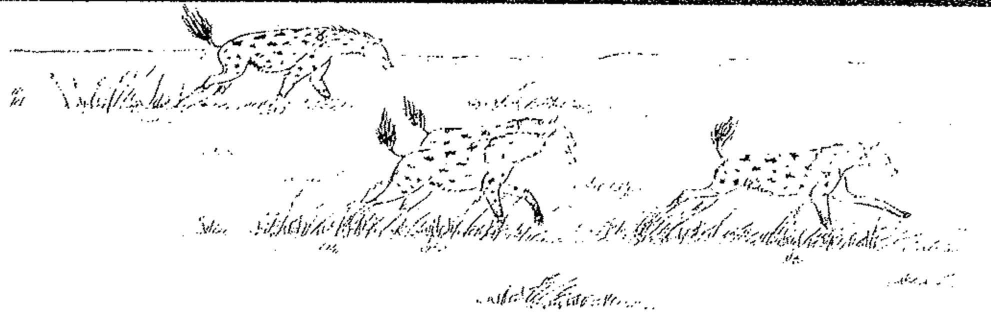
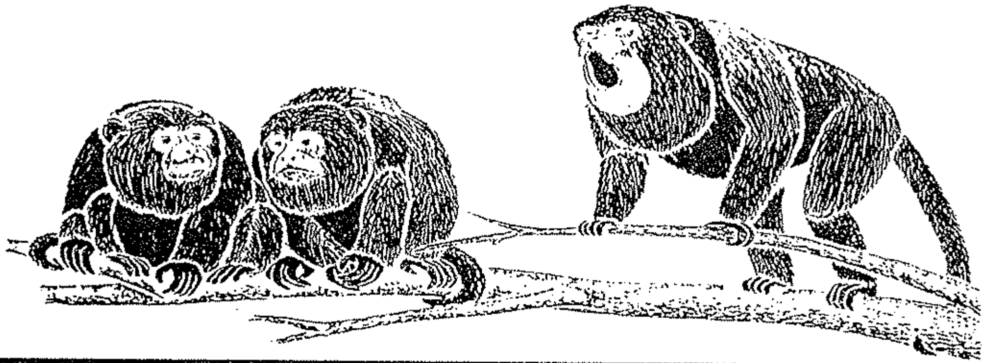
On the Move

How and Why Animals Travel in Groups





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How and Why Animals Travel in Groups

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CHAPTER FOURTEEN

Quo Vadis? Tactics of Food Search and Group Movement in Primates and Other Animals

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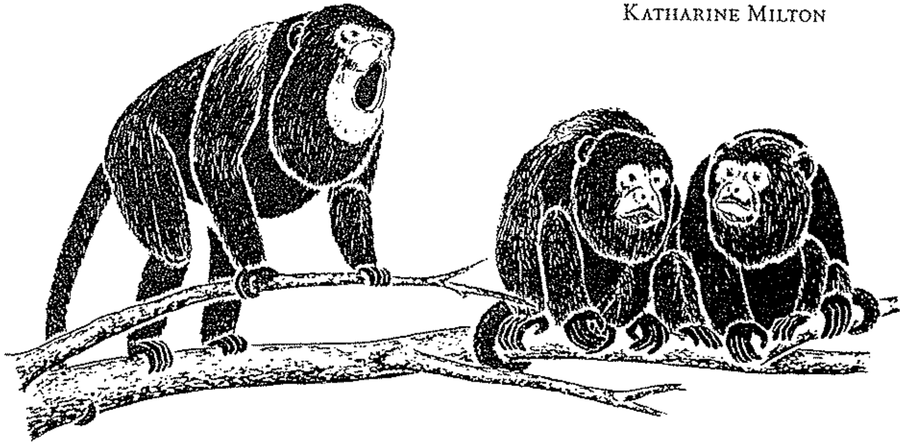

> When comparative psychologists want to study a particular cognitive skill . . . they would do well to search the animal kingdom for taxa that solve similar problems.
>
> (P. Tyack, 138) 1993

The question posed in this section of this volume is whether taxonomic differences in the group movements of primates reflect differences in the ways in which species process information. In primates, group movement (travel) almost invariably occurs in the context of foraging. Thus, to explore this question, I begin with a detailed analysis of food search behavior in mantled howler monkeys *(Alouatta palliata),* then use information generated by this analysis to examine features of group movement in four other primate taxa: spider monkeys, chimpanzees, bonobos, and human foragers. I then extend this examination beyond primates, seeking common attributes of food-associated group movement and cognitive processes across ordinal boundaries by looking at the foraging and travel behavior of members of two other taxa; namely, dolphins and parrots.

The different sections of this chapter are somewhat disjunct because in each case, the type and amount of available information varied. For howler monkeys, I had detailed field data that could be used to examine quantitatively some features of foraging behavior, whereas for other taxa, both primate and nonprimate, I relied largely on information from the literature, generally extensive. When I turned to foraging behavior and its associated cognitive processes in my own species, the amount of potentially relevant data increased exponentially. For this reason, comment on group movement and food search behavior in human foragers is limited to a small subset of case studies.

Background

In 1974, when I began my study of the dietary ecology of wild howler monkeys *(Alouatta palliata)* in Panama, primatologists working with more "lively" species often remarked that they couldn't understand how I could spend so much time with such an inactive monkey. Didn't I get bored? they asked. Couldn't I just predict most events in a howler monkey's day? Suffice it to say that I did not find howlers predictable (in my view, the predictable animal is extinct since predators and parasites would have little trouble tracking a predictable organism), and probably for this reason, did not find them boring. Particularly in the early months of my study, the monkeys were continually eating food plants that were new to me, and it was extremely rare for a sample period to pass in which I was not led to one or more huge fruiting or flushing trees whose existence I had never suspected. Indeed, I often found myself hard pressed to keep up with all of the information my "inactive" study subjects were continually supplying in terms of their dietary activities.

By the conclusion of my one-year study, I'd learned the general extent of the home range area of each of my two study troops and where clusters of productive food trees could be found such that, when a howler troop began to travel, I could at times predict where they were going and what they might eat when they got there (Milton 1977, 1980). But compared with the monkeys, I was still largely a novice at finding rich food sources. Furthermore, it was still not uncommon for my study subjects to travel in a directed manner to huge fruiting trees whose existence I had never suspected.

The lowland tropical forest on Barro Colorado Island (BCI) in Panama, where my study took place contains about 200 large (≥ 60 cm in circumference breast height, CBH) trees per hectare (100 × 100 m) as well as numerous smaller trees, saplings, shrubs, bushes, vines, and other vegetation. Visibility, both on the ground and in the canopy, is limited, and thus my lack of information as to the locations of some of the thousands of trees in the 32-hectare home range of my two study troops isn't that surprising. After all, I spent only 5 days per month with each of my two study troops. If I had spent an entire year with only one troop, following it about the forest every day for 365 days, I'm sure I would have learned considerably more about the locations of most preferred fruit trees in its home range. But even based on only 10 days of fieldwork per month, it was clear that howler monkeys had a food search strategy that often appeared goal directed.

Goal-Directed Travel

When howlers set out to travel (actively moving from tree to tree for a distance of 100 meters or more), they did not move about the forest in a hesitant or random manner, but rather traveled slowly but steadily through the canopy in single file, typically finishing their journey at a large tree that contained edible fruits or a large crop of new leaves—a tree that could not be seen from our starting point and whose location and phenological condition appeared to be anticipated by the monkeys before they began to move (Milton 1980; see also Smith 1977). As this happened with new leaf as well as fruit crops, it seemed doubtful that olfactory cues were being utilized, though this remains to be demonstrated (Able 1996; Garber, chap. 10, this volume).

Howler monkeys are not the only primates that have been observed to travel to food trees in this manner. Many primatologists report that their study subjects travel confidently and directly to food sources located some distance away from the initial starting point (Kummer 1968a; Sigg and Stolba 1981; Garber 1989; Garber, chap. 10, this volume; Byrne, Whiten, and Henzi 1990; Byrne, chap. 17, this volume; Boinski 1996; Boinski, chap. 3, this volume). In particular, Garber's (1989) study of foraging patterns of two *Saguinus* species in Peru showed that a high percentage of travel to food trees was goal directed and that animals could move directly to the nearest conspecific neighbor of a particular fruiting tree over long distances; the monkeys could also reach these particular trees by various arboreal pathways, depending on where they were in their home range when travel was initiated.

In the laboratory, controlled experiments have shown that some monkey and ape species have well-developed and highly flexible memory strategies for remembering food locations (Menzel 1973a; MacDonald and Wilkie 1990; Gallistel and Cramer 1996). Experimental subjects of several species also minimized the travel distance to food locations even though there were no obvious experimental constraints on either time or distance traveled (MacDonald and Wilkie 1990; Gallistel and Cramer 1996). As goal-directed travel behavior and computation of the optimal (most efficient) travel route to one or more foraging goals has been demonstrated for primates both in the wild and under captive conditions, the problem thus becomes one of determining how this might be accomplished and what benefits may accrue to its practitioners as a result. The theory of foraging strategy offers testable predictions that aid in such investigation.

Foraging Strategy Theory

The theory of foraging strategy (or optimal diet theory) predicts that the efficiency of foraging is maximized by natural selection (Schoener 1971). In early models associated with this theory, the optimal diet was viewed as the set of food choices that maximized net energy yield/foraging time, or some other units believed to reflect fitness. The usual variables were the caloric value of foods and the time spent in search and pursuit of edible prey. However, researchers interested in the foraging behavior of plant-eating animals soon pointed out that the foods of primary consumers (plant eaters) differed in certain important respects from those of secondary consumers (flesh eaters) and that such differences often called for somewhat different foraging solutions (Westoby 1974; Pulliam 1975; Pyke, Pulliam, and Charnov 1977; Milton 1980, 1981a,b; Sih and Milton 1985).

One important difference is that for secondary consumers, potential foods (animal prey) tend to be mobile and evasive, while the plants and plant parts eaten by primary consumers are sessile—tree locations tend to be predictable over the lifetime of a given primate. Thus, for primary consumers (and most anthropoids and some prosimians can be viewed in this light: Schultz 1969; Milton 1980, 1987), the pursuit of mobile prey is generally not the most critical variable in foraging efficiency (Westoby 1974), and indeed, in many cases (e.g., gorillas, howler monkeys, spider monkeys), is not important at all.

A second important difference between the foods of secondary and primary consumers is that the foods of primary consumers vary far more in their nutritional (and toxic) content than foods from the second trophic level (Freeland and Janzen 1974; Westoby 1974; Milton 1980). Leaves, for example, particularly young leaves, tend to be high in protein though low in available energy; in contrast, ripe fruits tend to be high in digestible energy but low in protein (Milton 1980, 1981b). Yet primates require both adequate protein and energy (as well as other nutrients and water) to remain in good health.

Because of the characteristics of their foods, the foraging objective of many primary consumers should be to optimize the nutrient mix within a given fixed bulk of food, rather than simply maximizing net energy yield/foraging time (Westoby 1974). Being selective in feeding, however (selectivity being called for to obtain the best possible dietary mix of high-quality plant parts), would increase the time spent searching for food (since high-quality plant parts are generally less abundant than low-quality plant parts). This would increase foraging costs, both directly in terms of the energy expenditure required to find high-quality foods and indirectly in the sense of opportunity lost—time spent seeking food could be devoted to some other beneficial activity, such as seeking out mates. Prolonged food search could also increase the risk of exposure to predators (e.g., van Schaik 1983; Terborgh and Janson 1986) or accidents (Milton 1980).

For all of these reasons, we would predict that primary consumers might exhibit features (both behavioral and morphological) that function to reduce the costs of their selectivity (Schoener 1971; see Milton 1980, chap. 6 for discussion of behavioral and morphological features that reduce the costs of selectivity in *A. palliata*). In particular, when preferences for certain dietary items are marked and such items are patchily distributed in space and time—which is precisely the case for most higher primates—selection should favor behaviors that improve the forager's probabilities of encountering desirable high-quality foods with the lowest expenditure of time or energy. Examination of the food search strategy of howler monkeys provides insight into how certain travel behaviors might function to enhance their foraging efficiency.

Study Subjects

Howler monkeys on BCI live in relatively closed social units (troops) averaging nineteen individuals and composed of some three to four adult males, five to eight adult females, and five to seven immature animals. Adult males weigh between 7 and 9 kg, about 20% more than adult females. During most of the year, howler monkeys eat a mixed diet composed of about 48% leaves, 42% fruits, and 10% flowers. The number of food species used per day is about 8: 5.1 leaf species, 1.7 fruit species, and 0.8 flower species (Milton 1977, 1980). However, during the transition period between the wet and dry seasons on BCI, when ripe fruits are in short supply, howler monkeys rely heavily (85–100% of feeding time per day) on leaves as a dietary staple; the daily number of food species during this period is also about 8, but the diet is now composed of 7 leaf species, 0.6 fruit species, and 0.9 flower species (Milton 1977, 1980). Howler monkeys can live on diets high in leaves for weeks at a time (Glander 1978; Milton 1980). Feeding data show that, generally, howlers orient their feeding around one or two primary food trees (a primary food tree being a food source that is used for >20% of feeding time per day) and a variety of secondary food sources fed in for shorter, often extremely brief, periods of time (Milton 1977, 1980).

A howler monkey troop tends to perform all of its daily activities as a unit. When one animal is eating, there is a strong probability that most or all other animals in its troop are eating too; when one monkey is traveling through the canopy, there is a high probability that other members of the troop are likewise traveling. On BCI, howler troops generally do not fission into subgroups during the day to forage except in rare instances, as on peninsulas, whose narrow configuration makes foraging as a cohesive unit difficult, or when feeding on scattered leaf sources. For most of the year, a typical howler troop on BCI can be thought of as a tight-knit social unit whose constituent parts move through the forest together, feed and rest together, howl together, do everything together—howler monkey troops on BCI are the essence of togetherness.

Travel Initiation

The decision as to which direction a howler troop will travel in seems to be made by the alpha male (Carpenter 1934). This male generally makes a few low clucking or rumbling vocalizations to alert other troop members; he may walk a few steps in a particular direction, then sit down again. These behaviors, in some manner, appear to indicate to other troop members the direction in which the troop will travel (Carpenter 1934). Other animals will then

slowly begin to file out of the tree, passing by the alpha male, who may sit until most troop members are already moving along the travel route. My observations indicate that the alpha male does not then run to the head of the procession, but may be found traveling at almost any position. This travel pattern indicates that though one animal may suggest or choose the travel destination, once this is somehow "decided," many other troops members "know" the arboreal pathway to take to move directly to that new locale and feeding tree, as animals can and do travel to their destination in almost any processional order.

However, the subject of how group movement is initiated in howler monkeys warrants further study. Prins (1996), for example, observed buffalo cows reaching travel direction consensus through subtle stretching and gazing behavior during periods of resting; this behavior (termed "voting behavior") served to coordinate later group movement (see also Kummer 1968a; Sigg and Stolba 1981; Byrne, chap. 17, this volume; Wilson, chap. 9, this volume). In howler monkeys, it is possible that travel path decisions result from subtle troop consensus rather than the decision of a single dominant member. As the knowledge possessed by the group as a whole should add up to more than the knowledge of any one member, animals might do better (be more efficient foragers) by using some type of consensus mechanism to direct their major episodes of food travel, rather than just playing follow the leader (e.g., Wilson 1997a).

Foraging Efficiency on Patchily Distributed Foods

Examination of the distribution pattern of potential howler diet items on BCI showed that the seasonal items howler monkeys prefer to eat (tender young leaves, soft ripe fruits, flowers) are far more patchily distributed in space and time in the BCI forest than largely ignored perennial foods such as mature leaves. Study of the relative availability of foods in particular dietary categories (mature leaves, new leaves, flowers, green fruits, ripe fruits) showed notable differences, with ripe fruits showing by far the most patchy distribution, both by species and by individual tree (tables 14.1 and 14.2; see Milton 1977, 1980 for additional details).

Given the uneven distribution of preferred howler foods, procurement costs for these foods, as measured in the time or energy spent seeking them out, must be considerably higher than if the monkeys focused more of their feeding time on more uniformly dis-

Table 14.1 Number of months in a year when seasonal foods are available from twelve tree species drawn at random from the Barro Colorado Island forest

Species	Number of months Young leaves	 Fruits	 Flowers
Hirtella triandra	10	4	4
Jacaranda copaia	7	5	2
Tabebuia rosea	10	2	6
Ceiba pentandra	12	2	2
Apeiba membranacea	9	11	7
Triplaris cumingiana	9	2	4
Palicourea guianensis	11	6	3
Ormosia coccinea	8	0	2
Ocotea cernua	6	3	3
Paullinia turbacensis	4	7	3
Zuelania guidonia	4	3	3
Cecropia insignis	8	8	6

Table 14.2 Mean number of months in a year during which seasonal foods were observed on twelve tree species drawn at random from the Barro Colorado Island forest

Food category	Species	Individual trees
Young leaves	6.81 ± 2.53	5.26 ± 2.53
Mature leaves	11.75 ± 0.46	11.03 ± 1.22
Green and ripe fruits	3.67 ± 2.92	2.08 ± 1.80
Ripe fruits	1.13 ± 1.27	0.78 ± 1.00
Flower buds and flowers	2.73 ± 2.00	1.84 ± 1.12

tributed and abundant foods such as mature leaves. These additional procurement costs must compensated for, at least in part, by the higher nutritional quality of these preferred seasonal foods (Milton 1980). Even so, the potential return in nutrients is limited, and the howler digestive tract can hold only a limited amount of food at any one time (Milton 1980; Milton 1981b). In particular, during seasonal low points in the availability of energy-rich fruits, howler monkeys should be under particularly strong pressure to minimize the energy they expend in food search. How are howler monkeys able to afford the costs of their selectivity?

One important way to lower the costs associated with food procurement would be to minimize the time and energy spent searching for food. This could be achieved by a food search strategy that maximized the probabilities of encountering preferred high-quality foods. The optimal search strategy would depend on the distribution patterns of preferred foods. If, for example, preferred foods were uniformly distributed in time and space, the most efficient search strategy would be to cover the entire supplying area in a "lawn mower" pattern, moving back and forth in even, nonoverlapping swaths until the entire area had been covered. But if the distribution of preferred foods was extremely patchy in space and time, as is the case for howler monkey foods on BCI (Milton 1977, 1980), the most efficient strategy would be to use a pattern of goal-directed travel—that is, to move directly to important sources of preferred foods (primary food species) when and where they were available without wasting valuable time and energy in random search.

As noted above, considerable field data suggest that howler monkeys often show a pattern suggesting goal-directed travel to primary food sources. To travel in this fashion, however, monkeys would somehow have to know, prior to travel initiation, *when* a particular highly desirable food source was available as well as *where* the particular tree was in their home range *and* the most direct route to it. Thus, to be effective, the food search strategy of howler monkeys would have to have at least two essential components: (1) the monitoring over a fairly substantial (32 hectares) area of a large number of specific trees such their phenological state could be tracked, and (2) the ability to determine each day which primary food trees were to be used such that monkeys could travel by the most economical route (straight line) to them.

Use of Two Ficus *Species*

To investigate the pattern of food search used by howler monkeys, I focused on the use of two important and highly preferred food species (*Ficus yoponensis* and *F. insipida,* Moraceae) by one howler monkey troop (14–18 individuals) living in the Lutz Ravine area on BCI (Milton 1980). This area of the forest consists of various large areas of old second growth interspersed with patches of mature primary forest, undisturbed perhaps for centuries (Hubbell and Foster 1990). Monkeys in the Lutz Ravine study troop spent 25.3% of their annual feeding time eating fruits and leaves from these two fig species (Milton 1980). Out of a total of 40 sample days, howlers ate foods from one or both *Ficus* species on 26 days (65% of total sample). Yet the relative density of these two fig species together was only 0.00371% (relative density was calculated from an examination of the number of trees ≥60 cm CBH in 30,000 m^2 of the 32 ha home range of the monkeys and a direct count of the total number of adult fig trees of these two species within this total supplying area).

Phenological data (Milton 1991) showed that, unlike many tree species on BCI, these two *Ficus* species were intraspecifically asynchronous in fruit production. Further, individual trees of each species produced fruit crops at different times each year. Trees of both species often produced small quantities of new leaves and, once or twice per year, large crops of new leaves (Milton 1991). Thus there appeared to be a strong incentive to howlers for visiting ("keeping an eye on") individuals of these *Ficus* species, since they tended to offer nutrient "rewards" for vigilance on a species-wide basis more frequently than most other tree species in the habitat. Most other tree species in the BCI forest are intraspecifically synchronous in their production of ripe fruits or new leaves, producing these seasonal items at best only once per year and producing them at approximately the same time each year (Milton 1980).

If howler monkeys have features that increase food search efficiency, field data should show that they are encountering individuals of *Ficus yoponensis* and *F. insipida* more frequently than if they were traveling around their home range at random. To test this assumption, I used data from my study in a search path model, as indicated in table 14.3. The supplying area of this study troop was determined by measuring all travel routes used on each of the 40 sample days (8 months of 5-day sampling designed to cover all portions of an annual cycle) (Milton 1977, 1980). These travel routes were referenced to a baseline point and plotted by computer onto a map of the study area. The area of the least convex polygon that enclosed all movements of the troop in the 40 sample days was regarded as the supplying (home range) area (Waser and Floody 1974; Milton 1980). All data on tree distributions were calculated within this 32 ha area.

Table 14.3 Search path model parameters

Number of days in sample	40
Mean daily travel time (t)	1.22 hrs ± 0.46
Mean daily travel distance (d)	392 m ± 127
Mean radius of tree crowns (r_1)	7.00 m
Mean radius of fig tree crowns (r_2)	11.70 m
Width of effective search path (s)	37.40
Area covered by troop per day (A)	14,660.80 m^2
Mean density of trees per m^2 (q)	.0185
Number of trees "sampled" in 40 days (n)	10,848.99
Relative density of fig trees (p)	.0037
Number of encounters with fig trees (X)	75

Note: r_1 is from a random sample of 20 trees in the Barro Colorado forest with a circumference at breast height (CBH) of 60 cm or more. r_2 is from a random sample of 20 mature fig trees (10 *Ficus yoponensis* and 10 *F. insipida*) in the Barro Colorado Island forest. $s = 2(r_1 + r_2)$. $A = ds$. q is for trees with a CBH of 60 cm or more from three 1 ha sample plots. $n = 40\,Aq$. p is from 3 ha of the troop's 32 ha supplying area in which all *Ficus* were tagged and mapped. X was counted from trees used as food sources or encountered on travel routes by the study troop.

Since the monkeys almost invariably traveled in single file through the forest canopy, rather than spreading out and covering a wide swath, I used the mean crown diameter of canopy trees in their supplying area as the width of the troop's search path. The measurements of crown diameter were taken in a random sample that measured 20 trees (≥60 cm CBH) at the widest points of branch extension, so the results should be an overestimate. The "effective search path" should include the width of the food patches (i.e., the crown diameters of the two species of fig trees), as pointed out by Holling (1966) and Pulliam (1975). The effective search path for this howler troop was estimated at 37.4 meters (table 14.3).

It is possible that the actual search path was wider than my estimate, but a circle with the assumed radius of effective search would include a mean of 20 trees with a CBH of >60 cm. It would also include smaller trees, vines, and lianas with a heavy overlap of crowns, so that most of the time the visual range of the monkeys must have been severely restricted by the dense foliage. The area covered by this troop in an average day's travel ($\bar{X}$ daily travel distance = 392 ± 127 m) should also be an overestimate, since the calculation assumes that the troop never covered the same area twice in the same day. However, in reality, whenever the troop changed direction, there would have been an overlap of the area covered, as demonstrated by Morrison (1975).

Results showed that howlers were encountering individuals of *Ficus yoponensis* and *F. inspida* significantly more frequently than if they had been "sampling" the forest at random ($Z = 5.51$, $p < .0001$), where

$$Z = \frac{X - np}{\sqrt{np(1 - p)}},$$

with X, n, and p as defined in table 14.3. This result supports the hypothesis that howlers have features that increase their efficiency in food search. The question thus posed is, what might such features be?

Features of Food Search

In observing their daily travel patterns, I noted that howlers appeared to concentrate travel in areas of their home range with relatively high densities of fig trees. An analysis of the ranging data showed that three of the four heaviest concentrations of travel routes also contained relatively high numbers of *F. yoponensis* and *F. inspida* (Milton 1980). There were an estimated twenty-one individuals of these two fig species in the 32 ha home range of the study troop. The 3 ha with maximal travel concentration contained ten of these twenty-one individuals (48%), six individuals in one hectare, four in another, and one in the third. Thus howler monkeys were concentrating travel in areas of their home range where chances of encountering these preferred foods were relatively high. As Tullock (1971) has phrased it, they were "shopping in the cheapest market."

Howler monkeys elsewhere have likewise been reported to forage in areas where fig tree densities are high (Sekulik 1981). Indeed, the home range size of one red howler monkey *(Alouatta seniculus)* troop studied by Sekulik (1981) in the llanos of Venezuela was so small (3.9 ha), particularly in terms of the sections containing trees (about 49% of the home range was open grassland), that rather than shopping in the cheapest market, these howlers might well be said to have been living in the market itself.

Another key feature of howler travel both on BCI and elsewhere is the repeated use of particular arboreal pathways that tend to connect areas of the home range where the densities of preferred food trees are relatively high (Milton 1977, 1980; Sekulik 1981). Similar arboreal pathways have also been noted for some other primate species and are likely to be characteristic of all primate species. For example, MacKinnon (1974, cited in Bell 1991) remarked on the use of distinct arboreal "highways" by orangutans and noted that such highways often followed natural environmental features such as ridges or streams and were used by various individuals.

As noted, howlers in the Lutz Ravine area of BCI traveled an average of 392 m per day (table 14.3). During travel, they typically visited one or more primary (≥20% feeding time per day) food sources and various secondary (<20% feeding time per day) food sources, often moving in a loop away from a primary source and then returning to it later that same day, or on subsequent days within a 5-day sample period (Milton 1977, 1980). Primary food sources are almost invariably fruits, whereas secondary food sources generally are leaves. Further, as discussed above, howlers tended to concentrate foraging activity in areas of their home range where fig tree density was relatively high.

The combination of these foraging behaviors could be very efficient. By using a known food source as a primary reference point and traveling a relatively predictable distance away from it each day, howlers would never be more than a normal day's travel from any productive food source in their entire home range (Milton 1977, 1980). Thus they avoid unpleasant "surprises" in terms of unexpectedly long day ranges and are able to keep their daily energetic expenditures (i.e., travel costs) both predictable and relatively constant. At the same time, they can also take advantage of any other high-quality food sources encountered while traveling as well as monitoring the phenological condition of other important food trees in their home range. Wrangham (1977), for example, has noted that chimpanzees at Gombe show daily travel patterns that at times suggest they are monitoring the phenological condition of particular fruit trees and can return to them at the optimal moment for harvest (see also van Roosmalen 1985).

Operations Research and Search Theory

Operations research is a field of study which, by assessing the overall implications of various alternative courses of action in a given management system, tries to predict the optimal policy or suggest an improved basis for decisions (see, for example, Pocock 1956). It has been termed "the science of generalized strategies and tactics" (Camp 1956, 102). Operations research seeks to discover regularities in apparently unrelated or random activities, drawing on techniques such as linear programming, game theory, search theory, and dynamic programming, among others (Pocock 1956; Hillier and Lieberman 1967). Barnett (1976) used search theory to construct a model designed to predict the optimal search pattern for preventive activities of police officers in cars who were interested in visiting potential crime sites in such a way as to intercept crimes in progress. Visiting every potential crime site was not feasible; further, some locales were far more likely to be (had a higher probability of being) the scene of a crime than others. In his model, Barnett showed that for events of limited duration (i.e., crimes) arising randomly in time at several discrete points, if an optimal search policy exists, then there is a cyclic optimal policy; that is, a regular pattern of visiting points that generate events less frequently every k units of time and busier points the rest of the time (see Barnett 1976 for a full description of the parameters of this model). In essence, Barnett's model appears applicable to the problem of howler foraging behavior in terms of finding fruiting fig trees.

Fig trees are not totally random in fruit production, but individual trees do alter the time(s) of year at which they produce fruit crops and, to a lesser extent, leaf crops as well (Milton 1991). This variation makes it difficult for howlers to predict precisely when an individual fig tree in their supplying area will initiate a fruit crop or produce new leaves, but it makes fig trees relatively worth monitoring (fig trees, in this sense, are like areas with higher probabilities of violent crime). From the point of view of howlers, it would appear that fig trees (and perhaps other tree species with similar traits, such as other members of the Moraceae; Milton 1991) can be regarded as "random busier points" to be visited on a fairly frequent basis and other, either less productive or more predictably productive food species, points to be visited every *k* units of time. Therefore, if there is an optimal food search strategy for howlers, it could well resemble the one shown by this study troop and predicted by Barnett's search theory model.

Estimates of Efficiency

Relative efficiency in howler food search can be measured in terms of time spent searching. Based on the data in table 14.3, the expected time needed for howlers to encounter one fig tree in random search would be $t/dspq$ = 1.22 hours. The actual mean search time per fig tree was $40t/X$ = 0.65 hours. Thus for fig trees, these howler monkeys were 47% more efficient in food search than if they had been traveling at random. This is a quite substantial improvement over a policy of random search.

It is easy to see the effect of this food search behavior on the predictions of some models for optimal diet. In the graphic models of MacArthur and Pianka (1966), a reduction in search time would have the same effect as increasing food density—that is, it would reduce the predicted number of different items in the diet. Thus the animal could be more *selective* in its choice of food. In the models of Emlen (1966), Schoener (1971, 1974) and Pulliam (1975), a reduction in search time would also result in a prediction of greater selectivity on the part of the forager. Thus in all four models, the animal can be more selective in its choice of diet at the same level of food density.

A corollary effect of a reduction in search time would be to lower the level of food density at which an item would be excluded from the diet. This is in accord with Westoby's (1974) prediction that the

choice of diet by large herbivores will be constrained by availability of foods only at rather low levels. As he points out, for such animals, pursuit time is not a variable, being small and similar for all food items, and the probability of capture is essentially 1 (a plant part cannot escape from an herbivore). This should be true for all terrestrial primary consumers, though the probability of capture may be somewhat less than 1 for arboreal primary consumers due to the possible inaccessibility of some food items (e.g., at the tips of small, flexible branches). Search time, however, is a variable, and since the "prey" items of primary consumers are stationary and also relatively predictable in time, there is clearly much room for improvement over a strategy of random search.

Given the potential payoff, it is reasonable to expect that primary consumers such as howler monkeys should have behavioral adaptations that enable them to locate preferred foods more efficiently than if they were searching at random. Application of Barnett's (1976) model to my data on howler monkey foraging behavior suggests that they do. These features may have been selected for early in primate evolution and should be characteristic of many other primate species eating plant-based diets (Milton 1979b, 1981a, 1988).

Examination of food search strategy in howler monkeys leads naturally to consideration of the cognitive processes involved in such behavior. When a given troop sets out in a purposeful manner and travels for 300 m or more through the canopy to a fruiting tree by a direct route, how is the travel route being determined?

Memory Strategy in Howler Monkeys

As discussed above, laboratory experiments and actual field data indicate that primates use memory strategies to locate preferred foods (Menzel 1971a; MacDonald and Wilkie 1990; Gallistel and Cramer 1996). Currently, there seems fairly general agreement that many mammals, including primates, navigate to particular travel goals by means of path integration (or dead reckoning) in combination with landmark information (e.g., Sherry 1996, 163; Etienne, Maurer, and Séguinot 1996; Gallistel and Cramer 1996). Recently, Gallistel and Cramer (1996) proposed a model suggesting that cognitive maps (mental representations of space possessed by the animal and used in navigation: Sherry 1996) consist of landmarks placed on a geocentric frame of reference by vector addition. According to this model, animals determine their geocentric position by path integration and take positional fixes on known landmarks to deal with the error accumulation of path integration.

For many researchers, one test for a cognitive map has been whether an animal can use its map to derive a novel shortcut—a direct route between two places that are familiar but have never before been visited successively (Tolman 1948; O'Keefe and Nadel 1978; Sherry 1996). Bennett (1996) recently reviewed evidence for novel shortcuts (hence proof of cognitive maps) for a variety of different organisms, including nonhuman primates and humans, and concluded that until other simplier explanations for such behavior have been tested and rejected, all claims for cognitive maps based on the premise of a novel shortcut are premature.

In the case of howler monkeys, the question of a cognitive map *sensu* Tolman and O'Keefe and Nadel cannot even be addressed, as I have no data on the use of novel shortcuts. Nor can I address the utility of the model proposed by Gallistel and Cramer (1996), though it has much to recommend it (Bennett 1996). Even the use of long-term spatial memory by howlers is uncertain, as they may actually not have to remember a great deal about the locations of potential foods in their supplying area. Rather, in line with the systems model discussed above, howler monkeys could simply keep moving steadily for a fairly set distance day after day, over traditional arboreal pathways that lead directly from one cluster of important food trees ("random busier points") to another, checking less busy points as they pass by them. For howlers and other primates with similar travel patterns, such daily group movement would actually kill two birds with one stone. Howler monkeys not only have to know *where* particular trees are and how to travel efficiently to them, but they also have to monitor particular key food trees in their home range such that they know *when* to visit them. Both of these demands could be satisfied in large part by the system of travel shown by howler monkeys, as discussed above.

Data show that the Lutz Ravine study troop covered between 32% and 64% of its total home range (32 ha) in six 5-day sample periods (April, July, Aug., Sept., Oct., Nov.), averaging 47% home range coverage per sample. In the dry season, average home range coverage per 5-day sample was 64%, while in the rainy season it was 43%. In January of 1975 (dry season), the travel movements of one howler troop were observed for 20 continuous days; at the end of this period, the troop had covered almost exactly two-thirds of its total home range area. Average *daily* coverage of the home range during 3 months of the rainy season (Aug., Sept., Oct.) was 19.3%, with a low of 8% and a high of 32% (Milton 1977, 1980).

These estimates indicate that a howler troop routinely covers about 50% of its home range every 5 days or less. Ripe fruit crops do not appear overnight, but rather can be seen on individual trees for a period of weeks before immature fruits are sufficiently ripe to harvest. The travel pattern shown by howlers should permit a troop to keep a fairly close eye on phenological activity within its total home range without the need for strong dependence on long-term memory. However, though howlers could be relying on more or less continuous monitoring of "potential hot spots" in their home range to detect most important food crops, their skill in moving across their home range directly to distant food sources at the opportune moment for harvest suggests that they do make some use of longer-term memory to enhance foraging efficiency (Milton 1979b, 1981a, 1988). Howler monkeys show a smaller brain size for their body mass than similar-sized frugivorous anthropoids (Milton 1979b; 1981a, 1988). Since they have a demonstrably efficient system for locating high-quality dietary resources within their home range (at least in terms of the two *Ficus* species considered above), larger brain size might not net them a higher return in foraging efficiency, but could prove costly due to the energetic demands of brain tissue (Milton 1988).

Long-Term Occupancy of Home Ranges

The main travel routes (arboreal pathways) that each howler troop follows within its home range may have been worked out through trial and error learning over many successive generations and then passed on through social facilitation and other means to new generations of descendants (Milton 1981a). Field data from BCI covering more than 25 years show that particular howler monkey troops and their descendants use the same general home range area over many consecutive generations; particular troops in particular locales also tend to remain at approximately the same size over time (K. Milton, unpub.). As howler monkeys live in cohesive troops composed of animals of different ages, and as some animals in each troop are philopatric, there are always some monkeys familiar with the principal arboreal pathways and primary food sources in that home range. Foraging efficiency can be greatly enhanced by pooled information about features of diet as well as detailed knowledge of one's foraging range and resource locations (Bell 1991). Furthermore, as has been suggested for social carnivores (e.g., lions: Packer and Ruttan 1988), group living and group size in primates may relate, at least in part, to the need to have a social group of a particular size and composition such that key dietary information can be passed on smoothly and efficiently from generation to generation.

Group Movement and Food Search in Spider Monkeys (*Ateles* spp.)

> Brains are metabolically expensive and don't get bigger (phylogenetically) unless in some fashion they are more than paying for their upkeep. (Hockett 1978, cited in Ridgway 1986)

What happens when we turn to consideration of a primate species that shows a different pattern of group movement than howler monkeys while living in precisely the same forest and even using many of the same fruit trees; namely, spider monkeys *(Ateles geoffroyi)* on BCI? Spider monkeys, which as adults are approximately the same size as howler monkeys, eat a diet composed primarily of ripe fruits, the most patchily distributed high-quality plant food in the BCI canopy see (tables 14.1 and 14.2). Ninety percent or more of the daily feeding time of spider monkeys may be devoted exclusively to ripe fruits, and the monkeys generally manage to devote 65% or more of their feeding time to ripe fruits at all times of the year (Milton 1981a,b, 1993b; Symington 1988a,b).

The daily travel path of spider monkeys is considerably longer than that of howlers. On BCI, daily travel by spider monkeys averages 900 m (as contrasted with 392 m for howlers), and on occasion, they may travel more than 3 km in a single day (Milton 1991; K. Milton, unpub.). At other sites, spider monkeys have been observed to travel as much as 5 km per day in search of food (van Roosmalen 1985). Thus, for spider monkeys, the use of visual or olfactory cues to locate ripe fruit crops at a distance seems even less probable than for howler monkeys.

In contrast to the fig trees preferred by howlers, many tree species used as primary fruit sources by spider monkeys ripen only a small portion of the total fruit crop each day (Milton 1982, 1991). In effect, this pattern forces these specialist fruit eaters to visit many different trees of a given species each day to secure sufficient fruits to meet their nutritional demands (van Roosmalen 1985). Probably also because of this fruiting pattern, members of a spider monkey troop tend to forage in small subgroups of only a few animals, rather than in a single cohesive troop like howler monkeys (Cant 1977; van Roosmalen 1985; Symington 1988a,b, 1990). If all members of a given spider monkey troop were to remain together over the course of the day, many individuals probably would not be able to obtain sufficient ripe fruit, or the entire group would have to travel farther. Thus, in essence, the diet of spider monkeys can be said to underlie their fission-fusion pattern of social organization (e.g., Cant 1977; van Roosmalen 1985; Symington 1990).

Traplining

On 7 consecutive days in October 1978, I followed spider monkey subgroups as they foraged in the BCI forest seeking fruits of *Spondias mombin,* a tree species that produces a sugar-rich, soft-pulped fruit with a single large, hard seed. On BCI, *S. mombin* shows a clumped spatial distribution (also characteristic of many other important fruit species utilized by spider monkeys), and generally one encounters several large trees of this species within a small area (Milton 1977, 1980). The spider monkey subgroups I observed were, in essence, "traplining" different patches of *S. mombin.* The term *traplining* describes a pattern of foraging behavior analogous to the movements of fur trappers. The trapper knows where his traps are, and follows a set schedule designed to minimize his travel path such that all traps are visited, and yet the trapper never wastes effort by doubling back over his path or revisiting traps already checked that day (see Thomson, Slatkin, and Thomson 1997 for a discussion of the difficulties both of defining and demonstrating traplining with free-ranging animals).

In seeking fruiting trees, spider monkey subgroups moved directly from one patch of *S. mombin* to another, harvesting fruits from one or more trees in each patch. They were not observed to double back on their trail or revisit patches already visited that day, though on occasion, other spider monkeys from their community were already present in a patch or entered a patch after the subgroup I was following arrived there (see also van Roosmalen 1985). Because of the tendency of many tree species on BCI to show a clumped spatial distribution, the presence of another subgroup in a patch would not necessarily imply that all fruit had been eaten. On successive days, animals generally visited at least some *S. mombin* patches utilized the previous day, but one, two, or more new patches were visited as well. This foraging pattern would permit spider monkeys to visit individual trees or species patches that they knew had fruit available (from their visit the day before, or in the very recent past) and, at the same time, monitor or feed from new patches of *S. mombin*. But, of course, they would have to know in advance where such patches were—otherwise they could not have moved directly to "new" patches by the shortest route—which, like Garber's (1989) *Saguinus* species, they did. Often, too, travel to new patches was extremely rapid, a feature likewise suggesting prior knowledge of the route and destination. Janson and Di Bitetti (1997) have noted that increased travel speed appears to decrease the probability of encountering food patches by chance unless animals pass within 10 m of a large patch.

Sex Differences in Travel Patterns of Spider Monkeys

Because of its dependence on ripe fruit, a spider monkey troop has a huge home range relative to a howler troop of similar size. On BCI, adult male spider monkeys may forage over most portions of the entire island. In my view, a 300 ha supplying area is a conservative estimate for an adult male spider monkey on BCI (> 500 ha might be more often the case), and 200 ha is conservative for an adult female. In Manu National Park, Symington (1988b) estimated home range size for troops of some 18–24 spider monkeys at 200 ha, while in Suriname, van Roosmalen (1985) estimated home range size (usable supplying area) for a troop of 15–20 spider monkeys at 220 ha.

Field data from BCI, Suriname, and Manu show that spider monkey females, particularly females with infants, have a shorter average day range than males (van Roosmalen 1985; Symington 1988a,b, 1990; Milton 1993b); furthermore, each adult female (and her dependent offspring) has a core area in which she tends to forage, particularly when ripe fruits are in short supply (van Roosmalen 1985; Symington 1990; Milton 1993b). Individual females have an extremely detailed knowledge of food sources in their particular core area (van Roosmalen 1985). Individual male spider monkeys also have core areas; these are larger than those of females and may overlap the core areas of two females (van Roosmalen 1985; Symington 1990).

Though males and females may forage together when fruit is abundant, generally on BCI and at some other sites, male spider monkeys tend to be found frequently in all-male associations; on BCI, on average, males spend about two-thirds of their daylight hours apart from females and young (Eisenberg and Kuehn 1976; Milton 1991). Adult males may forage for a short time each day with females and young, but typically at some point, generally sooner rather than later, males leave females and travel away at great speed to feed in other areas of the forest, where they may remain for most or all of the day (Symington 1988a,b; K. Milton, pers. obs.). Male spider monkeys are at times observed foraging alone, though on BCI this is rare. In Suriname, spider monkeys show a pattern somewhat similar to that reported for bonobos *(Pan paniscus)* (Hohmann and Fruth 1994): particular adult males often appear to associate with particular leading females, and all-male bands or male-male associations are not common (van Roosmalen 1985).

"Leading Females"

In his anecdotal descriptions, van Roosmalen (1985) differentiated between "leading females," generally older females who tended to lead foraging subgroups, and "other females" (see also Rowell 1972a). Leading females generally left sleeping trees first, traveled in front of a subgroup most of the time, always fed on the food sources that determined the route that was taken, and initiated most travel activity. Leading females took the shortest routes between important food sources and usually did not hesitate while traveling. They also appeared to check particular trees, often over a long period of time, in order to incorporate them into the foraging itinerary at the proper moment in the days or weeks to come.

Moreover, van Roosmalen suggested that a leading female probably roughly mapped out a foraging route in her mind for a particular day early that day, or even the day before. If, however, a leading female temporarily joined another subgroup that was following a different foraging route, later that same day she might have difficulty picking up her former route and could be observed backtracking to a particular food source already visited or moving back and forth between trees already visited earlier that same day—apparently trying to pick up the proper environmental cues to continue with her initial planned travel itinerary. Non-leading females (probably younger and less experienced) were described as foraging with less confidence than leading females, hesitating and traveling back and forth between the same food sources, rather than striking out rapidly and directly to new distant food patches (van Roosmalen 1985).

Because of the variable and uneven characteristics of their principal items of diet and the fact that they often forage in small subgroups (which may contain only a single adult) or alone, to be efficient, spider monkeys must formulate individual foraging paths each day such that they maximize encounters with abundant, high-quality fruit resources and, at the same time, monitor potential "hot spots" over a large area. As discussed above, the speed and skill with which some individuals move from patch to patch of the same fruiting tree species shows that they clearly recognize that when one individual of that species is in fruit, other members of that species are likewise in fruit, and suggests that they possess knowledge of specific tree locations that enables them to map out a travel route and then move between a certain number of these food sources by the most direct means. But, as noted above, female spider monkeys with dependent young do not, on average, forage as far each day as male spider monkeys, nor do they have as large a supplying area. How, then, can females and young benefit from the wider pool of dietary information available to males in their social unit?

Food Long Calls in Spider Monkeys

It is worth the effort to travel to a rich food source if no similar food patches are nearby and you know that fruits will be there when you arrive. On the other hand, if you do not pass through a given area sufficiently frequently to monitor its trees, traveling to that area could be a waste of energy if you do not find ample food there when you arrive. Perhaps to counteract this potential problem, individual spider monkeys have been observed to give loud calls at fruiting trees (van Roosmalen 1985; Chapman and Lefebvre 1990; Chapman and Weary 1990; K. Milton, pers. obs.)—calls that ostensibly signal to other group members the location of the food source. Individuals or subgroups interested in such information can then travel to that tree if they choose.

Chapman and Lefebvre (1990) investigated food calling behavior in free-ranging Costa Rican spider monkeys *(Ateles geoffroyi).* Though both males and females gave food calls (a "whinny," described as a "long-range vocalization"), females were reported to call more frequently than males (Chapman, Wrangham, and Chapman 1995). On occasion, other subgroups responded to the calls and traveled to the food tree. There was a positive relationship between subgroups with dominant individuals and frequency of calling, and the frequency of calling positively affected the number of conspecifics that arrived (Chapman and Lefebvre 1990). There was some suggestion that particular females formed coalitions to monopolize rich food resources (Chapman, Wrangham, and Chapman 1995).

Observing another loud, long-distance vocalization, the "whoop," Van Roosmalen (1985) noted a clear sex-based difference in the food calls of *Ateles paniscus* in Suriname. At this site, only male spider monkeys gave "food long calls," generally just before or during feeding on a primary food source. However, in contrast to the situation in Costa Rica, other subgroups usually did not join the caller. In van Roosmalen's view, the food long call signaled to other group members that they should *not* travel to the location as the food source was being depleted. The different calling patterns and subgroup reactions to calls that have been noted between Costa Rican and Suriname spider monkeys are puzzling and warrant further study (that fact that two different calls are being discussed may also relate to the different reactions described). But it does not really matter whether the calls are meant to attract or repel other community members—the end result is still the passing of key dietary information over long distances, information that can either attract group members to rich food sources (provide energy) or save them the trouble of traveling to foods being depleted (conserve energy), in either case enhancing their foraging efficiency. This energetic savings could be particularly critical for females, as it could permit them to invest more energy in reproductive efforts than otherwise would be the case as well as improving their own nutritional status.

Food Long Calls in Chimpanzees and Bonobos

Spider monkeys are not the only primates observed to use long calls (apparently) to communicate dietary information to conspecific group members. Both bonobos *(Pan paniscus)* and common chimpanzees *(P. troglodytes)* are reported to give loud food calls (Goodall 1986; Hohmann and Fruth 1994; VanKrunkelsven et al. 1996). Like spider monkeys, both chimpanzee species show a fission-fusion pattern of social organization, tend to forage primarily in small subgroups, and focus the majority of their feeding on ripe fruits (Goodall 1986; Symington 1990; VanKrunkelsven et al. 1996).

Captive male bonobos are hypothesized to utter food calls to attract potential mates, and apparently are willing to give up the discovered food resources in return for sex; food call frequency increases when finding larger amounts of food (VanKrunkelsven et al. 1996). Free-ranging common chimpanzee males likewise are reported to give loud calls—pant-hoots—to signal the location of rich food sources, with more intense calling at richer, divisible food sources (Hauser and Wrangham 1987; Mitani et al. 1992; Clark and Wrangham 1993; Hauser 1996), and females and young are reported to respond to these calls (Goodall 1986). It is adult male chimpanzees who call most often and most loudly at desirable food sources (Goodall 1986; Mitani 1996); females tend to utter only soft food grunts (Goodall 1986). The pant-hoot call of adult males has a third phase, the climax phase, that adult females typically do not give (Marler and Hobbett 1975; Mitani et al. 1992).

The pant-hoot vocalizations of two geographically distinct chimpanzee communities (Gombe and Mahale) differed statistically, suggesting that different communities might possess different "dialects" (Mitani et al. 1992), a feature that could help identify community members (Green 1975). Chimpanzees apparently can also identify distant long calls as being those of particular individuals (Marler and Hobbett 1975, Mitani et al. 1992), and community members react differently to calls of known versus strange conspecifics (Mitani et al. 1992; Mitani 1996; Baker and Aureli 1996). Loud calls of individual chimpanzees are said to vary depending on social context (Clark and Wrangham 1993). Similarly, human observers can identify particular spider monkeys or chimpanzees from their long calls (Marler and Hobbett 1975; van Roosmalen 1985). Masataka (1986) suggested that spider monkeys might both recognize one another as individuals by their calls and direct calls to particular individuals.

In effect, there appears to be a continuum of call complexity in anthropoids (see, for example, Marler 1970, 1976b; Cheney and Seyfarth 1982; Boinski and Mitchell 1997, Boinski, chap. 15, this volume). Most calls are "intragroup calls"—that is, they are intended to be heard and reacted to by one's own group members (Marler 1970; Boinski, chap. 15, this volume), who generally are in fairly close proximity to the caller. Calls directed over a long distance, on the other hand, such as the roars of howler monkeys, tend to be aggressive intergroup calls, broadcast to repulse strange conspecifics at a distance (Harrington 1987; Whitehead 1987). However, in fusion-fission species such as spider monkeys, chimpanzees, and bonobos, it would appear that various loud long-distance calls have been elaborated into an intragroup call system—a system of calls directed at one's own community members.

Long-distance intragroup calls might require more skill to "decode" than most other intragroup calls, which are often simple calls exchanged between individuals in fairly close proximity (proximity permitting the use of other cues simultaneously—facial gestures, hand or body gestures, environmental context, and so on; e.g., Marler 1976b). In support of this view, Marler and Hobbett (1975) have commented that in common chimpanzees, individuality is especially marked in those sounds used for long-range communication, while Hohmann and Fruth (1994) describe the high-hoots of bonobos as the major device used to regulate and maintain the social network of the bonobo community. Mitani et al. (1992) speculate that the social system of chimpanzees (and, by analogy, other fusion-fission species) may have created an appropriate selective milieu particularly favoring the evolution of vocal learning.

Avoiding Cognitive Overload in Foraging

One striking characteristic of most extant primates, which appears to set them apart from many other plant-eating arboreal mammals, is the large number of food species they exploit, both on a daily and an annual basis (Milton 1987). It is not unusual to find that a given group of monkeys or apes has taken foods from more than 150 different plant species over an annual cycle. As tropical forests have a high diversity of species, and most species occur at very low densities, and as each plant species has its own phenological pattern, the amount of information a primate might theoretically have to deal with is immense.

But primates have ways of getting around potential information overload. Field studies show that though primates eat a large number of plant species, typically only a small percentage of these make up the bulk of the daily or annual diet. For example, for howler monkeys on BCI, the overall pattern in the differential use of food species, as measured in percentage of feeding time per species, is that a few tree species are used rather heavily but most are used hardly at all. The same pattern is seen if differential use of food species is measured by the number of days a species is eaten. A few species are eaten on many days, but many are eaten on only a single day of observation (Milton 1977, 1980). Though on BCI, howlers eat an average of 8 plant species per day, only 1.5 of these are primary food sources (i.e., contribute ≥ 20% of feeding time). A species used as a primary food source in more than one sample month of my study was considered a *staple* resource. Very few species could be regarded as staples because of the high turnover rate of most howler food sources, particularly leaf species. Combined data from both study troops showed that, overall, only 9 plant species were used as staple foods by howler monkeys over the total study (Milton 1977, 1980). Similar feeding patterns are found in a large number of other primate species.

Howler monkeys and other primates thus appear to counteract the great diversity of their food species by concentrating heavily on a select number of staple species and using many others largely opportunistically. This strategy greatly reduces the amount of information an animal needs to retain, both in terms of species worth monitoring and in knowing where particular individuals of those species are located. Howlers, for example, use an average of only 1.5 primary food sources per day; a large amount of spatial memory does not seem necessary to travel to 1.5 trees per day, particularly when well-traveled arboreal pathways connect many important resource clusters (Milton 1977, 1980).

In spider monkeys, a very similar pattern is found. As spider monkeys trapline particular fruit species, they typically deal with only a single or perhaps two primary fruit species per day, and one (or two) species may serve as their primary source of ripe fruits for weeks at a time (K. Milton, pers. obs.). However, in contrast to howler monkeys, each spider monkey or spider monkey subgroup has to visit a number of different trees of a primary species each day to get sufficient fruit, an activity that could prove costly. But since many such tree species show a clumped spatial distribution, travel to one fruiting individual generally results in finding a number of other individuals of that species in close proximity (Milton 1980).

Feeding data suggest that, on average, a spider monkey subgroup travels to three or four patches of primary fruit trees per day. Like howler monkeys, spider monkeys have arboreal pathways through the forest such that an observer can often predict where a subgroup is going and the route it will take as it begins travel. To supplement their primary foods, as noted, spider monkeys and howler monkeys (and probably most primate species) feed opportunistically on any desirable dietary items encountered as they travel between primary sources (Milton 1977, 1980).

As chimpanzees are considerably larger than spider monkeys, an individual chimp needs absolutely more ripe fruit per day than a spider monkey. All else being equal, this could necessitate travel to more fruit trees per day, perhaps the use of more primary fruit species or trees per day, and a larger home range area. Furthermore, chimpanzees at some sites—apparently more so than spider monkeys—may often have to forage alone or only in the company of dependent young. These various travel and foraging pressures would seem to call for enhanced navigational abilities and the need for more memory, both short and long term, in these considerably larger fruit-eaters.

Cognitive Abilities with Respect to Multi-Destinational Routes

To examine some features of spatial memory in primates with respect to such foraging challenges, Cramer (Gallistel and Cramer 1996) carried out experiments with vervet monkeys *(Chlorocebus aethiops)* to test their ability to choose a multidestinational foraging route. Each subject watched in a holding area as grapes were hidden in a number of holes within its outdoor enclosure. The monkey was then released into the enclosure. Because the grapes were hidden, the monkeys had to rely on memory to compile a multidestinational route and collect the grapes. The vervets never remembered more than six locations (Gallistel and Cramer 1996).

In contrast, similar experiments by Menzel (1973a) using young chimpanzees as subjects showed that these apes were able to retrieve pieces of hidden fruit from as many as eighteen different hiding sites in a single rapid foraging expedition (described in Gallistel and Cramer 1996). The route the ape took bore no relationship to the one the experimenter had taken while hiding the fruits, and it appeared to minimize the distance traveled. Earlier work by Tinkelpaugh (1932), in which the memory capacities of rhesus monkeys *(Macaca mulatta),* common chimpanzees, and humans were tested gave the same result (six locations for the monkeys; sixteen or more for both chimps and humans).

The ability to map out a mental multidestinational route in vervets seems to be predicated on what has been termed "a three-step look-ahead"—that is, when planning its route, the monkey is able to consider at least two further destinations beyond the next destination (Gallistel and Cramer 1996). Most arboreal primates are not particularly large in size and, like vervet monkeys, may therefore require no more than a three-step look-ahead to plan their daily foraging activities. The food requirements of larger-bodied anthropoids such as great apes, however, would appear to be considerably higher, and this might account for their enhanced ability to plan more complex, multidestinational foraging routes and their larger brain-to-body ratio.

Group Movement and Food Search in Humans

> At the simpliest level, the significance of material culture lies neither in the establishment of chronology nor as a measure of relationships, but as an indicator of efficiency in obtaining food. (Bartholomew and Birdsell 1953, 492–93)

With humans, much of the speculation that marks the above discussion is avoided. Humans can describe how they will travel to or locate particular dietary resources, and they can explain why they seek certain foods in preference to others, or why they choose to hunt alone or with others. Though Bennett (1996) has called into question evidence supporting the use of cognitive maps, *sensu* Tolman and O'Keefe and Nadel, even for humans, we know that humans can mentally visualize complex geographic areas and describe the most efficient travel route from point to point (mentally calculate direction and distance). But generally in such examples we are dealing with human knowledge of a familiar landscape, or an experiment in which the human subject has previously studied some scaled layout of landmarks or been led blindfolded over a simple route and asked to return to the starting point (Fujita et al. 1993). What happens when blindfolded human subjects are taken some distance into an unfamiliar area—an area in which they have not been before? Can they, for example, point to the direction of home?

Formerly, it was speculated that humans, like some other vertebrates, might be able to orient themselves toward home or familiar landmarks (goal orientation) without instruments or celestial cues through the use of a magnetic sense organ (Baker 1980). Repeated experiments have consistently failed to provide any convincing evidence that humans utilize a magnetic sense organ (Gould and Able 1981). Humans, therefore, must learn certain landmarks, celestial cues, or navigational "rules" in order to move about in a goal-directed (directional) rather than a haphazard manner (see, for example, Etienne, Maurer, and Séguinot 1996; Gallistel and Cramer 1996) when carrying out daily activities over more than a short distance, including movement associated with food procurement. How, then, do human foragers (as, for example, indigenous hunters) behave when traveling through an unfamiliar landscape in search of food?

Orientation When Foraging

The indigenous hunters I work with in Brazil (lowland tropical forest dwellers in the Amazon Basin) generally select their hunting area the night before and depart in a group well before daybreak. If they leave from the village, they follow a trail, and even distant areas may contain trails. If hunters leave in a boat, they may travel by river for several hours, then enter the forest where, often, there are no trails. If three or fewer men are hunting, they may all walk along together in single file while looking and listening for game. However, if more men are hunting, they typically fan out once they enter the hunting area, with each man taking a somewhat different route. The hunters may hunt all day (8 hours or more), and each one is somehow able to return to the boat or trail by dusk. Hunters often call out loudly on their return, both to signal their location and to aid others in walking by the most direct route to the reunion site—calls from hunters already near or at such sites are particularly useful here.

Indigenous hunters tell me they use the angle of the sun to help orient themselves while in the forest. Apparently, use of the sun is very important, for one Mayoruna hunter (Pacha) told me that if it were a cloudy or rainy day, hunters might not be able to return to the boat or trail and would have to sleep in the forest. Amazonian hunters may also mentally keep track of landscape details—hills, streams, the direction of the main river, and so on—to help orient themselves when moving through the forest.

Yost and Kelley (1983), in working with the Waorani in Ecuador, noted that unless tracking a large terrestrial animal, hunters almost always hunt by trail, and trails almost always follow the tops of ridges, paralleling the streams and rivers. Though cutting across ridges and rivers would take the hunter through a richer variety of biotopes, hunters prefer to hunt along the ridge tops (where trails have been created through such use). Apparently the extra physical effort required to cross rivers, climb hills, and so on is viewed as too costly energetically, especially when one is burdened with game (Yost and Kelley 1983; K. Milton, pers. obs.). Thus, hunters are more efficient (i.e., net a higher return in exchange for their hunting efforts) if they follow the ridges (Yost and Kelley 1983), and for this reason, over time, trails have been created in these areas rather than others.

Food-Related Calls and Other Acoustical Cues

To aid in prey procurement, groups of Matis hunters use calls in order to keep themselves spaced well apart as they move through the forest (e.g., Hill and Hawkes 1983). A hunter also calls to "tell" other hunters if he encounters game and what type of game it is; these calls are cryptic and not detected as human calls by game (monkeys, wild pigs, etc.), but all of the hunters understand their meaning (just as spider monkeys and chimpanzees "understand" the meaning of their long calls). Hunters will then close in to try to make a kill.

The use of calls to space hunters at some regular (presumably optimal) distance over the landscape should improve the probability of encounters with game. If a hunter encounters a singleton game animal, he can pursue and hopefully kill it himself, but if he encounters more game than he can kill by himself, or game more likely to be killed in large numbers if surrounded by hunters, he can summon others to the area with calls before he begins to shoot.

Amazonian (and other) hunters use subtle features of the environment (overturned leaves, hollow logs, animal prints or scats, plant fragments on the forest floor, odors) to determine the presence or passing of game species (Winterhalder 1981; Henley 1982; O'Dea 1992; K. Milton, pers. obs.). They also know the calls of literally every species in the forest as well as the significance of particular noises such as falling fruits or moving branches. Little escapes their attention, and their reflexes seem amazingly quick relative to mine. As one nonindigenous man who had done considerable hunting with the Mayoruna remarked to me at the end of a successful hunt, "I pity the animal who crosses the path of a Mayoruna."

In reflecting on the sensory modality most important for hunting success in Amazonia, Yost and Kelley (1983) made the following observation:

> Undoubtedly, the Wao(rani) hunter depends on hearing more than upon any other sense to locate potential game. He learns to distinguish among the animals in the canopy by the sound they make as they move; the frequency of the movements, the loudness of the rustling leaves, the distance between movements, the kinds of trees the animals are in are all clues to the species. It is not unusual for hunters to know what kind of animal is present long before they see it or hear it call. The dense growth of the canopy often obscures animals from view, but knowledge of what species is present, combined with an understanding of that species' behavior, can make it possible for a hunter to predict an animal's next move without ever seeing the animal. Obviously, the better the hunter understands the species' behavior, the greater his chances of success in the hunt.

Vision is generally viewed as the most important sensory modality for primates, including humans, but reliance on auditory skills may be underrated in terms of its influence on the trajectory of human evolution. Anthropoids have a long evolutionary history of relying strongly on acoustical signals to aid in carrying out routine activities each day (Mitani et al. 1992; Boinski, chap. 15, this volume), and human language continues this trajectory.

Learning as the Key to Foraging Success

In his book *Hunters of the Northern Forest,* Nelson (1973) provides a detailed examination of the hunting behaviors of the Kutchin, indigenous inhabitants of the Chalkyitsik region, Alaska. This book helps emphasize for the urbanized Westerner the amazing number of different skills a human hunter (and, for that matter, with certain modifications, a human gatherer) has to master to be successful (see also Gladwin 1970; O'Dea 1992). The required knowledge includes the characteristics of the hunting landscape, the behaviors of the many different prey animals, the different hunting tactics and the manufacture and use of the weapons or tools needed to capture particular animal species, highly honed navigation skills of many different types (e.g., Gladwin 1970), the logistics of hunting, survival tactics under difficult or critical environmental conditions, and hundreds of other things. The life of "natural man" is most emphatically not a "remarkably easy one" (i.e., Humphrey 1976, 307). And all of this information has to be learned—none is encoded genetically in the human forager (e.g., Milton 1992).

A Division of Labor in Foraging

With human foragers, we also find some unusual behavioral adaptations related to group movement and food procurement that have antecedents, but no parallels, among other extant mammals, including other primates; namely, a division of labor between the sexes and food sharing (Lancaster 1978; Isaac 1978). Some other mammals show a division of labor in terms of food acquisition—for example, a pride of lions, a pack of wolves—and there are examples of food sharing in some bats and particularly among the social carnivores, which may also bring food back to a den (home base) to feed pups. But in no case do we find a sex-based division of labor in terms of food acquisition like that which apparently characterized ancestral hunter-gatherers *(Homo)* and still characterizes most hunter-gatherer groups today, a division of labor typically directed at foods from two trophic levels and in which foods obtained are shared with most or all members of the social unit. Human young are also provisioned entirely or partially for a very protracted time period, which should greatly facilitate their survivorship to reproductive adulthood (Lancaster 1978). Though the particularly human type of labor division was undoubtedly initiated in response to foraging pressures, it can be extended into almost all spheres of activity. As Hutchins (1995) points out:

> In anthropology there is scarcely a more important concept than the division of labor. In terms of the energy budget of a human group and the efficiency with which a group exploits its physical environment, social organizational factors often produce group properties that differ considerably from the properties of individuals . . . a particular kind of social organization permits individuals to combine their efforts in ways that produce results . . . that could not be produced by any individual . . . working alone. (Hutchins 1995, 175)

In short, the human division of labor is ergonomically efficient. One interesting aspect of group foraging in humans is that, typically, men hunt and women gather. Animal prey, unlike plant foods, is not sessile but mobile. Various aspects of food search strategy optimal for sessile plant foods would not be equally efficient for mobile animal prey, perhaps necessitating some fairly radical modifications in behavior and perhaps morphology to deal efficiently with these new foraging challenges (e.g., Milton 1981b).

A Foraging Complexity Continuum

In effect, howler monkeys, spider monkeys, chimpanzees, and human foragers can be viewed as successive points along a foraging complexity continuum. In general, spider monkeys and chimpanzees do not appear to have elements in their foraging behavior that could not be found in less complex form in howler monkeys or most other primates. Even the long call given at rich food sources by spider monkeys and chimpanzees appears to have its antecedents in calls some other primates give on encountering unusually rich food sources (e.g., toque macaques, *Macaca sinica:* Dittus 1984). Differences noted in group movement among anthropoids appear to originate from a common pool of cognitive potential shared by all anthropoids, elements of which are expressed or developed to a greater or lesser degree in a particular taxon in response to the challenges posed by its particular dietary niche. In the case of spider monkeys and chimpanzees, such challenges appear to have resulted in a set of very similar behavioral solutions (e.g., Symington 1990) in spite of phyletic distance, a considerable difference in body size, and presumably, differences in the two genera's respective forest environments.

Are Primates "Special"?

As an order, Primates are noted for their large brains and enhanced capacity for learning and retention, as well as their remarkable degree of behavioral plasticity (Eisenberg 1973; Milton 1981a). However, though monkeys and apes may seem particularly clever and special to us, their closest living relatives, it is important to realize that there are a number of other animal taxa that show many similar characteristics. We have seen that distantly related primate lineages can exhibit very similar behaviors on a number of levels, apparently in response to similar dietary challenges. To test the broader validity of this observation, it is useful to examine group movement and its attendant behaviors in two nonprimate taxa that, like spider monkeys, chimpanzees, and human foragers, eat very high quality foods, live in social groups, and show a fission-fusion pattern of group movement; namely, dolphins and parrots. For brevity, my discussion is focused primarily on a single species in each taxon, but many observations are likely to be equally valid for other members of that taxon as well.

Group Movement and Food Search in Bottlenose Dolphins

Bottlenose dolphins *(Tursiops truncatus),* like all Cetaceae, are secondarily aquatic, their ancestors (and ancestral neocortex) having evolved on land (whales are thought to have returned to the water some 70–90 mya) (Morgane, Jacobs, and Galaburda 1986). Dolphins (unless otherwise specified, the term "dolphin" here will refer only to *T. truncatus*) feed on mobile prey—principally fish. Some prey species are solitary or form small schools, while others form large schools. Thus, depending on the particular prey type being exploited, dolphins sometimes forage alone or in small parties, while at other times, frequently alerted by conspecifics, numerous dolphins converge on large schools of fish (large food patches) and pursue them, capturing individual fish, apparently aided by their echolocation system.

Dolphins are regarded as fission-fusion foragers (Smolker, chap. 19, this volume). This fluid grouping pattern appears to relate to their fluctuating and unevenly distributed food supply, which calls for constantly fluctuating subgroup size and composition. Data suggest that, as in spider monkeys and chimpanzees, mother-dependent offspring may be the only constant social association in bottlenose dolphins. However, it has been repeatedly observed that within specific locales, there are long-term association patterns between particular dolphin females and particular dolphin males, and that male-female localized associations or communities appear to exist—communities, however, that may also be constantly entered and left by noncommunity (or less frequently seen community) members (Smolker, chap. 19, this volume).

Individual Recognition

As dolphins appear to live in fairly discrete, localized communities but do not forage as a cohesive social unit, they are faced with the problem of maintaining and efficiently coordinating the activities of their group members at a distance. Like the above-discussed fission-fusion primate foragers, they appear to rely heavily on acoustic signals (and attendant cognitive processes) to accomplish this task.

Observational data suggest that dolphins can recognize conspecifics as individuals. Until recently, it was also believed that each dolphin produced a distinctive "signature whistle" developed during ontogeny (Tyack 1993). This observation has been challenged as recent research on whistle production by individuals from three different dolphin communities failed to detect evidence for individual signature whistles, though some data did support the possibility of community-based dialects (McCowan and Reiss 1995a). The dolphin whistle system is regarded as an open-ended system of communication (Tyack 1993) analogous to the open-ended system of verbal communication in humans (and similar in this respect to the "graded" calls of some nonhuman primates).

The Echolocation System

In addition to whistles, dolphins possess an echolocation system—a mental system of amazing precision that enables a given dolphin not only to locate an individual fish, even in a large school, but also to follow its rapid flight and (apparently) "stun" it by emitting a burst of signals (Wood and Evans 1980). However, blindfolded dolphins can capture live prey without producing any detectable echolocation sounds, apparently using their keen sense of hearing (Wood and Evans 1980). Within the dolphin brain, the echolocation system appears distinct from the signature call system. The call system appears to be localized primarily in the thin cerebral cortex,

particularly the temporal cortex, while the echolocation system occupies a large area in the midbrain (Tyack 1993). Ridgway (1986) suggests that much of the great hypertrophy of the dolphin's auditory system—and perhaps the entire cerebrum—results from the animal's need for great precision and speed in processing sound—a key attribute of human speech (and the human brain).

These and other data suggest that the large brain size of dolphins is functionally linked to the rapid processing of sound. I can appreciate the need for such abilities when foraging for rapidly moving prey, particularly in turbid water. But rapid sound processing seems less urgent in terms of *social* signaling, unless acoustic signals facilitate hunting efficiency, predator avoidance, or some other critical behavior(s) that requires a rapid response. Until recently, conspecific food calls had been reported only for animals foraging on plants. However, Janik (1997) has presented data describing a unique low-frequency two-part call in wild bottlenose dolphins that is associated with feeding on large fish. Dolphins produced these low-frequency calls in 94% of all observed feeding events, and in each case, the feeding dolphins were rapidly joined by conspecifics. It was suggested that such calls could function to alter prey behavior, to increase food intake of close kin, or to recruit conspecifics to approach and thus chase fish backward toward the callers (improving prey catch efficiency). To feed efficiently, dolphins must also possess navigational skills such that they can orient themselves within their foraging range, travel to seasonal foraging sites, travel rapidly and directly to fast-moving schools of prey from a distance, and so on.

As discussed, dolphins appear to know one another as individuals, and Janik's (1997) data suggest that they communicate information about prey size and location to one over long distances. As noted for primates, there appear to be long-term, multigenerational communities of dolphins loyal to particular foraging areas. Dolphin young take some 10 years to mature. This suggests that, like the young of some other large-brained mammals, they require a long period of practice and learning to become successful adults.

As yet, it is difficult to speculate on what dolphins are doing with the various components of their brains because so little is known about the specifics of communication feedback among dolphins when foraging or pursuing schools of fish (or doing anything else). The dolphin case is particularly interesting because dolphins clearly can do so many things besides echolocate and whistle (Tyack 1993).

Captive dolphins easily learn elaborate "trick" routines, often cued by signals from their trainers; they appear able to observe an action and replicate it; they are reported to imitate sounds, mimic the behavior of other animals, and so on (Herman 1980, discussed in Griffin 1992). Does signaling about and honing in on mobile prey require such a rich repertorie of behavioral capabilities? Perhaps enhanced cognitive capabilities with respect to a particular set of foraging challenges can be generalized to many other situations.

Group Movement and Food Search in Parrots

Parrots are highly social birds, noted for their complex vocalizations and their ability to acquire new sounds from the environment (Nottebohm 1970; Wright 1996, 1997). They are not the only birds possessing this ability, however, and more than one factor almost certainly can select for it. Data on wild parrots are not abundant, as they are extremely hard to study in the natural environment. Here comments are limited largely to information on the foraging and social behavior of the yellow-naped amazon *(Amazonas auropalliata)* in Costa Rica, supplemented with more general information on some other psittaciformes.

In the wild, many parrots (e.g., *Amazonas* spp., *Ara* spp.), like primates, have diets made up primarily of patchily distributed plant foods, principally fruits and seeds—foods that vary over an annual cycle in abundance and quality. Many seeds parrots feed on are protected by a thick, hard husk or shell. Parrots use their powerful bills to pry or bite open these hard-shelled fruits. Unlike those of most other birds, the tongues, feet, and toes of parrots are highly manipulative and serve as important foraging aids. They are used to position fruits for opening, remove food from the shell, and turn and position fruits and seeds for ingestion. This manipulative behavior is quite precise and enables parrots, like many primates, to discard the lower-quality, less digestible portions of their food items, ingesting only the most select, high-quality material (K. Milton, pers. obs.).

Grouping and Foraging Patterns of the Yellow-naped Amazon and Some Other Species

Parrots are long-lived birds that form long-lasting pair bonds. Available data suggest a three-tiered social structure for some *Amazonas* species. At the simplest level there is a mated pair; various pairs appear to associate in a type of loose "flock" (some thirty to fifty individuals who associate with one another frequently); and finally there is a large communal roost at which dozens to hundreds of conspecific parrots that appear to be members of the same community congregate at night (Ridgely 1982; Wright 1996, 1997; K. Milton, pers. obs.). On leaving the night roost each morning, parrots deploy themselves in various groupings, which can change over the course of a day, such that only a single pair, a flock, or a large congregation may be seen at a given feeding site. As members of a larger social unit (night roost) that appear to forage in subgroups of changing size and composition (other than the bonded pair), at least some parrot species would appear to be fission-fusion foragers. As such, they are faced with the challenge of maintaining social bonds, coordinating foraging activities, defending themselves from predators, and sharing important information with fellow group members, though often apart. Much of this social coordination and maintenance may be achieved through vocalizations (Saunders 1983).

Regional and Night Roost Dialects

The "contact" call is the most frequently uttered component of the vocal repertorie of many parrots. Contact calls appear to initiate group activities and maintain contact between flock members and mates (Saunders 1983; Wright 1996). In yellow-naped amazons, the contact call is used by individuals of both sexes and all ages in a number of social contexts, and is particularly common at night roosts and nest sites (Wright 1996, 1997). As discussed for primates and dolphins, data suggest that various parrots (*Amazonas* spp., some cockatoos) can recognize individual family members or flockmates by their calls (Saunders 1983; Wright 1996). It is possible for a human observer to sex and identify individual black cockatoos *(Calyptorhynchus funereus latirostris)* from their calls (Saunders 1983).

Study of the contact calls of free-ranging yellow-naped amazons in Costa Rica indicates that this species exhibits call variation at two geographic scales: (1) at the regional level (termed "dialects" and shared by members of various night roosts in a given geographic area) and (2) at the level of the individual night roost within a dialect ("within-dialect variation," Wright 1996, 1997). Regional dialects are defined by large-scale shifts in the structure of the contact call, while within-dialect variation exists in the fine-scale structure of the contact calls at each particular night roost (Wright

1997). Some birds at roosts bordering two regional dialects use the calls of both neighboring dialects interchangeably. Dialect borders thus appear to act as barriers to the spread of "foreign" calls (e.g., Hardy 1966; Nottebohm 1970; Wright 1996).

Night roost size in yellow-naped amazons ranges from twenty to three-hundred birds, and night roosts occur in highly traditional sites that are used throughout the year (Wright 1997). In this species, birds respond strongly to, and may interact only with, birds from their own night roost, ignoring other conspecifics regardless of dialect (Wright 1996, 1997). This observation strengthens the contention that features of each particular night roost subdialect define its members and help identify them as such to one another. This recognition could facilitate the transmission of survival information (e.g., food sites, nest sites, etc.) to roostmates. As yet, our understanding of avian dialects is hampered by a lack of information as well as by the possibility that they may serve different functions in different lineages (see Hardy 1966; Nottebohm 1970; Wright 1996, 1997 for discussion of hypotheses related to avian dialects).

Night Roosts as Information Centers?

Why many parrot species form communal roosts is not known. Ward and Zahavi (1973) suggest that night roosts serve as "information centers" for the social group, functioning primarily in the sharing of information about food and only secondarily as any type of antipredator defense. It has been noted that avian species that feed in flocks upon an unevenly distributed food supply tend to roost communally, while those that feed solitarily on more evenly distributed foods roost alone (Ward and Zahavi 1973). Other environmental characteristics also appear to influence flock size, as J. D. Gilardi and C. A. Munn (unpub.) report that *Amazonas* species in their study area (Manu, Peru) foraged in small family groups composed of three to five birds—apparently a mated pair and their immature offspring—and, at least in the dry season, did not form large communal roosts. However, communal roosts have been noted for *Amazonas* species in the Bahamas, Puerto Rico, Guatemala, Panama, and as noted, Costa Rica (J. D. Gilardi and C. A. Munn, unpub.; Wright 1996, 1997; K. Milton, pers. obs.). Information sharing at communal roosts is hypothesized to confer "massive" foraging enhancement (Ward and Zahavi 1973). Leaving each day from a communal roost could also help to deploy groups of parrots over the landscape in the most favorable configuration for maximizing individual foraging returns.

The high-quality foods many parrots depend on may be distributed over huge home ranges, estimated to cover many square kilometers (Ridgely 1982). Some flocks (ten to fifty individuals) of the pink cockatoo *(Cacatua leadbeater)* in Australia are estimated to forage over more than 300 square kilometers (Rowley and Chapman 1991). It has been noted that the largest associations occur at night roosts when food is scant—the time when parrots need the largest possible pool of information (Ward and Zahavi 1973). At the night roost, parrots are speculated to gain information on food sources over a wide area through association with roostmates who have fed in productive areas that day (Ward and Zahavi 1973). It is not known how birds distinguish successful foragers, but well-fed parrots may have behaviors, special vocalizations, or even olfactory cues that indicate this to their conspecifics.

Because particular parrot pairs come to a common roost site at night (or to a particular tree hole when nesting), they can be considered central-place foragers. As pointed out by Galef (1993), social birds or mammals that forage from a central site can benefit from exchange of information with conspecifics about the availability and distribution of foods. Such information pools may be particularly helpful for younger individuals by aiding them in finding their widely scattered dietary resources. Because parrots form long-term pair bonds and live for many decades in the same area, it would seem that, over time, a particular area might become populated by many parrots sharing strong kinship ties (first a pair, then a flock, and ultimately, a community), who would sleep at a communal roost, share important information with one another, and often associate at the same feeding sites during the day. Rowley and Chapman (1991) provide considerable information on the complex flock structure and feeding patterns of the pink cockatoo in western Australia, but in general, data on this topic are scant.

The widely appreciated longevity of parrots suggests that the accumulation and transfer of information from generation to generation, presumably at least in part about types, locations, and production patterns of particular food species, is a critical feature in the eventual foraging success of offspring. Rowley and Chapman (1991) described the behavior of pink cockatoos who took their dependent progeny to places where food and water were conveniently available. Young parrots appear to require a long period of maturation, learning, and practice to develop the skill and strength to find, manipulate, and open the variety of hard seeds and other foods that provide them with much of their diet, as well as to fly long distances between food sites. Like spider monkeys, chimpanzees, bottle-nosed dolphins, and humans, parrots show a large brain-to-body ratio (Pearson 1972; MacPhail 1982).

Overview

With the exception of howler monkeys, all of the vertebrates discussed above are fission-fusion foragers. This pattern of social organization appears to be directly related to the uneven patterning of their high-quality items of diet, a trait that also appears to necessitate a large suppling area. In all of these taxa, individuals known to one another (and many probably closely related) are part of distinct, often closed, social units—troops, groups, communities, pods, flocks, roosts—whose members come together and drift apart in subgroups whose size and composition (other than mother-dependent offspring or, in parrots, the mated pair) varies. These taxa all have a large brain in relation to their body mass, they are all highly social (for a discussion of the difficulty of defining sociality and social complexity, see Blumstein and Armitage 1997), and they are all strongly dependent on a highly elaborated system of acoustic communication aid in foraging coordination and efficiency and the maintenance of their social network. All of these species have a lifestyle that calls for a relatively long period of maturation during which a considerable amount of learned information and skill must be acquired for successful adulthood.

Within its particular lineage, each of these fission-fusion taxa appears to represent a somewhat extreme position in terms of body size *and* dietary quality—two traits that in many mammals, particularly herbivores, tend to be antagonistic and mutually exclusive rather than complementary, as they are in the fission-fusion species discussed above (e.g., Milton 1987). To counteract this seeming paradox, the niche each species occupies appears to require unusually well-developed cognitive abilities of various types in order for its holders to be successful—such behaviors bound up in the large brain size of the species.

For such species, it seems maladaptive for most information to be coded genetically, since environmental conditions (including those of the social environment) are constantly changing (Milton 1981a, 1988; Provenza and Cincotta 1993). Rather, what seems to

be called for is an increasing reliance on cognitive skills, particularly learning and memory, as well as sufficient behavioral plasticity to respond rapidly to changes in the environment (Milton 1981a, 1988). Provenza and Cincotta (1993) have stressed that learning is vital to securing rapid adaptation, and point out that foraging models have not yet incorporated learning as a within-or between-generational adaptive process. And, if you are going to have to learn a great deal before you can function successfully as an adult, it also seems of utility to have a long life span to give you the chance to put some of this knowledge to good use.

As these fission-fusion taxa are all highly social, I conclude that their basic requirements (i.e., obtaining food, avoiding danger, reproducing successfully) or some other requirements (e.g., information transfer between generations, provisioning of offspring, passing on a supplying area to descendants) are best realized in association with known conspecifics. However, because these species forage in subgroups rather than cohesively, benefits postulated to accrue to cohesively foraging groups (e.g., van Schaik 1983; van Schaik and von Hooff 1983; Bell 1991) might have to be obtained by somewhat different methods.

The calls discussed above (loud calls, whistles, food calls, contact and other calls) seem particularly important in this respect—they are speculated to be communication devices that permit scattered community members to "e-mail" one another during the day, touching bases and apparently sharing information (often about dietary resources but also about reunion sites, strange conspecifics, predators, and other features) that may be critical to group maintenance and coordination and foraging efficiency. In some species, total group size is not particularly large, and average subgroup size, where known, tends to be small (e.g., Wrangham 1977; van Roosmalen 1985). This suggests that it may not be the quantity of individuals in the social unit that is important in the development of complex cognitive abilities, but rather the quality of the interactions between them.

These behaviors seem familiar because they are also representative of our own species, *Homo sapiens*. Particularly in our hunter-gatherer past, it would appear that we too lived in relatively closed social units with a high degree of relatedness and showed a fission-fusion pattern associated with food procurement, a well-developed acoustic repertorie, and highly elaborated affiliative behaviors. Symbolic language, the hallmark characteristic of the human species, is most parsimoniously viewed as a labor-saving device. Human language is a low-cost behavior relative to its potential for enhancing ergonomic efficiency. Medawar (1976) views human language as essential for "the human system of heredity," that is, cultural evolution: "this characteristic human system of heredity calls for and depends upon the existence of language and other forms of conceptual communication." (Medawar 1976, 502)

The Other Side of the Coin

The identification calls, food-related calls, communication repertoires, and "dialects" of parrots, spider monkeys, dolphins, and chimpanzees have another aspect that needs to be addressed. On the one hand, these calls identify and provide a shared communication matrix for group members, but on the other hand, these acoustic traits also serve to identify nongroup members, whose detection, at least in nonhuman primates, typically elicits highly negative, defensive behaviors (Mori 1983; Goodall 1986; Baker and Aureli 1996). Similarly, most hunter-gatherer groups I have worked with in Amazonia show only the most intense animosity toward neighboring groups, and any suspicion that members of a neighboring group have been seen within the supplying area of its residents engenders an immediate hostile reaction (Milton 1992). Moore (1981) provides a detailed discussion of the particular benefits potentially accruing to centrally based human foragers through exclusive use of their supplying area.

Just as dialects may emerge between distinct social groups of nonhuman conspecifics and aid them in distinguishing kin or affiliated group members from nonkin/outsiders, language differences between human societies may emerge because a distinctive dialect or language that cannot be easily understood by one's neighbors could help a given human population safeguard particular facets of its unique behavioral (cultural) heritage, thereby securing or maintaining a competitive advantage over its neighbors. Nottebohm (1970), Barbujani (1991), Lieberman (1992), and others have pointed out that dialects and languages may also act as barriers to gene flow between human populations, perhaps contributing to microevolutionary processes.

In terms of our own species, the enormous number of different languages and dialects representative of human societies living at the same time in the same geographic region (e.g., Papua New Guinea, pre-contact South America) may well have developed not only through isolation or drift, but rather to some extent though an active interest in impeding intergroup communication and, in this way, discouraging potential "information parasites" ("free-riders" *sensu* Enquist and Leiman 1993; see also Wright 1997; Wilson 1997a). If this notion seems far-fetched, let me point out that it is not uncommon to find such behavior even *within* subgroups of particular human populations. Cockney, pig latin, and the languages invented by twin siblings are good examples of this. Among the Kutchin, hunters who live in small, economically self-sufficient, kin-based groups, the traplines of different families often pass through portions of the same geographic area. In such cases, trappers have been noted to hide or bury their trapping devices so that members of the neighboring group cannot see them and learn their unique design (Nelson 1973). Western fly fishermen exhibit the same behavior, developing "secret" lures that they do not wish to show to anyone for fear the lure will be copied and their individual fishing prowess eroded. The old saying "monkey see, monkey do," as we now realize is most correctly applied to our own species—and with good reason. As has been suggested, true imitation (*sensu* Galef 1988) may well be our most uniquely "human" trait (Meltzoff 1988).

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