Spatial Memory during Foraging in Prosimian Primates: *Propithecus edwardsi* and *Eulemur fulvus rufus*

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**Abstract**

A variety of anthropoids travel efficiently from one food source to another, although there is disagreement over how this is accomplished over large-scale space. Mental maps, for example, require that animals internally represent space, geometrically locate landmarks, use true distance and direction, and generate novel shortcuts to resources. Alternately, topological or route-based maps are based on a network of fixed points, landmarks and routes so that one food patch can be linked with another. In this study we describe travel patterns between food sources for two prosimian species found in southeastern Madagascar, *Propithecus edwardsi* and *Eulemur fulvus rufus*. Both species are dependent on fruit and have large home range sizes. By comparing inter-patch distances, patch size and turning angles, we found that both species prefer nearest neighbor food patches and *P. edwardsi* travels in relatively straight lines. The amount of backtracking seen in *E. f. rufus* may be linked to their large group size and dependence on large-crowned fruit trees. We suggest that the goal-oriented foraging of both prosimian species is dependent on a topological or route-based map. These are rare behavioral data relevant to ecological and social contexts of primate cognitive evolution.

**Introduction**

Many researchers agree that anthropoid primates do not forage randomly over their home ranges; instead, travel seems to be goal oriented with relatively straight-line movement between food sources [Carpenter, 1934; Kummer, 1968; Altmann,
Presumably, animals learn the relative positions of major food sources and other features in their environments to travel efficiently from one food source to another. This implies that anthropoids must be able to spatially represent, or mentally map, their food sources. What is not agreed upon, however, is ‘what kinds of representations these are, how they are used, or what their costs are in terms of computation and neural network size’ [Barton 2000, p. 230].

Mental maps are internal representations of space (with corresponding neural substrate) used by organisms to navigate through their environments [Gallistel and Cramer, 1996; Sherry, 1996]. It is generally assumed that many animals, including primates, use path integration, or dead reckoning, along with landmark information to reach their travel goals. More specifically, a mental map refers to the ability to geometrically locate landmarks and other environmental features of a large-scale space (i.e. Euclidian or vector map) [Byrne, 1979; Bennett 1996; Gallistel and Cramer, 1996]. This ability allows an individual to locate its position, compare true distances and directions from one food source to food sources that are out of sight, and estimate angles between landmarks to compute optimal travel routes, including novel shortcuts, to achieve the best reward for its effort. There is, however, little current evidence that animals have such mapping abilities [Bennett, 1996; Byrne, 2000]. Poucet [1993] offers an alternative explanation, in which animals may use a route-based representation of their home ranges that is made up of a network of travel routes, nodes (or fixed points), landmarks and topological features that are learned and are encoded in individuals. The use of route-based maps has been documented for several anthropoids including mantled howler monkeys [Milton, 1988; Garber and Jelinek, 2005], spider monkeys [van Roosmalen, 1985; Milton 1988], proboscis monkeys [Boonratana, 2000], hamadryas baboons [Sigg and Stolba, 1981] and orangutans [MacKinnon, 1974].

However, the use of spatial memory and the generation of foraging decisions are poorly documented for prosimian primates, as most reports are anecdotal [Kappeler, 2000]. Therefore, in this study we describe the foraging movements of two lemur species found in southeastern Madagascar. Propithecus edwardsi is a large-bodied (5.9 kg), diurnal primate that lives in small groups (2–9 individuals) with an average home range of 56 ha [Wright, 1995; Hemingway, 1996; Pochron and Wright, 2003; Lehman et al., 2005]. P. edwardsi spends the majority of its annual feeding time on ripe fruit and seeds and has low dietary diversity [Hemingway, 1998]. Eulemur fulvus rufus is smaller (2.7 kg), cathemeral, lives in larger groups (6–16 individuals) and has a home range size of up to 100 ha [Overdorff, 1993a; Overdorff et al., 1999]. E. f. rufus also has low dietary diversity and concentrates primarily on ripe and unripe fruits [Overdorff, 1993b]. The primary fruit sources used by the study species are typically clumped in distribution, tend to be medium to large in size but are not predictable in terms of yearly production [Overdorff 1993b; Ganzhorn, 1995; Hemingway, 1998; Gould et al., 1999; Wright, 1999]. We address the question: Do P. edwardsi and E. f. rufus exhibit goal-oriented foraging behavior by selecting nearest neighbor food patches and traveling in relatively straight-line progressions?
Study Site and Study Species

Ranomafana National Park (RNP) was established in 1991 and encompasses 41,500 ha (21°2′–21°25′ S, 47°18′–47°37′ E) of lowland to montane rain forest in southeastern Madagascar. This region supports 10 primate species in addition to *P. edwardsi* and *E. f. rufus* [Wright, 1992]. This study was conducted at the Vatoharanana study site that lies 5 km south from the main RNP research site. Monimiaceae, Cunoniaceae, Lauraceae and Myrtaceae are predominant plant families [Schatz and Malcomber, 1993]. Research has been ongoing at this site since 1988 [Overdorff, 1991]. At this study site, cooler, drier months occur between May and September (rainfall <150 mm/month, range 4–20 °C), and warmer, wetter months fall between October and March (rainfall >150 mm/month, range 11–31 °C). Food resources, particularly fruit, are typically least abundant in the austral winter; however, fruit production is temporally variable from year to year [Overdorff, 1993b; Ganzhorn et al., 1999; Wright, 1999] as some species produce fruit on irregular, asynchronous or alternate year cycles [Overdorff, 1993b; Hemingway, 1995; Overdorff, 1996; Powzyk, 1997; Balko, 1998].

Previously habituated groups of *P. edwardsi* and *E. f. rufus* were used in this study [Overdorff, 1993a; Hemingway, 1995; Overdorff, 1996]. Two groups of *P. edwardsi* were studied during the birth season from May to August 1996 (PEI n = 74 h; PEII n = 78 h), and one group of *E. f. rufus* was studied during the time of gestation from May to August 1997 (EFR n = 166 h). These groups have been studied intensively for many years by several different researchers (*E. f. rufus* from 1988 [Overdorff, 1993]; *P. edwardsi* from 1992 [Hemingway, 1995]). Groups contained at least 1 adult male and adult female (table 1). Individuals could be identified based on their uniquely colored nylon collar and metal pendant [for methods, see Glander et al., 1991]. Fruit was usually abundant during the study period, and *P. edwardsi* and *E. f. rufus* fed primarily on this patchy resource (table 1), although they concentrated on a small number of species. Both *P. edwardsi* groups spent approximately 95% of their fruit-feeding time on *Chrysophyllum boivinianum* and *Syzygium* sp., while the *E. f. rufus* group spent 97% of its fruit-feeding time on *Harungana madagascariensis*.

### Table 1. Diet, home range, daily path length (DPL) and group composition for *P. edwardsi* and *E. f. rufus* study groups

<table>
<thead>
<tr>
<th>Feature</th>
<th>PEI</th>
<th>PEII</th>
<th>EFR</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diet, %</td>
<td>88.6</td>
<td>70.1</td>
<td>84.6</td>
</tr>
<tr>
<td>FR</td>
<td>8.2</td>
<td>1.2</td>
<td>0.05</td>
</tr>
<tr>
<td>FL</td>
<td>3.2</td>
<td>24.9</td>
<td>14.4</td>
</tr>
<tr>
<td>NL</td>
<td>0</td>
<td>3.8</td>
<td>0.05</td>
</tr>
<tr>
<td>Home range, ha</td>
<td>19</td>
<td>55</td>
<td>45</td>
</tr>
<tr>
<td>Mean DPL, m</td>
<td>919 (n = 9)</td>
<td>702 (n = 11)</td>
<td>1,170 (n = 15)</td>
</tr>
<tr>
<td>DPL range, m</td>
<td>652–1,363</td>
<td>881–1,103</td>
<td>237–3,180</td>
</tr>
<tr>
<td>Group size</td>
<td>1 M, 3 F, 2 J</td>
<td>3 M, 1 F</td>
<td>4 M, 2 F, 1 J</td>
</tr>
</tbody>
</table>
| FR = Fruits (ripe and unripe) and seeds; FL = flowers; NL = new leaves; ML = mature leaves; M = adult males; F = adult females; J = juveniles (individuals 2 years or younger).

### Methods

Goal-Oriented Foraging

Each group was sampled for a number of days to assess goal-oriented foraging (PEI n = 9 days, PEII n = 11 days, EFR n = 15 days). Additional sampling days were used to measure and
map food patches. On each sampling day, all patches used for food (>2.5 cm diameter breast height) by 50% of the adult group members were marked and located on a two-dimensional map of the study site following Overdorff [1993b]. The word ‘patch’ is defined here as a single tree or liana used by a study subject for food and includes fruit, flower and leaf resources. Each patch was identified by genus and species names, and crown volume was estimated as a measure of patch size following Overdorff [1996]. All feeding patches and resting trees used by *P. edwardsi* (PEI n = 99; PEII n = 118) and *E. f. rufus* (n = 127) were tagged with a unique marker and mapped. These data were then used to calculate daily path lengths, home range size (table 1) [for methods, see Overdorff, 1993a], distances between individual food patches and patch sizes (table 2). Home range sizes were estimated by calculating the area of the minimum convex polygon that encompassed all daily path lengths for the study period using the Pathfinder 1.5 program [Winslett, unpubl. program].

We followed the same assumptions that Garber [1989] made during his study that (1) only patches previously used by *P. edwardsi* and *E. f. rufus* were considered for these analyses, and (2) patches previously used for food during the day were not considered as potential nearest neighbor patch (NNP) choices for subsequent feeding bouts. Intertop distances were used to determine how often *P. edwardsi* and *E. f. rufus* groups selected the nearest patch of a particular plant species as the next food patch [Garber, 1989]. For each feeding bout, the linear distance was calculated between the current food patch to each individual food patch of the next plant species used by *P. edwardsi* or *E. f. rufus*. These patches were then ranked from 1 (which represented the nearest potential food patch of that plant species, Nearest Neighbor Patch = NNP) to n. Patches less than 15 m apart were ranked similarly. A G test with Williams correction was used to determine how often study groups used NNP and if the distances traveled to NNP in lower ranks were shorter than distances traveled to higher-ranked patches.

A similar ranking procedure was used to determine if patch size, as an estimate of food availability, influenced group movements. Crown volume was calculated for each food patch and ranked from 1 to n within plant species. For each feeding bout, it was determined if the group visited the largest patch of that plant species, the second largest, etc. The distance rank and mean patch size (crown volume in cubic meters) were then compared for each feeding bout for each study group using a Kruskal-Wallis test to determine if distance and/or patch size influenced group movements. Differences between study groups were compared using a Mann-Whitney U test.

### Table 2. A summary of the food patches used by *P. edwardsi* and *E. f. rufus* (standard deviations in parentheses)

<table>
<thead>
<tr>
<th></th>
<th>Rank 1</th>
<th>Rank 2</th>
<th>Rank 3</th>
<th>Rank 4+</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>PEI patches (n = 49)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number per distance rank</td>
<td>28</td>
<td>10</td>
<td>6</td>
<td>5</td>
</tr>
<tr>
<td>Percent per distance rank</td>
<td>57</td>
<td>21</td>
<td>12</td>
<td>19</td>
</tr>
<tr>
<td>Mean distance traveled, m</td>
<td>58.1 (52.0)</td>
<td>142.8 (63.1)</td>
<td>148.0 (57.7)</td>
<td>325.0 (111.1)</td>
</tr>
<tr>
<td>Mean patch size (crown volume), m³</td>
<td>630.9 (1,570.1)</td>
<td>436.7 (447.1)</td>
<td>531.9 (796.4)</td>
<td>489.8 (557.8)</td>
</tr>
<tr>
<td><strong>PEII patches (n = 85)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number per distance rank</td>
<td>70</td>
<td>9</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>Percent per distance rank</td>
<td>82</td>
<td>11</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>Mean distance traveled, m</td>
<td>52.4 (42.1)</td>
<td>158.9 (90.4)</td>
<td>202.5 (80.2)</td>
<td>350.2 (103.4)</td>
</tr>
<tr>
<td>Mean patch size (crown volume), m³</td>
<td>791.1 (1,238.8)</td>
<td>649.5 (872.7)</td>
<td>753.5 (633.9)</td>
<td>256.3 (334.5)</td>
</tr>
<tr>
<td><strong>EFR patches (n = 75)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number per distance rank</td>
<td>59</td>
<td>7</td>
<td>5</td>
<td>4</td>
</tr>
<tr>
<td>Percent per distance rank</td>
<td>79</td>
<td>9</td>
<td>7</td>
<td>5</td>
</tr>
<tr>
<td>Mean distance traveled, m</td>
<td>33.9 (23.5)</td>
<td>133.4 (70.6)</td>
<td>164.7 (69.3)</td>
<td>219.3 (82.4)</td>
</tr>
<tr>
<td>Mean patch size (crown volume), m³</td>
<td>1,050.1 (1,317.1)</td>
<td>759.1 (458.1)</td>
<td>454.6 (274.1)</td>
<td>288.8 (177.5)</td>
</tr>
</tbody>
</table>
Travel for the *P. edwardsi* groups was typically linear, with one animal following the one in front of it, and the *E. f. rufus* group traveled cohesively with a group spread of approximately 7–14 m [Overdorff and Erhart, unpubl. data]. As a group was followed throughout the day, the compass bearing of the group's travel was recorded every 10 min to note the direction of travel. Because compass bearings were independent at this time interval (Fisher's exact test [So- kal and Rohlf, 1995]), all data were used to calculate successive changes in travel patterns. An index of turning [Zimmerman, 1979; Garber, 1989] was used to determine if *P. edwardsi* and *E. f. rufus* groups traveled in straight lines between patches or backtracked from food patch to food patch. Turning angles vary from 0° to 180° so angles ≤90° indicate that groups travel in a relatively straight line, while angles >90° indicate that groups are backtracking [Garber, 1989]. We calculated the proportion of turning angles for each study group that were ≤90° and >90°, and then compared them using a G test with Williams correction.

**Results**

**Nearest Neighbor Food Patches**

The study groups used about 10 food patches per day (PEI: mean = 10.2, standard deviation, SD = 4.7; PEII: mean = 10.1, SD = 2.5; EFR: mean = 9.1, SD = 2.8). All groups selected NNP significantly more often than would be expected by chance (G test, PEI: G = 10.36, d.f. = 3, p = 0.02; PEII: G = 25.79, d.f. = 3, p < 0.0001; EFR: G = 20.19, d.f. = 3, p = 0.0002, table 2). PEII and EFR used NNP more often than PEI (3-way G test, G = 22.04, d.f. = 6, p < 0.0001, table 2). The forest at the Vatoharanana study site is dense, with vegetation growing at all levels, and both species traveled in the middle and lower parts of the canopy [Overdorff and Erhart, unpubl. data]. Thus, their field-of-view for locating NNP was limited, and we do not think they are able to visually locate fruits of NNP at distances of 34 and 55 m.

The actual distance traveled in each rank varied significantly by group (3-way G test, G = 17.35, d.f. = 6, p < 0.01). All groups traveled shorter distances to NNP although PEI traveled slightly shorter distances between patches in ranks 2 to 4+ than PEII (G test, G = 9.51, d.f. = 3, p < 0.02, table 2), and *E. f. rufus* traveled shorter distances for ranks 1, 2 and 4 compared to the *Propithecus* groups.

Although patch size was not a significant variable when comparing patch size and distance rank for *P. edwardsi* (Kruskal-Wallis test, PEI: H = 0.95, d.f. = 3, p = n.s.; PEII: H = 1.9, d.f. = 3, p = n.s.), it was a significant variable for *E. f. rufus* (Kruskal-Wallis test, EFR: H = 13.0, d.f. = 3, p < 0.005) with patches decreasing in size from distance rank 1 to distance rank 4+ (table 2). *E. f. rufus* also used significantly larger patches in distance rank 1 compared to both *P. edwardsi* groups (Mann-Whitney test, PEI: Z = –2.11, p < 0.04; PEII: Z = –2.01, p < 0.05; table 2). The use of larger NNP by *E. f. rufus* may relate to the larger average group size for this species (9.5 individuals) [Overdorff et al., 1999] compared to *P. edwardsi* (5.3 individuals) [Pochron and Wright, 2003].

**Straight-Line Travel**

Both *P. edwardsi* groups progressed in relatively straight lines of travel based on the proportion of turning angles ≤90° (PEI: 73.5%, total n = 161; PEII: 85.3%, total n = 162, fig. 1). PEI had a greater proportion of turning angles >90° compared to PEII (G test, G = 4.43, d.f. = 1, p < 0.04, fig. 1), and thus backtracked more often. We suggest that differences in the travel patterns of the *P. edwardsi* groups may be related...
to differences in daily path length, differences in home range size and shape, and to differing amounts of fruits and leaves in their diets (table 1). Although PEI had slightly longer daily path lengths compared to PEII (Mann-Whitney test, $Z = 1.80$, $p = n.s.;$ table 1, fig. 2), PEI used a home range less than half the size of PEII (19 vs. 55 ha; G test, $G = 7.3, d.f. = 1, p < 0.01$, table 1, fig. 2). In addition, the home range of PEI was less elongated and more rounded in shape compared to that of PEII. Finally, the straighter travel of PEII may be the result of ‘snacking’ on leaves as the group traveled between fruit sources. This is supported by a significant difference in feeding bout duration between the groups (PEI: mean duration = 9.38 min, SD = 12.06; PEII: mean duration = 5.93 min, SD = 6.72; Mann-Whitney U: $Z = -2.33, p = 0.02$) and is reflected in a significant difference between the time PEII spent feeding on fruits versus ‘snacking’ on young leaves (fruit: mean = 11.29 min, SD = 9.00; leaves: mean = 4.38 min, SD = 4.36; Mann-Whitney U: $Z = -6.49, p < 0.0001$).

*E. f. rufus* did not progress in straight lines, having a greater proportion of turning angles $>90^\circ$ (EFR: 60.9%, total n = 115, fig. 1). During the study period, *E. f. rufus* typically traveled in a loop, returning to patches of *H. madagascariensis* (for further explanation, see Discussion).

**Discussion**

Memory and learning have recently played a central role in primate foraging theory. The location and distribution of feeding sites and the distance between food patches have been suggested as information retained by animals and used in foraging decisions [Carpenter, 1934; Kummer, 1968; Altmann, 1974; Milton, 1980; Sigg
Spatial Memory in Prosimians

and Stolba, 1981; Garber, 1988; Chapman et al., 1989; Garber, 1989; Menzel, 1997; Janson, 1998; Garber, 2000; Janson, 2000; Milton, 2000; Menzel et al., 2002; Garber and Jelinek, 2005]. An individual’s proficiency at remembering the locations and phenological patterns of resources are thought to increase foraging success [Milton, 1981; Garber, 2000; Janson, 2000; Milton, 2000] and, ultimately, reproductive success.

Several environmental factors common to Madagascar, including poor soils, low plant productivity and an erratic and severe climate, would seem to encourage behavioral adaptations in lemurs that would enable them to locate foods efficiently. Soils in the eastern rain forests of Madagascar are acidic and extremely infertile because of high concentrations of iron and aluminum and low levels of phosphorus [Johnson, 1994]. Tree growth is slower and fruit productivity lower compared to sites in South America and Africa [Struhsaker, 1997; Terborgh et al., 1997]. In addition, cyclones are an almost yearly event in Madagascar’s eastern rain forests, and they can result in little to no fruit or leaf production for about a 9-month period [Ganzhorn, 1995]. As a result, lemurs have low dietary diversity and rely on fruits whose production is unpredictable and highly seasonal [Overdorff 1993b; Ganzhorn, 1995; Hemingway, 1998; Gould et al., 1999; Ganzhorn et al., 1999; Wright, 1999]. Goal-oriented foraging, along with characteristics such as small group size (compared to anthropoids), cathemerality, fissioning during feeding, female dominance and targeted female-female aggression during reproductive periods, are possible strategies that reduce foraging costs and increase foraging success for frugivorous lemurs [Kappeler, 1999; Wright, 1999].

It is clear to us that P. edwardsi and E. f. rufus possess considerable information about the availability and distribution of food sources, particularly fruit, within their home ranges. Based on our comparisons of interpatch distances, patch sizes

**Fig. 2.** Home range size and shape for PEI (19 ha), PEII (55 ha) and EFR (45 ha). One representative daily path length (lighter solid line) is shown for each group to demonstrate how PEII backtracked less often than PEI. Solid circles indicate food patches. Larger circles indicate feeding bouts of 10 min or longer, smaller circles indicate feeding bouts of less than 10 min.
and turning angles, both species prefer NNP and *P. edwardsi* travels in relatively straight lines. Therefore, selection of feeding sites appears to be goal oriented. The amount of backtracking seen in *E. f. rufus* may be linked to their dependence on a particular fruit tree, *H. madagascariensis*. *Harungana* grows in closely distributed, densely packed clumps [Balko, 1998] and has high ‘spatial apparency’, meaning that it is highly synchronous in terms of fruit production but has shortened temporal availability [Balko and Underwood, 2005]. *Harungana* fruit made up the bulk of the fruit portion of the *E. f. rufus* diet (97% of the time spent feeding on fruit). *E. f. rufus* often traveled in a loop, moving away from a clump of *Harungana* and returning to it later in the same day or within a few days. This pattern is similar to the foraging of some howler monkeys that tend to backtrack to areas of their home ranges where preferred fruit density is relatively high, ensuring that they are always within reach of productive fruit sources [Milton, 1980]. Thus, backtracking may not be inconsistent with goal oriented foraging.

Although our work with *P. edwardsi* and *E. f. rufus* does indicate nonrandom use of home ranges, does this mean that these species are able to form mental maps? The use of NNP may not be evidence of mental maps since simple rules can generate many nonrandom patterns and still solve complex problems [Bennett, 1996; Janson, 1998, 2000]. Indeed, at no point in this study did we witness study groups using a novel shortcut to a food source, a necessary component of a mental map in its strictest sense (i.e. Euclidian or vector map) [Byrne, 1979; Bennett, 1996; Gallistel and Cramer, 1996; Byrne, 2000]. Instead, the main travel routes used by *P. edwardsi* and *E. f. rufus* to move from one food patch to the next were traditional travel routes [Overdorff, 1991; Hemingway, 1995], and group movements were initiated and led primarily by adult females [Erhart and Overdorff, 1999]. Female leaders in each of the study groups were philopatric and so were presumably familiar with the locations of fruit sources and pathways within their home ranges. The use of traditional travel routes allows primates to check resources along the way as they move from one important food source to another [Milton, 2000], particularly resources that are out of sight from a current location.

Primates may use an objective in foraging that Janson [2000] calls ‘shortest-path satisficing’. In other words, primates may choose from among the available resources the subset that (1) can be visited within a day or fulfills a relatively fixed daily food requirement and (2) minimizes the distance traveled that day’ [Janson, 2000, p. 169]. Thus, as long as primates are able to find enough essential foods on a daily basis, they will be under weak selection pressure to form mental maps. One way that primates, including *P. edwardsi* and *E. f. rufus*, could choose the best subset of resources is to use a topological or route-based map. When using a route-based map, individuals are dependent on known routes and sequences of routes to efficiently find food, particularly over large-scale spaces [Poucet, 1993]. Because of increasing distance and decreasing visibility when traveling over large-scale spaces, animals may not be able to use true distances and directions to find the most efficient way to move from one food source to the next, and use topological information instead. Such information could be learned over time as animals explore their environments and result in a network of fixed points, landmarks and routes so that one food patch could be linked with others. A network, then, could allow animals to select among routes to minimize travel distance or combine portions of different routes, and this would result in reuse of routes over time. We suggest that a route-based map is consistent with the
travel patterns of *P. edwardsi* and *E. f. rufus*. However, although we feel that we have good preliminary data on the issue of goal oriented foraging in *P. edwardsi* and *E. f. rufus*, our group sizes were small and our sample was restricted to one season of the year. Thus, future testing is necessary to confirm our results.

Finally, it has been hypothesized that finding spatially and temporally diverse foods like fruit was the major selective force in the development of advanced cerebral complexity in anthropoids [Milton, 1981]. Frugivorous primates have larger brain to body size ratios and larger home range sizes compared to folivorous primates [Clutton-Brock, 1977; Clutton-Brock and Harvey, 1980]. The large home ranges of frugivores would then necessitate a powerful spatial memory for the efficient exploitation of their major food source [Clutton-Brock and Harvey, 1980; Milton, 1988]. From these relationships we would not expect to see small-brained prosimians, such as *P. edwardsi* and *E. f. rufus*, efficiently find fruit in their home ranges, yet they seem to do so. How, then, can this result be explained? One explanation relates to the fact that brains are metabolically expensive organs [Martin, 1981; Armstrong, 1983]. Milton [2000] asserts that when primates with smaller brain sizes (e.g. howler monkeys) are able to find efficiently high-quality, seasonal foods (e.g. fruit and young leaves), a larger brain size would not be a benefit, but a cost, and would therefore be selected against. Another explanation comes from focusing on parts of the brain rather than overall brain size. Barton [2000] has found that the hippocampus, which is involved in spatial memory, does not differ in size between the primate suborders and so concludes that the large anthropoid brain cannot be explained by selection for mental mapping. Rather, he suggests that visual differences in acuity and color vision are at least partially responsible for differences in relative neocortex size and overall brain size between the primate suborders [Barton, 1999, 2000]. Much of the neocortex of monkeys and apes is involved in visual processing and is correlated with diurnality, frugivory and social group size [Barton et al., 1995; Barton, 2000].

These explanations have important implications for the study of the evolution of spatial and cognitive abilities in primates. One behavioral line of inquiry might be to focus on how variables, such as age, sex, group composition, group size, individual preferences, dominance relationships and social structure, affect decisions regarding group movement from one food source to the next [Boinski, 2000]. Challenges, such as monitoring other group members’ foraging intentions, negotiating where groups move or relocating group members when groups have fissioned into subgroups during foraging, could significantly increase the amount of information processing individuals must accomplish to forage efficiently. Thus, future studies of primate foraging strategies and group movement need to consider the interaction between social and foraging demands [Barton, 2000].

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