *Presbytis senex* and *P. entellus* show a seasonal increase in sugar intake, only the latter shows fluctuations over the year in intake of protein and lipids. Thus, we have a contrasting effect in biochemical terms in two sympatric species during the same period. It is likely that many other inter-specific differences in food composition and in patterns of variation will be recorded when this aspect is studied more fully.

Local variations in diet

Some populations have slight differences in diet because of the local availability of food plants, as in *Macaca fuscata* (Iwamoto, this volume). In one species at least, *Cercopithecus aethiops*, the local variations can be so marked that the intraspecific differences in diet (Galat and Galat-Luong, this volume) are much greater than those commonly seen between species. This case might represent the early stages of speciation, since the selection of a specialized molar model (Kinzey, this volume) might follow the use of a large protein source such as the mangrove crabs. On the other hand, the flexibility afforded by a generalized dental morphology might have greater survival value for a species living in a heterogeneous environment. Local differences in the diets of human populations (de Garine, this volume) can be maintained solely by cultural processes without morphological specializations.

FEEDING BEHAVIOUR IN RELATION TO FOOD COMPOSITION

Two different sets of physiological mechanisms have been invoked to explain the regulation of feeding behaviour in primates (Hladik *et al.*, 1971).

Long-term effects of nutrients

The first mechanism is a long-term response, with conditioning through the beneficial effects of ingestion and absorption of foods; this depends on the morphology and enzymes of the gastro-intestinal tract adapting to foods of certain composition. It is also partly dependent on tooth structure since food preparation may be very important for efficient digestion (Kinzey, this volume). Long-term conditioning can be induced by the toxic effect of any maladaptive diet. During this symposium several references have been made to toxic compounds; their avoidance can be acquired by this conditioning mechanism. Laboratory tests are generally made on a two-sample choice; Snowdon and Jacobson (this volume) have shown how dietary deviations can be induced artificially, but these are unlikely to happen in the wild. The case of *Hylobates syndactylus* searching for *Sloetia* leaves more intensively than *H. lar* (Raemaekers, this volume) might be explained biochemically, in terms of the dietary composition of both species and the need for one of them to compensate for the lack or excess of some elements.

Food taste stimulation

The second mechanism for regulating food intake is the immediate effect and conditioning of taste. In the case of *Presbytis entellus* and *P. senex* from Sri Lanka, there are no clear anatomical differences, even in gut histology, to explain the differences in food choice. There are small differences in molar structure (giving greater shearing efficiency to the more folivorous *senex*, Kay, 1975), but contrasting intensities of the immediate taste response in each species is the most likely explanation. Soluble substances that are likely to be detected by taste, such as sugars and organic acids, are especially abundant in the diets of primates which need the maximum effect of immediate conditioning to direct them to dispersed food species (Hladik *et al.*, 1971). Further tests are necessary to confirm this hypothesis, which could explain one of the ways whereby specific dietary patterns can be achieved, integrating species into the pyramid of production.

Negative and positive effects of secondary compounds

It is topical to suggest that toxic secondary compounds play a major role in food choice (Janzen, 1970). In the absence of supporting evidence, it is likely that substances of this kind, which are usually tasty and present in the leaves of many species of rain-forest tree (for example, the alkaloids tested in Gabon by A. Hladik, 1977) are harmless because in low concentration (or non-active molecular configuration): they might play a conditioning role among primates helping in the identification and selection from various tree species of important nutrients, undetectable by taste, with which they are associated.

A few plant parts have potentially toxic alkaloids. Primate species with complex bacterial flora capable of 'detoxifying' such substances can obviously benefit from being able to exploit a slightly wider variety of foods.

Among 41 food plants tested for alkaloids in Sri Lanka (Hladik, 1977a) only three are likely to be toxic; among them, the fruits of *Strychnos potatorum* were avoided by the macaque but eaten by the leaf-monkeys. In the specialized habitat surveyed by Gartlan and McKey (this volume) there seems to be a higher proportion of toxic plants, protected against defoliation on a poor soil low in nutrients where leaf replacement is difficult; this exerts a strong influence on the feeding strategy of *Colobus satanas*.

Further analysis is necessary to determine the extent to which the different chemicals can be beneficial or harmful to primates. At all times it is important (1) to recognise the dynamic process of coevolution between plant and animal, (2) to distinguish carefully between seed destruction and seed dispersal, with the latter perhaps more prevalent in primates than other animals, and (3) to appreciate that high levels of secondary compounds in leaves might represent intermediate biproducts of plant metabolism, while in seeds might have been selected as end-products to prevent destruction.

FUTURE DEVELOPMENTS

Our knowledge of specific physiological adaptations among primate species is very limited in terms of the long-term effects of different nutrients and of psycho-sensory physiology. Descriptions of the physical properties of natural food resources, and the sensory discriminations that must be performed by primates in locating and identifying their food, may help to define particular adaptations more precisely (Snodderly, this volume).

The variety of field methods - sampling or continuous observation of feeding, measurement of food intake by kind or weight, analysis of stomach contents, the choice of which is dictated by local circumstances - have resulted in real progress in defining and explaining specific food choices and feeding strategies; they *do* allow comparisons to be made.

Thus, the ecological background has been clarified considerably, but fuller laboratory studies are necessary before we can implement on any practical scale the theoretical approach of feeding 'economy' advanced by Altmann (this volume), and more quantitative data on food intake must be accumulated before comparisons can be made with human nutrition (de Garine, this volume).

The continued collection of quantitative data in both field and laboratory is necessary to consolidate our understanding of the energetic and nutritional aspects of feeding and of the dynamics of primate communities - to explain how and why diets are strictly maintained in the different ecological niches.

REFERENCES

Charles-Dominique, P. (1975). *In* "Phylogeny of the Primates" (W.P. Luckett and F.S. Szalay, eds), pp. 69-88. Plenum, New York.

Charles-Dominique, P. (1976). "Ecology and Behaviour of Nocturnal Primates". Duckworth, London.

Charles-Dominique, P. and Hladik, C.M. (1971). *Terre et Vie*, 25, 3-66.

Chivers, D.J. (1973). *In* "Comparative Ecology and Behaviour of Primates" (R.P. Michael and J.H. Crook, eds), pp. 101-146. Academic, London.

Chivers, D.J. (1974). *Contrib. primatol.*, 4, 1-335.

Chivers, D.J. (1977). *In* "Primate Ecology: studies of feeding and ranging behaviour in lemurs, monkeys and apes" (T.H. Clutton-Brock, ed.), pp. 355-382. Academic, London.

Chivers, D.J., Raemaekers, J.J. and Aldrich-Blake, F.P.G. (1975). *Folia primatol.*, 23, 1-49.

Curtin, S. (1976). "Niche differentiation and social organization in sympatric Malaysian colobines". Ph.D. dissertation, University of California, Berkeley.

Curtin, S.H. and Chivers, D.J. (1977). *In* "The Ecology of Arboreal Folivores" (G.G. Montgomery, ed.). Smithsonian Institution, Washington.

Eisenberg, J.F., Muckenhirn, N.A. and Rudran, R. (1972). *Science*, 176, 863-874.

Gillon, D. and Gillon, Y. (1974). *Terre et Vie*, 28, 429-474.

Hladik, A. (1977). *In* "The Ecology of Arboreal Folivores" (G.G. Montgomery, ed.). Smithsonian Institution, Washington.

Hladik, A. and Hladik, C.M. (1969). *Terre et Vie*, 23, 25-117.

Hladik, C.M. (1975). *In* "Sociology and Psychology of Primates" (R.H. Tuttle, ed.), pp. 3-35. Mouton, The Hague.

Hladik, C.M. (1977a). *In* "Primate Ecology: studies of feeding and ranging behaviour in lemurs, monkeys and apes" (T.H. Clutton-Brock, ed.), pp. 323-353 and 481-501. Academic, London.

Hladik, C.M. (1977b). *In* "The Ecology of Arboreal Folivores" (G.G. Montgomery, ed.). Smithsonian Institution, Washington.

Hladik, C.M. and Hladik, A. (1972). *Terre et Vie*, 26, 149-215.

Hladik, C.M., Hladik, A., Bousset, J., Valdebouze, P., Viroben, G. and Delort-Laval, J. (1971). *Folia primatol.*, 16, 85-122.

Janzen, D.H. (1970). *American Naturalist*, 104, 501-528.

Leigh, E. (1977). *In* "The Ecology of Arboreal Folivores" (G.G. Montgomery, ed.). Smithsonian Institution, Washington.

Kay, R.F. (1975). *Amer. J. phys. Anthrop.*, 43, 195-216.

Moynihan, M. (1976). "The New World Primates". Princeton University Press, New Jersey.

Odum, E.P. and Odum, H.T. (1959). "Fundamentals of Ecology". Saunders, Philadelphia.

Raemaekers, J.J. (in prep.) Synecology of Malaysian hylobatids. Ph.D. dissertation, Cambridge.

Struhsaker, T.T. (1975). "The Red Colobus Monkey". University of Chicago Press, Chicago.

Whitmore, T.C. (1975). "Tropical Rain Forests of the Far East". Clarendon, Oxford.

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