

# The Relative Importance of Size of Food and Interfood Distance in Eliciting Aggression in Captive Rhesus Macaques (*Macaca mulatta*)

Jeffrey W. Mathy Lynne A. Isbell

Department of Anthropology, University of California, Davis, Calif., USA

---

## Key Words

Primates · Rhesus macaques · *Macaca mulatta* · Contest competition · Aggression · Food distribution · Food size

---

## Abstract

We conducted an experiment on a group of captive rhesus macaques (*Macaca mulatta*) in which we manipulated both food size and interfood distance independently to examine which factor was more important in causing aggressive competition. For each of 254 trials, the monkeys were offered simultaneously two apple pieces ranging in size from 1 to 40 g at interfood distances ranging from 1 to 5 m. In contrast to other studies, food size and interfood distance were not conflated in this study. Multiple regression analyses revealed that food size was a better predictor of aggression whereas interfood distance was a better predictor of the ability to monopolize foods. Growing evidence suggests that factors such as food size, quality and depletion time are more important than interfood distance in influencing aggression within groups.

Copyright © 2001 S. Karger AG, Basel

## Introduction

Competition is thought to be inevitable when individuals live in social groups primarily because closer proximity increases the likelihood of agonism over food and other resources [1]. The spatial distribution of food has long been implicated as a causal factor in bringing individuals closer together and therefore in increasing aggressive competi-

---

## KARGER

Fax + 41 61 306 12 34  
E-Mail [karger@karger.ch](mailto:karger@karger.ch)  
[www.karger.com](http://www.karger.com)

© 2001 S. Karger AG, Basel  
0015-5713/01/0725-0268\$17.50/0

Accessible online at:  
[www.karger.com/journals/fpr](http://www.karger.com/journals/fpr)

L.A. Isbell, Department of Anthropology  
University of California at Davis  
Davis, CA 95616 (USA)  
Tel. +1 530 754 9718, Fax +1 530 752 8885  
E-Mail [laisbell@ucdavis.edu](mailto:laisbell@ucdavis.edu)

tion. That is, clumped foods are thought to increase aggressive competition whereas dispersed foods are thought to minimize aggressive competition [2–10].

The terms ‘distribution’ and ‘clumping’ are deceptively simple, however. In reality, the dispersion of resources can be notoriously difficult to quantify, in part because the answer one gets is so strongly dependent on the scale at which one measures the resources. Food resources can be measured at a scale as small as the individual food item or as large as that which allows all group members to feed together, but it is not clear what scale is appropriate for understanding aggressive competition within groups [11].

Experimental studies designed to test the hypothesis that spatial distribution of food determines the frequency of aggressive competition have consistently failed to reject it [12–15]. Generally, previous studies have involved varying the distance between foods while maintaining a constant level of overall food abundance. This requires a simultaneous (conflating) change in the size of the food, which could affect its depletion time. In a study of free-ranging brown hares (*Lepus europaeus*), for example, apple quarters were placed either into one pile with a diameter of 0.5 m or at 1-meter distances over an area of 50 m<sup>2</sup> [13]. Similarly, in a study of captive rhesus macaques (*Macaca mulatta*), 300 pieces of food (bananas, apples and carrots) were placed either in one pile or in three piles 5 m apart [15]. In both studies, the single pile was meant to represent a clumped distribution of food whereas the alternative was meant to represent a dispersed distribution of food.

Although controlling for overall food abundance may have been done to avoid introducing a potential confounding factor in these experiments, it inadvertently ties spatial distribution to food size or depletion time. By making fewer piles of food larger, such experiments change not only spatial distribution but also the amount of food per pile, and therefore its intrinsic value and the time it takes to deplete each pile. The experimental piles were either large and clumped or small and dispersed. It is not possible to determine from these experiments whether aggression is caused more by distance between foods or by food size/depletion time or whether the factors must interact to influence aggression.

As a first step in determining the importance of spatial distribution of food on aggression relative to other factors, we conducted an experiment on captive, group-living rhesus macaques in which we separated interfood distance from food size and measured aggression in response to the presence of the food. Here we report the results of that experiment.

## Methods

### *Subjects*

We conducted the experiment at the California Regional Primate Research Center (CRPRC) on the campus of the University of California, Davis, over 9 days from May to July 1999. The subjects were an established group of 74 rhesus macaques (33 males ranging from infancy to 15 years, including 16 adult males, and 41 females ranging from infancy to 11 years, including 22 adult females) that were kept in an outdoor 0.2-ha enclosure (NC 2) in which they were free to move about. The walls and roof of the enclosure are made of wire fencing, and the surface is natural ground cover of dirt and grass, supplemented with pebbles. Water and monkey chow were continuously available, while fresh seasonal fruits were provided regularly but less frequently by CRPRC staff.

### *Procedure*

We used apples supplied by the CRPRC as the experimental food. Apples were chosen for ease in obtaining precise weights for apple pieces and the monkeys' familiarity with and interest in them. The apples were cut and the pieces weighed with a portable scale just prior to each day's trials. Pieces ranged in size from < 1 to 40 g. The upper limit was capped at 40 g when it became clear that that size was obviously associated with increased aggression. We used a larger range of smaller food sizes because it was not obvious what the lower limit was, i.e., what size of food is not worth contesting.

To begin a trial, two apple pieces of the same size were simultaneously thrown over the top of the enclosure so that they would land somewhere in the enclosure. Initially, one observer hid behind a visual barrier while throwing the food to minimize expectant behavior but we found that the monkeys learned quickly to associate our appearance at the enclosure with the food, and we no longer attempted to hide after the second day of trials. This also allowed us to vary the location of the foods in the enclosure; no systematic attempt was made to randomize the location. Apple pieces of particular sizes were chosen for each trial with the goal of balancing sample sizes across all combinations of food size and interfood distance. The order in which we provided foods of different sizes was therefore dependent to a large extent on where the foods landed in the enclosure.

J.W.M. recorded the following data for each trial: food size (g), estimated distance between apple segments at landing (m), number of individuals in the area, identities of those in closest proximity to the food, the identity of the first to approach the food, the identities of those who ate the food, and behaviors that occurred at the food sites after the food landed. We divided the behaviors into six categories: (1) *no interaction*: one individual approaches food and eats it without interference from others; (2) *stealing*: one individual takes food away from another but without apparent aggression; could include taking food from the individual's mouth or hands; (3) *scramble*: multiple individuals rush to grab food with no aggression following; (4) *aggression following scramble*: multiple individuals rush to grab food with aggression occurring after the food has been obtained, where aggression is defined as attacking, chasing, or threatening another; (5) *aggression alone*: at least one individual attacks, chases, or threatens another individual without scrambling or stealing, and (6) *monopolization*: one individual consumes both apple pieces in a given trial.

Behaviors were scored using 1–0 sampling. This sampling technique was chosen because the rapidity with which the animals approached the food and interacted with others required quick assessment, making other sampling methods less reliable. Behaviors that occurred over at least one of the two food pieces were given a score of 1; more than one behavior could be recorded in any one trial. Data collection was terminated after the food was consumed, i.e., completely eaten or stored in cheek pouches. Since only two apple pieces were used per trial, each trial ended quickly (typically in < 10 s) and we were able to conduct an average of 25 trials per observation day (range 10–54; mean inter-trial interval 2.1 min).

### *Statistical Analyses*

Although we could control food size, we could not fully control interfood distance from outside the enclosure, and we had fewer of some food size/interfood distance combinations than others. For statistical analyses, we combined apple pieces < 1 g into the category of 1 g, those 2–4 g into the category of 3 g, those 6–10 g into the category of 10 g, and those of 30–40 g into the category of 30 g, the categories 5 g and 20 g contained apple pieces of those exact weights, for a total of six categories (table 1). Each category thus included foods of similar size, i.e., we did not combine into the same category foods of widely disparate sizes. We combined interfood distances of < 1 m into the category of 1 m; other distances were estimated to the nearest whole meter during the trials. Statistical analyses included five categories of interfood distance: 1, 2, 3, 4 and 5 m. The number of trials per combination ranged from 1 to 26; total sample size was 254 trials after excluding combinations with a sample size of 1 (table 1). Scores for 26 of 30 possible combinations remained after these exclusions. For each of the 26 combinations we calculated mean scores of each of the behaviors to minimize potential bias resulting from uneven sample sizes among combinations. These means converted our data from presence/absence data into percentages. We analyzed the means statistically using the software program JMP (SAS Institute, Cary, N.C., USA), conducting multiple regression tests for the independent contributions of food size and interfood distance on 'aggression alone', 'aggression following scramble', 'scramble', and 'monopolization'. We did not conduct tests on 'stealing' (too few

**Table 1.** Sample sizes per combination of food size and interfood distance: each combination was weighted equally by using mean values; means for combinations with a sample size of 1 cannot be calculated and were excluded from analyses

Food size	Interfood distance				
	1 m	2 m	3 m	4 m	5 m
1 g	23	26	18	4	4
3 g	7	6	4	3	12
5 g	5	12	14	1	3
10 g	2	11	6	2	1
20 g	21	15	3	1	1
30 g	8	10	13	13	5

cases) or on ‘no interaction’ (although the lack of interaction might be useful in understanding feeding preferences of individuals, it was not germane to our study other than as a possible outcome other than aggression, the behavior of interest here). Each trial was numbered consecutively based on chronology for each day. Means were obtained for each trial number having at least two data points ( $n = 43$ ). These means were correlated with the two categories of aggression to determine whether aggression increased as the number of trials progressed. Statistical significance of the correlation tests were taken from Zar [16].

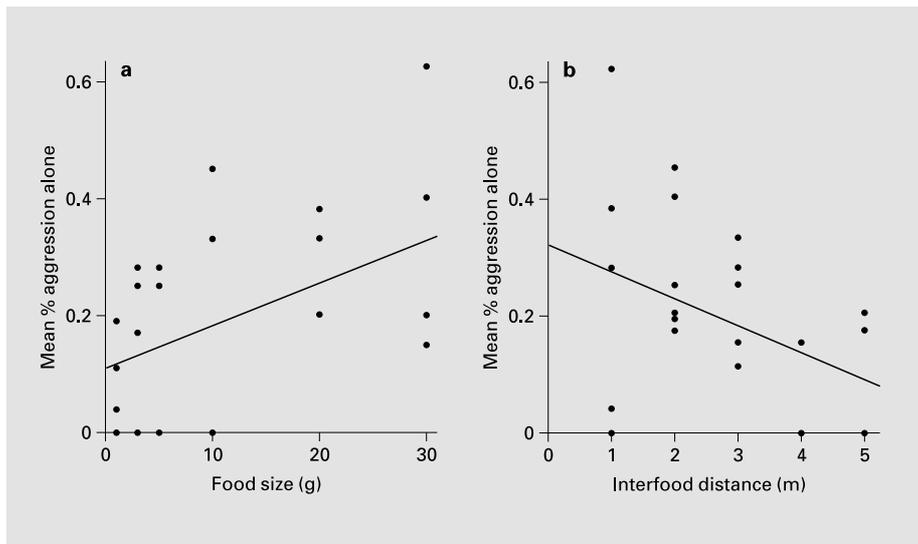
## Results

### *Relative Effects of Food Size and Interfood Distance*

Food size and interfood distance were not significantly correlated with each other ( $r = -0.05$ ,  $p > 0.50$ ,  $n = 26$ ). That is, larger foods were not more likely to be clumped than smaller foods; foods could be small and clumped, small and dispersed, large and clumped, or large and dispersed.

‘Scramble’, in which individuals rushed to grab food, was the most frequent response to the arrival of the food and occurred in 123 of 254 trials (48%), followed by ‘no interaction’, which occurred in 95 trials (37%). ‘Aggression alone’, in which at least 1 monkey attacked, chased, or threatened another monkey near the food, and ‘aggression following scramble’, in which aggression occurred after multiple monkeys rushed to get the food, occurred in 54 (21%) and 37 (15%) trials, respectively. ‘Stealing’ occurred in only five trials (2%).

Together, food size and interfood distance significantly influenced the occurrence of aggression alone (table 2), although food size had a stronger effect than interfood distance. When the two characteristics of food were tested separately, food size explained 22% of the variance in aggression alone (fig. 1a) while interfood distance explained 15% of the variance (fig. 1b). Only food size influenced the occurrence of aggression following scramble, however (table 2). When they were tested separately, food size explained much more variation than interfood distance in aggression following scramble (food size 60%, fig. 2a; interfood distance 0.8%, fig. 2b). Scramble, a behavior that did not involve any kind of overt aggression, was not significantly affected



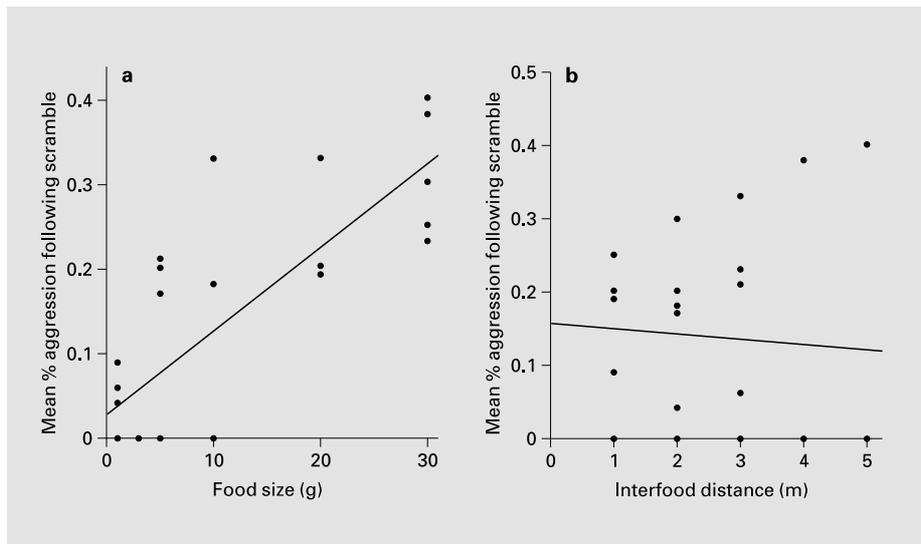
**Fig. 1.** The influence of food size (**a**) and interfood distance (**b**) on the mean percentage of trials in which aggression occurred alone. In both cases, food size was a statistically significant predictor of aggression (see text for statistical values).

**Table 2.** F ratios and significance levels of multiple regression on the independent effects of food size and interfood distance on behavior

	Food size	Interfood distance
Aggression alone	F = 6.68, p = 0.02	F = 4.18, p = 0.05
Aggression following scramble	F = 35.56, p < 0.0001	F = 0.20, p = 0.66
Scramble	F = 1.55, p = 0.22	F = 0.46, p = 0.50
Monopolization	F = 1.36, p = 0.26	F = 9.41, p = 0.005

by either food size or interfood distance (table 2). Analyses of subsets of food sizes (1, 10 and >30 g; 1, 10, 20 and >30 g) did not change the outcome of the results.

Despite a large number of trials occurring over a relatively short period of time, neither aggression alone nor aggression following scramble increased across trials within a given day, but both were negatively correlated with the order of trials (aggression alone:  $r = -0.52$ ,  $n = 43$ ,  $p < 0.001$ ; aggression following scramble,  $r = -0.39$ ,  $p < 0.01$ ). The decrease in aggression over time likely reflects changes in food size over time: food size was also negatively correlated with trial order ( $r = -0.85$ ,  $p < 0.001$ ). Scramble was not significantly correlated with trial order ( $r = 0.13$ ,  $p > 0.20$ ), indicating that the animals were interested in the food throughout the day's trials and therefore that the reduction in aggression over time was not a result of satiation.

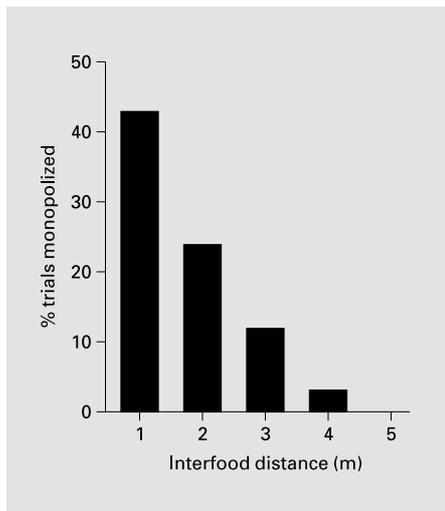


**Fig. 2.** The influence of food size **(a)** and interfood distance **(b)** on the mean percentage of trials in which aggression occurred following scramble. Food size only was a statistically significant predictor of aggression following scramble (see text for statistical values).

Although food size influenced aggression, it did not apparently determine whether one individual would monopolize both food pieces. Aggression in general (aggression alone and aggression following scramble combined) was as likely to occur with nonmonopolized trials as with monopolized trials ( $\chi^2 = 2.4$ ,  $p = 0.12$ ). Instead, the ability to monopolize both pieces of food was determined largely by interfood distance (table 2). Interfood distance explained 27% of the variance in monopolizability, whereas food size explained only 3% of the variance. Foods were monopolized most often at interfood distances of 1 m and decreased with successive interfood distances until the interfood distance of 5 m, at which no monopolization occurred (fig. 3).

#### *Individual Involvement in Food Acquisition*

Although 55 of the 74 animals in the enclosure (74%) were observed to eat at least one apple piece, the 9 members of the highest-ranking matriline [the U matriline; G. Vicino, pers. commun.] were observed to eat at least 269 of 508 (53%) apple pieces. Within the U matriline, 3 individuals were most frequently involved. Ultro, 5 years old and the beta male [G. Vicino, pers. commun.], obtained at least one apple piece in 86 of 254 trials (34%) and ate at least 113 of 508 apple pieces (22%). Umpy, a 1-year-old male, obtained at least one apple piece in 40 trials (16%) and ate at least 43 apple pieces (8%). Uriah, a 3-year-old female, obtained at least one apple piece in 39 trials (15%) and, like Umpy, ate at least 43 apple pieces (8%). The most successful individual outside the U matriline was the alpha male, who obtained at least one apple piece in 28 trials (11%) and ate at least 35 apple pieces (7%). Adult females outside the U matriline were noticeably uninvolved in the trials. Although these 19 adult females represented



**Fig. 3.** The percentage of food trials in which both apple pieces were eaten by the same individual ( $n = 252$  with 2 unknown cases). Interfood distance, but not food size, significantly predicted monopolizability (see text for statistical values).

26% of the group, they were involved in only 26 trials (10%). Interest by only a subset of available individuals has also been observed in similar food trials with a wild group of vervets [Isbell, unpubl. data].

## Discussion

The problem of previous experimental studies in conflating food size with spatial distribution was eliminated in this study; food size was not correlated with interfood distance. Dissociating the two factors revealed that food size predicted general aggressive behavior better than interfood distance, largely because food size was especially important in influencing aggression after multiple individuals rushed to get the food and the food was consumed. The possibility exists that this form of aggression occurs simply as the result of heightened defensiveness as multiple individuals rush for the same food and come into very close proximity. Alternatively, it may function as a future deterrent to lower-ranking animals attempting to get the food. The animals that were successful in obtaining the food were mainly high-ranking animals, and thus in a position to punish others. Aggression by higher-ranking individuals only after they have consumed the food has also been observed toward lower-ranking individuals that attempted to get the food during similar food trials in a group of wild vervets [Isbell, unpubl. data]. Although food size was better at influencing aggression, interfood distance was better at predicting the ability to monopolize foods. Indeed, aggression and monopolizability were not associated with each other.

Larger foods may exert their effect by having longer depletion times. Depletion time has been found to be important in determining aggressive interactions in several species. In vervets and patas monkeys, the rate of aggression of adult females corresponded better with feeding site depletion time (FSDT) than with interfood distance. The rate of aggression among vervets was higher in *A. xanthophloea* habitat, the habitat in which they spent longer at food sites [10–11], and lower in *A. drepanolobium* habitat, the habitat in which they spent less time at food sites. The rate of aggression among female vervets in *A. drepanolobium* habitat and the time they spent at food sites also converged with the behavior of patas monkeys in the same habitat [10, 11]. In brown capuchins (*Cebus apella*), aggressive interactions occurred more frequently over foods that were depleted more slowly [17]. In yellow baboons (*Papio cynocephalus*), higher-ranking individuals had longer feeding bouts (and therefore probably longer FSDTs) and were less likely to be aggressively interrupted during feeding bouts than lower-ranking individuals [18]. Depletion time was not an issue in this study, however, because all foods were consumed immediately.

Larger foods may also exert their effect by having greater intrinsic value than smaller foods. The benefits of aggressive behavior are likely to counter the risk of injury as foods increase in value. In Hanuman langurs (*Semnopithecus entellus*) aggression occurred more frequently over foods that were higher in nutritional quality [19]. Because we did not vary the kind of food, its value could have only changed as a result of size.

Aggression decreased as trials increased, which could suggest satiation. Satiation is not intrinsic to food value but is extrinsic and depends largely on the motivational state of the animals. There was no indication that the animals became satiated, however, because they maintained interest in the foods throughout a given day's trials and the foods were always consumed quickly. Food size also decreased as trials increased, and it is likely that aggression was spuriously negatively correlated with trial order through its positive correlation with food size.

The results presented here revealed that interfood distance affected the ability to monopolize foods. Although the ability to act aggressively to obtain foods is often equated with the ability to monopolize foods [e.g., 3–5, 20], they are not always the same. These abilities may be coupled only for high-ranking individuals under the condition of short interfood distances. It will be important in future research to specify whether competitive relationships are based on the ability and potential to usurp foods from others, either directly by supplanting or indirectly by aggression, or on the ability and potential to hold onto resources. Usurpability may be affected by the quality of a food (food size in the case here), or by FSDT, a temporal component of food resources, whereas the ability to hold onto food resources may be affected by interfood distance, a spatial component of food resources. In our study, the area over which the two food sites were monopolized dropped off as interfood distance increased; the interfood distance of 5 m appeared to be impossible to monopolize by any individual, regardless of rank. It would be intriguing to examine species differences in the size of the area of monopolizability and the degree of elasticity of that area within species as social conditions, i.e., rank and density of individuals, change.

The question arises that if food size, quality, or FSDT actually elicits aggressive competition, why has spatial distribution traditionally been considered the causal factor? We can think of four potential reasons. First, interfood distance may influence aggressive competition, albeit to a much smaller extent than food size, quality, or

FSDT. Second, because humans are visually oriented, spatial influences on behavior may be more easily identified than temporal influences. Third, human perceptual responses may be different for small, numerous foods and few, large units [21, 22]. When humans are presented with a spatial configuration composed of many small units, e.g., flowers in a tree, we appear to perceive independence between the larger configuration and the smaller units, and we preferentially recognize the larger configuration (the tree). In contrast, when presented with a spatial configuration composed of few large units, e.g., a solitary moose or a group of deer, we appear to perceive both the units (the individual animals) and the larger configuration (the group) similarly [21, 22]. This suggests that small foods may become clumped, depending on the scale at which they are measured, but that large foods are always considered clumped regardless of the scale. If this is true, it then becomes difficult to find in nature large and dispersed foods or small and clumped foods on scales that are relevant to the individual animal. Finally, and perhaps most importantly, when clumping of smaller foods occurs at the scale of small, monopolizable areas, it may increase the opportunity for aggression by increasing effective food size. This may have been the case in previous experiments that found correlations between food distribution and aggression.

### Acknowledgments

We thank the personnel at the California Regional Primate Research Center, particularly G. Vicino and K. Anderson, for facilitating our efforts to conduct this study. We also thank V. Cummins for assistance during the experiments, T. Bazaine, S. Betts, M. Nakamura, and M. Sockol for constructive comments during the study, and T. Young for particularly insightful discussions and comments on the manuscript. This study was funded in part by instructional funds from the University of California, Davis, and was covered under protocol #8661 of the UC Davis Animal Care and Use Committee. During the preparation of the manuscript, L.A.I.'s research was supported by grants from the NSF (BCS-9903949), the Wenner-Gren Foundation for Anthropological Research, the L.S.B. Leakey Foundation, and by funds from the Faculty Research Grant program and the Dean's Office of the College of Letters and Science, University of California at Davis.

### References

- 1 Alexander RD: The evolution of social behavior. *Annu Rev Ecol Syst* 1974;5:325–383.
- 2 Chalmers NR: Group composition, ecology and daily activities of free living mangabeys in Uganda. *Folia Primatol* 1968;8:247–262.
- 3 Wrangham RW: An ecological model of female-bonded primate groups. *Behaviour* 1980;75:262–300.
- 4 Van Schaik CP: The ecology of social relationships amongst female primates; in Standen V, Foley RA (eds): *Comparative Socioecology: The Behavioural Ecology of Humans and Other Mammals*. Oxford, Blackwell Scientific, 1989, pp 195–218.
- 5 Isbell LA: Contest and scramble competition: Patterns of female aggression and ranging behavior in primates. *Behav Ecol* 1991;2:143–155.
- 6 Milinski M, Parker GA: Competition for resources; in Krebs JR, Davies NB (eds): *Behavioural Ecology: An Evolutionary Approach*, ed 3. Oxford, Blackwell Scientific, 1991, pp 137–168.
- 7 Barton RA: Sociospatial mechanisms of feeding competition in female olive baboons, *Papio anubis*. *Behav Ecol Sociobiol* 1993;38:321–239.
- 8 Phillips KA: Foraging-related agonism in capuchin monkeys (*Cebus capucinus*). *Folia Primatol* 1995;65:159–162.
- 9 Saito C: Dominance and feeding success in female Japanese macaques, *Macaca fuscata*: Effects of food patch size and inter-patch distance. *Anim Behav* 1996;51:967–980.
- 10 Pruettz JD, Isbell LA: Ecological correlates of female aggression in vervets (*Chlorocebus aethiops*) and patas monkeys (*Erythrocebus patas*) living in simple habitats. *Behav Ecol Sociobiol* 2000;49:38–47.

- 11 Isbell LA, Pruett JD, Young TP: Movements of vervets (*Cercopithecus aethiops*) and patas monkeys (*Erythrocebus patas*) as estimators of food resource size, density and distribution. *Behav Ecol Sociobiol* 1998;42:123–133.
- 12 Southwick CH: An experimental study of intragroup agonistic behavior in rhesus monkeys (*Macaca mulatta*). *Behaviour* 1967;28:182–209.
- 13 Monaghan P, Metcalfe NB: Group foraging in wild brown hares: Effects of resource distribution and social status. *Anim Behav* 1985;33:993–999.
- 14 Boccia ML, Laudenslager M, Reite M: Food distribution, dominance, and aggressive behaviors in bonnet macaques. *Am J Primatol* 1988;16:123–130.
- 15 Brennan J, Anderson JR: Varying responses to feeding competition in a group of rhesus macaques (*Macaca mulatta*). *Primates* 1988;29:353–360.
- 16 Zar JH: *Biostatistical Analysis*, ed 2. Englewood Cliffs, Prentice Hall, 1984.
- 17 Janson CH: Ecological consequences of individual spatial choice in foraging groups of brown capuchin monkeys, *Cebus apella*. *Anim Behav* 1990;40:922–934.
- 18 Post DG, Hausfater G, McCuskey SA: Feeding behavior of yellow baboons (*Papio cynocephalus*): Relationship to age, gender and dominance rank. *Folia Primatol* 1980;34:170–195.
- 19 Koenig A, Beise J, Chalise MK, Ganzhorn JU: When females should contest for food – Testing hypotheses about resource density, distribution, size, and quality with Hanuman langurs (*Presbytis entellus*). *Behav Ecol Sociobiol* 1998;42:225–237.
- 20 Sterck, EHM, Watts D, van Schaik CP: The evolution of female social relationships in primates. *Behav Ecol Sociobiol* 1997;41:291–310.
- 21 Kimchi R, Palmer SE: Form and texture in hierarchically constructed patterns. *J Exp Psychol* 1982;8:521–535.
- 22 Kimchi R, Palmer SE: Separability and integrality of global and local levels of hierarchical patterns. *J Exp Psychol* 1985;11:673–688.