Be early or be tolerated: vervet monkey, *Chlorocebus pygerythrus*, foraging strategies in a dispersed resource

Ming Fei Li [a] , T. Jean M. Arseneau-Robar [a], Eve A. Smeltzer [a], Julie A. Teichroeb [a, b, *]

[a] *Department of Anthropology, University of Toronto, Toronto, ON, Canada*
[b] *Department of Anthropology, University of Toronto Scarborough, Toronto, ON, Canada*

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Among social foragers, individuals can actively search for and find food (the producers) or join already discovered food patches (the scroungers). Compared to scroungers, producers often occupy more dangerous outer spatial positions in the group, but they benefit from the finder's advantage, which is the amount of food eaten before the arrival of others. Scroungers may occupy safer positions but they face feeding competition when joining a patch already occupied by others. Here, we report factors influencing intragroup spatial position, feeding strategies and feeding success for a group of wild vervet monkeys, *C. pygerythrus*, at Lake Nabugabo, Uganda. We collected data using behavioural observations and field experimentation ($N = 132$ trials) where we set up an artificial food patch with dispersed food rewards. We found that individuals who spent more time in the front-outer position of a moving group produced more. Producers that had a greater finder's time advantage (fed undetected by group members for longer periods) had a greater finder's advantage (consumed more food items before the arrival of other group members), and scroungers that arrived earlier had greater overall feeding success. We found that when the scrounger was higher ranking than other individuals at the patch, they used displacement scrounging (supplanted at least one individual from the patch to gain access to the food resource). However, feeding success did not differ between displacement scrounging and tolerated scrounging (when the scrounger fed at the patch with at least one other individual). Interestingly, we did not find higher-ranking individuals to have greater feeding success than lower-ranking individuals. Our findings corroborate previous studies showing that even among species with a linear dominance hierarchy and high occurrences of within-group contest competition, dominant individuals do not benefit from feeding advantages at large, dispersed food patches since they cannot monopolize the resource. Furthermore, our results emphasize the need to understand factors influencing feeding tolerance, particularly for subordinate individuals, who need to process ecological and social elements to maximize their food acquisition.

Socially foraging animals have to trade off the benefits of group living (e.g. reduced predation risks, information sharing) with the costs of within-group competition for resources such as food, space and mating opportunities (van Schaik, 1983, 1989). Optimal foraging theory predicts that individuals should forage in a manner that maximizes their net energy intake to improve overall fitness (Charnov, 1976; Pyke, 1984; Schoener, 1971). Foraging strategies are affected by ecological factors such as resource distribution (clumped versus dispersed) (van Schaik, 1989; van Schaik & Janson, 1988), the rate of depletion (Charnov, 1976) and habitat risk (Barta, Liker, & Mónus, 2004; Sih, 1980; Stephens, 1981). For group-living animals,

the payoff of a foraging strategy is also frequency dependent on the strategies of other group members who are competing for shared resources (Giraldeau & Beauchamp, 1999; Giraldeau & Dubois, 2008; Giraldeau & Livoreil, 1998). When foraging in a group, individuals can either actively search for and find food (the producers) or join an already discovered food patch (the scroungers) (Barnard & Sibly, 1981; Ranta, Peuhkuri, Laurila, Rita, & Metcalfe, 1996). Compared to scroungers, producers invest more time and energy into discovering resources and are more likely to encounter risks in the environment while foraging (Caraco & Giraldeau, 1991; Janson, 1990b; Mathot & Giraldeau, 2007). However, producers benefit from the finder's advantage, which is the number of food items eaten before the arrival of other group members (Caraco & Giraldeau, 1991; Giraldeau, Hogan, & Clinchy, 1990; Ranta et al., 1996;

* Corresponding author.
E-mail address: julie.teichroeb@utoronto.ca (J. A. Teichroeb).

Vickery, Giraldeau, Templeton, Kramer, & Chapman, 1991). While scroungers exploit the discovery of other group members and are exposed to fewer environmental risks, they face increased feeding competition when joining a patch already occupied by other individuals. In other words, in addition to individual foraging strategy (producer versus scrounger), it is also important to examine an individual's decision to join a patch (i.e. to scrounge or not) in the presence of intragroup competition. Therefore, in addition to the influence of environmental factors on foraging behaviours, social foragers are greatly affected by the social context, and these factors determine their foraging strategy and success.

Among species with a marked dominance hierarchy, dominance rank mediates access to resources, with dominant individuals having priority of access due to their ability to outcompete subordinates via contest competition (Isbell, 1991; Sterck, Watts, & van Schaik, 1997; van Schaik, 1989). Barta and Giraldeau (1998) predicted that strong differences in competitive ability will result in dominants mainly using the scrounger strategy and subordinates using the producer strategy. The preference for scrounging by more dominant individuals has been reported in several taxa (e.g. emperor tamarins, *Sanguinus imperator,* and saddleback tamarins, *Sanguinus fuscicollis*: Bicca-Marques & Garber, 2005; Mexican jays, *Aphelocoma ultramarina*: McCormack, Jablonski, & Brown, 2007; house sparrows, *Passer domesticus*: Lendvai, Liker, & Barta, 2006). The effects of social status are expected to be most pronounced when resources are clumped and defendable (for reviews see Giraldeau & Dubois, 2008; Grant, 1993; van Schaik, 1989). Studies with primates (King, Isaac, & Cowlishaw, 2009; Lee & Cowlishaw, 2017; Whitten, 1983) have shown that dominants have greater feeding success (i.e. obtain more food) when patches are rich and clumped. Even among species with a linear dominance hierarchy and generally high within-group contest competition, a high-ranking individual is unable to defend a large food patch (Hirsch, 2007; van Schaik, 1989). Therefore, when resources are dispersed (i.e. accessible to all group members and cannot be monopolized by one or a few individuals), scramble competition should take precedence and resource access becomes less dependent on the dominance hierarchy. Although most studies have found that dominant individuals tend to be scroungers, some studies have found the opposite or no effect of social status on foraging strategy (common marmosets, *Callithrix jacchus*: De la Fuente et al., 2019; rooks, *Corvus frugilegus*: Jolles, Ostojić, & Clayton, 2013; vervets, *C. pygerythrus*: Teichroeb, White, & Chapman, 2015; zebra finches, *Taenopygia guttata*: Beauchamp, 2006).

Within-group competition also occurs for intragroup spatial positions, and studies have shown that dominant individuals tend to occupy central positions in a group, especially when predation risk is high in their environment (Barta, Flynn, & Giraldeau, 1997; Dostie et al., 2016; Hall & Fedigan, 1997; Heesen, Macdonald, Ostner, & Schülke, 2015; Janson, 1990; but see Josephs, Bonnell, Dostie, Barrett, & Henzi, 2016). Central positions in a group are safer since the risk of predation is lower in the middle than on the periphery of the group (Bumann, Rubenstein, & Krause, 1997; Hamilton, 1971). Individuals' intragroup spatial positions while the group is moving can in turn influence their foraging strategies (Beauchamp, 2008; Hirsch, 2007; Janson, 1990a, 1990b; Mónus & Barta, 2008). Animals at the leading edge of a foraging group are more likely to discover food sources and assume the producer strategy. From an ecological perspective, the front-central position (just behind the leading edge) in a foraging group is an ideal location for scroungers to monitor and exploit other's food discoveries (Barta et al., 1997; Di Bitetti & Janson, 2001). This is particularly advantageous for dominant individuals who can displace the producer from the food patch and exploit their discovery. However, when producing confers greater feeding success

than scrounging or when predation risk is low in the environment, dominants may trade off the safety of a central position for a front peripheral position where they could assume a more advantageous foraging strategy (Teichroeb et al., 2015). Furthermore, producers can increase their finder's advantage by increasing their interindividual distance, which can increase the time delay before the arrival of scroungers (Bicca-Marques & Garber, 2005; Di Bitetti & Janson, 2001; Dubuc & Chapais, 2007).

It is apparent that an individual's intragroup spatial positioning, foraging strategy and feeding success are interrelated. However, field studies on producer–scrounger strategies are rare compared to work on captive subjects, and results from existing studies provide conflicting evidence for the predictive capabilities of various socioecological variables on individual spatial positions and foraging strategies. In this study, we use an experimental approach to investigate the effects of age, sex and dominance rank on intragroup spatial position, foraging strategy and feeding success in a group of wild vervet monkeys, *C. pygerythrus*, at Lake Nabugabo, Uganda. We collected observational data on intragroup spatial position, both while the group was stationary (i.e. middle and outer positions) and moving (i.e. front-outer, front-middle and back positions) (Appendix, Fig. A1). Our experimental set-up was inspired by previous work on vervet monkeys at Lake Nabugabo that compared foraging strategies using small and large clumped food patches (Teichroeb et al., 2015). Our experiment consisted of trials in which we set up an artificial food patch for the group to discover. The provided food patch was large enough for multiple individuals to feed at the same time and food items were dispersed enough that dominant individuals were not able to monopolize the entire food patch. This set-up facilitated scrounging, allowing us to gain a greater understanding of vervet foraging strategies.

Adult males are larger and have longer canines than female vervet monkeys and are therefore less vulnerable to predators (Isbell, 1994). Males are also the dispersing sex, so they are more likely to spend time on the periphery of the group to detect and interact with neighbouring groups. Therefore, we expected adult and subadult males to be in the outer position of the group and be more likely to produce than other individuals (Appendix). Furthermore, we expected individuals who showed a greater propensity to spend time in the front-outer position to be more comfortable moving further ahead of the group, and that these individuals would tend to arrive at food patches earlier and obtain a greater finder's advantage as a result. We predicted that higher-ranking individuals would be in the middle of the group both while stationary and moving since central positions are generally preferred due to their safety from predators (Hamilton, 1971; Janson, 1990a; Robinson, 1981). We also expected higher-ranking individuals to scrounge more and obtain more food as scroungers than lower-ranking individuals.

In addition to the binary producer–scrounger strategies, we also investigated different types of scrounging used by individuals. A study on free-ranging ravens, *Corvus corax*, found that the use of different scrounging techniques (e.g. aggressive displacement, stealing) was dependent on social status and state of food depletion (Bugnyar & Kotrschal, 2002). Studies on producer–scrounger strategies rarely explore the different ways that individuals scrounge, which can have important implications for their feeding success. In our study, we classified scrounging into three types: (1) displacement scrounging, when the scrounger supplants at least one individual from the patch and gains access to the food resource; (2) tolerated scrounging, when the scrounger feeds at the patch with at least one other individual; and (3) untolerated scrounging, when the scrounger either snatches food from the patch and quickly departs or attempts to feed at the patch but receives aggression from another individual. We decided to include 'snatch

and go' scrounging as untolerated scrounging because individuals who used this type of scrounging likely anticipated being untolerated and wanted to avoid aggressive interactions at the patch. Although we refer to these as scrounging types, we want to highlight that while displacement scrounging is the action of the scrounger, the other two scrounging types reflect the actions of group members in response to the scrounger (i.e. tolerating or not tolerating the scrounger) rather than the actions of the scrounger themselves. We predicted that displacement scrounging would be used more by higher-ranking individuals and would be the scrounging type that provided the greatest feeding success. We also predicted that females would be tolerated more than males by foragers of both sexes since (1) within-group females are more likely to be related to each other and tolerance to food sharing may be a strategy to maximize inclusive fitness (Chapais & Belisle, 2001; King, Clark, & Cowlishaw, 2011) and (2) males may be more tolerant towards female scroungers as a way of trading feeding tolerance for mating opportunities (Dubuc, Hughes, Cascio, & Santos, 2012; Noë & Hammerstein, 1994).

METHODS

Study Site and Subjects

We carried out this study at Lake Nabugabo, Masaka District, central Uganda (0°22′−12°S, 31°54′E). Lake Nabugabo (8.2 × 5 km) lies at an elevation of 1136 m and is a satellite lake to Lake Victoria. The study subjects were a habituated group of vervet monkeys, *C. pygerythrus*, called KS group, that has been followed continuously since 2016. Vervet monkeys live in multimale, multifemale groups and despite females' smaller body and canine sizes, studies have demonstrated that females can outrank males and vervet monkeys can have an integrated hierarchy with both sexes (Hemelrijk, Wubs, Gort, Botting, & van de Waal, 2020; Struhsaker, 1967; Young, McFarland, Barrett, & Henzi, 2017). The home range of KS group consists of a mix of open woodland, grassland and farmland and a few buildings. The landscape of Lake Nabugabo is highly human-modified, and although the vervet monkeys at our study site primarily feed on natural foods, they will supplement their diet with anthropogenic foods (Chapman et al., 2016). Despite having more access to human foods throughout the year compared to groups in more natural and less disturbed habitats, resources are still limited and not sufficient to satiate all members of the group. Thus, feeding competition is prevalent in KS. Because of their flexible diet and semiterrestriality, vervet monkeys are an ideal species for foraging experiments. We were able to identify all individuals in the group by their natural features. At the beginning of the study, KS group consisted of 42 individuals: six adult males, 11 adult females, three subadult males, five subadult females and 17 juveniles and infants. Over the course of the study, one adult male and one subadult male dispersed, two infants died of unknown causes and one infant was born. KS group had participated in foraging experiments in the past (Kumpan et al., 2019, 2020).

Behavioural Observations

We followed KS group during 0730−1700 hours, 6 days a week, for 3 months (June−August 2019). We collected behavioural data using scan sampling, instantaneous focal animal sampling, all occurrences sampling and ad libitum sampling (Altmann, 1974). Every 30 min, we conducted a scan of the group over a 10 min period, during which the instantaneous activity and position of each individual was recorded, for as many individuals as possible. We collected a total of 366 group scans and 4657 individual scans. During these scans, we recorded the time, individual identity (ID),

state behaviour (feeding, resting, moving or social) and spatial position. See Appendix for how we recorded intragroup spatial positions. In between group scans, we opportunistically conducted 5 min instantaneous focal animal samples on adults and subadults (N = 539, 45 h). We generated a randomized list of focal individuals to ensure that individuals were sampled at different times during the day. During instantaneous focal animal samples, we recorded the individual's state behaviour at the beginning of every minute (Altmann, 1974). In other words, there were six 'focal points' within each focal sample period (0, 1, 2, 3, 4, 5 min). At each focal point, we recorded the time, IDs of near neighbours within 5 m and the focal individual's state behaviour (e.g. feed, rest, move, social). Throughout the focal, we recorded all-occurrences of social (including actor and recipient) and self-directed events. We collected focal data on an iPad using the Animal Observer application (v.1.2.2) designed by Damien Caillaud from the Dian Fossey Gorilla Fund International.

In addition, we used ad libitum sampling to record social behaviours (i.e. agonistic, affiliative and sex interactions) that occurred outside of focal animal samples. Sampling bias was minimal since observers were always moving around the group during group scans, which ensured random samples of individuals and behaviours. The majority of KS group's home range was open and had excellent visibility, so upon hearing a conflict, we were able to record the agonistic interaction, including the outcome and identities of individuals who were involved. We compiled all agonistic interactions from focal and ad libitum data into a win−loss sociomatrix for each sex. We confirmed a linear hierarchy among adults and subadults for both females (N = 16 individuals, 367 interactions, $h' = 0.70$, $P < 0.001$) and males (N = 9 individuals, 278 interactions, $h' = 0.81$, $P = 0.001$) (de Vries, 1995). We used the updated I&SI method, which is a way to calculate ordinal ranks where there is linearity in the hierarchy (Schmid & de Vries, 2013), to determine the best intrasex dominance rank for each individual (Spearman rank correlation: $r_S = 0.98$ for females and 0.98 for males). We also constructed an integrated dominance hierarchy with adults and subadults from both sexes (N = 25 individuals, 866 interactions, $h' = 0.44$, $P < 0.001$; Spearman rank correlation: $r_S = 0.89$). We found that the alpha female (ASP) ranked third in the integrated hierarchy, following the alpha and beta males, and that several adult and subadult females ranked above subadult males. Just like Young et al.'s (2017) finding from vervet monkey groups in South Africa, females in KS group also showed co-dominance with males. We assigned individuals to the upper, middle or lower rank tier based on whether they were in the upper third, middle third or lower third of the integrated hierarchy. The upper tier consisted of all adult males and the alpha and beta females. We used rank tiers because these are more robust to slight changes in dyadic relationships compared to ordinal ranks. Because of the lack of agonistic interactions recorded for juveniles and infants, we did not assign ordinal ranks for them. We placed juveniles and infants (N = 10) below their mothers, within the same rank tier as their mother, since matrilineal inheritance of rank and maternal coalitionary support exists in many cercopithecines (Chapais, 1992), including vervet monkeys (Fairbanks & McGuire, 1984; Horrocks & Hunte, 1983). We placed orphaned juveniles and infants (N = 5) who were without maternal support in the lower tier. We did not include juveniles and infants that were born or had died during the study period. Information on intrasex and integrated dominance ranks of individuals in KS group are included in the Appendix (Table A1).

Foraging Experiment

We set up an artificial 'discovery food patch' by evenly distributing 20 slices of matoke (*Musa acuminata*) on a 1.75 × 1.75 m blue

plastic tarp (Fig. 1). Matoke, also known as the East African Highland banana, is a starchy variety of banana and is a staple crop in Uganda. It is widely available for purchase from farmers around our study site and vervet monkeys often feed on discarded matoke, so they recognize this as a food resource. The continued use of the blue tarp allowed the monkeys to have a salient visual cue indicating the presence of food. The discovery patch was placed in random locations ahead of the group's foraging path. Since we were familiar with KS group's daily movement patterns, we were mostly able to anticipate their line of travel and efficiently set up experimental trials. All experiment equipment was hidden inside our backpacks, and if any individual saw us setting up the patch, we terminated the trial. It was important that the patch was set up randomly since this experiment depended on the monkeys' ability to discover the food patch rather than predict where it would be. Several trials had to be abandoned because no individual discovered the patch. We ran a total of 132 trials during the study period, with a maximum of five trials per day, but not all trials reached completion (see Data Analyses section). We videotaped the trials and one author (M.F.L.) coded the videos using the BORIS v.7.7.3 software (Friard & Gamba, 2016).

Once an individual looked directly at the patch and started quickly moving towards it, we assigned the individual as a 'Discoverer' and recorded their ID and the distance from that individual's position to the tarp (m). The first individual to reach the patch was the 'Producer' and subsequent individuals who joined the patch were the 'Scroungers'. We conducted focal animal sampling on each participant in the trial and recorded their times of discovery, arrival time, departure time, number of matoke slices obtained and all occurrences of social interactions. For scroungers, we identified the type(s) of scrounging used. Since there was often more than one individual at the patch when a new scrounger arrived, some scroungers used multiple types of scrounging during the same trial. For example, a scrounger can simultaneously displace certain individuals from the patch and also be tolerated by other individuals at the patch. Therefore, we noted the IDs of the receivers (i.e. individuals already on that tarp) for each scrounging type. For scrounging interactions that occurred among individuals of the same sex, we assigned relative dominance according to their ordinal ranks. For scrounging interactions that occurred among individuals from different sexes, we assigned relative dominance according to their rank tiers, with the exception of the top two ranking males (JLY and OTS), who were higher ranked than all females. We also used rank tier for interactions involving juveniles and infants, with the exception of interactions between mother and offspring, in which case the mother always ranked higher. Relative

Figure 1. Foraging experiment set-up of discovery patch (1.75 × 1.75 m blue plastic tarp) with 20 matoke slices spread out on top.

dominance categories were: 'higher' when the scrounger was higher ranked than all other individuals at the patch, 'lower' when the scrounger was the lowest ranked, 'mixed' when the scrounger ranked differently relative to different individuals at the patch and 'same' if they were in the same rank tier.

Ethical Note

The methods used in this study were approved by the Uganda Wildlife Authority (permit no. UWA/COD/96/02), the Uganda National Council for Science and Technology (Protocol Approval no. NS 537) and the University of Toronto Animal Care Committee (UACC Protocol no. 20011416). The methods also adhered to the ASAB/ABS Guidelines for the use of animals in research. This group of vervet monkeys was fully habituated and all individuals were comfortable with humans in proximity. Observers kept a minimum of 5 m from the monkeys during behavioural observations and foraging trials. We specifically designed the experiment using a much larger patch size than the set-up from a previous study (Teichroeb et al., 2015) in order to reduce food competition and mitigate conflict. Individuals were not captured, handled or restrained in any way. Participation in foraging trials was voluntary and individuals were free to depart from the food patch at any time.

Data Analyses

See Appendix for analyses on stationary and moving intragroup spatial positions. For the tendency to produce, we ran a GLMM with binomial distribution and set the response variable as '1' if the individual produced and '0' if they did not. Our predictors were age−sex class, rank tier and propensity to be found in the front-outer position (calculated as the number of scans an individual was in the front-outer position divided by the total number of moving group scans for that individual). For all categorical variables with multiple levels, we set one level as the reference against which all other levels were compared; reference levels are specified in our results tables. Since only one trial had a juvenile producer, we excluded this trial from our analyses ($N = 131$ trials) and only looked at adults and subadults ($N = 25$ individuals). Some trials did not start with 20 pieces due to the previous trial being incomplete (e.g. trial was interrupted, producer abandoned the patch after eating a few pieces and no other individuals showed up), so we had set up a 'half-trial' with the remaining pieces. We decided to include these half-trials for the tendency to produce model because the number of pieces on the discovery patch should not affect the propensity to produce, since vervet monkeys would still be able to discover the blue tarp. We set individual ID as the random effect since we had repeated measures for several individuals. We also included trial order across the day as a random effect because the timing of the trial could affect animals' motivation to participate. For example, individuals might be less motivated to produce during later trials in the day because they were already satiated from feeding in their home range and/or from a previous trial. We removed all data from one adult male from our analysis, as his observations were outliers that exerted strong leverage on the model. This male was actively seeking dispersal opportunities, as he was commonly on the extreme periphery of the group, often approached neighbouring groups without behaving aggressively and dispersed during the study. As a result, we believe his propensity to be in the front-outer position was due to his prospecting behaviour rather than his adopting a producer foraging strategy. The results reported reflect the final GLMM with this outlier excluded. In examining the factors explaining the tendency to scrounge, we used a GLMM with a binary response variable and the same predictors as our tendency to produce model. However, in

this model we included juveniles and infants ($N = 40$ individuals) as this age class often scrounged. For each trial, we excluded the individual that produced since they cannot produce and scrounge in the same trial. We only included trials in which the tarp had been stocked with 20 pieces of matoke at the onset and there was at least one scrounger ($N = 107$ trials, $N = 350$ scrounging events). Again, we included individual ID and trial order as a random effect in this model.

To look at feeding success, we ran four GLMMs using a Poisson distribution: (1) finder's advantage (i.e. number of pieces of matoke eaten in each trial before first scrounger arrived); (2) producer's feeding difference (i.e. the difference between the total amount of food eaten and the finder's advantage in each trial); (3) scrounger's feeding success (i.e. number of pieces eaten as a scrounger per trial); (4) overall feeding success (i.e. total amount eaten per trial, in producer and scrounger roles). Since all four response variables showed overdispersion, we included observational level random effects (OLRE) by assigning a unique number for each row of observation (Harrison, 2014). OLRE was used in all four models to account for overdispersion in a Poisson distribution (Elston, Moss, Boulinier, Arrowsmith, & Lambin, 2001; Harrison, 2014). We set individual ID (to control for repeated measures of individuals) and trial order (to control for changes in individual motivation throughout the day) as random effects. With the exception of the producer's feeding success model, we included individual ID as a nested random effect within trial number because the identities of participants in a particular trial could affect how much food an individual was able to obtain in that trial. The other random effects were crossed. See Table 1 for a summary of the predictor variables and random effects included in each feeding success model.

To look at the different scrounging types, we only included scrounging events in which there was at least one receiver already present and feeding at the patch when the scrounger arrived ($N = 358$ scrounging events). We ran a multinomial logistic regression with scrounging type as the response variable (displacement scrounging as the reference category) and set predictors as age—sex, rank tier, relative rank and arrival time. To assess whether feeding success differed between the scrounging types, we used a GLMM with Poisson distribution and set the number of pieces obtained per trial as the response variable and scrounging type as the predictor (tolerated scrounging set as reference category). For this model, we only included the scrounging type(s) of individuals that participated once (i.e. we excluded scroungers that left and then returned to the patch) ($N = 292$ scrounging events). We set individual ID, trial number, trial order and observation number (to account for overdispersion) as random effects. Once again, individual ID and trial number were nested while the other random effects were crossed.

All statistical analyses were performed in R Studio (v.1.1.463, 2009—2018 RStudio Inc.; R v.4.0.1) for Mac OS X (R Core Team, 2020). We used the following packages: 'compete' for constructing dominance hierarchies (Curley, 2016), 'lme4' for fitting GLMMs (Bates, Mächler, Bolker, & Walker, 2015), 'nnet' for multinomial logistic regressions (Venables & Ripley, 2002), 'MuMIn' (Bartoń,

2020), 'DHARMa' for model diagnostics (Hartig, 2020) and 'ggplot2' for creating figures (Wickham, 2016). Overall model significance was determined by comparing the final model with the null model, which included only the random effects, using a likelihood ratio test. We also report the marginal and conditional R^2 values for all GLMMs and the McFadden pseudo R^2 for the multinomial logistic regression. The marginal R^2 reflects variance explained by the fixed effects while the conditional R^2 reflects variance explained by both fixed and random effects (Nakagawa & Schielzeth, 2013). All statistical tests were two-tailed, with alpha set to 0.05 for significance.

RESULTS

Producer—Scrounger Strategies

During our foraging experiment ($N = 132$ trials), 22 (21 adults/subadults, one juvenile) out of 40 individuals produced and 37 individuals scrounged at least once. One adult female and two infants never participated in the experiment, so they were not counted as producers or scroungers in any trial (Fig. 2). In two out of 132 trials, the identity of the discoverer differed from the producer. On average, individuals discovered the patch while they were 25.04 m away ($\pm$ SD 13.73) and 3.27 individuals ($\pm$ SD 2.06) scrounged during a trial. Rank tier did not significantly affect an individual's tendency to produce, but age—sex and the use of the front-outer position did have effects (Table 2). Adult females with an infant produced less than adult males ($\beta = -1.80$, $P = 0.009$) (Table 2). Individuals that showed a greater propensity to spend time in the front-outer position produced more ($\beta = 6.79$, $P < 0.001$). Age—sex and rank tier had significant effects on an individual's tendency to scrounge (Table 2). Subadult females ($\beta = 1.48$, $P = 0.044$) and subadult males ($\beta = 1.94$, $P = 0.007$) scrounged more than adult males (Table 2). Tendency to scrounge did not differ between adult females and adult males, or between juveniles/infants and adult males (Table 2). Individuals in the lower ($\beta = -2.27$, $P < 0.001$) and middle ($\beta = -1.47$, $P = 0.004$) rank tiers scrounged less compared to individual in the upper tier (Table 2). The proportion of front-outer position use did not have an effect on the tendency to scrounge (Table 2).

Feeding Success

Producers obtained a mean finder's advantage of 5.13 pieces ($\pm$ SD 3.78), a mean total of 7.42 pieces ($\pm$ SD 4.17) and had a mean time advantage of 1.83 min ($\pm$ SD 1.87) before scroungers arrived. We did not find significant effects of age—sex or rank tier on the finder's advantage (Table 3). Only the finder's time advantage significantly affected the finder's feeding advantage; producers that were able to feed undetected by their group members for longer time periods consumed significantly more food ($\beta = 0.21$, $P < 0.001$; Table 3, Fig. 3a). None of the predictors (i.e. age—sex and rank tier) were significant in the producer's feeding difference model, and the overall model was also not significantly different

Table 1
Summary of feeding success models with indication of which variables were included

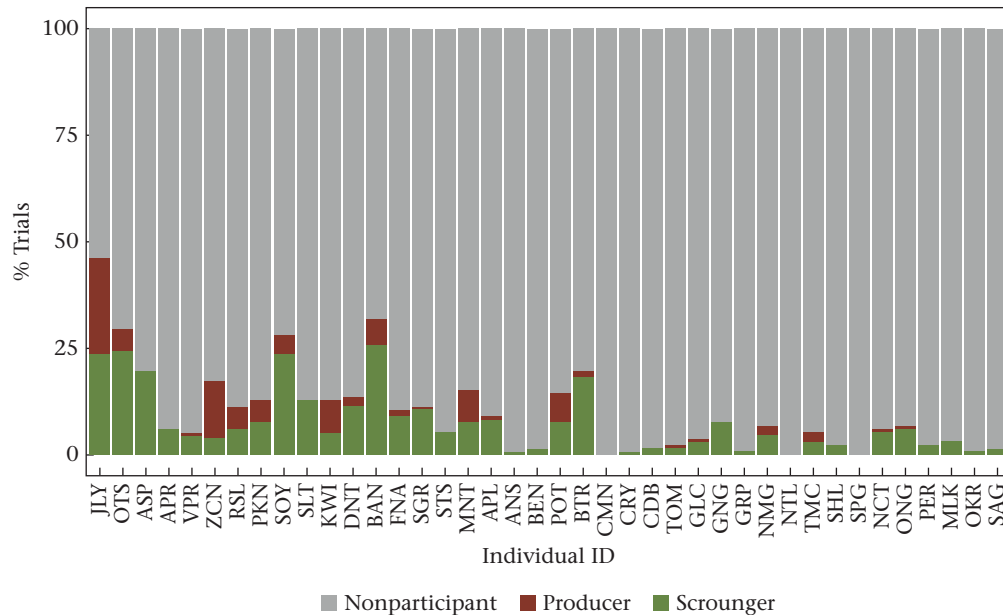| Model	Predictor variable					Random effect			
	Age—sex	Rank tier	Time advantage	Arrival time	Foraging strategy	Ind ID	Trial num.	Trial order	Obs. num.
Producer's success	×	×	×			×		×	×
Producer's difference	×	×				×	×	×	×
Scrounger's success	×	×		×		×	×	×	×
Overall success	×	×		×	×	×	×	×	×

Figure 2. The percentage of trials ($N = 132$) in which an individual produced, scrounged and did not participate. Individuals are ordered based on intersex dominance rank from high (left side of the figure) to low (right side).

Table 2
Summary of GLMM for the effects of age−sex, rank tier and proportion of front-outer position use on the tendency to produce and scrounge

Predictor variable	β (SE)	z	P
Tendency to produce[a]			
(Intercept)	−4.56 (0.64)	−7.18	<0.001
Age−sex			
Adult male (reference)	—	—	—
Adult female	−0.03 (0.59)	−0.06	0.954
Adult female + infant	**−1.80 (0.69)**	**−2.61**	**0.009**
Subadult female	−0.72 (0.67)	−1.06	0.288
Subadult male	−0.60 (0.65)	−0.92	0.359
Rank tier			
Upper (reference)	—	—	—
Lower	−0.45 (0.59)	−0.76	0.447
Middle	0.88 (0.59)	1.50	0.133
Front-outer use	**6.79 (1.72)**	**3.95**	**<0.001**
Tendency to scrounge[b]			
(Intercept)	−1.84 (0.79)	−2.34	0.019
Age−sex			
Adult male (reference)	—	—	—
Adult female	0.84 (0.74)	1.14	0.256
Adult female + infant	0.58 (0.70)	0.83	0.405
Subadult female	**1.48 (0.73)**	**2.02**	**0.044**
Subadult male	**1.94 (0.72)**	**2.69**	**0.007**
Juveniles and infants	0.01 (0.80)	0.02	0.986
Rank tier			
Upper (reference)	—	—	—
Lower	**−2.27 (0.46)**	**−4.92**	**<0.001**
Middle	**−1.47 (0.51)**	**−2.88**	**0.004**
Front-outer use	−0.49 (1.97)	−0.25	0.804

Significant effects ($P < 0.05$) are shown in bold.
[a] Overall model fit compared to the null model, which included only the random effects: $N = 3144$, $\chi^2 = 35.85$, $P < 0.001$. Marginal $R^2 = 0.31$, conditional $R^2 = 0.33$.
[b] Overall model fit compared to the null model, which included only the random effects: $N = 4173$, $\chi^2 = 33.50$, $P < 0.001$. Marginal $R^2 = 0.20$, conditional $R^2 = 0.31$.

Table 3
Summary of producer's feeding success GLMM for the effects of age−sex, rank tier, and finder's time advantage on the finder's advantage in a given trial

Predictor variable	β (SE)	z	P
Intercept	1.21 (0.10)	12.19	<0.001
Age−sex			
Adult male (reference)	—	—	—
Adult female	-0.12 (0.26)	-0.47	0.642
Adult female + infant	0.43 (0.43)	1.01	0.312
Subadult female	-0.34 (0.39)	-0.86	0.392
Subadult male	-0.23 (0.37)	-0.64	0.526
Rank tier			
Upper (reference)	—	—	—
Lower	-0.12 (0.39)	-0.32	0.753
Middle	-0.12 (0.33)	-0.38	0.705
Time advantage	**0.21 (0.03)**	**7.86**	**<0.001**

Overall model fit compared to the null model, which included only the random effects: $N = 106$, $\chi^2 = 64.05$, $P < 0.001$. Significant effects ($P < 0.05$) are shown in bold. Marginal $R^2 = 0.41$, conditional $R^2 = 0.41$.

$P < 0.001$), adult females with an infant ($\beta = -0.60$, $P < 0.001$), subadult females ($\beta = -0.60$, $P < 0.001$) and juveniles/infants ($\beta = -1.27$, $P < 0.001$) obtained significantly less food as scroungers compared to adult males (Table 5). Subadult males also tended to obtain less food than adult males, but the difference was not significant ($\beta = -0.37$, $P = 0.054$). Rank tier did not have a significant effect on scrounger's feeding success, although there was a nonsignificant tendency for individuals in the lower rank tier to obtain more food than individuals in the upper tier ($\beta = 0.29$, $P = 0.054$; Table 5). There was no difference in feeding success between scroungers in upper and middle tiers (Table 5). Arrival time had a significant negative effect, which meant scroungers that arrived at the patch later obtained significantly less food ($\beta = -0.09$, $P < 0.001$; Table 5; Fig. 3b).

On average, each participant in the foraging experiment obtained a mean of 4.41 pieces ($\pm$ SD 3.68). We found that foraging strategy, age−sex and arrival time had significant effects on the total number of pieces eaten (Table 6). Producers obtained significantly more total food than scroungers ($\beta = 0.25$, $P = 0.003$; Table 6, Fig. 4). Adult females ($\beta = -0.41$, $P < 0.001$), adult females
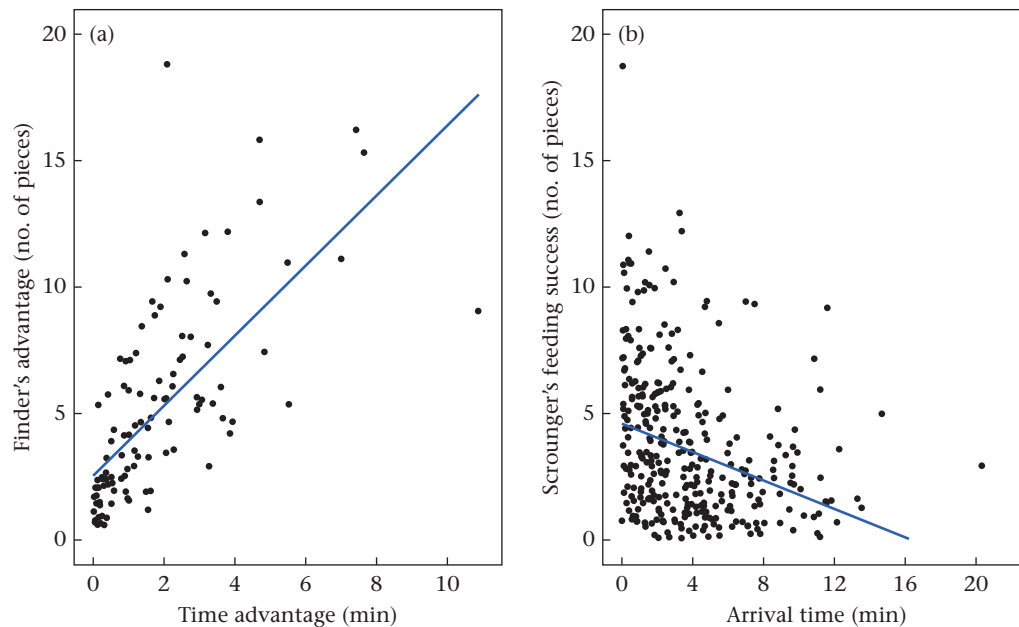
from the null (overall model: $N = 106$, $\chi^2 = 4.16$, $P = 0.655$; Table 4).

Scroungers obtained a mean of 3.51 pieces ($\pm$ SD 2.98), and the mean arrival time was 3.87 min ($\pm$ SD 3.28) after a trial had started. We found that age−sex and arrival time had significant effects on the scrounger's feeding success (Table 5). Adult females ($\beta = -0.46$,

Figure 3. Relationship between feeding success and time. (a) Finder's advantage as a function of time advantage for producers. (b) Total food obtained as a function of arrival time for scroungers. Blue lines represent the linear regression trendline.

with infants ($\beta = -0.54$, $P < 0.001$), subadult females ($\beta = -0.57$, $P < 0.001$), subadult males ($\beta = -0.41$, $P = 0.009$) and juveniles/infants ($\beta = -1.29$, $P < 0.001$) obtained significantly less food at experimental patches than adult males. Arrival time had a negative effect on overall feeding success ($\beta = -0.08$, $P < 0.001$), which meant that individuals who arrived at the patch later obtained less food (Table 6). Rank did not have a significant effect on the total number of pieces eaten, but there was a tendency for individuals from the lower rank tier to obtain more food than those in the upper rank tier ($\beta = 0.26$, $P = 0.053$; Table 6).

Scrounging Types

The most frequently used scrounging type was tolerated scrounging ($N = 199$), followed by displacement scrounging ($N = 119$) and untolerated scrounging ($N = 40$). When comparing tolerated and untolerated scrounging against displacement scrounging, we found that only relative dominance had a significant effect (Table 7). As relative dominance increased (i.e. from lower to same/mixed to higher), tolerated ($\beta = -1.33$, $P < 0.001$) and untolerated scrounging ($\beta = -2.36$, $P < 0.001$) occurred less than displacement scrounging (Table 7, Fig. 5). The mean number of pieces obtained was 4.00 ($\pm$ SD 3.22) using displacement scrounging, 3.31 ($\pm$ SD 2.81) using tolerated scrounging and 1.04 ($\pm$ SD 1.06) using untolerated scrounging. We found that scrounging type had a significant effect on the number of pieces eaten (Table 8). Scroungers who were not tolerated at the patch obtained significantly less food than scroungers who were tolerated ($\beta = -1.10$, $P < 0.001$). Feeding success did not differ between tolerated and displacement scrounging ($\beta = 0.14$, $P = 0.119$).

DISCUSSION

Our findings demonstrate that intragroup spatial positions influence foraging strategy and that individuals that travel on the front, leading edge of the group are more likely to discover food patches. We found that producers benefitted most when scroungers arrived later because this allowed producers to increase

their finder's advantage. In addition, scroungers that arrived earlier during the trial had greater feeding success since food was not yet depleted. During our experiment, subadults of both sexes scrounged more than other age–sex classes, and individuals in the upper rank tier scrounged more than those in the two lower tiers. Adult males obtained the most food as scroungers and surprisingly, upper-tiered scroungers did not obtain more food than middle- and lower-tiered scroungers. This unexpected finding may be due to that fact that feeding success did not differ between displacement and tolerated scrounging. This means that even though higher-ranking individuals tended to use displacement scrounging to gain access to more food, lower-ranking individuals were still able to attain a substantial amount of food when they were tolerated at the experimental patch.

We found that the propensity to be in the front leading edge of a moving group was the most important predictor of producing. We did not find dominance rank effects on the use of the front-outer position (Appendix, Table A3), so it is not surprising that rank did not affect the likelihood of producing. Adult females with infants were the only age–sex class that produced less than adult males, likely because mothers maintained proximity to their infants, who rarely searched for and located food patches. Furthermore, we found that juveniles and infants occupied central positions in the group and only a single juvenile produced once in our experiment (Appendix). This is compelling evidence that intragroup spatial positions, particularly while the group is moving, greatly determine the use of the producer strategy (Beauchamp, 2008; Flynn & Giraldeau, 2001; Hirsch, 2007).

We found that the time advantage was the only significant predictor for the finder's advantage. In other words, regardless of age–sex and rank, producers that spent more time alone at the patch before scroungers arrived were able to consume more food. Age–sex and rank also did not affect the producer's feeding success after the arrival of scroungers. This means that for producers, it was extremely beneficial to feed at a patch as long as possible without being detected, or joined, by other group members. We did not find a significant positive correlation between the proportional use of the front-outer position and finder's time advantage. But an individual's

Table 4
Summary of producer's feeding difference GLMM for the effects of age−sex and rank tier on the difference between total number of pieces eaten and finder's advantage for producers

Predictor variable	β (SE)	z	P
Intercept	0.22 (0.31)	0.71	0.476
Age−sex			
Adult male (reference)	−	−	−
Adult female	0.64 (0.69)	0.93	0.351
Adult female + infant	1.30 (1.22)	1.07	0.284
Subadult female	1.69 (1.02)	1.66	0.098
Subadult male	0.79 (1.02)	0.78	0.434
Rank tier			
Upper (reference)	−	−	−
Lower	−1.33 (1.06)	−1.26	0.209
Middle	−1.24 (0.87)	−1.42	0.156

Overall model fit compared to the null model, which included only the random effects: $N = 106$, $\chi^2 = 4.16$, $P = 0.655$. Marginal $R^2 = 0.04$, conditional $R^2 = 0.66$.

Table 5
Summary of scrounger's feeding success GLMM for the effects of age−sex, rank tier and arrival time on the total number of pieces eaten for scroungers in a given trial

Predictor variable	β (SE)	z	P
Intercept	1.85 (0.09)	21.33	<0.001
Age−sex			
Adult male (reference)	−	−	−
Adult female	**−0.46 (0.14)**	**−3.36**	**<0.001**
Adult female + infant	**−0.60 (0.14)**	**−4.27**	**<0.001**
Subadult female	**−0.60 (0.18)**	**−3.38**	**<0.001**
Subadult male	*−0.37 (0.19)*	*−1.92*	*0.054*
Juveniles and infants	**−1.27 (0.17)**	**−7.60**	**<0.001**
Rank tier			
Upper (reference)	−	−	−
Lower	*0.29 (0.15)*	*1.92*	*0.054*
Middle	0.08 (0.14)	0.59	0.556
Arrival time	**−0.09 (0.01)**	**−6.13**	**<0.001**

Overall model fit compared to the null model, which included only the random effects: $N = 350$, $\chi^2 = 116.9$, $P < 0.001$. Significant effects ($P < 0.05$) are shown in bold and trends ($P < 0.08$) are italicized. Marginal $R^2 = 0.33$, conditional $R^2 = 0.38$.

Table 6
Summary of overall feeding success GLMM for the effects of foraging strategy, age−sex, rank tier and arrival time on the total number of pieces eaten for producers and scroungers in a given trial

Predictor variable	β (SE)	z	P
Intercept	1.80 (0.07)	24.40	<0.001
Foraging strategy			
Scrounger (reference)	−	−	−
Producer	**0.25 (0.08)**	**3.01**	**0.003**
Age−sex			
Adult male (reference)	−	−	−
Adult female	**−0.41 (0.12)**	**−3.53**	**<0.001**
Adult female + infant	**−0.54 (0.13)**	**−4.17**	**<0.001**
Subadult female	**−0.57 (0.16)**	**−3.62**	**<0.001**
Subadult male	**−0.41 (0.16)**	**−2.61**	**0.009**
Juveniles and infants	**−1.29 (0.16)**	**−8.25**	**<0.001**
Rank tier			
Upper (reference)	−	−	−
Lower	*0.26 (0.13)*	*1.94*	*0.053*
Middle	0.05 (0.12)	0.42	0.674
Arrival time	**−0.08 (0.01)**	**−6.20**	**<0.001**

Overall model fit compared to the null model, which included only the random effects: $N = 457$, $\chi^2 = 214.32$, $P < 0.001$. Significant effects ($P < 0.05$) are shown in bold and trends ($P < 0.08$) are italicized. Marginal $R^2 = 0.42$, conditional $R^2 = 0.42$.

proportional use of the front-outer position does not tell us how far away they were from other group members. It is possible that producers who had a longer time advantage maintained greater interindividual distances (Bicca-Marques & Garber, 2005; Di Bitetti &

Janson, 2001; Dubuc & Chapais, 2007). Although we did not record interindividual distances in this study, previous research by Teichroeb et al. (2015) found that the scroungers' distance from the finder did not affect the finder's share in vervet monkeys. The finder's time advantage could also be increased by delaying food calls, as shown in capuchins (Di Bitetti & Janson, 2001). During our experiment, food calls occurred in less than 10% of the trials and most of them were given by scroungers, so it appears that producers did not communicate the discovery of a food patch to the rest of the group. Unfortunately, we do not have a baseline frequency of food-associated calls in this group, so we cannot conclude that the lack of food calls was an intentional tactic used by producers to increase their finder's time advantage. We found that producers obtained more total food than scroungers at the patch, so while producers invested more in searching for food, they benefited from greater feeding success. Other studies have also found greater success in producing compared to scrounging (Beauchamp, 2014; De la Fuente et al., 2019). Nevertheless, not all members of this vervet monkey group had equal chances of producing since the tendency to produce appeared to be constrained by intragroup spatial positioning. In theoretical producer−scrounger games, the relative frequencies of producers and scroungers can be calculated under stable equilibriums (i.e. when both strategies have equal feeding success) (Vickery et al., 1991). However, when foraging strategy is limited by individual characteristics (e.g. age, sex, dominance rank, intragroup spatial position), the success of a strategy is no longer strictly frequency dependent and becomes phenotype-limited (Barta & Giraldeau, 1998). Indeed, we found that phenotype affected scrounging tendency and success.

We found that subadult males and females tended to scrounge more than adult males, although adult males obtained more food as scroungers than all other age−sex classes, likely due to their larger body size and higher dominance in the group, which aided the use of displacement and tolerated scrounging. At our study site, there are few natural predators, so scrounging may be a riskier foraging strategy than producing since food-related aggression is quite common in this group. Subadult females were not constrained by the presence of offspring and could more freely scrounge during the experiment compared to adult females, who often travelled with offspring and would not have wanted to risk being aggressed by intolerant individuals at the patch. In this group, all three subadult males were at the bottom of the male dominance hierarchy and they did not benefit from female coalitionary support as much as subadult females. Because of this, subadult males were arguably the most precarious age−sex class in the group and they may have been more reliant on scrounging as a strategy to obtain food. Blaszczyk (2017) found that subadult males were bolder than adult females in novel object tests and this may be because they are the age−sex group that must prepare for natal dispersal (see Cote, Clobert, Brodin, Fogarty, & Sih, 2010 for review). Future studies should uncover the influence of age-dependent personality on foraging strategies in vervet monkeys as the shy−bold and exploratory−unexploratory continuums have been linked to individual preference in foraging strategy (barnacle geese, *Branta leucopisis*: Kurvers et al., 2010; Eurasian tree sparrows, *Passer montanus*: Fülöp et al., 2019; rooks: Jolles et al., 2013; sheep, *Ovis aries*: Michelena, Sibbald, Erhard, & McLeod, 2009; zebra finches: Beauchamp, 2006).

Interestingly, we found that feeding success of lower-ranking scroungers at the patch did not differ significantly from that of higher-ranking scroungers. This is contrary to what we had predicted for this despotic primate species characterized by strong within-group competition and a linear dominance hierarchy (Sterck et al., 1997). Scrounging at a large food patch may be a way for subordinates to obtain high-quality food that they would otherwise not be able to access if the patch was small enough for dominant individuals to defend (Whitten, 1983).
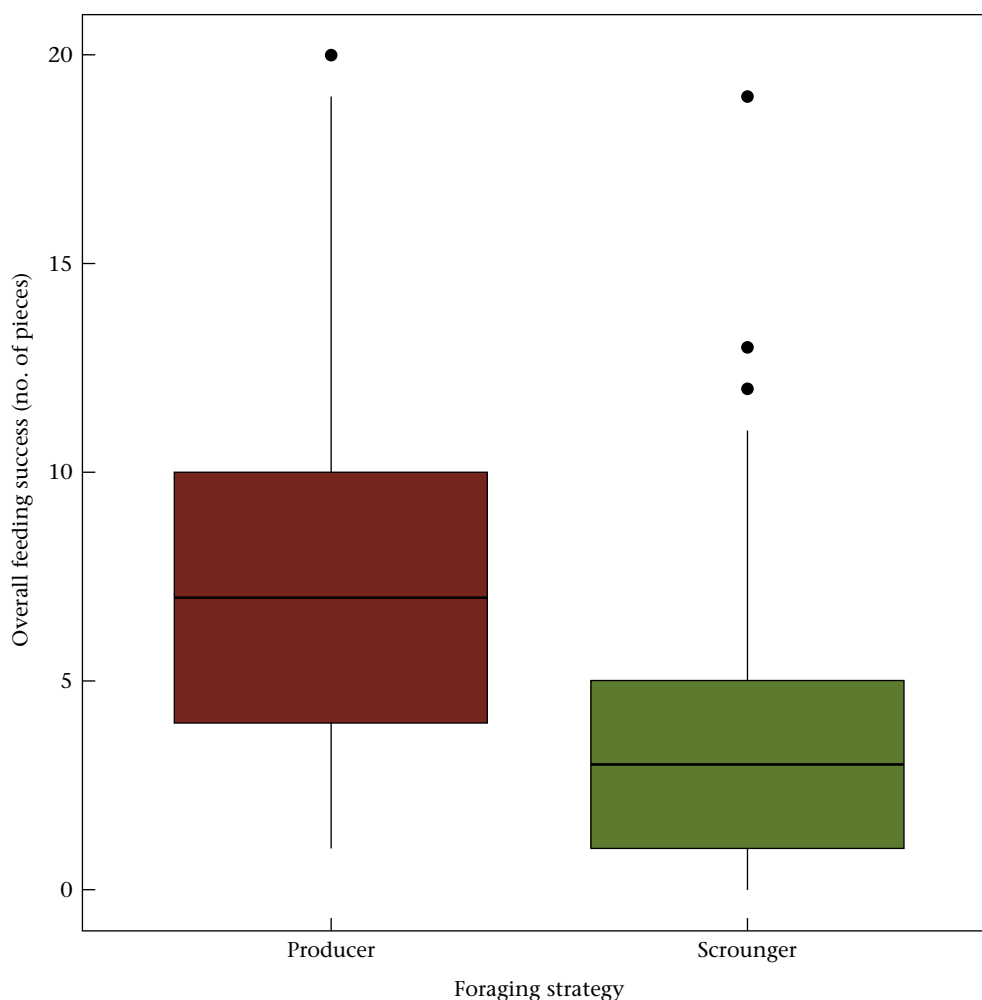
Figure 4. Box plot for the total amount of food obtained as producer and as scrounger (*N* = 107 trials). The 25% and 75% quartiles (box), medians (lines in the boxes), minimum and maximum values within the range of 1.5 times the respective quartiles (whiskers) and outliers (filled circles) are shown.

Although high-ranking individuals scrounged more than lower-ranking individuals, they did not disproportionately benefit more from scrounging. Higher-ranking individuals may have scrounged more because they faced fewer risks while scrounging since they were less likely to be aggressed or displaced by conspecifics. Lower-ranking individuals, on the other hand, faced greater risks while scrounging at a patch, which might have deterred many individuals from participating. Nearly half (48%) of scrounging events from lower-ranking individuals were attributed to three individuals, which made up only 15% of the lower rank tier (Appendix, Table A1). In comparison, around half (54%) of scrounging events from high-rankers came from 33% of individuals in the upper rank tier (Appendix, Table A1). However, low-rankers that did participate in this high-risk, high-reward trade-off benefited from greater feeding success. It is important to make a distinction between feeding strategies of high-ranking members from those of low-ranking members in a group. Displacement scrounging was used more by higher-ranking individuals and provided the greatest mean feeding success, similar to Bugnyar and Kotrschal's (2002) findings for ravens. That being said, the amount of food obtained via displacement scrounging and tolerated scrounging did not differ. Lower-ranking individuals, who could not rely on displacing others to gain access to food, were still able to acquire a considerable amount of food by being tolerated at the patch.

Feeding tolerance has been studied from a biological market approach in which tolerance functions as a commodity than can be exchanged for other commodities such as grooming, mating opportunities or reciprocal tolerance (Barrett, Henzi, Weingrill, Lycett, & Hill, 1999; Borgeaud & Bshary, 2015; de Waal, 1997; Dubuc et al., 2012; Harten et al, 2018, 2019; King et al., 2009; Noë & Hammerstein, 1995; Ventura, Majolo, Koyama, Hardie, & Schino, 2006). Without genetic data for this group of vervet monkeys, it is difficult to disentangle the influence of social affiliation from relatedness (Hamilton, 1964). Unfortunately, due to a small sample size and lack of power, we could not test our predictions regarding the sex-specific nature of tolerance (i.e. whether females were tolerated more than males). Future studies might test feeding tolerance during the mating season to further explore whether vervet monkeys trade 'food-for-sex' as was recently found in Egyptian fruit bats, *Rousettus aegyptiacus* (Harten, Prat, Ben Cohen, Dor, & Yovel, 2019).

The vervet monkeys at Lake Nabugabo feed on a mix of natural and anthropogenic foods (e.g. crops, garbage, human handouts), and a neighbouring group (M group) at this site demonstrated more flexible birthing seasons compared to populations in less disturbed habitats (Schoof, Twinomugisha, Teichroeb, Rothman, & Chapman, 2015). Nevertheless, in KS group, there is a still a seasonal trend in births and all but one female gave birth between September and December in the year prior to this study. This is clear evidence that

Table 7
Summary of multinomial logistic regression model for the effects of age—sex, relative rank and arrival time on scrounging type (reference category was set to 'displacement scrounging')

Predictor variable	β (SE)	z	P
Tolerated scrounging vs displacement scrounging			
(Intercept)	3.54 (0.66)	5.35	<0.001
Age—sex			
Adult male (reference)	—	—	—
Adult female	0.33 (0.41)	0.81	0.421
Adult female + infant	−0.45 (0.43)	−1.06	0.289
Subadult female	0.74 (0.47)	1.60	0.111
Subadult male	−0.50 (0.60)	−0.84	0.400
Juveniles and infants	0.73 (0.61)	1.95	0.232
Relative dominance	**−1.33 (0.21)**	**−6.26**	**<0.001**
Arrival time	−0.01 (0.04)	−0.20	0.842
Untolerated scrounging vs displacement scrounging			
(Intercept)	3.33 (1.31)	2.54	0.011
Age—sex			
Adult male (reference)	—	—	—
Adult female	0.67 (1.00)	0.67	0.505
Adult female + infant	−0.83 (1.05)	−0.79	0.428
Subadult female	0.786 (1.03)	0.76	0.447
Subadult male	−11.72 (119.51)	−0.10	0.919
Juveniles and infants	0.90 (1.11)	0.81	0.418
Relative dominance	**−2.36 (0.40)**	**−5.86**	**<0.001**
Arrival time	0.04 (0.07)	0.58	0.563

Overall model fit compared to the null model, which included only the random effects: $N = 358$, $\chi^2 = 144.85$, $P < 0.001$. Significant effects ($P < 0.05$) are shown in bold. McFadden's pseudo $R^2 = 0.22$.

Table 8
Summary of GLMM for the effects of scrounging type on the total number of pieces eaten by a scrounger in a given trial

Predictor variable	β (SE)	z	P
Intercept	1.07 (0.08)	13.46	<0.001
Scrounging type			
Tolerated (reference)	—	—	—
Displacement	0.14 (0.09)	1.56	0.119
Untolerated	**−1.10 (0.26)**	**−4.19**	**<0.001**

Overall model fit compared to the null model, which included only the random effects: $N = 292$, $\chi^2 = 24.67$, $P < 0.001$. Significant effects ($P < 0.05$) are shown in bold. Marginal $R^2 = 0.12$, conditional $R^2 = 0.64$.

smaller patches and found that high-ranking individuals were much less tolerant towards other members trying to feed at the patch (i.e. scroungers either displaced others or 'stole' food and ran away). This lack of tolerance was also found in a previous study at this site (Teichroeb et al., 2015) using approximately the same amount of food (20 halves of small bananas) but on a much smaller patch (0.65 × 0.47 m platform). The effects observed in this study was greatly mediated by the choice in experimental design and demonstrates that feeding tolerance is dependent on patch size (also see Borgeaud & Bshary, 2015).

Conclusions

Our findings from this group of vervet monkeys support intragroup spatial position being an important determinant of foraging strategies. In addition, our results raise the question of how the influence of various factors (e.g. social interactions, feeding competition) differ for a stationary versus moving group, particularly in populations that have low predation pressure (see Appendix). In this group, producing provided greater overall feeding success than scrounging, and the finder's advantage was primarily dependent on the length of time the producer enjoyed the absence of feeding
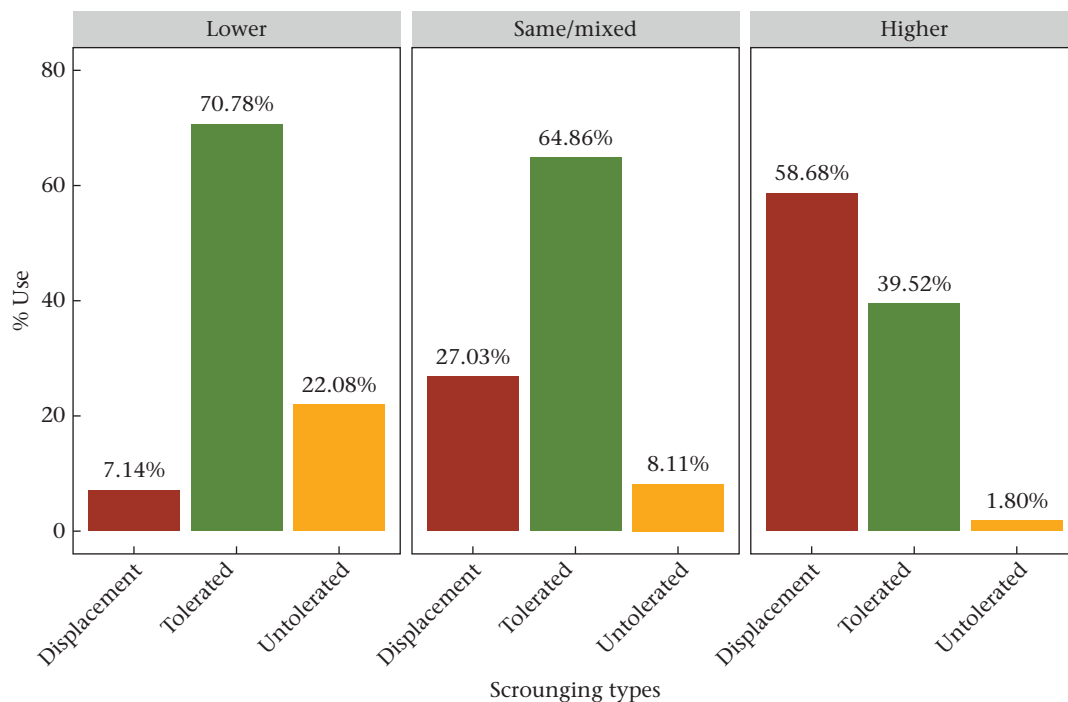
there are still limitations to resource availability at this site and that these monkeys are subject to the same food competition that shapes foraging behaviours of populations in more natural habitats. In this study, we intentionally increased patch size to prevent dominant individuals from monopolizing the resource, which subsequently facilitated tolerated scrounging in this group. Prior to deciding on the 1.75 × 1.75 m tarp for the experimental set-up, we tested

Figure 5. Scrounging type used by scroungers of different relative dominance rank. The three types are displacement scrounging, tolerated scrounging and untolerated scrounging. The relative dominance ranks are lower (left panel), same or mixed (middle panel) and higher (right panel).

competition, mirroring that of a solitary forager (Rita & Ranta, 1998). More accurate methods for recording and analysing spatial data (e.g. time-stamped GPS coordinates) that can clarify the sequence of events leading up to the discovery of a food patch will be instrumental in explaining how producers gain greater time advantages. The unexpected finding that lower-ranking individuals did not obtain less food than higher-ranking individuals may help us better understand how subordinates in a group navigate social and ecological contexts to ensure that they meet their energy requirements in lieu of within-group competition. Whether our findings pertain to all vervet monkeys will require future studies to examine producer–scrounger dynamics in populations under different ecological (i.e. greater predation pressure, less anthropogenic disturbances) and social (i.e. different group size and degree of feeding competition) conditions. Future work should also examine foraging types in other socially foraging species, particularly those with a marked dominance hierarchy. In this study, we have shown that manipulating foraging experimental set-up can increase tolerance to scrounging. Field experimentation can provide opportunities to explore topics relating to feeding networks, biological markets and cooperation among social foragers in their natural environment.

Acknowledgments

References

Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour, 49*(3–4), 227–266. https://doi.org/10.1163/156853974X00534

Barnard, C. J., & Sibly, R. M. (1981). Producers and scroungers: A general model and its application to captive flocks of house sparrows. *Animal Behaviour, 29*(2), 543–550. https://doi.org/10.1016/S0003-3472(81)80117-0

Barrett, L., Henzi, S. P., Weingrill, T., Lycett, J. E., & Hill, R. A. (1999). Market forces predict grooming reciprocity in female baboons. *Proceedings of the Royal Society B: Biological Sciences, 266*(1420), 665–670. https://doi.org/10.1098/rspb.1999.0687

Barta, Z., & Giraldeau, L.-A. (1998). The effect of dominance hierarchy on the use of alternative foraging tactics: A phenotype-limited producing-scrounging game. *Behavioral Ecology and Sociobiology, 42*(3), 217–223. https://doi.org/10.1007/s002650050433

Barta, Z., Flynn, R., & Giraldeau, L.-A. (1997). Geometry for a selfish foraging group: A genetic algorithm approach. *Proceedings of the Royal Society B: Biological Sciences, 264*(1385), 1233–1238. https://doi.org/10.1098/rspb.1997.0170

Barta, Z., Liker, A., & Mónus, F. (2004). The effects of predation risk on the use of social foraging tactics. *Animal Behaviour, 67*(2), 301–308. https://doi.org/10.1016/j.anbehav.2003.06.012

Bartoń, K. (2020). *MuMIn: Multi-model inference* (R package version 1.43.17) https://CRAN.R-project.org/package=MuMIn.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software, 67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Beauchamp, G. (2006). Phenotypic correlates of scrounging behavior in zebra finches: Role of foraging efficiency and dominance. *Ethology, 112*(9), 873–878. https://doi.org/10.1111/j.1439-0310.2006.01241.x

Beauchamp, G. (2008). A spatial model of producing and scrounging. *Animal Behaviour, 76*(6), 1935–1942. https://doi.org/10.1016/j.anbehav.2008.08.017

Beauchamp, G. (2014). A field investigation of scrounging in semipalmated sandpipers. *Behavioral Ecology and Sociobiology, 68*(9), 1473–1479. https://doi.org/10.1007/s00265-014-1755-2

Bicca-Marques, J. C., & Garber, P. A. (2005). Use of social and ecological information in tamarin foraging decisions. *International Journal of Primatology, 26*(6), 1321–1344. https://doi.org/10.1007/s10764-005-8855-9

Blaszczyk, M. B. (2017). Boldness towards novel objects predicts predator inspection in wild vervet monkeys. *Animal Behaviour, 123*, 91–100. https://doi.org/10.1016/j.anbehav.2016.10.017

Borgeaud, C., & Bshary, R. (2015). Wild vervet monkeys trade tolerance and specific coalitionary support for grooming in experimentally induced conflicts. *Current Biology, 25*(22), 3011–3016. https://doi.org/10.1016/j.cub.2015.10.016

Borgeaud, C., Sosa, S., Sueur, C., & Bshary, R. (2017). The influence of demographic variation on social network stability in wild vervet monkeys. *Animal Behaviour, 134*, 155–165. https://doi.org/10.1016/j.anbehav.2017.09.028

Bugnyar, T., & Kotrschal, K. (2002). Scrounging tactics in free-ranging ravens, *Corvus corax. Ethology, 108*(11), 993–1009. https://doi.org/10.1046/j.1439-0310.2002.00832.x

Bumann, D., Rubenstein, D., & Krause, J. (1997). Mortality risk of spatial positions in animal groups: The danger of being in the front. *Behaviour, 134*(13–14), 1063–1076. https://doi.org/10.1163/156853997X00403

Caraco, T., & Giraldeau, L.-A. (1991). Social foraging: Producing and scrounging in a stochastic environment. *Journal of Theoretical Biology, 153*(4), 559–583. https://doi.org/10.1016/S0022-5193(05)80156-0

Chapais, B. (1992). The role of alliances in social inheritance of rank among female primates. In A. H. Harcourt, & F. B. M. de Waal (Eds.), *Coalitions and alliances in humans and other animals* (pp. 29–59). Oxford, U.K.: Oxford University Press.

Chapais, B., & Belisle, P. (2001). Tolerated co-feeding in relation to degree of kinship in Japanese macaques. *Behaviour, 138*(4), 487–509. https://doi.org/10.1163/156853901750382124

Chapman, C. A., Twinomugisha, D., Teichroeb, J. A., Valenta, K., Sengupta, R., Sarkar, D., et al. (2016). How do primates survive among humans? Mechanisms employed by vervet monkeys at Lake Nabugabo, Uganda. In M. T. Waller (Ed.), *Ethnoprimatology. Developments in primatology: Progress and prospects* (pp. 77–94). Cham, Switzerland: Springer. https://doi.org/10.1007/978-3-319-30469-4_5.

Charnov, E. L. (1976). Optimal foraging, the marginal value theorem. *Theoretical Population Biology, 9*(2), 129–136. https://doi.org/10.1016/0040-5809(76)90040-X

Cheney, D. L., & Seyfarth, R. M. (1983). Nonrandom dispersal in free-ranging vervet monkeys: Social and genetic consequences. *American Naturalist, 122*(3), 392–412. https://doi.org/10.1086/284142

Cote, J., Clobert, J., Brodin, T., Fogarty, S., & Sih, A. (2010). Personality-dependent dispersal: Characterization, ontogeny and consequences for spatially structured populations. *Philosophical Transactions of the Royal Society B: Biological Sciences, 365*(1560), 4065–4076. https://doi.org/10.1098/rstb.2010.0176

Curley, J. P. (2016). *Compete: Analyzing competitive interaction data* (R package version 0.1) https://github.com/jalapic/compete.

De la Fuente, M. F., Schiel, N., Bicca-Marques, J. C., Caselli, C. B., Souto, A., & Garber, P. A. (2019). Balancing contest competition, scramble competition, and social tolerance at feeding sites in wild common marmosets (*Callithrix jacchus*). *American Journal of Primatology, 81*(4), Article e22964. https://doi.org/10.1002/ajp.22964

Di Bitetti, M. S., & Janson, C. H. (2001). Social foraging and the finder's share in capuchin monkeys, *Cebus apella. Animal Behaviour, 62*(1), 47–56. https://doi.org/10.1006/anbe.2000.1730

Dostie, M. J., Lusseau, D., Bonnell, T., Clarke, P. M. R., Chaplin, G., Kienzle, S., et al. (2016). Proof of principle: The adaptive geometry of social foragers. *Animal Behaviour, 119*, 173–178. https://doi.org/10.1016/j.anbehav.2016.07.011

Dubuc, C., & Chapais, B. (2007). Feeding competition in *Macaca fascicularis*: An assessment of the early arrival tactic. *International Journal of Primatology, 28*(2), 357–367. https://doi.org/10.1007/s10764-007-9118-8

Dubuc, C., Hughes, K. D., Cascio, J., & Santos, L. R. (2012). Social tolerance in a despotic primate: Co-feeding between consortship partners in rhesus macaques. *American Journal of Physical Anthropology, 148*(1), 73–80. https://doi.org/10.1002/ajpa.22043

Elston, D. A., Moss, R., Boulinier, T., Arrowsmith, C., & Lambin, X. (2001). Analysis of aggregation, a worked example: Numbers of ticks on red grouse chicks. *Parasitology, 122*(5), 563–569. https://doi.org/10.1017/S0031182001007740

Fairbanks, L. A., & McGuire, M. T. (1984). Determinants of fecundity and reproductive success in captive vervet monkeys. *American Journal of Primatology, 7*(1), 27–38. https://doi.org/10.1002/ajp.1350070106

Flynn, R. E., & Giraldeau, L.-A. (2001). Producer–scrounger games in a spatially explicit world: Tactic use influences flock geometry of spice finches. *Ethology, 107*, 249–257.

Friard, O., & Gamba, M. (2016). BORIS: A free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution, 7*(11), 1325–1330. https://doi.org/10.1111/2041-210X.12584

Fülöp, A., Németh, Z., Kocsis, B., Deák-Molnár, B., Bozsoky, T., & Barta, Z. (2019). Personality and social foraging tactic use in free-living Eurasian tree sparrows (*Passer montanus*). *Behavioral Ecology, 30*(4), 894–903. https://doi.org/10.1093/beheco/arz026

Gall, G. E. C., & Manser, M. B. (2018). Spatial structure of foraging meerkat groups is affected by both social and ecological factors. *Behavioral Ecology and Sociobiology, 72*(5), 77. https://doi.org/10.1007/s00265-018-2490-x

Giraldeau, L.-A., & Beauchamp, G. (1999). Food exploitation: Searching for the optimal joining policy. *Trends in Ecology & Evolution, 14*(3), 102–106. https://doi.org/10.1016/S0169-5347(98)01542-0

Giraldeau, L.-A., & Dubois, F. (2008). Social foraging and the study of exploitative behavior. *Advances in the Study of Behavior, 38*, 59–104. https://doi.org/10.1016/S0065-3454(08)00002-8

Giraldeau, L.-A., & Livoreil, B. (1998). Game theory and social foraging. In L. A. Dugatkin, & H. K. Reeve (Eds.), *Game theory and animal behavior* (pp. 16–37). Oxford, U.K.: Oxford University Press.

Giraldeau, L.-A., Hogan, J. A., & Clinchy, M. J. (1990). The payoffs to producing and scrounging: What happens when patches are divisible? *Ethology, 85*(2), 132–146. https://doi.org/10.1111/j.1439-0310.1990.tb00393.x

Grant, J. W. A. (1993). Whether or not to defend? The influence of resource distribution. *Marine Behavior & Physiology, 23*(1–4), 137–153. https://doi.org/10.1080/10236249309378862

Hall, C. L., & Fedigan, L. M. (1997). Spatial benefits afforded by high rank in white-faced capuchins. *Animal Behaviour, 53*(5), 1069–1082. https://doi.org/10.1006/anbe.1996.0392

Hamilton, W. D. (1964). The genetical evolution of social behaviour. II. *Journal of Theoretical Biology, 7*(1), 17–52. https://doi.org/10.1016/0022-5193(64)90039-6

Hamilton, W. D. (1971). Geometry for the selfish herd. *Journal of Theoretical Biology, 31*(2), 295–311. https://doi.org/10.1016/0022-5193(71)90189-5

Harrison, X. A. (2014). Using observation-level random effects to model over-dispersion in count data in ecology and evolution. *PeerJ, 2*, e616. https://doi.org/10.7717/peerj.616

Harten, L., Matalon, Y., Galli, N., Navon, H., Dor, R., & Yovel, Y. (2018). Persistent producer–scrounger relationships in bats. *Science Advances, 4*(2), Article e1603293. https://doi.org/10.1126/sciadv.1603293

Harten, L., Prat, Y., Ben Cohen, S., Dor, R., & Yovel, Y. (2019). Food for sex in bats revealed as producer males reproduce with scrounging females. *Current Biology, 29*(11), 1895–1900. https://doi.org/10.1016/j.cub.2019.04.066. e3.

Hartig, F. (2020). *DHARMa: Residual diagnostics for hierarchical (multi-level/mixed) regression models* (R package version 0.3.2.0) https://cran.r-project.org/web/packages/DHARMa.

Heesen, M., Macdonald, S., Ostner, J., & Schülke, O. (2015). Ecological and social determinants of group cohesiveness and within-group spatial position in wild Assamese macaques. *Ethology, 121*(3), 270–283. https://doi.org/10.1111/eth.12336

Hemelrijk, C. K., Wubs, M., Gort, G., Botting, J., & van de Waal, E. (2020). Dynamics of intersexual dominance and adult sex-ratio in wild vervet monkeys. *Frontiers in Psychology, 11*, 839. https://doi.org/10.3389/fpsyg.2020.00839

Hirsch, B. T. (2007). Costs and benefits of within-group spatial position: A feeding competition model. *Quarterly Review of Biology, 82*(1), 9–27. https://doi.org/10.1086/511657

Horrocks, J., & Hunte, W. (1983). Maternal rank and offspring rank in vervet monkeys: An appraisal of the mechanisms of rank acquisition. *Animal Behaviour, 31*(3), 772–782. https://doi.org/10.1016/S0003-3472(83)80234-6

Isbell, L. A. (1991). Contest and scramble competition: Patterns of female aggression and ranging behavior among primates. *Behavioral Ecology, 2*(2), 143–155. https://doi.org/10.1093/beheco/2.2.143

Isbell, L. A. (1994). Predation on primates: Ecological patterns and evolutionary consequences. *Evolutionary Anthropology: Issues, News, and Reviews, 3*(2), 61–71. https://doi.org/10.1002/evan.1360030207

Janson, C. H. (1990a). Social correlates of individual spatial choice in foraging groups of brown capuchin monkeys, *Cebus apella. Animal Behaviour, 40*(5), 910–921. https://doi.org/10.1016/S0003-3472(05)80993-5

Janson, C. H. (1990b). Ecological consequences of individual spatial choice in foraging groups of brown capuchin monkeys, *Cebus apella. Animal Behaviour, 40*(5), 922–934. https://doi.org/10.1016/S0003-3472(05)80994-7

Jolles, J. W., Ostojić, L., & Clayton, N. S. (2013). Dominance, pair bonds and boldness determine social-foraging tactics in rooks, *Corvus frugilegus. Animal Behaviour, 85*(6), 1261–1269. https://doi.org/10.1016/j.anbehav.2013.03.013

Josephs, N., Bonnell, T., Dostie, M., Barrett, L., & Henzi, S. P. (2016). Working the crowd: Sociable vervets benefit by reducing exposure to risk. *Behavioral Ecology, 27*(4), 988–994. https://doi.org/10.1093/beheco/arw003

King, A. J., Clark, F. E., & Cowlishaw, G. (2011). The dining etiquette of desert baboons: The roles of social bonds, kinship, and dominance in co-feeding networks. *American Journal of Primatology, 73*(8), 768–774. https://doi.org/10.1002/ajp.20918

King, A. J., Isaac, N. J. B., & Cowlishaw, G. (2009). Ecological, social, and reproductive factors shape producer–scrounger dynamics in baboons. *Behavioral Ecology, 20*(5), 1039–1049. https://doi.org/10.1093/beheco/arp095

Kumpan, L. T., Rothman, J. M., Chapman, C. A., & Teichroeb, J. A. (2019). Playing it safe? Solitary vervet monkeys (*Chlorocebus pygerythrus*) choose high-quality foods more than those in competition. *American Journal of Primatology, 81*(7). https://doi.org/10.1002/ajp.23002

Kumpan, L. T., Smeltzer, E. A., & Teichroeb, J. A. (2020). Animal cognition in the field: Performance of wild vervet monkeys (*Chlorocebus pygerythrus*) on a reversal learning task. *Animal Cognition, 23*(3), 523–534. https://doi.org/10.1007/s10071-020-01356-5

Kurvers, R. H. J. M., Prins, H. H. T., van Wieren, S. E., van Oers, K., Nolet, B. A., & Ydenberg, R. C. (2010). The effect of personality on social foraging: Shy barnacle geese scrounge more. *Proceedings of the Royal Society B: Biological Sciences, 277*(1681), 601–608. https://doi.org/10.1098/rspb.2009.1474

Lee, A. E. G., & Cowlishaw, G. (2017). Switching spatial scale reveals dominance-dependent social foraging tactics in a wild primate. *PeerJ, 5*, Article e3462. https://doi.org/10.7717/peerj.3462

Lendvai, A. Z., Liker, A., & Barta, Z. (2006). The effects of energy reserves and dominance on the use of social-foraging strategies in the house sparrow. *Animal Behaviour, 72*(4), 747–752. https://doi.org/10.1016/j.anbehav.2005.10.032

Mathot, K. J., & Giraldeau, L.-A. (2007). Increasing vulnerability to predation increases preference for the scrounger foraging tactic. *Behavioral Ecology, 19*(1), 131–138. https://doi.org/10.1093/beheco/arm114

McCormack, J. E., Jablonski, P. G., & Brown, J. L. (2007). Producer–scrounger roles and joining based on dominance in a free-living group of Mexican jays (*Aphelocoma ultramarina*). *Behaviour, 144*(8), 967–982. https://doi.org/10.1163/156853907781492717

Michelena, P., Sibbald, A. M., Erhard, H. W., & McLeod, J. E. (2009). Effects of group size and personality on social foraging: The distribution of sheep across patches. *Behavioral Ecology, 20*(1), 145–152. https://doi.org/10.1093/beheco/arn126

Mitchell, D. J., Dujon, A. M., Beckmann, C., & Biro, P. A. (2019). Temporal autocorrelation: A neglected factor in the study of behavioral repeatability and plasticity. *Behavioral Ecology, 31*(1), 222–231. https://doi.org/10.1093/beheco/arz180

Mónus, F., & Barta, Z. (2008). The effect of within-flock spatial position on the use of social foraging tactics in free-living tree sparrows. *Ethology, 114*(3), 215–222. https://doi.org/10.1111/j.1439-0310.2007.01472.x

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution, 4*(2), 133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x

Noë, R., & Hammerstein, P. (1994). Biological markets: Supply and demand determine the effect of partner choice in cooperation, mutualism and mating. *Behavioral Ecology and Sociobiology, 35*(1), 1–11. https://doi.org/10.1007/BF00167053

Noë, R., & Hammerstein, P. (1995). Biological markets. *Trends in Ecology & Evolution, 10*(8), 336–339. https://doi.org/10.1016/S0169-5347(00)89123-5

Pyke, G. H. (1984). Optimal foraging theory: A critical review. *Annual Review of Ecology and Systematics, 15*(1), 523–575. https://doi.org/10.1146/annurev.es.15.110184.002515

R Core Team. (2020). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/.

Ranta, E., Peuhkuri, N., Laurila, A., Rita, H., & Metcalfe, N. B. (1996). Producers, scroungers and foraging group structure. *Animal Behaviour, 51*(1), 171–175. https://doi.org/10.1006/anbe.1996.0014

Rita, H., & Ranta, E. (1998). Group foraging, gain and the finder's advantage. *Oikos, 82*(3), 515–521. https://doi.org/10.2307/3546372

Robinson, J. G. (1981). Spatial structure in foraging groups of wedge-capped capuchin monkeys *Cebus nigrivittatus. Animal Behaviour, 29*(4), 1036–1056. https://doi.org/10.1016/S0003-3472(81)80057-7

van Schaik, C. P. (1983). Why are diurnal primates living in groups? *Behaviour, 87*(1–2), 120–144. https://doi.org/10.1163/156853983X00147

van Schaik, C. P. (1989). The ecology of social relationships amongst female primates. In V. Standen, & R. Foley (Eds.), *Comparative socioecology: The behavioural ecology of humans and other mammals* (pp. 195–218). Oxford, U.K.: Blackwell Scientific.

van Schaik, C. P., & Janson, C. H. (1988). Recognizing the many faces of primate food competition: Methods. *Behaviour, 105*(1–2), 165–186. https://doi.org/10.1163/156853988X00502

Schmid, V. S., & de Vries, H. (2013). Finding a dominance order most consistent with a linear hierarchy: An improved algorithm for the I&SI method. *Animal Behaviour, 86*(5), 1097–1105. https://doi.org/10.1016/j.anbehav.2013.08.019

Schoener, T. W. (1971). Theory of feeding strategies. *Annual Review of Ecology and Systematics, 2*(1), 369–404. https://doi.org/10.1146/annurev.es.02.110171.002101

Schoof, V. A. M., Twinomugisha, D., Teichroeb, J. A., Rothman, J. M., & Chapman, C. A. (2015). Vervets in an anthropogenic landscape: Reduced breeding seasonality and mixed diet. *American Journal of Physical Anthropology, 154*(Suppl. 60), 279–280.

Sih, A. (1980). Optimal behavior: Can foragers balance two conflicting demands? *Science, 210*(4473), 1041–1043. https://doi.org/10.1126/science.210.4473.1041

Stephens, D. W. (1981). The logic of risk-sensitive foraging preferences. *Animal Behaviour, 29*(2), 628–629. https://doi.org/10.1016/S0003-3472(81)80128-5.

Sterck, E. H. M., Watts, D. P., & van Schaik, C. P. (1997). The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology, 41*(5), 291–309. https://doi.org/10.1007/s002650050390

Struhsaker, T. T. (1967). Social structure among vervet monkeys (*Cercopithecus aethiops*). *Behaviour, 29*(2–4), 83–121. https://doi.org/10.1163/156853967X00073

Teichroeb, J. A., White, M. M. J., & Chapman, C. A. (2015). Vervet (*Chlorocebus pygerythrus*) intragroup spatial positioning: Dominants trade-off predation risk for increased food acquisition. *International Journal of Primatology, 36*(1), 154–176. https://doi.org/10.1007/s10764-015-9818-4

Venables, W. N., & Ripley, B. D. (2002). *Modern applied statistics with S* (4th ed.). New York, NY: Springer.

Ventura, R., Majolo, B., Koyama, N. F., Hardie, S., & Schino, G. (2006). Reciprocation and interchange in wild Japanese macaques: Grooming, cofeeding, and agonistic support. *American Journal of Primatology, 68*(12), 1138–1149. https://doi.org/10.1002/ajp.20314

Vickery, W. L., Giraldeau, L.-A., Templeton, J. J., Kramer, D. L., & Chapman, C. A. (1991). Producers, scroungers, and group foraging. *American Naturalist, 137*(6), 847–863. https://doi.org/10.1086/285197

de Vries, H. (1995). An improved test of linearity in dominance hierarchies containing unknown or tied relationships. *Animal Behaviour, 50*(5), 1375–1389. https://doi.org/10.1016/0003-3472(95)80053-0

de Waal, F. B. M. (1997). The chimpanzee's service economy: Food for grooming. *Evolution and Human Behavior, 18*(6), 375–386. https://doi.org/10.1016/S1090-5138(97)00085-8

Whitten, P. L. (1983). Diet and dominance among female vervet monkeys (*Cercopithecus aethiops*). *American Journal of Primatology, 5*(2), 139–159. https://doi.org/10.1002/ajp.1350050205

Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. Cham, Switzerland: Springer International.

Young, C., McFarland, R., Barrett, L., & Henzi, S. P. (2017). Formidable females and the power trajectories of socially integrated male vervet monkeys. *Animal Behaviour, 125*, 61–67. https://doi.org/10.1016/j.anbehav.2017.01.006

Zhang, S., Ren, B., Li, B., Liang, B., & Wang, L. (1999). Spatial pattern in the foraging group of Sichuan golden monkeys. *Chinese Science Bulletin, 44*(15), 1369–1372. https://doi.org/10.1007/BF02885983

Appendix

Table A1
Information on individuals in KS group, including age–sex, dominance, proportional use of the front-outer position and the frequency of foraging strategy used during our experiment

Ind. ID	Age–sex [a]	Intrasex ordinal rank	Integrated ordinal rank	Rank tier	Proportion front-outer position use	Producer frequency (N = 132)	Scrounger frequency (N = 350)
JLY	AM	1	1	Upper	0.40	30	31
OTS	AM	2	2	Upper	0.24	7	29
ASP	AFI	1	3	Upper	0.23	0	26
APR	JI	–	–	Upper	0	0	9
VPR	AM	3	4	Upper	0.55	1	6
ZCN	AM	4	5	Upper	0.44	18	4
RSL	AM	5	6	Upper	0.35	7	6
PKN	AM	6	7	Upper	0.22	7	8
SOY	AF	2	8	Upper	0.19	6	29
SLT	JI	–	–	Upper	0.05	0	17
KWI	SAM	7	9	Middle	0.27	10	7
DNT	SAF	3	10	Middle	0.09	3	13
BAN	SAF	4	11	Middle	0.20	8	31
FNA	SAF	5	12	Middle	0.11	2	9
SGR	AFI	6	13	Middle	0.21	1	13
STS	JI	–	–	Middle	0.04	0	7
MNT	AF	7	14	Middle	0.11	10	10
APL	AFI	8	15	Middle	0.04	1	10
ANS	JI	–	–	Middle	0.05	0	1
BEN [b]	AFI	10	16	Middle	0.04	0	2
POT	SAM	8	17	Lower	0.43	9	9
BTR	SAM	9	18	Lower	0.19	2	23
CMN [b]	AFI	9	19	Lower	0.13	0	0
CRY	JI	–	–	Lower	0.10	0	1
CDB	JI	–	–	Lower	0.03	0	2
TOM	AF	11	20	Lower	0.14	1	2
GLC	AFI	12	21	Lower	0.06	1	3
GNG	JI	–	–	Lower	0.03	0	7
GRP	JI	–	–	Lower	0.07	0	1
NMG	AFI	13	22	Lower	0.21	3	6
NTL	JI	–	–	Lower	0.04	0	0
TMC	SAF	14	23	Lower	0.21	3	4
SHL	AF	15	24	Lower	0.15	0	2
SPG	JI	–	–	Lower	0.07	0	0
NCT	SAF	16	25	Lower	0.24	1	6
ONG [c]	JI	–	–	Lower	0.10	1	8
PER [c]	JI	–	–	Lower	0.07	0	2
MLK [c]	JI	–	–	Lower	0.04	0	4
OKR [c]	JI	–	–	Lower	0	0	1
SAG [c]	JI	–	–	Lower	0.09	0	1

[a] Age–sex classes: AM = adult male, AF = adult female, AFI = adult female with infant, SAM = subadult male, SAF = subadult female, JI = juveniles and infants.
[b] Rank order in integrated hierarchy different from rank order in intrasex hierarchy.
[c] Juveniles and infants with unknown mothers.

Additional Information on Intragroup Spatial Positions

Members of a group can compete for spatial positions, and central positions are often preferred due to their lower exposure to predation risks (Bumann et al., 1997; Hamilton, 1971). An individual's intragroup spatial position while the group is moving can in turn influence their foraging strategy (Beauchamp, 2008; Hirsch, 2007; Janson, 1990a, 1990b; Mónus & Barta, 2008). Animals at the leading edge of a foraging group are more likely to discover food sources and assume the producer strategy. When producing confers greater feeding success than scrounging or when predation risk is low in the environment, dominant individuals may trade off the safety of a central position for a front peripheral position where they could assume a more advantageous foraging strategy (Teichroeb et al., 2015). Furthermore, producers can increase their finder's advantage by increasing their interindividual distance, which can increase the time delay before the arrival of scroungers (Bicca-Marques & Garber, 2005; Di Bitetti & Janson, 2001; Dubuc & Chapais, 2007). In this study, we looked at the effects of age, sex and dominance rank on intragroup spatial positions both when the group was stationary and when the group was moving.

Adult males are larger and have longer canines than female vervet monkeys and are therefore less vulnerable to predators (Isbell, 1994). Males are also the dispersing sex, so they are more likely to spend time on the periphery of the group to detect and interact with neighbouring groups. This is applicable to both subadult and adult males, who are preparing for natal and secondary dispersals, respectively (Cheney & Seyfarth, 1983). Therefore, for intragroup spatial position, we predicted that males would be more likely to be in the outer position of the stationary group and front-outer position of the moving group than females, juveniles and infants. We also predicted that higher-ranking individuals would be in the middle of the group both while stationary and moving since central positions are generally preferred due to their safety from predators (Hamilton, 1971; Janson, 1990a; Robinson, 1981).

Methods

Behavioural observations. We did a scan sample of the group every 30 min ($N = 366$ group scans, $N = 4657$ individual scans) and tried to instantaneously sample as many individuals as possible within a 10 min window (Altmann, 1974). During these scans, we recorded the time, individual identity (ID), state behaviour (feeding, resting, moving or social) and spatial position. For spatial position, we first determined whether the group was moving or stationary. We defined the group as moving if the centre of the group moved more than 15 m in 15 min. If the group was stationary, we recorded whether the focal individual was in the 'middle' spatial position (there were individuals more peripheral to them) or the 'outer' spatial position (they were the outermost individual in the group) (Fig. A1a). If the group was moving, we recorded the focal individual's spatial position using the elliptical clock method (Janson, 1990a, 1990b; Teichroeb et al., 2015). The direction of travel corresponds to 12 o'clock and the individual's position in the group was recorded as a number on the clock. We also recorded whether the focal individual was in the middle or outer position, resulting in a total of 24 possible spatial positions when the group was moving (Fig. A1b). For analyses, we consolidated these positions into three categories (after Hall & Fedigan, 1997; Janson, 1990a, 1990a; Teichroeb et al., 2015): front-outer (FO), front-middle (FM) and back (BK) (Fig. A1c). Since this study was focused on food discovery and producer−scrounger strategies, we were especially interested in positions near the front of the group, so we made sure to start the group scan from the front of the group towards the back. To the best of our ability, we determined the front of the group as the direction of travel. When the group changed direction in the middle of a scan, we recorded the focal individual's relative spatial position in the instant the individual was scanned. For example, if two individuals were both in 12M (12 o'clock, middle) but the group changed directions by 180 degrees (i.e. turn back), then the individual who was scanned before the change would be in 12M and the individual who was scanned after the change in direction would now be in 6M (6 o'clock, middle). As a change in movement direction was relatively uncommon, we believe that the spatial positions recorded are representative of an individual's preferred position in the group.

Data analyses. To look at spatial position use while the group was stationary, we ran a generalized linear mixed model (GLMM) with binomial distribution and set spatial position as the outcome variable (middle, outer) and assigned the fixed effects as age−sex class and rank tier. We used 'adult male' and 'upper tier' as the reference categories. We controlled for temporal autocorrelation (Mitchell, Dujon, Beckmann, & Biro, 2019) by fitting models using scans taken at different time intervals and found that stationary group scans taken 5 h apart no longer had temporal autocorrelation (Durban−Watson test: $d = 1.77$, $P = 0.402$), so that was the model we chose. For moving spatial position use, we ran a multinomial logistic regression with spatial position (front-outer, front-middle, back) as the outcome variable and set 'front-outer' as the reference category. We used the same predictors and reference categories as our stationary position model. Once again, we tested for temporal autocorrelation and used moving group scans taken 6 h apart (Durban−Watson test: $d = 1.88$, $P = 0.281$).

Results

We collected 641 stationary individual scans with a minimum of 5 h between consecutive scans and 602 moving scans with a minimum of 6 h between consecutive scans. When the group was stationary, age−sex and rank tier significantly affected spatial position use (Table A2). We found that adult females ($\beta = -1.93$, $P = 0.027$), adult females with infants ($\beta = -3.13$, $P < 0.001$), subadult females ($\beta = -3.16$, $P = 0.002$) and juveniles/infants ($\beta = -4.30$, $P < 0.001$) used the outer position less than adult males (Table A2). Subadult males also tended to use the outer position less than adult males ($\beta = -1.90$, $P = 0.069$; Table A2). Individuals in the lower rank tier were in the outer position more than individuals in the upper tier ($\beta = 2.03$, $P = 0.016$; Table A2). We did not find a difference between individuals in the middle and upper tiers (Table A2). When the group was moving, age−sex class significantly affected spatial position use (Table A3). Compared to adult males, juveniles/infants used the front-middle ($\beta = 2.12$, $P < 0.001$) and back positions ($\beta = 1.76$, $P = 0.003$) more than the front-outer position. Adult females and subadults of both sexes did not differ significantly from adult males in their use of the front-outer position compared to the other two positions (Table A3). Rank tier did not have a significant effect on moving spatial position use (Table A3).
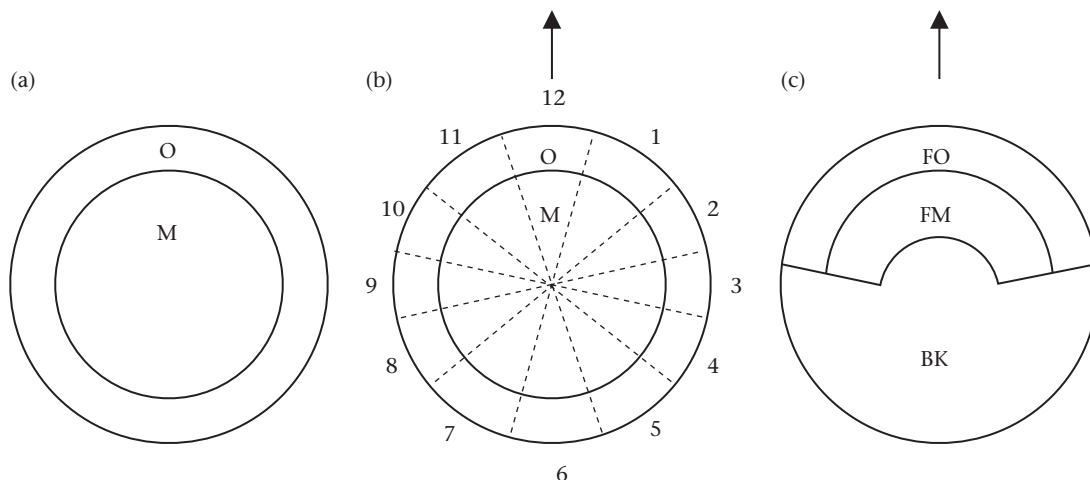

Figure A1. Elliptical clock method for recoding individual spatial positions during group scans (modified from Janson, 1990a; 1990b): (a) while the group was stationary (O: outer, M: middle); (b) while the group was moving, with arrow depicting the direction of travel; (c) consolidated categories for analyses (FO: front-outer; FM: front-middle; BK: back).

Table A2
Summary of generalized linear mixed effects model for the effects of age–sex and rank tier on stationary spatial position (reference category was set to 'middle')

Predictor variable	β [a] (SE)	z	P
Intercept	−0.52 (0.35)	−1.47	0.141
Age–sex			
Adult male (reference)	–	–	–
Adult female	**−1.93 (0.87)**	**−2.21**	**0.027**
Adult female + infant	**−3.13 (0.93)**	**−3.35**	**<0.001**
Subadult female	**−3.16 (1.01)**	**−3.11**	**0.002**
Subadult male	*−1.90 (1.04)*	*−1.82*	*0.069*
Juveniles and infants	**−4.30 (0.95)**	**−4.53**	**<0.001**
Rank tier			
Upper (reference)	–	–	–
Lower	**2.03 (0.84)**	**2.42**	**0.016**
Middle	1.25 (0.87)	1.43	0.154

Overall model fit compared to the null model, which included only the random effects: $N = 641$, $\chi^2 = 2.09$, $P < 0.001$. Marginal $R^2 = 0.28$, conditional $R^2 = 0.37$. Significant effects ($P < 0.05$) are shown in bold and trends ($P < 0.08$) are italicized.
[a] Positive coefficient values mean that the predictor increased the log-odds, while negative values mean the predictor decreased the log-odds, of being in the outer position.

Table A3
Summary of multinomial logistic regression model for the effects of age–sex and rank tier on moving spatial position (reference category was set to 'front-outer')

Predictor variable	β [a] (SE)	z	P
Front-middle vs front-outer			
(Intercept)	0.39 (0.25)	1.58	0.115
Age–sex			
Adult male (reference)	–	–	–
Adult female	0.79 (0.56)	1.42	0.156
Adult female + infant	0.68 (0.52)	1.32	0.187
Subadult female	0.90 (0.64)	1.41	0.158
Subadult male	0.63 (0.68)	0.93	0.355
Juveniles and infants	**2.12 (0.60)**	**3.54**	**<0.001**
Rank tier			
Upper (reference)			
Lower	−0.55 (0.49)	−1.14	0.254
Middle	0.33 (0.52)	0.63	0.530
Back vs front-outer			
(Intercept)	0.47 (0.25)	1.90	0.058
Age–sex			
Adult male (reference)	–	–	–
Adult female	0.88 (0.55)	1.60	0.111
Adult female + infant	0.56 (0.51)	1.10	0.273
Subadult female	0.94 (0.63)	1.50	0.134
Subadult male	−0.12 (0.70)	−0.18	0.861
Juveniles and infants	**1.76 (0.60)**	**2.95**	**0.003**
Rank tier			
Upper (reference)	–	–	–
Lower	−0.21 (0.48)	−0.44	0.663
Middle	0.42 (0.52)	0.82	0.414

Overall model fit compared to the null model, which included only the random effects: $N = 602$, $\chi^2 = 33.76$, $P = 0.002$. Significant effects ($P < 0.05$) are shown in bold. McFadden's pseudo $R^2 = 0.03$.
[a] Positive coefficient values mean that the predictor increased the log-odds, while negative values mean the predictor decreased the log-odds, of being in the front-middle or back position.

Discussion

In this group of vervet monkeys, we found that when the group was stationary, adult males were more likely to occupy the outer position than all other age–sex classes. When the group was moving, adults and subadults of both sexes were equally as likely to be found in the front-outer position, while juveniles and infants were less likely to be in the front-outer position, than adult males. When the group was stationary, upper-ranking individuals were more likely than low-rankers to occupy central positions. However, dominance rank had no effect on spatial position when the group was moving. Their consistent propensity to be central in the group suggests that juveniles and infants were the most sensitive to the higher risk of predation when in the group's periphery. Similar findings have been observed in several species (Assamese macaques, *Macaca assamensis*: Heesen et al., 2015; meerkats, *Suricata suricatta*: Gall & Manser, 2018; Sichuan golden monkeys, *Rhinopithecus roxellana*: Zhang, Ren, Li, Liang, & Wang, 1999; tufted capuchins, *Cebus apella*: Janson, 1990a). Our prediction that adult and subadult males would be equally as likely to be on the periphery of the group was not upheld. Instead, we found that adult males were in the outer position more than subadult males while the group was stationary. This could be because adult males were less vulnerable to predators due to their larger body size (Isbell, 1994), so they assumed the outer position more than the smaller subadults. A social explanation could be that subadult males were in the centre of the group more than adult males because they had stronger social bonds with natal group members and were thus more central in the group's social network.

Contrary to our predictions, adult and subadult females of all ranks were equally as likely to travel at the front of the group as adult males. This finding may arise because the overall predation risk at this field site is low. At Lake Nabugabo, the vervet monkeys occasionally encounter snakes, but aerial predators and terrestrial predators are largely absent, with the exception of dogs. The monkeys seemed able to discern between dogs that were threats from those that were harmless, and typically detected potential threats early enough that they posed a relatively low risk. The lack of predators may mean that females have little incentive to mitigate predation risk, allowing them to decrease feeding competition by opportunistically spending time in the front edge of the group. When the group was stationary, females, subadult males and high-rankers tended to occupy more central positions. These findings may arise because when the group is stationary, the valuable food patches in the area have already been detected, decreasing the benefit of being peripheral. Therefore, dominant individuals, and females in particular, may choose to prioritize minimizing predation risk over avoiding feeding competition, and to gather in central positions where they can maintain important social relationships with group members (Borgeaud, Sosa, Sueur, & Bshary, 2017).

Our results resemble those from a group of vervet monkeys in South Africa, where dominance rank had no effect on the distance from the front of the group (Josephs et al., 2016). Conversely, our findings differ from previous work on a neighbouring group (i.e. M group) at the same field site, which found that higher-ranking individuals tended to be in the front-outer position of a moving group (Teichroeb et al., 2015). KS had a bigger group size ($N = 40$) than M group ($N = 24$) and KS had a much larger home range that included areas with higher risks such as a military base and a bordering village where inhabitants chased monkeys to deter crop foraging (Chapman et al., 2016). Greater environmental risks could explain why high-rankers in KS displayed inconsistent use of the front-outer position, dependent on risk levels, while higher-rankers in M group were more willing to be on the leading edge consistently.