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Spatial position and feeding success in ring-tailed coatis

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Abstract The location of an animal within a social group has important effects on feeding success. When animals consume quickly eaten food items, individuals located at the front edge of a group typically have greater foraging success. When groups feed at large clumped resources, dominant individuals can often monopolize the resource, leading to higher feeding success in the center of the group. In order to test these predictions, behavioral data relating foraging success to within-group spatial position were recorded from two habituated groups of ring-tailed coatis (*Nasua nasua*) in Iguazu, Argentina. Foraging success did not fit expected patterns. When feeding on small ground litter invertebrates, coatis had the same foraging success at all spatial positions. This pattern likely resulted from an abundance of invertebrates in the ground litter. When feeding on fruit, individuals in the front of the group had greater feeding success, which was driven by the relatively quick depletion of fruit trees. Dominant juveniles were often located in the front of the group which led to increased access to food. This resulted in higher feeding success on fruits but simultaneously increased their risk of predation. Although groups typically became more elongated and traveled faster when feeding on fruit, it did not appear that the coatis were drastically changing their spacing strategies when switching between the two food types. Paradoxically, spatial position preferences during invertebrate foraging appeared to be driven by fruit trees. Because fruit trees were encountered so frequently, juveniles ranging at the front edge of the group during invertebrate foraging were the first to arrive at fruit trees and thus had higher foraging success. This study demonstrates the importance of how food patch size and depletion rate affect the spatial preferences of individuals.

Keywords Coati · Social foraging · Dominance · Within-group spatial position · Food depletion · Feeding competition · Predation

Introduction

As a group of animals moves through the environment, individual group members encounter and consume food items. If food items are small and quickly eaten, individuals at the back of the group may forage in areas which have already been stripped of resources. This often results in individuals at the back of the group having lower feeding success. This pattern of front-to-back food depletion has been found in several studies (O'Connell 1972; Robinson 1981; Janson 1990b; Black et al. 1992; Krause et al. 1992; Krause 1993; Hall and Fedigan 1997; Stahl et al. 2001; Rowcliffe et al. 2004; Romey and Galbraith 2008). However, when food is abundant, it may be impossible for individuals at the front of the group to deplete food resources before the arrival of individuals at the back of the group, which leads to equal feeding rates from front to back of the group (e.g., Hall and Fedigan 1997 during the wet season).

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When food items occur in sparsely distributed and defensible patches, front-to-back food depletion is not predicted to occur (Hirsch 2007a). Fruit trees which contain large numbers of fruit in a relatively small area are often defensible resources. In many frugivorous primate species, central individuals have the highest food intake rates (*Cebus nigrivittatus*, Robinson 1981; *Cebus apella* and *Cebus albifrons*, Janson 1986, 1990b; *Macaca fascicularis*, van Schaik and van Noordwijk 1986, 1988; *Papio anubis*, Barton 1993). This occurs because central dominant individuals are able to aggressively monopolize the concentrated resource (Janson 1996; Grant et al. 2002). Subordinate group members are then left to seek alternate food resources which may be located far away from the group, or wait for the dominants to leave a central food resource before entering (Vogel and Janson 2007). This can lead to a pattern where dominant individuals are found in the center of the group more frequently than other group members, which has been found in several mammal species (for review, see Hirsch 2007a). The same food resources which can lead to higher feeding success in central individuals are often important food resources, such as fruit trees, and individuals may be able to remember the locations of these trees in time and space (Garber and Paciulli 1997; Janson 1998, 2000; Janmaat et al. 2006; Janson and Byrne 2007). When individuals know the location of food resources, individuals may use this knowledge to change their spatial position preferences in a manner which increases their food intake (Hirsch 2007a). In particular, subordinate brown capuchin monkeys (*C. apella*) have been observed to run far ahead of the group before approaching a fruit tree (Janson 2000). By "jumping ahead" of the group, subordinates are often able to consume a share of the food resource before dominants arrive and monopolize the resource. Alternately, subordinate brown capuchins who want to avoid aggression often enter a food tree only after the dominants have left the tree after feeding (Janson 1990a, b).

In cases where the locations of food items are unknown, some individuals can act as scroungers. Rather than independently search for food, scroungers search for conspecifics which have found food and then join the food discoverers (Giraldeau and Caraco 2000). When food joining opportunities are present, central and front-center spatial positions may be ideal for monitoring food joining opportunities and quickly joining feeding individuals (Barta et al. 1997; Janson and Di Bitetti 1997). Because food joining often takes the form of aggressive kleptoparasitism, dominants are predicted to be scroungers more often than subordinates and thus may choose front-center spatial positions more than food finders (Janson and Di Bitetti 1997; Hirsch 2007a; McCormick et al. 2007). The combination of food abundance, depletion time, and prior knowledge of resources is predicted to influence an individual's choice of within-group spatial position differently depending on their dominance status (Hirsch 2007a).

Coatis are an ideal species to test predictions related to within-group spatial position because they are mostly terrestrial, have linear dominance hierarchies, and forage on both large clumped items and small dispersed items (fruit and invertebrates) (Hirsch 2007b, 2009). Before making predictions as to how coatis should optimally choose spatial positions, it is important to quantify food depletion and understand how patch size affects food depletion. The main purpose of this paper is to determine which spatial positions lead to higher feeding success and how food depletion affects group geometry and spatial position preferences. It was hypothesized that coatis would exhibit front to back food depletion while feeding on invertebrates, but have higher feeding success in the middle of the group while feeding on fruit. Because fruit and invertebrate food abundance changes throughout the year, these patterns are predicted to change over time and be dependent on which species the coatis are consuming. Previous work on ring-tailed coati fruit foraging suggests that several fruit species consumed in Iguazu are quickly depleted, which could lead to front-to-back food depletion (Hirsch 2009). In addition to determining which spatial positions result in the highest food intake rates, it is predicted that dominant coatis, which are not constrained by social dominance interactions, should choose spatial positions consistent with maximizing their food intake.

Methods

This study was conducted at the Iguazu National Park, Argentina between March 2003 and September 2004 (for details of the field site, see Brown and Zunino 1990; Di Bitetti 2001a, b). The study area is part of the Atlantic Costal forest ecoregion, has a relatively high abundance of fruit trees (two to three per hectare, Placci and Janson unpublished data), and an intact community of felid predators (Di Blanco and Hirsch 2006, Di Bitetti et al. 2006). Ring-tailed coatis are medium-sized, social Procyonids, which spend most of their foraging time searching for invertebrates (millipedes, spiders, insects, and annelid worms) in or below the forest leaf litter (Hirsch 2009). Coatis in Iguazu spent between 69.7% and 97.5% of their monthly foraging time foraging for invertebrates, but travel and movement patterns of coati groups were mostly determined by the presence of ripe fruit (Hirsch 2009). Coatis spent more of their fruit foraging time exploiting pindo fruits (*Syagrus romanzoffianum*) than any other fruit species (Hirsch 2009).

Coati groups were comprised of adult females (24 months of age or older), subadults (12–24 months of age), juveniles (2–12 months of age), and one adult male (generally 36 months or older). Two coati groups (PQ and PSG) were used in this study, and group size varied between nine and 29 individuals. Group composition changed over time, and subadults were absent in the PQ group during 2004, and the PSG group during 2003 (see Table 1 in Hirsch 2010a). Between one and three adult females per group were fitted with radio collars which were used to locate the groups. Coatis were captured using Tomahawk or similar traps, anesthetized, and either fitted with radio collars or given a unique combination of multi-colored plastic eartags for individual identification (Dalton Rototags). Groups of coatis were usually habituated within 2 to 3 weeks. Habituated coatis would allow observers to silently walk within 2 m of a focal animal. Each group was followed for at least 60 h per month and typically more than 100 h per month.

Continuous focal samples were taken on known individuals from August 2002 to October 2004. Focal samples were 10 s in duration and the same individual was not resampled within 10 min. During the focal samples, I recorded the identity of the focal individual, within-group spatial position, individual and group activity (invertebrate foraging, rest, alert, travel), individual and group terrestriality (arboreal or terrestrial), group speed (ranked from 0 to 3 with 0 being no movement and 3 being rapid travel), the number and identity (when possible) of all individuals within 3 m of the focal, and the number of food items ingested. Short focal samples were used because many of the associated variables recorded during the focal samples changed frequently and rapidly. This was particularly important for accurately measuring neighbor density (number of individuals <3 m of focal). The use of a 3 m radius to measure coati density was chosen because this distance corresponds to the maximum radius of the fruit shadow of the most commonly eaten fruit species (*S. romanzoffianum*), thus this distance should have some biological relevance. The species of fruit eaten during samples was recorded and included in subsequent analyses because feeding rates (number of fruits eaten per sample) varied considerably by species. Individuals were selected opportunistically. Due to poor overall visibility in the dense forest, it was not feasible to select individuals based on a pre-determined order. Adults were preferentially targeted over juveniles, especially during 2004 when both groups had large numbers of juveniles.

Spatial position of individuals was recorded in the same manner as Janson (1990a, b). The group spread was visually divided into three concentric ellipses: (1) center, (2) middle, and (3) edge. The location of the focal animal within these circles was then further subdivided into 12 positions based on the number of a clock, with 12 being the front most position and 6 representing the back of the group. These 36 spatial positions were then summarized into five spatial position categories for analysis: (1) front edge, (2) front middle, (3) center, (4) back middle, and (5) back edge (Fig. 1).

Data on group spread and geometry was taken during 15-min scan samples of the group. During these samples, the length and width of the group was estimated to the nearest 5 m. All samples were taken by the author and these estimations were periodically checked for accuracy. When double-checking the group spread estimations, one field assistant and I would locate and mark the front and back edges of the group. After the group had moved away, we would measure this distance using a 50-m fiberglass tape. Group behavior and feeding data taken during the 15-min scan samples included the percentage of arboreal individuals, group activity, group speed, and the number and location of fruit trees in the group spread (if present).

To determine if coatis arrived at fruit trees in a particular order, a series of tree focal samples was recorded (Vogel and Janson 2007). When I was able to arrive at a fruit tree before the arrival of the group, I recorded the number and identity (or age/sex class) of all individuals eating at the fruit tree every minute. Prior to the start of the sample, I set the timer on my watch to beep every minute. The tree focal sample started with the first beep after the arrival of the coati group, thus the sample could have started between 1 and 59 s after the arrival of the group. At each beep I recorded either the number of all feeding individuals, the number of feeding individuals in each age/sex class, or the ID of all feeding individuals.

Statistical analyses

Individual focal samples taken during periods of invertebrate foraging and fruit feeding were analyzed to test the relationship between feeding success and spatial position using the STATISTICA statistical package (version 6.1, StatSoft, Inc, 2003). Before the analysis was performed, the independence of consecutive samples was tested using the

Fig. 1 Spatial position categories with the top representing the direction of group movement. *1* Front edge, *2* front middle, *3* center, *4* back middle, *5* back edge
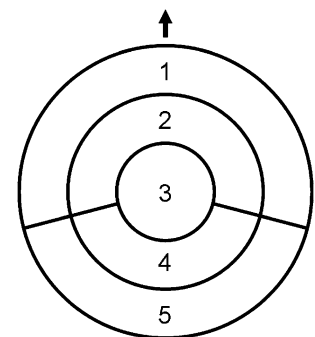
method reported in Appendix 2 of Schoener (1981). The number of samples recorded per month varied between 104 and 479 (fewer samples were taken during the birthing season from October to December). A total of 67 individuals were sampled. Because it was not possible to systematically sample individuals in a predefined order, an unequal number of samples were taken on different individuals and different age/sex classes (adult females total number of samples $N=1,902$, number of samples per individual ranged from 171 to 264, subadults $N=835$, range 46–172, juveniles $N=1,499$, range 4–102, adult males $N=238$, range 3–155). The different number of individuals in each age/sex class also contributed to unequal numbers of samples for each age/sex class. Outer spatial positions were larger in area than inner spatial positions and the density of coatis varied by spatial position. These factors led to considerable differences in the number of samples recorded at each of the five spatial positions (N for spatial positions $1=1,423$, $2=731$, $3=740$, $4=652$, $5=928$).

Two generalized linear models were conducted with fruit or invertebrate feeding success as the dependent variable and several potential predictor variables entered into the models (time of day, group speed, group size, age/sex class of individual, and the number of neighbors within 3 m). All test statistics were two-tailed except where reported otherwise. Because month is a circular variable, both the month (represented by numbers 1–12) and month squared were entered as variables to test for nonlinear seasonal patterns. Because group ID was not a significant predictor variable in the generalized linear models, individuals in the two study groups were pooled into the same data set for all analyses. Although two other habituated study groups were not included in the analyses due to small sample sizes, within-group spatial position patterns appeared to be highly similar in these groups as well. To test for possible pseudoreplication, separate generalized linear models were run with individual ID as a predictor variable rather than age/sex class. Because individual ID was not a significant predictor variable and the slopes and P values of the other predictor variables were very similar, it was determined that repeated sampling of individuals did not skew the statistical conclusions.

To test whether different age/sex classes differed in their spatial position preferences, the focal samples were entered into a contingency table with four age/sex classes and five spatial positions ($N=20$ cells). χ^2 models were calculated from the contingency tables and the distribution of age/sex classes by spatial position were significantly different from random in the total model for both fruit feeding and invertebrate foraging. Expected cell wise values were then calculated for each age/sex class and spatial position based on the total number of samples recorded for each age/sex class and the total number of samples recorded at each

spatial position. The relative deviations from these expected values were calculated by subtracting the observed values from the expected values, and then dividing these by the expected values. To test whether particular age/sex classes were more or less likely to be found in certain spatial positions, G tests were performed to determine if each age/sex class had spatial preferences that differed from random, and if so, cell wise χ^2 values were calculated for each spatial position. All significant values ($\alpha=<0.05$) are noted in Fig. 3. This same analysis was repeated for samples taken during fruit feeding. To test whether the spatial position preferences of the four age/sex classes were different when feeding on fruit than when feeding on ground litter invertebrates, a logistic regression test was run with spatial position as the dependant variable (as a categorical 1–5 variable) ($N=4,474$). Age/sex class, fruit feeding, and the interaction of fruit feeding and age/sex class were entered as independent variables in the multivariate analysis.

Data from fruit tree focal samples were analyzed in JMP (5.1, SAS Institute 2004). For consistency, the analysis was restricted to periods of feeding on pindo fruit and only data from the PSG group during 2004 was used. All known individuals were lumped into their respective age/sex classes. The number of individuals feeding per age/sex class was divided by their total number in the group to control for differing numbers of group members by age/sex class. A series of ANOVAS and Tukey–Kramer paired comparisons were used to test for differences in the presence of the four age/sex classes at pindo trees during each minute. Not all pindo trees were depleted in the same amount of time, thus the number of samples for each time step differed (total of pindo trees used=160). In addition, the minute in which the last individual to leave the tree varied according to the depletion time. In order to correct for this latter variation and test whether some age/sex classes were more often found at the back of the group during pindo foraging, an additional analysis was conducted using data taken during the last minute of pindo feeding (only trees fed on for 2 min or more were used in this analysis, $N=129$).

Results

When feeding on ground litter invertebrates, coatis typically consumed prey items very quickly (1 s or less). In some cases, they would spend over 15 s consuming a particularly large annelid worm. Even though the consumption of invertebrates was generally quick, coatis could sometimes spend much longer excavating the prey. Coatis were occasionally observed spending over 2 min digging holes which reached up to 20 cm in depth searching for

subterranean invertebrates. In general, invertebrate search times were much shorter, and it appeared that most items were found directly beneath a leaf or only a few centimeters below the leaf litter.

Fruit trees were depleted more slowly than invertebrates, ranging from 2.50 to 12.5 min on average (using the eight most common fruit species; Hirsch 2009). Some large *Ficus* trees were particularly productive and coatis were recorded feeding continuously for up to 45 min in one tree. On the other hand, small *Cecropia* trees were depleted relatively quickly (average=2.5 min, N=37). The most common fruit species eaten by coatis was pindo palm fruit (*S. romanzoffianum*) which were depleted in an average of 5.68 min (N=406, Hirsch 2009). Species that were consumed more slowly than pindo had negative slope values in the generalized linear model, while species with smaller, more quickly eaten fruits had positive slope values (Table 3). Although many fruit trees were re-visited frequently, more than once per day in some cases, it was not common to find fresh fruits underneath the trees after a coati group visited (Hirsch 2009). The major exception to this pattern was when coati groups visited large ficus trees which could be fed in for hours without depleting al the fruit (I observed only two trees like this in the home ranges of the PQ and PSG groups).

The average length and width of the two groups was 23.23 m by 14.34 m, respectively (SD length=18.22, SD width=9.29). Both group length and width were significantly positively related to group size (length, $F_{1,2208}$= 244.10, P<0.001, width, $F_{1,2208}$=160.66, P<0.001). The average length and width of small groups (between eight and 15 individuals) was 16.83 m by 11.67 m (SD length= 10.11, SD width=6.77). The group spread in large groups (25–31 individuals) was 28.87 m by 17.10 m (SD length= 21.99, SD width=10.65). The group spread was generally greater in length than width, and this elongation increased as the group increased travel speed (length/width ratio during no movement=1.70, slow travel=1.85, moderate travel speed=2.56, rapid travel=3.60, χ^2=109.05, df=3, P<0.001). When group speed, group size, and the percentage of individuals eating fruit were entered into a multiple regression model, fruit eating was positively related to an increased group length/width ratio ($F_{1,5}$= 10.11, P=0.002).

The spatial position preferences of the four age/sex classes during fruit feeding were similar to the patterns seen when foraging on invertebrates (Table 1). Although both fruit feeding and age/sex class were significant in the final logistic regression model with spatial position as the dependant variable, the interaction was not (whole model, df=28, R^2=0.026, χ^2=364.92, P<0.001; food×age/sex class, df=12, χ^2=11.75, P=0.466). The lack of effect of the interaction variable is consistent with the hypothesis

that the spatial position preference of the age/sex classes did not change markedly when feeding on fruit versus invertebrate foraging. Adult females, subadults, and juveniles had statistically significant spatial position preferences during invertebrate foraging, but only subadults had preferences which differed from random during fruit feeding (G test P values for age/sex class <0.05). These results were likely influenced by the lower number of samples recorded during fruit feeding (fruit feeding N= 1,045, invertebrate foraging N=3,429), and low sample sizes recorded for adult males (fruit feeding N=50, invertebrate foraging N=188). Subadults were less likely to be found in the center and more likely to be found at the back edge of the group when feeding on fruit (front edge, χ^2=5.21, P=0.023; back edge, χ^2=5.99, P=0.014) compared to other age–sex classes. During fruit feeding, it was much more common to record individuals in the center of the group compared to invertebrate foraging (χ^2=115.28, P<0.001). This was either a result of biased data collection or, more likely, a higher density in the group center during fruit feeding.

When feeding on ground litter invertebrates, individuals at the front of the group did not have higher food intake rates (slope estimate=0.000, P=0.994). Three predictor variables had significant effects on invertebrate foraging rates: group size, month, and month squared (Table 2). Invertebrate feeding success was negatively related to group size (slope estimate=−0.019, P=0.003). Invertebrate feeding rates were lowest during the winter (June–August). Winter months are typically colder and invertebrate abundance declines during this period (Di Bitetti 2001a; Beisiegel and Mantovani 2006; Alves-Costa et al. 2004). Spatial position had no effect on invertebrate food intake even during the winter months when fewer invertebrates were available (χ^2=0.229, P=0.632). Invertebrate feeding success was negatively related to group speed, but only if a one-tailed test was used (slope estimate=−0.129, one-tailed P=0.044). Because greater feeding success with increasing group speed was considered highly implausible, it was previously determined that a one-tailed test was appropriate for this effect.

Table 1 Nominal logistic model testing factors which affect the number of samples recorded in each individual spatial position (categorical 1–5)

Variable	df	χ^2	P value
Food (fruit or invertebrate)	4	90.59	<0.001
Age/sex class	12	76.19	<0.001
Food×age/sex	12	11.75	0.466

N=4,474, df=28, R^2=0.026, χ^2=364.92, P=<0.001

Table 2 Results of generalized linear model for factors affecting the food intake of coatis searching for ground litter invertebrates

Variable	df	Slope	Standard error	P value
Month	1	−0.195	0.067	0.004
Month^2	1	0.014	0.005	0.007
Time of day	1	0.000	0.000	0.402
Group speed	1	−0.129	0.076	0.044
Group size	1	−0.019	0.006	0.003
Age/sex	3			
Adult female		0.000	–	–
Adult male		0.106	0.140	0.448
Subadult		−0.128	0.096	0.181
Juvenile		0.045	0.085	0.591
Neighbor density	1	0.031	0.023	0.187
Spatial position (front to back)	1	0.000	0.028	0.994

$N=3{,}429$, $df=10$, $\chi^2 =23.739$, $P=0.008$

Feeding rates differed depending on the species of fruit being eaten (Table 3). Individuals eating fruit had higher intake rates at the front of the group (slope estimate front-to-back$=-0.103$, $P=0.034$). When the interaction of the fruit species and spatial position variables was entered into the generalized linear model, both variables remained significant and the interaction did not, indicating that this pattern of front–back fruit depletion occurred for all eight fruit species. Fruit intake decreased with increasing neighbor density and was positively correlated with larger group size, time of day, and increased group speed (Table 3). Although no differences in fruit intake rates were seen between the different age/sex classes, age/sex classes differed in their use of pindo fruit trees over time (P values for all ANOVAS <0.001) (Fig. 2). Tukey–Kramer analyses were used to investigate pairwise comparisons of all age/sex classes and positive P values indicated significant differences. Juveniles were more likely found feeding in pindo trees than subadults and adult males during the first minute of fruit feeding (Tukey–Kramer paired comparison with adult females $P=0.008$, subadults $P=0.011$, adult male $P=0.057$). The presence of adult females and subadults did not differ during the first minute of pindo feeding ($P=-0.022$). During the second minute, juveniles were present more often than subadults ($P=0.001$) and adult males ($P=0.037$), and adult males were less likely to be present than all other age/sex classes. During minutes 3–4, the only significant difference found was that adult males were less likely to be found feeding on pindo than juveniles. From minute 5–10, no significant differences in the presence of individuals of each age/sex class at pindo trees was found. Tukey–Kramer analyses on the last minute of pindo feeding failed to identify any significant age/sex class differences (negative P values for all comparisons).

Discussion

Invertebrate feeding success

There was no significant relationship between an individual's within-group spatial position and their feeding success on ground litter invertebrates, which may indicate that invertebrates were common enough that coatis were unable to deplete these food resources as they passed over them (Hall and Fedigan 1997). This pattern was even found during the Argentine winter, when invertebrates were less abundant. The negative relationship between group size and invertebrate foraging success may be evidence of invertebrate food depletion in large groups, but this hypothesis is contradicted by the lack of effect of spatial position and neighbor density on invertebrate foraging rates. The lack of a front-to-back depletion effect during invertebrate foraging is different from expected. Field experiments and intensive monitoring of the ground litter invertebrate community are needed to further understand why this pattern was not found.

A potential strategy to avoid conspecific feeding interference during foraging is to travel in a phalanx formation. If a group is spread out further in width than length, individuals may be able to increase the amount of food items encountered, while simultaneously reducing the amount of food depletion from front-to-back of the group (Altmann 1974; Hirsch 2007a). Coati groups rarely traveled in a phalanx formation (15% of all samples), despite spending most of their time foraging for invertebrates. The ability of the groups to form phalanxes may have been impeded by frequent traveling to fruit trees. When groups traveled to fruit trees, they typically sped up before arriving, which often leads to group elongation and a higher density of individuals at the front of the group (Bumann et al. 1997; Pochron 2001; Hemelrijk and Kunz

Table 3 Generalized linear model for factors affecting the food intake of coatis feeding on fruit

Variable	df	Slope	Standard error	P value
Month	1	−0.133	0.153	0.385
Month^2	1	0.000	0.013	0.972
Time of day	1	0.000	0.000	0.070
Group speed	1	0.300	0.127	0.018
Group size	1	0.034	0.014	0.011
Age/sex	3			
Juveniles		0.026	0.127	0.839
Subadults		−0.232	0.162	0.151
Adult females		0	–	–
Adult male	1	0.179	0.242	0.459
Neighbor density	1	−0.045	0.020	0.021
Spatial position (front to back)	1	−0.103	0.048	0.034
Species	7			
Syagrus romanzoffianum		0	–	–
Cecropia pachystachia		−0.425	0.459	0.355
Maclura tinctorea		0.530	0.369	0.151
Ficus sp.		0.747	0.225	0.001
Citrus sp.		−0.782	0.220	<0.001
Crysophyllum gonocarpum		−0.685	0.251	0.006
Hovenia dulcis		0.463	0.187	0.013
Eriobotrya japonica		−0.070	0.360	0.845

$N=1,045$, $df=17$, $\chi^2 =87.481$, $P=<0.001$

2005). Because these fruit tree visits were so frequent, it may have been difficult or impossible for the groups to rapidly switch between a phalanx and an elongated group formation.

Fruit feeding success

Individuals at the front of the group had higher fruit feeding rates than individuals in the back. This effect remained when the species of fruit was controlled for in the generalized linear model, meaning that front-to-back food

Fig. 2 The proportion of individuals of each age/sex class at a target pindo fruit tree per unit of time. Time 1 equals the first minute of arrival at the fruit tree. *Error bars*=±standard error. *N*=number of fruit tree focal samples

depletion was found while foraging on all fruit species. Smaller, more abundant fruits (such as *Hovenia dulcis* and *Ficus* sp.) led to higher intake rates compared to fruits which were larger or more spread out in the tree canopy (*Citrus* sp. and *Crysophyllum gonocarpum*). A negative relationship between neighbor density and fruit intake rate was found, which is consistent with interference or "scramble" competition (van Schaik and van Noordwijk 1988). On the other hand, group size was positively related to individual fruit feeding success (which is not consistent with high scramble competition). The two main study groups almost doubled in size during 2004 (Hirsch 2007b), so it was difficult to separate the effects of group size and year of study. When both year and group size were entered into the generalized linear model, neither variable was significantly related to fruit intake rate. Further data is needed to determine if these patterns are the result of a bumper fruit crop in 2004, or a group size effect.

Within-group spatial position preferences

The four age/sex classes all had different spatial position preferences (Figs. 3 and 4). These preferences did not significantly differ when foraging on fruit compared to invertebrate foraging (see Hirsch 2010a for further details on age/sex class differences). The fruit tree focal samples were a useful double check of the results derived from individual focal samples during fruit foraging and in many
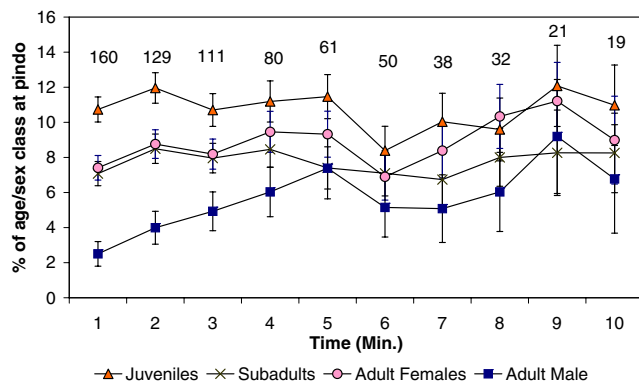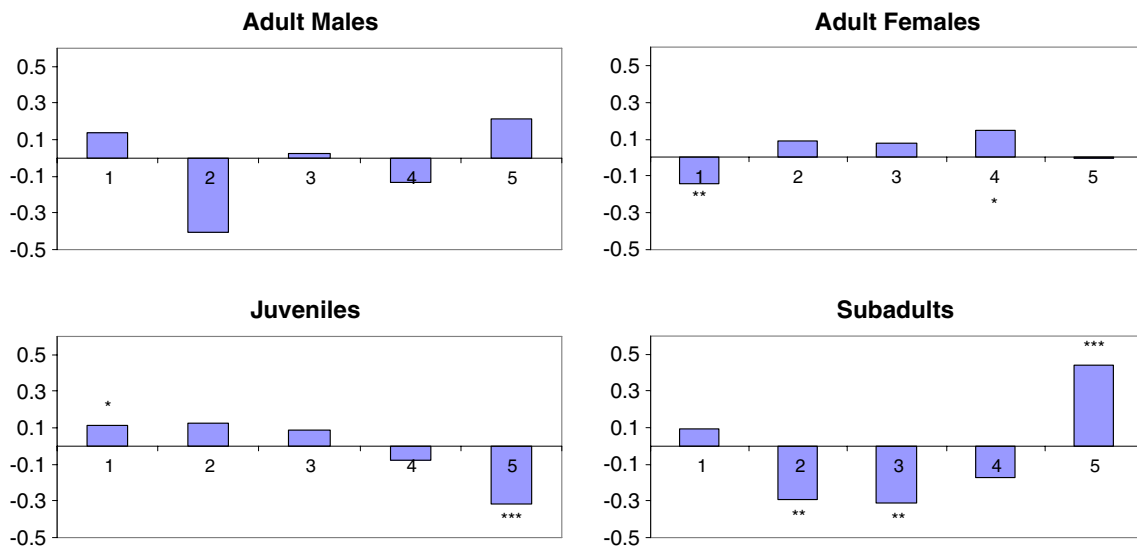
Fig. 3 Deviations from expected values of within-group spatial position when feeding on terrestrial invertebrates during the entire year. Spatial position numbers are continuous with 1=front edge of group 5=back edge of group. *P=<0.05, **P=<0.01, ***P=<0.001. N=3,429. Total model R^2=0.010, df=12, χ^2=110.018, P=<0.001, N= 3,429

cases these two datasets resulted in similar patterns. During periods of invertebrate foraging, juveniles were found to be on the front edge of the group more often than predicted, but not during fruit foraging. Juveniles were over represented during the first 1–2 min at a fruit tree, which indicated that juveniles who were at the front of the group during invertebrate foraging also arrived at fruit trees before other age/sex classes. Although juveniles were not able to increase their invertebrate feeding success when at the front edge of the group, this spatial preference resulted in higher foraging success at fruit trees.

Because juveniles are generally dominant over adult females and subadults during dyadic agonistic encounters, it was predicted that juveniles would be less constrained by social factors than these other age/sex classes (Hirsch 2007b). Given that invertebrate foraging success was similar throughout the group spread, it could be predicted that juveniles should forage in the center of the group during invertebrate foraging, where predation pressure is lowest, and at the front of the group during fruit foraging. This pattern was not found. By locating themselves at the front edge spatial position during invertebrate foraging,
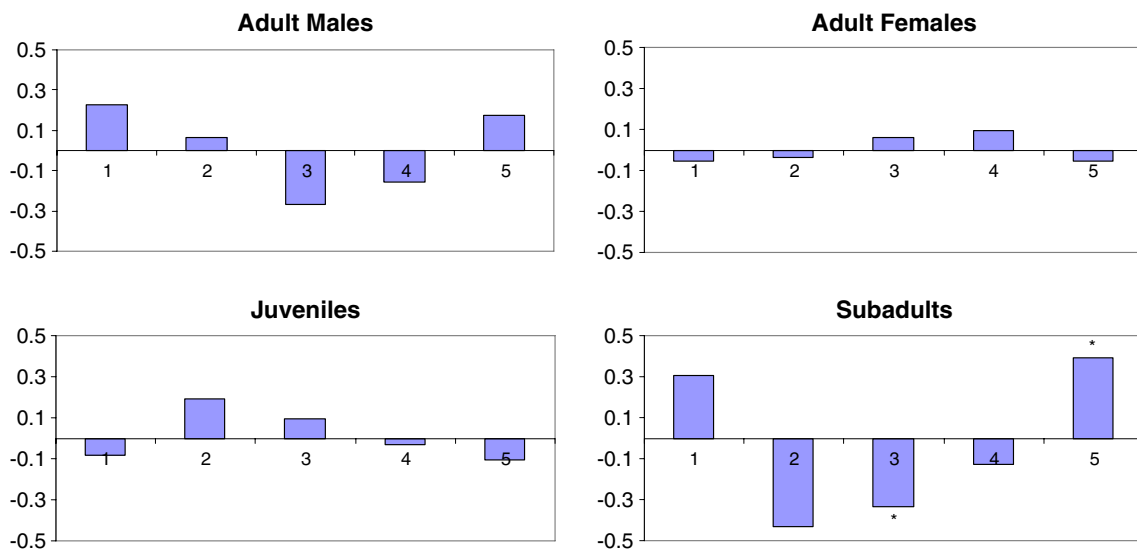

Fig. 4 Deviations from expected values of within-group spatial position when feeding on fruit during the entire year. Spatial position numbers are continuous with 1=front edge of group and 5=back edge of group. *P=<0.05, **P=<0.01, ***P=<0.001. N=1,045. Total model R^2=0.008, df=12, χ^2=26.688, P=<0.001, N=1,045

juveniles were able to arrive first at fruit trees and increase their total fruit intake. This strategy appears to be particularly advantageous if juveniles have no prior knowledge as to when the group will encounter a new fruit tree. However, it is highly likely that coatis know the location of fruit trees before visiting them. Coatis generally travel between fruit trees in straight lines, and increase travel speed before re-visiting fruit trees (Hirsch unpublished data). These patterns are highly consistent with the hypothesis that coatis have prior knowledge of fruit trees (Janson 2000; Pochron 2001; Janson and Byrne 2007). It seems plausible that juveniles could switch their within-group spatial strategies depending on the food source being used. During invertebrate foraging, they could range in the center of the group, then, before arriving at a fruit tree, they could run up to the front of the group to feed before others (Di Blanco and Hirsch 2006; Hirsch 2007a). It appears that the juveniles were not spacing themselves according to this strategy, but instead, consistently foraged near the front edge of the group, despite an increased predation risk in this position (Di Blanco and Hirsch 2006). A possible reason for this seemingly sub-optimal pattern displayed by the juveniles was that fruit trees were so common in the environment, and they were visited so frequently, it always paid to be located at the front of the group. The average distance between fruit trees visited by coatis was 108 m (median=53 m, N=423; Hirsch unpublished data). Coati groups visited on average 17.8 fruit trees per day or one tree every 27 min (Hirsch 2010b). It appeared that the distance between fruit tree visits was generally too short to allow juveniles enough time to switch spatial strategies when using different resources. In many cases, individuals at the front of the group entered a new fruit tree while individuals at the back of the group were still feeding on a previous fruit tree. Paradoxically, juvenile spatial choice during invertebrate foraging appears to be the driving factor which increased their fruit foraging rates.

Because subadults were subordinate to all other age/sex classes, and thus more constrained in their spatial position choices, they were predicted to use a "jumping ahead" strategy. This pattern has commonly been seen in subordinate capuchin monkeys and may allow subordinates to feed upon resources before the arrival of dominant individuals who can monopolize the resources (Janson 1990b; Hirsch 2007a). There is conflicting evidence that subadult coatis used this strategy. There was a trend for subadults to be found more often at the front edge during fruit feeding (χ^2=3.081, P=0.079) and the spatial position data appears to support the hypothesis that subadults were using a bimodal strategy of ranging in either the front edge or the back edge of the group. However, this pattern was not detected during the fruit tree focal samples. Subadults were significantly less likely to be found at pindo trees than juveniles during

the first minute and were not found at pindo trees more frequently during the last minute of feeding. The discrepancy between the fruit tree focal method and the individual focal samples may be the result of a limitation in the focal tree data. Focal tree samples were recorded at 1-min increments, and finer-scale data collection (every 10–15 s) may have been needed to detect other patterns. For example, if a subadult arrived at a fruit tree before the rest of the group, spent 15 s consuming a couple of fruits, and then left upon the arrival of the juveniles and adult females, this behavior might not have been recorded.

Although adult males were found in the front–middle spatial position less often during invertebrate foraging, no statistically significant differences were detected due to low sample sizes (only one male was found in each group). Adult males were consistently underrepresented at fruit trees during the first 4 min. It seemed that adult males did not rush ahead to fruit trees and generally avoided the front position regardless of foraging behavior. Given that adult males were typically the most dominant group members during dyadic interactions, there seemed to be little reason for adult males to avoid a concentrated source of food (Hirsch 2007b). In white-nosed coatis, Gompper et al. (1997) found that adult female coatis in larger groups were able to form coalitions and chase away adult males from fruit tree shadows. Despite adult male dominance, based on dyadic interactions, adult males may have avoided pindo trees to reduce the possibility that multiple individuals would form a coalition to drive them out (Hirsch 2007b). Philopatric adult females may have been less tolerant of adult males compared to adult females, whom are likely related to each other, thus areas of the group with high coati density could have been more of a threat to adult males than adult females.

The relationship between food size and feeding success in relation to within group spatial position was different than expected. Although fruit feeding success was lowest at the back of the group, ground litter invertebrates feeding success was not. This may be evidence that ground litter invertebrates in Iguazu National Park were too abundant to be easily depleted. Given these patterns of feeding success, the distribution of age/sex classes within the group was different than expected as well. The most dominant individuals, adult males and juveniles, were predicted to locate themselves at the front edge of the group during fruit feeding more than other group members. Juveniles were commonly found at the front edge of the group, but adult males were not, and appeared to avoid fruit trees. Because the juveniles were most commonly found in the location in the group with the highest threat of predation, the spatial position preferences of juvenile ring-tailed coatis appear to be more focused on foraging benefits than predation risk. Additionally, social factors such as avoiding aggression may have driven individuals to locate themselves in positions that were suboptimal for obtaining the

highest foraging success possible (Hirsch 2010a). Such social effects may explain why adult males that were dominant during dyadic agonistic encounters, but had few or no allies, chose not to forage in the optimal spatial position for feeding.

Ethical standards This study complied with all laws and regulations of Argentina, the Administración de Parques Nacionales, and ASAB/ABS guidelines for animal welfare.

Conflict of interest The author declares that he has no conflict of interest.

References

Altmann SA (1974) Baboons, space, time, and energy. Am Zool 14:221–248

Alves-Costa CP, Da Fonseca GAB, Christofaro C (2004) Variation in the diet of the brown-nosed coati (Nasua nasua) in Southeastern Brazil. J Mammal 85:478–482

Barta Z, Flynn R, Giraldeau L-A (1997) Geometry for a selfish foraging group: a genetic algorithm approach. Proc R Soc Lond B Biol Sci 264:1233–1238

Barton RA (1993) Sociospatial mechanisms of feeding competition in female olive baboons, Papio anubis. Anim Behav 46:791–802

Beisiegel BM, Mantovani W (2006) Habitat use, home range and foraging preferences of the coati Nasua nasua in a pluvial tropical Atlantic forest area. J Zool 269:77–87

Black JM, Carbone C, Wells RL, Owen M (1992) Foraging dynamics in goose flocks—the cost-of-living on the edge. Anim Behav 44:41–50

Brown AD, Zunino GE (1990) Dietary variability in Cebus apella in extreme habitats: evidence for adaptability. Folia Primatol 54:187–195

Bumann D, Krause J, Rubenstein D (1997) Mortality risk of spatial positions in animal groups: the danger of being in the front. Behaviour 134:1063–1076

Di Bitetti MS (2001a) Home range use by the tufted capuchin monkey (Cebus apella nigritus) in a subtropical rainforest of Argentina. J Zool 253:33–45

Di Bitetti MS (2001b) Food-associated calls in tufted capuchin monkeys (Cebus apella). Ph.D. thesis, State University of New York at Stony Brook

Di Bitetti MS, Paviolo A, De Angelo C (2006) Density, habitat use and activity patterns of ocelots (Leopardus pardalis) in the Atlantic Forest of Misiones, Argentina. J Zool 270:153–163

Di Blanco Y, Hirsch BT (2006) Determinants of vigilance behavior in the ring-tailed coati (Nasua nasua): the importance of within-group spatial position. Behav Ecol Sociobiol 61:173–182

Garber PA, Paciulli LM (1997) Experimental field study of spatial memory and learning in wild capuchin monkeys (Cebus capucinus). Folia Primatol 68:236–253

Giraldeau LA, Caraco T (2000) Social foraging theory. Princeton University Press, Princeton

Gompper ME, Gittleman JL, Wayne RK (1997) Genetic relatedness, coalitions and social behaviour of white-nosed coatis, Nasua narica. Anim Behav 53:781–797

Grant JWA, Girard IL, Breau C, Weir LK (2002) Influence of food abundance on competitive aggression in juvenile convict cichlids. Anim Behav 63:323–330

Hall CL, Fedigan LM (1997) Spatial benefits afforded by high rank in white-faced capuchins. Anim Behav 53:1069–1082

Hemelrijk CK, Kunz H (2005) Density distribution and size sorting in fish schools: an individual-based model. Behav Ecol 16:178–187

Hirsch BT (2007a) Costs and benefits of within-group spatial position: a feeding competition model. Q Rev Biol 82:9–27

Hirsch BT (2007b) Spoiled brats: an extreme form of juvenile dominance in the ring-tailed coati (Nasua nasua). Ethology 113:446–456

Hirsch BT (2009) Seasonal variation in the diet of ring-tailed coatis (Nasua nasua) in Iguazu, Argentina. J Mammal 90:136–143

Hirsch BT (2010a) Within-group spatial position in ring-tailed coatis: balancing predation, feeding competition, and social competition. Behav Ecol Sociobiol. doi:10.1007/s00265-010-1056-3

Hirsch BT (2010b) Tradeoff between travel speed and olfactory food detection in ring-tailed coatis (Nasua nasua). Ethology 116:671–679

Janmaat KRL, Byrne RW, Zuberbuhler K (2006) Evidence for a spatial memory of fruiting states of rainforest trees in wild mangabeys. Anim Behav 72:797–807

Janson CH (1986) The mating system as a determinant of social evolution in capuchin monkeys (Cebus). In: Else JS, Lee PC (eds) Primate ecology and conservation. Cambridge University Press, New York, pp 169–179

Janson CH (1990a) Social correlates of individual spatial choice in foraging groups of brown capuchin monkeys, Cebus apella. Anim Behav 40:910–921

Janson CH (1990b) Ecological consequences of individual spatial choice in foraging groups of brown capuchin monkeys, Cebus apella. Anim Behav 40:922–934

Janson CH (1996) Towards an experimental socioecology of primates: examples from Argentine brown capuchin monkeys (Cebus apella nigritus). In: Norconk MA, Rosenberger AL, Garber PA (eds) Adaptive radiations of Neotropical primates. Plenum, New York, pp 309–325

Janson CH (1998) Experimental evidence for spatial memory in foraging wild capuchin monkeys, Cebus apella. Anim Behav 55:1229–1243

Janson CH (2000) Spatial movement strategies: theory, evidence, and challenges. In: Boinski S, Garber PA (eds) On the move: how and why animals travel in groups. University of Chicago Press, Chicago, pp 165–203

Janson CH, Byrne R (2007) What wild primates know about resources: opening up the black box. Anim Cogn 10:357–367

Janson CH, Di Bitetti MS (1997) Experimental analysis of food detection in capuchin monkeys: effects of distance, travel speed, and resource size. Behav Ecol Sociobiol 41:17–24

Krause J (1993) The relationship between foraging and shoal position in a mixed shoal of roach (Rutilus rutilus) and chub (Leuciscus cephalus)—a field study. Oecologia 93:356–359

Krause J, Bumann D, Todt D (1992) Relationship between the position preference and nutritional state of individuals in schools of juvenile roach (Rutilus rutilus). Behav Ecol Sociobiol 30:177–180

McCormick JE, Jablonski PG, Brown JL (2007) Producer-scrounger roles and joining based on dominance in a free-living group of Mexican jays (Aphelocoma ultramarine). Behaviour 144:967–982

O'Connell CP (1972) The interrelationship of biting and filter feeding activity on the northern anchovy (*Engraulis mordax*). J Res Fish Board Canada 29:285–293

Pochron ST (2001) Can concurrent speed and directness of travel indicate locational knowledge in free-ranging yellow baboons (*Papio h. cynocephalus*) of Ruaha National Park, Tanzania? Int J Primatol 22:773–785

Robinson JG (1981) Spatial structure in foraging groups of wedge-capped capuchin monkeys *Cebus nigrivittatus*. Anim Behav 29:1036–1056

Romey WL, Galbraith E (2008) Optimal group positioning after a predator attack: the influence of speed, sex, and satiation within mobile whirligig swarms. Behav Ecol 19:338–343

Rowcliffe JM, Pettifor RA, Carbone C (2004) Foraging inequalities in large groups: quantifying depletion experienced by individuals in goose flocks. J Anim Ecol 73:97–108

Schoener TW (1981) An empirically based estimate of home range. Theor Popul Biol 20:281–325

Stahl J, Tolsma PH, Loonen MJJE, Drent RH (2001) Subordinates explore but dominants profit: resource competition in high Arctic barnacle goose flocks. Anim Behav 61:257–264

van Schaik CP, van Noordwijk MA (1986) The hidden costs of sociality: intragroup variation in feeding strategies in Sumatran long-tailed macaques (*Macaca fascicularis*). Behaviour 99:296–315

van Schaik CP, van Noordwijk MA (1988) Scramble and contest in feeding competition among female long-tailed macaques (*Macaca fascicularis*). Behaviour 105:77–98

Vogel E, Janson CH (2007) Predicting the frequency of food related agonism in white-faced capuchin monkeys (*Cebus capucinus*), using a novel focal tree method. Am J Primatol 69:533–550