



Original Article

Interindividual spacing affects the finder's share in ring-tailed coatis (*Nasua nasua*)

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Received 24 April 2019; revised 15 August 2019; editorial decision 13 September 2019; accepted 27 September 2019; Advance Access publication 23 October 2019.

Social foraging models are often used to explain how group size can affect an individual's food intake rate and foraging strategies. The proportion of food eaten before the arrival of conspecifics, the finder's share, is hypothesized to play a major role in shaping group geometry, foraging strategy, and feeding competition. The variables that affect the finder's share in ring-tailed coatis were tested using a series of food trials. The number of grapes in the food trials had a strong negative effect on the finder's share and the probability that the finder was joined. The effect of group size on the finder's share and foraging success was not straightforward and was mediated by sociospatial factors. The finder's share increased when the time to arrival of the next individual was longer, the group was more spread out, and the finder was in the back of the group. Similarly, the total amount of food eaten at a trial was higher when more grapes were placed, arrival time was longer, and the number of joiners was smaller. Individuals at the front edge of the group found far more food trials, but foraging success was higher at the back of the group where there were fewer conspecifics to join them. This study highlights the importance of social spacing strategies and group geometry on animal foraging tactics and the costs and benefits of sociality.

Key words: coati, *nasua*, producer-scrounger, Social foraging, within-group spatial position.

INTRODUCTION

In many animals, gregariousness leads to increased feeding competition, while simultaneously reducing predation risk (Krause and Ruxton 2002). Within cohesive social groups, food intake rates can vary according to age/sex class, dominance status, within-group spatial position, foraging strategy, and a variety of other factors (Janson 1990a, 1990b; Black et al. 1992; Altmann 1974, 1998; Hirsch 2007a, 2011a, 2011b; King et al. 2009). By understanding how these factors influence an individual's food intake rate, researchers can better understand the mechanisms that drive sociality and varying social systems. Most current social foraging models focus on how group size affects individual food intake rates and foraging strategies (Giraldeau and Caraco 2000). However, the manner by which group size mediates foraging strategies via group spread, interindividual distances, and joining times is unclear in most study systems. The primary aim of this article is to determine the spatial mechanisms by which group size affects social foraging.

Increasingly, individual foraging strategies have been modeled using game-theoretical approaches (Barnard and Sibly 1981; Vickery et al. 1991; Ranta et al. 1996; Ruxton et al. 2005). In particular, a growing body of work has used producer–scrounger models in which animals can either search for food or join conspecifics who have found food (which can also be termed finders and joiners; see also Caraco and Giraldeau 1991; Ranta et al. 1996). When an animal finds a patch of food, it typically consumes a fraction of the resource before the arrival of another group member, which is defined as the “finder's share.” As the finder's share increases, the frequency of scroungers in a group is predicted to decline and the proportion of producers is predicted to increase (Giraldeau and Caraco 2000). This proportion is hypothesized to play a major role in shaping group geometry, feeding competition, and competitive regimes (Barta et al. 1997; Giraldeau and Caraco 2000; Di Bitetti and Janson 2001; Dubois and Giraldeau 2004). The finder's share and size of resource patches are particularly important factors in the evolution of competitive regimes and kleptoparasitism. When food patches are small, they are often consumed before the arrival of a conspecific; thus, the finder's share is essentially 100%, and it is generally not possible to compete aggressively

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over food (Dubois et al. 2003; Dubois and Giraldeau 2004). When food items are larger, the ability to compete over food depends on a combination of the finder's share, competitive inequalities between group members, food dispersion, group geometry, and the ability to monopolize food (Di Bitetti and Janson 2001; Hirsch 2007a; King et al. 2009).

Giraldeau and Caraco (2000) note that the distance between individuals, group spread, foraging area, and food detectability are likely to be important factors that influence social foraging, yet few authors have incorporated interindividual spacing into foraging models. To address these questions, a series of feeding trials were conducted using wild groups of ring-tailed coatis (*Nasua nasua*) feeding on patches of introduced fruit. Coatis represent a useful model to study social foraging strategies because their interindividual spacing is highly variable; thus, they have the opportunity to discover food both close to and far away from conspecifics (Gompper 1996; Hirsch 2011a, 2011b; Hirsch and Gompper 2017). Coatis mostly travel on the ground, are easily observed at close distance, and can be videotaped with no effect on their behavior. A series of predictions concerning the outcome of the coati feeding trials was made based on previous empirical and theoretical work:

1. The amount of food available in a patch will be negatively related to the finder's share (Giraldeau and Caraco 2000). For example, if an animal always eats 5 food items before the arrival of a conspecific (regardless of all other factors), the finder's share would be 100% for a patch of 5 food items and 5% for a patch of 100 items.
2. Group size and the finder's share should be negatively related (Giraldeau and Livoreil 1998). The group size effect should occur because as the number of potential joiners in a group increases, the chance that the finder will be joined, or joined more quickly, will increase (Di Bitetti and Janson 2001; Flynn and Giraldeau 2001).
3. The total amount of food consumed by the finder should be negatively affected by the number of individuals that arrive at the food trial and the speed at which they arrive (Giraldeau and Caraco 2000).
4. Individuals at the front edge of the group will discover more food trials (Barta et al. 1997; Hirsch 2010), but should have lower overall foraging success if they are joined by higher numbers of conspecifics.

METHODS

Study area and species

The study was conducted in 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, 2001b). Observations and feeding trials were conducted on 2 study groups (PQ and PSG). Ring-tailed coati groups generally consist of adult females and their offspring (juveniles = 0–12 months of age, subadults = 12–24) (Hirsch 2007c; Hirsch and Gompper 2017; Hirsch and Maldonado 2011) and each group in this study contained one adult male (Hirsch 2011c). During 2004, the subadults (individuals between 1 and 2 of age) in the PQ broke off and formed their own subgroup (3–6 individuals). To increase the sample size for small groups, the PQ subadult subgroup and temporary foraging subgroups were used in the trials whenever

possible (PQ juveniles $n = 5$ trials, PQ $n = 69$, PSG $n = 90$). In general, the PQ and PSG groups foraged cohesively and the average length and width of small groups (between 8 and 15 individuals) was $16.83 \text{ m} \times 11.67 \text{ m}$ and large groups (25–31 individuals) $28.87 \text{ m} \times 17.10 \text{ m}$ (Hirsch 2011b). Group sizes remained relatively stable within a given year (PQ 2003 = 15, 2004 = 25–31; PSG 2003 = 9–12, 2004 = 25–27) (Hirsch 2007b, 2009). In one case, the PQ group was joined by the PQ subgroup, leading to a group of 35 individuals.

One to three adult females per group were fitted with radio-collars to help locate the groups. Coatis were captured using $32 \times 10 \times 12$ inch Tomahawk or similar traps, anesthetized, and either fitted with radio-collars or given multi-colored plastic eartags for individual identification (Dalton Rototags). Eartags were placed on juveniles older than 4 months of age, and we were able to recognize all individuals during the food trials. This study complied with all institutional, national, and ASAB/ABS guidelines for animal welfare. Local permission was granted from Argentina National Park service and animal handling procedures were approved by the SUNY Stony Brook Institutional Animal Use and Care Committee (IACUC# 20021175).

Groups of coatis were usually habituated within 2–3 weeks. Habituated coatis would allow observers to silently walk within 2 m of a focal animal. It did not appear that the coatis changed their foraging and travel behavior due to being observed, with the exception of startle reactions to occasional accidental loud noises made by the observers (such as loudly breaking a branch). If a food item such as a pindo palm fruit (*Syagrus romazoffianum*) was encountered within $<1 \text{ m}$ of an observer, the coatis would approach the food (even if the fruit was below the boot of an observer).

Coatis spent 70% or more of their foraging time searching for ground litter invertebrates, with the remaining foraging time spent foraging for fruit (Hirsch 2009). This behavior of searching for widely distributed small food items, punctuated by larger clumped food sources influences the movement behavior of the coatis (Hirsch et al. 2013). When coatis detect a fruit patch, they typically speed up and run directly to the food patch, presumably to consume as much food as possible before conspecifics arrive (Hirsch 2010). Agonistic interactions are more commonly seen during fruit feeding compared with other activities, and subordinate individuals (especially subadults) were sometimes excluded or driven away from the grape trials (Hirsch 2007b, 2007c, 2009).

Trials

Feeding trials were conducted using medium-sized green table grapes, and methods were previously described in Hirsch (2010). For most trials, between 5 and 100 (5, 10, 20, 50, or 100) grapes were placed in a 1 m^2 area on the forest floor. For the 100 grape treatments, fruit were placed in 30 cm^2 , 70 cm^2 , 1 m^2 , and 2 m^2 areas for a concurrent study of feeding competition ($n = 47$ trials that were larger or smaller than 1 m^2). When coatis fed on the most common native fruit species in Iguazu, pindo palms, they consumed an average of 98.80 fruits per group visit (Hirsch 2009); thus, the 100 grape trials are most similar to what coatis experience in nature. The major difference is that coatis often remember the location of fruit trees (Hirsch et al. 2013). This prior knowledge of food resources leads to cases that are by definition not able to generate producer–scrounger tactics. However, when trees produce fruit unpredictably, or when the first fruits of the season are available, coati social foraging patterns should resemble the 100 grape trials.

A DVC video camera was set up on a portable tripod approximately 2.5 m from the trial site. Feeding trials were always conducted with 2 or more observers who communicated with radios and hand signals. One observer would stay with the group, whereas the other arranged the fruit and video camera. When a group approached within 25 m of the trial, the researcher walking with the coatis stopped in a location where they could see the coatis closest to the trial, whereas the other researcher remained near the trial and started the video camera. In order not to disturb the coatis during the detection process, both researchers tried to remain stationary or walk as softly as possible. When coati groups approached the trial, both observers carefully watched the behavior of the coatis nearest to the site. The observers would often coordinate their observations to track the individuals that were in the best positions to discover the site. To prevent the coatis from cuing on the sight of the tripod or the sound of the radios, we regularly used both outside the context of the feeding trials. If the coatis were using the sight or sound of the tripod setup as a cue, we would have expected that coatis would approach tripods during nontrial periods. We never observed coatis approach the tripod, and the changes in travel direction and sniffing behavior observed during the trials were only witnessed in the presence of fruit or other food (Hirsch 2010).

Coatis regularly find food by olfaction, and not by sight (Hirsch 2010). The behaviors associated with olfactory food detection allowed us to pinpoint the distance at which coatis detected the feeding trials, and what factors influenced food discovery (Hirsch 2010). Although we were able to observe the finder's discovery readily, the method by which joiners found food items was not regularly observed, and is not discussed in this manuscript. Coatis do not emit food calls. It is the impression of the authors that the joiners used 3 cues to find the trials: 1) visual detection of the finder eating the grapes, 2) olfactory detection of the trial (with and without visual confirmation of the finder's presence), and 3) auditory information. The last method seemed to coincide with periods of loud fighting. It appeared that the likelihood of further joiners detecting the trial was much greater following periods of loud fighting at the trial site, although this remains to be confirmed.

The observers recorded several variables in conjunction with the trial discoveries, including the identity and spatial position of the finder, and the distance from the finder to its nearest neighbor. Additional group-level factors recorded were the group length and width, and the distance of the trial to the group center (at the time of arrival of the finder). The group length and width were estimated visually by the 2 observers. Once the location of the group edges was determined by both observers, the lead author visually estimated the group width and length, and the accuracy of visual estimations was regularly compared to distances measured with measuring tape. All other distances were measured using a 50-m fiberglass tape after the trial was completed. The group spread estimates were double checked when measuring the distance between the trial and group center. When the detection distance was subtracted from this latter number, the resulting number should have been close to the radius of the group, which was the case during all trials. The activity and speed of the finder and group were recorded whenever possible. Fine-scale behavioral categories were condensed into 2 categories: feeding/foraging or traveling. Speed was measured on a scale of 1–4 in the same manner as Hirsch (2010).

The authors later watched the recorded tapes to determine the number of grapes which the finder ate before the arrival of a conspecific (the finder's share), whether a finder was joined, and if so, the time to arrival of the finder. All videos were annotated using

Behavioral Observation Research Interactive Software (BORIS) (version 3.41, Friard and Gamba 2016). All times were rounded to the nearest second. The number of grapes eaten by the finder and other group members throughout the feeding trials and the total number of individuals in the group who visited the trial while grapes were still on the ground was also transcribed from the trial videos.

The spatial position of the finder was recorded in the same manner as Janson (1990a, 1990b). The group spread was visually divided into 3 concentric circles: 1) center, 2) middle, and 3) edge. The coati's location within these circles was then further subdivided into 12 positions based on the numbers 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 5 spatial position categories (as in Janson 1990a, 1990b); 1) front edge, 2) front middle, 3) center, 4) back middle, and 5) back edge (Figure 1). A total of 185 trials were conducted, but due to missing data for some variables, incomplete videos, or incomplete trials, we used a subset of 164 complete trials for analysis. Of the associated variables, the nearest neighbor to the finder was sometimes impossible to record ($n = 25$); thus, the sample size on analyses with the nearest neighbor had lower sample sizes.

Statistical methods

All data were entered into the STATISTICA statistical program (version 5.5, TIBCO Software Inc. 2017). Generalized linear models were run with up to 8 independent variables without interaction variables (the all subsets approach). Best subsets models were chosen based on the lowest Δ AIC values (Symonds and Moussallii 2010). Dependent variables were identity, probit, or logit linked as appropriate for the variable (Tables 1 and 2; Supplementary Tables S2–S4). The first analysis used the finder's share as the dependent variable, with distance to nearest neighbor, distance to group center, group length and width, spatial position of finder, group size, grape density, and the number of grapes (log transformed) as the independent variables. Because the number of trials detected in the center and middle positions was low (Hirsch 2010), the spatial position variable was treated as a continuous variable with one being the front edge of the group and 5 the back edge. Trials with no joiners were excluded from the finder's share analyses. Additional generalized linear model (GdLM) analyses used the number of

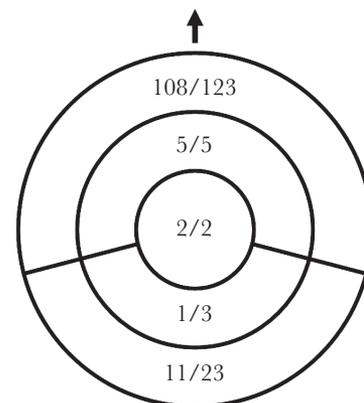


Figure 1 Number of discoveries when the finder was joined by a conspecific divided by the total number of discoveries per spatial position. The top of the figure represents the direction of group movement.

grapes eaten by the finder, the proportion of total grapes eaten by the finder, number of individuals that arrived at the trial, and the presence or absence of a conspecific joiner as dependent variables (with the previously listed variables entered as independent variables when appropriate). The last analysis used the complete dataset that included trials when the finder was not joined. The inclusion of variable interactions did not change the resultant best subsets models in any analysis.

RESULTS

All 5 best subset models identified by the Akaike analyses were significant overall ($P < 0.001$) and highly correlated predictor variables were excluded from being entered into the same model (Supplementary Table S1). Variance inflation factors for individual variables ranged from 1.03 to 1.96. The finder's share was higher when there were fewer grapes, the time to conspecific arrival increased, the nearest neighbor was further away, group length was longer, group size smaller, when the finder traveled slower, and when the finder was in the back of the group (Table 1). The average finders share was 4.9 grapes, or 15.4% of available food ($n = 133$), and finders ate roughly 3 times more grapes than later arrivals (finders = 15.9 grapes, joiners = 4.5, $n = 164$, $t = 13.56$, $P < 0.001$). The total amount of grapes eaten by the finder at a trial was positively correlated with the number of grapes and the time to arrival of the next conspecific, and negatively related to the number of individuals that arrived at the food trial (Table 2). Similar results were found when the proportion of grapes eaten was entered as the independent variable (Supplementary Table S2). Even after subtracting the finder's share of grapes, finders ate more grapes than later arrivals (8.4 vs. 5.6 grapes, $n = 164$, $t = 9.34$, $P < 0.001$). The

Table 1
Generalized linear model for factors affecting the finder's share

	df	Estimate	χ^2	Standard error	P
Number of grapes (log)	1	-1.007	83.683	0.137	<0.001
Time to joiner	1	0.011	44.785	0.002	<0.001
Finder's speed	1	-0.848	33.470	0.173	<0.001
Group length	1	0.036	24.295	0.007	<0.001
Group size	1	-0.061	22.003	0.014	<0.001
Spatial position	1	0.163	6.189	0.064	0.013
Distance to group	1	-0.025	4.665	0.012	0.031

Finder's share was normally distributed and logit linked in the model ($n = 119$).

Table 2
Generalized linear model for factors affecting the total number of grapes eaten by the finder

	df	Estimate	χ^2	Standard error	P
Number of grapes (log)	1	7.753	114.803	0.559	<0.001
Time joined	1	0.092	44.507	0.012	<0.001
Number of coatis at trial	1	-0.791	38.176	0.118	<0.001
Group size	1	0.163	4.123	0.079	0.042
Group activity	1	1.308	2.023	0.916	0.155
Finder's speed	1	0.592	0.611	0.757	0.434
Distance to group	1	-0.011	0.029	0.065	0.865

Number of grapes eaten was normally distributed and identity linked in the model ($n = 125$). Group activity estimate indicates the number of grapes eaten increased during foraging compared with group travel.

number of individuals to arrive at a trial was positively correlated with the number of grapes and number of individuals in the group, and negatively correlated with the time until the first joiner arrived and group travel behavior (Supplementary Table S3).

Whether or not a finder was joined by a conspecific was positively correlated with the number of grapes and negatively related to the distance to the nearest neighbor, being located at the back of the group, and group travel (Supplementary Table S4). The average time between the finder's arrival and the arrival of a joiner was 21.23 s (± 38.04 SD). Whether an individual was joined or not had a large influence on the amount of grapes eaten. Finders who were not joined ate more grapes (21.3 ± 13.72 SD) than those that were joined (14.7 grapes ± 11.02 SD, $df = 1$, $F = 8.605$, $P = 0.004$). The total amount of time needed to consume all grapes in the trials was longer when an individual was never joined by a conspecific (solo visits – average 104.5 ± 84.9 SD, multiple individuals – average 158.6 ± 99.0 SD).

Food trials were far more likely to be discovered at the front edge of the group than the back edge ($n = 156$, $F = 8.237$, $P = 0.005$, Figure 1). The front of the group generally contains a higher density of individuals, and the average number of individuals within 3 m of a focal animal was almost twice as high in the front of the group (front edge = 1.50, back edge = 0.88, $n = 124$, $F = 19.90$, $P < 0.001$). As the number of individuals in a particular spatial position increases, so does the number of potential joiners in close proximity. Although spatial position was not a significant predictor variable of the proportion of grapes eaten in the GdLM models, finders at the back edge ate an average of 17.2 (47.1%) of the trial grapes compared with 14.3 (35.0%) of grapes at the front edge (Figure 2, $n = 144$, $F = 8.726$, $P = 0.004$). This difference was in part due to variation in the chances of being joined. Of the 123 trials which were discovered by front edge individuals, all but 15 finders were joined by conspecifics (87.8%), compared with less than half of the finders in the back periphery (11 of 23 = 48%, $n = 144$, $F = 23.584$, $P < 0.001$).

DISCUSSION

The number of grapes used in the trials had a large negative effect on the finder's share. As the number of grapes increased, the finder was able to eat a proportionally smaller amount of the total before the arrival of a conspecific, which is consistent with studies in other animals (Giraldeau and Caraco 2000; Hansen et al. 2016; Kok et al. 2017). In addition, the probability of being joined ranged from 65.0% when only 5 grapes were placed, to 88.9% when 100 grapes were placed. This result makes sense because the probability of being joined should increase as the time spent feeding increases,

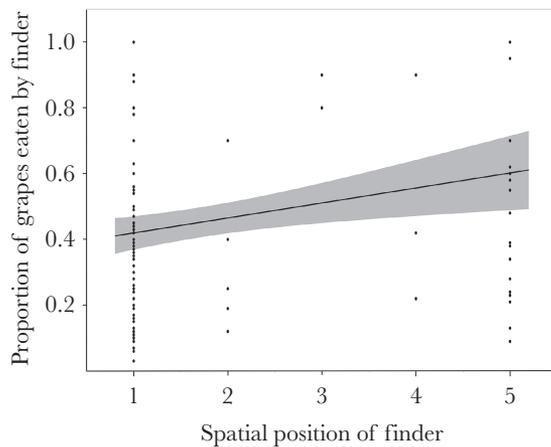


Figure 2

Proportion of grapes eaten by the finder for the duration of the food trial by spatial position of the finder ($n = 156$, $F = 8.2372$, $P = 0.005$, $R^2 = 0.051$).

which in turn increases with the number of fruit in the patch. The total proportion of grapes eaten by the finder during the duration of the food trial decreased as the number of grapes increased. These results suggest that the payoffs to being a finder or a joiner depend strongly on the amount of food in a patch (Giraldeau et al. 1990; Giraldeau and Livoreil 1998).

In many producer–scrounger models, it is assumed that food eaten before being joined (i.e., the finder's share) is the primary benefit of finding a new food source. In this study, we found that finders ate almost 3 times the number of grapes than the average joiner, and almost twice as many grapes as conspecifics *after* being joined. We believe that this is a result of the timing of the arrival of joiners. If all joiners arrived at the same time, the foraging success of the producer post-joining should be roughly equal to the joiners. If conspecifics arrive at a food site in a staggered manner, each individual will have a different amount of time at the food source for feeding, and food intake rate should be closely related to the amount of time spent at the food patch (Beauchamp 2008). This result suggests that a more appropriate measure of the finder's advantage may need to include post-joining feeding rates (see Beauchamp 2014).

The behavior and speed of the finder and coati groups generally did not have significant effects on the finder's share or amount of food eaten by the finder once other variables were controlled for. Finders that were traveling faster did have smaller finder's shares, but the reason for this effect is unknown. Coatis that travel faster generally have more difficulty discovering food sites (Hirsch 2010), but this should not affect their finder's share. Faster travel speed of individuals is correlated with faster group travel (Supplementary Table S1), but group travel speed was not a significant predictor variable in the finder's share model.

Group size was negatively correlated with the finder's share and positively correlated with the probability that a finder would be joined by a conspecific, which has been found in previous studies (Giraldeau and Caraco 2000). However, the total amount of food eaten by the finder was weakly positively correlated with group size after controlling for other factors (Table 2). This paradoxical result is due to other variables playing a stronger role in determining the amount of food eaten by the finders. Both the finder's share and the amount of food eaten by the finder were more strongly influenced by the time to arrival of the second individual. The total

amount of grapes eaten by the finder was also heavily influenced by the total number of individuals that arrived at the food trial. Individuals that were further away from their nearest neighbor and located at the back of the group were less likely to be joined at a trial (Supplementary Table S4), and when they were joined, the time to arrival was positively correlated with the nearest neighbor distance ($n = 111$, $F = 21.7$, $P \leq 0.0001$, $R^2 = 0.167$). These results indicate that foraging away from other group members can increase an individual's finder's share (DiBitetti and Janson 2001; Flynn and Giraldeau 2001). In a similar manner, finder's shares were larger when the length of the group was longer. As groups become more elongated, the density of individuals, especially at the front of the group, should thin out, thus leading to fewer conspecific joiners at the front edge of the group.

Traditional producer–scrounger models have primarily focused on the effects of group size, but the results here indicate that interindividual spacing and group geometry are the likely mechanisms driving group size effects (see Flynn and Giraldeau 2001; Beauchamp 2008). The time to arrival of the second coati was the strongest predictor variable (other than the number of grapes) of the finder's share and grapes eaten by the finder. Given that the distance to nearest neighbor and time to arrival are highly correlated ($n = 113$, $F = 53.3$, $P \leq 0.0001$, $R^2 = 0.324$), individuals that are located away from other group members should have increased food intake, which is consistent with other studies (Di Bitetti and Janson 2001; Carbone et al. 2003; Hirsch 2011b). This study supports the hypothesis that interindividual spacing and within-group spatial position may be a more important driver of behavioral decisions than group size, which has also been seen in other behavioral contexts such as feeding and vigilance (Lima and Zollner 1996; Stillman et al. 2000; Blumstein et al. 2001; Hirsch 2002; Fernandez-Juricic et al. 2007; Treves 1998). Given the central importance of group size in several foundational theories of behavioral ecology (Krebs and Davies 1996; Giraldeau and Caraco 2000; Krause and Ruxton 2002), the results found here that group size effects are mediated through interindividual spacing have important implications on the theoretical underpinnings of animal behavior.

Coatis at the front edge of the group were more likely to discover food trials and be joined by conspecifics after they found the grapes (Figure 1). This is consistent with previous studies showing that producers are more likely to be located at the front of the group (Flynn and Giraldeau 2001; Monus and Barta 2008; King et al. 2009). Individuals at the back of the group were located over twice as far from their nearest neighbors as individuals at the front of the group (front edge average neighbor distance = 3.29 m, back edge = 7.61 m). This decrease in animal density at the back edge of the group can help explain why individuals on the front edge of the group had smaller finder's shares than individuals at the back of the group. Finders at the front of the group ate a smaller proportion of grapes than finders at the back of the group (Figure 2); however, spatial position was not a significant predictor variable in the GdLM model (Table 2). Although the amount of food eaten when the finder was located in the back of the group was greater than the front, the greater than 5 times increase in discovery rate at the front of the group combined with the almost 3-fold increase in total grapes eaten by the finder resulted in the front edge of the group being the best location for food intake.

To fully understand constraints on social foraging strategies, it is also important to understand the costs and benefits of spacing in relation to predation and agonism (King et al. 2009). Previous work on these coati groups has shown that vigilance levels rise when

coatis have fewer neighbors and are in the front edge spatial position (Di Blanco and Hirsch 2006). These patterns indicate that individuals who choose to forage away from others to increase food intake are simultaneously increasing their risk of predation (Romey 1995, 1997; Hirsch and Morrell 2011; Ioannou et al. 2019). Adult males are larger than other age/sex classes, and presumably safer from predation (Gompper 1996); thus, it could be predicted that they should be more likely to be located at the front of the group. However, this is not the case, and the age/sex class most likely to be located in the front of the group were juveniles who are presumably at the highest risk of being predated (Hirsch 2011a, 2011b). It has previously been assumed that the need for juvenile coatis to obtain food for quick growth outweighs their risk of predation at front edge spatial positions (Hirsch 2011a, 2011b). Dominance relations can also constrain where individuals are able to locate themselves within the group (Ron et al. 1996; Hemelrijk 1998, 2000; Hirsch 2007c; Hirsch et al. 2012). Subadult ring-tailed coatis are subordinate to other age/sex classes and are regularly driven away from juveniles and feeding patches. These subadults are more likely to be located at the back edge of the social group (Hirsch 2011a, 2011b). The results here indicate that subordinate individuals choose peripheral spatial positions not as an alternate tactic to gain access to more food, but to avoid receiving aggression from dominant individuals.

To date, a few studies have used spatially explicit foraging models to understand producer–scrounger payoffs (e.g., Rands et al. 2004, 2006; Beauchamp 2008). Barta et al. (1997) used individual-based modeling to predict that finders (or producers) will be preferentially located at the group periphery. This and other studies are consistent with this prediction (Di Bitetti and Janson 2001; Flynn and Giraldeau 2001; Monus and Barta 2008; King et al. 2009). Similarly, Beauchamp (2008) predicted that the finder's share should be smaller when forager density is higher, a pattern also found in this study. A major advantage of using individual-based models is that spatial factors can be incorporated into the model (food detection distance, neighbor distance, and predation threat). Because the group size effects on social foraging variables are largely mediated through spatial factors, as shown in this study, individual-based models may be a more biologically realistic method for understanding the costs and benefits of sociality than game-theoretical models that do not incorporate important biological phenomena.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

FUNDING

This study was funded in part by an NSF grant (BCS-0314525).

We thank Santiago Escobar, Carolina Ferrari, Mauro Tamone, and Fermino Silva for help and assistance during the course of the fieldwork. We also thank Viviana Muñoz for her veterinary assistance. We are particularly grateful to Charles Janson for the immeasurable amount of advice he provided during all aspects of this project and letting us borrow several pieces of much-needed field equipment. We are also very thankful for the consistently helpful comments and advice from Mario Di Bitetti. This article has benefited tremendously thanks to comments by Charles Janson, Mario Di Bitetti, Andreas Koenig, and 4 anonymous reviewers. We thank the Argentina National Park for permission to carry out work in Iguazu.

Data accessibility: Analyses reported in this article can be reproduced using the data provided by Hirsch et al. (2019).

Handling Editor: Andrea Griffins

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