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Route-based travel and shared routes in sympatric spider and woolly monkeys: cognitive and evolutionary implications

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Abstract Many wild primates occupy large home ranges and travel long distances each day. Navigating these ranges to find sufficient food presents a substantial cognitive challenge, but we are still far from understanding either how primates represent spatial information mentally or how they use this information to navigate under natural conditions. In the course of a long-term socioecological study, we investigated and compared the travel paths of sympatric spider monkeys (*Ateles belzebuth*) and woolly monkeys (*Lagothrix poeppigii*) in Amazonian Ecuador. During several field seasons spanning an 8-year period, we followed focal individuals or groups of both species continuously for periods of multiple days and mapped their travel paths in detail. We found that both primates typically traveled through their home ranges following repeatedly used paths, or ''routes''. Many of these routes were common to both species and were stable across study years. Several important routes appeared to be associated with distinct topographic features (e.g., ridgetops), which may constitute easily recognized landmarks useful for spatial navigation. The majority of all location records for both species fell along or near identified routes, as did most of the trees used for fruit feeding. Our results provide strong support for the idea that both woolly and spider monkey use route-based mental maps similar to those proposed by Poucet (Psychol Rev 100:163–182, 1993). We suggest that rather than remembering the specific locations of thousands of individual feeding trees and their phenological schedules, spider and woolly monkeys could nonetheless forage efficiently by committing to memory a series of route segments that, when followed, bring them into contact with many potential feeding sources for monitoring or visitation. Furthermore, because swallowed and defecated seeds are deposited in greater frequency along routes, the repeated use of particular travel paths over generations could profoundly influence the structure and composition of tropical forests, raising the intriguing possibility that these and other primate frugivores are active participants in constructing their own ecological niches. Building upon the insights of Byrne (Q J Exp Psychol 31:147–154, 1979, Normality and pathology in cognitive functions. Academic, London, pp 239–264, 1982) and Milton (The foraging strategy of howler monkeys: a study in primate economics. Columbia University Press, New York, 1980, On the move: how and why animals travel in groups. University of Chicago Press, Chicago, pp 375–417, 2000), our results highlight the likely general importance of route-based travel in the memory and foraging strategies of nonhuman primates.

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Introduction

For wild primates, successful survival requires that animals be able to navigate their home ranges in search of food and other resources. Over the last several decades, questions concerning navigational skills and the mental representation of space have drawn particular attention from primate biologists (Boinski and Garber 2000), in part because the challenges of finding and monitoring hundreds of feeding patches is suggested to be a critical selective factor in the evolution of primate brain size (Milton 1981). Primates are intriguing models for exploring how animals utilize changing information about the environment (e.g., the spatial and temporal pattern of food availability) when making decisions about foraging and ranging, and, in a number of taxa, individuals clearly integrate information about the location, size, and quality of many different potential feeding patches when making these decisions (e.g., Garber 1989; Janson 1998; Suarez 2003; Cunningham and Janson 2007; Janson 2007). Moreover, for many primate taxa home ranges can be quite large and can contain hundreds or thousands of potential feeding sites from a diverse array of plant species, and these sites are often located hundreds of meters apart, out of sight from one another. Clearly an ability to remember the locations of and to travel efficiently among feeding patches would help to minimize energy expenditure by reducing the time and energy spent searching for food items (Milton 2000).

A number of recent studies of range use and foraging behavior have convincingly demonstrated that primates have the ability to remember and return to hidden food items, to choose short and direct routes when traveling among feeding sites, to weigh the relative values of particular food patches, and to update information on the locations of food items (see recent reviews by Byrne 2000; Garber 2000; Janson 2000). Nonetheless, these skills themselves do not provide insight into the fundamental question of just how primates represent space mentally in order to successfully navigate their environments—that is, into the forms of their so-called ''mental'' or ''cognitive'' maps—and the exact forms that these mental representations take are much debated in the animal navigation literature (Gallistel 1989; Bennett 1996).

At one extreme is the idea that animals possess highly detailed information about the spatial relationships among salient features of the environment (e.g., feeding trees, sleeping sites), and that they represent these features mentally as either a set of specific locations in a coordinate system or as a series of angles and distances among those features (Tolman 1948; O'Keefe and Nadel 1978). Such a representation, also known as a geometric, Euclidean, or vector mental map, has been likened to possessing a mental image of the environment much as humans would picture a folding map with a ''view from above'', encompassing all landscape features in some form of coordinate system external to the animal itself. Euclidean maps implicitly demand that an animal mentally store information about the locations of important features in its environment, along with information on the distance and angle relationships among all of those features, even those that are not perceivable from one another. Theoretically, possessing such a map would allow animals to calculate efficient and, importantly, novel routes between any two features of their environments. However, the notion that animals really possess such detailed maps has been seriously challenged, not least because proving or disproving the existence of such a mental representation would be extremely difficult since the observer would need to demonstrate that animals can choose both efficient and novel travel routes (Janson 2000). It is also argued that the cognitive demands of storing sufficient information to maintain a Euclidean mental map would be overwhelming (Bennett 1996). At present, there is little evidence to support this type of mental representation of spatial information in any animal taxon (Poucet 1993; Benhamou 1996; Bennett 1996; Byrne 2000).

One alternative to using a Euclidean map is to navigate the environment using the process of ''path integration'', whereby an animal continually updates its mental representation of its location in the environment by tracking and integrating all of the small, directional changes in position made while moving. Path integration, coupled with the use of known visual landmarks, is hypothesized to be an important mode of navigation for animals generally (Etienne et al. 1996; Gallistel and Cramer 1996), but the process remains to be tested—and, indeed, would also be difficult to demonstrate—in many mammalian taxa that occupy large home ranges and have long daily path lengths. As with a Euclidean map, path integration would allow animals to generate novel routes among distant features of their environment, with the restriction that some landmark should always be visible.

Yet another alternative to the Euclidean map is referred to variously as a topological, network, or route-based map, and it envisions that an animal's mental representation of locations and features in its environment consists of a set of interconnected, learned travel routes among sites (Byrne 1979, 1982; Milton 1980, 2000; Poucet 1993). With such a mental map, routes can be complex and can intersect with one another, and those intersections or ''nodes'' may be sites where animals can jump from one route to the next. Possessing such a mental representation of the environment could allow animals to navigate quite efficiently, even taking different routes between the same two sites, but it does not require that an animal store spatial information about the global geometric relationships among features of the environment that cannot be perceived from one

another, nor does it suppose that animals need to constantly update their position by path integration as they move. A number of researchers have documented the use of route-based travel in nonhuman primates (e.g., orangutans: Mac Kinnon 1974; howler monkeys: Milton 1980, 2000; hamadryas baboons: Sigg and Stolba 1981), and Milton (2000) has suggested that the repeated use of traditional arboreal pathways is ''likely to be characteristic of all primate species'' (p. 386).

In this paper, we examine the travel patterns of two neotropical primates—white-bellied spider monkeys (*Ateles belzebuth*) and lowland woolly monkeys (*Lagothrix poeppigii*)—found at our study site in Yasuní National Park in Amazonian Ecuador, and we interpret these patterns in light of the perspectives described above about how animals may represent and use spatial information. These species constitute an excellent pair for comparative investigations of socioecology and cognition as they both (1) rely on similar resources (indeed, in our study site they feed from many of the same trees), (2) are highly social, living in large groups or communities, (3) range widely and visit multiple feeding trees per day, and (4) are long-lived with long periods of juvenile dependency, hence possessing the opportunity for learning about spatial characteristics of the environment.

Using GIS software, we first characterize the travel routes used by both spider and woolly monkeys. We then examine the relationship between route-based travel, range use, and feeding site locations, and we evaluate the association between identified route segments and the topography of the environment. Finally, we discuss the implications that route-based navigation may have for understanding the selective pressures underlying the evolution of primate brain size and cognitive capabilities, as well as for influencing the structure and dynamics of tropical forests.

Methods

Study site and subjects

Spider and woolly monkeys are closely related and highly frugivorous primates. Spider monkeys typically utilize home ranges of 100–400 ha and live in multimale–multifemale, ''fission–fusion'' communities comprising 20–40 individuals, where individuals forage in small, temporary parties or subgroups that change in size and composition frequently (Klein and Klein 1977; van Roosmalen 1985; Symington 1990; Chapman et al. 1995). Woolly monkeys also live in large multimale–multifemale groups, but, unlike spider monkeys, they only infrequently split into subgroups that range independently of one another. Instead, groups tend to remain socially cohesive, although indi-

viduals from the same group may be spread over a considerable area while foraging and may be out of sight of most other group members. Home range sizes for woolly monkeys vary from 110 to over 1,000 ha (Peres 1994; Stevenson et al. 1994; Defler 1996), but in Yasuní fall toward the lower end of that range (Di Fiore 2003).

The data analyzed here were collected during several field seasons between April 1995 and July 2003 on one community of spider monkeys and three groups of woolly monkeys living in the Proyecto Primates Research Site (75°28′W, 0°42′S). Four sets of data—two for each species—were collected at different times using slightly different methodologies, but for each the raw data consist of location records collected at specified intervals during continuous follows of focal individuals or groups of each species, plus the paths connecting these locations. In the field, we recorded locations as distances and bearings from previously mapped trails and feeding trees.

The first spider monkey dataset comes from a single community that has been studied almost continuously since 1995. Between March 1999 and May 2000, location records ($N = 15,103$) were collected every 5 min during ten 2-week follows of three adult females, with three follows each on two of these subjects, and four follows of the third. Community size at the time was ~16 individuals, and the community used a total home range of ~300 ha (Suarez 2003). The second set of *Ateles* data comes from the same community studied between July 2002 and July 2003. Here, location records ($N = 7,159$) were taken in similar fashion during shorter 10 min to 12-h focal follows of all adult members of the community. At this time, the community comprised ~23 animals and used a total home range of ~266 ha (Di Fiore and Link, unpublished data).

The first woolly monkey dataset comes from three social groups of woolly monkeys ranging in size from ~18 to ~25 animals studied between April 1995 and March 1996. During this period, location records ($N = 6,314$) for the rough geographic center of a focal group were taken every 10 min during the context of behavioral scan sampling. During sampling, the observer changed positions under the group frequently, and the group location recorded represents the average location of the individual animals detected during a scan (Di Fiore 2003). The second set of *Lagothrix* data comprises location records ($N = 2,358$) for one of these groups studied again between July 2002 and July 2003. In this case, the focal group had grown in size to over 30 animals, and records were collected every 15 rather than every 10 min.

Analytical procedures

All location records were entered into ArcView GIS 3.3 or 8.0, and successive records for the same focal animal or

group were then joined to create daily paths (or partial daily paths for less than full-day samples). For the purposes of analysis, records separated by more than 30 min (e.g., if a focal animal was lost for a series of sampling points) were not connected when we drew daily paths. However, we note that focal animals and groups were seldom lost for more than 30 min and, in most cases, were followed continuously until the end of the day or until researcher deliberately left the subjects. Path segments reflecting obvious errors in location data (e.g., aberrant trajectories that suggested a mapping error in the field) were also omitted.

Initial determination of repeatedly used routes was made for each of the four datasets separately by overlaying all recorded daily paths and then identifying, by eye, all paths that appeared to have been used multiple times. These initial routes were sketched and digitized and were then confirmed by superimposing, one at a time, the set of individual paths recorded in each dataset. A route was permanently included in the map when sections of the paths followed by the same spider monkey or group of woolly monkeys on at least two different days—or by two different individual spider monkeys or groups of woolly monkeys on the same day—were clearly concordant with the proposed route, i.e., they followed the same trajectory as the proposed route for ~100 m or more and lay within ~25 m of the proposed route. In practice, nearly all path segments on the routes identified within each of the datasets were used three or more times—and segments common to routes in multiple datasets were used even more often—confirming the highly nonrandom nature of the overlap between path segments and supporting the appropriateness of our method for identifying routes. The result of this process was a system of overlapping and intersecting travel paths, resembling a network. Where two or more paths within this network crossed, the location was defined as an ''intersection''. The section of a route bordered on each end by an intersection was then defined as a ''route segment''.

The junction of route segments may simply be an arbitrary intersection of two travel paths, or they could be points where monkeys make decisions about where to travel next, being free to choose to turn down any of the intersecting paths. To test whether the intersections of route segments in the network map were truly points of decision, hereby defined as ''nodes'' (Poucet 1993), daily paths for each dataset were overlaid on the route map one at a time. The direction of approach and direct taken at each intersection were tallied, and when at least two alternate paths were selected at a single intersection from any single approach direction, or when the same path was taken at an intersection following approaches from different directions, the junction was scored as a node.

Routes identified within the various datasets were superimposed to assess the degree of concordance among them. A crude quantitative measure of route concordance across time for each species was determined by calculating the proportion of all location records falling within 25 m of the route network for one dataset for that species that also then fell within 25 m of the route network identified in the other dataset. To examine the extent to which particular route segments were common to both species and across years, we defined a 25 m buffer around the network identified in each dataset, intersected these areas, and redigitized a smaller set of common routes based on the areas of intersection. We examined the extent to which route use influenced ranging and foraging behavior by constructing a series of successive buffers around the routes in the network and counting the cumulative number of location records and feeding sites that fell within these regions. Finally, we visually assessed the concordance between route use and topography by superimposing identified routes on a digital elevation model of the site constructed using the Spatial Analyst Extension in ArcView GIS 3.3 from ~90 m × 90 m resolution Shuttle Radar Topography Mission (SRTM) data available from the US Geological Survey's EROS Data Center.

Results

Repeatedly used pathways

Plotting all location records and daily paths for each dataset on maps of the study area reveals areas of heavy use for both spider monkeys and woolly monkeys for each of two different points in time and clearly demonstrates repeated path use. Immediately apparent are the concentrations of location records and paths in narrow bands in many areas and the absence of points in other large portions of the home range. Based on superimposing the daily paths connecting these locations following the method outlined above, we identified a set of repeatedly used routes and intersections among these routes for each dataset (Fig. 1a–d). Consistent with the idea of a topological or network mental map, most of the intersections were also confirmed decision points, or nodes.

Temporal stability in route-use and the common use of routes

Comparing both spider and woolly monkey route use across years (Fig. 1), it is clear that many of the same routes and nodes are temporally stable for each taxon, and among the three woolly monkeys groups studied in 1995–1996, multiple groups were found to use several of the

Fig. 1 Location records (*dots*) and daily travel paths (*fine lines*) of spider and woolly monkeys in Yasuní National Park, Ecuador with the network of repeatedly used travel paths (*thicker grey lines*) superimposed. **a** *Ateles*, 1999–2000. **b** *Ateles*, 2002–2003. **c** *Lagothrix*, 1995–1996. **d** *Lagothrix*, 2002–2003
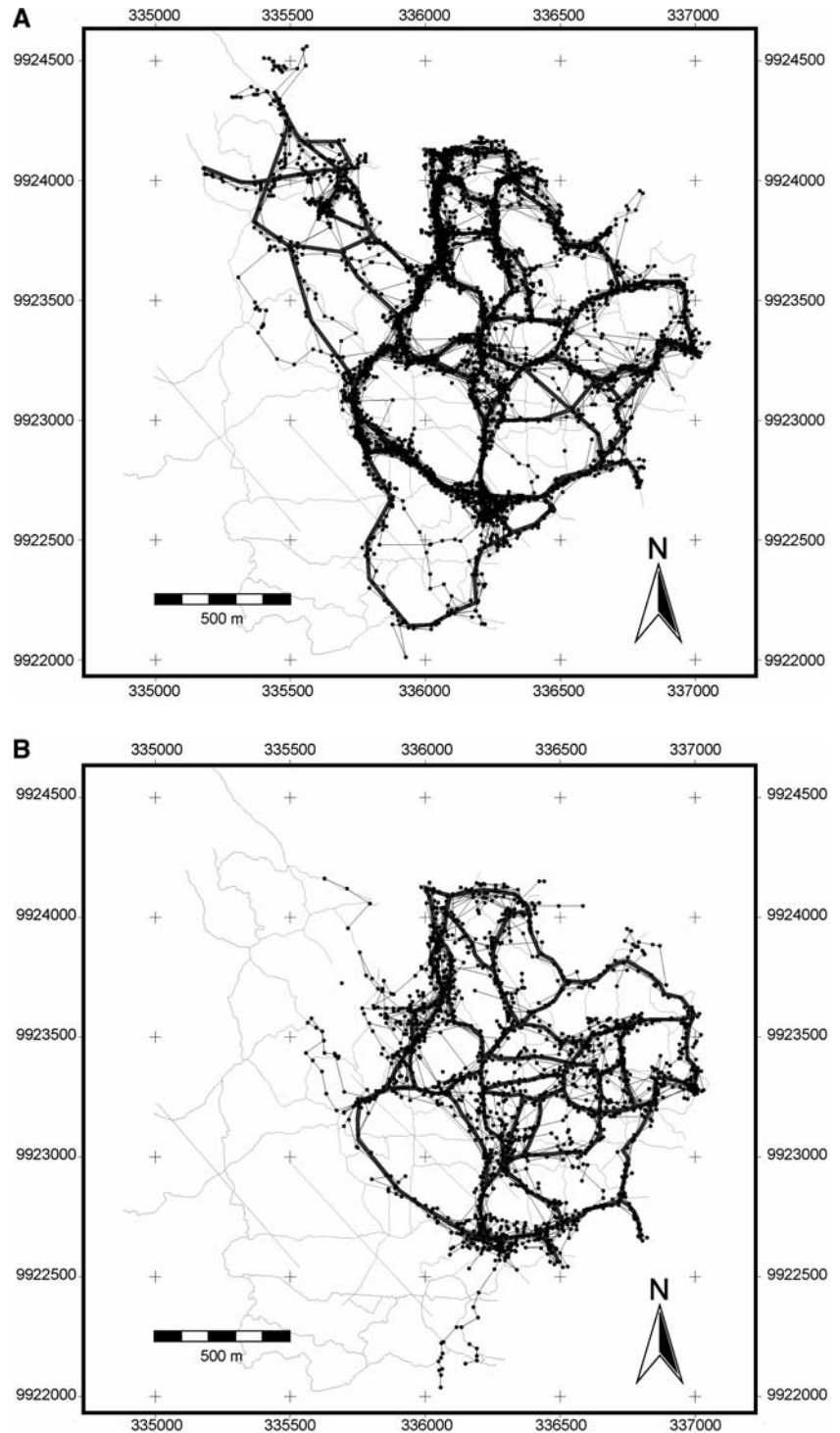
same travel routes in areas of range overlap. For spider monkeys almost 75% of the location records that fell within 25 m of routes identified in one of the two study periods also fell within 25 m of routes identified in the other study period. For woolly monkeys, 41% of locations records falling within 25 m of the route network for three groups in 1995–1996 also fell within 25 m of the route network for the lone study group (Group 3) 6 years later, and nearly 72% of the records within 25 m of Group 3's network in 2002–2003 fell within 25 m of the earlier route network. These results might not be surprising for spider monkeys, since the same community was studied in both time periods; however, for the woolly monkeys two of the original study groups (Groups 1 and 2) were heavily hunted

Fig. 1 continued
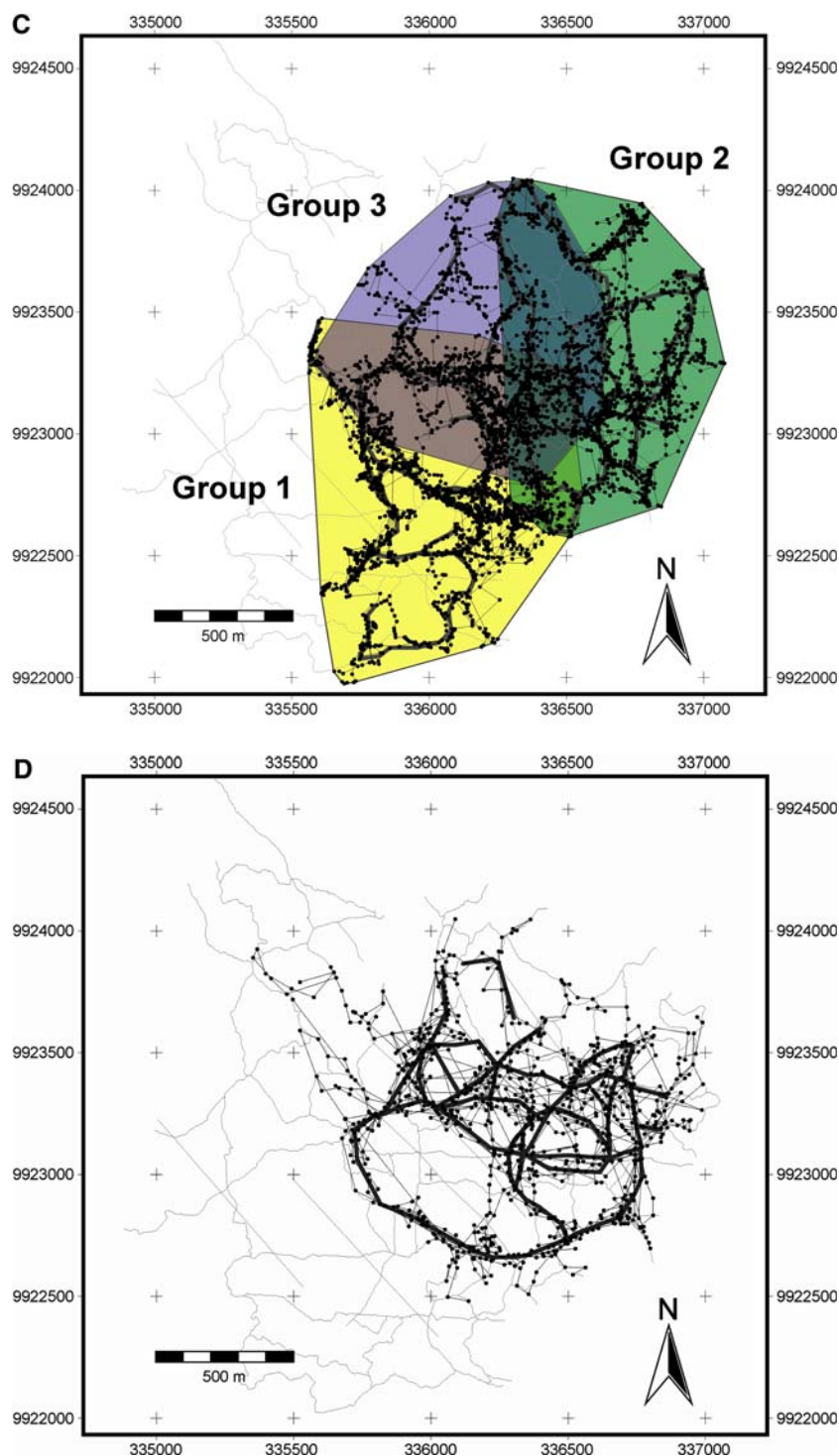
early on during the 6 years between the datasets, and, over that time, the range of the third group expanded to encompass a substantial portion of the former groups' ranges. Interestingly, in 2002–2003 Group 3 was found using some of the same route segments used by Groups 1 and 2 that had previously been located outside of Group 3's original range.

Association between routes, range use, and foraging behavior

Figure 2a to d plot the total number of location records falling within successive 10 m bands around the routes identified in each dataset. For the first *Ateles* dataset, almost 50% of all location records fell within 10 m of

Fig. 2 Cumulative number of location records falling within successive 10 m buffers around the route networks of spider and woolly monkeys. **a** through **d** as in Fig. 1
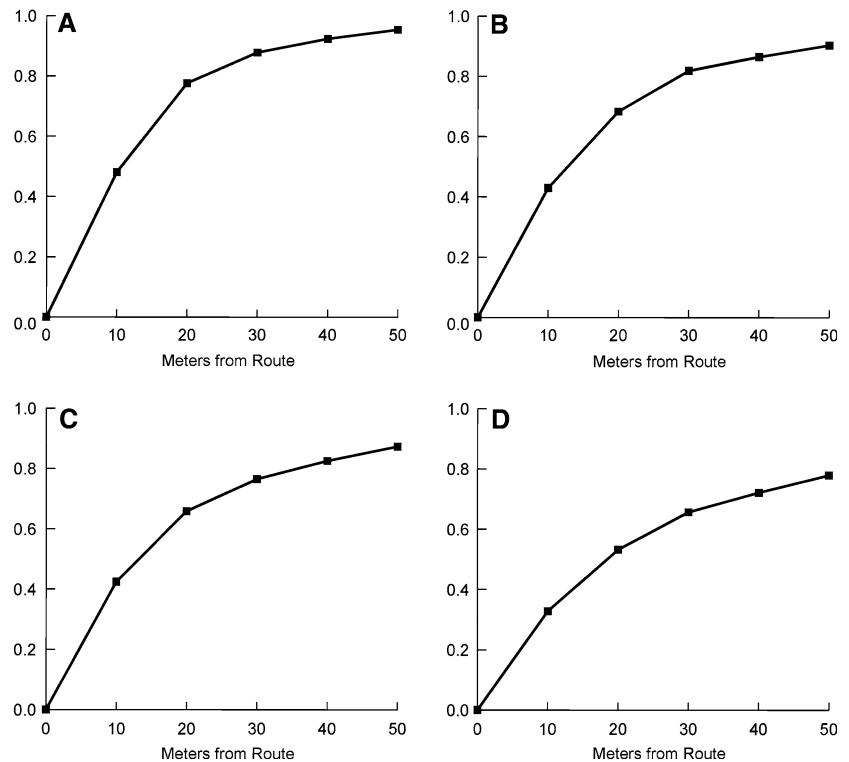
identified routes, and over 95% fell within 50 m of routes. For the second *Ateles* dataset, the same strong association was seen: 43% of location records fell within 10 m of routes and over 90% fell within 50 m of routes. The same pattern was seen in the two *Lagothrix* datasets: 87 and 78% of all location records fell within 50 m of the route network in 1995–1996 and 2002–2003, respectively.

To examine the association between routes and sites used for feeding, we placed 25 and 50 m buffers around the set of routes and then plotted the locations of all feeding trees used during follows. For the 1999–2000 *Ateles* dataset, 68% of 1,057 used feeding trees were located within 25 m of identified routes, and 88% were located within 50 m. A comparably strong association was seen between routes and *Ateles* feeding trees in 2002–2003, where 69% of 419 trees were located within 25 m of the route network and 87% were located with 50 m. A similar pattern was again seen in the two *Lagothrix* datasets: in 1995–1996, 69% of 989 used feeding trees were located within 25 m of the route network, and 87% of used trees were located within 50 m, and in 2002–2003, these values were 53% and 76% of 407 trees, respectively.

Shared routes and the association between routes and topography

Finally, we examined the extent of concordance among routes across all four datasets and the relationship between routes and the topography of our study site. Figure 3a plots the altitude above sea level for ~90 m × 90 m quadrats across the study site gleaned from SRTM data and the 5 m elevation contour lines extrapolated from this data. In Fig. 3b we have superimposed the set of consensus routes common to all four dataset on top of the contour map. The total length of the set of common routes identified (~4,900 m) represents between 26 and 50% of the total length of the route network identified in any one of the datasets. For these common routes, there is a clear association between routes and ridges, with routes generally falling slightly to one side of ridge apices. Figure 4 plots a 3D view of an exemplary spider monkey travel path superimposed on the topography of the study site to demonstrate the clear way in which most of the path follows or parallels ridges.

Discussion

Route-based travel in spider and woolly monkeys

Our results demonstrate that rather than covering all portions of their home range evenly, Yasuní spider and woolly monkeys commonly traveled through their home ranges following a network of repeatedly used paths, or ''routes''. Many of these routes were common to both species and showed a strong degree of permanency, being repeated

Fig. 3 Relationship between topography and shared travel routes. **a** SRTM data and extracted topography (5 m contour lines) for the Proyecto Primates Research Site. **b** Contour lines, trail map, and set of travel routes common to all four datasets
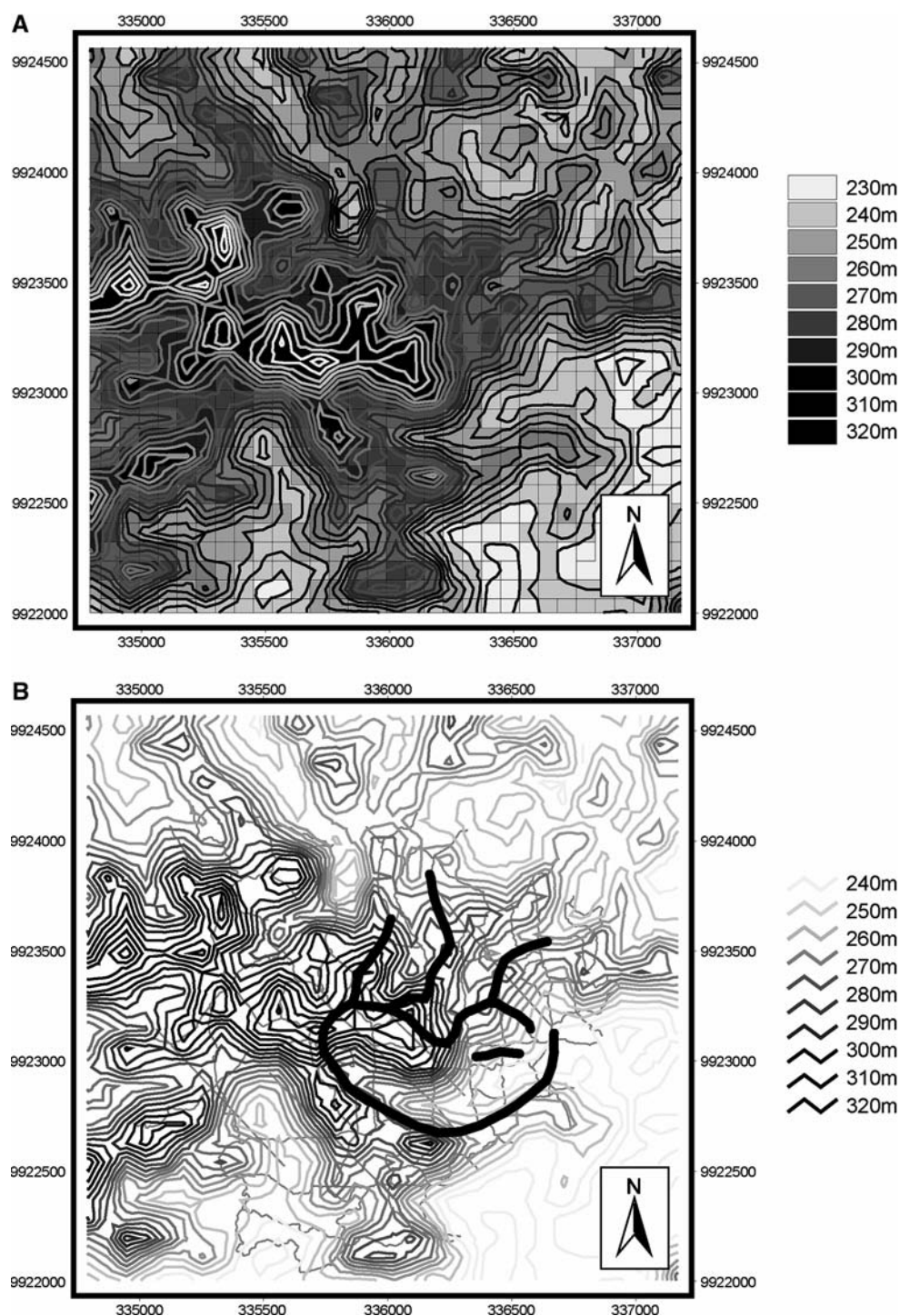
across the year during individual studies, as well as across multiple study years. Additionally, the vast majority of location records for both species fell along or near identified routes, as did most of the fruit feeding trees used by each species, and several important routes appeared to be associated with distinct topographic features. By traveling along these routes, selecting among the alternative path segments available at an intersection (node), and then continuing along the next segment, Yasuní spider and woolly monkeys were clearly able to effectively navigate their home range in their daily search for food.

The fact that a very high proportion of location records fell within 25 m of identified route networks for both species indicates that neither spider nor woolly monkeys typically take novel paths among distant parts of their home ranges. Given that novel path use is predicted by both the Euclidean

and path integration models of spatial memory and navigation, our observations of fidelity to repeatedly used paths by both of these highly frugivorous species suggest that a different model may be more appropriate. In particular, our results are consistent with Poucet's (1993) model of topological or route-based mental maps, and a number of field studies of other nonhuman primates are also consistent with this model. For example, MacKinnon (1974) described the repeated use of particular paths or ''arboreal highways'' by Bornean orangutans in traversing their home ranges. Similarly, Sigg and Stolba (1981) documented that hamadryas baboons travel between important sections of their home range using various combinations of repeatedly used ''street segments'' of ~500 m. Finally, Milton (1980, 1981, 2000) observed the same use of arboreal highways in both howler monkeys and spider monkeys in Barro Colorado Island, Panama. These arboreal pathways appeared to be traditional routes used to connect areas of the home range where the density of preferred food trees was relatively high, and she suggested that these routes may develop and persist across several generations.

Routes, topography, and travel efficiency

Although the specific tree-to-tree and branch-to-branch paths traveled along route segments varied, repeatedly used routes often followed topographic features for both spider and woolly monkeys. The Proyecto Primates Research Site

consists of a series of high, interconnected ridges that can rise more than 100 m above the bottoms of the drainages between them. In many cases, route segments followed or paralleled the locations of ridges almost perfectly (e.g., Fig. 4), with shorter route segments crossing between them. Indeed, almost all of the route segments common between taxa were ones that followed ridges.

There are several reasons why an association between routes and ridges might be expected. First, traveling along ridges may be preferred as it offers excellent visibility of the surrounding terrain, allowing animals to potentially monitor feeding sites or conspecifics at a great distance. Second, traveling along ridges may be energetically less costly than direct travel if that involves crossing valleys or going up and down slopes (see Milton 2000 for a discussion of this point relevant to travel by indigenous Amazonian humans). Third, ridges may provide convenient landmarks to use for navigation.

Interestingly, the monkeys did not typically travel along the tops of the ridges. Rather, they tended to travel in tall trees along one side of the slope, typically at or just above the height of the ridge itself. There are several possible explanations for this observation. First, despite providing a superior view of surrounding terrain, travel along the tops of the ridges might cause the greatest exposure to aerial predators such as harpy eagles (*Harpia harpyja*) or crested eagles (*Morphnus guianensis*), known predators of both species. Second, fewer tall trees are available on the ridge

Fig. 4 Sample daily path of a spider monkey demonstrating the association between travel paths and ridges
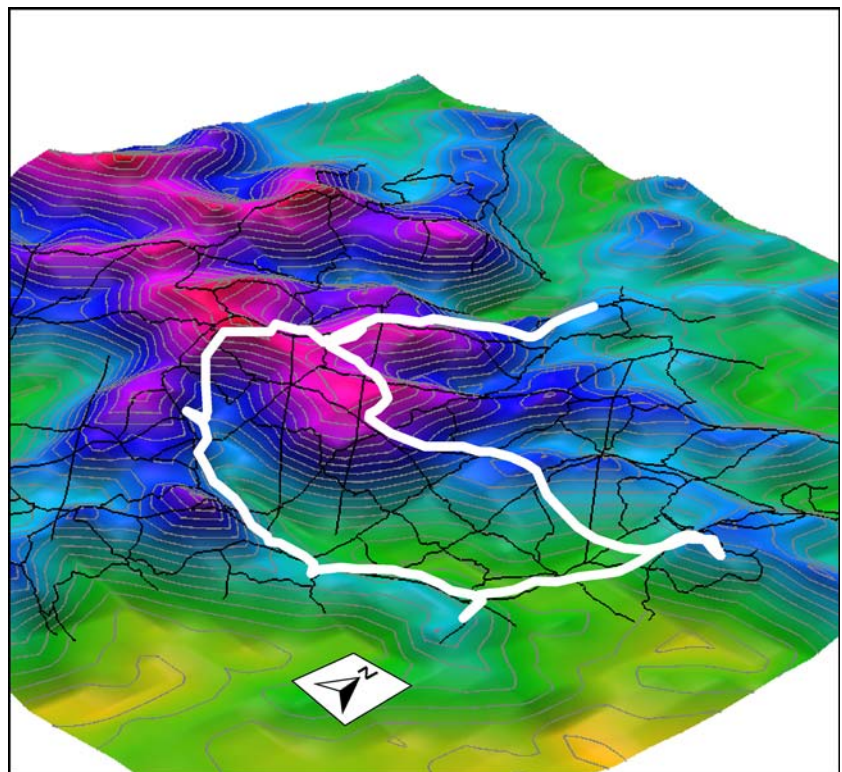
tops, presumably because these are more likely to be knocked down by strong winds. Spider and woolly monkeys spend most of their time traveling in the tops of tall trees, more than 20 m above ground level (Di Fiore 1997; Dew 2001), where they are best able to travel along strong branches from tree to tree (Cant et al. 2001). Travel along the sides of ridges may thus represent a compromise between maximizing the view of the surrounding area, while simultaneously minimizing exposure to aerial and terrestrial predators and retaining the ability to travel along a preferred substrate.

Route segments were not limited to following ridges, however. Shorter routes crossed between ridges, and most of these did not follow obvious geographic features. Moreover, the lowest areas in our study site are generally flat, wet, and covered by tall primary forest; nonetheless, regular routes were also discernable in these topologically featureless areas. Observation of travel in these areas suggests that preferred trees or tree types (Cant et al. 2001) might dictate regular travel routes. The relatively large body size of both spider and woolly monkeys may mean that they are constrained by the size of support branches available for travel, having to avoid branches too thin to support their weight. In some places, such as those where large support trees are less common, routes may be funneled along these trees.

Specific route segments may also have developed because they provided the most efficient travel within a terrain type. Spider and woolly monkeys often traveled circuitous routes along ridges, rather than opting for more direct paths that would require them to cross valleys or traverse ridges perpendicularly. Ridge travel would primarily be in a horizontal plane, rather than involving the up-and-down climbing that would often be demanded by more direct travel. Thus, travel along ridges could theoretically pay off on energetic grounds.

Cognitive and evolutionary implications of route-based travel

Poucet (1993) suggested that a topological, or route-based, mental map would be an efficient mental system for storing the spatial data animals need for navigating about an environment. In fact, by using a route network, animals should be able to navigate effectively and relatively efficiently even with only a minimal understanding of the general spatial relationships among nodes in the network. Mental representation of the routes linking the nodes would require only storage of distance information and a series of linked views so that the animal would recognize the route during travel, and these would be reinforced by repeated use of the routes. Additionally, using routes for navigation could reduce an animal's need for ''on-line processing''

and updating of their mental map of the spatial and temporal relationships among landscape features as the animal moves (Barton 2000), something that would be required if either a Euclidean cognitive map or path integration were being used for navigation.

By following obvious geographic features, such as ridges, the memorization and learning of specific routes would be made even simpler. The use of visual cues, called ''landmarks'', to orient to important locations has been well documented for many animals, including insects, birds, and various mammals, including several primates (e.g., Sigg and Stolba 1981; Gould 1987; Garber 1989; Hitchcock and Sherry 1990; Jacobs and Liman 1991; Etienne et al. 1996; Gould-Beierle and Kamil 1996; Vlasak 2006a, b). In fact, geographical features such as ridges, streams, forest edges, and cliffs are known to be associated with primate travel routes in several taxa (MacKinnon 1974; Sigg and Stolba 1981; Garber 1989; Janson 1998). Ridges are ideal landmarks because their location does not change and their size allows them to be seen from hundreds of meters away.

If spider and woolly monkeys do indeed utilize topology-based mental maps to navigate their home ranges, several interesting implications arise. First, examination of the initial range maps (Fig. 1) shows that there are large areas within the bounds of each species' and group's home range that were almost never visited. Although microhabitat differences (e.g., primary forest versus disturbed areas) likely account in part for this pattern, much of the unvisited portion of the home range appeared to be suitable for use (Di Fiore and Suarez, unpublished data). However, because visual distance in tropical forests is limited to ~50 m (Janson and Di Bitetti 1997), traveling primarily via a route network could mean that monkeys are effectively unable to discover feeding trees located far off the route system. This, in turn, is likely to affect animals' own assessments of resource abundance in their habitats and thus influence their foraging behavior. Socioecologists investigating how resource abundance and dispersion influence various aspects of primate social systems should bear this in mind when designing floristic surveys and phenological studies.

Second, the use of a topological mental map also provides the foundation for an interesting model for the updating of a primate's knowledge of the location and condition of fruit-bearing trees in their environment (Wrangham 1977; Milton 1981, 2000; van Roosmalen 1985) and for avoiding what Milton (2000) has referred to as ''cognitive overload''. If an animal is passing many potential feeding trees as it travels around its home range, it may be easy to check their phenological status directly rather than trying to keep track of that status mentally. For animals such as spider and woolly monkeys, which each feed on a minimum of over 220 different species of fleshy

fruits (Di Fiore 2004; Suarez 2006), this could represent a significant adaptation.

Moreover, as animals travel particular routes to feed in trees currently bearing fruits, it is likely that they will pass near other trees in earlier stages of fruit ripeness. These trees can be monitored during daily travel, and then incorporated into the repertoire of current feeding trees as they begin to bear desirable fruit. This could also allow them to indirectly monitor fruiting patches along routes not recently used by the animals. In a clever experiment, Menzel (1991) demonstrated that Japanese macaques applied phenological information learned at one specific feeding patch to other patches of the same species. In the experiment, he placed ripe fruit beneath a vine of the same species that was out of season and not bearing fruits. When the macaques discovered this, they traveled to other vines of the same species (also out of season) and visually inspected them, as if expecting to find ripe fruits there, too.

If spider and woolly monkeys have the same ability to generalize fruit condition, then monitoring potential fruit-bearing trees along their more common daily routes would also indirectly allow them to monitor the status of additional trees in less recently traveled areas, thereby reducing time and energy expenditure. In this way, animals would not need to commit as many cognitive resources to storing information on the locations of all potential feeding trees or to keeping track of or trying to predict the temporally shifting phenological status of all of those trees, a proposition that Milton (1981, 2000) raised based on her study of howler monkey travel patterns. If navigating by repeatedly used routes does, indeed, yield some cognitive savings in terms of storing or processing spatial and/or phenological information, it might be taken as evidence that ''foraging cognition'' has not been as important in driving the evolution of primate brain size as selection for either social cognition or visual information processing power (Barton 2000).

Third, route-based foraging also has implications for several components of sociality in atelines and other primate taxa characterized by flexible patterns of spatial association among group members. For both spider monkeys (who live in highly flexible fission–fusion societies and often forage alone or in small parties) and woolly monkeys (who, while traveling in cohesive social groups, often forage out of sight of other group members), the fact that animals navigate their home ranges using the same predictable routes may help prevent them from losing social contact with travel partners or facilitate their locating one another again if they do become separated. Route-based travel may, in fact, reduce the intensity of overt contest competition among members of a foraging group or subgroup, since animals traveling together would not need to actually remain in close spatial proximity to one another

to nonetheless reap whatever benefits that association might provide in terms of increasing foraging efficiency, reducing the risk of predation, etc. Indeed, overt contest competition appears rare in spider and woolly monkeys (e.g., Di Fiore and Campbell 2007). Additionally, for *Ateles* in particular, route-based travel could allow animals foraging in different subgroups to more easily find one another and join together. Although not analyzed formally here, many spider monkey subgroup fusions appeared to take place at key nodes within the route network, particularly where nodes corresponded with sleeping or resting sites or with long-term-use feeding trees (Suarez 2003). In fact, it appeared common for a subgroup to approach one of these ''reunion sites'' and wait there until they were joined by additional animals from other subgroups. Route-based travel may thus facilitate animals' flexible and strategic use of socio-spatial associations.

A final implication of route-based foraging concerns the potential ecological and evolutionary impacts of animal ranging behavior on their environments. Both spider and woolly monkeys are important seed dispersers (Yumoto et al. 1999; Stevenson 2000; Dew 2001; Stevenson et al. 2002; Russo 2003), and because travel for these species is largely confined to a route-based system, defecation of seeds tends to occur along highly used route segments (Di Fiore and Link, unpublished data). If routes are used across many years, as our data suggest, then it is plausible that over time spider and woolly monkeys may significantly influence the distribution of fruiting trees throughout their home ranges, as Milton (1980) speculated might be true for howler monkeys, resulting in a higher concentration of dietary fruiting trees along travel routes than off of them and contributing to the modification or construction of their own ecological niches (Odling-Smee 1988; Jones et al. 1994; Odling-Smee et al. 1996, 2003; Laland et al. 1999). This possibility highlights a real need for biologists to undertake spatial analyses of forest structure (both of the floristic composition and of the population genetic structure of important species in the diet) in relation to routes used by their dispersers.

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