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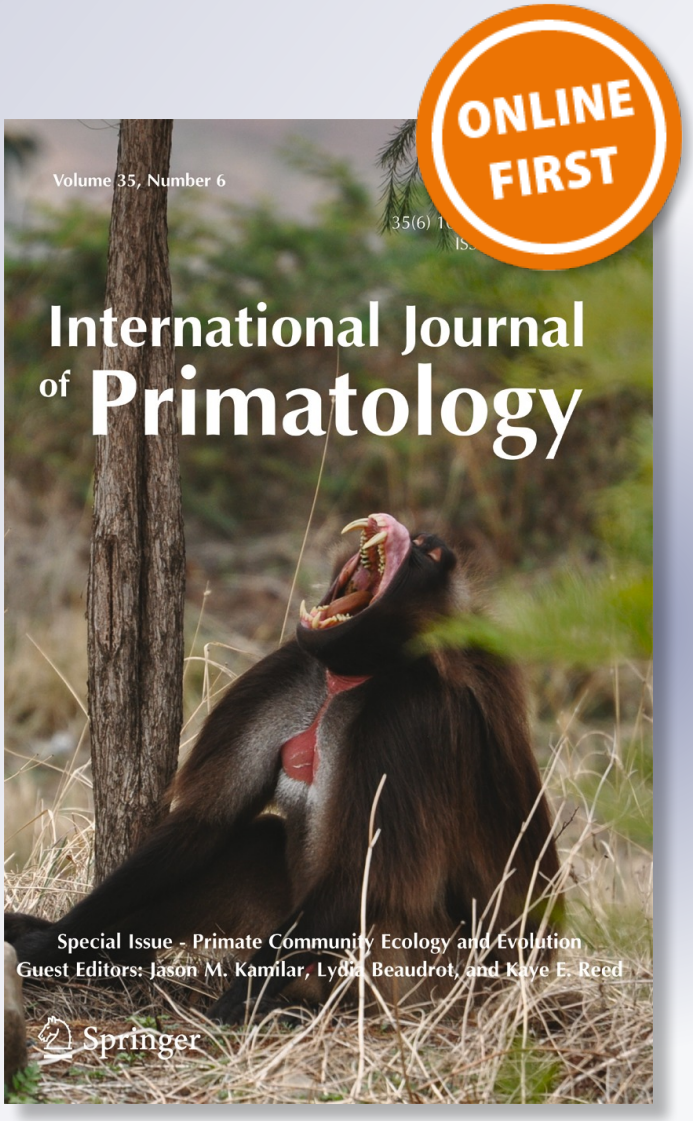

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Vervet (*Chlorocebus pygerythrus*) Intragroup Spatial Positioning: Dominants Trade-Off Predation Risk for Increased Food Acquisition

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Abstract The costs and benefits of group-living are not distributed evenly among group members. Individuals that maintain positions on the front, outside edge of the group encounter most predators first, but are more likely to access food patches before others. Therefore a trade-off exists in which a strategy maximizing safety, by staying in the group's center, may lower foraging success, whereas a strategy maximizing food acquisition may increase predation risk. We examined intragroup spatial positions for vervets (*Chlorocebus pygerythrus*) at Lake Nabugabo, Uganda relative to sex, age, dominance rank, and activity when the group was moving and when it was stationary. We used artificial food patches of varied richness to examine which individuals found new food sources and what share they obtained. When the group was stationary, high-ranking females tended to be at the group's center, while males and subordinates were at the group's edge. Moving and feeding occurred more than expected at the edge, while social behavior took place in the center. When the group was moving, most females stayed in the center of the group, but dominant males and the alpha female foraged at the front, outside edge of the group. These dominants also found more artificial food patches and foraged at greater interindividual distances than those in the center. Whether they found patches or scrounged at the patches found by others, high-ranking individuals obtained more food than subordinates, but their overall share was

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greatest when they acted as producers rather than scroungers. This likely explains why dominant individuals traded off predation risk for food acquisition by consistently foraging on the front, outside edge of the group farther from conspecifics.

Keywords *Chlorocebus pygerythrus* · Finder's share · Group living · Producer-scrounger strategies · Spatial position

Introduction

Two of the most important benefits of group living have been identified as a reduction in predation risk (Pulliam 1973; Roberts 1996; van Schaik 1983) and an increase in food acquisition through food defense and communal searches for resources (Pitcher *et al.* 1982; Wrangham 1980). However, owing to variation in spatial positioning, group members do not share these benefits equally (Krause 1994; Rubenstein 1978). Individuals on the periphery face a high risk of predation (Beecham and Farnsworth 1999; Hamilton 1971; Vine 1971), particularly individuals on the front, outside edge of group progressions because they move into new areas first and encounter predators before others (Bumann and Krause 1993; Bumann *et al.* 1997). With fewer neighbors, edge individuals also benefit less from the dilution effect and shared vigilance (Hall and Fedigan 1997; Hamilton 1971; Treves 1998), though actual predation risk depends on predator attack mode (Hirsch and Morrell 2011; Morrell *et al.* 2011). Despite the danger, individuals that forage on the front, outside edge of the group come into contact with resources first and benefit because these resources are not yet depleted (Beecham and Farnsworth 1999; Black *et al.* 1992; Eggers 1976; Janson 1990a,b; Krause 1994; Krause *et al.* 1992; Robinson 1981; Rowcliffe *et al.* 2004).

In species with a dominance hierarchy, high-ranked individuals tend to maintain positions in the center of the group to maximize safety from predation (primates: Hall and Fedigan 1997; Janson 1990a; Robinson 1981; spiders, birds, fish, ungulates: reviewed in Krause 1994), and modeled simulations replicate these results (Barta *et al.* 1997; Evers *et al.* 2011; Hemelrijk 1998, 2000). Presumably, dominants shape their group's spatial organization by choosing their preferred positions, as they are avoided by and able to displace subordinates (Hall and Fedigan 1997; Janson 1990a;). Dominants at the center of a group are less likely to find food patches (act as producers), which can be a costly loss when food items are small and quickly depleted. At larger, more slowly depleted food sites, central dominants can easily supplant subordinates (act as scroungers) to obtain resources (Barta and Giraldeau 1998; Hirsch 2007a; Liker and Barta 2002). Variability in resource size and richness may explain why dominants in some primate species take an intermediate strategy in which they forage at the front-central position of the group, just behind those at the front of the progression, but close enough that they can quickly monopolize most food that is found, i.e., wedge-capped capuchin (*Cebus olivaceus*: Robinson 1981) and tufted capuchin (*C. paella*: Di Bitetti and Janson 2001; Janson 1990a, b). Subordinates may be forced to the edge of the group, putting them at an increased risk of

predation, but they can make the best of this situation by foraging at the front, outside edge and acting as producers (Barta and Giraldeau 1998; Di Bitetti and Janson 2001; Liker and Barta 2002). Feeding first may allow them to acquire many or all of the food items in small patches and a greater share of the food in larger or richer patches before dominants approach (the "finder's advantage"; Barnard and Sibly 1981; Giraldeau and Beauchamp 1999; Giraldeau and Livoreil 1998; Goldberg *et al.* 2001; Hirsch 2007a; Smith *et al.* 2002; Vickery *et al.* 1991). One way to examine the importance of food acquisition vs. safety from predation in a landscape is to look at the distance that those at the front edge of the group maintain from others. Producers gain a greater share of resources when they are as far away as possible from scroungers (Barta *et al.* 1997), but maintaining smaller interindividual distances reduces an individual's predation risk (Bumann *et al.* 1997; Hamilton 1971).

Age and sex also influence intragroup spatial position for primates. Adult and subadult males tend to be at the front of moving groups of several species: olive baboons (*Papio anubis*: Harding 1977), yellow baboons (*P. cynocephalus*: Collins 1984; Rhine and Westlund 1981; Rhine *et al.* 1979), chacma baboons (*P. ursinus*: King *et al.* 2008), Celebes crested macaque (*Macaca nigra*: Watanabe and Brotoisworo 1982), and mountain gorilla (*Gorilla beringei beringei*: Watts 2000). However, juveniles may stay more central (*P. cynocephalus*: Rhine *et al.* 1981; *P. ursinus*: Rhine *et al.* 1985; *Cebus apella*: Janson 1990a) because they face the greatest risk of predation and may rely on adults for vigilance (Arnez and Leger 2000; Boukhriss *et al.* 2007; Janson and van Schaik 1993). Females typically stay closer to the group's center but this may be dependent on dominance rank, with more dominant females taking central positions, pushing subordinate females to the edges [*C. apella*: Janson 1990a; white-faced capuchin (*C. capucinus*: Hall and Fedigan 1997); *P. ursinus*: Ron *et al.* 1996].

We examined the intragroup spatial positioning of vervets (*Chlorocebus pygerythrus*) at Lake Nabugabo, Uganda. Vervets are female philopatric, matrilineal cercopithecines with a wide geographic distribution across East and South Africa. Their diets vary, depending on the habitat they occupy (Jaffe 2011), but they eat a primarily frugivorous diet (77%) at Nabugabo, supplementing with insects (10.6%), flowers (7.6%), and young leaves (4.0%) (C. A. Chapman, *unpubl. data*). Vervets are considered semiterrestrial, spending *ca*. 19% of their time on the ground and an additional 29% within 5m of the ground (Rose 1979). Predation rates on this species can be very high in certain environments (Isbell 1990) because of threats from both ground and aerial predators (Seyfarth *et al.* 1980). At Nabugabo, humans have modified the range of our vervet troop, so some of the larger predators, e.g., leopards, are extirpated and the primary predators are now domestic dogs. Venomous snakes also occur frequently in the vervet's range, as do constricting snakes, e.g., ball pythons (*Python regius*), but eagles specializing in primates (crowned-hawk eagles, *Stephanoaetus coronatus*) have not been observed (C. A. Chapman, *unpubl. data*).

In this study, we examined the intragroup spatial positions of individual vervets in a single group when the group was stationary vs. when it was moving. Different ecological and social pressures affect groups during rest periods compared to periods of movement, which may affect positioning. For instance, whereas

predation risk may decrease from the outer edge to the interior of stationary groups (Hamilton 1971), this threat shows a front-to-back gradient in moving groups (Bumann *et al.* 1997). Affiliative social behaviors should occur more often in stationary groups where grooming is possible, while food competition should increase in moving groups that are actively foraging. We determined the individual effects of age, sex, rank, and activity on spatial position. We used clumped, artificial food patches ("discovery patches") that varied in richness (poor vs. rich) to determine which individuals acted as producers and the amount of food they managed to obtain in a food patch (the "finder's share") relative to their rank and position (Barnard and Sibly 1981; Vickery *et al.* 1991).

In accordance with the male-biased dispersal pattern in vervets, we predicted that sex would have a strong effect on spatial position, with females maintaining central positions in stationary and moving groups and males more often on the group's periphery (Table I). As a result of this positioning, we expected males to find more discovery patches than females. We predicted that juveniles would be positioned in the group's center owing to their greater risk of predation and because of this positioning we did not expect juveniles to discover many experimental food patches. We did not predict any age differences in spatial position between adults and subadults. Activities in certain spatial positions were predicted to differ only while the group was stationary. Because food may be depleted in the center of stationary groups (though this depends on the richness of a food patch; Hirsch 2007a; Whitten 1983), especially if the group has been in one position for some time, we expected feeding to occur on the periphery. Social behaviors were predicted to occur in the center of groups because vigilance may be compromised while engaging in these behaviors (Cords 1995; Cowlishaw 1998; Maestripieri 1993). We did not expect resting and moving to occur in particular spatial positions in stationary groups. We predicted that dominant individuals would maintain central positions, both when the group was stationary and while it was moving (Clifton 1991; Robinson 1981). However, because moving groups usually search actively for food, we expected to find dominants in front-central positions in these groups, just behind those on the front, outside edge. We predicted that subordinates would be restricted to the outside edge of stationary groups, but would be found at the front of moving groups (Di Bitetti and Janson 2001; Dubuc and Chapais 2007; Hall and Fedigan 1997; Janson 1990a,b; Liker and Barta 2002; Stahl *et al.* 2001) so that they could act as producers, finding more discovery patches than dominants and those in other spatial positions. Whether acting as scroungers or producers, we predicted that dominants would gain a greater share of resources than subordinates in the same roles. In line with the predictions in the preceding text, we expected that those in positions on the front, outside edge of groups would find more discovery patches than those in other spatial positions. We predicted that the finder's share would be greater when a poor food patch was discovered relative to a rich patch, or when scroungers were further away and had to travel further to feed in the discovered patch (Di Bitetti and Janson 2001). We predicted that the proportion of a patch acquired by scroungers (the "scrounger's share") would be greater for dominant animals, in rich patches, and when the scrounger arrived soon after a patch was discovered (Barnard and Sibly 1981; Vickery et al. 1991).

Table I Variables and predictions for use of intragroup spatial positions[a] by vervets (*Chlorocebus pygerythrus*) at Lake Nabugabo, Uganda (June – July 2012)

Variables		Predictions		Discovery patches
		Stationary group	Moving group	
Sex:	Males:	Peripheral	Peripheral	Find > patches than females
	Females:	Central	Central	Find < patches than males
Age:	Juveniles:	*Central*	*Central*	Find < patches than other aged individuals
Activity:	Feed:	> on outside edge[b]	No spatial variation	
	Rest:	No spatial variation	No spatial variation	
	Move:	*No spatial variation*	No spatial variation	
	Social:	> in center	No spatial variation	
Dominance:	High-ranking:	Central	*Front-central*	*Find < patches than subordinates* > share than subordinates when scrounging > share than subordinates when producing
	Low-ranking:	Peripheral	*Front-outside edge*	*Find > patches than dominants* < share than dominants when scrounging < share than dominants when producing
Spatial position:	Front-outside edge:			Find > patches than those in other positions
Patch richness:	Rich:			Finder's share smaller Scrounger's share larger
	Poor:			Finder's share larger Scrounger's share smaller
Interindividual spacing (mean distance of closest neighbor):	Large:		*Smaller on front-outside edge than the center*	*Finder's share larger*
	Small:			*Finder's share smaller*

Predictions in italics were not upheld.

[a] Defined as the most frequent location of individuals relative to others in the group.

[b] May depend on how long the group has been in one position to give time for resources to be depleted.

To decrease their risk of predation by domestic dogs, we also predicted that those at the front edge of the group would consistently show smaller

interindividual distances compared to those in the center (Bumann *et al.* 1997; Hamilton 1971).

Methods

Study Site and Subjects

We carried out this research at Lake Nabugabo, Masaka District, central Uganda (0°22′–12°S and 31°54′E). Lake Nabugabo (8.2 × 5 km) is a satellite lake to Lake Victoria lying at an elevation of 1136 m. The landscape around the lake features mostly wetlands, grasslands, and patches of swamp forest, but a small portion is modified by humans with farmers' fields, degraded forest, and a few buildings. We followed one habituated group of vervets called M group for 2 mo (June–July 2012) from dawn to dusk; 5 d/wk (41 d). M group contained 24 individuals (2 adult males, 5 adult females, 3 subadult males, 3 subadult females, 9 juveniles, and 2 infants). We employed dye marking at the beginning of the study, after which we could identify all adult and subadult individuals by their unique features. During a single day, we baited individuals that were difficult to identify with popcorn and sprayed nontoxic, commercially available hair dye onto their bodies using a syringe, carefully avoiding the face area. Dye marks lasted for an average of 2 wk, but allowed enough time for observers to learn to differentiate individuals by their natural features. Individual identification of juveniles was less reliable than that of adults and subadults, so data for juveniles has been lumped in the following analyses.

Data Collection

We collected behavioral data using instantaneous sampling, focal animal sampling, and all-occurrences sampling, as well as *ad libitum* (Altmann 1974). During full-day follows (N = 41), we recorded instantaneous samples of single, randomly chosen individuals every 15 min (N = 1348) during which we recorded information on their identity, activity, spatial position, the distance and identity of their nearest neighbor, and the number of individuals within 5 m. A minimum of 2 h passed between consecutive samples on the same individual. Because recording of juvenile identities was not always possible, no unidentified juveniles of the same sex were sampled within 2 h of one another. We recorded state behaviors for individuals during instantaneous samples in four categories: feed (manipulation and ingestion of food), rest (remaining stationary), move (change of location by any means), social (an interaction between two or more individuals), and other (behaviors such as vocalizing and autogrooming). We also noted *ad libitum* aggressive and submissive behaviors, copulations, alarm calls, behavior during intergroup encounters, and other rare events, including information on participants.

When the group was moving, i.e., the geographical center of the group was progressing in a certain direction, we recorded the spatial position of an individual relative to other group members during instantaneous samples using the elliptical clock method (Janson 1990a,b). The 12 o'clock position indicated the direction of travel and individuals' positions were marked according to their location relative to the numbers

on the clock, e.g., those leading the group would be at the front outer edge of the clock, in a position such as 11 o'clock (11O; Fig. 1a). This system provides 36 possible locations; however, for analyses we collapsed these locations into four categories that contained a roughly equal number of samples. Area 1 was the front, outside edge of the group and included the individual samples spent in the 9 o'clock to 3 o'clock positions [area 1: 9O (outside), 10O, 11O, 12O, 1O, 2O, 3O, $N = 187$ samples, Fig. 1b]. Area 2 was the front-central position just behind those at the front of group progressions [9M (middle), 10M, 11M, 12M, 1M, 2M, 3M, $N = 155$]. Area 3 was the position in the center [8M, 7M, 6M, 5M, 4M, and all the positions in the interior (I), $N = 183$], while area 4 was the rear outer edge of the group [8O (outside), 7O, 6O, 5O, 4O, $N = 162$] (after Hall and Fedigan 1997; Janson 1990a,b). This scheme allowed overall analyses of individual spatial position because each of these areas was ordered from the front to the back of a moving group. If the group was not traveling at the time, i.e., the geographical center of the group was stable or not progressing in a single direction, individual positions were marked only as inner, middle, and outer relative to the position of others.

We set up "discovery patches" containing food rewards of two different sizes, in the vervet groups' range to examine producer-scrounger roles relative to spatial position. Vervets make ideal subjects for foraging experiments because they are partially terrestrial, eat a varied diet, and easily take food from human sources (Teichroeb and Chapman 2014). This allowed us to conduct experiments on the ground and to offer

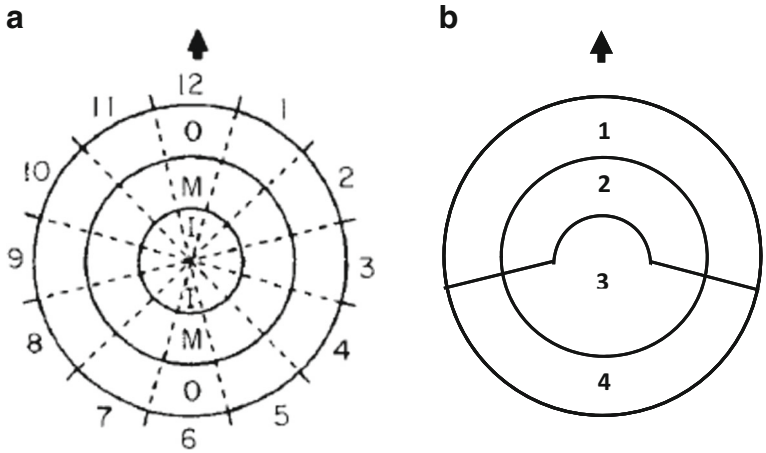

Fig. 1 **(a)** The elliptical clock method used to determine individual spatial position during instantaneous samples where the vervet (*Chlorocebus pygerythrus*) group at Lake Nabugabo, Uganda (June–July 2012) was moving, from Janson (1990a). O = outside; M = middle; I = interior. (Reprinted with permission from Elsevier). The arrow indicates the direction of travel of the foraging group. For analyses of individual spatial position while the group was stationary, we collapsed the 36 categories into the outside (area 1), middle (area 2), and interior (area 3) areas. **(b)** For analyses on the group while it was moving, we collapsed the 36 categories recorded in **(a)** into the four shown (after Janson 1990a,b; Hall and Fedigan 1997). Area 1 (9 o'clock to 3 o'clock) represents those that are on the outer leading edge. Area 2 is a front-central position that may be beneficial for both predation protection and access to food. Area 3 is the central section of the group, while individuals in area 4 (8 o'clock to 4 o'clock) are on the outer trailing edge.

locally grown bananas as food rewards. During full-day follows, we opportunistically set up discovery patches containing rich (20 half bananas, $N = 20$) or poor food rewards (3 half bananas, $N = 20$) on the ground in the groups' line of travel. We used a black, rectangular, hard, plastic bin (Rubbermaid Action Packer, 37 cm tall, 65 cm × 47 cm wide) to transport the bananas and then flipped it over with the food stacked on top to use as the feeding platform (Fig. 2). To ensure that the monkeys did not anticipate the experiments, which would have led to biased results, we set up the platforms randomly with respect to location and time of day and never carried the plastic bin while we followed the group. The vervets have a small home range (5.61 ha) and a relatively predictable daily path, which allowed J. A. Teichroeb to anticipate their future trajectory from their current location. We cut up and counted reward bananas at the field station and then carried the bin to a random location in the anticipated line of travel of the monkeys. On three occasions this method meant that the vervets did not discover the platform. Once an individual found the platform (gazed directly at it and began moving quickly toward it), we recorded the following data: the identity of the producer (finder), the distance at which the producer discovered the platform (m), the distance of the producer's nearest neighbor (m) at the time of discovery, and the time (s) it took for the producer to arrive at the platform (Di Bitetti and Janson 2001). We videotaped the platform and the area around it on each trial from the first approach of the producer until all the food was gone, and we recorded all occurrences of feeding (the number of half bananas obtained by the producer and subsequent scroungers), as well as the identity of scroungers, and the time that each scrounger arrived.

We collected 5-min focal animal samples ($N = 600$, 50 h) on adult and subadult members of the group during full-day follows to provide data on dominance relationships to add to *ad libitum* observations. We conducted focal samples opportunistically with at least an hour left between those on the same individual. We also made an effort to record the same number of samples per individual. We determined dominance relationships by constructing a matrix using all agonistic interactions (aggressive and/or submissive) that occurred during *ad libitum* and focal observations. We found a linear hierarchy for all adult and subadult individuals ($N = 15$ individuals, 42

Fig. 2 Three individual vervets (*Chlorocebus pygerythrus*) feed on the remains of a rich discovery patch at Lake Nabugabo, Uganda, June–July 2012.

interactions, $h' = 0.73$, $P = 0.024$, de Vries 1995). When constructing the dominance hierarchy, we excluded agonistic interactions that occurred between adult males and females in a mating context and between mothers and alloparents during infant handling because these were often coalitionary and it was difficult to determine winners and losers. Unless otherwise stated, we used the sex-specific dominance rank in all analyses.

Definitions

M group had been followed for *ca.* 1 yr before the study began, so we knew the exact age of some infants and juveniles, while we estimated the age of other individuals from their relative size. We defined infants as those that were unweaned and juveniles as those that were weaned but smaller than subadults. Subadult females were smaller than adult females and, to our knowledge, had not given birth. We defined adult females as those that had reached first parturition, as indicated by observation or the presence of elongated nipples. Young subadult males were larger than juveniles and the same size as subadult females. Older subadult males were the same size, or slightly larger than, adult females, but their testicles had yet to drop and become bright blue. Adult males were larger than adult females and had descended bright blue testicles.

Data Analyses

We summarize the data collected for each individual in Table II. To examine factors influencing individual spatial position when the group was stationary and when it was moving we used multinomial logistic regressions with the categorical variable of spatial position as the dependent variable. Given that samples of consecutive spatial position for each individual were at ≥2 h apart, we considered them independent. For the stationary model, we classified individual spatial position as 1 = outside, 2 = middle, and 3 = interior (Fig. 1a) and for the moving model, we used areas 1–4 (Fig. 1b) to represent spatial positions from the front to the back of the moving group. We examined the effect of age, sex, dominance rank, and activity on spatial position in each regression.

We used linear mixed-effects models to examine the impacts of several variables on the finder's and scrounger's share of discovery patches. For the model examining influences on the scrounger's share, we set the proportion of each discovery patch obtained by each scrounger as the dependent variable. Fixed factors in this model included dominance rank, time of arrival at the patch, and patch richness. For the linear mixed-effects model determining influences on the finder's share, we used the proportion of each discovery patch obtained by the producer as the dependent variable with dominance rank, patch richness, and the distance of the nearest neighbor when the patch was found as fixed factors. We included animal ID and age–sex class as random factors in both of these models, and in addition, included observation number for each individual as a repeated measure. We compared Akaike information criterion (AIC) values for all models generated with different covariance parameters and considered those with the lowest AIC values as best-fit models.

For some factors that had significant effects in the multinomial logistic regressions and linear-mixed effects models, we performed *post hoc* analyses to determine where differences lay. For the stationary analyses, we used chi-square tests to determine whether certain activities occurred more often than expected in particular spatial positions. We calculated expected values for each activity as the proportion of all observations in each of the three spatial positions (interior, middle, outside). Because spatial position categories for the stationary analyses were ordered, i.e., 1 = outside, 2 = middle, and 3 = interior, and represented a greater tendency to be near the group's center as numbers increased, we used mean spatial positions over all samples for each individual for the remainder of the stationary *post hoc* analyses. We used Mann–Whitney

Table II Description of the sample size, spatial positioning, and foraging strategies of individual vervet monkeys (*Chlorocebus pygerythrus*) at Lake Nabugabo, Uganda (June–July 2012)

Ind.	Age/sex[a] class	Dominance rank (intrasex)	*N*	Most frequent spatial position[b] (percent of time spent there in parentheses)		Producer frequency	Mean finder's share	Scrounger frequency[c]	Mean scrounger's share
				Stationary (%)	Moving (%)	*N* = 40 patches		*N* = 40 patches	
JK	AM	1	102	2 (44)	1 (45)	4	0.59	12	0.34
NM	AM	4	108	1 (86)	4 (55)	8	0.51	4	0.13
LM	OSM	2	89	1 (71)	1 (58)	2	0.6	10	0.19
EL	OSM	3	99	1 (59)	1 (50)	5	0.52	10	0.22
ST	OSM	5	86	1 (51)	1 (33)	4	0.76	6	0.14
OT	YSM	6	37	1 (72)	2 (67)	3	0.62	16	0.17
CL	YSM	7	24	1 (59)	2 (29)	3	0.37	5	0.07
GT	AF	1	107	2 (47)	1 (37)	3	0.5	13	0.22
DT	AF	5	92	2 (68)	3 (44)	1	1	6	0.13
PT	AF	7	112	2 (60)	3 (39)	1	0.67	1	0.1
LP	AFwI	3	108	2 (71)	3 (40)	0	—	5	0.05
TS	AFwI	6	118	1 (26), 2 (26)	3 (53)	2	0.23	6	0.05
RM	SF	4	56	2 (76)	4 (35)	0	—	4	0.11
TB	SF	2	74	2 (54)	3 (32)	2	0.46	22	0.13
MA	SF	8	40	2 (50)	3 (46)	1	0.67	5	0.09
9 Ind	J		261	1 (43)	4 (30)	0	—	17	0.08

[a] Age/sex class definitions: AM = adult male; OSM = Older subadult male; YSM = younger subadult male; AF = adult female; AFwI = adult female with infant; SF = subadult female; J = juveniles.

[b] Number for spatial position refer to those in Fig. 1.

[c] Not all experimental patches provided scrounging opportunities to each individual because some were depleted before the individual had a chance to encounter them.

U tests to examine the relationship between mean spatial position and the two variables of sex and dominance rank. We further investigated the effect of dominance rank on spatial position using Spearman correlations on data from each sex. For the moving *post hoc* analyses, we used a Wilcoxon test to determine if there was a difference in the number of near neighbors for individuals when the group was moving vs. when it was stationary. We used a Fisher's exact test to examine the proportion of samples in central positions (positions 2 and 3) vs. outer positions (1 and 4) for males vs. females. In addition, we used a chi-square test to examine the proportion of samples spent in each spatial position by individuals of different dominance rank and we set expected values as equal for each spatial position (areas 1–4).

For the results of the foraging experiments, we compared the number of scroungers in rich versus poor patches with a *t*-test. To examine the effects of sex, age, and dominance rank on the tendency of individuals to act as producers, we used a multiple regression after checking for the normality of residuals. We used a Mann–Whitney *U* test to examine the interindividual spacing (the mean distance of the nearest neighbor during instantaneous samples) maintained by those on the front, outside edge (area 1) of progressions vs. those in the center (area 3). Finally, we used a Wilcoxon exact test to compare the share of patches that dominants obtained with producing vs. scrounging to determine why they maintained positions on the front edge of the group. We defined "dominants" in this context as individuals in the upper half of a mixed-sex dominance hierarchy, i.e., the top 7 of 15 individuals. We performed model selection and statistical tests in PASW version 22.0 and calculated linearity indices for dominance with R 3.1.1 (R Development Core Team, 2014). Statistics were two-tailed with $\alpha = 0.05$ set for significance.

Results

Stationary Group

When the group was stationary, sex, activity, and dominance rank significantly affected individual spatial position (Table III). Age showed no significant effect on individual spatial position while the group was stationary. *Post hoc* analyses showed that females (mean position 1.75) were near the group's center more often than males (mean position 1.48) (Mann–Whitney *U*: $N_{\text{females}} = 14$, $N_{\text{males}} = 6$, $Z = 2.06$, $P = 0.04$). Feeding (chi-square: $N = 192$, $\chi^2 = 13.32$, df = 2, $P = 0.001$) and moving ($N = 145$, $\chi^2 = 6.46$, df = 2, $P = 0.04$) took place on the periphery more often than expected and social behaviors took place in the center of the group more than expected ($N = 179$, $\chi^2 = 37.15$, df = 2, $P < 0.0001$). There was no significant variation from expected in where resting ($N = 380$, $\chi^2 = 0.08$, df = 2, $P = 0.96$) or other behaviors took place ($N = 15$, $\chi^2 = 0.97$, df = 2, $P = 0.62$). Despite the significant effect of dominance rank on spatial position in the regression, *post hoc* analyses did not find an association. Mean position for individuals ranked 1–4 was 1.67, while for individuals ranked 5–8, it was 1.69 (Mann–Whitney *U*, $N_{\text{rank 1–4}} = 8$, $N_{\text{rank 5–8}} = 6$, $Z = 0$, $P = 1.0$). The effect of

dominance rank on position in the regression may have been driven by higher ranked females being nearer the center of the group, though the relationship between rank and mean spatial position in females was not significant (Spearman, $N = 8$, $r_s = -0.66$, $P = 0.07$). Males showed no correlation between rank and mean spatial position ($N = 7$, $r_s = 0$, $P = 1.0$).

Moving Group

When the group was moving, individuals maintained fewer neighbors within 5 m (mean 1.56 ± SD 0.55) than when the group was stationary (mean 1.96 ± SD 0.65) ($N = 15$, $Z = -2.88$, $P = 0.004$). Sex and dominance rank significantly affected spatial position within moving groups, but age and activity did not (Table III). We observed females near the group's center (in positions 2 and 3) in a higher proportions of samples than males, who were more likely to be found on the outside of the group (in positions 1 and 4, Fisher's exact test, $P < 0.0001$). In contrast to stationary groups, we observed high-ranking individuals on the front, outside edge of the group more often than in other spatial positions (Fig. 4). The alpha, beta, and gamma males, as well as the alpha female, most frequently occupied area 1, the position at the head of moving groups (Fig. 3). Indeed, when using a dominance hierarchy that integrated both males and females, the more dominant half of the group (7 of the 15 individuals) had a significantly greater proportion of samples in this area (area 1: 35.3%) than in other areas [areas 2 (20.7%), 3 (17.8%), and 4 (26.2%); chi-square, $N = 309$, $\chi^2 = 21.91$, df = 4, $P < 0.0001$]. Two natal subadult males most often occupied area 2, the front-central position just behind those at the front edge. Besides the alpha female, all other adult females (two of which had infants during the study) and two subadult

Table III Multinomial logistic regression models describing influences on intragroup spatial position while the vervet (*Chlorocebus pygerythrus*) group was stationary and moving (Lake Nabugabo, Uganda, June–July 2012)

Variable	χ^2	df	*P*
Stationary[a]			
Age	1.91	4	0.75
Sex	67.80	2	<0.0001*
Dominance rank	31.01	16	0.01*
Activity	36.89	10	<0.0001*
Moving[b]			
Age	7.15	3	0.07
Sex	33.41	3	<0.0001*
Dominance rank	69.94	21	<0.0001*
Activity	9.15	12	0.69

[a] Overall model: $N = 3{,}921$, pseudo-$R^2 = 0.22$, $\chi^2 = 161.12$, df = 32, $P < 0.0001$.

[b] Overall model: $N = 4{,}687$, pseudo $R^2 = 0.27$, $\chi^2 = 161.96$, df = 39, $P < 0.0001$.

*Significant effect.

females most often occupied area 3 at the center of the group. A mid-ranking and peripheral adult male, as well as a mid-ranking subadult female, most often occupied area 4, the position at the rear of moving groups. We observed juveniles in a mix of positions but found them most frequently in area 4, trailing the rest of the group (Fig. 3).

Producers and Scroungers

During our foraging experiments, 13 of 15 adult and subadult individuals acted as both producers and scroungers, while two adult females never produced and only scrounged. Juveniles never acted as producers, i.e., found discovery patches. Producers discovered feeding platforms at a mean distance of 12.63 m (± SD 10.29) but this was highly variable (range: 4–50 m), depending on the structure of the vegetation in the area. Once producers found a platform, they took a mean of 13.57 s (± SD 12.38) to reach it and had a mean of 75.79 s (± SD 75.94, range: 1–298 s) to feed before the first scrounger arrived. It took vervets a mean of 39.4 s (± SD 16.4, $N = 11$ from 3 individuals) to eat a single half-banana but they would often snatch banana halves from the platforms and run off with them, particularly when confronted by a higher ranking individual. Scrounging occurred in 100% (20/20) of rich patches, but in only 40% (8/20) of poor patches; thus, rich patches had significantly more scroungers than poor patches (*t*-test, $N_{large} = 20$, $N_{small} = 20$, $t = -11.35$, df = 38, $P < 0.0001$). When scrounging, individuals gained a greater share of the food in a patch if they were higher ranked, arrived earlier, or if the patch was poor and hence had few other scroungers present (Table IV). Individuals had a larger finder's share when they were higher ranked and the patch

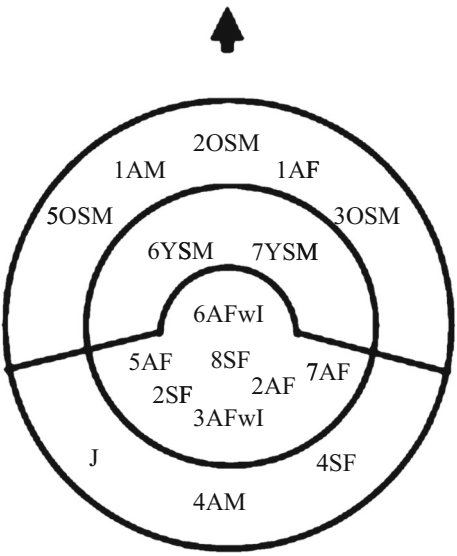

Fig. 3 Most frequent intragroup spatial position of individual vervets (*Chlorocebus pygerythrus*) at Lake Nabugabo, Uganda (June–July 2012) while the group was moving. The arrow indicates the direction of travel of the foraging group. The number represents the intrasex dominance rank of each individual. AM = adult male; AF = adult female; AFwI = adult female with infant; OSM = older subadult male; YSM = younger subadult male; SF = subadult female; J = juveniles.

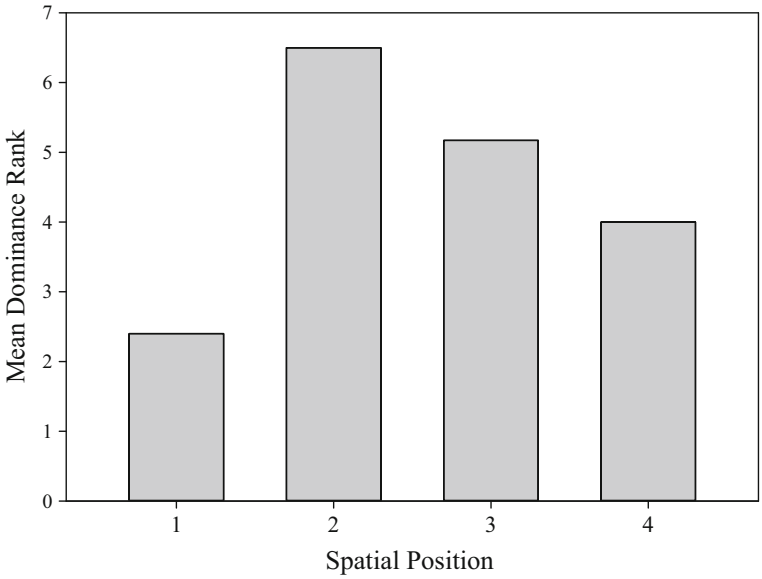

Fig. 4 Mean sex-specific dominance rank of individual vervets (*Chlorocebus pygerythrus*) in each spatial position (positions 1–4 representing those going from the front to the back of the group while it was moving) at Lake Nabugabo, Uganda, June–July 2012.

was poor (Table V). Producers were able to access all or most of the food in poor patches (mean proportion = 0.83, $N = 20$), but were less successful in monopolizing the resources in rich patches (mean proportion = 0.24, $N = 20$). The distance of the nearest neighbor at the time the patch was found did not influence the finder's share.

Individuals that most frequently foraged in area 1, found more discovery patches than those in other spatial positions (chi-square, $N = 40$, $\chi^2 = 9.51$, df = 3, $P = 0.02$, Fig. 5). High-ranking individuals foraged on the front edge of moving groups but dominance rank had no effect on the proportion of patches in which an individual acted as a producer (multiple regression, $\beta = -0.001$, $P = 0.79$). Age also had no effect ($\beta = -0.03$, $P = 0.15$) on the proportion of patches in which an individual acted as a producer but sex did have an effect ($\beta = -0.08$, $P = 0.002$), with males finding more patches than females (overall model fit, $R^2 = 0.61$, $N = 3{,}15$, $F = 5.68$, $P = 0.01$). Overall, the mean distance of the closest neighbor for individuals was 3.51 m (± SD 1.8) while the group was moving. However, contrary to our prediction, individuals that we observed more

Table IV Linear mixed-effect model examining the variables affecting the proportion of discovery patches obtained by scrounging (the scrounger's share) in vervets (*Chlorocebus pygerythrus*) at Lake Nabugabo, Uganda (June–July 2012)

Model term	Estimate (SE)	*F*	df	*P*
Dominance rank	–0.01 (0.01)	5.14	24.3	0.03*
Patch richness	–0.24 (0.03)	78.48	109.2	<0.0001*
Time of arrival	–0.0008 (0.03)	11.77	99.7	0.001*

*Significant effect.

Table V Linear mixed-effect model examining the variables influencing the proportion of discovery patches obtained by producing (the finder's share) in vervets (*Chlorocebus pygerythrus*) at Lake Nabugabo, Uganda (June–July 2012)

Model term	Estimate (SE)	*F*	df	*P*
Dominance rank	–0.04 (0.01)	21.99	26.1	<0.0001*
Patch richness	–0.69 (0.04)	307.08	28.1	<0.0001*
Distance of nearest neighbor	–0.02 (0.002)	1.04	21.4	0.32

*Significant effect.

frequently at the front edge of the group maintained larger interindividual distances (mean 4.33 ± SD 1.32 m) than those usually observed in the center (mean 2.3 ± SD 0.38 m) (Mann–Whitney U, $N_{\text{Area 1}} = 5$, $N_{\text{Area 3}} = 6$, $U = 1.5$, $P = 0.02$).

Interaction of Dominance, Share of Resources, and Spatial Position

Dominant individuals foraged at the front, peripheral edge of the group; however, they gained a greater share of resources than lower ranked individuals regardless of whether they found a patch or scrounged from others. We thus questioned why dominants took on the presumably riskier tactic of foraging on the front, outside edge. To examine this we looked at the share of resources obtained by the most dominant individuals (the top 7 ranked adult and subadults of the 15) when acting as producers compared to when acting as scroungers. We found that dominants obtained a greater proportion of available resources when they acted as producers compared to when they acted as scroungers (Wilcoxon exact test, $N = 6$, $Z = -2.20$, $P = 0.03$). When dominants acted as

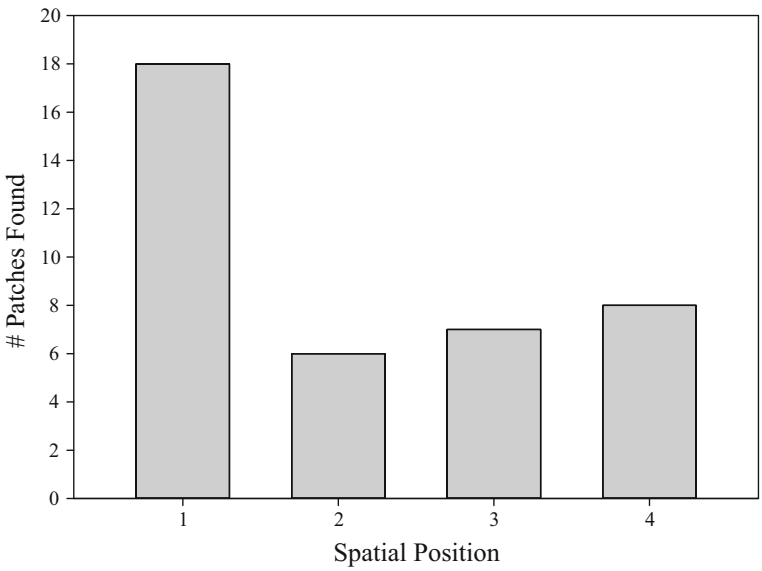

Fig. 5 The number of discovery patches found by individual vervets (*Chlorocebus pygerythrus*) at Lake Nabugabo, Uganda that were most frequently in each spatial position (positions 1–4 representing those going from the front to the back of the group while it was moving), June–July 2012.

producers, they gained a mean proportion of 0.53 ($N = 6$ individuals) of the food in the patch compared to 0.21 when they acted as scroungers ($N = 7$ individuals). This equaled 10.6 half bananas in rich patches and 1.6 in poor patches for high-ranking producers, relative to 4.2 and 0.63 half bananas respectively, for high-ranking scroungers.

Discussion

For vervets at Lake Nabugabo, a number of factors influenced intragroup spatial position and this was a function of whether the group was stationary or moving. The only consistent effect was that of sex. Regardless of the state of the group, females stayed more often near the center, while most males occupied peripheral positions. This might be a result of vervet social structure, where females are philopatric and tightly bonded (Cheney and Seyfarth 1990; Seyfarth 1980) and it is consistent with findings from some other female-philopatric primate species (*Papio cynocephalus*: Collins 1984; *P. ursinus*: Ron *et al.* 1996; *Cebus apella*: Janson 1990a; *C. capucinus*: Hall and Fedigan 1997). However, this result might also be due to patterns of sexual dimorphism. With a larger body size and longer canines males may be more tolerant of the predation threat at the edge of the group because they inherently face a lower risk than females (Rhine and Westlund 1981; Rhine *et al.* 1979).

Individual activity influenced spatial positioning when the group was stationary. Those engaged in social behavior were found in the center. The majority of social interactions were allogrooming, where vigilance has been shown to be compromised [rhesus macaques (*Macaca mulatta*: Maestripieri 1993), blue monkeys (*Cercopithecus mitis*: Cords 1995), and *Papio ursinus*: Cowlishaw 1998]; if one's attention must be diverted from being vigilant, being surrounded by others may be a good strategy to avoid predation. However, this result is likely confounded by the fact that females were more often in the center and they allogroom more often (16.6% of our sample) than males (2.4%). Vervets that were feeding and moving were more likely to be on the periphery of the group when it was stationary. Depending on the resources in the area (Whitten 1983), food may be quickly depleted at the center, so foraging would likely be more efficient on the edge of an unmoving group. In contrast, when the group was moving, we found no effect of activity on spatial position. Moving groups generally forage or travel from one food site to another so most individuals, regardless of position, would be alternating between moving and feeding.

The influence of dominance rank on spatial position was reversed in stationary and moving groups. When the group was stationary, more dominant females were in the center with subordinate females and males on the edge. In contrast, when the group was moving, high-ranking males and females tended to be on the front, outside edge. High-ranking males tend to be at the front of moving groups of several primate species (*Papio anubis*: Harding 1977; *P. cynocephalus*: Collins 1984; Rhine and Westlund 1981; Rhine *et al.* 1979; *P. ursinus*: King *et al.* 2008; *Macaca nigra*: Watanabe and Brotoisworo 1982; *Gorilla beringei beringei*: Watts 2000). However, this effect has been found less often for females; *cf.* black-and-white ruffed lemurs (*Varecia variegata*: Overdorff *et al.* 2005). In our case, the alpha female showed this effect most strongly,

spending the majority of her instantaneous samples on the front, outside edge of moving groups.

Theoretically, those foraging on the front edge of the group face a trade-off, giving up safety from predators to access food patches first (Romey 1995, 1997) and indeed in ring-tailed coatis (*Nasua nasua*), individuals in this spatial position showed more vigilance than those in other spatial positions (Di Blanco and Hirsch 2006). In this study, those that were most often on the front, outside edge of the group found more food patches than those in other spatial positions, an effect seen in several species (birds: Flynn and Giraldeau 2001; Monus and Barta 2008; *Cebus apella*: Di Bitetti and Janson 2001; *Papio ursinus*: King *et al.* 2009). Vervets on the front, outside edge also maintained greater interindividual distances while foraging compared to individuals in the center, which may have further compromised their safety (Fernández-Juricic and Beauchamp 2008; Hamilton 1971; Quinn and Cresswell 2006; Robinson 1981; Romey 1995, 1997) and required greater investment in vigilance to avoid predation (Blumstein *et al.* 2001; Cowlishaw 1998; Hirsch 2002; Pöysä 1994; Teichroeb and Sicotte 2012; Treves 1998). This suggests that the need to find food constrains the behavior of vervets at Nabugabo more than predation risk, a result that may be due to the fact that their range is partly modified by humans. Some previously forested areas have been cleared for cultivation, likely decreasing the availability of large fruiting trees and altering the predator community. During three years of research on M group, we did not observe any predation attempts by aerial predators and snakes, but we recorded two successful instances of predation by domestic dogs (C. A. Chapman, *unpubl. data*). Dogs are "pursuit" predators that attack individuals from relatively long distances, so those on the periphery of groups face higher risk (Hirsch and Morrell 2011); yet high-ranking vervets chose to tolerate this threat to increase their access to food.

Because high rank allows dominants to displace subordinates at food sites and maintain better food intake rates [*Cebus apella*: Janson 1985; *C. capucinus*: Vogel 2005; Japanese macaques (*Macaca fuscata*: Saito 1996); and gray langurs (*Semnopithecus entellus*: Koenig 2000)], we expected that high-ranking animals would act as scroungers more often and maintain safer spatial positions in the center of the group compared to lower ranked individuals (Barta and Giraldeau 1998; Bicca-Marques and Garber 2005; King *et al.* 2009; Liker and Barta 2002). The data did not uphold this prediction. Even though dominant vervets obtained a larger share of resources than subordinates when acting as producers or scroungers, they foraged on the front, outside edge of the group. Our analyses showed that dominant vervets may forage in this riskier spatial position because they obtained proportionately more resources when acting as producers than when acting as scroungers. In other species besides vervets, dominant individuals have been shown to predominantly act as producers rather than scroungers (birds: Beauchamp 2006; Giraldeau and Lefebvre 1986; Giraldeau *et al.* 1990; Robinette Ha and Ha 2003).

Compared to other spatial positions, individuals on the front, outside edges of groups have the largest influence on the direction of group movements (Bumann and Krause 1993; Burns *et al.* 2012; Couzin and Krause 2003; Huth and Wissel 1992). We do not have evidence that vervets that maintained positions on the front, outside edge controlled group movements. However, any influence over the direction of group movement may have been beneficial for higher ranking vervets. Being on the outside edge provides foraging advantages in several ways. For large food resources that are

known to the whole group, such as fruiting trees, arriving first may allow individuals to get prime feeding sites within the patch; in addition, small, high-quality food items such as insects are often randomly positioned in space and consumed by the first individual to find them (Hirsch 2007a). These foraging benefits may outweigh the potential risks of being on the periphery of the group. Indeed, though vervets at Nabugabo often ate from large fruiting trees, they primarily moved through their range on the ground, foraging as they went, on insects in grass and low shrubs. Because patch richness was an important factor determining the number of scroungers at a discovery patch (Giraldeau and Beauchamp 1999; Giraldeau and Livoreil 1998; Vickery *et al.* 1991; this study) and producers could only monopolize all or most of the food in poor patches, the importance of small, mobile insects for foraging vervets at Nabugabo may mean that the benefits of being on the front, outside edge for dominant individuals could be tremendous.

We found no significant effect of age on intragroup spatial position. Adults, subadults, and juveniles were found throughout the group. We expected juveniles to stay in the group's center owing to their greater risk of predation compared to adults (Janson and van Schaik 1993); however, they most frequently brought up the rear of the group. Likely as a result of this spatial positioning, juveniles never found discovery patches. It is possible that, when the vervet group was feeding on rich patches or foods that required a longer time period to deplete (*cf.* long-search substrates, Janson 1990b), individuals ended up at the rear of moving groups because they were still feeding and the group kept moving forward past them. A more thorough investigation of foraging strategies in relation to spatial position is needed to determine if this is the case.

Individual vervets were flexible in the degree to which they used producer or scrounger strategies at our discovery patches, as shown for other species, e.g., birds (Beauchamp 2001; Giraldeau and Lefebvre 1986; Giraldeau *et al.* 1994; Morand-Ferron *et al.* 2007), emperor's tamarins (*Saguinus imperator*), saddleback tamarins (*S. fuscicollis*: Bicca-Marques and Garber 2005), and *Papio ursinus* (King *et al.* 2009). Only 2 of 15 individuals used a single tactic. Two adult females only scrounged and never found patches, though given greater opportunities (a larger sample) this result may not persist. Both of these females consistently foraged in the center of the group and were mid-ranking. One of these females also had the youngest infant. In fact, during our research, both females that had young infants maintained positions in the center of the group. It would be informative to replicate this study at a time when the alpha female has an infant to see whether she alters her strategy of foraging on the front, outside edge.

The finder's share for vervets at Lake Nabugabo decreased with larger patch richness and increased with rank. These results resemble those found for *Cebus apella* by Di Bitetti and Janson (2001). However, Di Bitetti and Janson (2001) also found that the finder's share increased for individuals of all ranks when conspecifics were further away and it took longer for them to arrive at a food site. We did not find that the distance of conspecific scroungers at the time of patch discovery affected the finder's share. This may be due to the openness of the area. We often set discovery patches in areas that could be seen from a long distance; so once they had been detected by the producer, other individuals that were quite far away would detect them as well and quickly approach on the ground. Replication of this study in more densely forested

areas, with food patches set in trees, may demonstrate that producers gain an advantage when they are further from conspecifics and sight lines are blocked.

In summary, vervets differed from some other species (primates: Di Bitetti and Janson 2001; Hall and Fedigan 1997; Janson 1990a; Robinson 1981; spiders, birds, fish, ungulates: reviewed in Krause 1994) and modeled simulations (Barta *et al.* 1997; Evers *et al.* 2011; Hemelrijk 1998, 2000) by showing a pattern of high-ranking individuals maintaining positions on the front, outside edge of their group. They appeared to tolerate increased predation risk in this position to access food patches first. Our results are intriguingly similar to those obtained for a member of the racoon family (Procyonidae), the ring-tailed coati (*Nasua nasua*). Hirsch (2007c, 2011a,b) also found that, despite the increased risk of predation (Di Blanco and Hirsch 2006), dominant coatis maintained positions on the front edge of moving groups (though in this case, dominant individuals were juveniles) and had higher feeding success. Adult female coatis were also most often found in the center of the group. Notwithstanding their evolutionary distance, vervets and coatis share several behavioral and physical traits. These medium-sized mammals both form mixed-sex groups of phylopatric females and immigrant males with linear dominance hierarchies. Both species forage (often terrestrially) for fruit and invertebrates and exploit new food types opportunistically (Hirsch 2007b,c, 2009, 2011a; Jaffe 2011). Why vervets would be more similar to coatis in their spatial positioning than other examined primate species is a subject for debate, but it may be related to an evolved response to predation risk by relatively terrestrial animals. Sit-and-wait predators are suggested to attack at short distances and may thus be able to capture individuals at all spatial positions in a group (Hirsch and Morrell 2011). Perhaps terrestrial foragers face a higher risk from sit-and-wait predators than from pursuit predators, relative to primarily arboreal animals. Thus, the evolved response to avoid dangerous areas on the edge of the group may not be as strong, despite current predation pressure. This hypothesis awaits further investigation.

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