

How do wild baboons (*Papio ursinus*) plan their routes? Travel among multiple high-quality food sources with inter-group competition

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Abstract How do humans and animals travel between multiple destinations on a given foraging trip? This question is of theoretical and practical interest, yet few empirical data exist to date. We examined how a group of wild chacma baboons travelled among multiple, simultaneously fruiting mountain fig trees (*Ficus glumosa*). In the course of a 16-month study, this highly preferred fruit was available during a 3-week period, from relatively few sites, which were also utilized by four larger baboon groups. We used directness of route and travel speed of 13 days of observation, and approach rates of 31 days of observation to differentiate between purposeful and opportunistic encounters with 50 fig trees. The study group visited a total of 30 fig trees overall, but only 8 trees per day on average. Each morning, they travelled along a highly repetitive route on all days of observation, thereby visiting 2–4 fig trees. They approached these trees rapidly along highly directed paths without intermittently exploiting other food sources that were available in large quantities. Then, they abruptly changed behaviour, switching to lower travel speed and less directed routes as they foraged on a variety of foods. They approached additional fig trees later in the day, but approach rates were similar to those at times of year when fruit of this

fig species was unavailable; this suggested that encounters with trees after the behavioural switch were not planned. Comparing visits to purposefully and opportunistically encountered trees, we found no difference in the average time spent feeding or frequency of feeding supplants, suggesting that purposefully and opportunistically visited trees had similar values. We conclude that when foraging for mountain fig fruit the baboons' cognitive maps either contain information on relatively few trees or of only a single route along which several trees are situated, leading to very limited planning abilities.

Keywords Route planning · Primate · Spatial knowledge · Cognitive map · Satisficing · Travelling salesman

Introduction

Animals that need to visit several resources in the course of each foraging trip face a problem, one that is exacerbated if their diet is complex and seasonally varying. For a baboon who largely relies on seasonally occurring plant foods, many food sources are available only for short periods at regular or irregular intervals, some are more rewarding than others, and some are found in patches separated by large distances, and thus are out of sight of each other. Such animals would profit from a cognitive map containing information not only on where to find a particular food type, but also when best to exploit it and what payoff to expect from each patch. Additional map information might also be valuable. For food sources that are scarce and attract competitors, it would pay to integrate the risk that a resource will be found depleted upon arrival; when predators share the range, it would pay to know about the

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locations of safe refuges. And in most instances, animals would benefit from using these memories to find the shortest possible route connecting all food places of a given day to be determined and planned in advance, to save time and travel expenses. To date we have little knowledge about the content and complexity of the cognitive maps used by foraging primates (reviewed in Janson and Byrne 2007). Yet understanding these capacities is important, since memory and cognition in general are likely to have evolved partly in response to the pressure of finding enough food to survive and reproduce.

Efficient travel between multiple locations seems to be a widespread foraging strategy of a variety of species, from hymenoptera (Ohashia et al. 2007, 2008) to primates (e.g. Mackinnon 1978; Milton 1981; Garber 1988; Normand and Boesch 2009). For example, humans are reported to attempt efficiency in their shopping trips by first choosing the location farthest away and then minimizing local distances between several close-by shops (Gärling and Gärling 1988). However, finding the shortest possible route among several resource places becomes increasingly complex and computationally expensive with increasing numbers of places to visit (Lawler et al. 1990). For example, a travelling salesman intending to minimize his route among six locations needs to calculate and compare the lengths of 720 possible routes, and possibilities rise to nearly 40 millions when 11 locations are involved (Wiener and Tenbrink 2008). While an efficient solution for this general problem is still lacking in computational mathematics, researchers interested in animal cognition agree that their subjects are unlikely to perform such large numbers of computations. Instead, animals are assumed to use relatively simple heuristics coupled with some form of spatial memory that gives an approximation to the optimal solution, which may be almost as efficient for survival and reproduction (Janson and Byrne 2007; Wiener and Tenbrink 2008).

Indeed, captive vervet monkeys (Cramer and Gallistel 1997) and rhesus macaques (Tinkelpaugh 1932; reported in Gallistel and Cramer 1996) found fairly short routes among six feeding sites, and young chimpanzees (Menzel 1973) did well when 18 locations were presented in small experimental arenas in which all target locations could be perceived at once. In humans, most work on the “travelling salesman problem” (TSP) has tested the participants’ ability to connect several points on a computer screen with the shortest possible line, and has not involved active navigation (reviewed in Wiener and Tenbrink 2008). A few studies on humans are directly comparable with the above primate work: e.g. Wiener et al. (2008) used coloured symbols arranged on a regular test grid within a large experimental room, and participants were asked to visit a given subset of symbols. Neither the nonhuman primates’

nor the humans’ behaviour could entirely be explained by the heuristic ‘always visit the nearest location’. Instead, the relative positions of additional feeding sites (or symbol sites) seemed to play an important role for the sequence in which sites were visited: thereby, both vervet monkeys and humans seemed to integrate spatial information of several sites to plan an efficient route. Vervet monkeys took into account at least two further locations beyond the nearest neighbour (Gallistel and Cramer 1996). Humans typically combined several neighbouring locations to clusters and preferred to visit larger clusters first; they first planned a coarse route on the region level, and then refined this plan during navigation by inserting nearby target places ad hoc (Wiener and Tenbrink 2008).

It is not clear how these findings relate to the strategies that wild primates use to find food and refuges, however. Some species may confront greater problems than these experimental tests, if they range over large areas where all resources cannot generally be perceived at once. In this situation, planning beyond the nearest resource may require an integrated memory for the relative spatial properties of several resource places.

In fact, many researchers have found that wild primates do not seem to plan their routes at all, but often move to the nearest available resource (Janson 1998; Menzel 1997). They share this simple foraging rule with animals possessing comparatively humble neural substrates, such as bumble bees (Ohashia et al. 2007).

However, recent work suggests that mammals may be able to plan travel between multiple destinations in the absence of direct stimuli. Certainly, some species remember large numbers of resource sites. For example, meerkats (*Suricata suricatta*) have been reported to know the locations of several hundreds of shelter locations in their home range, enabling them to escape quickly from predators at any time (Manser and Bell 2004). Also, there is good evidence from the lab and from the wild that many mammal species have integrated memories about resource type and spatial location (e.g. Kaminski et al. 2008). In the wild, Japanese macaques (*Macaca fuscata*) instantly search akebi trees when experimentally confronted with akebi fruit out of season (Menzel 1991, 1997). When the route to a fruit feeding site is blocked, baboons sometimes visit alternative fruit feeding sites at a distance of several kilometres, suggesting that they have access to integrated information of “where” and “what” (Noser and Byrne 2007b).

There is an ongoing debate about whether animals possess a higher order cognitive structure (e.g. a cognitive map) in which several “what-where” memories are integrated to a single entity, allowing access to several represented locations simultaneously in order to plan efficient travel among several locations. Possession of a cognitive

map should allow foragers to anticipate where food sources of a certain type can be encountered in the near future. Evidence for anticipation of out-of-sight resources comes again from wild baboons: hamadryas baboons living in the Ethiopian semi-desert have been reported to increase travel speed long before arriving at water holes (Sigg and Stolba 1981). Chacma baboons departed significantly earlier from their sleeping site when foraging for distant, scarce fruit than when foraging for abundant fruit in a habitat with high levels of scramble competition (Noser and Byrne 2007a). Apparently, baboons can anticipate some qualities of the resources well before they can see them.

In addition, primate groups in the wild seem to use some knowledge about productivity of resources. Many primates bypass close unproductive feeding sites in favour of distant productive ones (Garber 1989, Janson 1998, Cunningham and Janson 2007; Noser and Byrne 2007a). For instance, wild baboons bypass seed feeding sites next to their sleeping site, and first visit distant, out-of-sight fruiting trees that otherwise may quickly become depleted by competitors, before returning to the abundant seeds (Noser and Byrne 2007a). Wild mangabeys remember previous feeding experiences in individual trees (Janmaat et al. 2006a) and anticipate the daily change of payoff of fruit-bearing trees, possibly by using temperature and solar radiation as cues (Janmaat et al. 2006b).

In summary, animals seem to possess the “cognitive tool kit” to qualify as good travelling salesmen: they integrate memories for “where” and “what” to find single resources, they seem to integrate several “where-what” memories into a cognitive map, and they anticipate events that will take place in the near future. This should enable them to plan travel among several resource sites, keeping travel routes short.

In this paper, we examine the foraging strategy of wild chacma baboons (*Papio ursinus*) visiting multiple resources on a single route, including their travel efficiency and its possible cognitive basis, taking advantage of the fact that mountain figs, occurring in 50 small-sized trees, were synchronously fruiting during a 3-week period at our study site. Mountain figs were highly preferred by the baboons. Four competing baboon groups were present in the area: although we did not systematically observe them, we frequently heard or saw them next to fig trees. Thus, baboon groups competed for the fig fruit, and trees were likely to suffer the risk of depletion. In this situation, travelling salesmen abilities could be particularly important. This conjecture is supported by our earlier finding that these baboons used a particular time-minimizing strategy when foraging for mountain figs (Noser and Byrne, 2007a): they departed from their sleeping site significantly earlier during the fig fruiting season than during other times of year when fig fruit were unavailable, and this result was robust to

variability in time of sunrise and day temperatures. We therefore expected our study group, once departed from their sleeping site, to economize on time expenditure by minimizing travel distance and maximizing travel speed between trees. In addition, we focused on the fraction of the available trees our group was able to exploit, and their flexibility of route choice among trees.

Methods

Study site

Mountain fig trees (*Ficus glumosa*) fruited synchronously during a 3-week period in December 2001 and January 2002 at Blouberg Nature Reserve (BNR; 22°58'S, 29°09'E) in the Limpopo Province, South Africa (see Noser and Byrne 2007a, for details). During that time, the woodland savannah offered a rich variety of additional fruit sources to the baboon population (Noser 2004). In contrast to all other fruit sources, *Ficus glumosa* occurred in restricted quantities. Fig trees grew only in a specific part of the baboon home range, the north-facing slopes of an elevation, “the hill” (Fig. 1), in an area of about 1.6 × 1.2 km.

Baboons and fig tree population

The data presented in this study are part of a 2-year study (August 2000–August 2002). During that time, we

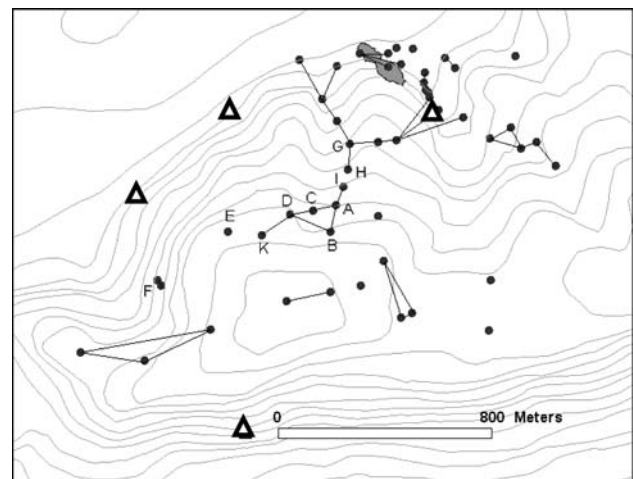


Fig. 1 Distribution of 50 mountain fig trees (*Ficus glumosa*; dots) in the study group’s home range. *Black lines* connect specimens that were visible from one another. (Note that the *black line* between A and C is part of the line connecting A and D: fig tree C was growing in a rocky valley, whereas trees A and D were growing on the slope of the hill. Thus, A could be seen from D, and vice versa, C was visible from D, but not from A.) *Grey lines* 20 m contour lines of the hill. *Grey area* Sleeping site area of the study group. *Triangles* Sleeping sites of four neighbouring baboon groups

identified nine baboon groups at BNR, five of which slept in cliffs at the foot of the hill (Fig. 1). Our study group was the smallest of them and had 25 members during the mountain fig fruiting season, including two adult males and eight adult females. From May 2001 onwards the study group allowed us to follow them on foot at a distance of 10–40 m. Home range size at the end of data collection was 13.5 km² (Noser 2004). The study group used a single sleeping site throughout our fieldwork. Ad libitum observations of other baboon groups at dawn suggested that sleeping site fidelity was common at BNR.

We recorded the locations of 50 mountain fig trees with GPS (Trimble Geoexplorer 3). This was likely to be the whole population in the study group's home range. Also, we recorded the locations of all baboon sleeping sites (Fig. 1).

We determined how far each tree was visible: one person waved a white flag next to each tree, and a second person walked in a large circle around the tree and took GPS waypoints in small time intervals at the locations where the flag just disappeared from sight. Thus, the waypoints bordered the areas within which each individual tree was visible. With this information we determined whether two subsequently visited trees had been visible from each other. In Fig. 1, trees that were visible from each other are connected with a black line.

Data collection procedure

During the mountain fig fruiting season, we followed the study group on 13 days (including seven whole days and, due to adverse observation conditions, six half days) for a total of 114 h. We recorded the group's location with GPS at intervals of 5 min (see Noser and Byrne (2007a) for details on data collection procedure) and viewed the line connecting the waypoints as the group's travel route.

In order to assess the amount of food the group extracted from each of the fig trees, we performed "focal tree samplings": as soon as a minimum of three baboons started feeding from a tree, this tree became the focus of our observations. Due to the relatively large distance from which the baboons were observed, we could not unambiguously tell individuals apart. As a consequence, we were unable to assess feeding times for individual baboons separately. Therefore, we recorded for each min how many baboons entered and left the focal tree. This allowed us to assess the number of animals feeding in this tree in each min of observation, until all baboons left. To corroborate these observations, and to prevent confounding fig feeding with other activities that sometimes occurred in the trees, we took scan samples of the behaviour occurring in the focal tree (feeding, sitting, playing or grooming) in intervals of 1 min. This "focal tree sampling" technique was

intended to give an approximate measure of the value to the baboons of a visit to a fig tree.

During focal tree sampling, we recorded all occurrences of aggressive interactions between any two individuals in the fig trees ("behaviour sampling", Martin and Bateson 1993). These included pronounced threats, chases and pulling hair by the aggressor, followed by screaming and withdrawing of the recipient. Again, due to the relatively large distance to the baboons, we may have missed milder forms of aggression (e.g. eye flashes followed by weak responses of recipients). Because these aggressive interactions occurred during fig feeding, we viewed them as feeding supplants.

Data analysis

We analysed route linearity and travel speed between each two successively used resources. Route linearity was given by the dispersion of the vectors between two successively used resources, measured by their r value (Batschelet 1965; Noser and Byrne 2007a). Travel speed was calculated as the distance travelled between two resources divided by the time needed to cover it.

We defined "payoff" of each tree as the sum of minutes feeding across all baboons in the group. (Thus, variability in payoff may be due to variability in feeding time as well as in the number of baboons that used a tree). Note that payoff is a measure of tree usage, rather than an objective measure of fig availability per tree, or nutritive value.

In order to assess the impact of a visit of a baboon group on the feeding behaviour of subsequent visitors, we compared payoffs of trees that were visited twice the same day by our baboon group. Since we suspected that the ripening process of fig fruit was relatively slow, we expected payoff of the second visit to be smaller than payoff of the first visit.

Several factors may have affected how our study group used trees, for example presence of other groups, hunger level, tiredness, perceived danger of a location, etc. We were able to control only some of them. In particular, we used feeding supplants as a rough measure of motivation to feed on fig fruit to address the question of motivational changes in the course of day. We assumed that, in an average-sized tree with an average amount of fruit, aggression levels and motivation covary: high numbers of supplants over fig fruit occur when motivation to feed on figs are high (e.g. due to high hunger levels). Then, as the baboons get slowly satiated, the numbers of supplants decrease. In particular, we expected high supplant frequencies when the group was hungry (e.g. in the mornings), and a decrease in supplant rate in the course of a day, because we supposed that satiation increased. We defined supplant rate as the number of feeding supplants occurring during a visit to a fig tree per min feeding during that visit.

During the fruiting season, the study group did not feed from all fig trees they encountered in the course of a day. We defined an “approach” *posthoc*, as when the study group had come within 30 m of a fig tree specimen. We used 30 m to define an approach to ensure that the group could have seen and assessed the fig tree in question: across fig trees, our visibility estimates varied from 32 to 498 m. We also suspected that a tree’s fruiting state could only be determined from very short distances, probably only when in the tree, due to the fruit’s small size (1 cm in diameter) and its position on the branches (axillary, well hidden between branch stems and leaf petioles). We recorded the group’s position as the position of the individual walking at the rear; given the spread of group members, individuals walking at the front may have been able to assess a tree’s fruiting state when those at the rear were 30 m away.

An approach could either be followed by a “visit” of the tree, or by “passing by” the tree. A visit was scored when at least three baboons started feeding from a tree, and each of them fed for a minimum of 1 min. When none of the baboons entered a tree, when 2 or less individuals fed from a tree, or when all individuals left a tree within 1 min we scored this tree as passed by. We used this criterion to have some certainty that a visit captured only those trees that were of some importance to at least a part of the group.

Since approaches to fig trees are only possible when moving but not when feeding or resting, we calculated the time spent moving on the hill during the fig fruiting season by discounting the time spent feeding and resting at a location from total observation time. We defined as “approach rate” the number of approaches to fig trees per hour moving on the hill (where fig trees occurred). Since baboons are likely to approach a certain number of trees just because they move through this area and the trees happen to occur next to their route to other resources, we calculated a “baseline approach rate”. This was the approach rate to fig trees in other times of year, when fig fruit was unavailable. The corresponding body of data was collected between August and October 2001. During that time, the study group spent less time on the hill, and a larger part of that time resting, than during the fig fruiting season. Thus, to get a comparable amount of time spent moving on the hill, 18 days of observation were used for calculating baseline approach rate.

Statistics

Statistical tests are two-tailed; a single exception is mentioned in the text. We used Lowess (locally weighted scatterplot smoothing, Cleveland 1979) to qualitatively examine changes in supplant frequency. A Lowess curve is a smoothed curve plotted through a set of data points. In contrast to conventional regression models, which consider

all data points of the entire set at a time and describe overall patterns with straight lines, Lowess uses only some adjacent data points at a time to find local patterns. Thus, it does not require a specific global function of any form to fit a model to the data, but fits the data locally. Each smoothed value is given by a weighted linear least squares regression over the smoother span, or tension. The smoother span gives the proportion of points in the plot that influence the smoothing at each value. Larger smoother span values give more smoothness and waver the least in response to fluctuations of the data; the smaller the value, the closer the regression function will conform to the data. Thus, using small smoother span values increase the likelihood that the regression function will eventually start to capture the random error in the data; values typically lie in the range 0.25–0.66. Here, we used a smoother span of 0.66.

Results

The study group visited 8.0 ± 1.9 fig trees per day on average (mean \pm SD; $n = 7$ records of whole day’s ranging). Visits were confined to 30 of the 50 available specimens. Seven of the 20 unvisited trees were situated outside their ranging area during the fig fruiting season; the remaining 13 specimens were sometimes approached, but then bypassed (Fig. 2a).

On all mornings the baboons climbed the hill as a coherent group and first visited a series of fig trees, none of which they had been able to see from their sleeping site. The choice of trees and the sequence of visits were highly repetitive from day to day: from the sleeping site they walked south, then turned west at tree B, before heading towards trees E and F (Fig. 2b). Ten fig trees were situated along that repetitively visited route, two of which were never visited (trees C and G, Fig. 1; Table 1). The baboons did not visit all of the remaining 8 trees each day, but only 2–4 per morning (see Table 1 for identity of trees and duration of visits).

At 6:24 a.m. \pm 14 min, or 67 ± 14 min (mean \pm SD) after departure from the sleeping site, the baboons’ highly consistent daily route dissipated in the area next to trees E and F, the junction between the repetitively travelled sector and the rest of the day’s ranging (Fig. 2a, b). At the same time, a sudden change occurred in their behaviour. While they had travelled fast and linearly among fig trees and exclusively fed on figs before that point, both travel speed and route linearity decreased after it, and they subsequently used other food types intermittently (e.g. grass corms *Brachiaria spp* and milkplum fruit *Englerophytum magaliesmontanis*). We use the term ‘on route’ to refer to the behaviours observed along the repetitively travelled route and ‘off route’ to refer to those away from it. This

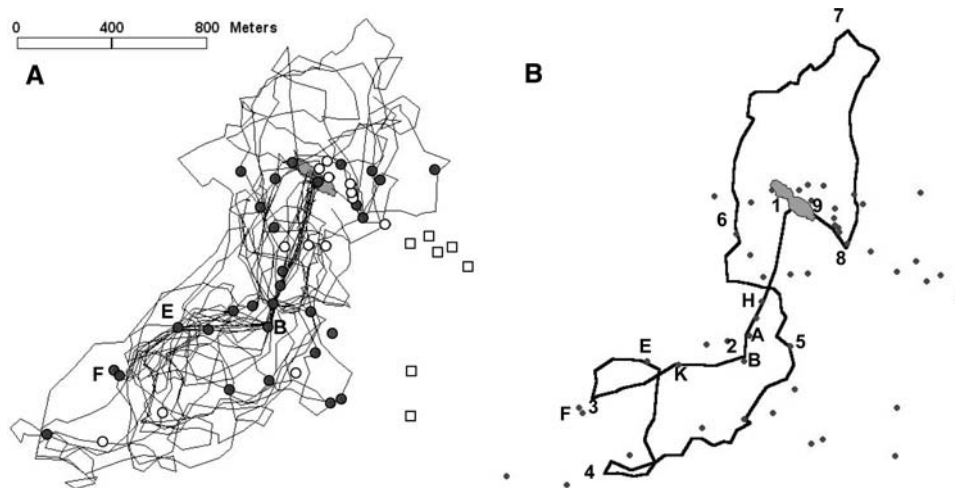


Fig. 2 Ranging patterns during the mountain fig fruiting season during seven whole and six half days. B, E and F indicate three fig trees (see also Fig. 1). Grey circles visited trees ($n = 30$); white circles bypassed trees $n = 13$; squares trees situated outside the area used for fig foraging, excluded from analyses ($n = 7$). **a** Ranging patterns during a single day (December 24). (1) Departure from sleeping site at 5:12 a.m., visits to trees H and A. (2) Visit to tree B at 5:45 am, visit to tree K at 6:00 am. (3) Drop of travel speed next to trees F, then slow travel feeding on grass corms from 6:16 onwards. A

competing group's long-distance calls can be heard from a short distance SW of figs F at 6:20 am. Study group turn north, travel-feed on grass corms, pass by fig E, then turn south. (4) Feeding on grass corms at 7:40 am. (5) Visit to fig tree at 9:15 am. (6) Visit to fig tree, then rest in the shade between 10:10 and 12:10 am. (7) Travel-feed on a variety of foods in the plain from 1:40 pm onwards, while moving towards water hole. (8) Arrival at water hole at 3:19 pm, rest until 4:10 pm. (9) 4:11 pm travel-feeding and frequent grooming until arriving at sleeping site at 5:26 p.m.

Table 1 Total number of visits to fig trees A-K situated on route, number of visits during on route travel, total payoff in min, average payoff in min, standard deviation of payoff, and number of bypassing at a distance of maximally 30 m

| Tree | A | B | C | D | E | F | G | H | I | K |
|---------------------|------|------|---|------|------|------|----|------|-----|------|
| Total no. of visits | 19 | 9 | 0 | 6 | 10 | 2 | 0 | 2 | 1 | 2 |
| No. on route visits | 13 | 9 | 0 | 3 | 8 | 2 | 0 | 2 | 1 | 2 |
| Feeding time | 384 | 178 | 0 | 76 | 258 | 30 | 0 | 48 | 5 | 25 |
| Bout length | 20.2 | 19.8 | – | 19.0 | 25.8 | 15.0 | – | 24.0 | 5.0 | 12.5 |
| SD | 8.4 | 9.5 | – | 10.9 | 17.0 | 9.9 | – | 26.9 | – | 9.2 |
| Bypassed | 3 | 2 | 3 | 3 | 4 | 3 | 11 | 11 | 18 | 9 |

distinction was made on the basis of behaviour, and not on the basis of tree location; a tree situated along the repetitively travelled route qualified as 'on route' when it was visited during the journey along the repetitively travelled route, and as 'off route' when it was visited later in the day, off the repeatedly travelled route. Trees A, D and E were visited in both conditions, on and off route (Table 1).

Whether or not subsequently approached fig trees were visible from each other seemed to be unimportant to the baboons: 51.1% of the 229 approaches recorded in total concerned fig trees that were visible from the previously

approached specimen, and 48.9% concerned trees that were out of sight ('on route': total 89 approaches, thereof 50.6% to visible trees, 49.4% to out-of-sight trees; 'off route': total 140 approaches, thereof 51.4% to visible trees, 48.6% to out-of-sight trees).

Travel speed and route linearity 'on route' were 23.5 ± 4.8 m/min and 0.959 ± 0.051 (mean \pm SD), respectively. They dropped to 16.8 ± 4.5 m/min and 0.741 ± 0.197 'off route'. Figure 3 illustrates these differences. Both were significant (unpaired t tests, linearity: mean diff = -0.209 , $t_{2,48} = 4.628$; travel speed: mean diff = 6.71 , $t_{2,48} = -5.032$; both $P < 0.001$). Note that travel 'on route' included travel uphill from the sleeping site to tree B, and then travel along the contour lines to tree E. In contrast, travel 'off route' mainly included travel downhill, or travel along contour lines (and only on very few occasions short uphill segments). Since the baboons' 'on route' travel was significantly faster than 'off route' travel, slope of the hill did not account for this difference in travel speed.

Of the 114 h of observation during the fig fruiting season, the baboons ranged on the hill for 97 h, and in the plain for 17 h (they never spent an entire day on the hill). When ranging on the hill, they were stationary for 11 h, and moving during 86 h. These 86 h were used to analyse approach rate. The baboons approached 2.7 ± 1.4 fig trees per h on average. To calculate baseline approach rate, we used 71 h of observation on the hill during the non-fig season, in which the group had moved for 51 h. This

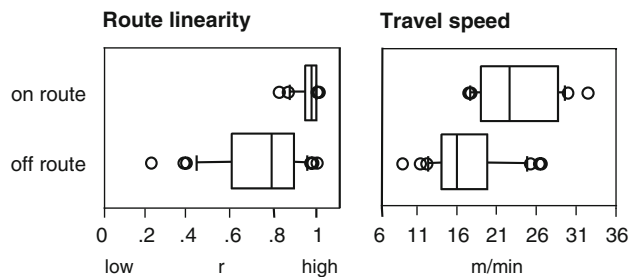


Fig. 3 Route linearity and travel speed on and off route. Dots indicate values above the 90th and below the 10th percentiles. Left panel r values are a measure of concentration of vectors (each calculated from two subsequent GPS readings) about the mean direction: the closer r approaches value 1, the smaller the angular deviation of the vectors (Batschelet 1965)

resulted in a baseline approach rate of 1.5 ± 0.4 per hour of movement. We took this to indicate the value that was likely to occur opportunistically when moving on the hill, and compared it with the approach rate during the mountain fig season. Approach rate was significantly higher than baseline approach rate (unpaired t test, $t = -3.103$, $p = 0.0048$). Figure 4 shows that this was mainly due to on route travel, with 5.9 ± 1.2 approaches per hour. Approach rate off route was 2.1 ± 1.1 per hour. An Anova with the factors ‘baseline approach rate’, ‘approach rate on route’ and ‘approach rate off route’ revealed that only approach rate on route significantly differed from the baseline value, but not approach rate off route ($MS = 77.626$, $F_{2,40} = 76.711$, $P < 0.001$, Dunnett test: mean diff_(on route) = 3.812, $P < 0.05$, mean diff_(off route) = -0.501 , $p > 0.05$; see Zar 1999). Thus, ‘on route’ trees were approached one after the other in a highly linear way, fast, and at high frequency. In contrast, off route trees were approached slowly, along less linear routes and at a frequency suggesting opportunistic encounters during feeding on other food sources.

Did visits on and off route differ in payoff? Overall payoff was 21.2 ± 15.3 min per visit on average ($n = 90$),

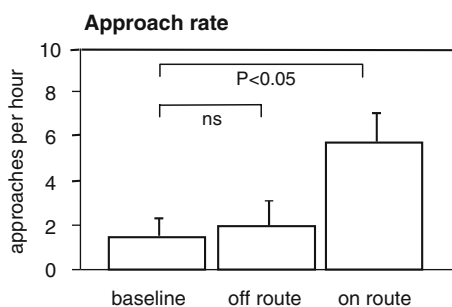


Fig. 4 Approach rate to fig trees outside the fig fruiting season (baseline), and during the fig fruiting season (on and off route). Approach rate on route is significantly higher than baseline, approach rate off route does not differ from baseline

ranging between 4 and 91 min. Payoff from on route visits was 21.6 ± 12.8 min (mean \pm SD; range: 4–55 min; $n = 38$ visits), and payoff from off route visits was 20.9 ± 17.1 min on average (range: 4–91 min; $n = 52$ visits). This difference was not statistically significant (unpaired t test, ln-transformed data, $t_{2,88} = -0.614$, $p > 0.05$). Thus, the baboons spent the same amount of time feeding in trees, whether on route or off route. Although of similar average payoff, visits to fig trees on and off the route might nevertheless differ in variability of payoff. We performed a variance ratio test (Zar 1999). The difference was not significant (ln-transformed data, $F_{51,37} = 1.079$, $p > 0.05$). Thus, the payoff of on route visits was as variable as the payoff of off route visits.

In order to control for the effect of time of day, we investigated feeding supplants occurring during fig feeding. 68 feeding supplants occurred during a total of 90 visits to fig trees: 32 during on route visits ($n = 38$), and 37 during off route visits ($n = 52$). The difference of supplant rates was statistically not significant (Mann–Whitney U test, mean rank_{on} = 46.4, mean rank_{off} = 44.9, $p > 0.5$). To see whether supplants decreased in the course of the day, we performed a correlation between time since leaving the route and supplant rate. This correlation was indeed negative, but the effect was weak and non-significant (Pearson correlation, $r_{45} = -0.132$, $P > 0.3$). Certainly, analyses of feeding supplant rate did not suggest a steady decrease in motivation over the course of the day. To investigate further, we applied a Lowess smoother to supplant rates in relation to time of day (Fig. 5): a distinct decrease occurred only around 300 min after the baboons had left the route. Thus, time of day did seem to affect motivation to feed on fig fruit: feeding supplant rate decreased around noon, when temperatures were highest. However, there was no temporal link between the decrease of motivation and the switch of foraging strategy (from ‘on route’ to ‘off route’ feeding and ranging), 5 h earlier than the noon dip in motivation (Fig. 6).

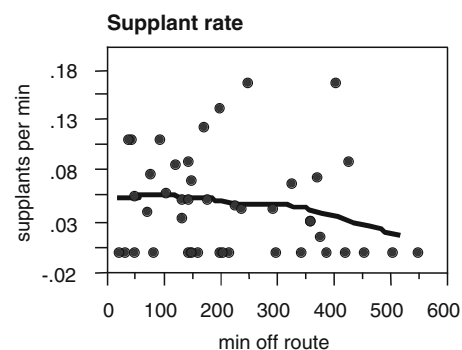


Fig. 5 Within-group feeding supplant rate during visits to fig trees off route in relation to time since leaving the repetitive route

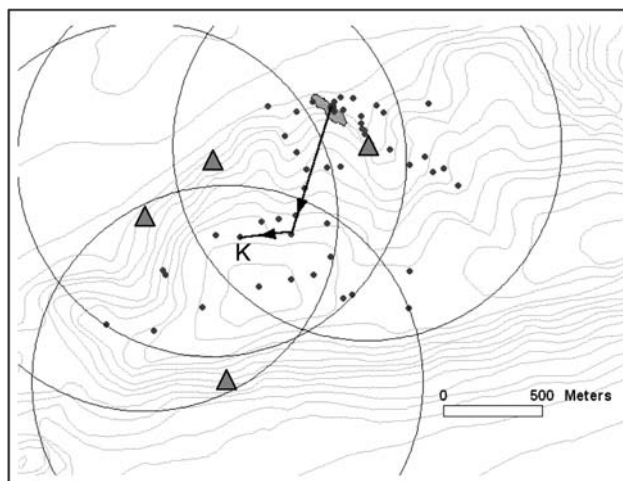


Fig. 6 Proposed pattern of inter-group competition for mountain fig fruit at the study site. Four baboon groups may have visited all available fig trees (circles) in the time needed by the study group to reach fig K (arrow), given similar departure time from the sleeping sites (triangles) and similar travel speed

Scramble competition could give another possible origin of the difference in foraging behaviour on and off route: other baboon groups might reach off route fig trees and deplete the best (ripe) fruit before our study group arrived. As a result, our group might have encountered ripe fruit only in the early part of each morning, and switched foraging strategy by the time when fruit quality decreased. To see whether this scenario was a realistic one, we examined the ‘on route’ distance travelled each morning by our study group in relation to the distances that the remaining resident groups could potentially travel in the same time, assuming similar departure times from the sleeping sites and similar travel speeds of all five baboon groups in the area. This revealed that the four competing groups could have reached and depleted all remaining fig trees by the time our study group arrived at tree K, approximately. This was indeed the area where the switch of foraging strategy occurred. (Whether any group other than the study group had in fact done so on a given day will inevitably have depended on many other factors).

To further strengthen this point, we assessed the impact that a visiting baboon group could have on the payoff of a tree left for subsequent visitors of that tree. We examined the difference in payoff of all fig trees that were visited twice a day by our own study group ($n = 9$ cases). Time between leaving and revisiting a specimen later the same day ranged between 115 and 526 min. Payoff of first visits was 23.9 ± 8.4 min; it decreased to 13.2 ± 9.1 min during second visits. This difference was significant (one-tailed paired t test, $t = 2.46$, $p < 0.02$). Thus, although some fruit seemed to be left after a visit to a fig tree, more time was spent feeding in trees that had not been visited by a baboon

group on a given day than in trees that had been visited earlier that same day.

Discussion

We have used data collected during a brief period when mountain fig trees (*Ficus glumosa*) were synchronously fruiting to investigate how a group of chacma baboons organized their travel among multiple destinations on a given foraging trip. Given the small data set and the purely observational character of our study, this analysis does not of course exhaustively cover the question of how baboons plan multi-destination routes. Many of the results reported here were unexpected, however, and give rise to some ideas on how external factors may interact with route planning in animals living in their natural habitats.

Most strikingly, our study group started each day by focusing on a small set of the available trees, only 10 out of 50, and by approaching them along linear routes and at high speeds. This, combined with the fact that the group did not intermittently feed on other available food sources during this phase of their day journey suggests that their travel was goal-directed. Moreover, this first travel phase was highly inflexible: the baboons approached the same fig trees each morning, in the same order along a single, stereotyped route (“on route” travel). During the rest of the day they approached a larger set of trees, but less directly and at lower speeds, and these visits were interspersed with feeding on other resources. The rate of approaches to mountain fig trees was thus much slower during the rest of the day (“off route”), and similar to that observed at other times of year when no fig fruit was available, suggesting that these were opportunistic approaches.

These findings suggest that the baboon group used two different search strategies for exploiting mountain fig trees. Approaches to fig trees on the stereotyped route seemed purposeful and anticipated in advance, whereas approaches to fig trees off this route and later in the day were unplanned. These trees may simply not form part of the baboons’ cognitive map. Support for this possibility comes from the work of Cramer and Gallistel (1997), who found a comparable limitation of spatial abilities in captive vervet monkeys: they only memorised six locations at a time, where food sites were presented in a relatively small arena. Also, our own study on evasive manoeuvres in response to other groups (Noser and Byrne 2007b) suggested that baboons do not flexibly travel among several resource places, but are tied to a network of familiar, memorised routes. Repetitive use of a single ‘fig-route’ may allow our study group to go by many fig trees in very short time. Since they use only a few trees along this route each day, it is possible that the large number of ‘bypasses’ is simply a

side effect of travelling to the mainly used trees (e.g. trees A, B and E; Fig. 2; Table 1).

These findings cannot be explained by the baboons' weak familiarity with the hill, because our study group often foraged in this area, not only during the fig fruiting season, but also at most other times of year. Nor can temporally changing factors such as motivation, nutrient-specific satiety (Provenza 1996) or tiredness, account for many of our findings. Such factors would be expected to change steadily and slowly over time. We analysed frequency of feeding supplants occurring during visits to fig trees as a rough measure of motivation to feed on fig fruit. Feeding supplants occurred on and off the stereotyped route, and declined only around noon when temperatures were highest. Up until this point the baboons behaved as if they perceived all fig trees as equally preferred resources, irrespective of their location in space. However, the abrupt change from goal-directed to opportunistic travel took place ca. 5 h earlier, between 6 and 7 am, only about an hour after departure from the sleeping site.

We found no difference in the estimated payoff of fig trees before and after this switch in foraging strategy. Under the simple assumption that time spent feeding from a resource is to some degree related to its quantity, this implies that the amount of fig fruit found did not differ according to whether a tree was visited deliberately or opportunistically. Note, however, that our measure of payoff, the sum of all individuals' time spent feeding from a fig tree, reflected the baboons' behaviour and was only an indirect measure of tree productivity. Therefore, we cannot exclude the possibility that the value of fruit from trees on and off the 'fig-route' differed in subtle ways that our measure was unable to capture: for example, we may have missed a decrease in ingestion per time spent feeding, or a decrease of sugar content. Also, since payoff was a group measure rather than one based on detailed observation of individuals, baboon identity during purposeful and opportunistic visits may have differed. Possibly, dominant individuals that led the group may have fed on fig fruit during fig-route travel, thus eating particularly ripe fruit, while they consumed other food sources during travel off the fig-route. On the other hand, subdominant individuals may have been able to enter the trees only off the fig-route when dominants were satiated. Our notes of *ad libitum* observations on individual baboons did not suggest so, however: at least the alpha male was seen to feed on fig fruit (and to supplant his group mates) throughout the day.

Another possibility is that travel speed, route linearity and approach rate may not always provide appropriate means to distinguish between purposeful and opportunistic foraging. In the dry woodland savannah of Blouberg, this baboon group consistently travelled at high speed along highly linear routes to water-holes and to scarce high-

quality food sources. In contrast, travel to abundant low-quality food sources was typically undirected and slow (see also Sigg and Stolba 1981; Milton 2000). However, there was a single exception: the single sleeping site of the group, undoubtedly a critical resource, was also approached at low linearity and speed (Noser and Byrne 2007a). This opens the possibility that the same might have occurred in the case of fig foraging: the baboons may have remembered the spatial locations of trees off the fig-route just as well as those on the fig-route, but some unknown factors other than a limitation in spatial competence affected travel routes and approach rates.

Unpredictability of resources, possibly due to high levels of scramble competition, may have been such a factor. Evidence for this comes from several sources. When our study group visited the same fig tree twice the same day, payoff of the second visit was substantially and significantly reduced. Under the assumption that our payoff measure was some measure of fruit quality and/or quantity, this suggests that a visit of a baboon group to a fig tree may alter a tree's value to subsequent visitors. Thus, a worthwhile quantity of new figs may need more than a few hours to ripen, possibly an entire day. As a consequence, the most successful foragers may be those who are the first to visit a mountain fig tree in the morning. We have earlier shown that our study group departed particularly early from the sleeping site when foraging for mountain figs (Noser and Byrne 2007a); and in the current study we found that exceptionally high travel speed and route linearity correlated with exclusive fig-foraging. In addition, we observed a conspicuous switch in foraging strategy, which is hard to explain by factors that change slowly over time, such as increasing satiation or tiredness. Similarly, a need to supplement the diet with other important foods is unlikely to account for our findings. Possibly, an important food source (unknown to us) was only available in the area where the stereotyped route ended, but not along it; this could explain why the baboons intermittently used food sources other than fig fruit only after the first hour of travel, but not from the beginning of the journey. However, it does not explain the sudden change of travel speed and route linearity, which coincided with the choice of alternative food types.

This switch occurred just at the time of day when other baboon groups could have potentially depleted all fig trees remaining in the area. We suggest that scramble competition is the only single factor able to explain all the above behaviours at once. In contrast to simultaneously foraging pairs of captive gorillas who only visited the portion of feeding sites that the partner had not visited (Gibeault and MacDonald 2000), our baboons may have used a heuristic strategy, one not requiring explicit knowledge about the causal relations between competitors and depleted

resources. Given a general aversion towards unpredictability (Kacelnik and Bateson 1996), coupled with the fact that alternative and probably more predictable food sources were available in large quantities at that time of year, the baboons could have adopted a strategy of switching from fig-foraging to general-foraging at a specific time of day and location in space, when the availability of desirable figs dropped off. This strategy also imposes low cognitive demands on spatial knowledge.

Arguably, baboons might integrate information more easily into their cognitive map when experiencing resources as stable in time. In contrast, unstable or even contradicting experience gained during multiple encounters with a resource may hamper integration of the corresponding information. This hypothesis could explain why our baboons showed signs of knowledge of only such a limited number of trees: they may have only mapped those which with predictable payoff. However, the inflexible use of a single route each morning would need additional explanation: lack of time is insufficient on its own to explain our findings. As a possibility, the five baboon groups that simultaneously foraged for mountain figs each morning may each have adopted a strategy to avoid encountering each other, leading to a rather inflexible manner of resource use in each group. Group avoidance could also explain why our study group did not use a route enabling them to pass the largest possible number of fig trees in the shortest possible time—and they clearly did not. For example, ten fig trees were situated SE of their sleeping site, within a circle of only about 200 m (Fig. 1). The study group may have refrained from visiting these trees in the early mornings because another baboon group spent their nights at the nearby sleeping site.

While we are far from understanding the interaction of factors affecting baboon foraging decisions, and many of our ideas remain speculative, at this stage we adhere to the most parsimonious explanation for our findings: that our baboons' cognitive map contained information on only a single route along which a few fig trees were situated. This limited capacity made planning beyond a small number of trees impossible, but this single route gave a satisfactory if not optimal yield. Then, once all known locations had been visited, the baboons were forced to adopt an opportunistic foraging mode.

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