Distribution Patterns of Tropical Plant Foods as an Evolutionary Stimulus to Primate Mental Development

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Primates are noted for their mental abilities but the selective basis for such traits has remained obscure. It is hypothesized that the element of predictability associated with the spatial and temporal distribution patterns of plant foods in tropical forests has served to stimulate mental development in primates taking much of their food from the first trophic level. Primates able to remember the locations and phenological patterns of a wide variety of plant foods could move directly to such foods when and where available without wasting time and energy in random search. This would enhance overall foraging success by lowering procurement costs associated with a varied and patchily distributed plant diet. Membership in a cohesive social unit, that utilized the same supplying area over many consecutive generations, would also enhance foraging success by serving to transmit important information about diet to close kin. Data on the foraging behavior of howler and spider monkeys are presented to test certain implications of this hypothesis. Similar selective pressures, but applied to foods from the second trophic level, may have been of critical importance in the mental development of hominids. [primates, evolution, intelligence, plant foods, *Ateles*, *Alouatta*]

Most primates show a remarkable capacity for learning and retention. As noted by Eisenberg (1973), what appear to set primate societies apart from those of other relatively long-lived and large-brained animals are particular sets of attributes related to the storage and retrieval of a great deal of independently acquired information about the environment. The complex brain of higher primates forms the basis for a plasticity of behavior that permits a wide variety of responses to a given situation (Napier 1970). Hominids are at the zenith of this trend and many hypotheses have been advanced as to why increasing mental complexity might have been favored in their evolution. Hunting is frequently singled out as a critical factor (Washburn and Lancaster 1968). According to this hypothesis, proto-humans living in savanna-mosaic areas during the Pliocene may

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have become increasingly dependent on animal protein in the diet. This dependency, in time, could have resulted in strong selective pressure toward increased hunting efficiency through cooperative hunting, food sharing, manufacture of tools and a symbolic system of communication (Hockett and Ascher 1964; Holloway 1967). It is indeed possible that selective pressures related to increased hunting efficiency may have served as an important stimulus in the evolution of the hominid brain. What is omitted from this and similar explanations, however, is why increasing mental complexity might have been favored in hominid evolution in the first place.

The key to understanding any adaptive trait comes not only from a knowledge of current selective pressures but also from the past evolutionary history of the species in question. New adaptations are not creations sui generis but rather are modifications of past adaptations. Some critical pressures in the evolutionary history of certain higher primates resulted in an increasing dependence on memory and learning—the hominid line represents an intensification of what must have been a preexisting trend in primate evolution.

Early primate field studies were largely concerned with the behavior of savanna-living primates since these were thought to offer possible analogues for hominid evolution (Washburn and DeVore 1961). It must be remembered, however, that proto-humans did not evolve in the savannas, but rather came gradually to them from tropical forests, bringing with them many millions of years of adaptations to forest conditions. To understand the origins of mental complexity in hominids, we must look not only at life in the savannas but also at life in tropical forests, for it is here that the first steps toward an increasing dependence on mental abilities must have been taken. What pressures on forest-living primates might have stimulated evolution along these lines?

Larger, forest-living primates today are all either partially or entirely primary consumers—that is to say, the bulk of their diet is taken from plant foods. In a forest, increasing body size apparently makes it uneconomical to specialize on limited, small, and discrete food particles such as insects (C. Hladik 1978). It seems reasonable to assume that the ancestral line leading to hominids may also at one time have been either partially or entirely dependent on plant foods. But, though tropical forests have often been viewed as unlimited sources of food for plant-eating animals, recent research has made it clear that this is a misleading assumption. Tropical forests are highly dynamic, fluctuating systems and often require dietary strategies of considerable complexity to meet the nutritional needs of an animal over all phases of an annual cycle. This is particularly true in the case of large-bodied primates eating a diverse set of plant resources distributed over a large home-range area.

It is my hypothesis that the extreme diversity of plant foods in tropical forests and the manner in which they are distributed in space and time have been a major selective force in the development of advanced cerebral complexity in certain higher primates.

FRAMEWORK FOR THE HYPOTHESIS

1. *Body size, diet, and home-range size.* Larger primates require absolutely more food than smaller primates. Thus, in general, they require a larger supplying area (Milton and May 1976). Young leaves are more patchily distributed in space and time in tropical forests than mature leaves; ripe fruit is more patchily distributed than young leaves (see below; see also Milton 1977a, 1980). Primates eating primarily young leaves should have larger supplying areas than those specializing more on mature leaves, while fruit specialists should have larger supplying areas than leaf specialists (with body size and all other considerations being equal) (Milton and May 1976; Clutton-Brock and Harvey 1977).

2. *Spatial distribution of potential plant foods.* Tropical forests are generally characterized by a high diversity of tree species. Most species have very low densities. An analysis of data collected on all trees 60 cm. and over in circumference breast height in a set of quadrats (6 one-hectare quadrats) representing 60,000 m.^{2} of lowland tropical forest in central Panama showed that 65% of all species encountered occurred less than once per hectare. Only one of the 135 different tree species identified in this study had a relative density in the total sample greater than 5%. When tested for pattern, data showed that most species tended toward a significantly clumped rather than random or uniform distribution (see Milton 1977a, 1980). Thus potential food sources for plant-eating primates in such forests can be described as patchy in space.

3. *Temporal distribution of potential plant foods.* Phenological data were collected on leaf, flower, and fruit production in this same lowland tropical forest for a five-year period. Each week the phenological status of 394 different trees representing 145 species was recorded. An analysis of these data showed that there were pronounced peaks and valleys in the production of seasonal items (new leaves, flowers, fruits) and that individual trees of most species generally showed some degree of intraspecific synchrony in phenology (Milton 1977a, 1980; Leigh and Smythe 1978). To quantify how long particular categories of seasonal dietary items might be available from particular species, I drew 12 species at random from the 145 species represented in the phenological sample and noted the months in which new leaves, fruits, and flowers, respectively, were observed on these species for one annual cycle. Young leaves were available on particular species for a mean of 6.8 months of an annual cycle, green and ripe fruits for 3.7 months, and flower buds and flowers for 2.7 months. Ripe fruits, however, were available on particular species for only 1.1 months. Further, these items were available on individual trees for even shorter periods of time: new leaves for a mean of 5.3 months, green and ripe fruits for 2.1 months, and flower buds and flowers for 1.8 months. Ripe fruits were available for individual trees for only 0.8 month. Examination of the nutrient content of some of these dietary items showed that in individual cases some of these items apparently were optimally edible for no more than 72 hours per annum (e.g., flush leaves of *Ceiba pentandra*) (Milton 1980). Thus potential foods for primates in such forests can be described as patchy in time and generally ephemeral in terms of optimal nutritional quality.

These features of plant foods in tropical forests should make it difficult for large plant-eating primates to specialize on only one or a few food species. An enormous supplying area would be required for such a specialist and dietary items would have to be available on a year-round basis. Thus, in general, larger primates are under considerable pressure to diversify their diets and show considerable dietary flexibility.

4. *Predictability in space and time.* Though plant foods, particularly preferred seasonal foods such as young leaves, flowers, and fruits are very patchily distributed in space and time in tropical forests, they share an important feature that could work to the advantage of a primary consumer. This is the degree of *predictability* associated with their spatial and temporal distribution (Milton 1977b, c). Once the location of a particular food tree is known, it becomes a dependable seasonal resource in terms of its location for the lifetime of a primate. Further, though each tree species has a particular phenological pattern, most such patterns show some degree of predictability as well (Augspurger 1978). This element of predictability with respect to the spatial and temporal distribution of potential foods helps to *counteract* the patchiness component associated with such a diet. It may have served as a critical stimulus in the development of cerebral complexity in higher primates for it places them under somewhat different selective pressures than secondary consumers with respect to certain important features of their foraging behavior.

5. *Food search efficiency.* Secondary consumers, carnivores, typically are faced with

mobile and evasive prey items which must first be located and then pursued and captured. Models dealing with foraging strategies of secondary consumers generally emphasize the importance of *both* the search and the pursuit components of foraging (MacArthur and Pianka 1966; Schoener 1971). Primary consumers, however, do not have to devote any notable expenditure of time or energy to the pursuit of prey since their foods—leaves, fruit, and flowers—are sessile and pursuit costs are small and similar for all items (Westoby 1974). We might therefore predict that primary consumers are under strong selective pressure with respect to increased food search efficiency since this should be a feature of major importance in overall foraging success. Increasing food search efficiency would lower foraging costs related to both time and energy expended in foraging. It would also reduce the risk of exposure to predators. In this respect, the predictability in space and time of particular items of diet could work to the advantage of primary consumers. Rather than wasting time and energy seeking out patchily distributed foods in a random fashion, such animals could move directly to particular dietary items when and where they were available.

How might selection function to improve food search efficiency when dealing with patchily distributed plant foods? It seems maladaptive in general, given the dynamic nature of tropical forests, to try and code a great variety of dietary information genetically. Rather, what appears to be required is a great deal of behavioral flexibility—flexibility to respond to continually changing forest conditions. Increasing mental complexity with a strong emphasis on learning and retention is one direction selection could take. This would accomplish the dual purpose of improving an animal's ability to recognize and remember the locations and timing of a variety of preferred foods as well as provide the required behavioral flexibility. In time, "wise" primates that could seek out the most nutritious foods with the least expenditure of time and energy should outcompete "less wise" primates relying primarily on a strategy of chemosensory cues or random search.

For maximum efficiency, some means other than genetic coding should also be developed to transmit such essential information to offspring since such foods are not only patchy within home-range areas but also vary from one home range to another (Richard 1977; Milton 1977a, 1980). Membership in a relatively cohesive social unit, that utilized essentially the same supplying area over successive generations, would greatly enhance efficient food search by serving to transmit information (either through imitation, learning, or a combination of the two) on types and distribution patterns of preferred foods to new generations of kin.

If the implications presented above are valid, when we examine the behavior of forest-living primates that are primary consumers, we should find that they fall along a continuum. All else being equal, those primate species dependent on the most hyperdispersed and patchy foods should show greater evidence of mental development than primates eating more uniform dietary resources. To test this hypothesis, I examined the diet and foraging behavior of two primate species, both primary consumers, living sympatrically in the lowland tropical forest on Barro Colorado Island in central Panama and then, using data from other sources, I related my results to estimates of their relative cranial capacities as well as the cranial capacities of other primate species. The two species selected for detailed examination were howler monkeys (*Alouatta palliata*) and spider monkeys (*Ateles geoffroyi*).

HOWLER AND SPIDER MONKEYS

Howler and spider monkeys are large Neotropical primates, averaging approximately the same adult body weight (7-9 kg.). They are found living sympatrically over much of their extensive geographical range. Both species are highly arboreal, eat an exclusively plant-based diet, and have relatively unspecialized digestive tracts when compared with

certain other plant-eating primates, particularly the leaf-eating colobines and indriids (C. Hladik 1967; Milton, Van Soest, and Robertson 1980). Both species live in relatively closed mixed social groups; strange conspecifics are generally repelled (Milton 1977a, 1980; Klein and Klein 1977). My own long-term data indicate that a high degree of interrelatedness exists between troop members of both species.

Troops of both species live in specific home-range areas that overlap with home ranges of conspecific troops (Milton 1977a, 1980; Klein and Klein 1977). My data indicate that these home ranges are used over various generations by members of the same social network. Therefore animals living in a particular section of the forest may be the descendents of animals living there some generations ago. Thus, in a great many important respects, these two primate species share common characteristics.

Howler monkeys and spider monkeys differ considerably, however, in dietary focus. Though both species eat primarily leaves and fruit, howlers are more folivorous while spider monkeys are more frugivorous. On Barro Colorado howlers spent an annual average of 48% of feeding time eating leaves, 42% eating fruit, and 10% eating flowers and flower buds. At certain times of the year, however, when fruit was in short supply, howlers switched to a diet consisting almost entirely of leaves (Milton 1977a, 1980). At such times, they spent as much as 90% or more of daily feeding time eating only leaves. Similar high percentages of leaf-eating over prolonged periods of time have been reported for howler monkeys living in other habitats (Glander 1975, 1978).

In contrast to howler monkeys, spider monkeys on Barro Colorado spent an annual average of 72% of daily feeding time eating fruit, 22% eating leaves, and 6% eating flowers and flower buds. When fruit was scarce in the forest and howlers turned to a heavily leaf-based diet, spider monkeys still were able to spend a daily average of 60% of feeding time eating fruit by carefully seeking out what appeared to be all available fruit sources in the habitat. Hladik and Hladik (1969) have estimated that 80% wet weight of the annual diet of spider monkeys on Barro Colorado comes from fruit pulp; at no time do these monkeys become strongly dependent on leaves. Similar feeding data have been obtained for spider monkeys living in other locales (Klein and Klein 1977).

As noted above, fruit is a more patchily distributed food resource in tropical forests than leaves—even young leaves. This difference is reflected in the considerable difference between the two species in the size of their supplying area. On Barro Colorado, where troop size for howlers averages some 19 animals, average home-range size is 31 hectares. In contrast, one troop of 15 spider monkeys uses a home-range area of around 800 hectares. Supplying areas of similar size have been reported for similar-sized troops of *Ateles belzebuth* in evergreen forest in Colombia (Klein and Klein 1977).

Thus spider monkeys are faced with a far more complex problem than howlers with respect to locating their food sources since, in effect, they are dealing with a supplying area over 25 times as large. How might selection have operated on the foraging behavior of these two primary consumers so as to improve their respective foraging efficiencies?

HOWLER MONKEYS: THE SOCIAL GROUP AS THE INFORMATION UNIT

Data show that over an annual cycle, howlers eat foods from more than 150 different plant species, primarily large trees. An average of seven different plant species are eaten each day and daily turnover of species averages 51%. Chemical analyses confirm that howlers generally choose foods of a high nutritional quality. Given the wide variety of potential foods in tropical forests, how do howler monkeys know what to eat and where to find it?

Data from several lines of investigation indicate that food choices are determined in large part by learning. Howler troops living in different areas of the Barro Colorado forest had different dietary traditions that were not totally explicable in terms of the relative abundances of particular tree species or relative availability of foods in each area (Milton 1977a, 1980). Similar patterns have been reported for other primate species eating strongly plant-based diets (e.g., Japanese macaques, Kawamura 1959; chimpanzees, van Lawick-Goodall 1973; sifakas, Richard 1977). Further, temporarily caged wild howlers consistently refused to eat nutritious but unfamiliar plant foods such as bananas, apples and lettuce even though they were obviously hungry; they did, however, readily accept all familiar wild foods offered them (Milton, Van Soest, and Robertson 1980). Young howlers raised in captivity will eat a wide variety of different foods, including eggs, cottage cheese, and meat. This too suggests that learning plays a critical role in determining what a wild adult howler will perceive as food.

Young howlers do not have a protracted period of maternal dependence. By six months of age a young howler, though still nursing, locomotes independently and feeds on solid foods with the troop. A long period of strong maternal dependence has been correlated with the need for a long period of information input and learning (Bartholomew and Birdsell 1953; Schultz 1968). Though howlers eat a diverse diet, young animals apparently do not have to maintain long-term close bonds with their mothers to master the dietary traditions of their area. I hypothesize that this is at least partially because they are part of a tight-knit social system. Members of a howler troop tend to perform all activities as a unit—when one animal is feeding, the rest of the troop is generally feeding too, typically in the same tree. Thus all a young howler has to do is stay with the troop and do what other members do in order to learn what to eat and how to locate such foods efficiently. After spending several years in the same home range, a young howler should master, through imitation and learning, the complexities associated with a diverse and patchily distributed diet.

Given that howler monkeys gradually learn to recognize preferred foods, the question remains as to whether they take advantage of the element of predictability associated with their food resources in order to locate them with a minimal expenditure of time and energy. There is considerable evidence that they do. First, data show that howlers tend to concentrate the bulk of their foraging activities in parts of their supplying area where the densities of preferred food species are relatively high. This increases their probability of locating preferred foods. Howlers show patterns of goal-directed travel and further can apparently recognize particular tree species as individuals and remember either their locations or routes leading to them (Milton 1977a,b,c). To quantify whether, in fact, howlers were locating sources of preferred food more frequently than would be expected from a pattern of random search, travel routes and encounters with individuals of two important food species (*Ficus yoponensis* and *Ficus insipida*) were analyzed for one study troop for an annual cycle. It was found that howlers were significantly more efficient at locating sources of these preferred foods than if they had been traveling at random (Milton 1977b,c, 1980).

As leaf-eaters, howlers have relatively small home ranges, amenable to a program of constant monitoring. On Barro Colorado, average home-range size is 31 hectares. The howlers' success at food location appears to depend, in large part, on the adherence to very regular patterns of activity in which some 10% of the day is spent moving an average of 460 meters through their supplying area over what appear to be traditional arboreal pathways connecting important clusters of food trees. Howlers may therefore not have to remember the types and locations of preferred foods, at least for more than a short time. (Some observational evidence, however, indicates longer-term memory.) All howlers have to do is learn these pathways and keep moving over their home range in such a way as to maximize probabilities for encounters with preferred foods. For howler monkeys,

membership in a cohesive social group, living in a clearly delineated home-range are
and performing most essential activities as a unit appears to provide the mechanis
whereby essential information on dietary traditions and the locations of preferred food
are efficiently transmitted from one generation to another.

SPIDER MONKEYS: THE INDIVIDUAL AS THE INFORMATION UNIT

Like howlers, spider monkeys take foods from a wide variety of plant species and use
number of different food species each day. They, too, seek out seasonal foods of relativel
high nutritional quality (Milton 1981). However, in various important respects the fora
ing behavior of spider monkeys differs considerably from that of howlers. As note
spider monkeys are very strongly frugivorous. Apparently in response to selectio
pressures related to the patchy distribution patterns of their principal dieta
resources (ripe fruit), spider monkeys, unlike howlers, do not forage as a cohesive soci
unit. Rather, in a manner analogous to chimpanzees, spider monkey troops show a flui
grouping structure and members are often found foraging in small subgroups. Lone in
dividuals are also encountered.

Young spider monkeys, in contrast to howlers, have an extensive and protracted perio
of strong maternal dependence. They apparently require a far longer period of matura
tion and development to master essential foraging skills. At 24 months of age a youn
spider monkey may still be carried for long distances by the mother and is still nursing. I
addition, female spider monkeys spend time with their young offspring carrying o
behaviors that appear to teach immature animals how to travel alone along foragin
routes. A female spider monkey will begin to move along a foraging route but will then s
down. Eventually her infant grows tired of waiting and moves forward away from her
short distance through the trees along the route. The mother will then get up and mo
along behind the infant, reinforcing its independent locomotion through the trees in t
position of leader, *not* follower. This can be a time-consuming process. It requires what
human observer would describe as considerable patience on the part of the mother, wh
being hungry, should prefer to move rapidly to food trees rather than sit for man
minutes waiting for her offspring to take the traveling initiative. This type of behavi
appears to represent active teaching of the infant by the mother.

Since spider monkeys are generally found in small subgroups, a young spider monk
probably acquires most early dietary information from its mother. Many food species a
apparently learned through imitation but there is evidence that spider monkeys also a
quire new dietary information by direct experimentation. I have found that capti
young spider monkeys accept new foods far more readily than young howlers; capti
adult spider monkeys also readily accept any palatable novel food. There may be a sele
tive basis both for the flexibility of spider monkeys and the conservatism of howlers. A
fruit eaters, spider monkeys are not likely to encounter toxic chemicals in most foo
since ripe fruits are generally low in such substances. Leaf-eating howlers may often e
counter toxic chemicals since leaves are generally high in such substances (Milton 1979
Further, since spider monkeys tend to forage alone or in small subgroups, they may oft
encounter rare, unknown but palatable fruit sources. It may be advantageous for spid
monkeys to show greater behavioral flexibility than howlers with respect to sampling ne
foods since the risks are low and the gain could be considerable.

Data show that spider monkeys strongly utilize the element of predictability to impro
food search efficiency. Like howlers, they often travel over the same arboreal pathwa
through the forest. Further, their travel invariably seems goal-directed; single animals o
subgroups or the entire troop will move directly from one individual of a fruiting speci
to another, often traveling a considerable distance between fruiting trees without sto

ping to eat along the way. The following day one or two of the same trees may be revisited by various spider monkeys and from four to eight new individuals of the same fruiting species added to the day route by moving over a route that minimizes travel distances between such fruiting trees. These data show that spider monkeys know the locations of particular trees, recognize them as individuals and realize that when one individual of a species is producing ripe fruit that other individuals of this species are probably producing it as well. It further suggests that spider monkeys are capable of formulating a travel route in advance that takes them to a number of different fruiting individuals over the course of a normal day's travel such that they do not double back and cover areas already visited.

Given the distribution patterns of their resources, it is apparently most efficient for spider monkeys to forage in small subgroups rather than in one large unit like howlers (see also Klein and Klein 1977; Wrangham 1977). Each adult spider monkey would appear to use its own particular subset of the total pool of resource information represented by the troop to locate preferred foods. By foraging in small subunits, each spider monkey should obtain a more nutritious diet than otherwise would be the case. Many of the tree species favored by spider monkeys (e.g., *Spondias mombin, Dipteryx panamensis*), unlike the fruiting trees favored by howlers (i.e., *Ficus* spp.), ripen only a portion of their fruit crop each day. By dispersing over a wide area, and visiting a large number of different individuals of the same fruiting species each day, each spider monkey may obtain a better quality diet than if all members of the troop used the same few trees. Further, spider monkeys eat absolutely more fruit each day than howlers (Milton 1981). Their greater overall fruit requirement may also best be served by using many rather than one or a few fruiting trees each day.

Thus spider monkeys would appear to be under somewhat different selective pressures than howlers with respect to certain important features of their foraging strategy. There appears to be far more pressure on them *as individuals* to learn to recognize and remember types and locations of a great many different food species and to be able to add to this number by showing considerable behavioral flexibility. Spider monkeys also show a more complex set of social behaviors than howlers including a rich repertoire of facial gestures, elaborate bouts of allogrooming and various distinctive vocalizations, some of which carry long distances and appear to convey information of a dietary nature to members of the troop in other parts of the home range.

DISCUSSION

If, as hypothesized, a more patchily distributed plant-based diet is, in some manner, correlated with advanced mental abilities in primates, all else being equal, spider monkeys should show more evidence of mental development than howlers since they are dealing with a more complex foraging matrix. One way of approaching the question of mental development is to examine the absolute and relative brain size of each species. A study by Quirling (1950), which examined brain size in a number of primate species, showed that mean brain weight for 63 male and female *Ateles* was 107 grams ($\bar{X}$ body wt. = 7.6 kg.). In striking contrast, mean brain weight for 28 male and female *Alouatta* was 50.34 grams ($\bar{X}$ body wt. = 6.2 kg.). Bauchot and Stephan (1969) also showed that mean brain size for spider monkeys was almost double that of howlers. Jerison (1973), who compared both relative brain size (encephalization quotient (EQ) = the ratio of an animal's actual brain size to its "expected" brain size based on body size (see Jerison for a full discussion of techniques used in computing encephalization indices) and relative neural complexity for a large number of primate species, found that species of *Ateles* showed a relative brain size and degree of neural complexity approximately double that of *Alouatta* species.

Since howler monkeys eat considerable foliage, it might be assumed that the difference in relative brain size between the two species is an artifact effect produced by the presumably greater weight of the howler digestive tract. However, data compiled on the relative surface area of different sections of the digestive tract of howler and spider monkeys show that only in the area of the large intestine is there any notable difference in size between the two species (C. Hladik 1967; Milton 1981). Further, field observations suggest that spider monkeys consume a greater volume wet weight of food per day since they spend a greater percentage of their daylight hours feeding than howlers and spend more time eating fruit which generally can be ingested approximately twice as rapidly as leaves per unit wet weight (Milton 1980). Therefore, though there is some difference in gut size between the two species it does not appear sufficient to account for the considerable difference in brain weight between them (see Leutenegger (1973) for a discussion of exponents of allometry for brain/body size in primates).

It is recognized that indices of relative brain size as well as measures of neural complexity do not necessarily reflect relative mental abilities. The problems inherent in using such indices as evidence of increased mental abilities have been the topic of many elegant and thoughtful discussions as, for example, those of Jerison (1961, 1963, 1973), Holloway (1973), and Gould (1975). Avoiding speculation as to the precise significance of larger brain size in spider monkeys, it does appear clear that selection has favored an increase in brain size in this lineage far more than in howlers. The brain is an expensive organ to maintain and its considerable size in spider monkeys must in some manner be compensated for by benefits accrued. The most striking difference between spider monkeys and howler monkeys in terms of their basic ecology is their different dietary focus. Most other behavioral differences as well as many morphological differences seem secondarily related to this fundamental difference in diet. Selective pressures related to increased efficiency in exploiting an extremely patchily distributed plant-based diet would appear to be the most likely factor initially involved in the cerebral expansion of the *Ateles* lineage (For an interesting discussion of encephalization ratios of various divisions of the brain in a wide range of primates see Douglas and Marcellus (1975), who conclude "man must have a platyrrhine ancestry . . . more like that of an American wooley or spider monkey than like that of either the chimpanzee or the gorilla" [p. 179].)

Turning from a consideration of two primate genera to a wider examination of many primate genera, the same basic trend can be discerned. The comparative charts of Jerison (1973) present data on primate body size, brain size, and indices of cranial size and neural complexity. When viewed with respect to dietary focus, these indices offer support for the hypothesis that primate groups exploiting a more complex foraging matrix show greater evidence of cerebral complexity. Further, a recent paper by Clutton-Brock and Harvey (1980), which uses a measure of encephalization specifically designed to avoid some of the problems pointed out by Jerison (1973) (i.e., formula of Clutton-Brock and Harvey (1980); comparative brain size, CBS, (for a given genus) = log (brain wt.) − (elevation for Family + slope for Family × log (body weight)) shows that, in general, more strongly frugivorous primates show a trend toward greater cerebral expansion than more folivorous genera. For example, the primarily folivorous Indriidae show a lower comparative brain size than the more frugivorous or omnivorous Lemurinae. *Alouatta*, the most folivorous cebid, shows the lowest value of all cebids tested. The leaf eating Colobinae generally show lower values than the more frugivorous or omnivorou Cercopithecinae such as *Cercocebus*. The gelada baboon, *Theropithecus*, an animal that exploits a relatively uniform grassland substrate, shows a lower value than those terrestrial primates eating more hyperdispersed and patchy foods such as *Macaca* or *Papio*. The Hylobatidae and Pongidae show very high values and most are highly frugivorous a well (see Clutton-Brock and Harvey 1980).

As noted, all extant primate species take at least some portion of their diet from plants. Since all larger-bodied anthropoids are strongly dependent on plant foods, all of them face the same basic problems with respect to food search efficiency. But some dietary groups, particularly larger-bodied frugivores, tend to face somewhat more complex problems in terms of efficient food location than other dietary groups and these are the primates generally exhibiting maximal cerebral expansion. Interestingly enough, a recent study of the relative cranial volumes of members of the order Chiroptera showed that nectarivores and frugivores (taking foods from the first trophic level) had relatively larger cranial volumes than sanguivores, insectivores, or carnivores (taking foods from the second trophic level) (Eisenberg and Wilson 1978). Some features associated with hyperdispersed and patchy food resources, particularly plant resources, therefore appear to stimulate an increase in brain size across ordinal boundaries though the precise functional reason for such an increase has not as yet been determined.

In turning to a consideration of factors involved in the mental development of hominids, it is not difficult to imagine that an intensification of the process I have just described for spider monkeys, but in a savanna-mosaic setting, might produce a primate line even more strongly dependent on mental abilities. Comparative data show that savanna-living primates have home-range areas, both on an individual and on a troop basis, that are relatively larger than those of forest-living primates of similar body size (Milton and May 1976). Therefore, australopithecines, estimated to have been around the same size as extant chimpanzees, may have had very large home-range areas. Data indicate that the cranial capacities of australopithecines are relatively somewhat larger than those of extant pongids; further, the brain appears to have been organized along essentially human rather than pongid lines (Holloway 1973; Leutenegger 1973). The added complexity of efficient food location over a much larger home-range area, when combined with new logistical problems such as the probable need for a constant water supply (an additional challenge in terms of foraging efficiency since it can limit effective day range) and defense from terrestrial predators may have been sufficient to account for the relatively larger brain size of australopithecines. The added burden imposed by the need to communicate an increasingly complex set of learned behaviors to offspring may also have stimulated some modification of brain organization.

Early members of the genus *Homo* show a clear increase in relative cranial capacity over the australopithecines (Pilbeam and Gould 1974; McHenry 1976). This indicates that some shift in behavior of early members of this lineage favored an increase in brain size. As has been suggested, a climatic or other environmental change may have altered the australopithecine resource base in certain savanna-mosaic areas, particularly with respect to primary productivity, such that new foraging behaviors were favored by selection. Pilbeam and Gould (1974) have speculated that all australopithecines were strongly dependent on plant foods. The smaller body size of *Australopithecus africanus* implies a need for more concentrated, higher quality dietary resources than would be required by the larger bodied *A. robustus* (see Parra 1978; Milton 1979; Van Soest 1981 for discussion of the nutritional needs of herbivores of different body size). Certain groups of small-bodied australopithecines may well have turned to scavenging and/or hunting foods from the second trophic level to augment often scarce or nutritionally incomplete vegetable foods.

Both carbohydrates and proteins are essential nutrients. Carbohydrates taken into the body in excess of daily requirements can be stored by the body as fat and later utilized in times of energy shortage. Protein, however, is an essential nutrient that cannot be stored as such by the body except in minute quantities (Maynard and Loosli 1969). Proteins containing essential amino acids in the proper complements and proportions must be taken into the body via the food each day to provide the materials for human protein synthesis. Meat provides the proper amino acids in the proper complements and proportions for human protein synthesis. It is not improbable (and has often been suggested) that certain members of the australopithecine lineage may have become increasingly dependent on animal protein in the diet. Presumably, for many millions of years prior to this point, the ancestral line leading to hominids had been oriented strongly toward the efficient location of sessil plant resources, first in a tropical forest environment and perhaps later in a savanna-mosaic environment. The entire organization of the brain and the skills selected for by such a dietary focus were geared toward the exploitation of this type of a diet. A shift in behavior, favoring the increasing ability to exploit mobile foods from the second trophic level, particularly to hunting down and killing such prey with sufficient efficiency so that it could be depended on in the diet, should therefore have required some major changes in certain areas of the brain. With respect to diet, the ancestral line leading to hominids appears somewhat rare in that its members have apparently changed trophic levels not once but twice during their evolutionary history—first from basal insectivore to plant-eater and then from plant-eater to omnivore with a strong orientation toward meat as a protein source. It is difficult to say just what ultimate effect a change in trophic levels might have on an organism, but given the variety of factors, both behavioral and morphological, bound up in diet, such a change might well have a profound effect.

In this context, it is interesting to note that Marks (1976) in his examination of the hunting economy of the Valley Bisa of Zambia gives estimates of the success rates of various nonhuman hunting carnivores. Most show a very low rate of success. For example, in five years of observation on four species of European raptors, Rudebeck (1950, 1951) found that only 7.6% of the 688 observed attempts of these birds to kill prey were successful. Mech (1966) reports that only 7.8% of the moose he observed tested by wolves were actually killed. The two most successful hunters listed in Mark's review are the East African hunting dogs with a success rate of 85% (Estes and Goddard 1967) and the mountain lion with a success rate of 82% (Hornocker 1970). Early hominid hunters could not emulate the hunting prowess of the solitary mountain lion but could well have emulated the group hunting behavior of wild dogs. These data suggest that the cooperative behavior of many individuals, when directed toward prey species also consisting of many individuals in a cluster (i.e., plains-living ungulates) can have a very high rate of success. In addition, as pointed out by Jerison (1973), mobile prey items typically are evolving at the same or an even faster rate than their predators. Lacking the powerful jaws and claws characteristic of hunting carnivores and already *predisposed* to solve their dietary problems primarily through behavioral rather than morphological or physiological adaptations, these hunting hominids may have depended heavily on mental acuity to outwit and capture prey.

The role of protein nutrition, particularly with respect to the needs of pregnant and lactating females and immature individuals, has been stressed as an important factor affecting the health of the resulting adult population (Chaney and Ross 1971). Without belaboring the point, it seems clear that a hominid population able to secure a dependable source of high quality protein would be in a strong position in terms of fitness potential when compared with other hominid populations with a more precarious nutritional substrate (see also Holloway 1967).

Single-factor hypotheses are generally inadequate to explain complex evolutionary phenomena due to the number of variables typically involved. But such hypotheses can direct attention toward critical types of behavioral changes, such as, for example, a shift in diet leading ultimately to a change in dietary focus or trophic level (Szalay 1968). Such a behavioral change, in combination with the spiraling sequence of other responses typically involved in such a change (Holloway 1967; Gabow 1977) can result in the reorganization or modification of many existing traits as well as the strengthening of preadaptations of utility in the efficient performance of the new behavior. Since a trend in increased cranial capacity can be noted in primate groups strongly dependent on patchily distributed plant foods, it is probable that the ancestral line leading to hominids received its original mental impetus from similar selective pressures. In support of this hypothesis it should be noted that evidence suggests most early Miocene hominoids occupied a frugivorous dietary niche (Kay 1977). Thus members of this superfamily have an extremely long evolutionary history bound up with the exploitation of foods of this type. It also seems probable that a shift in dietary focus, which strongly emphasized mobile foods from the second trophic level as well as sessile foods from the first, may well have set in motion the evolutionary process ultimately resulting in the mental development and behaviors characteristic of members of the genus *Homo*. A dietary focus of this nature would facilitate the acquisition of adaptations such as a division of labor and food sharing, two behaviors that have been viewed as critical steps leading ultimately to human social systems based on reciprocity (Isaac 1978).

NOTES

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