



## Comparing capuchins and coatis: causes and consequences of differing movement ecology in two sympatric mammals



Ben T. Hirsch<sup>a,b,\*</sup>, Maria P. Tujague<sup>c,d,e</sup>, Yamil E. Di Blanco<sup>d,e</sup>, Mario S. Di Bitetti<sup>d,e</sup>, Charles H. Janson<sup>f</sup>

<sup>a</sup>Smithsonian Tropical Research Institute (STRI), Balboa, Panama

<sup>b</sup>School of Environment and Natural Resources, The Ohio State University, Columbus, OH, U.S.A.

<sup>c</sup>National Research Council (CONICET), Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Paseo del Bosque S/N, La Plata Buenos Aires, Argentina

<sup>d</sup>Instituto de Biología Subtropical, Facultad de Ciencias Forestales, Universidad Nacional de Misiones – National Research Council (CONICET), Puerto Iguazú, Misiones, Argentina

<sup>e</sup>Asociación Civil Centro de Investigaciones del Bosque Atlántico (CeIBA), Puerto Iguazú, Misiones, Argentina

<sup>f</sup>Division of Biological Sciences, University of Montana, Missoula, MT, U.S.A.

### ARTICLE INFO

#### Article history:

Received 30 October 2012

Initial acceptance 2 January 2013

Final acceptance 6 May 2013

Available online 3 July 2013

MS. number: A12-00819R

#### Keywords:

animal movement

capuchin

*Cebus apella nigrilus*

coati

foraging

*Nasua nasua*

straightness index

trapline

travel behaviour

travel cost

The mechanisms that shape animal movement decisions at the level of an individual or a group of animals can scale up to affect larger-scale ecological processes. Ecologists often use mechanistic animal movement models to understand these links, but animal movement models rarely connect empirically with an understanding of how animals actually decide to move around in their environment. To better understand this relationship, we compared the travel behaviour of two sympatric mammal species that have broadly similar diets: brown capuchin monkeys, *Cebus apella nigrilus*, and ring-tailed coatis, *Nasua nasua*. According to most mechanistic animal movement models, species that exploit the same resources should show similar movement patterns. Although the fruit component of coati and capuchin diets is very similar, coatis primarily feed on invertebrates in the leaf litter or soil, while capuchins forage on invertebrate prey in the forest canopy. We found that these two species showed markedly different movement patterns: while capuchins typically travelled between fruit trees in relatively straight lines, coatis had significantly more tortuous daily travel paths and frequently visited the same fruit trees more than once per day. These circular coati travel paths would not be predicted by most foraging models. We posit that these differences in coati and capuchin movement patterns are driven by differences in arboreal and terrestrial travel costs, exploitation of fallen fruits and shifts in foraging behaviour over the course of the day. Because these seemingly small differences between the two species lead to major differences in movement behaviour, we posit that animal movement models need to better incorporate (1) travel costs, (2) both directed travel and random food search and (3) realistic diet models that include resources with different nutrient compositions.

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The behaviour and movement patterns of animals scale up to affect population-level and community-level ecological processes (Morales & Ellner 2002; Bowler & Benton 2005; Holyoak et al. 2008; Revilla & Wiegand 2008; Nathan et al. 2009). To better understand how animal behaviour affects these large-scale ecological processes, it is necessary to understand the causes and consequences of fine-scale movement patterns at the level of individual animals or animal groups (Lima & Zollner 1996; Schick et al. 2008).

Recent improvements in tracking technology, computing power and theoretical models of animal movement have led to an increasingly integrative approach to movement ecology (Nathan et al. 2009). Despite these recent advances, a gap exists between theoretical models of animal movement and traditional ethological studies of animal movement.

The major theoretical foundation for animal movement models is based on random walk and random search models (Turchin 1998; Bartumeus et al. 2005). Although the assumptions of these models may be realistic for animals that have little or no prior knowledge of food locations, they are less than ideal for modelling the foraging behaviour of animals that use memory to exploit previously visited food resources. Many animal species feed on resources that persist over time, which facilitates the use of memory during foraging

\* Correspondence and present address: B. T. Hirsch, School of Environment and Natural Resources, The Ohio State University, 2021 Coffey Rd, Columbus, OH 43210, U.S.A.

E-mail address: [hirschb@si.edu](mailto:hirschb@si.edu) (B. T. Hirsch).

decisions. Animals that feed on 'known' food resources are often observed to travel consecutively from food patch to food patch in a process called 'traplining' (Gill 1988; Janson 1996). While a large body of research has been undertaken to understand the manner in which animals visit these known resources, little work has been done to integrate traplining and random search animal movements into the same model (Mueller et al. 2011). Some statistical techniques have been developed to identify if and when an animal switches from undirected food search to directed travel towards known locations (Nevitt et al. 2008; Byrne et al. 2009), but most theoretical models of animal movement still neglect to incorporate both food searching and goal oriented behaviour (but see Mueller & Fagan 2008; Mueller et al. 2011).

The degree to which animals use memory to find food items varies widely. Some animal species primarily exploit previously visited food sites, while other species constantly search for new food items. In reality, most animals probably fall somewhere on a continuum between these two extremes. For example, brown capuchin monkeys, *Cebus apella nigrinus*, have been observed to show long-distance directed movements towards large fruit trees, and it has been experimentally demonstrated that monkey groups have prior knowledge of the locations of fruit patches (Janson 1998, 2007). In between visits to fruit trees, capuchins typically feed on dispersed, cryptic arboreal invertebrates (Janson 1990). Because of the ephemeral nature of these invertebrates, it would be difficult or impossible for capuchins to reliably predict the locations of these small, scattered resources. The daily movement patterns of brown capuchins appear to be driven almost solely by the presence of ripe fruit trees (Janson 2007). Thus even though capuchins exploit both known and unknown food items, their travel behaviour appears to closely resemble trapline movements between known food resources. Another social mammal with a diet similar to capuchin monkeys is the ring-tailed coati, *Nasua nasua*. Coatis can also travel from fruit tree to fruit tree in relatively straight lines, and forage for invertebrates in the soil and leaf litter when not visiting fruit trees (Hirsch 2009, 2010). It has been concluded that coati movement patterns are primarily determined by the presence and location of ripe fruit (Hirsch 2009). Capuchins and coatis do differ in three respects: (1) capuchins are almost exclusively arboreal while coatis usually travel and forage on the ground, (2) the coati diet in Iguazú, Argentina includes a greater quantity of small, quickly depleted fruit resources (e.g. pindo palm trees, *Syagrus romanzoffianum*) compared to capuchins at the same field site, and (3) coatis have faster life histories, which may lead to different nutritional demands in comparison to capuchins (Hirsch 2009; Janson et al. 2012).

The purpose of our study was to test whether differences in feeding ecology, travel costs and nutritional requirements could impact the movement behaviour of two well-studied sympatric Neotropical frugivores: coatis and capuchin monkeys. Given that both species have similar diets and show movement patterns that appear to be driven by the availability of ripe fruit (Di Bitetti & Janson 2001a, b; Hirsch 2009), one could predict that these two species should travel through their environment in a similar manner. Alternately, differences in travel costs, food depletion or physiology could conceivably lead to differences in movement behaviour between these two species. While it may not be possible to conclusively determine the exact cause and effect of differences in movement patterns through a comparison of two species, by comparing two intensively studied sympatric mammals it is possible to identify what possible factors may shape differences in movement patterns. These factors can then be incorporated into future animal movement models and studied in closer detail through empirical studies.

In principle, optimal foraging theory predicts that both capuchins and coatis should travel in straight lines between consecutive, densely concentrated, long-lasting food resources (such as fruit trees) and opportunistically forage for dispersed ephemeral foods (such as invertebrates) between visits to consecutive fruit trees. The resulting travel patterns are predicted to closely resemble trapline foraging movements, and both species are predicted to show low levels of tortuosity (i.e. twisting, curvy paths) both between visits to consecutive food patches and during their total daily travel patterns. To test whether the two focal species behaved as predicted, we quantified measures of tortuosity and fruit tree revisits in these two species. We then investigated whether the observed travel patterns were consistent with the hypothesis that movement patterns were predominantly determined by the locations of fruit trees in these two species. Additionally, we discuss which, if any, differences between the two species (terrestriality, fruit tree size and life history) could have led to differences in movement patterns.

## METHODS

### Site

This study was carried out in the Iguazú National Park, Argentina (25°40'S, 54°30'W). The site has a humid subtropical climate with marked seasonality in daylength and temperature (Crespo 1982). Mean annual precipitation for the area is between 1900 and 2000 mm, with no marked dry season (Brown & Zunino 1990). The highly seasonal availability of fleshy fruits and arthropods is predictably lowest in winter (June–August) and reaches its peak between October and January in most years (Di Bitetti 2001a). While fruit availability does change from year to year, the yearly changes in fruit availability in Iguazú are relatively minor compared with seasonal variation in fruit availability (Placci et al. 1994). A network of trails covering a 6 km<sup>2</sup> area was used to follow the capuchin and coati study groups. These trails were marked at 50 m intervals by flagging tape that indicated trail name and distance. All trails were measured with compass and metric tape and then mapped using the custom-made computer program Tracker (C. H. Janson & P. Lee, unpublished data).

### Species

Brown capuchin monkeys are medium sized (~3 kg) arboreal monkeys that live in groups of 2–44 individuals (Di Bitetti & Janson 2001b; Janson et al. 2012). We collected data from two well-habituated social groups that varied in size between 12 and 23 individuals. The majority of capuchin activity budgets are spent searching for and consuming food (Janson 1998). Capuchins are omnivorous and primarily feed on ripe fruit and cryptic arboreal invertebrates. Capuchin groups often search for invertebrates between visits to fruit trees and this foraging accounts for 66% of capuchin active time budgets (i.e. time budget when not sleeping or resting; C. H. Janson, unpublished data). The average home range for Iguazú capuchin groups is 161 ha (range 81–293 ha; Di Bitetti 2001b). The two capuchin groups included in this study ('Rita' and 'Gundolph') were not provisioned at feeding platforms (e.g. Janson 1996, 1998, 2007) during the course of this study.

Ring-tailed coatis are medium-sized (3–6 kg) terrestrial mammals that live in groups of 8–64 individuals (Gompper 1995; Hirsch 2007a, b). We used data from two well-habituated groups that varied in size between 9 and 30 individuals (Hirsch 2007a). Coatis spend 70–98% of their monthly foraging time searching for ground-litter invertebrates, which is equivalent to 81% of their total active time budget (Hirsch 2009). Coatis have a highly developed sense of smell that they use to detect ground-litter invertebrates

and fruit (Hirsch 2010). Coatis typically eat fruits after they have fallen on the ground, but they can climb trees, and arboreal coatis often accidentally knock fruits from trees during feeding (Hirsch 2009). Coati home ranges in Iguazú are roughly twice as large as sympatric capuchin home ranges (Hirsch 2007b).

#### Movement and Feeding Data

Daily travel paths of the two species were recorded during complete full-day follows of the animal groups (i.e. groups were followed from sunrise to sunset). A total of 28 all-day follows were analysed for each species. We chose these 28 days based on the completeness of the data (animals were consistently within view of researchers throughout the day), similar group sizes of capuchins and coatis, and the month that the data were collected (Table 1). The collection of capuchin ranging data was unevenly distributed over the course of the year, so to control for seasonal effects, we selected an equal number of coati all-day follows from the same months (but different years) from a larger data set ( $N = 28$  days per species; March: 7 days; April: 13 days; September: 2 days; October: 2 days; November: 1 day; December: 3 days). For coatis, the location of the group was recorded continuously in the field (e.g. any change in position of more than 10 m was recorded) and was typically determined by direct observations of the group in relation to nearby trail markers (Hirsch 2010). Coati group locations were plotted on a detailed map containing all trails and trail markers. The location of any fruit tree visited by group members during the day was plotted on these maps. The handwritten maps were digitized using the Grab It XP program (DATATREND Software, Raleigh, NC, U.S.A.). For capuchins, group and fruit tree locations were recorded with hand-held GPS receivers (Garmin 60Cx). GPS locations were recorded in the centre of the group at least once every 15 min (unless the group was stationary for >15 min).

When a coati or capuchin group fed at a fruit tree, the location and amount of time spent feeding at that tree were recorded. In all cases included in this study, fruit trees had ripe fruit available for consumption. We excluded fruit trees from the analysis when only a few individuals (1–3 individuals) visited the tree while the remaining group members did not visit the fruit tree location. By eliminating these trees from the analyses, we were able to exclude trees that had little or no ripe fruit available, and thus were not desirable travel targets for an entire animal group. We calculated the distances between consecutively visited fruit trees as the shortest straight-line (i.e. Euclidean) distance between them. Travel distances between consecutive fruit trees were calculated by summing the straight-line distances between observed travel locations. When capuchin groups encounter other capuchin groups, they often change direction at the point of encounter (Crofoot et al. 2008; Scarry & Tujague 2012); thus, any travel bout from fruit tree

to fruit tree that was interrupted by an intergroup encounter was removed from our analyses of fruit tree travel distances ( $N = 9$ ). Coatis occasionally encountered conspecific groups, but no encounters were observed during the days included in this study.

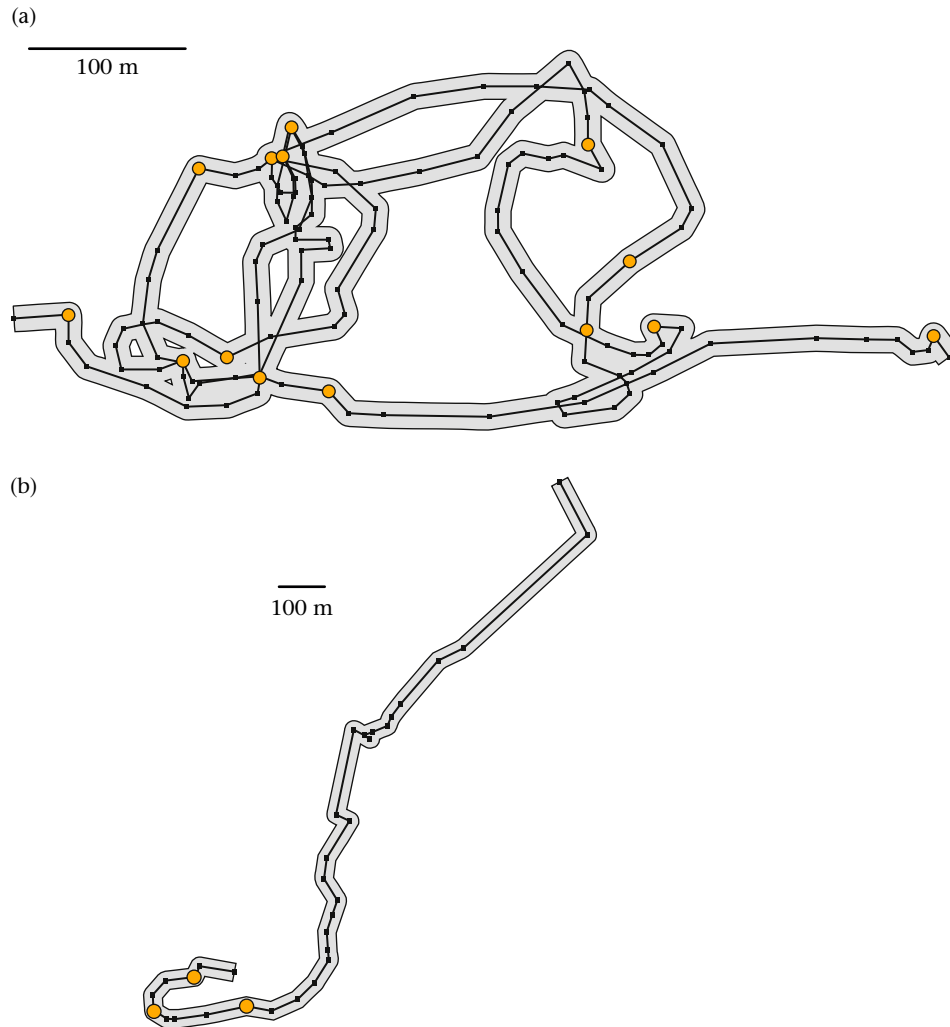
We recorded data on feeding success using focal scan samples (as in Hirsch 2009) for both capuchins and coatis. Fruit intake data, or the number of items eaten per minute, was recorded while animals were inside or below a fruit tree. To compare fruit intake rates of capuchins and coatis, we used 11 species of trees (*Cecropia pachystachya*, *Citrus* sp., *Eriobotrya japonica*, *Eugenia* sp., *Ficus guaraniticus*, *Hovenia dulcis*, *Inga marginata*, *Miconia* sp., *Nectandra lanceolata*, *Sorocea ilicifolia*, and *Syagrus romanzoffianum*). In addition, we tested whether coati fruit intake rates differed when feeding on the ground and feeding inside a fruit tree. We also recorded invertebrate foraging success during focal scan samples (capuchins:  $N = 924$ ; coatis:  $N = 3429$ ), and used the proportion of 10 s samples during which the focal individual consumed an item to determine relative intake rates between the two species (see also Hirsch 2009).

#### Tortuosity Measures

To compare the relative straightness of movement patterns, we chose to create an alternate measure of tortuosity that is computationally simple and biologically relevant to our two study species (see also Nams 2006). A major cost of travelling in a nonlinear path is that it is less efficient, both in terms of energy and time consumed, than travelling in straight-line movements when navigating towards specified goals (such as fruit trees). Nonlinear paths may also be more costly if animal groups pass over areas where they have previously foraged. If food resources are depleted after an animal group passes through the area, any circular movements or moving through previously visited areas should result in lower feeding success. For this reason, we decided to calculate the degree to which coatis and capuchins revisited the same area of their home range during their daily movement paths. Daily travel paths were plotted in ArcView GIS (v.9.3, Esri, Environmental Systems Resources Institute, Inc., Redlands, CA, U.S.A.), and each path was fitted with a buffer that corresponded to the average width of the animal group (Fig. 1). Despite having similar group sizes, coati groups are less spread out than capuchin groups, which may be due to the increased threat of predation on the ground (Hirsch 2002, 2011a; Di Blanco & Hirsch 2006). For coatis, the average group spread was 11.67 m diameter for small groups (8–15 individuals) and 17.1 m for large groups (25–31 individuals; Hirsch 2011b). These group spread estimates were recorded every 15 min during the course of the study, and group spread was estimated by observers that could see or hear all or almost all individuals in the group (see Hirsch 2011b). The average group spread of capuchin groups at Iguazú during this study were observed to be similar to previously recorded estimates (42 m diameter; Janson & DiBitetti 1997). These estimates for capuchin group spread were recorded by observers walking the length of the group and measuring the width in relation to trail markers (Janson & DiBitetti 1997). If a daily travel path was perfectly linear, the area of the day path buffers would be equal to the total daily travel distance multiplied by group spread. If travel paths were excessively curvy and/or groups passed over an area more than once per day, the area used per day (as calculated by the daily path buffer) would be lower than the area calculated for a straight-line path. To calculate tortuosity and the degree to which these groups revisited the same areas during the course of a day, we calculated the ratio of area used per day divided by the maximum area possible (daily travel distance  $\times$  group spread). The resultant foraging efficiency ratio is a measure of

**Table 1**  
Capuchin and coati group sizes, study parameters and results

Species	Capuchin	Coati
<b>Number of study groups</b>	2	2
<b>Group size by month/year/species</b>		
April, $N=6$	2010=12	2003=9–12
March–April, $N=14$	2011=20	2004=26–30
September–October, $N=4$	2009=19	2003=9–12
November, $N=1$	2010=23	2003=29
December, $N=3$	2010=23	2003=29
<b>Average home range size (ha)</b>	161	~300
<b>Average daily travel distance (km)</b>	2.24	3.02
<b>Average number of trees visited/day</b>	6.21	12.11
<b>Average straightness index</b>	0.86	0.86
<b>Average foraging efficiency ratio</b>	92%	83%



**Figure 1.** Examples of total daily travel paths for sympatric (a) coatis (3282 m) and (b) capuchins (2179 m). Solid circles indicate locations of fruit trees; grey buffers correspond to the average group spread (coatis: 17.1 m; capuchins: 42 m).

tortuosity and foraging efficiency with higher values (approaching 100%) indicating more efficient foraging and less tortuous paths.

Foraging efficiency ratios are a computationally simple method for calculating foraging efficiency and straightness of travel. To accurately calculate the efficiency ratios, it is necessary to record the average spread of the animal groups because the travel efficiency ratio value of a given path will change if the group spread changes. In general, travel efficiency ratios decrease as group spread increases. This pattern emerges because as animals forage in larger swaths, any change in direction or repeated use of the same location will result in a larger area of spatial overlap. We posit that these foraging efficiency ratios are the most biologically realistic measure available to describe the percentage of group travel that occurs in areas that have not been previously visited during that day. Another useful measure of tortuosity and directed travel is the straightness index ( $SI = \text{Euclidean distance}/\text{observed travel distance}$ ; Batschelet 1981). To determine whether coatis and capuchins engaged in directed travel between consecutively visited fruit trees (i.e. traplining), we calculated SI values for travel paths between consecutive fruit tree visits. The SI values range between 0 and 1, with lower values being more tortuous routes and 1 being equal to direct straight-line travel from one fruit tree to another.

#### Statistical Methods

Comparisons of coati and capuchin fruit intake rates were tested using paired *t* tests in the JMP computer program (v.5.1, SAS Institute, Cary, NC, U.S.A.). We used general linear mixed models (GLMMs) to test which factors influenced foraging efficiency ratios and fruit tree travel SI values. All GLMMs were run in the STATISTICA computer program (v.6.1, StatSoft Inc., Tulsa, OK, U.S.A.). In addition to testing differences between species, we also entered month as a random factor because daily travel distances and the number of ripe fruit trees vary by month (Di Bitetti 2001a, b; Hirsch 2010). For the daily travel analyses, we entered the total distance travelled during that day as a covariate, and for the fruit travel SI analysis, we entered the Euclidean distance between consecutive fruit trees as a covariate in the model. In many cases, coati groups revisited the same fruit tree more than once per day. To determine the degree to which coatis could still obtain fruit from these re-visits, we conducted paired *t* tests comparing the time spent feeding at a fruit tree during the first visit of the day compared to the second visit ( $N = 142$ ). If food intake rates are constant, then the amount of available fruit should be closely correlated with the amount of time spent foraging under fruit trees. Coati fruit intake rates do not decrease over the course of the day (Hirsch 2009,



2011a); thus, the amount of time spent feeding at a fruit tree should be closely correlated with the total amount of consumed fruits.

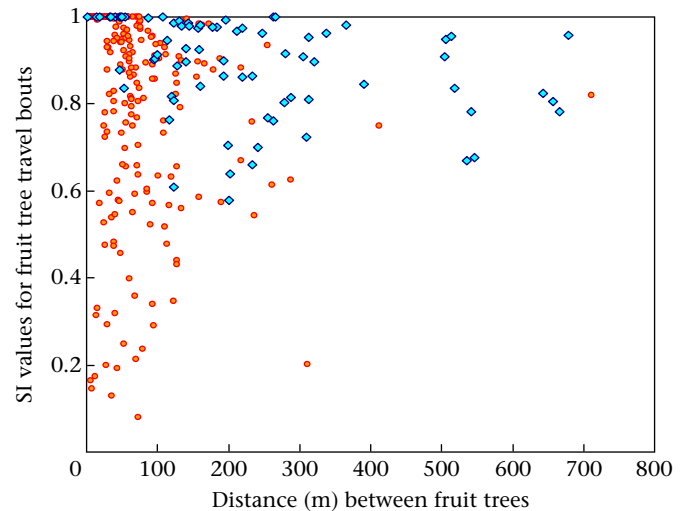
## RESULTS

Coatis travelled 25.8% further per day than capuchins (mean  $\pm$  SD: coatis:  $3.02 \pm 0.79$  km; capuchins:  $2.24 \pm 0.44$  km;  $t$  test:  $t_{28} = -4.57$ ,  $P < 0.001$ ) and visited almost twice as many fruit trees per day (mean  $\pm$  SD number of fruit trees/day: coatis:  $12.11 \pm 8.55$ ; capuchins:  $6.21 \pm 1.28$ ;  $t$  test:  $t_{28} = -4.62$ ,  $P < 0.001$ ). Although we did not record the average diameter at breast height (DBH) of fruit trees during our study, coatis at Iguazú exploit pindo palm trees more frequently than do capuchins (Di Bitetti 2001a, b; Hirsch 2010), suggesting that coatis concentrate feeding on smaller-sized fruit trees than capuchins.

Daily paths of coatis were more tortuous than those of capuchins. Mean  $\pm$  SD foraging efficiency ratio was  $92 \pm 0.06\%$  for capuchins and  $83 \pm 0.10\%$  for coatis (GLMM test for species effect:  $\chi^2_1 = 8.058$ ,  $P = 0.005$ ). Neither month nor the total distance travelled per day had a significant effect on the efficiency ratios (month:  $\chi^2_5 = 2.347$ ,  $P = 0.799$ ; distance:  $\chi^2_1 = 1.376$ ,  $P = 0.241$ ; Table 2).

Coatis also showed less directed travel between pairs of fruit trees, as assessed by the straightness index (SI). When we accounted for distance and month in the GLMM models, SI values of capuchins were significantly higher than those of coatis ( $\chi^2_1 = 6.52$ ,  $P = 0.010$ ). Both species had a high percentage of fruit travel bouts that were perfectly straight (SI = 1: capuchins: 20%; coatis: 44%), but coatis frequently had low SI values even when travel distances were short (<100 m; Fig. 2). In 27 cases, coatis had SI values lower than 0.5 (8.2%), which indicates that the coati group travelled over twice as far as needed to reach the next fruit tree. In contrast, capuchins had SI values <0.5 only five times (3.9%). As the Euclidean distances between fruit trees increased, SI values generally decreased (Table 3). We found relatively high SI values (>0.8) for both species, even when distances between fruit trees were long (>500 m), indicating that both species are capable of long-distance directed travel towards fruit resources (Fig. 2).

In contrast to capuchins, coati groups regularly visited the same tree more than once per day (capuchins: five occurrences in 28 days, 3% of fruit trees; coatis: 142 occurrences, 42% of fruit trees). When doing so, the coati groups spent a mean  $\pm$  SD of  $9.00 \pm 8.84$  min feeding on fruit during the first visit and a mean of  $6.77 \pm 6.25$  min feeding on fruit during the second visit (paired  $t$  test:  $t_{142} = 3.254$ ,  $P = 0.001$ ). The same pattern held for the most commonly eaten fruit species (pindo palms): first visit:  $7.37 \pm 5.41$  min; second visit:  $5.89 \pm 5.65$  min (paired  $t$  test:  $t_{99} = 2.763$ ,  $P = 0.007$ ). The average  $\pm$  SD time spent feeding on pindo trees that were not revisited on the same day was  $4.79 \pm 4.59$  min, which was not significantly shorter than the average time spent during second visits to pindo trees (ANOVA:



**Figure 2.** Straightness index (SI) values for fruit tree travel bouts as a function of the Euclidean distance (in metres) between consecutive fruit trees. Circles: coatis; diamonds: capuchins.

$F_{1,294} = 3.32$ ,  $P = 0.070$ ) but was significantly shorter than first visits ( $F_{1,294} = 18.94$ ,  $P < 0.001$ ).

Food intake rates during feeding on 11 common fruit species did not differ between the two species (capuchins: 7.94 fruits/min; coatis: 7.22 fruits/min; paired  $t$  test:  $t_{11} = 0.478$ ,  $P = 0.643$ ); thus, we found no evidence that the arboreal fruit feeding by capuchins was more efficient than coati terrestrial fruit feeding. Additionally, fruit intake rates for coatis were similar underneath and inside pindo trees (ANOVA:  $F_{1,510} = 0.082$ ,  $P = 0.775$ ). Coatis had higher invertebrate foraging efficiency than capuchins and they ate at least one item during invertebrate foraging scan samples almost twice as often as capuchins (capuchins: 11.04%,  $N = 924$ ; coatis: 19.69%,  $N = 3429$ ).

## DISCUSSION

Capuchin monkeys showed less tortuous daily travel paths and revisited fruit trees less frequently than coatis in Iguazú. For a given distance, capuchins travelled in a more direct, straight-line manner between consecutive fruit trees than coatis, and they rarely travelled in a curvilinear manner at relatively short distances. One caveat to comparing travel efficiency ratios between these two species is that the foraging efficiency measurements are sensitive to differences in group spread: if all other factors are equal, larger group spreads will result in lower foraging efficiency values. Because capuchins have wider group spreads, we expected their foraging efficiency values to be lower than those for coatis, but we

**Table 2**  
General linear mixed model of factors influencing daily travel path efficiency ratios

Variable	df	Estimate	P
<b>Species</b>	1	-0.041	0.005
<b>Daily travel distance</b>	1	0.000	0.241
<b>Month</b>	5		
March		0.000	–
April		0.020	0.369
September		-0.009	0.830
October		-0.019	0.651
November		0.026	0.637
December		-0.035	0.328

**Table 3**  
GLMM of factors influencing fruit tree to fruit tree travel straightness index (SI) scores

Variable	df	Estimate	P
<b>Species</b>	1	0.037	<0.011
<b>Euclidean distance</b>	1	-0.001	<0.001
<b>Month</b>	5		
March		0.000	–
April		0.055	0.108
September		-0.002	0.964
October		-0.036	0.522
November		0.127	0.353
December		-0.140	0.008

found the opposite result instead, suggesting that our observed differences are conservative. Despite this potential bias favouring more tortuous travel paths in capuchins, their trajectories were in fact less likely to overlap prior foraging routes.

What mechanisms could account for the more efficient foraging paths of capuchins relative to coatis? One possibility is that increased travel costs of travelling through tree canopies versus walking on the ground leads capuchins to minimize travel distances and avoid previously depleted areas more than coatis. While we do not possess physiological measures of the cost of locomotion for either of our study species, a previous analysis of energy budgets in capuchins estimated that arboreal travel was at least twice as costly per ground distance covered as equivalent movement on the ground (Janson 1988). Furthermore, our measures of capuchin group travel distances may underestimate the amount of travel by individual monkeys in the group because they are unable to travel in perfectly straight lines through canopy trees (see also Isbell et al. 1999). For these reasons, it is plausible to hypothesize that capuchins are more sensitive to maximizing travel efficiency than coatis. If these differences in the costs of arboreal versus terrestrial travel are generalizable, this leads to testable predictions about the relative tortuosity of travel paths in other species. As a general rule, tortuosity and food patch revisits should be more common in species with low travel costs. Indeed, there are numerous examples of flying animals revisiting food patches many times in a day (bats: Lemke 1984; Racey & Swift 1985; bumblebees: Thomson et al. 1982, 1997; Thomson 1996; euglossine bees: Janzen 1971; hummingbirds: Gill 1988; Garrison & Gass 1999), which is consistent with the observed lower energy costs of aerial travel (Schmidt-Nielsen 1972).

We posit that differences in terrestriality in relation to fruit feeding may help explain how and why coatis frequently revisit fruit trees during their daily travels. When coatis visit fruit trees, most individuals feed on the ground, while some individuals may climb the tree and feed arboreally (Hirsch 2009). Although we did not count the number of ripe fruits remaining after a coati group visited, typically very few fruits were left on the ground. In contrast, it was common for ripe fruits to remain in the tree canopy, especially if no coatis climbed up into the canopy. This seemingly minor difference in foraging behaviour between coatis and capuchins (i.e. coatis' greater reliance on felled fruits), could greatly affect their travel behaviour. Unlike capuchins, when a coati group revisits a fruit tree later in the day, there may be additional fruit remaining on the tree. If one or more individuals enter the canopy and knock ripe fruits out of the tree, this would make food available for group members remaining on the ground. Although coatis spent less time feeding on fruit trees during their second visit, these trees still contained sufficient fruit so that it was profitable to return and feed at the same tree twice in one day. This does not appear to be the case in capuchins, which have been found to deplete almost all fruit during visits to trees up to 20 m in diameter, which are much larger than the pindo palms commonly exploited by coatis (Janson 1988; Hirsch 2009).

Cognitive differences could conceivably play a role in driving differences in movement ecology between these two species. Primates, and capuchins in particular, have relatively large brains, which are generally linked to increased success in performing cognitive tasks (Stephan et al. 1981; Reader & Laland 2002; Dunbar & Shultz 2007). Carnivores generally have relatively smaller brains than primates, and the relative brain size of procyonids are at the mean level for carnivores (Gittleman 1986). It is conceivable that morphological and cognitive differences between these two species could result in greater travel efficiency behaviour for the 'smarter' species: capuchin monkeys. While we cannot rule out this hypothesis, we posit that cognitive differences may not be the source

of the observed differences in movement behaviour. The use of memory to navigate to fruit trees has been well documented and supported in capuchin monkeys (Janson 1998, 2007). Although the same tests have not been conducted with coatis, the straight-line travel behaviour towards fruit resources combined with an increase in travel speed when approaching within 25–40 m of a fruit tree (Hirsch 2010) is highly consistent with the hypothesis that coatis had prior knowledge of fruit tree locations (cf. Pochron 2001; Janson & Byrne 2007). Given that coatis appear to rely on memory for navigation to food resources and are able to exhibit straight-line travel at relatively long distances (>100 m), the pattern that coatis routinely take round-about routes between fruit trees at relatively short distances (<25 m) suggests that the inefficient travel routes by coatis are not due to their inability to remember the locations of nearby fruit trees.

An alternate hypothesis for differences in travel behaviour between capuchins and coatis is that differences in physiology and foraging ecology could have led to these differences in movement behaviour. The circular travel patterns of coatis may arise because coatis are more focused on finding invertebrates, with fruit trees being a resource of secondary importance (e.g. Alves-Costa et al. 2004). If this were the case, then coatis would be expected to only visit fruit trees in areas where they foraged for invertebrates. We find this unlikely because coatis were often observed to travel more than 100 m in straight lines between consecutive fruit resources. A more plausible hypothesis is that coatis 'switch' food search strategies during the course of the day for dietary reasons (Westoby 1974). The nutrient contents of fruit and ground litter invertebrates are likely to be very different. Fruits are generally high in sugars and simple carbohydrates, while invertebrate prey should contain higher concentrations of proteins (Levey & Karasov 1989; Lambert 1998). Coatis may have a greater need for proteins than do capuchins due to faster life histories (22 months from birth to adulthood for coati females; Kaufman 1962; ~5 years for capuchins: Janson et al. 2012). If coatis switch from directed fruit tree travel to invertebrate foraging during the course of the day, this could explain observations of high SI values during short travel bouts. Capuchin invertebrate foraging appears more opportunistic and typically occurs en route to other food sources. When fruit availability declines seasonally, capuchins reduce their daily travel and forage on relatively low-quality plant piths, suggesting that invertebrate foraging may not be energetically profitable (Di Bitetti 2001b). In comparison, when fruit availability declines, coatis increase their invertebrate foraging effort. In some months, coatis spend over 90% of their foraging time pursuing invertebrates, and seasonal fluctuations in invertebrate foraging success are relatively minor (Hirsch 2009).

Although this behavioural strategy of switching back and forth between foraging for particular nutrients has been predicted and observed in some empirical studies, to our knowledge, it has never been incorporated into mechanistic models of animal foraging behaviour. We posit that future models of animal movement behaviour need to include both multiple food resources and the ability of animals to switch search strategies between resources according to nutrient requirements and seasonal changes in food availability. Optimal foraging models that have incorporated these exact factors already exist (Simpson et al. 2004; Houston et al. 2011), and we concur with Simpson et al. (2010) that incorporating optimal nutrient foraging models into animal movement models will result in more realistic results.

Even when resource switching is taken into account, the observation that coatis routinely forage over the same area more than once per day is not easily explained by optimal foraging models. One insight that may shed light on this issue is the observation that coatis located at the back edge of their social

groups had similar invertebrate foraging success as individuals at the front of the group (Hirsch 2011a). Hirsch (2011a) posited that ground litter invertebrates may be so abundant in Iguazú that coati groups can forage in the same area more than once per day without appreciably depleting the quantity of invertebrate prey available. This contrasts strongly with the foraging behaviour of capuchin groups, which have been found to deplete invertebrates from the front to the back of groups (Janson 1990; Hall & Fedigan 1997). The primary difference between the two species may be the foraging substrate. When foraging for arboreal invertebrates, only a select number of locations such as tree crooks, underneath loose bark and inside leaves may provide effective hiding places for cryptic prey. In contrast, ground litter may provide more area for invertebrates to hide. This could conceivably make it harder to locate invertebrates on the ground, and the soil and leaf litter could potentially sustain a higher density of potential prey items. The observation that coatis consume almost twice the number of invertebrates during foraging than capuchins is highly consistent with the idea that the soil and ground litter contain a higher density of readily accessible invertebrate prey compared to trees.

Even though circuitous travel of coatis does not reduce invertebrate foraging success, it is unclear what advantage this travel behaviour would have compared to straight-line travel during invertebrate foraging. One potential benefit of circuitous travel could be a reduction in exposure to terrestrial predators. Coatis are most often preyed upon by medium- to large-sized felids (Hass & Valenzuela 2002). Because these felids, and particularly ocelots (*Leopardus pardalis*), the most abundant felid at Iguazú, are most active at night and typically rest during the day (Sunquist & Sunquist 2002; Di Bitetti et al. 2010), felid predators may be found in a different spatial location each morning. The threat of predation should thus be highest during the morning when prey groups enter areas of their home range for the first time during the day, while areas that are used for a second or third time during the day should be less likely to contain predators. We posit that the circuitous travel behaviour and the use of previously visited areas may lower the rates at which coatis encounter sit-and-wait felid predators.

In this study, we find that seemingly minor differences between two sympatric species with similar diets may lead to large differences in movement ecology. While there is evidence that both species use memory to travel relatively long distances to known food items, coatis show significantly more circuitous travel patterns. We suggest that the lower terrestrial travel costs in coatis reduce constraints on circular travel while the higher relative benefits of invertebrate foraging in coatis may promote less exclusive reliance on traplining behaviour between fruit trees. These differences in foraging ecology, which on the surface, appear to be minor, have arguably led to biologically significant differences in travel behaviour between these two species. While the travel paths of capuchins are qualitatively similar to predictions of trapline foraging models, the circuitous travel patterns of coatis are not. To our knowledge, no current optimal foraging model could have predicted movement patterns similar to those shown by coatis. We posit that detailed species-level studies are necessary to fully understand how food distribution, foraging preferences and predation risk affect movement patterns and can lead to patterns that would not have been predicted by current animal movement models. In turn, we think these results are important to the study of movement ecology because we have demonstrated that factors not currently incorporated into animal movement models (Table 4) can potentially lead to markedly different movement patterns. To further test the effects of these factors, it would be ideal to record detailed movement data in relation to food sources for multiple (>2) frugivores, in the same habitat, and test whether foraging

**Table 4**

Potential factors that could lead to deviations from trapline foraging by coatis in comparison to capuchin monkeys

Factors that could lead to deviations from trapline foraging	
1	Lower travel costs for terrestrial coatis lift energetic constraints of circuitous travel routes
2	Incomplete food patch depletion by coatis could promote patch revisits and circuitous travel
3	Coatis may switch from fruit to invertebrate foraging over the course of the day, while capuchin travel is almost exclusively driven by fruit tree locations
4	The lack of evident invertebrate prey depletion allows coatis to revisit locations with little or no reduction in foraging success
5	Cognitive differences could lead to different levels of foraging efficiency or movement strategies
6	Travelling in previously visited areas could reduce the chance of predator encounter for terrestrial coatis

efficiency correlates with factors such as arboreality, life history, nutrient requirements, predation risk and relative brain size.

### Acknowledgments

We thank Alex Alcocer Aldunate, Ana Alvarez, María Celia Baldivino, María Verónica Cifre, Santiago Escobar, Carolina Ferrari, Emanuel Galetto, Elizabeth González Valentín, Rosalyn Johnson, Daniel Lambruschi, Luis Molina, Viviana Muñoz, Juan Pablo Peretti, Noelia Rivas, Taylor Rubin, Fermino Silva and Mauro Tammone for help and assistance during the course of the field work. This paper has benefited tremendously thanks to comments by Margaret Crofoot, Esteban Fernández-Juricic and two anonymous referees. We thank the Administración de Parques Nacionales (APN) for permission to carry out work in Iguazú. This study was funded in part by National Science Fund grants (BCS-0314525 and BNS-9009023) to C.H.J. and B.T.H., an Argentine Research Council (CONICET) dissertation fellowship to M.P.T., grants from Idea Wild and American Society of Mammalogists to M.P.T., and a Fulbright to C.H.J.

### References

- Alves-Costa, C. P., Da Fonseca, G. A. B. & Christofaro, C. 2004. Variation in the diet of the brown-nosed coati (*Nasua nasua*) in southeastern Brazil. *Journal of Mammalogy*, **85**, 478–482.
- Bartumeus, F., Da Luz, M. G. E., Viswanathan, G. M. & Catalan, J. 2005. Animal search strategies: a quantitative random-walk analysis. *Ecology*, **86**, 3078–3087.
- Batschelet, E. 1981. *Circular Statistics in Biology*. New York: Academic Press.
- Bowler, D. E. & Benton, T. G. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological Reviews*, **80**, 205–225.
- Brown, A. D. & Zunino, G. E. 1990. Dietary variability in *Cebus apella* in extreme habitats: evidence for adaptability. *Folia Primatologica*, **54**, 187–195.
- Byrne, R. W., Noser, R., Bates, L. A. & Jupp, P. E. 2009. How did they get here from there? Detecting changes of direction in terrestrial ranging. *Animal Behaviour*, **7**, 619–631.
- Crofoot, M. C., Gilby, I. C., Wikelski, M. C. & Kays, R. W. 2008. Interaction location outweighs the competitive advantage of numerical superiority in *Cebus capucinus* intergroup contests. *Proceedings of the National Academy of Sciences, U.S.A.*, **105**, 577–581.
- Crespo, J. A. 1982. Ecología de la comunidad de mamíferos del Parque Nacional Iguazú, Misiones. *Revista MACN, Ecología*, **3**, 45–162.
- Di Bitetti, M. S. 2001a. Food-associated calls in tufted capuchin monkeys (*Cebus apella*). Ph.D. thesis, State University of New York at Stony Brook, Stony Brook.
- Di Bitetti, M. S. 2001b. Home-range use by the tufted capuchin monkey (*Cebus apella nigritus*) in a subtropical rainforest of Argentina. *Journal of Zoology*, **253**, 33–45.
- Di Bitetti, M. S. & Janson, C. H. 2001a. Social foraging and the finder's share in capuchin monkeys, *Cebus apella*. *Animal Behaviour*, **62**, 47–56.
- Di Bitetti, M. S. & Janson, C. H. 2001b. Reproductive socioecology of tufted capuchins (*Cebus apella nigritus*), in northeastern Argentina. *International Journal of Primatology*, **22**, 127–142.
- Di Bitetti, M. S., De Angelo, C. D., Di Blanco, Y. E. & Paviolo, A. 2010. Niche partitioning and species coexistence in a Neotropical felid assemblage. *Acta Oecologica*, **36**, 403–412.



- Di Blanco, Y. & Hirsch, B. T.** 2006. Determinants of vigilance behavior in the ring-tailed coati (*Nasua nasua*); the importance of within-group spatial position. *Behavioral Ecology and Sociobiology*, **61**, 173–182.
- Dunbar, R. I. M. & Shultz, S.** 2007. Understanding primate brain evolution. *Philosophical Transactions of the Royal Society B*, **362**, 649–658.
- Garrison, J. S. E. & Gass, C. L.** 1999. Response of a traplining hummingbird to changes in nectar availability. *Behavioral Ecology*, **10**, 714–725.
- Gill, F. B.** 1988. Trapline foraging by hermit hummingbirds: competition for an undefended, renewable resource. *Ecology*, **69**, 1933–1942.
- Gittleman, J. L.** 1986. Carnivore brain size, behavioral ecology, and phylogeny. *Journal of Mammalogy*, **67**, 23–36.
- Gompper, M. E.** 1995. *Nasua narica*. *Mammalian Species*, **487**, 1–10.
- Hall, C. L. & Fedigan, L. M.** 1997. Spatial benefits afforded by high rank in white-faced capuchins. *Animal Behaviour*, **53**, 1069–1082.
- Hass, C. C. & Valenzuela, D.** 2002. Anti-predator benefits of group living in white nosed coatis (*Nasua narica*). *Behavioral Ecology and Sociobiology*, **51**, 570–578.
- Hirsch, B. T.** 2002. Vigilance and social monitoring in brown capuchin monkeys (*Cebus apella*). *Behavioral Ecology and Sociobiology*, **52**, 458–464.
- Hirsch, B. T.** 2007a. Spoiled brats: an extreme form of juvenile dominance in the ring-tailed coati (*Nasua nasua*). *Ethology*, **113**, 446–456.
- Hirsch, B. T.** 2007b. Within-group spatial position in ring-tailed coatis (*Nasua nasua*): balancing predation, feeding success, and social competition. Ph.D. thesis, Stony Brook University, Stony Brook, New York.
- Hirsch, B. T.** 2009. Seasonal variation in the diet of ring-tailed coatis (*Nasua nasua*) in Iguazú, Argentina. *Journal of Mammalogy*, **90**, 136–143.
- Hirsch, B. T.** 2010. Tradeoff between travel speed and olfactory food detection in ring-tailed coatis (*Nasua nasua*). *Ethology*, **116**, 671–679.
- Hirsch, B. T.** 2011a. Spatial position and feeding success in ring-tailed coatis. *Behavioral Ecology and Sociobiology*, **65**, 581–591.
- Hirsch, B. T.** 2011b. Within-group spatial position in ring-tailed coatis: balancing predation, feeding competition, and social competition. *Behavioral Ecology and Sociobiology*, **65**, 391–399.
- Holyoak, M., Casagrandi, R., Nathan, R., Revilla, E. & Spiegel, O.** 2008. Trends and missing parts in the study of movement ecology. *Proceedings of the National Academy of Sciences, U.S.A.*, **105**, 19060–19065.
- Houston, A. I., Higginson, A. D. & McNamara, J. M.** 2011. Optimal foraging for multiple nutrients in an unpredictable environment. *Ecology Letters*, **14**, 1101–1107.
- Isbell, L. A., Pruett, J. D., Nzuma, B. M. & Young, T. P.** 1999. Comparing measures of travel distances in primates: methodological considerations and socioecological implications. *American Journal of Primatology*, **48**, 87–98.
- Janson, C. H.** 1988. Food competition in brown capuchin monkeys (*Cebus apella*): quantitative effects of group size and tree productivity. *Behaviour*, **105**, 53–76.
- Janson, C. H.** 1990. Ecological consequences of individual spatial choice in foraging groups of brown capuchin monkeys, *Cebus apella*. *Animal Behaviour*, **40**, 922–934.
- Janson, C. H.** 1996. Towards an experimental socioecology of primates: examples from Argentine brown capuchin monkeys (*Cebus apella nigrinus*). In: *Adaptive Radiations of Neotropical Primates* (Ed. by M. A. Norconk, A. Rosenberger & P. Garber), pp. 309–325. New York: Plenum.
- Janson, C. H.** 1998. Experimental evidence for spatial memory in foraging wild capuchin monkeys, *Cebus apella*. *Animal Behaviour*, **55**, 1229–1243.
- Janson, C. H.** 2007. Experimental evidence for route integration and strategic planning in wild capuchin monkeys. *Animal Cognition*, **10**, 341–356.
- Janson, C. H. & Byrne, R. W.** 2007. What wild primates know about resources: opening up the black box. *Animal Cognition*, **10**, 357–367.
- Janson, C. H. & DiBitetti, M. S.** 1997. Experimental analysis of food detection in capuchin monkeys: effects of distance, travel speed, and resource size. *Behavioral Ecology and Sociobiology*, **41**, 17–24.
- Janson, C. H., Baldovino, M. C. & DiBitetti, M. S.** 2012. The group life cycle and demography of brown capuchin monkeys (*Cebus (apella) nigrinus*) in Iguazú National Park, Argentina. In: *Long-term Field Studies of Primates* (Ed. by P. M. Kappeler & D. P. Watts), pp. 185–212. Berlin: Springer-Verlag.
- Janzen, D. H.** 1971. Euglossine bees as long-distance pollinators of tropical plants. *Science*, **171**, 203–205.
- Kaufman, J. H.** 1962. Ecology and the social behavior of the coati, *Nasua narica*, on Barro Colorado Island, Panama. *University of California Publications in Zoology*, **60**, 95–222.
- Lambert, J. E.** 1998. Primate digestion: interactions among anatomy, physiology, and feeding ecology. *Evolutionary Anthropology*, **7**, 8–20.
- Lenke, T. O.** 1984. Foraging ecology of the long-nosed bat, *Glossophaga soricina*, with respect to resource availability. *Ecology*, **65**, 538–548.
- Levey, D. J. & Karasov, W. H.** 1989. Digestive responses of temperate birds switched to fruit or insect diets. *Auk*, **106**, 675–686.
- Lima, S. L. & Zollner, P. A.** 1996. Towards a behavioral ecology of ecological landscapes. *Trends in Ecology & Evolution*, **11**, 131–135.
- Morales, J. & Ellner, S.** 2002. Scaling up animal movements in heterogeneous landscapes: the importance of behavior. *Ecology*, **83**, 2240–2247.
- Mueller, T. & Fagan, W. F.** 2008. Search and navigation in dynamic environments: from individual behaviors to population distributions. *Oikos*, **117**, 654–664.
- Mueller, T., Fagan, W. F. & Grimm, V.** 2011. Integrating individual search and navigation behaviors in mechanistic movement models. *Theoretical Ecology*, **4**, 341–355.
- Nams, V. O.** 2006. Improving accuracy and precision in estimating fractal dimension of animal movement paths. *Acta Biotheoretica*, **54**, 1–11.
- Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. & Smouse, P. E.** 2009. A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences, U.S.A.*, **105**, 19052–19059.
- Neivitt, G. A., Losekoot, M. & Weimerskirch, H.** 2008. Evidence for olfactory search in wandering albatross. *Proceedings of the National Academy of Sciences, U.S.A.*, **105**, 4576–4581.
- Placci, L. G., Arditi, S. I. & Cioeteck, L. E.** 1994. Productividad de hojas, flores, y frutos en el Parque Nacional Iguazú, Misiones. *Yvyraté*, **5**, 49–56.
- Pochron, S. T.** 2001. Can concurrent speed and directness of travel indicate purposeful encounter in the yellow baboons (*Papio hamadryas cynocephalus*) of Ruaha National Park, Tanzania? *International Journal of Primatology*, **22**, 773–785.
- Racey, P. A. & Swift, S. M.** 1985. Feeding ecology of *Pipistrellus pipistrellus* (Chiroptera, Vespertilionidae) during pregnancy and lactation 1. Foraging behavior. *Journal of Animal Ecology*, **54**, 205–215.
- Reader, S. M. & Laland, K. N.** 2002. Social intelligence, innovation, and enhanced brain size in primates. *Proceedings of the National Academy of Sciences, U.S.A.*, **99**, 4436–4441.
- Revilla, E. & Wiegand, T.** 2008. Individual movement behavior, matrix heterogeneity and the dynamics of spatially structured populations. *Proceedings of the National Academy of Sciences, U.S.A.*, **105**, 19120–19125.
- Scarry, C. J. & Tujague, M. P.** 2012. Consequences of lethal intergroup aggression and alpha male replacement on intergroup relations and home range use in tufted capuchin monkeys (*Cebus apella nigrinus*). *American Journal of Primatology*, **74**, 804–810.
- Schick, R. S., Loarie, S. R., Colchero, F., Best, B. D., Boustany, A., Conde, D. A., Halpin, P. N., Joppa, L. N., McClellan, C. M. & Clark, J. S.** 2008. Understanding movement data and movement processes: current and emerging directions. *Ecology Letters*, **11**, 1338–1350.
- Schmidt-Nielsen, K.** 1972. Energy cost of swimming, flying, and running. *Science*, **177**, 222–228.
- Simpson, S. J., Sibly, R. M., Lee, K. P., Behmer, S. T. & Raubenheimer, D.** 2004. Optimal foraging when regulating intake of multiple nutrients. *Animal Behaviour*, **68**, 1299–1311.
- Simpson, S. J., Raubenheimer, D., Charleston, M. A. & Clissold, F. J.** 2010. Modeling nutritional interactions: from individuals to communities. *Trends in Ecology & Evolution*, **25**, 53–60.
- Stephan, H., Frahm, H. & Baron, G.** 1981. New and revised data on volumes of brain structures in insectivores and primates. *Folia Primatologica*, **35**, 1–29.
- Sunquist, M. & Sunquist, F.** 2002. *Wild Cats of the World*. Chicago: University of Chicago Press.
- Thomson, J. D.** 1996. Trapline foraging by bumblebees: I. Persistence of flightpath geometry. *Behavioral Ecology*, **7**, 158–164.
- Thomson, J. D., Maddison, W. P. & Plowright, R. C.** 1982. Behavior of bumble bee pollinators of *Aralia hispida* Vent. (*Araliaceae*). *Oecologia*, **54**, 326–336.
- Thomson, J. D., Slatkin, M. & Thomson, B. A.** 1997. Trapline foraging by bumble bees: II. Definition and detection from sequence data. *Behavioral Ecology*, **8**, 199–210.
- Turchin, P.** 1998. *Quantitative Analysis of Movement: Measuring and Modeling Population Redistribution in Animals and Plants*. Sunderland, Massachusetts: Sinauer.
- Westoby, M.** 1974. An analysis of diet selection by large generalist herbivores. *American Naturalist*, **108**, 290–304.