

RESEARCH ARTICLE

Within-Group Female–Female Agonistic Interactions
in Taiwanese Macaques (*Macaca cyclopis*)

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Feeding-related agonism among wild female Taiwanese macaques was investigated in two study groups at ecologically diverse sites (Fu-shan and Ken-ting) to determine whether contest-feeding competition was present in these groups. Females that contest for food within a primate group are hypothesized to form dominance hierarchies and tend to be philopatric. In this study we tested 1) whether Taiwanese macaque females show higher agonism in a feeding context, 2) whether they exhibit stronger agonism over higher-quality foods, and 3) whether higher agonism rates occur in smaller food patches. Female Taiwanese macaques at both study sites showed similar agonism rates in a feeding context (0.30 events/hr). They exhibited higher agonism rates inside food patches than outside food patches in the spring. Higher agonism rates occurred during seasons of higher fruit availability, and a lower agonism rate occurred in winter when the macaques switched to feeding on fallback foods. Females in the Fu-shan group exhibited higher proportions of aggressive interactions over higher-quality foods, such as animal matter and the reproductive parts of plants. In the Ken-ting group, 95.8% of feeding-related agonistic interactions among females occurred over fruits. Agonistic interactions that occurred in small food patches tended to result in the agonism recipient leaving the food patch. We conclude that female Taiwanese macaques show contest feeding competition in certain contexts. The patterns we observed have also been documented in other primate species

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in which females are philopatric and form linear dominance hierarchies. *Am. J. Primatol.* 69:199–211, 2007. © 2006 Wiley-Liss, Inc.

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INTRODUCTION

Socioecological theory includes the hypothesis that within-group contest feeding competition among females shapes the social structure of females living in groups [Isbell, 1991; Sterck et al., 1997; van Schaik, 1989]. Female primates may face intense within-group contest feeding competition if they feed on defensible food resources [Saito, 1996]. The pressure of within-group contest feeding competition may contribute to female philopatry, since females may benefit from gaining better access to monopolizable food resources by cooperating with kin [Wrangham, 1980]. It is also thought that stable, matrilineal dominance hierarchies are formed among females that experience within-group contest feeding competition [Isbell, 1991; van Schaik, 1989].

When the dominant animals in a group monopolize a food resource and gain more food than other group members through displacement or aggression, it indicates that within-group contest feeding competition is present [Janson & van Schaik, 1988; van Schaik & van Noordwijk, 1988]. Higher rates of agonism are suggested to occur inside food patches in comparison to outside food patches [Range & Nöe, 2002; Sterck & Steenbeek, 1997]. If females contest for food resources within groups, patterns of agonistic interactions among females may be associated with food quality, the distribution pattern and size of food items, and the size of food patches [Pruetz & Isbell, 2000]. van Schaik and van Noordwijk [1988] suggested that long-tailed macaques (*Macaca fascicularis*) contest for food, since they observed variation in aggression rates among the macaques over various food resources. We studied feeding-related agonistic interactions in female Taiwanese macaques (*M. cyclopis*) to investigate whether within-group contest feeding competition exists in this species.

Keeping other feeders from gaining access to food resources requires energy, and may put an animal in danger. Therefore, it is predicted that higher-quality foods [Koenig et al., 1998; Range & Nöe, 2002] or food items in clumped distribution [Mathy & Isbell, 2001] are more likely to be monopolized. Defending higher-quality foods is rewarded by gaining a higher intake of energy and nutrition. This is considered to be the payoff for the energy expended on resource defense. Long-tailed macaques at Ketambe exhibited a higher relative aggression rate over fruits than leaves [Sterck & Steenbeek, 1997], and the size of food items has been associated with increased aggression over the food item in captive rhesus monkeys [Mathy & Isbell, 2001].

The distribution pattern of food resources has been demonstrated to affect agonism rates over food resources in both wild and captive primate groups. Spatially clumped food resources are more defensible than dispersed food resources [Barton, 1993]. Agonism increases when the distribution of food trees is clumped (e.g., vervet monkeys (*Chlorocebus aethiops*) [Pruetz & Isbell, 2000]). It has also been found that inside a given food patch, relatively greater agonism occurs over food items with clumped distribution patterns (e.g., capuchin monkeys (*Cebus capucinus*) [Phillips, 1995]). Females are also more likely to be displaced and/or show submission when they are approached by another female

in a food patch with clumped food items (e.g., long-tailed macaques [Sterck & Steenbeek, 1997]).

The size of a food patch is likely to be associated with the defensibility of that patch [Janson, 1985; Pruett & Isbell, 2000; Sterck & Steenbeek, 1997]. Small food patches are more likely to be monopolized. However, larger food patches may attract more feeders at a time because of the greater number of food items or feeding sites available. Differential rates of agonistic interactions occur in food patches of different sizes in some primate groups. Sterck and Steenbeek [1997] reported that in Thomas langurs (*Presbytis thomasi*), the relative aggression rate (the proportion of approaches that result in displacement or submission) decreased with an increase in food patch size as well as the number of food items available in the food patch. These researchers suggested that the monopolization of food items in a given food patch is associated with the size of the food patch. However, in another study, vervet monkeys displayed agonism more frequently in large food patches than in small food patches. This may result from a smaller number of feeding sites relative to potential feeders in the large food patches. The feeders compete for access to the relatively limited feeding sites in the large food patches, whereas there are too few feeding sites in the small food patches to attract many feeders [Pruett & Isbell, 2000].

Within-group contest feeding competition has been detected in many primate groups in which females are philopatric and form linear dominance hierarchies [Suzuki et al., 1998; van Schaik & van Noordwijk, 1988]. In Taiwanese macaques, females are philopatric and exhibit linear dominance hierarchies [Birky, 2002; Chi & Lee, 1990; Fooden & Wu, 2001; Su, 2003]. Daughters attain social rank equal to and adjacent to that of their mothers. Youngest-sister ascendancy [Datta, 1983; de Waal, 1977; Walters, 1980] was observed in two of three pairs of sisters in a wild group at Fu-shan [Su, 2003]. Group fission occurs along matriline [Hsu & Lin, 2001; Wu & Lin, 1992]. In addition, Taiwanese macaques feed on different food types, including various plant parts and animal matter [Fooden & Wu, 2001]. Fruits are considered their primary food source [Chang, 1999; Su & Lee, 2001].

We hypothesized that within-group contest-feeding competition would be found in this species. Based on this hypothesis we predicted that 1) females would exhibit agonism more frequently inside food patches than outside food patches, 2) they would exhibit stronger agonism over higher-quality foods, and 3) higher agonism rates would occur in smaller food patches.

MATERIALS AND METHODS

Study Site and Subjects

We observed two wild Taiwanese macaque groups from populations in Fu-shan and Ken-ting. Fu-shan is located in the northern part of Taiwan (24°46' N, 121° 34' E), and Ken-ting is located in southern Taiwan (120°48' E, 21°58' N). These two wild macaque groups depend solely on natural food resources and move freely within their natural habitat. The geographical characteristics, climate, and vegetation in the study site were described in a previous study [Birky & Su, 2005].

The Fu-shan group became habituated to the presence of researchers after a preliminary study was conducted from July to October 1998. Six adult females and two adult males were individually identified. Two subadult females, which gave birth for the first time in 1999 and 2000, respectively, were identified and categorized as adults in the following study period, and 12 offspring (10 juveniles and two infants) of the six adult females made up the rest of the group. Two mother-daughter pairs were identified in the group. The Ken-ting study group

averaged 25 individuals, including three males, six adult females, and their juveniles and infants. At both sites, all individuals in the groups were identified during the habituation period and data collection was focused on adult females.

Data Collection

Data on agonistic interactions in both study groups were collected during both focal animal sampling [Altmann, 1974] on the adult females and ad libitum observation [Martin & Bateson, 1986] of all group members. The Ken-ting group was observed for 1,365 hr between December 1996 and April 1998, and the Fu-shan group was observed for 1,187 hr between November 1998 and December 1999. Focal-animal sampling was conducted on all of the adult females in each study group. All focal-animal samples lasted 10 min. The focal female was randomly chosen prior to focal sampling. However, when the scheduled focal animal could not be located due to the dense vegetation present at both study sites, females that were in sight were randomly chosen for observation. For each female, the number of focal samples was distributed as evenly as possible during the day. If the focal sample lasted less than 5 min before the sampling was terminated, that focal sample was excluded from data analysis. The Fu-shan group was encountered for 7–23 days (mean \pm SD: 14.1 \pm 5.7) per month, and a total of 3,681 focal animal samples were collected. The amount of focal observation time for each of the seven adult females ranged from 78.7 to 124.5 hr (mean \pm SD: 96.6 \pm 18.2). The monthly distribution of the number of focal samples was similar in all females throughout the year (Spearman's correlation test, all $P < 0.05$). Similar hourly distribution patterns of focal samples were collected from each female (Spearman's correlation test, all P 's < 0.05). At Ken-ting, 1,716 focal animal samples were collected and the group was encountered for 4–24 days per month (mean \pm SD: 14.8 \pm 4.8). The focal observation time recorded for the six adult females ranged from 26.3 to 64.3 hr (mean \pm SD: 35.5 \pm 14.6).

Agonistic interactions were divided into two categories: displacement and aggressive interaction. If one individual approached another individual without displaying aggressive behavior, and the approached individual retreated from the spot it originally occupied, the interaction was categorized as displacement. Aggressive interactions were defined as when one individual approached another individual and displayed aggressive behaviors, which included threatening facial expressions, lunging, chasing, or physical attack, such as grabbing, beating, and biting [Chi & Lee, 1990]. Overt threat was involved in aggressive interactions but not in displacement.

Female activity was continuously recorded during focal-animal samples. The amount of time allocated to different activities, including feeding, foraging, resting, moving, and social activities was recorded. Feeding behavior was defined as gathering food by picking it up with the mouth or hand(s), ingesting food by biting food items or putting food items into the mouth, or chewing known food items. Foraging behavior was defined as searching for food with the limbs or mouth and/or visually scanning a food patch. Time spent feeding on each food item (represented by plant species and plant part eaten) and different food types, including fruit, flower, plant body, and animal matter, was determined for each female.

For each agonistic event observed, the context in which agonism occurred was recorded to indicate whether the agonistic interaction occurred in a feeding or nonfeeding context. If the individuals involved in the agonistic interaction were feeding or foraging within a food patch, the interaction was categorized as

agonism occurring in a feeding context. Otherwise, the agonistic interaction was categorized as occurring in a nonfeeding context, such as moving, resting, grooming, or social interaction. The individuals involved in these agonistic interactions were also identified and recorded. Individuals that showed aggressive behavior or approach were recorded as the initiators of agonism. Individuals that received aggressive behavior or were displaced were recorded as the recipients of agonism. If the agonistic interactions occurred during feeding, the food item over which the agonism occurred was identified and recorded. Whether the recipient of agonism stayed in or left the food patch immediately following the agonistic interaction was recorded at Fu-shan.

A food patch was defined as one tree crown or continuous tree crowns of a tree or shrub species in which the monkeys conducted feeding and/or foraging behavior (after Sterck and Steenbeek [1997]). At Fu-shan we estimated the size of a food patch by the volume of tree crowns. One of the authors (H.S.) measured the crown volume of 22 tree or shrub species that accounted for a major part of the fruit/flower food source in the macaques' diet. Time spent feeding on these 22 species accounted for 78.7% of the time spent feeding on fruits/flowers other than grains. Fifty other tree or shrub species accounted for the remainder of the time spent feeding on fruits/flowers other than grains [Su, 2003]. Measurements on one to five individual trees (mean \pm SD: 3.4 ± 1.2) from each of the 22 species were taken. These individual trees that were measured to estimate the tree crown volume of the species were preferentially consumed by the monkeys and were accessible to the researcher. The measurements taken from each individual tree included two diameters of the tree crown (d_1 and d_2), tree height (h_t), and height of first branch with leaves (h_1). The volume of the tree crown (V_c) was calculated by the following formula, with a shape value of 0.5 for the parabolic shape: $V_c = 0.5 * 1/4 * d_1 * d_2 * \pi * (h_t - h_1)$ [Pruetz & Isbell, 2000; Wenger, 1984]. The tree crown height equaled ($h_t - h_1$). If more than one tree was measured for a particular species, the average tree crown volume was used to represent the food patch size of that particular species. The mean tree crown volume of these 22 plant species ranged from 0.2 to 1,239.8 m³. They were categorized into small and large food patches based on the size distribution of their crown volumes (slope_{small patch} = 8.42, slope_{large patch} = 93.09). Species with tree crown volumes smaller than 89.1 m³ were categorized as small food patches, and those with volumes larger than 154 m³ were categorized as large food patches. Information on food patch size was collected only at the Fu-shan field site.

Statistical Analyses

Nonparametric analyses were conducted on the data sets in this report. The significance level for all tests was set at 0.05 (one-tailed). Incidents of agonistic interactions collected from both sampling methods were used in the tests. However, the agonism rate was calculated from events of agonistic interactions collected during focal animal samples. We analyzed agonistic interactions among females to test whether they competed for food, by using a matched-pairs design (Wilcoxon matched-pairs signed-ranks test) to compare agonism rates in feeding contexts with those in nonfeeding contexts. Fisher's exact test was used to assess how food quality affected agonism rates among females. One-tailed tests were employed because we predicted that there would be stronger agonism over higher-quality foods and within smaller food patches.

RESULTS

Agonistic Interactions Among Females

A total of 255 agonistic interactions among adult females in the Fu-shan group were recorded from November 1998 through December 1999, and a total of 258 incidents of agonistic interactions among adult females in the Ken-ting group were recorded from December 1996 through April 1998. These agonistic interactions occurred in both feeding and nonfeeding contexts, and were collected using both focal animal sampling and ad libitum observation methods. Agonistic interactions collected during focal animal samples (186 events in Fu-shan and 79 events in Ken-ting) were used to calculate agonism rates. Females in the two study groups exhibited similar rates of agonism in a feeding context (Fu-shan group: 0.29 events/focal hour; Ken-ting group: 0.30 events/focal hour).

In both groups, agonism rates in a feeding context were not significantly different from those in a nonfeeding context: 0.30 vs. 0.29 at Fu-shan (Wilcoxon test, $n = 7$, $z = -0.169$, $P > 0.05$), and 0.30 vs. 0.33 at Ken-ting (no statistical analysis was performed due to the small sample size). Since diet changed seasonally, a seasonal analysis of agonism in a feeding context was conducted for the Fu-shan females. The sample size for the Ken-ting females was not large enough for this analysis. The agonism rates for each female were significantly higher in the feeding context than the nonfeeding context during the spring (Wilcoxon matched-pairs signed-ranks test for small sample size, $n = 7$, $T^+ = 26$, $P < 0.05$). There was no significant difference in agonism rates in these contexts during the summer, fall, or winter seasons (Wilcoxon matched-pairs signed-ranks test, all $P > 0.05$).

At Fu-shan the rate of female–female agonistic interactions in a feeding context varied seasonally (Kruskal-Wallis test, $df = 3$, $H = 8.23$, $P = 0.04$). Among females, higher agonism rates occurred in the spring and summer than in the fall and winter (mean rank, spring: 18.43; summer: 19.43; fall: 10.86; winter: 9.29).

Responses of the Recipients to Different Types of Agonistic Interactions

A total of 195 female–female agonistic interactions in a feeding context were observed at Fu-shan. All observed agonistic interactions were included in the subsequent analysis. We categorized 36.9% (72/195) of these agonistic events as aggressive interactions, and 63.1% (123/195) as displacement. In the Ken-ting group, 72 incidents of female–female agonism in a feeding context were observed. We categorized 47.2% of these events as aggressive interactions, and 52.8% as displacement.

In terms of continuing feeding opportunity in a food patch, recipients of agonism displayed a variety of responses to the initiator of the agonistic interaction. Females who stayed in the food patch after receiving agonism continued to feed in the food patch they originally occupied, or joined the agonism initiator in feeding on the same kind of food item present in the food patch. Recipients that left the food patch after the agonistic interaction were deprived of continuing feeding opportunities in that food patch. At Fu-shan, there were 109 observed agonistic interactions in a feeding context involving food items contained in the tree/bush crowns or liana in which the response of the recipient could be determined. The recipients in 53 of these interactions left the food patch. The other 56 observed agonistic interactions resulted in the agonism recipient

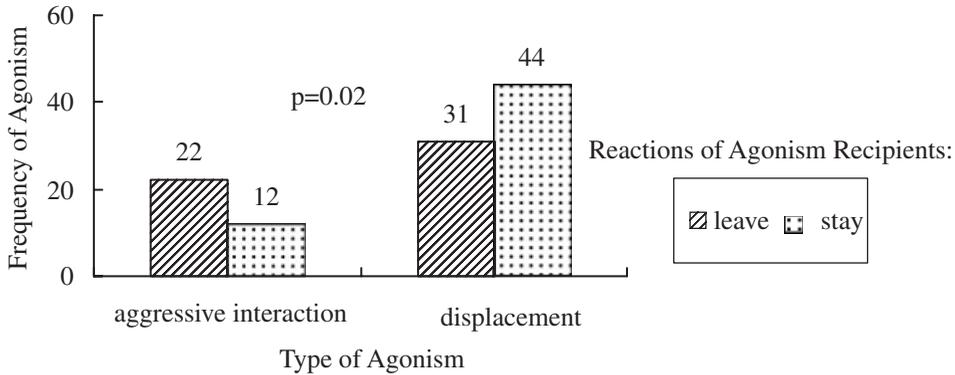


Fig. 1. Different types of agonistic interactions among females in the Fu-shan group resulted in different reactions from the recipients in terms of continuous feeding by the recipient in the food patch.

changing feeding sites and continuing to consume the same kind of food item at a new feeding site in the food patch.

Different types of agonistic interactions elicited different responses from the recipients. Aggressive interactions resulted in the recipients leaving food patches significantly more frequently than did displacement (Fisher's exact test, $P = 0.02$; Fig. 1). Aggressive interactions were more likely to terminate the feeding opportunities of the agonism recipients in the food patch where the agonism occurred.

Agonism Over Different Food Types

More aggressive interactions occurred when the females in the Fu-shan group competed for access to animal food or reproductive parts of plants. The Fu-shan females exhibited a higher proportion of aggressive interactions relative to displacement over animal foods than over plant foods (Fisher's exact test, $P = 0.045$; Fig. 2). Females of both groups exhibited a significantly higher proportion of aggressive interactions relative to displacement over the reproductive parts of plants (fruits and flowers) compared to that over nonreproductive plant parts (Fisher's exact test, $P < 0.001$; Fig. 3). At Ken-ting, 95.8% (69/72) of feeding-related agonistic interactions among females occurred over fruits or flowers, and almost 50% of these were categorized as aggressive interactions. The remaining 4.2% (3/72) of the feeding-related agonistic interactions occurred over leaves, and no threats were involved (Fig. 3).

There was no significant difference in the agonism rates over different food types, including animal food, reproductive parts of plants, and other plant parts (Wilcoxon matched-pairs signed-ranks test with a Bonferroni adjustment on the significance level for multiple comparisons, $n = 7$, all $P > 0.05$). In the Ken-ting group, however, females competed for the nonreproductive parts of plants at a very low frequency (4.2% of agonisms occurred in a feeding context).

Agonistic interactions over grass grains, such as *Paspalum conjugatum*, were compared with interactions that occurred over the fruits of trees or bushes. There was no significant difference in the proportion of aggressive interactions over the fruits compared to the grains (Fisher's exact test, $P = 0.2$).

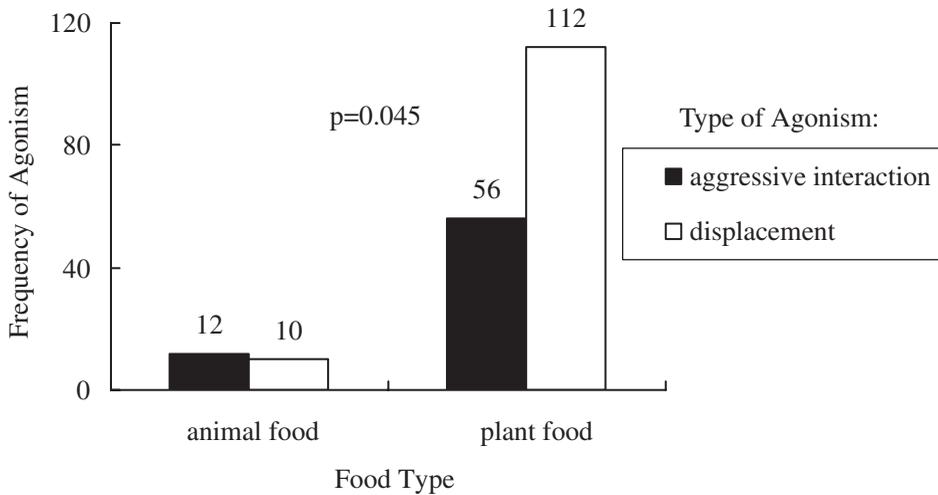


Fig. 2. A higher proportion of aggression among females in the Fu-shan group occurred over animal foods than over plant foods.

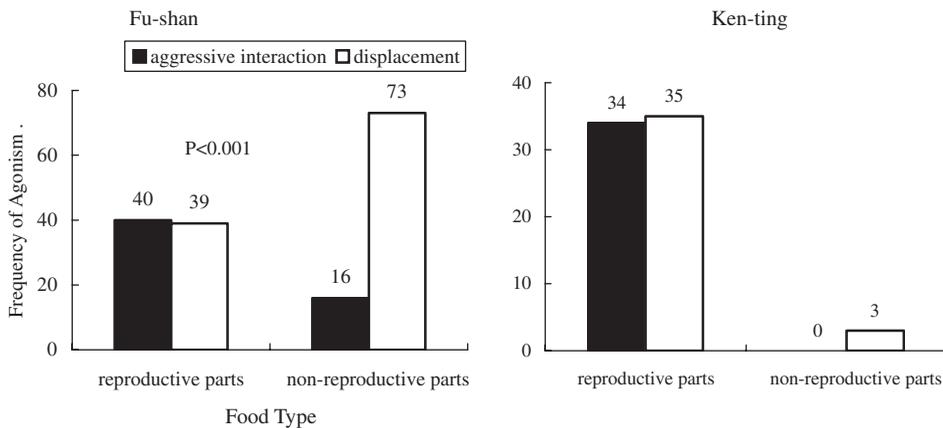


Fig. 3. A higher proportion of aggression among females in the Fu-shan group occurred over the reproductive parts of plants; 95.8% of agonistic interactions among females in the Ken-ting group occurred over the reproductive parts of plants.

Agonistic Interactions Over Fruits/Flowers in Food Patches Differing in Size

Agonistic interactions in food patches of different sizes (small vs. large) were compared in the Fu-shan group. The agonism rate over a particular plant species was calculated by dividing the total number of agonistic interactions among females over the given plant species by the time spent feeding on the fruits and/or flowers of this plant species by the females. There was no significant difference in agonism rates over fruits/flowers consumed in large and small food patches (Mann-Whitney test, $n_s = 10$, $n_l = 12$, $z = -1.55$, $P > 0.05$). However, females exhibited agonism over seven of the 10 plant species that were categorized as small food patches, and over six species of the 12 species categorized as large food

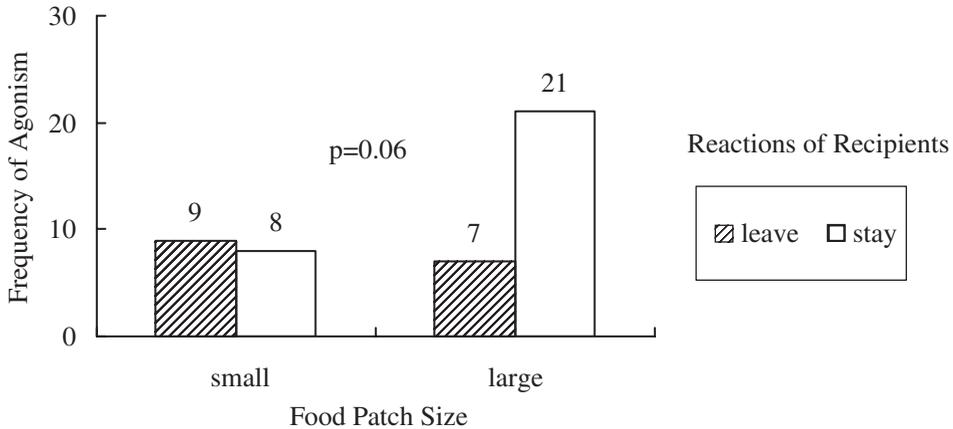


Fig. 4. Responses of the agonism recipients varied with the size of food patches in the Fu-shan group.

patches. Four of the seven females displayed agonism in small food patches more frequently, although the difference in agonism rates between the two sizes of food patches for each female was not significant (Wilcoxon matched-pairs signed-ranks test, $n = 7$, $z = -1.10$, $P > 0.05$).

The size of a food patch appeared to be the determining factor in terms of whether the recipient of agonism continued to feed in the food patch where the agonistic interaction occurred. Agonistic interactions that occurred in small food patches tended to result in the agonism recipient leaving the food patch in which the agonistic interaction occurred (Fisher's exact test, $P = 0.06$; Fig. 4). However, no higher proportions of aggressive interactions occurred in small food patches compared to large food patches (Fisher's exact test, $P = 0.51$).

DISCUSSION

Agonistic interactions among females from both the Fu-shan and Ken-ting study sites were observed in a feeding context at a rate of about 0.30 times per focal observation hour. This is the first report of feeding competition in this species. In their natural habitat, both groups were observed to feed on fruits as their major food source. They also showed similar patterns of seasonal variation in diet, in terms of the time spent feeding on various food types [Su, 2003; You, 2000]. This similar pattern of food resource utilization may explain why females in the two study groups, which inhabit areas that differ in vegetation and climate, exhibited similar agonism rates over food.

Although the feeding-related agonism rate among females appears to be low (about 0.30 events/hr), it was not much lower than rates reported for other macaques in the *fascicularis* group [Fooden, 1980]. In wild Japanese macaque groups, the reported agonism rate among females is also lower than one incident per feeding hour (0.19 and 0.75 for the Yakushima and Kinkazan groups, respectively) [Furuichi, 1983; Saito, 1996]. Female long-tailed macaques exhibited agonism 0.97 times per hour inside food patches [Sterck & Steenbeek, 1997]. However, note that in the provisioned Japanese macaque groups, the aggression rate was as high as 27.2 times per hour within the feeding area [Mori, 1977]. Provisioning is known to influence many aspects of social behavior, including the

frequency of aggression [Hill, 1999]. Macaques display much lower agonism rates while feeding under natural conditions, since the spatial distribution of food resources in nature may not be as clumped as they are for the provisioned troops.

The females in the Fu-shan group showed significantly higher rates of agonism during feeding only in the spring. They also competed over food more frequently in spring and summer compared to fall and winter. Contest competition over food is predicted to decrease when groups feed on less monopolizable and evenly distributed food resources [Barton & Whiten, 1993; Wrangham, 1980]. The study groups switched to mature leaves and twigs when fruit availability decreased in winter [Chang, 1999; Lin et al., 1997; Su, 2003]. This was as expected, since leaves are more abundant and evenly distributed in space and time than fruits [Harrison, 1984; Lin et al., 1997; van Schaik, 1989]. When feeding on leaves in winter, these macaques may be released from contest-feeding competition.

The intensity of food competition is predicted to be associated with food quality [Koenig et al., 1998; Parker, 1974; van Schaik, 1989]. Females in the Fu-shan group exhibited higher proportions of aggressive interactions over animal matter and the reproductive parts of plants, which are considered higher-quality food for macaques. Fruits generally contain more carbohydrates than leaves. Fruits are also more digestible than leaves, and are a major source of energy for these macaques [Kay & Davies, 1994]. When fruit and insects (caterpillars) are available at the same time, caterpillars are preferred [Chang, 1999]. Stronger competition over higher-quality foods has also been observed in Japanese macaques [Saito, 1996]. Within the Fu-shan group, overt aggression was observed when the subordinate females did not yield to the dominant females when approached. When competing over higher-quality food resources, the subordinates were more likely to attempt to stay with the food resource without retreating. The dominants then showed aggression to usurp the food resource. Furuichi [1983] suggested that dominant Japanese macaques behaviorally suppress subordinates only when they are closer than a certain distance (the "tolerance/intolerance" distance). However, in another study [Shopland, 1987], food quality was not found to be a good indicator of the intensity of feeding interference in yellow baboons (*Papio cynocephalus*).

It has been proposed that contest competition for food is associated with factors involving the defensibility of food patches, such as patch size [Isbell, 1991; Pruett & Isbell, 2000]. However, the association between the intensity of feeding competition and the size of food patches has not been verified in studies. In a study of Japanese macaques, more frequent agonistic interactions were observed in smaller food patches [Saito, 1996]. Approaches resulting in a higher proportion of aggression in smaller food patches have also been reported for Thomas langurs [Sterck & Steenbeek, 1997]. However, agonistic interactions among female long-tailed macaques at Ketambe have not been reported to be associated with the size of food patches [Sterck & Steenbeek, 1997]. In this study, the agonism rate among female Taiwanese macaques in smaller food patches was no higher than that in large food patches. It is possible that some small food patches do not attract enough feeders to compete, due to the small number of feeding sites available in the tree crown. The number of feeding sites in a food patch relative to the size of potential feeders in a social group may be associated with the intensity of feeding competition in a food patch. Pruett and Isbell [2000] reported that vervets exhibited agonistic interactions more frequently in larger food patches that contained a greater number of feeding sites but were not large enough to accommodate the whole group.

In the present study, H.S. observed that the entire group simultaneously fed on fruits in the large tree crown of *Machilus muthaensis* (maximum size of coveeding party = 16) during its peak fruiting period. Agonism over the fruit occurred when the monkeys changed feeding spots, and only 20% of the observed agonistic interactions resulted in the recipient leaving the tree crown. The tree crown of *M. muthaensis* seemed to be able to accommodate all of the group members. Mitchell and associates [1991] suggested that when squirrel monkeys (*Samiri sciureus*) feed in very large tree crowns (>25 m in diameter, such as *Ficus* spp.) in which fruits are abundant, the monkeys concentrate on consuming as many fruits as possible, rather than compete for feeding space. Thus, feeding-related agonism among squirrel monkeys is rare. Sterck and Steenbeek [1997] also suggested that Thomas langurs rarely compete for food resources in very large food patches. Animals are released from competition for food when the whole animal group can feed on abundant food items contained in large food patches [Mitchell et al., 1991; Sterck & Steenbeek, 1997].

Even though the female Taiwanese macaques competed for high-quality foods with greater intensity, the quality of food is not the primary factor that determines whether a food patch can be monopolized. Frequently, two or more females were observed feeding in a food patch simultaneously. However, they left the food patch more frequently after receiving agonism in a small food patch than in a large food patch. Monopolization of small food patches by females was not related to the intensity of agonistic interactions, since there was no significant difference in the proportion of aggressive interactions in small food patches compared to large food patches. In Japanese macaques the proportion of attacks relative to displacement did not significantly differ among different sizes of *Zelkova* patches [Saito, 1996].

The pattern of agonistic interactions among female Taiwanese macaques shows that they contest for food within groups. They exhibited higher agonism rates in a feeding context in the spring, and this feeding-related agonism was relaxed in the fall and winter seasons when they fed on evenly distributed and/or abundant foods. Seasonal differences in agonism rate in a feeding context may indicate that the monkeys contest for food only during certain times of the year. In addition, stronger agonism occurred over higher-quality foods. Although the feeding-related agonism rate among female Taiwanese macaques was relatively low (0.30 incident/hr), the patterns of agonistic interactions agree with the prediction that within-group contest-feeding competition would occur in female-bonded groups in which females form a linear dominance hierarchy and practice nepotism in terms of social rank acquisition [Sterck et al., 1997]. Therefore, we conclude that food plays a role in shaping female social relationships in Taiwanese macaques. Because overall female agonism rates were low, even though the contact hours for both field sites totaled more than 2,552 hr, we combined observations of agonistic incidents from focal-animal samples and ad libitum data in some of our analyses to increase our sample size. Ideally, more contact hours would increase the sample size, and we are currently collecting such data.

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