1   Regular paper to *Behavioral Processes*

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3   **Possible use of heterospecific food-associated calls of**

4   **macaques by sika deer for foraging efficiency**

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6   **Highlights**

7   Playback of macaque food calls under trees gathered significantly more deer than silence control

8   periods.

9   Deer can associate macaque food calls with foraging activities and use heterospecific calls.

10   Japanese sika deer, *Cevus nippon*, use heterospecific food calls of Japanese macaques, *Macaca*

11   *fuscata yakui*, for foraging efficiency.

Possible use of heterospecific food-associated calls of macaques by sika deer for foraging efficiency

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Abstract

Heterospecific communication signals sometimes convey relevant information for animal survival. For example, animals use or eavesdrop on heterospecific alarm calls concerning common predators. Indeed, most observations have been reported regarding anti-predator strategies. Use of heterospecific signals has rarely been observed as part of a foraging strategy. Here, I report empirical evidence, collected using playback experiments, showing that Japanese sika deer, *Cevus nippon*, use heterospecific food calls of Japanese macaques, *Macaca fuscata yakui*, for foraging efficiency. The deer and macaques both inhabit the wild forest of Yakushima Island with high population densities and share many food items. Anecdotal observations suggest that deer often wait to browse fruit falls under the tree where a macaque group is foraging. Furthermore, macaques frequently produce food calls during their foraging. If deer effectively obtain fruit from the leftovers of macaques, browsing fruit fall would provide a potential benefit to the deer, and, further, deer are likely to associate macaque food calls with feeding activity. The results showed that playback of macaque food calls

under trees gathered significantly more deer than silence control periods. These results suggest that

deer can associate macaque food calls with foraging activities and use heterospecific calls for

foraging efficiency.

Key words: heterospecific signals, polyspecific association, inter-species communication

1. Introduction

Heterospecific communication signals sometimes convey biologically relevant information for animal survival. Theoretically, if the signal receiver gathers potentially beneficial information from the heterospecific signals, the ability to use or eavesdrop on signals would be expected to evolve (for detailed recording procedure, see Method section and ref Bradbury and Vehrencamp 1998). Indeed, alarm signals are a well-known example of the use of heterospecific calls (Zuberbuhler 2003). It often occurs that several animals share common predators. Alarm signals of one species provide beneficial information not only for conspecific but also for heterospecific animals. Previous reports have demonstrated that several primates or birds respond appropriately to heterospecific alarm calls (Fallow and Magrath 2010; Goodale and Kotagama 2005, 2008; Hurd 1996; Rainey, Zuberbuhler, and Slater 2004, 2004; Ramakrishnan and Coss 2000; Randler 2006; Shriner 1998; Vitousek et al. 2007).

Furthermore, two different species may sometimes both recognise alarm calls for the same predators, meaning that they mutually obtain the potential benefit of avoiding predation risks. In these cases, the mutual recognition of heterospecific alarm signals is treated as true interspecies communication (Fichtel 2004; Oda and Masataka 1996; Zuberbuhler 2000).

Unlike alarm signals, the use of heterospecific signals has rarely been reported in the context of foraging strategies. Context-dependent signals are not restricted to anti-predator strategies but have also been found in connection with foraging strategy (Bradbury and Vehrencamp 1998). Indeed, food-associated signalling has been reported in many animals. Several birds and primates vocalise specific call types at food finds, attracting group members (Bugnyar, Kijne, and Kotrschal 2001; Clay and Zuberbuhler 2009; Di Bitetti 2003, 2005; Gros-Louis 2004, 2006; Hauser and Marler 1993,

1993; Kitzmann and Caine 2009; Slocombe et al. 2010; Valone 1996). Given that sympatric species share or compete for common food resources with each other, food-associated signals would be a reliable signal for the presence of food resources for the same and different species. Surprisingly, there are few empirical demonstrations showing the use of heterospecific food-associated calls to date. Here, I present the first report of the possible use of food-associated vocalisations of a primate, the Japanese macaque (*Macaca fuscata*), by an ungulate animal, the Japanese sika deer (*Cevus nippon*).

Sika deer and Japanese macaques both inhabit the lowland forests of Yakushima Island in southern Japan at extremely high population densities. In this area, longitudinal field research on the Japanese macaque has been conducted(Yamagiwa 2010). Although arboreal fruits are attractive food resources for deer, it would be difficult for deer, as entirely terrestrial animals, to obtain them. To increase their efficiency in foraging fruits, it has recently been found that deer rely considerably on fruit falls from macaques foraging trees in the area (Agetsuma, Agetsuma-Yanagihara, and Takafumi 2011). Indeed, there are anecdotal observations that deer often wait to browse fruit falls under the tree where a macaque group is foraging (Majolo and Ventura 2004). If deer effectively obtain fruits from the leftovers of macaques, browsing fruit fall would provide a potential benefit to the deer. Furthermore, given that Japanese macaques frequently make food-associated calls during their foraging (Koda, Shimooka, and Sugiura 2008; Sugiura 2007; Suzuki and Sugiura 2011), deer may associate macaque food calls with macaque foraging activity.

In this study, I experimentally played back macaque food calls under the lauraceous trees, the fruit of which is a common food item for deer and macaques during the experimental season here (Agetsuma, Agetsuma-Yanagihara, and Takafumi 2011; Agetsuma and Nakagawa 1998) to simulate the macaques' foraging. I predicted that macaque food-associated calls would recruit deer.

2. Materials and Methods

The research methodology complied with protocols approved by the guidelines of Primate Research Institute, Kyoto University and adhered to the legal requirements of Japan.

2.1. Study area and subject animals

I conducted playback experiments in the evergreen forests of the lowlands of Yakushima Island (30.4°N, 130.4°E) in southern Japan in October 2002. The total area of Yakushima Island is approximately 503 km^2, and the study site was located on the northwest coast (0–400 m above sea level). The mean annual temperature is approximately 21°C, and the annual rainfall is approximately 2600 mm. The site is covered with warm-temperate, broad-leaved forest species. The forest canopy consists mainly of Fagaceae and Lauraceae. The diversity of plant species is high within the study area (Agetsuma and Nakagawa 1998).

Japanese sika deer and Japanese macaques inhabit area at extremely high population densities (Agetsuma et al. 2003; Tsujino, Noma, and Yumoto 2004). Furthermore, the site is in an area where longitudinal study of Japanese macaques is ongoing and where more than 10 group have been habituated and identified by researchers for around 20 years (Yamagiwa 2010). Additionally, the wild deer are moderately habituated to human observers or tourists, and recently, it has been possible to observe their behaviours directly by focal animal sampling methods (Agetsuma, Agetsuma-Yanagihara, and Takafumi 2011). Previous research has revealed that some food items are shared between deer and macaques, and the deer rely considerably on fruit falls from macaques foraging in the trees (Majolo and Ventura 2004). This would suggest that deer obtain a potential

benefit from macaque fruit falls. Furthermore, there are no natural predators for both macaques and deer in this study site.

2.2. Playback stimulus

The food-associated calls of Japanese macaques are defined by both the emitted context and acoustic structures. Acoustically, food-associated calls are almost the same as contact calls, referred to as "coo calls," and have tonal acoustic structures (Koda 2004; Koda and Sugiura 2010). During foraging, the   macaques frequently produce there food-associated calls and exchange calls with group members within the food patch of the tree (Koda, Shimooka, and Sugiura 2008; Suzuki and Sugiura 2011). The rates of calling during foraging were estimated roughly at 1.1 per min for one subject (Koda, Shimooka, and Sugiura 2008). This high rate of calling would be related with no potential predators for macaques. The macaques usually continue to forage for more than 10 min (Agetsuma 1995), and thus, the exchange of calls is heard constantly during their foraging.

To simulate the foraging activities of Japanese macaques, I selected 15 food-associated calls from acoustic stimuli previously recorded for other studies (for detailed recording procedure, see Koda 2004). I prepared a 10-min-long stimulus of macaques exchanging of food-associated calls such that 15 calls appeared during each minute.

2.3. Playback procedures

The single experiment was designed to be 40 min long and consisted of three stages: 1) 20 min pre-experimental; 2) 10 min experimental; and 3) 10-min post-experimental. First, I put the active

speakers (Sony SRS-Z750) connected to a CD player (Sony D-EJ955) on the ground under the

camphor trees, *Cinnamomum camphora*. The fruits of camphor trees are ripe during the end of

summer (late August) through the autumn (November) and are important food items for both deer

and macaques in Yakushima (Agetsuma, Agetsuma-Yanagihara, and Takafumi 2011; Agetsuma and

Nakagawa 1998). The standard height of camphor trees in lowland forests of Yakushima is

approximately 20–30 m; thus, the deer never directly access the ripe fruits in the canopies of the

trees. The heights and abundance of the fruits in the canopy were equivalent among all target

camphor trees I chose; the height was approximately 20 m and 60 percent of fruits were ripe. I also

confirmed that the macaques group around the study area used the target trees routinely just during

the experiment periods. After I visually confirmed the absence of both of deer and macaque for at

least 5 min around the speakers, I moved away, at least 200 m from the speakers. When leaving the

speakers, I started to play the stimulus CD, which began with the 20-min pre-experimental stage.

During this stage, no sound was played. After this pre-experimental stage, the 10-min experimental

stage was started. During the experimental stage, the food-associated call stimuli were played for 10

min. Finally, in the post-experimental stage, no sound was played for 10 min. Furthermore, control

experiments were conducted. In the control experiment, the speakers were placed but no acoustic

stimulus was played for 40 min. The playback and control experiments were conducted 20 and 13

times, respectively. The experimental site was chosen from approximately 200 ha area intensively

studied by many researchers of Japanese macaques, and was changed for each experiment. I left at

least 30 min between experimental sessions. All experiments were recorded using a video camera

(Sony DCR-PC120) on a 1-m tripod. The video camera was placed 30 m away from the front of the

speakers. The vertical visual perspective was approximately 30 m, and approximate range of

recorded by camera were 500 m^2

2.4. Data analysis

The first 10-min silence period was ignored for analysis because deer and macaques might approach the playback site after setting up. Thus, the last 10-min period of silence was analysed as the pre-experimental stage. For the control experiments, the first 10 min was also ignored for analysis. Consequently, I used 30-min-long periods for the analysis.

In the video recordings, I counted the numbers of deer appearing on the video monitor. The maximum number of deer was measured for each stage. For comparisons with control experiments, the maximum numbers of deer was measured for every 10-min period. Also, the time when the maximum peak number of deer was reached (peak time, PT) was recorded. Here the PT was defined as the time from the onset time of 30-min-long periods for the analysis to the time when the maximum peak number of deer was first reached. If the same number of deer was observed in multiple times within a single experiment, the first times was used for analysis of PTs. If no deer appeared in a session, that session was excluded for calculating PT.

To examine the effect of experimental conditions (playback, control) and experimental stages (pre, experiment, post) on the maximum number of deer, I performed generalised linear mixed model (GLMM) procedures to estimate fitted models using the 'glmmML' method in 'glmmML' package in the 'R' software (ver. 2.12.1; R Development Core Team). In the model terms, experimental condition (playback, control) and experimental stages (pre, experiment, post) were considered explanatory fixed factors, and session was considered a random factor. Furthermore, I performed Mann-Whitney U tests to compare the PTs between playback and control conditions. To examine whether the PTs of playback conditions were over 10 min, we calculated the mean of the

PTs with 95% confidence intervals. Significance levels were all set at $P < 0.05$.

3. Results

Figure 1 shows the overall patterns of numbers of deer observed between experimental conditions at the experimental stages. The estimations of coefficients showed two significant interaction effects between the experimental stage and playback condition, and post-experimental stage and playback condition (Table 1). This suggested that the numbers of deer observed were not significantly different in the pre-experimental stage between control and playback conditions, while significantly increased in experiment and post-experimental stages of playback condition. That is, deer gathered close to the speaker after the stimuli playing back.

Figure 2 shows the overall patterns of PTs for the two experimental conditions. No deer appeared in 9 and 9 sessions for control and playback conditions, respectively. The Mann-Whitney U test revealed that PTs of playback condition were significantly higher than those of control condition ($N_{\text{control}} = 4$, $N_{\text{playback}} = 11$, W=1, $P = 0.0029$). The mean PT with 95 percent confidence intervals under the playback condition was computed as 17.9min (lower limit, 13.0; upper limit, 22.8. Given that the onset time of stimuli playback was 10 min, lower limit of 95% confidence interval showed that the mean PT under the playback condition was significantly later than the onset time of the playback.. These results suggest that deer started to gather near the speaker after the stimuli were played.

4. Discussion

These experiments demonstrated that deer gathered in response to the exchange of macaque

food-associated calls. Interestingly, the movements of the deer corresponded to the onset time of playbacks. The coincidence of the short time delay between the playback period and the deer's arrival is direct evidence that deer responded to the acoustic stimulus within a relatively short time. This is consistent with the higher number of deer observed during the experimental stage of playback.

The deer's use of macaque calls is supported by a recent ecological study of deer in the same area. Recent observations of the foraging behaviour of deer in the same area revealed that deer rely considerably on food falls from macaques foraging in trees (Agetsuma, Agetsuma-Yanagihara, and Takafumi 2011). Agetsuma and colleagues carried out direct observations of foraging behaviours by focal animal sampling, which is a method wherein the observer follows the focal deer at a close distance. They reported the time budgets of foraging and also calculated the percentages of time spent on each food category. Interestingly, the percentage of time spent on food falls from macaque tree foraging was 7%, which was not much less than the total time spent eating. They suggested that macaques facilitated deer's feeding on food falls. In the absence of potential predators, a high rate of calls is not costly behaviour (Koda, Shimooka, and Sugiura 2008). Consequently, the ecological background in this area potentially allows macaques to emit calls frequently. Given the high call rates of macaques in this area (Koda, Shimooka, and Sugiura 2008), it seems reasonable for deer to associate food-associated calls with feeding activity by a macaque group, recognising beneficial information from the macaque calls.

Although the deer may associate macaque calls with a good opportunity to feed on fruits, seeds, and leaves from the top of the canopy, which would be impossible to eat without the macaques, using macaque calls is apparently not an active strategy but rather an opportunistic strategy on the part of the deer. In fact, no deer gathered near the speaker in 9 of 20 sessions (45%) under the playback condition. This would suggest that the macaque food calls weakly attract deer

and that deer do not actively follow the macaques. Alternatively, if deer happen to hear macaque

food-associated calls in the near distance, deer may opportunistically move to the tree where the

macaque group is foraging. Previous observations also support the opportunistic use of macaque

leftovers (Agetsuma, Agetsuma-Yanagihara, and Takafumi 2011; Majolo and Ventura 2004). Even if

deer opportunistically use the macaque calls, it would provide a benefit for the deer because of the

ecological background of Yakushima Island. In the current field sites at Yakushima Island, the

population densities of deer and macaques are both very high. Recent investigations reported

>80 head / km^2 (Agetsuma et al. 2003) for deer, and 60–70 head / km^2 for macaques (Agetsuma and

Sugiura 2007). Given this high density of macaques, deer could easily have the opportunity to

encounter a macaque group foraging, even without actively searching and/or following a macaque

group.

To my knowledge, this is the first reported demonstration of heterospecific calls used in a

foraging strategy (i.e., a context other than anti-predator strategies). Polyspecific associations have

been reported for several mammals (Majolo and Ventura 2004; Newton 1989; Stensland, Angerbjorn,

and Berggren 2003; Tsuji et al. 2007). Most such reports are of associations between primates and

other species (Stensland, Angerbjorn, and Berggren 2003). Currently, there are two major hypotheses

proposed as ecological explanations for such polyspecific associations (Stensland, Angerbjorn, and

Berggren 2003). The first explanation is derived from an anti-predator strategy (Stojan-Dolar and

Heymann 2010; Leonardi et al. 2010; Hardie and BuchananSmith 1997) and suggests that animals

provide predation-risk information to associated animals, unidirectionally or mutually, because doing

so serves to decrease predation risks. The second hypothesis is based on foraging strategies (Bearzi

2006; Taylor and Skinner 2000; Minta, Minta, and Lott 1992) and argues that animals provide

food-resource information to their associated partner animal because doing so plays a role in

increasing foraging benefits. This appears to be the case with my observations. The marked

difference between the two explanations is that interactions via signals are necessary for the former but are not necessary for latter, which may explain why most inter-species communications that have been characterised concern sharing information by means of alarm signals. Signal production that provides foraging benefits would be seem to be a costly behaviour for the sender because such signals might help a potential predator to detect the signal senders, resulting in increased predation risks (Bradbury and Vehrencamp 1998). The two explanations are not mutually exclusive. In the case where foraging benefit is the main reason for a polyspecific association, interactions via signals may not fundamentally contribute to an association, but rather may be suppressed because of predation risks. The absence of potential predators would assist in enhancing heterospecific interactions via food-associated calls.

Of particular importance in my study was the demonstration of the possible use of heterospecific signals in a foraging strategy. My demonstrations provided evidence only of unidirectional signal use, but further investigations may also uncover the mutual use of heterospecific signals (i.e., inter-species communication). Furthermore, the diets of deer and macaques vary seasonally, and the dependency of deer on macaque leftovers also varied with seasonal variation in the diets of macaques (Agetsuma, Agetsuma-Yanagihara, and Takafumi 2011). In current study, I only focused on camphor trees, but experiments on different trees or during different seasons may provide different results. Deer could also associate macaque food-associated calls with a more complex learning process such as conditional discrimination.

Acknowledgements

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Table 1 Coefficients of estimated models

Parameters	Coefficient Estimates	Standard Errors	Z-values	*P*
(Intercept)*	- 1.72	0.76	-2.26	0.024
Condition: Playback condition	-0.22	0.91	-0.24	0.80
Stage: Experimental stage	-0.25	0.50	-0.50	0.61
Stage: Post-experimental stage	-0.59	0.56	-1.05	0.29
Interaction: Playback condition × Experimental stage	1.60	0.68	2.34	0.019
Interaction: Playback condition × Post-experimental stage	1.69	0.73	2.31	0.021

*Intercept was set as the coefficient of the pre-experimental stage of the control condition in the model.
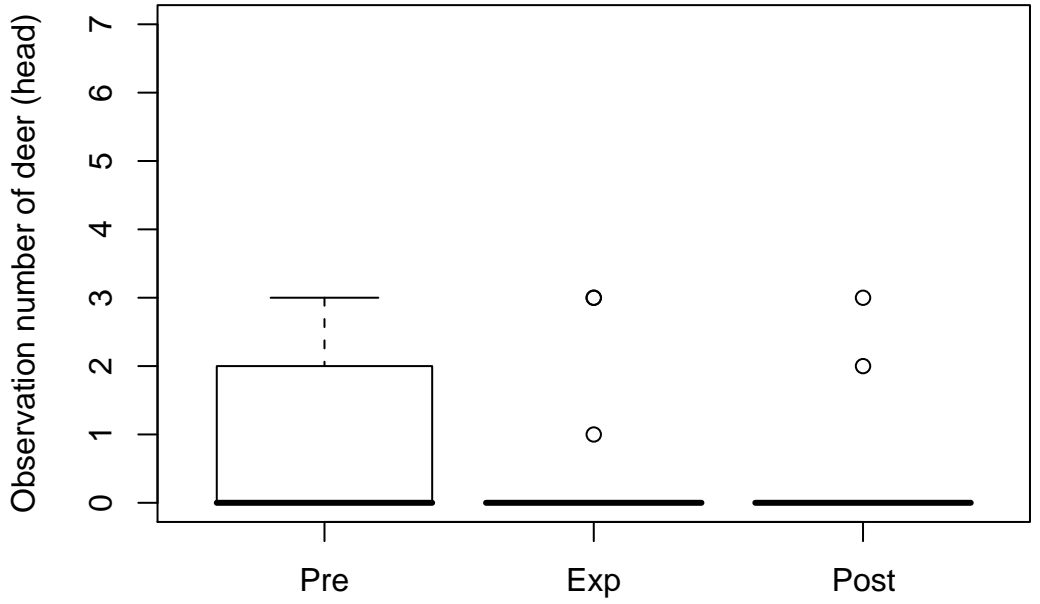
Figure legends

Fig. 1

Boxplots of observed numbers of deer in each experimental stage for each condition. Box plots represent the medians (horizontal bold lines), 25th and 75th percentiles (bottom and top of box), the $1.5 \times$ interquartiles range (whiskers), and outliers (circles).

Fig. 2

Boxplots of peak times (PTs) for each condition. Box plots represent the medians of PTs (horizontal bold lines), 25th and 75th percentiles (bottom and top of box), the $1.5 \times$ interquartiles range (whiskers).

Fig. 1

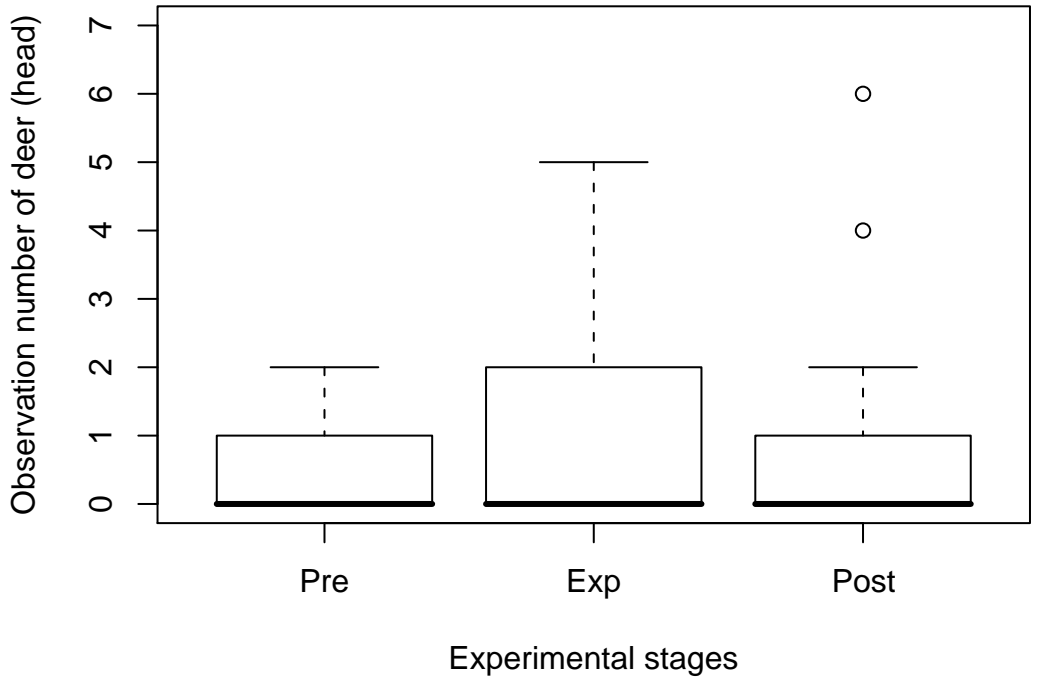## Control condition

Playback condition

Fig. 2

PT for each condition

Time (min)

Control   Playback

Experimental condition