Tradeoff Between Travel Speed and Olfactory Food Detection in Ring-Tailed Coatis (*Nasua nasua*)

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Abstract

The distance at which an animal can detect food has important ramifications for foraging behavior. Although some studies have investigated the factors which affect visual food detection, very little is known about what influences olfactory food detection abilities in wild animals. The food discovery behavior of ring-tailed coatis (*Nasua nasua*) was studied using experimental fruit plots. Coatis primarily used olfaction to detect these new food sources, and visual food discovery appeared plausible in only five of 148 trials. Coatis detected the fruit from longer distances when traveling compared with when foraging for invertebrates in the leaf litter. Travel speed had a negative effect on discovery distance. Coatis traveling slowly detected the fruit plots from further away, which demonstrated a tradeoff between speed and food detection. If this tradeoff is biologically important, slower groups should have visited more fruit trees per day, so data taken during full-day coati group follows were analyzed to determine whether this pattern occurred. Slower moving groups visited more fruit trees than faster groups once confounding factors such as daily travel distance, group identity, group spread, and year were controlled for. These results are consistent with the hypothesis that coatis exhibit a speed-accuracy tradeoff for olfactory food detection. This tradeoff appears to be an important factor influencing the movement ecology of animal groups.

Introduction

How animals detect and search for food is an important factor influencing optimal foraging strategies. For instance, animals with relatively large food detection distances are predicted to have higher food encounter rates in comparison with animals with shorter detection distances (Giraldeau & Caraco 2000). Higher encounter rates should in turn favor earlier departure from food patches and greater choosiness in entering food patches (Stephens & Krebs 1987). If an animal has poor detection abilities and uses replenishing food sources, they are predicted to increasingly exploit known food items rather than search for new food items (Janson & Di Bitetti 1997). This strategy is predicted to be particu-larly important in organisms which feed on large food patches with slow depletion times (such as large fruit trees).

One factor which has been hypothesized to have a major effect on food discovery is travel speed (Gendron & Staddon 1983; Janson & Di Bitetti 1997; Spaethe et al. 2001). All else being equal, if an animal travels a greater distance it should encounter more food items (Janson & Goldsmith 1995). On the other hand, as a predator moves faster, its ability to detect cryptic prey items should decrease due to limited attention (Dukas & Kamil 2001; Dukas 2002). This cognitive constraint should lead to a speed-accuracy tradeoff in foraging (Chittka et al. 2003, 2009). This pattern could also arise from decreased sensory input at higher travel speeds. For example, if

an animal passes through an odor plume quickly, fewer molecules would hit the receptive membranes, thus resulting in lower food detectability. Movement speed has also been used to make inferences about animals' knowledge of their resources (Janson & Byrne 2007). In general, when animals travel quickly and directly to a resource outside of their visual field, it is assumed that they have prior knowledge of that resource (Janson 1998; Pochron 2001; Janmaat et al. 2006; Janson & Byrne 2007). Researchers have hypothesized that the speed-detection tradeoff leads some animal species to move in a saltatory (pause-travel) fashion because freezing movement leads to better visual search abilities (Anderson et al. 1997; Kramer & McLaughlin 2001). Given how important food discovery is to an animal's movement patterns, understanding how travel speed affects food discovery is a major key needed to understand the movement ecology of organisms (Speakman 1986; Nathan et al. 2009).

Most studies which have investigated foraging speed-detection tradeoffs have looked at organisms which primarily use vision to find hidden food items (Gendron 1986; Speakman & Bryant 1993). There is evidence that olfactory speed-detection tradeoffs exist, but to my knowledge, no study has shown this pattern in wild animals (Rinberg et al. 2006; Chittka et al. 2009). Much of the work on olfactory food detection has been conducted on insects, birds, and bats (Jander 1998; Nevitt 2000; Korine & Kalko 2005; Wright et al. 2009). Accurately measuring flight speed and food detection distance may be difficult in these flying organisms and these studies do not typically measure or report food detection distance (but see Spaethe et al. 2001; Nevitt et al. 2008). Given that many species rely on olfaction to discover new food items, it is important to confirm or reject the hypothesis that a speed-detection tradeoff exists for these animals. If there are major differences between sensory mechanisms of food discovery, this could lead to differences in optimal food search strategies between animals which primarily use different sensory modalities (such as vision, olfaction, and hearing).

A series of fruit plot trials were conducted which tested the olfactory food detection abilities of ring-tailed coatis (*Nasua nasua*). Coatis spent most of their foraging time searching for invertebrates in and below the leaf litter, but fallen fruit accounted for a large portion of their diet as well (Hirsch 2009). Coatis typically spent their day searching for invertebrates while traveling between fruit trees. Fruit trees and sleeping sites were the main factors determining

the foraging paths of coatis (Hirsch 2009; Hirsch 2007). Coatis used their keen sense of olfaction to discover new food items, and nasal and cranial anatomies are consistent with a heavy reliance on olfaction (Chapman 1938; Compton 1973; Gompper 1996). Coatis typically searched for invertebrates by sticking their snouts in the leaf litter and soil and sniffing for prey (Kaufman 1962; Gompper 1996). Coatis were sometimes observed pointing their flexible snouts in an upwards position, sniffing the air for odors. This behavior usually occurred in response to a newly discovered food item and the coatis often traveled directly to the food source after sniffing the air (personal observation). Because coatis have a behavioral signal which indicates that food has been discovered, they are an ideal species for studying speed-accuracy tradeoffs in food detection.

If coatis primarily use olfaction to discover food items, they should find most new food sites by smell. If coatis exhibit a speed-accuracy tradeoff in olfactory food detection, when coatis move more slowly, their ability to detect food should increase, and they are predicted to detect food from longer distances than when traveling quickly. I used data on coati group foraging efficiency, travel speed, daily travel distance and fruit tree visits to test for possible speed-accuracy food detection tradeoffs during natural foraging. Even if coatis have prior knowledge and memory of food resource location, asynchronously fruiting trees result in variation in food location over time. If coatis are able to smell ripe fruits from further away, they should be able to both monitor and discover ripe fruit food sources more efficiently, which should lead to more fruit tree visits per day.

Methods

This study was conducted in the Iguazu National Park, Argentina between March 2003 and September 2004 (for details of the field site see: Brown & Zunino 1990; Di Bitetti 2001a,b). Data on natural fruit foraging and fruit discovery were taken from two study groups (PQ and PSG). The groups ranged in size between 11 and 15 individuals in 2003 and 25–30 during 2004. Coatis were captured using wire mesh live animal traps (32 × 10 × 12 inches), anesthetized, and given a unique combination of colored plastic eartags for individual identification (Dalton Rototags). Eartags were placed on juveniles older than 4 mo of age, making it possible to individually recognize all juvenile and adult group members. Between one and three adult females per group were fitted with radio-collars in order to locate the

study subjects. Groups of coatis were well habituated and observers could silently walk within 2 m of a focal individual without disturbing the animal. With the exception of occasional accidental loud noises made by the observers (such as breaking a branch), it did not appear that the coatis changed their travel and foraging behavior in response to observer presence. For instance, if a food item such as a pindo fruit was encountered near an observer, the coatis would approach the food regardless (even if the fruit was below the boot of an observer).

Daily travel distances and average group speed were based on 71 full-day follows during 2003–2004 when coati groups were followed from sun-up to sun-down and the speed of the group was recorded every 15 min. Location was recorded continuously in the field and was typically determined by direct observation of the group in relation to nearby trail markers (which were normally <75 m from the group at any given time). The group location was plotted on a detailed map containing all the trail markers. The location of any fruit tree visited by group members during the day was plotted on the map. The handwritten maps were digitized using the Grab It XP program (DATATREND Software, Raleigh, NC, USA) and total daily travel distances were calculated in Excel. Average daily group speed was calculated by averaging the group speed measures during the 15-min scan samples. Speed was recorded on a graded scale (1–3) based on gait and estimated speed. Based on the day range maps, these categories correspond to the following travel speeds: (1) slow – 0 to 0.29 km/h, (2) medium – 0.3 to 0.6 km/h, and (3) fast – >0.6 km/h. All group speed measures taken while the group was feeding at a fruit tree or during sleeping and resting were excluded from the analysis. During the scan samples, the length and width of the group spread was recorded (Hirsch 2007). The average group spread was calculated by adding the width plus length divided by two.

Feeding trials were conducted using medium-sized green table grapes. Because grapes are not a natural food item for coatis, the two study groups were presented with grapes. Coati groups were given grapes at least three times before the experimental feeding regime so that all individuals would have an opportunity to smell and feed on grapes. During the feeding trials, 5, 10, 20, 50, or 100 grapes were placed in a 1 m^2 plot. During the 100 grape treatments, the fruit plot varied in size between 0.3 and 2 m^2 (0.3, 0.7, 1, and 2 m^2). This variation in plot density was used for another concurrent study of feeding competition. A digital video camera was fixed to a portable

tripod approx. 2.5 m from the fruit plot to record feeding rates and other behaviors. Feeding trials were always conducted with two or more observers who communicated with radios and hand signals. One researcher would typically stay with the group, while the other arranged the fruit and video camera ahead of the group. When a group approached within 25 m of the fruit plot, the researcher walking with the coatis positioned themselves in a location where they could see those individuals closest to the food, while the other researcher remained 2–5 m from the food and started the video camera. The researcher near the camera was typically not located between the coati group and the plot, but rather behind or to the sides of the plot. In order to not disturb the coatis during the detection process, both researchers tried to remain stationary, or walk as quietly as possible. Observers would often coordinate their data collection to observe multiple individuals who were most likely to discover the fruit plot. A total of 229 trials were conducted. In 44 of these trials, the detection behavior of the coatis was either not observed or was insufficiently clear to the observers and therefore excluded from the analysis (for a total sample size of 185). The coati groups did not discover food in 37 of these 185 trials (N = 148 clearly observed discoveries).

Janson & Di Bitetti (1997) noted that upon discovery of a new food source, brown capuchin monkeys generally changed direction towards the food site and increased travel speed. This behavior was also observed in coatis, but with a notable addition. During a typical food discovery, the coatis would hold their heads up from the ground and sniff in the air. This was particularly noticeable due to the flexion of the tip of the nose, which was a clear indication of olfactory behavior. This behavior was typically followed by orienting toward the food site then increasing travel speed. In some cases, it was not possible to observe the sniffing behavior of the coatis due to poor visibility and thick vegetation, but it was clear that the coatis discovered a food site due to their increase in speed and a change in travel direction. By using a combination of behavioral cues to determine the presence of olfactory detection, the methods used here closely resemble those of previous studies (Nams 1991, 1997; Cablk et al. 2008).

During the discovery trials we were especially careful to minimize any possibility that the coatis could detect the fruit plots by 'cuing' in on our actions. Fruit was kept in sealed plastic containers inside a backpack which was regularly washed before the feeding trials. To prevent the coatis from

cuing on the sight of the tripod or the sound of the radios used during the trial, hand held radios and a video camera were regularly used outside the context of feeding trials. During the experiment, the tripod was often placed behind a tree or other visual obstruction to reduce the possibility that the coatis could cue on the tripod. Because the fruit were placed on the ground and vegetation was thick in many locations, it was probably difficult or impossible for the coatis to see the fruit at distances >5 m. Despite these controls, in some cases it appeared plausible that coatis may have been able to use visual information to detect the fruit plot. In the cases in which coatis would look in the direction of the fruit plot without sniffing in the air before approaching, we noted that visual detection might have occurred. If the area between the coati and the fruit plot was sufficiently dense with vegetation as to prevent visual detection we coded the detection as olfactory by default. In no cases did it appear that the coatis used the scent of the researchers or backpack to detect the food plots. If this occurred, we would have predicted that the coatis would travel directly to the researcher near the food plot rather than directly to the plot itself. After a coati detected the food plot, it always travelled to the plot and not in the direction of the researcher (unless the researcher was located immediately behind the plot).

When a discovery occurred, the identity, behavior, travel speed, travel direction, and spatial position of the discoverer were recorded. If the fruit plot was not discovered, the same data was taken on the individual who came closest to the fruit. At the point of discovery, or the closest approach without detection, the group behavior, group speed, group travel direction, distance from the fruit plot to the center of the group, and wind speed and direction were recorded. All distances were measured using 50-m fiberglass tape after the trial was completed. The distance at which an individual discovered the feeding site, or the distance to the nearest individual who did not discover the site was determined to be the nearest approach distance (NAD).

Speed measures during feeding trials were recorded from the food discoverer at the moment of discovery and were not based on scan samples. Although there was a connection between individual speed and behavior, the two variables were not perfectly correlated. An animal searching for terrestrial invertebrates could move at any speed, but typically moved at slow or medium speeds. Animals which were traveling and not searching for food typically traveled at medium or fast speeds.

Wind speed was difficult to record due to the low amount of wind in the forest. Attempts to measure wind speed using a digital wind meter were inadequate because the wind was only strong enough to set off the meter during one feeding trial. The presence and direction of wind was determined by using the flame of a lit match held next to a compass (after the experiment was completed). Individual behavior was divided into two categories: (1) travel – when the coatis were moving forward and not stopping to search for invertebrates, and (2) invertebrate foraging – when the coatis would search for ground litter invertebrates in between bouts of movement (Hirsch 2009). The spatial position of individuals was recorded using the elliptical clock method (as in Janson 1990a,b; Di Blanco & Hirsch 2006) and then summarized into seven spatial position categories: (1) front edge, (2) front middle, (3) center, (4) back middle, (5) back edge, (6) outer sides, and (7) middle sides.

Statistical Analyses

The distance at which the chance of detection reached 50% was calculated by plotting the percentage of trials discovered at ranked distance categories (0–5, 5–10, 10–15, 15–20, 20–25, 25–30 m) weighted by the number of observations. The polynomial formula obtained from this plot was then used to determine the distance at which detection of fruit plots reached 50%. A generalized linear multiple logistic regression (GDLM) was run on the trials which were successfully discovered (N = 148) to determine what factors influenced the distance at which coatis detected the introduced fruits. Eleven independent variables pertaining to the experiment and coati which discovered the experiment were entered into this model (month, month squared, age, individual activity, and speed, and the interaction of these two variables, within-group spatial position, presence and direction of wind, the number of grapes, and fruit plot density). The square of the numerical value for 'month' was entered into the analysis of detection distance after an initial inspection of the data indicated the possibility of a U-shaped pattern of discovery distance over time. Best subset models were identified using an Akaike analysis. A separate GDLM was run to determine what factors affected the number of fruit trees visited per day (N = 71 all day follows). Eight independent variables were entered into the model (month, month squared, year, coati group, group size, daily travel distance, average daily speed, and group spread).

Results

Of the 148 fruit plot discoveries, visual detection appeared possible in only five cases. It was clear and unambiguous that the coatis discovered food by olfaction in the remaining 143 experiments. The average distance at which the coatis detected the fruit plots was 8.9 m (SD ± 4.77). The probability of detecting the food site reached 50% at a NAD of 19.6 m (Fig. 1). A total of 42 different coatis discovered experiments and there was no effect of individual ID on detection distance (Kruskal–Wallis test, $\chi^2 = 44.580$, p = 0.247). In the complete model, there were no significant effects of year, month, group, age of discoverer, number and density of grapes, and presence and direction of wind on the distance of detection. The lack of wind speed and direction effects may have been due to unpredictable turbulence found on the forest floor. The variables which significantly influenced detection distance in the full model were; individual activity, individual speed, and the interaction of those two variables (Table 1). These three variables along with month and month squared, were the only variables remaining in the best subset model as identified by the AIC analysis. When coatis foraged for terrestrial invertebrates, travel speed had no significant effect on the distance of fruit plot discovery (Kruskal–Wallis $\chi^2_2 = 0.642$, p = 0.726). Coatis discovered the fruit at significantly shorter distances during rapid travel, compared with slower travel speeds (slope = −2.892, p = 0.007, Fig. 2). When traveling at slow and moderate speeds, the coatis were able to detect the fruit plots more than twice as far compared to when foraging or rapidly traveling (average slow and medium travel detection distance = 15.36, fast travel detec-
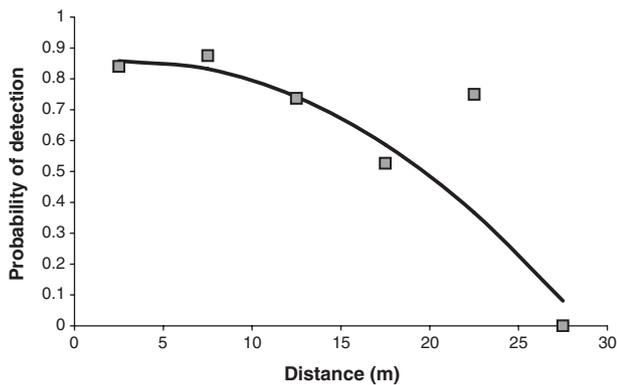
Table 1: Full generalized linear model for experiment detection distance

Independent variable	df	Estimate	Wald stat	p value
Month	1	−1.265	2.011	0.163
Month squared	1	0.124	3.166	0.075
Number of grapes	1	0.033	0.321	0.971
Density of grapes	1	−0.135	0.019	0.683
Presence of wind	1	−0.499	0.538	0.487
Experiment upwind	1	−0.089	0.003	0.924
Age of discoverer	2			
Adult		0.000	–	–
Juvenile		−0.597	0.199	0.356
Subadult		0.302	0.701	0.578
Spatial position	6			
Front edge		0.000	–	–
Front middle		1.422	0.528	0.466
Center		−1.378	0.276	0.535
Back middle		0.698	0.028	0.798
Back edge		−0.953	0.298	0.507
Side edge		−0.197	0.034	0.844
Side middle		−0.360	0.040	0.892
Individual activity	1			
Terrestrial foraging		0.000	–	–
Travel		2.219	12.084	0.003*
Speed	2			
Slow or no movement		0.000	–	–
Medium speed		0.814	2.185	0.348
Fast movement		−2.892	11.368	0.007*
Activity × Speed	2			
Slow travel		0.000	–	–
Medium travel		1.553	2.362	0.082
Fast travel		−3.261	8.932	0.002*

$\chi^2_{19} = 53.380$, p = <0.001. *Significant (<0.05) effects.
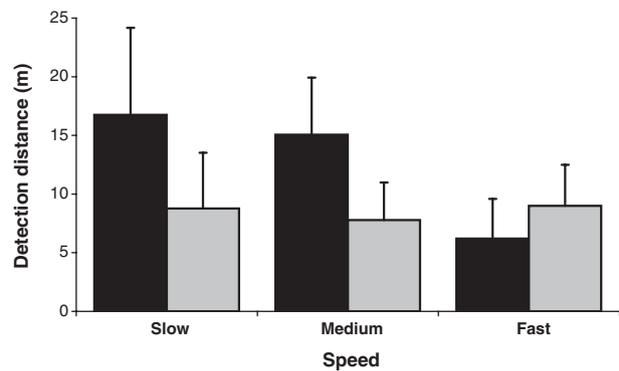

Fig. 2: Detection distance of fruit plots in relation to the speed of the discoverer in meters ±SE. Black bars indicate animals traveling during the discovery and gray bars terrestrial foraging. Slow speed = 0–0.29 km/h, medium speed = 0.3–0.6 km/h, and fast speed = >0.6 km/h.

Fig. 1: Probability of food detection as a function of nearest approach distance (NAD). Slope equation for discovery probability = 0.846 + 0.00793 × NAD − 0.0013 × NAD².

tion distance = 6.20). Coatis were more likely to discover fruit plots when foraging in the front and side edges of the group, but this had no effect on the

Table 2: Full generalized liner model for variables which affect the number of fruit trees visited per day

Independent variable	df	Estimate	Wald stat	p value
Month	1	0.110	22.689	0.149
Month squared	1	−0.010	16.802	0.160
Group size	1	−0.041	25.304	0.110
Year (2004)	1	0.816	2.080	<0.001*
Group (PSG)	1	−0.272	5.245	<0.001*
Travel distance	1	0.015	2.557	0.022*
Average speed	1	−0.345	1.971	0.023*
Group spread	1	0.012	5.167	0.035*

$\chi^2_7 = 103.964$, p = < 0.001. *Significant (<0.05) effects.

detection distance (front edge mean = 9.52 m, side edge mean = 9.28 m).

The average daily travel distance for the coati groups was 3.04 km (range = 1.14–4.84 km, N = 71). The groups visited an average of 17.8 fruit trees per day and the number per day was positively correlated with year (more trees during 2004), group (more trees visited by the PQ group), group spread and travel distance. The best subset model as identified by the Akaike analysis did not include the month or month squared variables. The number of fruit trees visited per day increased during 2004 and when the group was more spread out. The longer the daily travel distance was the more fruit trees were visited (Table 2). When these other independent variables were controlled for in the GDLM analysis, an increase in group travel speed resulted in fewer fruit trees visited per day.

Discussion

Coatis almost exclusively discovered fruit plots using olfaction. This is consistent with earlier experiments where coatis detected fruit hidden inside of boxes (Chapman 1938). The detection distances found in this study are larger than one would expect if the coatis were solely using vision to detect small fruits on the forest floor. This heavy reliance on olfaction may be related to their evolutionary history, as coatis are the only diurnal member of the order Procyonidae and their ancestral state was likely nocturnal (Koepfli et al. 2007). It is difficult to make any concrete conclusions as to whether the detection distances in these experiments were similar to natural fruit sources. Grapes were used in the experiments because they resembled the most commonly consumed fruit species in size (pindo palm – *Syagrus romanzoffianum*) and were available year round. It is not known if using natural fruits which might have

given off more odors would have resulted in larger detection distances. Anecdotal observations indicated that coatis did not commonly detect natural fruit trees from significantly longer distances than those reported here. It was also not known which chemical cues the coatis primarily used to detect the fruit, but studies of other mammals have pointed to the importance of alcohols, esters, and aldehydes (Laska & Seibt 2002a,b; Laska et al. 2003; Dominy 2004; Hodgkinson et al. 2007). In future studies, it would be ideal to control additional factors such as food 'smelliness,' temperature, height, and visibility in the canopy, learning, and search images (Murlis et al. 1992; Nams 1997; Dukas & Kamil 2001).

Coatis detected fruit plots from further away when traveling than when foraging for ground litter invertebrates. This pattern may be related to posture. When foraging for ground litter invertebrates, the coatis typically had their noses positioned down in the leaf litter or a small hole in the ground. It seems plausible that coatis were able to smell further away when their head position was upright. The shape of the odor plume could have had an effect on food discovery in this case. If coatis cued on relatively light chemical cues (such as ones important to other mammalian species) these smaller particles would be more likely to drift up into the canopy during inversion and not drop to the ground or enter the leaf litter (Conover 2007). Alternately, when the coatis were searching for ground litter invertebrates, they may have been using a particular olfactory search image for invertebrate prey (Nams 1991, 1997). If the coatis were primarily paying attention to invertebrate smells, they have been less likely to notice fruit odor cues. On the other hand, when the coatis were moving quickly between fruit trees, they may have been more likely to notice fruit odors.

The speed of the coati which discovered the fruit had a negative effect on fruit detection distance when traveling, but no effect when foraging. The first pattern was expected and is similar to previous results found in visual predators such as redshanks, bobwhite quail, and brown capuchin monkeys (Goss-Custard 1977; Gendron 1982; Speakman & Bryant 1993; Janson & Di Bitetti 1997). Additional evidence indicates that a speed-detection tradeoff occurred during invertebrate foraging as well. When coati group speed increased, invertebrate consumption rates declined, which may be evidence that olfactory detection for invertebrates was reduced as speed increased (Hirsch 2007, 2009). If this is correct, it means that individual speed during terrestrial foraging influences invertebrate detection but not

fruit detection and may be evidence that coatis were switching search images as they changed from invertebrate foraging to traveling between fruit trees.

The analysis of coati travel patterns and fruit tree visits provided further evidence that slow travel resulted in coatis foraging more efficiently. Although not significant in either GDLM model, fewer fruit trees were visited during the Argentine summer (Nov.–Jan.) when fewer trees contained ripe fruit (Hirsch 2009). Removing the seasonality variables did not affect the direction of effect for the other predictor variables in the best subsets model. Travel distance was positively correlated with the number of fruit trees visited, which fits previous predictions (Janson & Goldsmith 1995). Substantially more fruit trees were visited per day during 2004 (2003 = average of 7.55 trees per day, 2004 = 26.10). The group size for both study groups increased during 2004, but this variable was controlled for in the analysis, thus it appears that the amount of available fruit was greater in 2004 than 2003. Group spread was positively correlated with the number of fruit trees visited, but it was also positively correlated with group size and negatively correlated with group speed, thus it was an especially important variable to enter into the GDLM model (Hirsch 2007). Once these factors were controlled for, it was found that slower coati groups visited more fruit trees per day, which was predicted if a speed-accuracy tradeoff for olfactory fruit discovery exists in coatis.

Experimental and behavioral data are consistent with ring-trailed coatis exhibiting a speed-accuracy tradeoff during foraging and travel. This should result in coatis traveling at slower speeds than would be predicted if the trade-off did not exist. In general, the coatis rarely travelled at their fastest travel speed. The coatis typically sped up when they were within 25–40 m of previously visited fruit trees, presumably to arrive at the fruit tree first and gain priority access to the food (Hirsch 2007). This is an indication that the coatis had prior knowledge of some fruit trees (Janson 1998; Pochron 2001; Janson & Byrne 2007). The coati groups would also travel rapidly toward sleep sites, especially when daylight was fading. Outside of these contexts, it would not have been advantageous for the coatis to speed up because it would have resulted in fewer food discoveries. The patterns found in this study are consistent with the hypothesis that when coatis are traveling between known fruit resources they travel slowly in order to better discover new fruit resources or monitor the ripeness of previously known fruit resources.

The generally slow travel speeds of the coati groups had important effects on travel patterns as well. The typical daily path of coati groups involved far more sharp turning angles and extreme tortuosity than sympatric capuchin monkey groups (Hirsch, Di Bitetti and Janson, Unpublished data and personal observations). This comparison is particularly interesting because the fruit component of the diet of these two sympatric social mammals is highly similar (Di Bitetti 2001b; Hirsch 2009). Although the coati groups often made sharp changes in direction when leaving fruit trees, this behavior was particularly notable when groups spent a long period of time invertebrate foraging in one general location (typically >30 min.). In this case, coati foraging resembled area restricted search behavior (Benhamou 1992, 2004; Nevitt et al. 2000; Barraquand & Benhamou 2008). Experimental feeding studies have found that capuchin monkey groups rarely turn at sharp angles, which is likely tied to maintaining cohesion in their spread out groups (Janson 1998; Hirsch 2002). Slow travel and forage speeds should help coati groups maintain group cohesion, which allows them to make sharper turning angles and possibly make better optimal foraging decisions with respect to route choice.

Acknowledgements

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