



Punishment and competition over food in captive rhesus macaques, *Macaca mulatta*

REBECCA L. CHANCELLOR & LYNNE A. ISBELL

Department of Anthropology, University of California, Davis

(Received 1 May 2007; initial acceptance 5 July 2007;
final acceptance 1 November 2007; published online 18 April 2008; MS. number: A10762R)

Current socioecological models predict that clumped food resources influence aggression, yet definitions of clumped resources often include two concepts: time spent at the resource and distance between resources. To disentangle these two aspects of clumping, we conducted an experiment on 15 multi-male–multifemale groups (range 50–110 individuals) of captive rhesus macaques at the California National Primate Research Center in which we varied both food size and interfood distance independently to test which factor more significantly influenced two forms of feeding competition, contest competition and punishment. At interfood distances of 1–6 m, two same-sized apple pieces of 1 g, 5 g, 15 g or 30 g were offered to the monkeys simultaneously during each of 297 trials. Aggression was recorded 5 min before the arrival of the food, when the food arrived and 5 min after. Results of the independent effects of food size revealed that larger food size was significantly associated with both contest competition and punishment. Interfood distance was not significantly associated with either contest competition or punishment. These results suggest that the size or handling time of food may be a better predictor of within-group aggression than is the spatial distribution of food.

© 2008 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Keywords: aggression; contest competition; dominance hierarchy; feeding competition; food distribution; handling time; *Macaca mulatta* punishment; rhesus macaque

Many studies have documented the importance of aggression in competition over resources, and a major area of interest has been investigating direct competition, in which individuals aggressively compete over an existing resource (e.g. Southwick 1967; Alexander 1974; Milinski & Parker 1991; Kaminski et al. 2006). Current ecological models predict that clumped resources promote contest competition (Wrangham 1980; van Schaik 1989; Isbell 1991; Grant 1993), and a number of field studies have tested this prediction (e.g. Monaghan & Metcalfe 1985; Mitchell et al. 1991; Ganslosser & Dellert 1997; Koenig et al. 1998; Goldberg et al. 2001).

Accumulating evidence, however, suggests that indirect resource competition, such as punishment, is also

important in social contexts where conflicts of interest arise (Clutton-Brock & Parker 1995). Punishment is a behavioural tactic that increases the fitness of the punisher in the long run by dissuading the victim from performing an action again (Clutton-Brock & Parker 1995). It is usually carried out by dominant individuals, and can be a potent force (Clutton-Brock & Parker 1995; Dugatkin 2002). For example, male lesser grey shrikes, *Lanius minor*, punish female partners for extrapair copulations by physically retaliating against them (Valera et al. 2003). Female red-backed salamanders, *Plethodon cinereus*, punish socially polygynous male partners by threatening and biting them during the courtship season (Prosen et al. 2004). Dominant male red junglefowl, *Gallus gallus*, periodically challenge males that signal similar high status in order to test dominance status and therefore punish cheaters (Parker & Ligon 2002). As a result of punishment, victims often change their behaviour to avoid future aggression (Boyd & Richerson 1992; Clutton-Brock & Parker 1995).

Correspondence: R. Chancellor, Department of Anthropology, University of California, Davis, CA 95616, U.S.A. (email: rlchancellor@ucdavis.edu). L. Isbell is at the Department of Anthropology, University of California, Davis, CA 95616, U.S.A. (email: laisbell@ucdavis.edu).

Subordinates periodically test dominance relationships, and therefore punishment is an important feature of group-living animals where the likelihood of recurring contests is high (Clutton-Brock & Parker 1995). Indeed, punishment is so important that it can influence the evolution of social behaviour. For example, punishment may have played an important role in the evolution of cooperation in humans (Boyd & Richerson 1992). In primates, Bernstein (2006) suggested that punishment helps to preserve the social stability of a group because group members may punish an individual who breaks an established 'rule'. For example, in hamadryas baboons, *Papio hamadryas*, male harem leaders punish straying females by biting them on the neck (Kummer 1968). Rhesus macaques that do not give food calls at preferred food sources are more likely to be targets of aggression (Hauser 1992; Hauser & Marler 1993).

In a study of contest competition related to food distribution, Mathy & Isbell (2001) observed that consumers often directed aggression towards others after the experimental food had already been consumed. This observation was contrary to their expectations that aggression would primarily occur before the food was eaten, while individuals were directly contesting it. They hypothesized that dominant consumers use postcontest aggression to punish individuals that attempt to compete, which deters them from attempting to compete again. In nature, punishment tends to occur directly after a noncooperative act (Hauser 1992).

In this study, we tested Mathy & Isbell's (2001) hypothesis by investigating potential social and ecological factors influencing punishment. The factors we used were food size, interfood distance, consumer dominance and the presence of scramble and contest competition. Foods that are depleted more slowly or that have longer handling times elicit aggressive interactions, because the food is inherently more valuable or because there is more time to fight over the resource (Post et al. 1980; Enquist et al. 1985; Janson 1990; Isbell et al. 1998; Pruettz & Isbell 2000; Sirot 2000). In captive primates in particular, the size of the food is a better predictor of aggression than is the spatial distribution of food (Mathy & Isbell 2001). Therefore, our predictions were that high-ranking consumers would be more likely to punish as food size increases, but that interfood distance would not affect punishment by consumers. In choosing to vary food size instead of the number of food piles as other tests of spatial clumping have done, we aimed to separate spatial clumping from handling time. Varying the number of food piles would have changed not only the spatial distribution of food, but also the amount of food per pile, which would have affected both the intrinsic value of the food and the time that it took to deplete each pile (see Mathy & Isbell 2001).

We also predicted that the presence of a second competitor (contest or scramble competition) would increase the likelihood that high-ranking consumers punish in order to deter competitors from competing for the food the next time. Finally, we examined the potential benefits of punishment by consumers. Specifically, we asked whether consumers who punish are more likely to have

priority of access to food. If punishment is indeed an effective strategy, consumers who punish should be more likely to get food in multiple trials.

METHODS

Study Site and Subjects

This study was conducted during May–August 2001 at the California National Primate Research Center (CNPRC), University of California, Davis. The subjects were 15 multimale–multifemale groups of rhesus macaques (North Field Cages 1–6, 8–15, and 18). Group sizes ranged from 50 to 110 individuals, with an average of 84 individuals per group, totalling approximately 1265 subjects. Group sizes fell within ranges that have been reported for free-ranging rhesus macaques (i.e. 15–133 individuals/group: Malik et al. 1984; 104–142 individuals/group: Manson 1994). All were established groups, with the exception of those in cages 6 and 15, which were recently formed. Groups were housed in 0.2-ha wire-fenced field cages, in which all individuals were able to move about freely. All groups had continuous access to water and monkey chow. The CNPRC staff also periodically provided extra food items such as sunflower seeds and fruit.

Procedure

To test Mathy & Isbell's (2001) predictions, our experiment resembled theirs, with a few modifications. Their average interval between trials was only 2.1 min. This short duration could have biased the behaviour of the study animals, perhaps by heightening expectant behaviour. Therefore, we conducted comparable food trials using similar food sizes and interfood distances, but increased intertrial intervals to over 24 h. We also expanded the study from one to 15 groups to increase sample size and to prevent any one individual from significantly influencing the results. This design allowed us to replicate Mathy & Isbell's results more rigorously, while also testing the punishment hypothesis. We also recorded all occurrences of aggression 5 min before the food trial and 5 min after the food trial. By doing so, we were able to examine punishment in relation to aggression before, during and after each food trial. A food trial started immediately after the food was thrown into the subjects' cage and continued until both food pieces were claimed by a consumer (ca. <1 min). As soon as the two food pieces were claimed, the 5 min post-trial period began.

As in Mathy & Isbell (2001), we used apples supplied by the CNPRC as the experimental food. Before each day's trials, the apples were cut into pieces and weighed to 1 g (size of a raisin), 5 g, 15 g or 30 g (size of an egg) on a portable scale. Each day and for each cage, the size of the apple pieces was chosen to try to obtain equal combinations of food size and interfood distance. Interfood distances were estimated to a whole metre (1 m, 2 m, 3 m, 4 m, 5 m, 6 m). For each trial, two same-sized apple pieces were introduced simultaneously to the animals

over the top of the enclosure, so that they would land inside in one of eight randomly selected 6 × 6 m grids that surrounded the periphery of each cage, and were easily demarcated by internal support poles. When the apple pieces landed, we recorded the food size (g), the distance between the two food pieces (m), the number of individuals in the grid, the identities of the consumers (when known), and all trials in which one individual obtained both pieces (monopoly). As individuals in the grid went for the food, we recorded the following three behavioural responses: (1) Contest Competition, defined as the presence of one or more individuals aggressively threatening, chasing or attacking others as individuals moved in to try to obtain the food; (2) Scramble, defined as the presence of more than one individual moving in to obtain food accompanied by no aggression; and (3) No Interaction, defined as the absence of overt interference by others as an individual took the food. Based on the results of Mathy & Isbell (2001), these behaviours were considered sufficient to characterize the most common behavioural responses before food was seized by a consumer. Behaviour was scored using 1–0 sampling (i.e. whether the behaviour occurred or not) because behavioural responses occurred so quickly that all-occurrences sampling could not be used (see Martin & Bateson 1993).

During the 5 min periods before and after each food trial (i.e. before and immediately after the food was thrown and claimed by consumers), we recorded the behaviour that occurred in the grid containing the food and in the five grids surrounding it (a total of 216 m², 11% of the enclosure). Aggressive behaviour observed in the 5 min periods before and after each trial was scored using all-occurrences sampling. To investigate the occurrence of punishment, we recorded consumer-related aggression after the food was in possession of the consumer and not likely to be stolen (i.e. already swallowed, being chewed in the mouth, in the cheek pouch, or being transferred between hands and mouth). We defined Punishment as any threat, chase or attack performed by the consumer towards others who had either assembled around or approached the consumer. This behaviour was scored using 1–0 sampling.

Rank

On the subset of individuals for which we had a positive identification (N = 157), we divided high- and low-ranking consumers by grouping the top five males and the top five females of each enclosure into the high-ranking category. We separated male and female dominance hierarchies, correcting for potential sex bias among ranks. Individuals in the top five ranks were on average within the top 6% of their respective dominance hierarchies. We did not use matrilineal divisions because they were not clear in all cages.

We conducted an average of 10 trials per observation day (range 5–15). Enclosures were sampled in random order, and all 15 enclosures were sampled before another round of trials began. This resulted in intertrial intervals of more than 24 h, which minimized expectant behaviour and the chance that any one individual biased results. It

also allowed each cage to be sampled at varying times of the day, making food arrival both temporally and spatially unpredictable. We conducted a mean of 19.8 trials per enclosure (range 15–24).

To determine handling times of each food size, we separately conducted 80 trials (20 trials per food size) in which we threw one apple piece into a randomly selected cage and grid, and timed how long it took the consumer to completely finish it (i.e. it was no longer visible in the consumer’s hands, mouth or cheek pouch and appeared to be swallowed). This was done to determine whether foods used in this study were so small that they were all depleted immediately, or whether food size at the scale presented in the trials fairly reflected significantly different handling times.

Statistical Analyses

As in Mathy & Isbell (2001), we could control for food size, but could not completely control for interfood distance during food trials, so there were more of some food size/interfood distance combinations than others. For analyses, in order to achieve more even distributions of food size/interfood distance combinations across cages, we grouped 1 g and 5 g food sizes into a small category and 15 g and 30 g sizes into a large category. We then grouped 1 m, 2 m and 3 m interfood distances into a short category, and 4 m, 5 m and 6 m interfood distances into a long category. We conducted 297 trials, ranging from 60 to 86 trials for each of the four combinations of food size/interfood distance (Table 1).

We measured interfood distance and food size as possible predictors of three types of responses, including behavioural responses as individuals went for the food (contest competition, scramble, or no interaction), food monopoly and punishment by consumers. We fitted three

Table 1. Sample sizes for each combination of food size and interfood distance by cage (N = 297 trials)

Food size	Small		Large		Total
	Short	Long	Short	Long	
Interfood distance					
Cage					
1	7	1	3	7	18
2	7	5	4	4	20
3	5	6	4	5	20
4	6	3	6	4	19
5	4	5	8	4	21
6	7	1	6	6	20
8	4	3	6	2	15
9	8	5	4	7	24
10	6	2	6	6	20
11	3	5	6	4	18
12	3	10	5	5	23
13	7	4	5	7	23
14	8	2	4	5	19
15	6	4	7	3	20
18	5	4	5	3	17
Total	86	60	79	72	297

regression models for these outcomes. Since we could not completely control for interfood distance, this study is a mixture of controlled and observational designs. Because the possibility of heterogeneity in behaviour across cages existed, we performed a first stage analysis for each behaviour, fitting models that had variance components only for cages. When random effects for cages in these models were not significant, we proceeded to fit models with fixed effects only. We used a multinomial logit regression model for outcome, with fixed effects for distance and food size; we used logistic regression models for monopoly and punishment, with the same fixed effects as above. We used these models because even in completely observational studies these models give valid statistical inferences (Myers et al. 2002). The number of observations used for the regression models was 297, except for monopoly, which was 262. Monopoly did not occur in two cages, which presented a problem for modelling cage effects. For these cages, the variation in behaviour that was needed to fit a model was not present. Thus cages 3 and 8 were excluded from the model for monopoly.

On the subset of data in which consumers' identities were known ($N = 157$), we measured consumer rank as a possible predictor of punishment by fitting a logistic regression model, with fixed effects for consumer rank. We measured punishment by a consumer as a possible predictor of getting food in multiple trials by fitting a logistic regression model, with fixed effects for punishment by a consumer and consumer rank (to control for rank). For contingency table tests of the interactions between consumer rank, food size and food monopoly, only the first trial of multiple trials involving the same consumer was used to minimize dependence of the data. The frequency of punishment as a possible predictor of the frequency of getting food was investigated using a least squares regression model on the subset of consumers who punished ($N = 58$), with fixed effects for the frequency of punishment and consumer rank (to control for rank), and random intercepts for cage. Food handling time was analysed using least squares regression.

All analyses were conducted using the software programs SAS 9.1 and JMP 7 (SAS Institute Inc., Cary, NC, U.S.A.). Statistical significance was set at $P = 0.05$ and all tests were two tailed. We used SAS PROC NL MIXED to fit the logistic and multinomial logit models with random effects. Data and scripts are available upon request.

RESULTS

Influence of Food Size and Interfood Distance on Competition and Punishment

During the food trials, the least frequent response was contest competition, which occurred in 76 of 297 trials (25%). Scramble occurred in 106 trials (36%). The most frequent response was no interaction (115 trials, 39%). When the food was thrown, expectant behaviour appeared to be low because there was an average of only 1.7 individuals in the trial grid.

The independent effects of food size and interfood distance revealed that large food size significantly increased the frequency of both contest and scramble competition, whereas interfood distance did not have a significant effect. We checked for pairwise interactions of the two predictors and for cage effects, and they were not significant, so we describe only a main and fixed effects regression. Wald tests (Wald 1943) showed that food size was a significant predictor of scramble and contest competition ($\chi^2_2 = 25.8$, $P < 0.0001$), but interfood distance was a weak predictor of scramble and contest competition ($\chi^2_2 = 1.2$, $P = 0.56$). The estimated odds ratio comparing large versus small food size on the outcome contest competition was 5.3 (95% CI: 2.8, 10.2), and the odds ratio for the outcome scramble was 1.8 (95% CI: 1.0, 3.0); thus, on average, for a given interfood distance, large food size increased the odds of contest competition by a factor of 5.3, but increased the odds of scramble competition by a factor of only 1.8 (a value of 1.0 implies that an outcome is indifferent to the predictor). Consequently, a strong significant relationship existed between food size and contest competition (Fig. 1), while a weaker one existed between food size and scramble. These results are consistent with those obtained by Mathy & Isbell (2001).

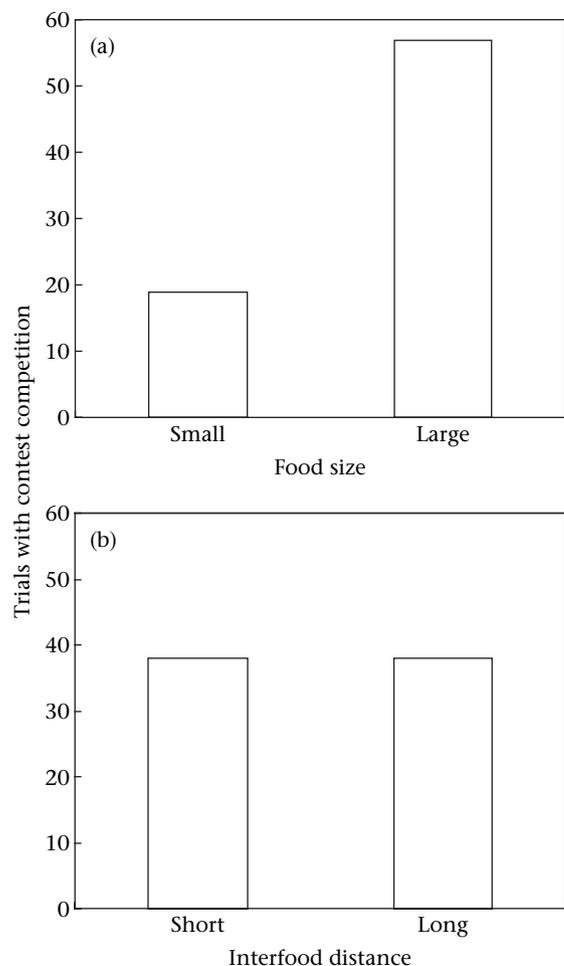


Figure 1. Number of trials in which contest competition occurred ($N = 76$) relative to (a) food size and (b) interfood distance.

Apple pieces were monopolized in 49 of 297 trials (16%). The independent effects of food size and interfood distance revealed that as interfood distance increased, the ability to monopolize both pieces significantly decreased, whereas food size did not have a significant effect (Fig. 2). We checked for pairwise interactions of the two predictors and for cage effects after excluding cages 3 and 8 (see Methods), and they were not significant, so we describe only a main and fixed effects regression. Wald tests showed that interfood distance was a significant predictor of monopoly ($\chi_1^2 = 19.5, P < 0.0001$), but that food size was not ($\chi_1^2 = 0.3, P = 0.57$). The estimated odds ratio comparing short versus long interfood distance was 7.5 (95% CI: 3.1, 18.5); thus, on average, for a given food size, short interfood distance increased the odds of monopoly by a factor of 7.5. Again, these results are consistent with those of Mathy & Isbell (2001).

The independent effects of food size and interfood distance revealed that large food size significantly increased the frequency of punishment, whereas interfood distance had no significant effect (Fig. 3). We checked for pairwise interactions of the two predictors and for cage

effects, and they were not significant, so we describe only a main and fixed effects regression. Wald tests showed that food size was a significant predictor of punishment ($\chi_1^2 = 17.3, P < 0.0001$), but that interfood distance was not ($\chi_1^2 = 0.002, P = 0.96$). The estimated odds ratio comparing large versus small food size was 2.8 (95% CI: 1.7, 4.4); thus, on average, for a given interfood distance, large food size increased the odds of punishment by a factor of 2.8.

When scramble and contest competition occurred, food was monopolized less than expected by chance, but when no interaction occurred, food was monopolized more than expected (Table 2). Contrary to our prediction, punishment was not significantly associated with either contest competition or scramble, and it was not associated with monopoly (Table 2).

Aggression and Punishment Before and After Food Trials

During the 5 min periods before and after the 297 trials, there were 576 occurrences of aggression. Of these

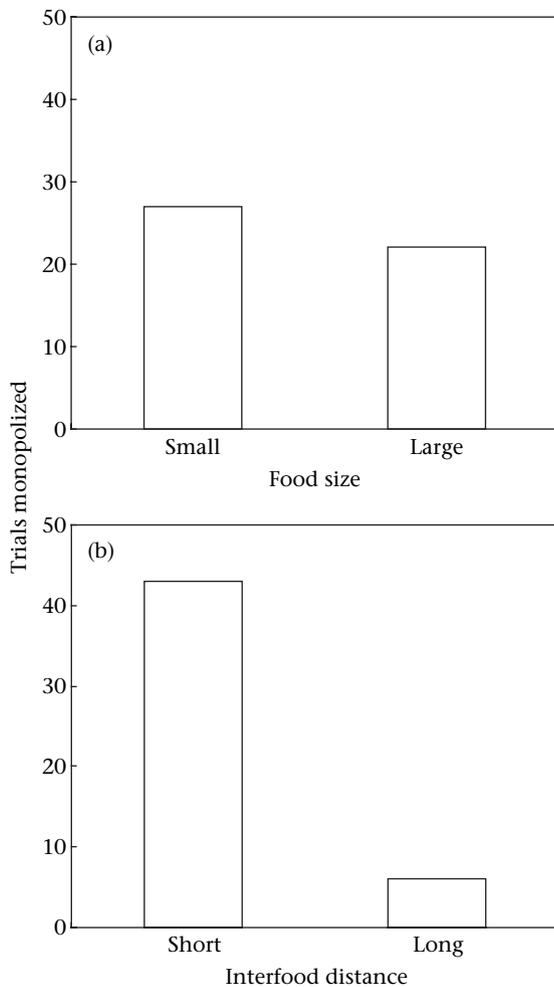


Figure 2. Number of trials in which the same individual ate both apple pieces (monopoly) ($N = 49$) relative to (a) food size and (b) interfood distance.

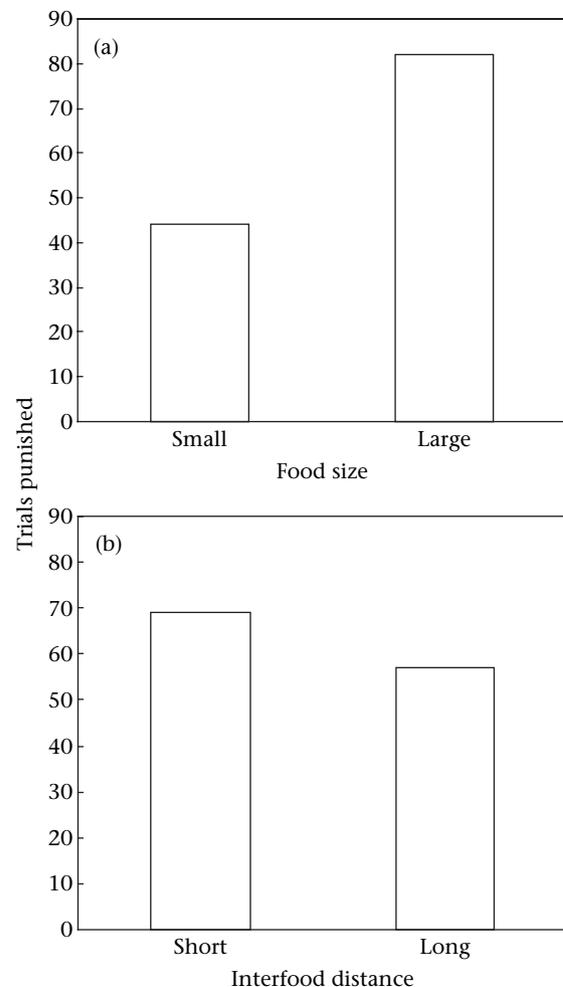


Figure 3. Number of trials in which punishment by consumers occurred ($N = 126$) relative to (a) food size and (b) interfood distance.

Table 2. Contingency table tests of the interactions between the initial behavioural responses to food, food monopoly and punishment by consumers ($N = 297$ trials) (expected counts in parentheses)

	Yes	No
<i>Food monopoly</i>		
Contest competition	4 (12.5)	72 (63.5)
Scramble	12 (17.5)	94 (88.5)
No interaction	33 (19)	82 (96)
	$\chi^2 = 21.9, P < 0.0001$	
<i>Punishment by consumer</i>		
Contest competition	37 (32.2)	39 (43.8)
Scramble	46 (45)	60 (61)
No interaction	43 (48.8)	72 (66.2)
	$\chi^2 = 2.5, P = 0.29$	
<i>Punishment by consumer</i>		
Food monopoly	19 (20.8)	30 (28.2)
No food monopoly	107 (105.2)	141 (142.8)
	$\chi^2 = 0.3, P = 0.57$	

occurrences, 159 (28%) occurred before the food trial, whereas 417 (72%) occurred after the food trial. Thus, overall aggression in the 15 enclosures, including both consumer and nonconsumer, increased from the 5 min period before the food trial (\bar{X} (95% CI) = 0.11 (0.08, 0.12) interactions/min, $N = 15$) to the 5 min period after the food trial (\bar{X} (95% CI) = 0.28 (0.24, 0.32) interactions/min, $N = 15$). During the 5 min period after the food trial, consumers were involved in aggressive interactions (\bar{X} (95% CI) = 0.17 (0.15, 0.2) interactions/min, $N = 15$) more often than nonconsumers (\bar{X} (95% CI) = 0.11 (0.09, 0.13) interactions/min, $N = 15$).

There was a possibility of 594 consumers as there were two apple pieces thrown for each of the 297 trials. Accounting for monopolized food, there were 545 consumers. Of these 545 consumers, 142 (26%) engaged in punishment. Only 48 (9%) consumers received aggression from others. Thus, consumers more often punished (\bar{X} (95% CI) = 0.13 (0.11, 0.16) interactions/min, $N = 15$) than received aggression (\bar{X} (95% CI) = 0.04 (0.03, 0.05) interactions/min, $N = 15$).

High Rank and Punishment

We were able to identify 285 of the 545 (52%) consumers. Of the 285 identified consumers, 94 (60%) got food in only one trial and 63 (40%) got food in more than one trial ($\bar{X} \pm SE = 1.8 \pm 0.1$ trials/individual, $N = 157$), so there were 157 individuals identified. Of the 157 individuals, 59 (38%) were male and 98 (62%) were female. There were 59 (38%) high-ranking consumers, 33 (56%) of which were females and 26 (44%) of which were males.

As expected, high-ranking consumers were better competitors than were low-ranking consumers. When food size was large, consumers were high-ranking more often than expected by chance. Rank, however, did not significantly affect food monopoly (Table 3). Of the 157 identified individuals, we found that, also as expected, high-ranking consumers were more likely to punish than were low-ranking consumers. We checked for cage

Table 3. Contingency table tests of the interactions between consumer rank, food size and food monopoly conducted on the subset of identified consumers ($N = 157$ consumers) (expected counts in parentheses)

	Consumer rank	
	High	Low
Small food size	24 (30.8)	58 (51.2)
Large food size	35 (28.2)	40 (46.8)
	$\chi^2 = 5.1, P = 0.02$	
Food monopoly	9 (6)	7 (10)
No food monopoly	50 (53)	91 (88)
	$\chi^2 = 2.6, P = 0.1$	

effects and found that they were not significant, so we describe only a fixed effects model. Wald tests showed that high rank was a predictor that a consumer would punish ($\chi^2_1 = 14.01, P = 0.0002$). The estimated odds ratio comparing high versus low rank was 3.7 (95% CI: 1.9, 7.4); thus, on average, a high-ranking consumer was 3.7 times more likely to punish than was a low-ranking consumer.

Influence of Punishment on Priority of Access to Food

To determine whether consumers who punished were more likely to get food in multiple trials, we conducted a logistic regression on the 157 identified consumers, controlling for rank. The independent effects of consumer rank and consumer punishment revealed that both high rank and punishment significantly increased the likelihood of obtaining food in multiple trials (15–24 trials/cage). We checked for pairwise interactions of the two predictors and for cage effects, and they were not significant, so we describe only a main and fixed effects regression. Wald tests showed that high rank was a significant predictor of getting food in multiple trials ($\chi^2_1 = 10.6, P = 0.001$), as was punishment ($\chi^2_1 = 6.6, P = 0.01$). The estimated odds ratio comparing high versus low rank was 3.3 (95% CI: 1.6, 6.7) and that comparing punishment versus no punishment was 2.6 (95% CI: 1.3, 5.3); thus, on average, for a given punishment outcome, high-ranking consumers were 3.3 times more likely to get food in multiple trials than were low-ranking consumers, and on average, for a given rank, consumers that punished were 2.6 times more likely to get food in multiple trials than were consumers that did not punish.

We then examined the importance of the frequency of punishment among the subset of consumers who punished ($N = 58$). We wanted to determine whether the percentage of trials in which a consumer punished was correlated with the percentage of trials in which the consumer obtained food, so we performed a least squares regression, controlling for rank and cage effects. We checked for pairwise interactions of the two predictors and they were not significant, so we interpret only the main effects.

The independent effects of consumer punishment and consumer rank revealed that the frequency of punishment significantly predicted the frequency of obtaining food, but rank did not (Fig. 4). The random effect variance for cage was essentially zero. Regression tests showed that the percentage of trials in which a consumer punished was a significant predictor of the frequency of obtaining food ($t_{55} = 4.9$, $P < 0.0001$), but high rank was not ($t_{55} = 1.0$, $P = 0.31$).

Food Size as a Proxy for Handling Time

The average handling time for a 30 g apple piece was over nine times that of a 1 g piece. The results of the regression analysis show that food sizes used were significantly correlated with their handling times (simple linear regression: $R^2 = 0.56$, $F_{1,78} = 101.5$, $P < 0.0001$). The slope showed that for each additional 5 g of food, handling time increased by 41 s on average. These results confirm that food size at the scale presented in the trials fairly reflected significantly different handling times.

DISCUSSION

Influence of Food Size and Interfood Distance on Competition and Punishment

Numerous studies have documented the importance of aggression in competition over resources (Alexander 1974; Milinski & Parker 1991). Aggression is used to acquire immediate resources through contest competition (Wrangham 1980; van Schaik 1989; Isbell 1991; Grant 1993) and to gain access to potential resources through punishment strategies that help to maintain dominance relationships (Clutton-Brock & Parker 1995). While the importance of aggression as a tool in resource competition has been generally accepted, the factors influencing it are less clear (see Isbell & Young 2002).

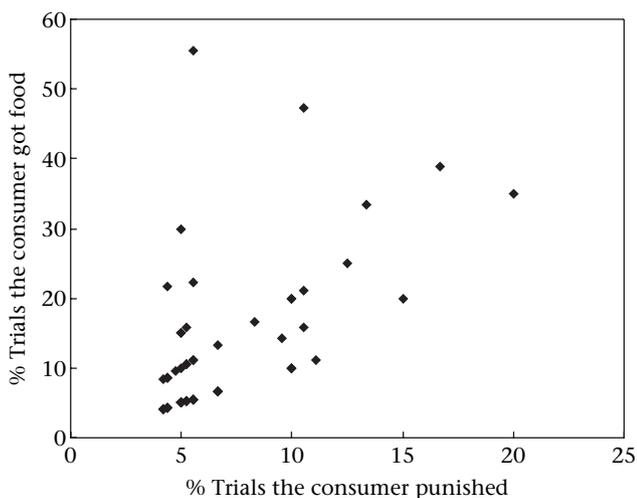


Figure 4. Relation between the percentage of trials in which a consumer punished and the percentage of trials in which the consumer got food ($N = 58$).

Current ecological models agree that clumped food resources elicit aggression, yet definitions of clumped resources often include two different concepts: time spent at the resource and distance between resources. Two of three main socioecological models consider the spatial quality of food to be important (Wrangham 1980; van Schaik 1989; Sterck et al. 1997). The third model considers temporal distribution on a short timescale (i.e. food site depletion time or handling time) to be more important than spatial distribution (Isbell et al. 1998; Mathy & Isbell 2001; Isbell & Young 2002). For example, Isbell and colleagues found that the same adult female vervet monkeys, *Cercopithecus aethiops*, had higher rates of aggression in a habitat where they spent longer at each food site than in a habitat where they spent a shorter amount of time at each food site (Isbell et al. 1998; Pruetz & Isbell 2000).

Our findings add to accumulating evidence that handling time of food, rather than its spatial distribution, may be more important in eliciting aggressive competition in the form of both contest competition and punishment. Similar to Mathy & Isbell (2001), results from this study suggest that food size is more important than interfood distance in eliciting aggressive competition.

In this study, foods with longer handling times appeared to provide greater opportunities for individuals to approach or gather around the consumer and for the consumer to punish them for their interest in the food, while foods that had shorter handling times and were consumed quickly, were often eaten before others noticed them. Larger food sizes may have also had greater intrinsic value, so that the benefit of punishment was greater for the larger pieces. In Hanuman langurs, *Semnopithecus entellus*, foods that are higher in nutritional quality have been found to elicit more aggression (Koenig et al. 1998).

We also found that when contest competition and scramble occurred, food was monopolized less than expected by chance, but when no interaction occurred, food was monopolized more than expected. This is probably because any type of competition makes it more difficult for one individual to monopolize food.

Punishment and Feeding Competition

Overall aggression, by both consumers and nonconsumers, increased from the 5 min period before the food trial to the 5 min period after the food trial. During the 5 min period after the food trial, consumers were involved in aggressive interactions more often than nonconsumers. Consumers also more often punished than they received aggression. Therefore, the presence of food was associated with heightened levels of aggression, but that aggression came primarily from the consumers in the form of punishment rather than competition to acquire available food.

Contrary to our prediction, punishment was not significantly associated with either contest competition or scramble, and it was not associated with monopoly. Most punishment happened soon after consumers obtained the food, usually when others approached and sat or stood near the consumer. Therefore, it appears that

consumers punished individuals for showing interest in the food after the food was already in possession of the consumer.

Since many of the consumers were of high rank, they were not under immediate threat of losing possession of the food. Therefore, there was no immediate reward for their aggression. Instead, consumers seemed to be using the food trials as opportunities to punish others to reinforce their rank and maintain their priority of access to future resources. Since subordinates test dominance (Clutton-Brock & Parker 1995), threats by high-ranking consumers could have also served as warnings to subordinates who, if not warned, might have attempted to take the food. However, very few consumers (9%), whether they punished or not, were actually threatened with aggression from others.

As expected, high-ranking consumers did better than low-ranking consumers. When food size was large, consumers were more likely to be of high rank. High-ranking consumers were also more likely to punish than were low-ranking consumers. This high-rank advantage is expected from what is known of the strict hierarchical social system of rhesus macaques (Sade 1967; Missakian 1972; Chapais 2004).

Influence of Punishment on Priority of Access to Food

Our results show that consumers who punished were more likely to get food in multiple trials. In addition, among punishers, consumers who punished the most were more likely to get food the most. These results suggest that individuals who punish have a greater chance of obtaining priority of access to future resources, and the more they punish, the greater their chances.

Clutton-Brock & Parker (1995) suggested five contexts in which punishment in animals may be observed, including the establishment and maintenance of dominance relationships, dissuasion of parasitism and cheating, establishment of mating bonds, conflict between parent and offspring, and enforcement of cooperative behaviour. Our study provides evidence for the role of punishment in the maintenance of dominance and priority of access to food. Investigation into the effects of punishment by consumers on the behaviour of the victims would help to further reveal the role of punishment in feeding competition.

Acknowledgments

We thank the personnel at the California National Primate Research Center, especially G. Vicino, for making it possible to conduct the study. We also thank M. Golden for his assistance in the food experiments. In addition, we thank M. Grote for help with statistical analyses, and A. Harcourt, A. Marshall and two anonymous referees for helpful comments on earlier drafts of this manuscript. This study was funded in part by research support to L.A.I. from the University of California, Davis and was covered under the IACUC Protocol for Animal Care and Use no. 8661.

References

- Alexander, R. D. 1974. The evolution of social behavior. *Annual Review of Ecology and Systematics*, **5**, 325–383.
- Bernstein, I. S. 2006. Social mechanisms in the control of primate aggression. In: *Primates in Perspective* (Ed. by C. J. Campbell, A. Fuentes, K. C. Mackinnon, M. Panger & S. K. Bearder), pp. 562–571. New York: Oxford University Press.
- Boyd, R. & Richerson, P. 1992. Punishment allows the evolution of cooperation (or anything else) in sizable groups. *Ethology and Sociobiology*, **3**, 171–195.
- Chapais, B. 2004. How kinship generates dominance structures: a comparative perspective. In: *Macaque Societies: a Model for the Study of Social Organization* (Ed. by B. Thierry, M. Singh & W. Kaumanns), pp. 186–204. Cambridge: Cambridge University Press.
- Clutton-Brock, T. H. & Parker, G. A. 1995. Punishment in animal societies. *Nature*, **373**, 209–216.
- Dugatkin, L. A. 2002. Cooperation in animals: an evolutionary overview. *Biology and Philosophy*, **17**, 459–476.
- Enquist, M., Plane, E. & Röed, J. 1985. Aggressive communication in fulmars (*Fulmarus glacialis*) competing for food. *Animal Behaviour*, **33**, 1007–1020.
- Ganslosser, U. & Dellert, B. 1997. Experimental alterations of food distribution in two species of captive equids (*Equus burchelli* and *E. hemionus kulan*). *Ethology, Ecology & Evolution*, **9**, 1–17.
- Grant, J. W. A. 1993. Whether or not to defend? The influence of resource distribution. *Marine Behavior and Physiology*, **23**, 137–153.
- Goldberg, J. L., Grant, J. W. A. & Lefebvre, L. 2001. Effects of the temporal predictability and spatial clumping of food on the intensity of competitive aggression in the zenaida dove. *Behavioral Ecology*, **12**, 490–495.
- Hauser, M. D. 1992. Costs of deception – cheaters are punished in rhesus monkeys (*Macaca mulatta*). *Proceedings of the National Academy of Sciences, U.S.A.*, **89**, 12137–12139.
- Hauser, M. & Marler, P. 1993. Food associated calls in rhesus macaques (*Macaca mulatta*). II. Costs and benefits of call production and suppression. *Behavioral Ecology*, **4**, 206–212.
- Isbell, L. A. 1991. Contest and scramble competition: patterns of female aggression and ranging behavior among primates. *Behavioral Ecology*, **2**, 143–155.
- Isbell, L. A. & Young, T. P. 2002. Ecological models of female social relationships in primates: similarities, disparities, and some directions for future clarity. *Behaviour*, **139**, 177–202.
- Isbell, L. A., Pruett, J. D. & Young, T. P. 1998. Movements of vervets (*Cercopithecus aethiops*) and patas monkeys (*Erythrocebus patas*) as estimators of food resource size, density, and distribution. *Behavioral Ecology and Sociobiology*, **42**, 123–133.
- Janson, C. H. 1990. Ecological consequences of individual spatial choice in foraging groups of brown capuchin monkeys, *Cebus apella*. *Animal Behaviour*, **40**, 922–934.
- Kaminski, J., Call, J. & Tomasello, M. 2006. Goats' behaviour in a competitive food paradigm: evidence for perspective taking? *Behaviour*, **143**, 1341–1356.
- Koenig, A., Beise, J., Chalise, M. K. & Ganzhorn, J. U. 1998. When females should contest for food: testing hypotheses about resource density, distribution, size, and quality with Hanuman langurs (*Presbytis entellus*). *Behavioral Ecology and Sociobiology*, **42**, 225–237.
- Kummer, H. 1968. *The Social Organization of Hamadryas Baboons: a Field Study*. Chicago: University of Chicago Press.
- Malik, I., Seth, P. K. & Southwick, C. H. 1984. Population growth of free-ranging rhesus monkeys at Tughlaqabad. *American Journal of Primatology*, **7**, 311–321.

- Manson, J. H.** 1994. Mating patterns, mate choice, and birth season heterosexual relationships in free-ranging rhesus macaques. *Primates*, **35**, 417–433.
- Martin, P. & Bateson, P.** 1993. *Measuring Behaviour: an Introductory Guide*. 2nd edn. Cambridge: Cambridge University Press.
- Mathy, J. W. & Isbell, L. A.** 2001. The relative importance of size of food and interfood distance in eliciting aggression in captive rhesus macaques (*Macaca mulatta*). *Folia Primatologica*, **72**, 268–277.
- Milinski, M. & Parker, G. A.** 1991. Competition for resources. In: *Behavioural Ecology: an Evolutionary Approach*. 3rd edn (Ed. by J. R. Krebs & N. B. Davies), pp. 137–168. Oxford: Blackwell Scientific.
- Missakian, E. A.** 1972. Genealogical and cross-genealogical dominance relations in a group of free-ranking rhesus monkeys (*Macaca mulatta*) on Cayo Santiago. *Primates*, **13**, 169–180.
- Mitchell, C. L., Boinski, S. & van Schaik, C. P.** 1991. Competitive regimes and female bonding in two species of squirrel monkeys (*Saimiri oerstedii* and *S. sciureus*). *Behavioral Ecology and Sociobiology*, **28**, 55–60.
- Monaghan, P. & Metcalfe, N. B.** 1985. Group foraging in wild brown hares: effects of resource distribution and social status. *Animal Behaviour*, **33**, 993–999.
- Myers, R. H., Montgomery, D. C. & Vining, G. G.** 2002. *Generalized Linear Models with Applications in Engineering and the Sciences*. New York: J. Wiley.
- Parker, T. H. & Ligon, J. D.** 2002. Dominant male red junglefowl (*Gallus gallus*) test the dominance status of other males. *Behavioral Ecology and Sociobiology*, **53**, 20–24.
- Prosen, E. D., Jaeger, R. G. & Lee, D. R.** 2004. Sexual coercion in a territorial salamander: females punish socially polygynous male partners. *Animal Behaviour*, **67**, 85–92.
- Post, D. G., Hausfater, G. & McCuskey, S. A.** 1980. Feeding behavior of yellow baboons (*Papio cynocephalus*): relationship to age, gender and dominance rank. *Folia Primatologica*, **34**, 170–195.
- Pruetz, J. D. & Isbell, L. A.** 2000. Ecological correlates of female aggression in vervets (*Chlorocebus aethiops*) and patas monkeys (*Erythrocebus patas*) living in simple habitats. *Behavioral Ecology and Sociobiology*, **49**, 38–47.
- Sade, D. S.** 1967. Determinants of dominance in a group of free-ranging rhesus monkeys. In: *Social Communication Among Primates* (Ed. by S. A. Altmann), pp. 99–111. Chicago: University of Chicago Press.
- van Schaik, C. P.** 1989. The ecology of social relationships amongst female primates. In: *Comparative Socioecology: the Behavioral Ecology of Humans and Other Mammals* (Ed. by V. Standen & R. A. Foley), pp. 195–218. Oxford: Blackwell Scientific.
- Sirota, E.** 2000. An evolutionarily stable strategy for aggressiveness in feeding groups. *Behavioral Ecology*, **11**, 351–356.
- Southwick, C. H.** 1967. An experimental study of intragroup agonistic behavior in rhesus monkeys (*Macaca mulatta*). *Behaviour*, **28**, 182–209.
- Sterck, H. M., Watts, D. P. & van Schaik, C. P.** 1997. The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology*, **41**, 291–309.
- Valera, F., Hoi, H. & Kristin, A.** 2003. Male shrikes punish unfaithful females. *Behavioral Ecology*, **3**, 403–408.
- Wald, A.** 1943. Tests of statistical hypotheses concerning several parameters when the number of observations is large. *Transactions of the American Mathematical Society*, **54**, 426–482.
- Wrangham, R. W.** 1980. An ecological model of female-bonded primate groups. *Behaviour*, **75**, 262–300.