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ARTICLE

Variation and social influence of bowing behavior by sika deer (*Cervus nippon*)

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Abstract Nara Park, Nara Prefecture, Japan is a sightseeing destination in which people have the unique custom of feeding specialized cookies to the park's free-ranging sika deer, *Cervus nippon*. Sika deer in Nara Park display a behavior akin to bowing to their human feeders. To characterize this bowing behavior and determine whether it is unique, we conducted feeding experiments with deer cookies on deer populations in Nara Park and Miyajima Island, Hiroshima Prefecture, where cookies are not available. Sika deer in Nara Park bowed more frequently than those on Miyajima Island. Within Nara Park, sika deer in busy areas bowed more frequently than those in quiet areas. These findings imply that bowing behavior has been acquired through encounters with humans. In Nara Park, adult deer showed the greatest number of bows, followed by yearlings and finally fawns. When bowing, up–down movement was relatively more common than slant movement in adults than in yearlings. These findings suggest that sika deer in Nara Park develop bowing behavior with age. Bowing behavior also differed among sexes and postures: more in females than males, and more in standing individuals than those sitting. Young individuals bowed more frequently after demonstrations of bowing behavior by adults than before, suggesting a social influence on this behavior.

Keywords Sika deer · Cultural behavior · Bowing behavior · Feeding experiment · Social influence

Introduction

In recent decades, many studies have suggested that, like humans, some animals have cultures (Rendell and Whitehead 2001; Laland and Hoppitt 2003). Cultural behavior is broadly defined as a behavior that is observed in two or more members of a social unit, is largely dependent on social means for its diffusion and maintenance, and is persistent across generations, or at least over a number of years (Fragaszy and Perry 2003). Animal culture has generally been studied by either investigating transmission mechanisms experimentally (Whiten and Ham 1992; Bonnie et al. 2007; Whiten et al. 2007; Thornton and Clutton-Brock 2011; Voelkl and Huber 2000; Battesti et al. 2012) or examining geographic variation in behavioral patterns that cannot be explained by genetic or environmental factors (Whiten et al. 1999; van Schaik et al. 2003; Gruber et al. 2009, 2011). However, few studies have demonstrated the transmission of behavior through social learning in wild populations (Biro et al. 2003; Allen et al. 2013; van de Waal et al. 2013; Hobaiter et al. 2014). Moreover, evidence for culture in wild animals has been reported mainly in primates, including Japanese monkeys (Kawai 1965; Huffman 1996), capuchin monkeys (Panger et al. 2002; Perry et al. 2003), chimpanzees (Whiten et al. 1999), and orangutans (van Schaik et al. 2003), and there have been a few reports relating to nonprimates (Rendell and Whitehead 2001; Hunt and Gray 2003). Furthermore, cultural behavior developed through habituation to humans has not been studied, except for the opening of milk bottle caps by British tit birds (Fisher and Hinde 1949; Hinde and Fisher 1951).

The sika deer, *Cervus nippon*, of Nara Park, Japan, are extremely tame as they are often fed vegetables or specialized "deer cookies" sold in the park by tourists and residents. This constant feeding likely influences sika deer

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behavior; indeed, deer in the park show display behavior that resembles bowing to their human feeders. Similar food-begging behavior is also known in red foxes in Shiretoko National Park, Hokkaido (Tsukada 1997). The details of this bowing behavior in sika deer remain unstudied; indeed, it is still unclear if it is unique to Nara Park, and it may be cultural. It is also unknown whether this behavior is socially transmitted.

In the study reported in the present paper, we conducted feeding experiments to characterize bowing behavior in relation to sex, body size, and posture, and to the degree of human influence. We also assessed the hypothesis that the bowing behavior could be a cultural variant unique to the sika deer in Nara Park by comparing their behavior with that of a sika deer population on Miyajima Island, where feeding by humans is rare, as well as by studying whether observations by young sika of the adults' bowing provokes bowing behavior in the young deer too.

Materials and methods

Study area

The study was conducted in Nara Park, Nara Prefecture (34°41′07″N; 135°49′58″E) and Miyajima Island, Hiroshima Prefecture (34°23′48″N; 132°27′35″E), central Japan. Nara Park (6.6 km^2) had a population of 1495 sika deer (384 males, 912 females, and 199 fawns) according to a census performed by the Nara Deer Foundation in July 2015. Sika deer in Nara Park are very tame and are often fed "deer cookies" or vegetables by tourists and residents. The park is not fenced, allowing the deer to move freely. However, the population is partly managed by the Nara Deer Foundation. Pregnant females are captured from April to July, and are allowed to bear fawns in an enclosure within the park. Males are captured from August to October to trim their antlers, after which they are released in October. Injured or sick deer are confined to the enclosure.

Miyajima Island housed about 500 wild deer in its 30.2 km^2 extent. Most sika deer occur in a residential area in the northeast according to a census conducted by the Hiroshima Prefectural Government from 2007 to 2008. As in Nara Park, sika deer on Miyajima Island are acclimated to man because residents protect them as they are symbols of the island. Although deer cookies were previously sold in Miyajima Island, their sale and the feeding of sika deer in any form have been prohibited since 2007.

Observation of bowing behavior in Nara Park

Sika deer in Nara Park were classified into seven classes by sex, body size, and antlers according to Kawamichi (1980): large males, generally with four-point antlers, estimated at ≥4 years old; small males, with two- or three-point antlers, estimated at 2 or 3 years old; male yearlings with spikes; large females, estimated at ≥4 years old; small females, estimated at 2 or 3 years old; female yearlings; and fawns <12 months old.

We conducted feeding experiments as follows. A deer cookie was provided to a sika deer from a distance of 1 m, and we noted whether the deer exhibited bowing behavior within 5 s. When the sika deer showed bowing behavior, the number of bows was recorded, together with the sex, size class, and posture (sitting or standing) of the bowing individual and the bowing type (up-and-down or slant movement; Fig. 1). We identified individuals using white spots on the body, antler configuration, and natural notches on the ears.

We performed several experiments testing bowing behavior in sika deer, which we refer to by number below. In experiment I, we observed bowing behaviors by individuals occurring in a busy area (area A) and those in a quiet area (area B) within Nara Park. Area A was located around Todaiji Temple Gate, covering 5.8 ha, where there were many visitors to Nara Park. Area B was located at the north and south edges of Nara Park, covering 4.3 ha, where there were few visitors. We conducted this experiment on 32 days from 21 May to 9 October 2012, from 1 to 3 pm, for 8 large males (7 in area A and 1 in area B) (number of feeding trials per individual, 4–18), 11 large females (7 in area A and 4 in area B) (3–15), and 5 small females (3 in area A and 2 in area B) (4–12), all of which were individually identified.

In experiment II, the bowing behavior by the individuals that occurred in both the busy area (area A) and the quiet area (area B and the adjacent area covering 2.9 h) was compared between the two areas. We conducted this experiment on 32 days from 17 July to 27 September 2013, once a day from 8 am until noon, for one large male, four small males, one male yearling, and four large females, all of which were individually identified.

Experiment III, which ran for 14 days from 15 to 28 February 2014, was conducted to compare bowing behavior between yearlings (both sexes) and fawns, once per day from 1 to 3 pm, in area A. Six yearlings (range of feeding trials per individual: 5–8) and 5 fawns (5–10), all of which were individually identified, were included.

Experiment IV, which was carried out on 8 November 2012 in area A and 12 November 2012 in area B, was conducted to compare bowing behavior between individuals with different body sizes and between sexes. In total, we observed 48 individuals (6 large males, 19 large females, 3 small males, 13 small females, 5 male yearlings, and 2 female yearlings) in area A and 15 (1 large male, 7 large females, 3 small males, 2 small females, 1 male

Fig. 1 Up–down (*left*) and slant (*right*) bowing movements by deer in Nara Park

yearling, and 1 female yearling) in area B, with one feeding trial for each individual.

Observation of bowing behavior on Miyajima Island

To study whether sika deer show bowing behavior in populations outside Nara Park, we carried out feeding experiments on Miyajima Island using the same methods as in Nara Park. Again, experiments were conducted in both busy (area C) and quiet (area D) areas on 15 September 2012 from 9 am to 3 pm. Area C was located in the town area, covering 20 ha, where there were many people. Area D was located in the remote area, covering 63 ha, where there were few people. Deer were classified into four groups (male adults, male yearlings, female adults, female yearlings) by sex and body size (male and female adults were estimated to be older than 2 years old). These feeding experiments were attempted on a total of 109 individuals (15 adult males and 35 adult females in area C, and 24 adult males and 35 adult females in area D).

Experiment investigating social influence

The experiment investigating social influence was carried out in area B and adjacent areas in Nara Park from 1 to 3 pm for 48 days from June to November 2014.

A fawn and 4 yearlings that never showed any bowing behavior in 10–15 feeding trials, and a yearling that showed bowing behavior on only one occasion in 10–15 feeding trials, were selected, individually identified, and shown a demonstration of bowing behavior in another adult deer. In the demonstration, we showed a sika cookie to an adult deer (demonstrator) to provoke up–down bowing near a target fawn or yearling (observer). Demonstrations by the same demonstrator to the same observer were repeated 10–23 times on the same day. Soon after the demonstrations, a sika cookie was shown to the observer deer and the occurrence and number of bows were recorded. These feeding trials were conducted once a day and repeated 2–12 times. The total number of demonstrators comprised 32 females and 3 males (2 females, 4 females, 5 females, 6 females, and 1 male, and 10 females and 2 males for individual observers).

Data analysis

For experiments I–IV in Nara Park, we used a generalized linear mixed model with a Poisson distribution and ln-link function to identify factors affecting the number of bows by sika deer. In experiments I and III, the number of bows by the individuals was the dependent variable, while individual was treated as a random effect. For experiment I, the explanatory variables were month (categorical variable), area (area A or B), deer sex, size (of females), and posture. For experiment II, the number of bows by the individuals was treated as the dependent variable, and area (area A or area B and adjacent areas), deer sex, and size (of males) were treated as explanatory variables. For experiment III, deer age was treated as the explanatory variable and the number of bows by the individuals as the dependent variable. In experiment IV, area (A or B), deer sex, and deer size were treated as the explanatory variables and the number of bows by the individuals as the dependent variable. For this experiment, we analyzed factors affecting bowing type using logistic regression. The dependent variable was the type (up–down or slant) of the first bowing by each individual and the explanatory variables were area, sex, and deer size.

To compare the frequency of bowing behavior between Nara Park (areas A and B) and Miyajima Island (areas C and D), we applied the Kruskal–Wallis test with nonparametric multiple comparison (Steel–Dwass test) to the respective feeding experiment results. We used the data for male adults and female adults and analyzed them separately.

Table 1 Result of a generalized linear mixed model that included five factors, i.e., month (May, June, July, August, September, or October), area (area A or area B), sex, size group (large or small within female), and posture (sitting or standing), as predictors of the number of bows in experiment I

Variable	Coefficient ± SE	*z* value	*P* value
Intercept	0.604 ± 0.471	1.283	0.2
Month: June	−0.195 ± 0.472	−0.413	0.68
Month: July	−0.390 ± 0.449	−0.868	0.39
Month: August	−0.138 ± 0.439	−0.314	0.76
Month: September	−0.207 ± 0.490	−0.422	0.67
Month: October	−0.615 ± 0.624	−0.987	0.32
Area: B	−0.634 ± 0.163	−3.895	<0.0001
Sex: male	−0.360 ± 0.122	−2.953	<0.001
Size: small	−0.025 ± 0.131	−0.191	0.85
Posture: standing	0.529 ± 0.148	3.576	<0.001

We analyzed whether bowing behavior in fawns and yearlings changed after they observed bowing by adults using a generalized linear model with a Poisson distribution and ln-link function. The dependent variable was the number of bows by the fawns and yearlings, and the explanatory variables were experiment timing (before or after the demonstration) and deer size. Respective individuals were treated as a random effect.

All analyses included interactions among all explanatory variables. If the interactions were not significant, we conducted the analysis excluding interactions. All analyses were conducted using JMP version 9 (SAS Institute Inc 2010 and Core Team 2015).

Results

Variation in bowing behavior in Nara Park

In experiment I, the number of bows differed significantly among areas, sexes, and postures, but there was no difference with regard to month or deer size (Table 1). The number of bows per feeding trial was larger in area A than in area B, in females than in males, and in standing individuals than in those sitting (Fig. 2).

Experiment II revealed that the number of bows differed significantly between areas (generalized linear mixed model, $\chi^2 = 7.99$, $p = 0.005$), size groups ($\chi^2 = 4.37$, $p = 0.04$), and sexes ($\chi^2 = 6.10$, $p = 0.047$). Individual deer bowed more frequently in area A (the number of bows by each deer per feeding trial: mean ± SD = 1.52 ± 0.56, range 0.64–2.50) than in area B (0.89 ± 0.42, 0–1.17).

In experiment III, the number of bows differed significantly between size groups (generalized linear mixed

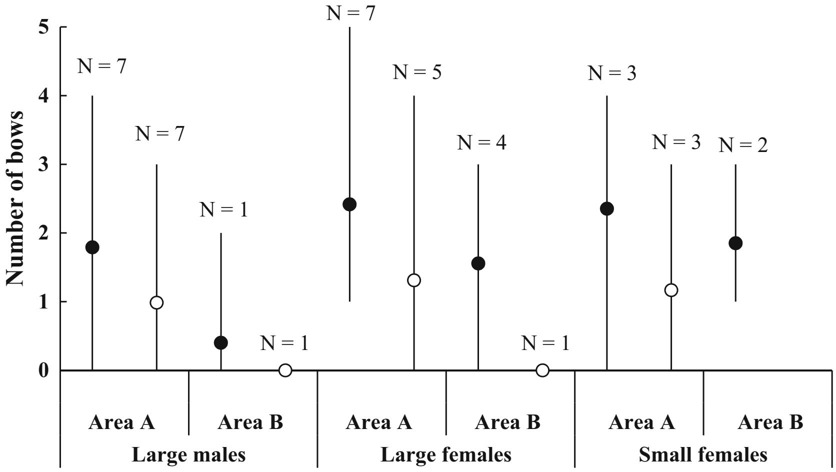

Fig. 2 Number of bows performed by deer in experiment I in Nara Park. *Circles* indicate the mean of number of bows by standing (*filled circles*) or sitting (*open circles*) individuals. *Solid lines* indicate the range from the *minimum* to *maximum* value. *N* number of individuals observed

model, $\chi^2 = 20.88$, $p < 0.0001$), with the number of bows per feeding trial larger in yearlings than in fawns (Fig. 3).

Experiment IV showed that the number of bows differed significantly between areas (generalized linear mixed model, likelihood ratio $\chi^2 = 7.74$, $p = 0.005$), whereas there was no difference between sexes (likelihood ratio $\chi^2 = 0.19$, $p = 0.66$) or size groups (likelihood ratio $\chi^2 = 4.93$, $p = 0.085$). The number of bows per feeding trial was larger in area A than in area B (Fig. 4). With respect to bowing type, the proportion of individuals showing up–down movement (Table 2) was significantly different only between size groups (generalized linear mixed model, likelihood ratio $\chi^2 = 9.80, p = 0.007$); there were no differences between areas (likelihood ratio $\chi^2 = 0.07, p = 0.79$) or sexes (likelihood ratio $\chi^2 = 0.17$, $p = 0.68$). Large and small adults (up–down: 38, slant: 4) had a higher proportion of individuals with up–down movement than yearlings (up–down: 1, slant: 3) (Fisher's exact probability test, $p = 0.009$).

Comparison of bowing behavior between Nara Park and Miyajima Island

The number of bows made by female adults in the feeding experiments differed significantly between the two areas of Nara Park and the two areas of Miyajima Island (Kruskal–Wallis test, $\chi^2 = 88.2$, $p < 0.001$); a nonparametric multiple comparison performed via the Steel–Dwass test showed significant differences between areas A and B ($p < 0.01$), areas A and C ($p < 0.001$), areas A and D ($p < 0.001$), and areas B and D ($p < 0.001$), but no differences between areas B and C ($p = 0.12$) or areas C and D ($p = 0.30$). The number of bows by male adults also differed significantly between Nara Park (area A only) and Miyajima Island (Kruskal–Wallis test, $\chi^2 = 32.3$, $p < 0.001$); the Steel–Dwass test showed significant differences between areas A and C ($p < 0.0002$) and areas A and D ($p < 0.0001$), but no difference between areas C and D ($p = 0.96$). Thus, female adults in area A of Nara Park exhibited more bows than those in area B or on Miyajima Island (Fig. 5), and male adults in area A exhibited more bows than those on Miyajima Island did (Fig. 6).

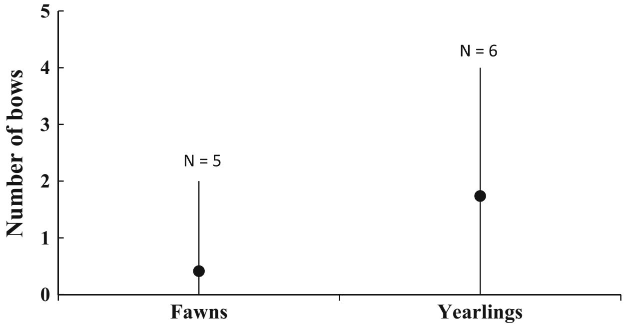

Fig. 3 Number of bows performed by deer in experiment III in Nara Park. *Circles* indicate the mean number of bows. *Solid lines* indicate the range from the *minimum* to the *maximum* value. *N* number of individuals observed

Experiment investigating social influence

The number of bows performed by individual fawns or yearlings before the demonstration differed significantly from the number of bows they made after the demonstration (generalized linear mixed model, $\chi^2 = 13.70$, $p = 0.0002$): the number of bows was greater after the demonstration (number of bows by each deer per feeding trial: mean ± SD = 0.63 ± 0.53, range 0–1.5) than before the demonstration (0.03 ± 0.08, 0–0.2), but no difference in number of bows was observed between deer sizes ($\chi^2 = 0.32$, $p = 0.57$).

Discussion

Bowing behavior in different areas

Comparing sika deer bowing behavior between different localities revealed that individuals in the busy areas of Nara Park bowed more than those on Miyajima Island. On Miyajima Island, where people generally do not feed deer,

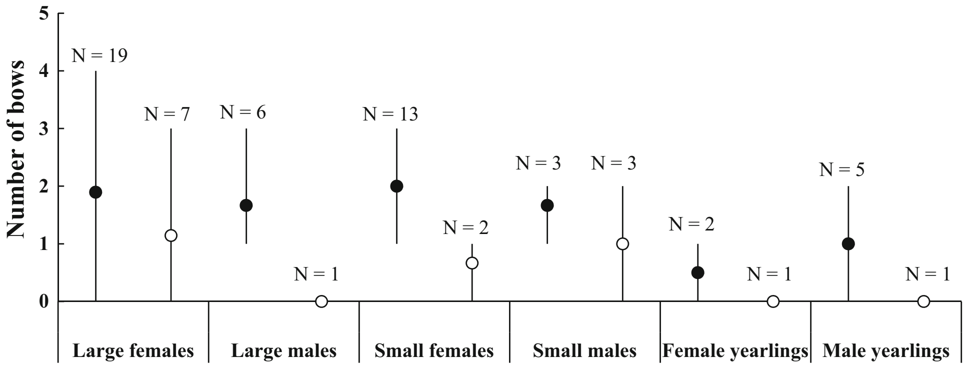

Fig. 4 Number of bows performed by deer in experiment IV in Nara Park. *Circles* indicate the mean number of bows performed in each area (*filled circles*: area A; *open circles*: area B). *Solid lines* indicate the range from the *minimum* to the *maximum* value. *N* number of individuals observed

Table 2 Proportion of individuals that showed up–down movement in bowing response in experiment IV in Nara Park

Area	Sex and size group	Proportion (%)
A	Large males	100 (6/6)
	Large females	92.9 (13/14)
	Small males	100 (3/3)
	Small females	81.8 (9/11)
	Male yearlings	33.3 (1/3)
	Female yearlings	0 (0/1)
B	Large females	100 (4/4)
	Small males	50 (1/2)
	Small females	100 (2/2)

Each individual was classified into one of the six classes by sex and size group

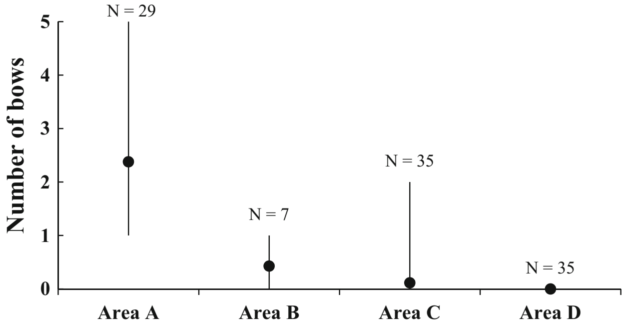

Fig. 5 Number of bows performed by female adults in the feeding experiment on various individuals in Nara Park (areas A and B) and Miyajima Island (areas C and D). *Circles* indicate the mean number of bows performed in each area. *Solid lines* indicate the range from the *minimum* to the *maximum* value. *N* number of individuals observed

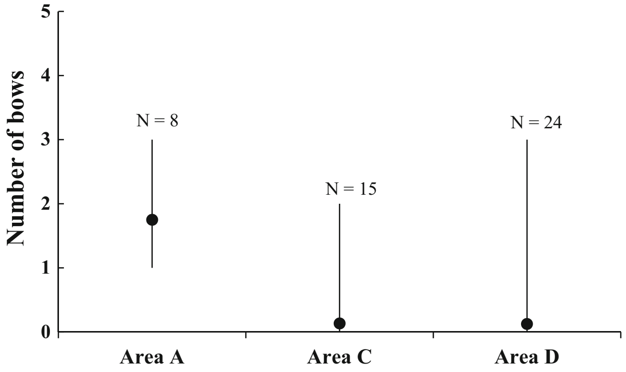

Fig. 6 Number of bows performed by male adults in the feeding experiment on various individuals in Nara Park (area A) and Miyajima Island (areas C and D). *Circles* indicate the mean number of bows performed by individuals in each area. *Solid lines* indicate the range from the minimum to maximum value. *N* number of individuals observed

few individuals—even in busy areas—showed bowing behavior. This result indicates that bowing behavior in sika deer is more developed in the Nara Park population.

We also found local differences in bowing behavior within Nara Park: individuals in (the busy) area A bowed more frequently than did those in (the relatively quiet) area B. Female deer in Nara Park generally congregate in the same areas during the daytime, and move from nighttime to daytime resting sites (Fukunaga and Kawamichi 1975) along almost the same routes each time (Kakizawa and Ando 1978). Moreover, Miura (1977) reported that individual male deer that spend the daytime feeding on deer cookies in area A remained consistent through time. Therefore, it is probable that individuals in areas A and B are separated in such a way that the former are confined to busy areas and the latter to quiet areas. On the other hand, some individuals that occurred in both areas A and B (one large male, small males, male yearlings, and large females) bowed more frequently in busy areas than in quiet areas. This implies that bowing by sika deer in Nara Park depends on human influence and that deer acquire the behavior through encounters with humans.

Age differences in bowing behavior

Experiment IV in Nara Park revealed that large and small adults displayed a greater number of bows than did yearlings, some of which barely bowed at all. Experiment III also showed more frequent bows by yearlings than by fawns. Conversely, experiment IV showed that bowing form differed between age groups: slant movement was more frequent than up–down movement in yearlings than in large adults. Thus, bowing behavior—both bowing frequency and bowing movement—develops with age.

Sexual differences in bowing behavior

In experiment I and experiment II in Nara Park, large females bowed more frequently than large males. Such differences between sexes have also been found in other studies. For example, Lonsdorf et al. (2004) found differences between the sexes in wild young chimpanzees learning to fish for termites at Gombe. Female chimpanzees achieved success on average >2 years earlier than males because infant females spent more time watching termite fishing by adults. In the Nara Park deer, young females remain in female groups that include their mothers even into adulthood, whereas some male yearlings leave the female groups during rutting season (Miura 1978). This suggests that young females have a stronger connection with adult females than do young males. The difference in the number of bows may have been caused by differing degrees of connection with adult females. The same explanation was proposed for a difference between the sexes of dolphins in the learning of feeding strategy from the mother (Man and Sargeant 2003).

Alternatively, the difference between the sexes in the number of bows may be related to differing demands for deer cookies. In Nara Park, competition for deer cookies is common, and males are more successful than females because they are better able to win the struggles that ensue (Kawamichi 1980). Thus, females may have a greater need for food than males. Since standing individuals presumably require food more than those sitting, and they more frequently displayed bowing behavior, we believe that bowing is related to food demand. However, more detailed studies should be conducted to elucidate the relationship between bowing behavior and food demand.

Social influence of bowing behavior

Our experiment revealed that young individuals that never or scarcely performed the bowing behavior enhanced their bowing inclination after observing bowing behavior by adults. This implies that young sika deer in Nara Park learn bowing behavior by observing adults bowing to people giving them deer cookies. However, this learning could be achieved not by imitation but by response facilitation (Byrne 1994), because the probability that the test animal (the observer) already had the bowing behavior in their behavioral repertoire before the demonstration cannot be denied.

Learning (e.g., foraging behaviors and tool use) has been shown in a broad range of taxa (Whiten and Mesoudi 2008). The most common methods with which to examine learning involve comparing between an experimental condition with a trained model and a control condition where no model is available (Stanley et al. 2008; Lefebvre 1986); that is, to compare two populations that have been exposed to different models (Whiten et al. 2005, 2007; Horner et al. 2006). Here, we compared the frequency of a behavior in individuals before and after they observed the same behavior in another, a method that has also been used for primates (Menzel et al. 1972) and birds (Curio et al. 1978a, b). The data we obtained using this method cannot, however, distinguish between the acquisition of novel behavior and facilitation of previously acquired behavior. Thus, an experiment that focuses on test animals (the observers) that have not observed bowing behavior since birth is required to explore this issue.

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