

Apparent feeding association between Japanese macaques (*Macaca fuscata yakui*) and sika deer (*Cervus nippon*) living on Yakushima Island, Japan

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Associations among animals of different species vary from parasitism to mutualism. The primate order is not well represented by studies on this subject, with scarce data concentrated on few species. This study is the first attempt to describe interactions between Japanese macaques (*Macaca fuscata yakui*) and sika deer (*Cervus nippon*), in an area where no natural predators exist.

Large quantities of food drop on the ground when Japanese macaques forage on the trees and deer were often observed to forage on these food items (i.e. gleaning). This observation may indicate that sika deer associated with Japanese macaque while feeding. Food quantity on a tree was the best predictor of this apparent feeding association. Yet, tree size, food quantity, and number of monkeys foraging on a tree significantly predicted the number of deer gleaning under that tree. Monkeys were rarely aggressive towards deer that were gleaning, although agonistic interactions among deer were frequently observed. Food dropped from the trees represents an additional, otherwise unavailable, source of energy for deer. Therefore, the deer probably improved their foraging efficiency by gleaning. These results suggest that deer gain some benefits by this behaviour while they apparently do not inflict any costs to monkeys. As such, interactions between sika deer and Japanese macaques may represent a case of commensalism, or of asymmetrical mutualism.

KEY WORDS: commensalism, association, Japanese macaque, *Macaca fuscata yakui*, mutualism, sika deer, Yakushima Island.

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INTRODUCTION

Associations among species are usually classified into three different categories: parasitism (i.e. one species benefits at the expense of the other), mutualism (i.e. both species benefit from the association), and commensalism (i.e. one species benefits and the other is unaffected by the association; WILSON 1975). Species are thought to gain two main benefits by participating to these associations (PULLIAM 1973, WILSON 1975, KREBS & DAVIES 1997): protection from predators (if predation risk per individual decreases as the number of animals associating increases, and/or if a species is sensitive to alarm calls of at least one other species in the association), and increased foraging efficiency (if, for example, one species consumes food discarded by the other or can obtain food otherwise unavailable). Feeding associations have been frequently reported among vertebrates (BRAGER 1998). For example, African jacanas (*Actophilornis africanus*) greatly increase their foraging efficiency by removing ectoparasites from forest buffalo (*Synceros caffer nanus*) and bongo antelopes (*Tragelaphus euryceros*), while these mammals benefit from the association through a reduction in ectoparasite loads and an increase in predator detection (as they react to the alarm calls of jacanas; RUGGIERO & EVES 1998). Seabirds of the North Sea often associate during feeding as the differentiation of the feeding methods employed by each species enables the seabirds to reach prey that would be otherwise unavailable to them (CAMPHUYSEN & WEBB 1999).

Primates foraging at different layers of the forest often form polyspecific associations (CORDS 1990). These associations improve the defence of these primates against predators (as each species responds to the anti-predator alarm calls of at least one other species participating in the association) and do not inflict any costs in terms of inter-specific food competition (as they have non-overlapping niches). Feeding associations have been documented among many primate species (WASER 1982, 1987; CORDS 1990; HONER et al. 1997), between primates and other vertebrates (usually ungulates; ELDER & ELDER 1970, MACKINNON 1974) or birds (SEAVY et al. 2001). For example, the bushbuck (*Tragelaphus scriptus*) was reported to forage on the food dropped from the trees by baboons (*Papio* sp.) in 35% of observations and the two species responded to each other's anti-predator alarm calls (ELDER & ELDER 1970). Although New World monkeys have been reported to associate with ungulates and even with lizards (GLANDER 1979, AGORAMOORTHY 1997), most of the studies focused on two only species: baboons and langurs (*Papio* sp. and *Presbytis* sp.; SENZOTA 1983, DUNBAR 1988, NEWTON 1989). Indeed, data on associations between primates and other vertebrates are not available for many species otherwise largely studied. This is the case of the Japanese macaque (*Macaca fuscata*), which has been intensively studied over the last fifty years but no systematic study has been conducted to analyse interactions with sympatric sika deer (*Cervus nippon*). Japanese macaques usually forage in the trees (HILL 1997) and, in doing so, large quantities of food drop on the ground, discarded by the monkeys or due to branch shaking. It is likely that deer forage on this food (i.e. gleaning) as it represents an additional, otherwise unavailable, source of energy.

The aims of this study, therefore, were to describe the effect of food dropping on deer behaviour, identify factors that predict the presence of deer gleaning under trees, and discuss the possible costs and benefits of interactions between monkeys and deer for each species.

METHODS

Study subjects and data collection

This study was conducted on Yakushima Island (31°N, 131°E), Japan, from January 26th to May 4th 2002. The island is inhabited by a large population of sika deer and an endemic sub-species of Japanese macaque (*Macaca fuscata yakui*). Monkeys and deer are the only large mammals on the island and no natural predator is present (NAKAGAWA 1998). The study area is covered by an evergreen broad-leaved forest (see AGETSUMA & NAKAGAWA 1998, NAKAGAWA 1998, YAMAGIWA & HILL 1998 for descriptions of habitat characteristics and social behaviour of Yakushima macaques). Subjects of this study were all 14 adult individuals of a non-provisioned troop of Japanese macaques (Nina A, consisting of 6 adult males, 8 adult females, 3 juveniles and 1 yearling) and the deer living in the area. The diet of sika deer comprises a large number of species and plant parts as they forage on herbs, grasses, young or mature leaves, fruits, and leaves (TAKADA et al. 2002). When food is limited, the diversity of their diet and the importance of food fallen from trees increase (DICTHCKOFF & SERVELLO 1998, TAKAHASHI & KAJI 2001). The abundance and ranging patterns of the two species was relatively unaffected by human presence.

Data were collected ad libitum (ALTMANN 1974) from 8.00 to 19.00 hr by the two authors. Inter-observer reliability was over 95%. Every time one or more monkeys were observed foraging on a tree we recorded: food category eaten by monkeys (i.e. leaves, seeds, or fruit), diameter of tree at breast height (DBH), food quantity available in the tree, and number of monkeys foraging on the tree. Food quantity was measured by estimating for each category by eye the amount of food available on the main branches of the tree and then transforming those data in percentages, grouped into four classes: 0-25%, 26-50%, 51-75%, 76-100%. Additionally, we recorded whether or not deer were with the monkeys, and, if so, the number of deer foraging on food items dropped from the tree by the monkeys. When deer were observed gleaning we recorded whether or not agonistic interactions between monkeys and deer or among deer were observed. A situation in which one or more monkeys were observed foraging on a tree was considered a single observation, regardless of the time that the monkeys spent foraging on that tree.

Data analysis

A series of Spearman rank correlations were run to evaluate correlations among independent variables (see below) used for logistic and multiple regressions. Logistic regression analysis was used to determine which variables best predicted the presence of deer gleaning under trees. The dependent variable was deer gleaning (nominal: yes or no) while the independent variables were food category eaten by the monkeys (nominal), DBH (continuous) and food quantity (ordinal) of the tree on which the monkeys were foraging, and number of monkeys foraging on the tree (continuous). Multiple regression was used to assess which of these independent variables best predicted the number of deer gleaning. For multiple regression we only considered observations in which monkeys and deer were observed together. A series of χ^2 tests were used to compare frequency of association in relation to the 3 food categories eaten by the monkeys.

RESULTS

A total of 149 observations was obtained. Leaves represented the main food source for macaques during this period of the year, whereas fruit accounted for a small proportion of their diet (see Fig. 1; HILL 1997). Deer were observed gleaning

41.6% (i.e. 62/149) of times that monkeys were foraging on the trees. When monkeys were foraging on leaves association between macaques and deer was less frequently observed than non-association ($\chi^2(1) = 10.3$, $P < 0.01$; see Fig. 1). An oppo-

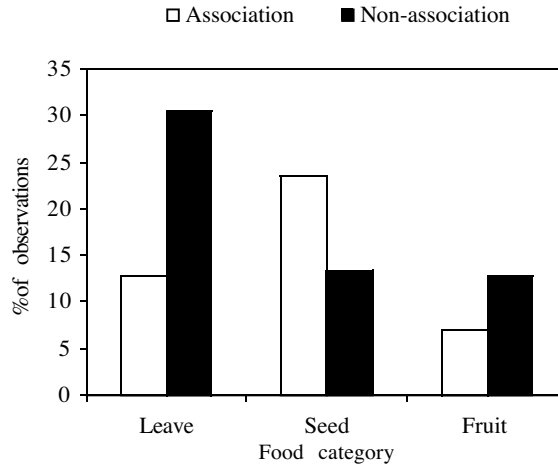


Fig. 1. — Variation in the occurrence of feeding association between monkeys and deer in relation to the three food categories eaten by the monkeys.

Table 1.

Results of the Spearman rank correlations between the independent variables used for the logistic and multiple regressions.

Variables	Rho values and significance
Food category × DBH	0.17, NS
Food category × food quantity	0.03, NS
Food category × no. of monkeys foraging	0.13, NS
DBH × food quantity	0.15, NS
DBH × no. of monkeys foraging	0.38, $P < 0.01$
Food quantity × no. of monkeys foraging	0.16, $P < 0.05$

Table 2.

Coefficients and significance for the variables used in the logistic regression (dependent variable: presence of deer gleaning).

Variables	β	Exp(β)	Significance
Food category	- 0.31	0.73	NS
DBH	- 0.02	0.98	NS
Food quantity	- 0.98	0.37	$P < 0.001$
No. of monkeys foraging	- 0.08	0.93	NS

Table 3.

Standard coefficients and results of the t-tests for the variables used in the multiple regression (dependent variable: number of deer gleaning).

Variables	Standard coefficients	T values and significance
Food category	- 0.04	- 0.35, NS
DBH	0.27	2.69, $P < 0.05$
Food quantity	0.40	4.02, $P < 0.001$
No. of monkeys foraging	0.57	5.61, $P < 0.001$

site result was found when monkeys were foraging on seeds ($\chi^2(1) = 3.8$, $P < 0.05$) while frequency of association did not differ in relation to time spent foraging on fruit ($\chi^2(1) = 2.3$, NS). Agonistic interactions between monkeys and deer were observed in 6.4% of the observations (i.e. 4/62). These interactions always consisted of a monkey threatening a deer in order to retrieve food items dropped from the tree. In contrast, agonistic interactions among deer were observed in 45.2% of observations (i.e. 28/62), apparently caused by competition for food dropped from the trees.

A series of Spearman rank correlations was used to analyse the relationship existing among the independent variables used for logistic and multiple regressions. DBH and food quantity were both positively related to the number of monkeys foraging on the tree while no other significant correlation was found (see Table 1). A logistic regression showed that all the variables were effective in predicting the presence of deer gleaning but food quantity was the variable that gave the best fit ($\chi^2(4) = 22.84$, $P < 0.001$, $-2 \log \text{likelihood} = 163.31$; see Table 2 for coefficients and significance of the variables in the equation). Moreover, all independent variables except food category were significant predictors of the number of deer gleaning. In particular, food quantity and number of monkeys foraging on the tree were the two factors mostly effective in predicting the number of deer gleaning ($R^2 = 0.48$, $F(4, 58) = 12.45$, $P < 0.001$; see Table 3).

DISCUSSION

In this study, deer were often observed gleaning. Although the deer living in the study area were familiar with human beings due to the continuous presence of primatologists and tourists, they were sometimes frightened by our presence, giving alarm calls and escaping if we approached within 30 m. This is likely to have partly prevented deer from gleaning whilst we were present. Deer might glean more frequently in undisturbed conditions than those recorded in this study. From the data collected we cannot determine whether the presence of deer gleaning under the tree represents a case of "active" association between monkeys and deer or if this is due to chance encounters between the two species (WASER 1982). Deer might associate with the monkeys only when they detect them foraging. Alternatively, they might actively follow the monkeys in order to forage on the food dropped by them. Which one of these two strategies does occur probably depends on the balance between the benefits in terms of increased foraging efficiency that deer would gain

by following the monkeys versus the costs of increased travel distance to remain with the monkeys.

The occurrence of association differed in relation to the food category eaten by the monkeys. This result suggests that deer showed some sort of food selection when they associated with macaques. However, this variable was the only one that did not predict presence or number of deer gleaning in the multivariate analyses. All the other variables were effective, although at a different level, in predicting the presence or the number of deer gleaning. Some of these variables were positively correlated one another. This result is not unexpected as larger trees usually bear greater quantities of food and they also allow larger numbers of monkeys to forage than smaller trees. Indeed, a positive relationship between food quantity, number of monkeys foraging, and the amount of food dropping from the tree (discarded by the monkeys or due to branch-shaking) have been found in other studies (e.g. HOWE 1980, OATES et al. 1980). Therefore, although we do not know which cue the deer use to detect the monkeys foraging (e.g. monkey vocalisations, branch-shaking), it is evident that the presence and number of deer gleaning clearly depends on the quantity of food dropped by the monkeys. Moreover, the quantity of food available on a tree also determines the amount of time that the monkeys spend foraging on that tree, which in turn may be positively related to the chances that deer have to spot the monkeys foraging. Data on the time the monkeys spent foraging in the tree were not collected and thus we cannot measure the importance of this factor in predicting the presence and number of deer gleaning. However, deer who were nearby quickly detected the monkeys foraging. Therefore, the time that the monkeys spent foraging probably affected more the total amount of food dropped than the number of deer gleaning.

In any case, it is likely that deer increased their foraging efficiency by gleaning. Sika deer, as many other ungulates, forage mainly on low vegetation and, as a consequence of this, they can greatly reduce the regeneration time of a forest (for example, foraging on young trees; TAKATSUKI & GORAI 1994, NOMIYA et al. 2003). Yakushima macaques, on the contrary, usually forage in the trees (HILL 1997). Therefore, sika deer have access by gleaning to food sources (i.e. ripe fruits, seeds, or young leaves) that otherwise would be seldom accessible to them. This hypothesis is supported by the high frequency of agonistic interactions observed among deer gleaning. The presence of additional food sources probably elicits food competition among deer. Increase in foraging efficiency for at least one species is one of the main reasons why feeding associations between species have evolved (the other one being defence against predators; RASA 1983, WASER 1987). If this is the case, we may suggest that the large population of macaques living on the island allows a larger population of deer than it would be sustainable by the habitat if there were no monkeys. Indeed, a recent study has shown that the population density of sika deer is higher in Yakushima than in other areas of Japan (AGETSUMA et al. 2003). This point needs further data to compare population dynamics in areas of Japan where the two species live sympatrically and in those in which one species is absent.

No natural predators live on the island and thus defence against predators may not be one of the reasons why monkeys and deer are observed together. However, it is possible that this factor led to the evolution of this behaviour in the past. Until the beginning of the 20th century macaques and deer were sometimes hunted by local people for their meat or to avoid crop raiding. Hence, we cannot completely rule out the possibility that macaques gain some benefits in terms of the detection of human presence or predators. However, monkeys were rarely observed to

look around when deer gave alarm calls. This observation may indicate that monkeys probably do not use deer alarm calls to detect predators. Therefore, the association between macaques and deer seems more likely to be a case of commensalism, or at least of asymmetrical mutualism, than of pure mutualism. Monkeys do not gain any evident benefit by associating with deer and they also incur low costs (as aggressive interactions between the two species in order to have access to food were rarely observed). On the contrary, gleaning probably increases the foraging efficiency of deer that, by associating with the macaques, have access to food sources otherwise unavailable.

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