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Author(s): Naofumi Nakagawa, Miki Matsubara, Yukiko Shimooka, and Mari Nishikawa

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Embracing in a Wild Group of Yakushima Macaques (*Macaca fuscata yakui*) as an Example of Social Customs

by Naofumi Nakagawa, Miki Matsubara, Yukiko Shimooka, and Mari Nishikawa

Recently, some primatologists have begun studying social customs, which had been neglected in research despite their importance to human culture. We observed embracing behaviors 64 times during 543.8 hours of focal animal sampling, targeting adult females in a wild group of Japanese macaques in Yakushima, Japan, and compared the results with those in macaques in Kinkazan. Embracing occurred immediately after the spontaneous pause of allogrooming, aggressions, and approach between dyads frequently exchanging antagonistic interactions, all of which are considered to be stressful conditions. Embracing in Yakushima may, therefore, serve to reduce stress; this may also be the case in Kinkazan. Despite this functional similarity, the forms of embracing in Yakushima are slightly different from those in Kinkazan. First, not only ventro-ventral embraces, but also ventro-lateral and ventro-dorsal embraces were found in Yakushima. Second, kneading another's fur by rhythmically opening and closing the palm occurred in Yakushima, instead of a rhythmic, body-rocking movement in Kinkazan. Because we cannot devise genetic or ecological explanations for the subtle local differences in embraces, this type of behavior may be identified as the first evidence for social customs in wild Japanese macaques.

Cultural behavior is defined as behavior that is shared among many group members and is socially, rather than genetically, transmitted from generation to generation (Nishida 1987; Whiten et al. 1999). Because it is difficult to prove social transmission in field studies, however, the following practical evidence for culture has been adopted: (1) the presence/absence of customary behavior among the population (van Schaik et al. 2003; Whiten et al. 1999); (2) the variation of patterns in customary behavior among a population (Panger et al. 2002; Santorelli, Schaffner, and Aureli 2011), both of which cannot be explained by either ecology or genetics (i.e., the "method of exclusion"; Krützen et al. 2006); and (3) the propagation of a newly innovated behavior in a population

(Huffman 1984; Kawai 1965; Matsusaka et al. 2006). However, many studies of animal culture have focused on technological and/or subsistence behaviors, such as tool use and extractive foraging (Panger et al. 2002; van Schaik et al. 2003; Whiten et al. 1999). By contrast, many aspects of human culture—such as social customs, religion, and institutions—are scarcely related to technological and/or subsistence behaviors (Richerson and Boyd 2005).

Recently, some cultural primatologists (*sensu* McGrew 1998) have begun studying neglected social customs: (1) the presence/absence of hand-clasp grooming (McGrew and Tutin 1978), social scratching (Nakamura et al. 2000), and other behaviors (see Nakamura and Nishida 2006) in chimpanzees; building nests for social play, kiss-squeaking with leaves/hands in orangutans (van Schaik et al. 2003); hand sniffing and finger-in-mouth games in white-faced capuchins (Perry et al. 2003); stone-banging displays in tufted capuchins (Moura 2005); stone-throwing displays in bearded capuchins (Faóitico and Ottoni 2013); kissing, false branch shaking, and others in Geoffroy's spider monkeys (Santorelli et al. 2011); and hand-holding communicative gestures in black howlers (Brockett et al. 2005); (2) variation of patterns in hand-clasp grooming (McGrew et al. 2001; Nakamura and Uehara 2004) and social scratching (Nishida, Mitani, and Watts 2004) in chimpanzees; and (3) the propagation of newly innovated hand-clasp grooming in chimpanzees (Bonnie and de Waal

Naofumi Nakagawa is Associate Professor at the Graduate School of Science of Kyoto University (Kitashirakawa-Oiwakecho, Sakyo, Kyoto 606-8502, Japan [nakagawa@jinrui.zool.kyoto-u.ac.jp]). **Miki Matsubara** is Adjunct Lecturer at Chukyo University (Yagotohonmachi 101-2, Shouwa, Nagoya, Aichi 466-8666, Japan). **Yukiko Shimooka** is Lecturer in the Faculty of Life and Environment Sciences of Teikyo University of Science (Yatsusawa 2525, Uenohara, Yamanashi 409-0193, Japan). **Mari Nishikawa** is Office Assistant at the Graduate School of Science of Kyoto University (Kitashirakawa-Oiwakecho, Sakyo, Kyoto 606-8502, Japan). This paper was submitted 17 II 14, accepted 10 IV 14, and electronically published XX I 15.

2006; de Waal and Seres 1997); eye covering gestures in mandrills (Laidre 2011); and social styles of low aggression/high affiliation in savanna baboons (Sapolsky 2006).

When compared to subsistence behaviors (Caldwell and Whiten 2006; Whiten and van Schaik 2007), social behaviors are less susceptible to the criticism that they were simply an adaptation to local environmental conditions due to their seemingly arbitrary nature (Laland and Hoppitt 2003; Perry and Manson 2003). When it comes to social behaviors exchanged concurrently and symmetrically (such as hand-clasp grooming in chimpanzees), kinesthetic social learning (de Waal and Seres 1997) or even molding (Nakamura and Nishida 2013), rather than observational learning, is likely to occur. “Initially, naïve individuals gain proprioceptive feedback while participating in grooming hand-clasp with an experienced partner, and then translate this into grooming hand-clasp with others” (Bonnie and de Waal 2006:33).

Shimooka and Nakagawa (2014) found an unreported “rocking-embrace” in a wild group of Japanese macaques (*Macaca fuscata fuscata*) living in Kinkazan Island, northern Japan. This behavior involves one individual ventro-ventrally encircling another individual, with both arms around each other in the sitting position, and rhythmically rocking their bodies back and forth; this may serve a sort of tension-reduction function. Recently, we have found behaviors whose functions seem to be similar, but whose motor patterns are slightly different, in a wild group of subspecies of Japanese macaques (*M. fuscata yakui*, hereafter, Yakushima macaques), living in Yakushima Island in southern Japan. No one has previously recognized this behavior, despite a number of researchers having been conducting field research on Yakushima macaques since the start of long-term, continuous observations in 1975 (Yamagiwa, Izawa, and Maruhashi 1998).

Stone handling is a well-known nonsubsistence culture behavior among Japanese macaques. Its presence/absence, the variation of patterns among groups and/or local populations (Leca et al. 2007), the propagation in a population (Huffman 1984), and its mechanisms of transmission (Leca et al. 2010) have been thoroughly scrutinized (see Huffman et al. 2010 for a review). However, stone-handling behavior is solitary play that is only found in provisioned groups, rather than social behavior in unprovisioned wild groups. On the other hand, all the candidates of social customs were also found in provisioned groups, including presence/absence of nonsexual alpha-male mounting on females and ordinary male-male mountings (Kawamura 1965); the variation of patterns in courtship gestures and postures of males and females (Stephenson 1973); the context of contact-call emissions (Sakura 1989); and newly innovated stone-grooming (Weinberg and Candland 1981). Provisioning gives macaques free time, allowing them to devote less time to feeding, and is likely to enhance the frequency of newly innovated behaviors, such as stone handling (Leca et al. 2008).

In this paper, we describe the forms and context of occurrences of embracing in Yakushima and compare them to

those in Kinkazan. Then, we discuss the significance of these findings, along with preliminary information about the presence/absence of this behavior in other populations, with special reference to culture. Thus, we provide the first evidence for cultural differences in wild unprovisioned Japanese macaques.

Methods

Study Sites and Subjects

We conducted field research from September 15 to December 19, 2005, and from October 15 to November 26, 2006, on the northwest coast of Yakushima (31°N, 131°E), a mountainous island of 503 km² located 70 km offshore of Kyushu, Japan (for location, see fig. 1). The mean annual temperature is about 21°C, and the annual rainfall is about 2,600 mm. The research site is covered with warm, temperate evergreen forests. The study troop was the E group of the Yakushima macaques. All the members of E group had been individually identified and habituated to human observers without pro-



Figure 1. Locations of the present study site of Yakushima Island, and of other long-term study sites where information on the presence/absence of embracing was obtained. *Triangle*: wild unprovisioned population; *circle*: provisioned population; *solid*: population where embracing was observed in at least one group; *open*: population where embracing has not been observed. Sources: Shimokita, Hakusan (Izawa 2010); Kinkazan (Shimooka and Nakagawa 2014); Arashiyama, Katsuyama, Takasakiyama (Nakagawa, Nakamichi, and Yamada 2011), Yakushima (this study).

visioning since 2004 (Nishikawa, Suzuki, and Sprague 2014). The age-sex composition of the E group was as follows: 2 adult males, 4 adolescent males, 7 adult females, 12 juveniles (all but 2 being females), and 1 infant female, totaling 26 individuals as of September 15, 2005; 2 adult males, 5 adolescent males, 8 adult females, 10 juveniles (all but 1 being females), and 5 infants (3 males and 2 females), totaling 30 individuals as of October 16, 2006, since 1 adolescent male and 1 juvenile male emigrated, 2 adolescent males immigrated, 1 adult female disappeared, 2 juvenile females sexually matured, and 5 infants survived out of 6 infants born. All the animals were individually identified. Mother-daughter, sisters, and grandmother-granddaughter were defined as kin with $r \geq 0.25$ in this study.

Comparative data were given by Shimooka and Nakagawa (2014) from a wild group (deemed the A group) of the Japanese macaques in Kinkazan, a small island of 10 km² (38°8'N, 141°4'E), located 700 m offshore from Honshu, and ca. 1,300 km northeast of Yakushima (see fig. 1). The mean annual temperature is about 11°C, and the annual rainfall is about 1,500 mm. The island is covered with cool, temperate, deciduous forests (for further details of vegetation at both sites, see Agetsuma and Nakagawa 1998).

Data Collection

This study targeted embracing, which we defined as a behavior wherein one individual encircles another with both arms in the sitting position. This behavior was always accompanied by lip smacking as a facial expression and, sometimes, a girney call (*sensu* Green 1975b). Lip smacking and girneys have been considered to serve as a way to reduce social tension (Itani 1963; Mori 1975).

Five (MN, TK, NC, GN, and DM) of 7 adult females were chosen as focal animals (Altmann 1974) in 2005. In place of TK, who had disappeared, another adult female, KE, was added to the focal animals in 2006. PN was excluded from focal animals in both years due to her old age. The focal animal sampling time per individual, in hours, was (mean $\pm$ SD = 94.9 $\pm$ 28.8, n = 6; for details, see table 1). Continuous sampling was used for embracing and antagonistic interactions (supplanting, threatening, lunging, chasing, and biting). Instantaneous sampling at 1-minute intervals was used for grooming interactions. Times of occurrence of each behavior for each participants were recorded. The study period coincided with the mating season. Estrus condition of adult females in the E group was judged based on their copulation or copulatory plug.

Comparative data from Kinkazan A group were collected through either the behavior sampling (Martin and Bateson 1990) or the sequence sampling method (Altmann 1974) in October 1997 (mating season; for details, see Shimooka and Nakagawa 2014).

Table 1. Focal animals and sampling time (in hours)

Name	2005		2006	
	Anestrus	Estrus	Anestrus	Estrus
MN ^a	26.5	21.2	25.0	0
TK	22.9	62.9	—	—
KE	—	—	16.9	50.8
NC ^a	30.8	12.3	31.7	32.7
GN	7.1	31.7	22.0	28.6
DM	17.0	56.6	36.6	36.0

^a MN is supposed to be a mother of NC.

Data Analyses

We compared the forms and contexts of embracing occurrences in Yakushima to those in Kinkazan. Although statistical analyses could not be undertaken due to the differences in sampling methods, we showed that the functions of embracing seemed similar in both groups, but posited that its different forms may be explained by culture.

Frequency of interaction between *A* and *B* is given by $[F_A(B) + F_B(A)] / [F(A) + F(B)] \times 100$. $F_A(B)$ or $F_B(A)$ is the total number of cases of embracing or antagonistic interactions or of sampling points of grooming interactions with *B* while *A* was followed, or with *A* while *B* was followed, respectively. $F(A)$ or $F(B)$ is the total focal animal sampling time of *A* or *B*.

Excel Statics was used to conduct the Wilcoxon signed-rank and the Kendall's rank correlation tests to examine the effect of estrus condition on the frequency of embracing and to examine the correlation between the dyadic frequency of antagonistic behaviors and that of embracing, respectively.

Results

Distribution and Forms of Embracing

We observed the embracing of macaques 88 times over some 569.1 hours of focal animal sampling. No significant differences were found in the frequency of embracing between anestrus and estrus conditions of each focal animal (Wilcoxon signed-rank test, z = 1.57, p = 0.12, two-tailed). The mean frequency of embracing was 0.16 ($\pm$ 0.13 SD, n = 6) per hour.

Table 2 shows the number of cases of the observed embracing in each participant dyad. Of the 88 cases of the behavior, 65 cases (74%) saw partners of the embrace in focal adult females to be adult females (24% of all possible partners in both 2005 and 2006), 22 cases (25%) saw partners to be juvenile females (40% and 31% of all the possible partners in 2005 and 2006, respectively), and 1 case of an adult males partner (alpha male). No non-alpha males, irrespective of age class, were involved in embraces with focal adult females. In 22 (27%) out of 83 cases between identified females, embracing occurred between maternal kin-related individuals,

Table 2. Number of observed cases of embracing in each participant dyad

Name	Age ^a	Sex ^b	MS	MN	MK	TK	TM	TR	KE	KT	NC	NJ	GN	PN	PK	DM	DB	UN ^c
MS	Adu	M		1	—	0	—	—	0	—	0	—	0	—	—	0	—	0/0
MN ^d	Adu	F	0		1 ^c	15	0	0/1	4	0	8 ^c	0 ^c	0	0	0/0	0	0	0/2
MK	Juv	F	—	0 ^c		0	—	—	0	—	4 ^c	—	0	—	—	0	—	—
TK ^d	Adu	F	0	7	0		0 ^c	1/0 ^c	3	0	3	0	0	0	0/0	0	0	0/0
TM	Juv	F	—	0	—	0 ^c		—	1	—	0	—	0	—	—	0	—	—
TR	Juv/Adu	F	—	0/1	—	1/— ^c	—		0/0	—	3/1	—	0/0	—	—	0/1	—	—
KE ^d	Adu	F	0	1	0	1	0	0/0		0 ^c	23	0	0	0	0/0	2	0	1/0
KT	Juv	F	—	0	—	0	—	—	—	—	3	—	0	—	—	0	—	—
NC ^d	Adu	F	0	3 ^c	2 ^c	1	0	2/1	13	1		2 ^c	0	0	0/0	0	0	1/0
NJ	Juv	F	—	0 ^c	—	0	—	—	0	—	2 ^c		0	—	—	0	—	—
GN ^d	Adu	F	0	0	0	0	0	0/0	0	0	0	0		1 ^c	0/1 ^c	0	0	0/0
PN	Adu	F	—	0	—	0	—	—	0	—	0	—	1 ^c	— ^c	—	0	—	—
PK	Juv/Adu	F	—	0/0	—	0/0	—	—	0/0	—	0/0	—	0/1 ^c	— ^c	—	1/0	—	—
DM ^d	Adu	F	0	0	0	0	0	0/1	2	0	0	0	0	0	1/0		4 ^c	0/0
DB	Juv	F	—	0	—	0	—	—	0	—	0	—	0	—	—	1 ^c		—
UN ^c	Juv/Adu	F	—	0/1	—	0/0	—	—	1/0	—	1/0	—	0/0	—	—	0/0	—	—

Note. Above and to the right of the diagonally blank cells is the entire data set; below and to the left of the diagonally arranged blank cells is the subset where embracing occurred immediately after approaching.

^a Adu: adult; Juv: juvenile; Juv/Adu: Juvenile in 2005 matured to adult in 2006. In columns for animals labeled Juv/Adu, the number before and after the slash (/) shows the value at juvenile and adult age class, respectively.

^b M: male; F: female.

^c UN: Unidentified individuals.

^d Focal animals

^e Estimated kin-related ($r \geq 0.25$) individuals.

which were composed of 16% and 19% of all the dyads among identified females in 2005 and 2006, respectively.

Table 3 summarizes the forms of embracing in Yakushima in comparison to those in Kinkazan. Embracing was always accompanied by lip smacking, and sometimes, girney calls. The Yakushima macaques embraced in one of three positions. Out of 82 cases where the positions were recorded, two individuals encircled each other ventro-ventrally with their arms around each other in 31 cases (38%); one encircled the other with both arms from her lateral in 50 cases (61%); one encircled the other with both arms from her backward in a single case. Unusually, we found the Yakushima macaques to knead one another's fur by rhythmically opening and closing their palms during the embrace (fig. 2).

Contexts of Occurrence of Embracing Behavior

Table 4 shows the behaviors immediately preceding the embrace. Out of 65 cases between adult females, we found 11 (17%) cases of spontaneous pause of allogrooming, 18 (28%) cases of antagonistic behaviors between participants involved in embracing or those between one of the two participants involved in embracing and a third party; 34 (52%) cases of approaching were preceded by neither allogrooming nor antagonistic behaviors.

With regards to embraces between focal adult females that were exhibited immediately after approaching, and were preceded by neither allogrooming nor antagonistic behaviors, the correlation between the dyadic frequency of embracing and that of antagonistic behaviors was also examined (fig. 3). The

more frequently the dyad was involved in antagonistic behaviors, the more frequently it exhibited embracing behaviors ($n = 15$, $\tau = 0.53$, $p = 0.01$, one-tailed). Since most of the embracing shifted to allogrooming (see below), the dyad exhibiting the embracing behavior was regarded as the dyad exhibiting allogrooming. In other words, the dyad that never exhibits allogrooming was regarded as the dyad that never embraces. When we removed the dyads that never exhibit allogrooming from the analysis, the Kendall's τ rank correlation coefficient grew to 0.60 ($n = 11$, $p = 0.01$, one-tailed).

Table 5 shows the behaviors immediately after the embrace. Of 62 cases between adult females in which behaviors immediately following the embrace could be identified, 51 (82%) cases shifted to allogrooming. Upon the inclusion of seven cases where likely subsequent allogrooming was interrupted by a third party, this value grew to 94%.

Discussion

Similarities in Context of Occurrences and Function of Embracing Behaviors between Yakushima and Kinkazan

Although quantitative comparisons could not be conducted as a result of different methods of data collection, main behaviors not only immediately preceding the embrace (i.e., spontaneous pause in allogrooming, antagonistic behaviors, and approaches that were not preceded by the former two behavior; see table 4), but also immediately following it (i.e., allogrooming; see table 5), were quite similar between Yak-

Table 3. Summary of forms of embracing in Yakushima in comparison to those in Kinkazan

	Yakushima	Kinkazan ^a
Mean frequency	0.16/hr (88/569.1 hr) ^b	0.48/hr (88/183 hr) ^c
Mean duration	Not measured but much shorter than duration in Kinkazan	17 s (range = 4–46)
Position of embracing	Ventro-ventral, ventro-lateral or ventro-dorsal	Ventro-ventral
Rocking movement of the body	No	Yes
Lip smacking	Yes	Yes
Girney call	Yes (sometimes)	Yes (sometimes)
Open-close movement of the palm	Yes	No

^a Data from Shimooka and Nakagawa (2014).

^b Focal animal sampling.

^c Behavior sampling and sequence sampling.

ushima and Kinkazan. Given that non-kin-related grooming partners in Kinkazan embraced more frequently than kin-related ones after such approaches, Shimooka and Nakagawa (2014) concluded that embracing in Kinkazan may have occurred under stressful conditions, and could function as a mechanism to reduce tensions. We could not examine the differences in frequency of embracing between kin and non-kin (see fig. 3), since only one kin dyad (MN and NC) was present among the focal animals. Instead, significant positive correlations were found between the dyadic frequency of embracing and that of antagonistic behaviors: the more frequently the dyad was involved in antagonistic behaviors, the more frequently it exhibited embracing. Given that proximity to dominant or unfamiliar individuals induced stressful conditions (Kutsukake 2003; Manson and Perry 2000; McDougall 2011; Pavani et al. 1991; Schino et al. 1990), embracing behavior in Yakushima was likely to have occurred under stressful conditions, and could serve the function of reducing social tension. This may also be the case in Kinkazan.

Subtle Differences in Embracing Behavior between Yakushima and Kinkazan as Evidence of Social Customs

Despite the aforementioned functional similarities, however, embracing behaviors in Yakushima were slightly different from those in Kinkazan (see table 3). First, not only ventro-ventral embracing, but also ventro-lateral and ventro-dorsal embracing were found in Yakushima. Second, kneading another's fur by rhythmically opening and closing the palm occurred, instead of a rhythmic, body-rocking movement.

Shimooka and Nakagawa (2014) mentioned that ventro-ventral embraces—a behavioral component of embracing in Kinkazan—were shared with other macaque species, while rocking the participant's body back and forth (another component of embracing) was not. On the other hand, overall behavioral components of embracing in Yakushima seemed to be shared with other species of macaques. It has been reported that ventro-ventral embracing accompanies kneading the other's fur in Tonkean (Thierry 1983), rhesus (Maestripieri and Wallen 1997), Barbary (Hesler and Fischer 2007), pigtail, and stump-tailed macaques (Maestripieri 2007). Moreover, embracing in ventro-lateral and ventro-dorsal po-

sitions seems to be equivalent to variations of a “hug” in Sulawesi macaques. The ethograms of the social behavior of Sulawesi macaques (Thierry et al. 2000:211) defined “hug” as follows: “An individual passes one or both hands, or one or both arms, around the body of another in multiple combinations. There may be a simultaneous grasping of the fur. Ventro-ventral contact is excluded. This is an affiliative contact that may be accompanied by lip smack.”

Such a behavioral similarity between Yakushima macaques and rhesus macaques, the closest allied species to Japanese macaques (Marmi et al. 2004), may possibly imply that Yakushima macaques are genetically closer to rhesus macaques than are the macaques in Kinkazan. However, genetic data show that Japanese macaques form a monophyletic group and can be differentiated from rhesus macaques (Hayasaka et al. 1988; Nozawa et al. 1977). Moreover, no genetic evidence has supported the validity of subspecies status for Yakushima macaques (Hayasaka et al. 1988; Kawamoto et al. 2007; Marmi et al. 2004; Nozawa et al. 1977). Although much longer hair lengths than those expected from the latitude of Yakushima (31°N)—one of the morphological pieces of evidence for a subspecies of Yakushima macaques (Hamada and Yamamoto 2010)—may enable them to knead each other's fur quite easily, this explanation does not seem to be related to the behavioral difference between Yakushima macaques and the macaques in Kinkazan belonging to a higher latitude (38°8'N) than Yakushima. Geographical cline in hair lengths, along with hair density, can be explained by adaptation to cold climates for increasing heat insulation (Hamada and Yamamoto 2010). Additionally, other climatic (Yamagiwa, Izawa, and Maruhashi 1998), ecological (Agetsuma and Nakagawa 1998; Maruhashi, Saito, and Agetsuma 1998), and socio-ecological differences (Nakagawa 1998; Saito et al. 1998; Takahashi and Furuichi 1998; see also Nakagawa 2010) between the Yakushima and Kinkazan populations have been found. Nevertheless, we cannot devise any genetic or ecological explanations for subtle, local differences in embracing, as might be the case with subtle behavioral variations in chimpanzees, including social ones (Nakamura and Nishida 2006). Chimpanzees at Mahale, Tanzania, engage in hand-clasp grooming, while those at Gombe, Tanzania (170 km to the north) engage in branch-clasp

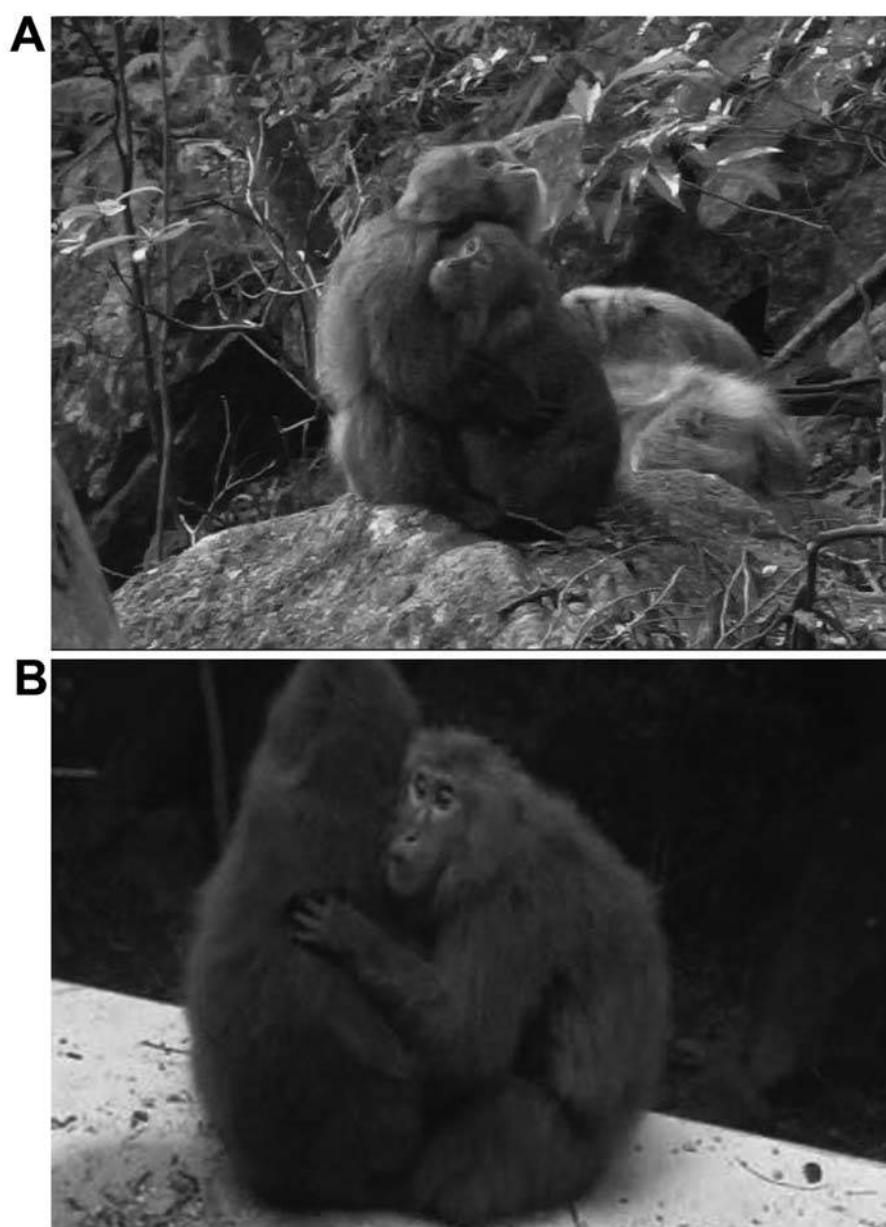


Figure 2. Embracing between an adult male and an adult female in a ventro-ventral (A) and between adult females in a ventro-lateral position (B). Note that A was from an unidentified group, while B was from E group (captured from video footage of ESMs 1 and 2, respectively, which were filmed by Nishikawa. ESM 1: Embracing between an adult male and an adult female in a ventro-ventral position in Yakushima Island; ESM 2: Embracing between adult females in a ventro-lateral position in Yakushima Island. A color version of this figure and both videos are available online.

grooming (McGrew and Tutin 1978). Chimpanzees at Ngogo, Uganda, scratch by using their fingers to “poke” the body of their partners, while those at Mahale use flexed fingers to “stroke” the body (Nishida, Mitani, and Watts 2004). Therefore, we posit that the local difference in embracing between Yakushima and Kinkazan macaques may be a cultural difference in social customs.

Presence/Absence of Embracing Behavior among Population as Evidence for Social Customs

Izawa (2010) observed embracing behaviors not only in Kinkazan, but also in two other wild unprovisioned populations: Shimokita and Hakusan (see fig. 1). Nakagawa, Nakamichi, and Yamada (2011) obtained the negative information on

Table 4. Behaviors immediately prior to embracing in Yakushima, compared to those in Kinkazan

Behaviors ^a	Yakushima	Kinkazan ^b
Approach	34 (46)	42 (44)
Spontaneous pause of allogrooming:		
Between participants involved in embracing	8 (11)	8 (10)
Between 1 of the 2 participants involved in embracing and a third party	3 (5)	0 (0)
Intervention of allogrooming by a third party	0	5 (5)
Embracing	1 (1)	0 (0)
Just sitting aside	1 (1)	0 (0)
Aggression:		
Between participants involved in embracing	9 (10)	5 (5)
Between 1 of the 2 participants involved in embracing and a third party	9 (14)	2 (2)
Lactating	0 (0)	0 (1)
Unknown	0 (0)	16 (21) ^b
Total	65 (88)	78 (88)

Note. The number of cases of embracing between adult females is shown. The total number of cases is shown in parentheses.

^a Four cases of “aggression between a pair of third parties” in Kinkazan were categorized as “Unknown” in this table, since “aggression between a pair of third parties” was not a target for data collection in Yakushima.

^b Data from Shimooka and Nakagawa (2014).

embracing in the provisioned Japanese macaques at three long-term study sites: Arashiyama, Katsuyama, and Takasakiyama. Questionnaires on infrequently observed behavior in Japanese macaques were given to primatologists undertaking yearlong or longer field research at each site who were shown video footage (to assist in the identification of behaviors) of two locally different embracing behaviors. As a result, no one confirmed embracing in all these three provisioned groups (Nakagawa, Nakamichi, and Yamada 2011).

The sole negative reliable evidence in unprovisioned groups comes from Tatsuro Kawazoe (personal observation cited in Izawa 2010), who conducted field studies for at least 6 years, targeting a C2 group at Kinkazan. Kawazoe never observed the embracing exhibited by the members of the C2 group. Judging from the history of fissions of the six groups at Kinkazan (Izawa 2009), along with the presence of embracing in each group, including two mother groups of B1/B2 and C1/C2 (fig. 4), the most likely scenario is that embracing had been acquired in the original mother group and transmitted from generation to generation, even after group fissions, because this behavior hardly ever occurred in adult males that transferred across groups. Finally, embracing behavior disappeared in the C2, and possibly C1, groups. Absence of embracing in the C2 group is evidence against the genetic determination of embracing and relevance of the absence of embracing to provisioning. With regard to Yakushima, the absence of embracing or presence of the other form of em-

bracing in other groups of Yakushima macaques would provide strong evidence of social custom.

In contrast to the subtle behavioral differences mentioned above, it is possible that the presence/absence of embracing was caused by factors such as social tension, since embraces serve the function of tension reduction. However, embracing as a tactile signal is redundant (*sensu* Partan and Marler 1999), since its accompanying lip smacking (as a visual signal) and girneys (as auditory signals) also serve equivalent functions (Shimooka and Nakagawa 2014). Although further study is needed to confirm this, particular factors of social tension may not be needed to explain the interpopulation or intergroup differences in the presence/absence of embracing.

Propagation of Embracing Behavior as an Evidence for Social Customs

Regrettably, the process used to propagate embracing is unknown. Nakagawa first noticed unreported embracing in the A group of Japanese macaques at Kinkazan in October 1984 (unpublished data), about one and a half years after the start of long-term, continuous observations of this population by Kosei Izawa and his students (Yamagiwa, Izawa, and Maruhashi 1998). In addition, Izawa (2010) reported, in 1982, the first observation of embracing behavior during the A group's habituation process (see fig. 4).

In March 2004, Nishikawa happened to notice embracing during the field studies in the E group of the Yakushima macaques. No one had yet reported this, although a number of researchers had conducted field research on Yakushima macaques since the start of long-term, continuous observations in 1975 (Yamagiwa, Izawa, and Maruhashi 1998). We confirmed that embracing had already spread among all the adult females of each group in December of 1984 (Nakagawa unpublished data for Kinkazan) and in September of 2004 (Nishikawa unpublished data for Yakushima). This value satisfies the condition enough to call it “customary,” for which

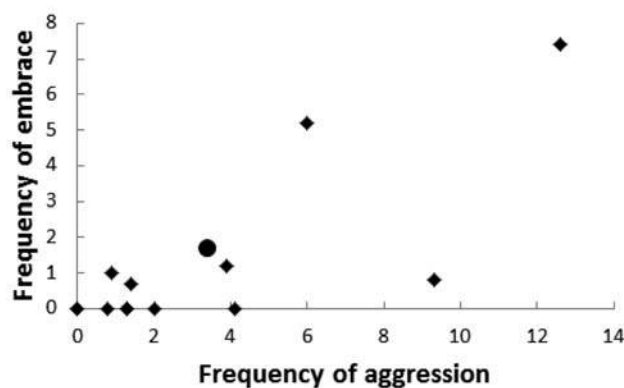


Figure 3. Relation between the dyadic frequency of embracing (per 100 hr) and that of antagonistic behaviors (per 100 hr). Circle: mother (MN)–daughter (NC) dyad.

Table 5. Behaviors immediately after the embracing in Yakushima in comparison to those in Kinkazan

Behaviors	Yakushima	Kinkazan ^a
Allogrooming	51 (66)	66 (73)
Embracing	0 (1)	3 (3)
Being driven away by a third party	7 (10)	5 (5)
Leaving	4 (5)	3 (4)
Just sitting aside	0 (1)	0 (1)
Unknown	3 (5)	1 (2)
Total	65 (88)	78 (88)

Note. The number of cases of embracing between adult females is shown. The total number of cases is shown in parentheses.

^a Data from Shimooka and Nakagawa (2014).

the behavior occurs in all, or most, able-bodied members of at least one age-sex class (*sensu* Whiten et al. 1999). As for durability of the behavior, other conditions for the culture (McGrew and Tutin 1978), Shimooka and Nakagawa (2014)) and Nakagawa (personal observation) confirmed the presence of embracing in the Kinkazan A group in October 1997 and March 2014, respectively. The most recent confirmation of embracing in the Yakushima E group was made in March 2014 by Nishikawa (personal observation). Thus, social customs of embracing occurred in each group, for at least 29 (Kinkazan A group) and 9 years (Yakushima E group), respectively.

The First Evidence for Cultural Differences in Social Customs in Wild Unprovisioned Populations of Japanese Macaques

Although sweet-potato washing and stone handling are textbook examples of cultural behaviors in Japanese macaques, these are subsistence behaviors and nonsubsistence solitary play behaviors, rather than examples of social behavior. In addition, sweet-potato washing and stone handling behaviors stem from the provisioning situation. Needless to say, sweet-potato washing has never occurred without the provision of sweet potatoes to the monkeys. Leca et al. (2008) hypothesized that the increase in the monkeys' free time through provisioning may have been the origin of stone handling. McGrew and Tutin (1978) pointed out that many cultural behaviors exhibited by Japanese macaques result either directly (e.g., sweet-potato washing, wheat-placer mining) or indirectly (e.g., snowball making, hot-spring bathing, and ladder-and-piton use) from provisioning. The sole evidence where it is difficult to see causation of provisioning is the interpopulation difference in the context of uttering a contact call (Sakura 1989). The local differences in embracing behaviors that we found were the first evidence of cultural differences in wild unprovisioned Japanese macaques.

Our data in this study, as well as our companion paper (Shimooka and Nakagawa 2014), were collected during the mating seasons of two groups, from two different populations. Given the function of embracing, a seasonal change in the behavior is expected in accordance with changes in social

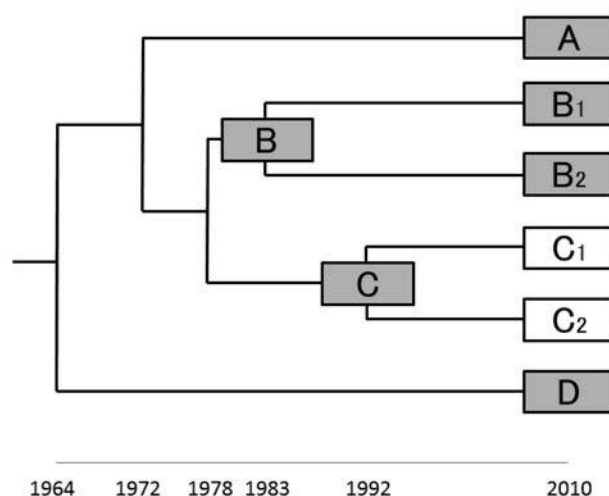


Figure 4. Groups where information on the presence/absence of embracing was obtained and chronology of group fissions in Kinkazan. *Shaded*: group where embracing was observed; *open*: group where embracing has not been observed. Sources: A group (Shimooka and Nakagawa 2014, Izawa 2010); B, B₂, C, and D groups (Izawa 2010), B₁ group (Isaji 2010; Izawa 2010); C₁ (Kiyomasa Miki, personal communication cited in Izawa 2010); C₂ (Tatsuro Kawazoe, personal communication cited in Izawa 2010); chronology of group fissions (Izawa 2009).

stress. Considering the plasticity of embracing, patterns of embracing will vary across groups in a population, as is the case with stone handling in Japanese macaques (Leca et al. 2007) and hand-clasp grooming in chimpanzees (McGrew et al. 2001). Nakamura and Uehara (2004) examined whether consistent behavioral patterns were observed at an individual level to investigate the proximate factors for different patterns of hand-clasp grooming in chimpanzees. In the future, such an analysis can be conducted in the E group of Yakushima macaques that exhibit three types of embracing at the group level: ventro-ventral, ventro-lateral, and ventro-dorsal.

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Comments

Kristin E. Bonnie

Department of Psychology, Beloit College, 700 College Street, Beloit, Wisconsin 53511, U.S.A., and Lester E. Fisher Center for Study and Conservation of Apes, Lincoln Park Zoo, Chicago, Illinois 60614, U.S.A. (bonniek@beloit.edu). 1 IX 14

Social customs are ubiquitous across human cultures. But, the habits we learn from others (de Waal 2001) or “the way we do things” (McGrew 2004) can be so engrained in our everyday behavior that we are sometimes unaware of their significance until we encounter people for whom customs differ from our own. These cultural differences, whether subtle or extreme, have been documented by cultural anthropologists through detailed ethnographies (e.g., Mead 1928), and used to explain psychological processes from cognition to child development (e.g., Heine 2011).

Although the ethnographic method is not without flaws (Aunger 1995), objective observation and detailed description provide the necessary foundation for understanding the behavior of individuals and groups. But, whether it is a valid tool for studying social customs and other cultural behaviors in nonhuman primates has been debated. Ingold (2001), for example, argued that the ethnographic method cannot be applied to the study of nonhuman primates because it “fails to achieve an understanding that is sensitive to the intentions and purposes of the people themselves, to their values and orientations, to their ways of perceiving, remembering, and organizing their experience, and to the contexts in which they act” (337). More recently, Laland and Janik (2006) have argued that the ethnographic method is weak for both conceptual and interpretive reasons. In particular, Laland and Janik criticize the method of exclusion, through which genetic and ecological explanations for patterns of behavior must be ruled out, yet has been the primary method of recognizing cultural behaviors in nonhuman primates for at least the last 15 years. In recent years, enhanced phylogenetic analysis (e.g., Lycett, Collard, and McGrew 2007, 2009), improvements in detailed genetic analyses of primate groups (e.g., Langergraber et al. 2011) and focused ecological studies specific to purported cultural behaviors (e.g., Gruber et al. 2012; Koops, McGrew, and Matsuzawa 2013) have contributed to the debate.

Yet, as Nakagawa et al. point out, the majority of studies reporting on, or examining the innovation and transmission (via social learning) of, cultural behaviors in primates have focused on food-related (Watson and Caldwell 2009) and technological/subsistence behaviors for which the method of exclusion may be a more relevant tool. Thus, I agree with Nakagawa et al. that “social behaviors are less susceptible to the criticism that they were simply an adaptation to local environmental conditions due to their seemingly arbitrary nature.” Moreover, as with the customs that are definitive of human cultures, social customs often go unnoticed to ob-

servers familiar to the group (Nakamura and Nishida 2006), but are not any less important to our understanding of the evolution of culture.

Nakagawa and colleagues provide a welcomed report on social customs among nonhuman primates. Importantly, this research adds breadth to a literature that is mostly dominated by reports of social customs in one species—chimpanzees (for exceptions, see works cited in target article). Together with the recent paper by van Leeuwen et al. (2014) describing the “grass in ear” behavior of chimpanzees, the study by Nakagawa et al. should serve as reminder that to fully understand cultural behavior patterns we must not forget the root of cultural primatology and to look for the often subtle ways in which group-living individuals do things, even if the exact purpose cannot be determined.

Jean-Baptiste Leca

Department of Psychology, University of Lethbridge, 4401 University Drive, Lethbridge, AB T1K 3M4, Canada (jeanbaptiste.leca@uleth.ca). 1 IX 14

Arbitrary Cultural Behavior Patterns Are Not Unique to Humans

While there is increasing evidence for cultural variation in a wide range of animal taxa, some behavioral domains are far more represented than others in the literature. On the one hand, there are numerous examples of animal material culture, including food preferences, food processing techniques, tool use, and medicinal plant use. On the other hand, reports on animal social culture, such as communicative rituals, courtship displays, allogrooming patterns, social play behaviors, and interspecific interactions, are relatively rare (reviewed in Frigaszy and Perry 2003; Laland and Galef 2009). By providing additional data to the latter, the study by Nakagawa and his colleagues is a timely and important contribution to the field of cultural primatology. Their findings have the potential to fuel the debate between evolutionary biologists who claim that culture is present in thousands of species (Lumsden and Wilson 1981) and sociocultural anthropologists who argue that “animal behavioral traditions” and “human culture” should be considered analogous rather than homologous because the content of what is transmitted is radically different (i.e., simple food-related utilitarian behavioral patterns versus elaborate social norms/conventions and ceremonial/symbolic customs based on complex beliefs; Hill 2009).

In nonhuman animals, material and social cultures differ in several ways. The former involves physical objects (e.g., food items, plant materials, and tools) that are used in subsistence-related contexts (e.g., feeding, self-medication) via the expression of adaptive behaviors that are reinforced by direct benefits to the performers and become the primary targets of natural selection. Thus, the form and sequence of

the motor patterns found in animal material culture are generally nonarbitrary. For example, efficient nut-cracking behavior requires the combination of specific objects with precisely coordinated and hierarchically organized behavioral patterns (Inoue-Nakamura and Matsuzawa 1997; but see Leca et al. 2011 for a notable example of arbitrary material culture in nonhuman animals).

The latter involves social interactions whose usage is far less obvious, as they occur in the context of social conventions or playful activities (reviewed in Nakagawa et al.). Apparently, these interactions are not reinforced by direct benefits to the performers, and therefore, they may not be the primary targets of natural selection. As such, they can be categorized as nonadaptive cultural behaviors. Relaxed functional constraints on social culture generally result in flexible and arbitrary behavioral patterns. Indeed, contrary to stone tool use, there are no optimal hand-clasp grooming postures in chimpanzees (cf. McGrew et al. 2001) and no possible “mistake” in expressing social greetings through hand sniffing, eye poking, or any other social games observed in white-faced capuchins (cf. Perry et al. 2003). According to Stephenson (1973), behavioral arbitrariness is usually a function of individual experience, but can also be influenced culturally through social interactions with other group members. Despite Nakagawa et al.’s (undemonstrated) claim that embracing behavior in Japanese macaques may serve to reduce social stress, this social custom is not likely to affect survival or reproductive success. Arguably, the apparent lack of direct fitness consequences and the arbitrariness of embracing positions (i.e., ventro-ventral, ventro-lateral, and ventro-dorsal) and rhythmic movements (i.e., opening and closing palm and body rocking) make it easier to rule out obvious ecological factors and thereby examine cultural factors as potential causes of intergroup variation (cf. Leca et al. 2007).

Interestingly, a recent study found marked intergroup differences and covariation in the frequency and form of two types of nonconceptive sexual behaviors in female Japanese macaques (i.e., female-female mounts and female-male mounts; Leca et al. 2014). Whereas male mounting posture should be optimal (i.e., precisely coordinated and invariant) in order to achieve penile intromission during heterosexual copulation, female mounting is less functionally constrained, which allows for more flexible and arbitrary behavioral patterns. Leca et al. (2014) showed that the customary occurrence, high prevalence, and great diversity of female-female and female-male mounts at Arashiyama may be the result of combined favorable sociodemographic conditions, namely few resident males, most of them being old, sexually undermotivated, and less aggressive and controlling than the average male Japanese macaques living in the other study groups at Minoo and Jigokudani. They suggest that female-female and female-male mounts may be cultural sexual practices in the Arashiyama monkeys; in most other populations, all the aforementioned favorable sociodemographic conditions are not met, and although female mounting may occasionally be ex-

pressed by several group members, it does not reach the group-level cultural status. In line with Nakagawa et al.’s account for group-specific forms of embracing behavior, Leca et al. (2014) argued that although genetic explanations for such intraspecific variation cannot be ruled out, *arbitrary* behavioral patterns such as intergroup differences in female mounting postures in Japanese macaques could be purely cultural, as any alternative explanation is difficult to imagine. As group-level social tolerance is key to explain cultural variation (Bonnie and de Waal 2006), future research could explore whether embracing behavior is more common in groups with a “mellow” social style.

William C. McGrew

Department of Archaeology and Anthropology, University of Cambridge, Cambridge CB2 1QH, United Kingdom (wcm21@cam.ac.uk). 20 VIII 14

Nakagawa et al. give us a valuable addition to the ethnography of nonmaterial culture in nonhuman primates, with their detailed description of stylized embracing in Japanese macaques. They rightfully point out that such social customs (i.e., those lacking any necessary contributions from external objects or the physical environment) have been reported far less often than the material cultural patterns of elementary technology and subsistence. Moreover, they offer a cross-populational comparison that reveals intergroup differences, suggesting that this behavioral constellation is flexible, perhaps as a result of social learning processes. The kneading versus rocking contrast is fascinating, as both involve kinesthetic cues. What follows here is a series of queries, posed in hopes that the authors will amplify or clarify some of the points that they have raised.

Culture Defined

This has always been a thorny area, both conceptually and terminologically. For example, transgenerational, vertical cultural transmission may characterize traditions, but within-generational, horizontal cultural transmission may give rise to fads, or pop culture. Both are culture. Similarly, the differences between intra- versus inter- and population versus group comparisons need to be made clear.

Material Culture

The authors’ distinction between social versus technological/subsistence seems to be confounded: 5 of their 11 examples (play nest, kiss squeak, stone bang, stone throw, branch shake) cited as social customs necessarily involve external objects. Perhaps a more clear-cut distinction might be material versus nonmaterial culture? (See McGrew 1992 and 2004 for fuller discussion.) A classic example of nonmaterial culture in Japanese monkeys is found in Green’s (1975a) wide-ranging

comparison of vocalizations across troops. These debates will run and run; for example, how should one classify a food taboo, as material or nonmaterial or both? In any event, embracing, kneading, and rocking as described here are clearly independent of direct environmental influences, as the authors state.

Provisioning

The authors often cite this independent variable. They argue that provisioning frees time from foraging and that this leisure time is likely to enhance the rate of innovation. In the absence of evidence for this causal sequence, it might be that provisioning yields habituation, and habituation increases the probability of observation of rare behavioral patterns. Whether provisioning or habituation is the causal variable is easily testable by comparing groups that were or were not provisioned in the process of habituation.

Tension Reduction

The authors repeatedly attribute the function of embracing to tension reduction in socially stressful contexts. They cite data from other studies that close proximity to dominant or unfamiliar individuals is stressful but provide no data for this in their work. They then offer circular reasoning regarding the mating season as being linked to stress but again provide no data. Testing of the tension-reduction hypothesis would seem to require either direct physiological measures (e.g., corticosteroid levels) or proven behavioral proxies (e.g., self-scratching).

Mating Season

Data were collected only during the mating season, for unstated reasons. Helpfully, within-subjects comparison of estrus versus nonestrus shows no differences in rate of embracing, but it would be interesting to see to what extent embracing occurs outside the mating season, when copulation and contest competition for mates is absent.

Sex and Kinship

Both of these key independent variables are mentioned in attempting to explain the occurrence of embracing. The female predominance in embracing is clear, but why such a sex difference exists is not. The picture for matrilineal kinship is uncertain: Without knowing how many related dyads versus nonrelated dyads showed embracing, we cannot say if kinship is important or not.

Individual Differences

Table 2 shows huge individual differences in performance of embracing, whether one looks at raw frequencies or at rates adjusted for observation time. Two of the focal subjects (MN,

KE) showed 57% of the total embracing seen in the 15 identified subjects. If only the six focal subjects are included, that proportion rises to 78%. Furthermore, only two of the possible 110 dyads (MN-TK, KE-NC) showed 43% of the observed embraces. Can these strong biases be explained?

Correction

The authors state that McGrew and Tutin (1978) cited ladder-and-piton use in Japanese macaques as effects of provisioning. Actually, they cited ladder-and-piton use in captive chimpanzees (McGrew et al. 1975).

Overall, these queries aside, Nakagawa et al. (see also Nakagawa 2013) make a strong case for adding embracing, and its associated patterns of body rocking and hair kneading, as social customs in Japanese macaques. Also, their questionnaire results suggest that there is more such nuanced variation to be described, as they and other investigators scrutinize this behavior in other groups and populations.

Michio Nakamura

Wildlife Research Center, Kyoto University, 2-24, Tanaka-Sekiden-Cho, Sakyo, Kyoto 606-8203, Japan (nakamura@wrc.kyoto-u.ac.jp). 24 VIII 14

Nakagawa et al. report the first clear evidence of social custom in wild (unprovisioned) Japanese macaques. In general, I appreciate the firsthand information given in this paper; therefore, here I will comment mainly on the background issues and the interpretation of the findings, in an attempt to facilitate further discussions.

The first issue I want to raise is related to the historical and disciplinary background of studies of Japanese macaque culture. I found it rather surprising that a paper on culture in wild Japanese macaque groups had not been published before. Given the long research history—over more than half a century at multiple sites—and the considerable number of researchers working on this species, there should have been more research about the behavioral diversity of this well-studied macaque species. As authors may be aware, “culture” (or “*kaluchua*”; see Nakamura and Nishida 2006) was one of the most important topics in the early days of Japanese primatology. Following a prophetic essay by Imanishi (1952), early researchers accumulated observations and discussions of Japanese monkey culture (e.g., Itani and Nishimura 1973; Kawai 1965; Kawamura 1956). Therefore, some readers, especially nonprimatologists, may wonder why, after this initial research, the theme of culture has long been almost neglected in studies of Japanese monkeys. The parallel may be seen in baboon studies, where long-term studies at multiple sites, comparable to or even longer than great ape studies, have been conducted with little discussion about the possibility of cultural differences (an exception is Sapolsky and Share 2004). I wonder whether this is a reflection of different degrees of motivation

to address this topic among researchers studying different primate taxa.

Second, I would emphasize the importance of incorporating into the discussion more examination of the cultural behaviors already reported for provisioned Japanese macaque groups. Following this first evidence of culture from unprovisioned groups, how can the cultural behaviors already proposed for the provisioned groups (e.g., Kawamura 1956) be reevaluated? Some of them (e.g., stone handling) may be interpreted relatively easily as by-products of provisioning, but others may not. Some authors (e.g., Whiten and van Schaik 2007) have proposed a criterion by which only those species with enduring traditions in *multiple* behavioral domains are judged to possess culture. Therefore, it is important to scrutinize other seemingly cultural variations to assess whether embracing is a single, rare example of a tradition that has naturally emerged in Japanese macaques, or whether more such examples are likely to exist.

The third issue concerns the scenario of how behavioral differences can emerge. Although Nakagawa and colleagues' main finding is the subtle differences in embracing behavior between two unprovisioned groups, they also present preliminary results regarding its presence/absence at several Japanese macaque study sites. One thing that Nakagawa et al. do not explicitly explain is why some groups completely lack this behavioral pattern. As the authors summarize, ventro-ventral embracing is commonly found among several other *Macaca* species and its function seems identical. Therefore, it may be more parsimonious to assume that this ventro-ventral embracing pattern already existed in the ancestral *Macaca* species, rather than assuming independent multiple emergences of seemingly identical behavior. If ancestral *Macaca* already had this behavioral pattern, we need to explain why some (mostly provisioned) Japanese macaque groups seem to have lost it. Similarly, since it took about 30 years of research before embracing was noticed in the Yakushima E group, this behavior must have once disappeared in the past, and then somehow reemerged again in the group. This is another puzzling, but interesting, point, because such a possible reemergence, as far as I am aware, has not yet been mentioned in the animal culture debate.

Current discussions of cultural differences in animals have largely been based on (likely) emergences of new behavioral patterns by innovation. Tomasello, Kruger, and Ratner's (1993) term "ratchet effect" indicates how we are prone to think that cultures are characterized by the "addition" of new behavioral patterns; thus, they are progressive in nature. Nakagawa et al.'s data possibly show that "subtraction" of a common behavioral pattern, and/or "re-addition" of a once lost behavioral pattern, can be alternative pathways to realize cultural diversity. Repeated innovations, underpinned by high intelligence, may be indispensable for the development of complex technologies. However, we should not forget that we are "cultural" beings, even outside of the technological domain; for instance, no one would deny that humans display

different greeting behaviors according to their cultures. Culture in the social domain may not change progressively and unidirectionally, and may have little to do with intelligence, yet nobody dismisses its importance in human societies. What, then, about its significance in nonhuman animal societies? One thing seems apparent: we still have very limited knowledge about the social domain of animal culture.

Claire Santorelli

Department of Psychology, University of Chester, Parkgate Road, Chester CH1 4BJ, England (c.santorelli@chester.ac.uk). 15 IX 14

Considering the immense number of traditions and individual behavior differences that exist across human cultures, papers such as Nakagawa et al.'s, which document behavioral comparisons across sites in other primate species, should be welcomed and encouraged. Additionally, a focus on a social behavior, rather than tool or subsistence behaviors, comes with a unique set of considerations. Effective study of cross-site social behaviors requires a great degree of field time and collaboration between researchers working at similar field sites. Nuances of behavior that differ on an individual level are easy to miss or ignore if they are not the main focus of an investigation, and this is particularly true for social behaviors that can be less apparent than tool use or subsistence behaviors. While this paper presents a number of noteworthy topics for discussion, I will limit my comments to two main points.

In general, studies of social traditions benefit greatly from incorporating data sets from all group members, as potential social learning opportunities are dependent on the actions of other individuals (Laland 2002). Additionally, social learning opportunities are likely to be influenced by a number of factors including, age, sex, social structure, season, time of day, social rank, and so on. Confining an examination of a behavioral occurrence to a particular subcategory of individuals, such as females as done in Nakagawa et al.'s study, risks overlooking how the use of a tradition may additionally function on a larger scale. For example, behavior variants might be used to identify and reinforce group membership. We suggest this function for some behavioral variants observed in spider monkeys (*Ateles geoffroyi*) when one variant offered no clear advantage over the alternate variant (Santorelli et al. 2011). Nakagawa et al. conclude that at both study sites embracing may serve to reduce tension. However, the arbitrariness of "body-rocking" versus "fur-kneading" embraces, and the variation in embrace positions examined, might offer a similar example of behavior variants that, once established within a group, are maintained by functioning as a signal of group identity in Japanese macaques.

A minor critique of this paper is the use of patterns of embracing variants to speculate on potential genetic relatedness between Japanese macaque subspecies. It seems precarious, as well as unnecessary, to use variants of a single

behavior to suggest one study group might be more closely related to another macaque species than the other study group is. It would be more parsimonious to examine patterns of a number of socially learned behaviors taking into consideration learning opportunities that neighboring Japanese macaque groups might have during intergroup encounters and emigrations, over time and geographical space. Across large geographic ranges, genetic variation invariably exists and is likely to be greatest between more geographically distant groups. In spider monkeys (Santorelli et al. 2011) we expected to find that if genetic differences alone were responsible for explaining behavioral variation across sites, patterns of shared behavior variants would diminish the further apart groups were, as was reported across orangutan field sites (van Schaik et al. 2003). Yet, we found that geographic distance did not correlate with the number of shared behavior variants. However, there are many features of transmission processes that might affect the dispersal of socially learned behaviors between groups that do not affect behaviors based on proximate genetic causes. These features include restrictions imposed by geographical features and immigrants acting as poor demonstrators of a behavior. For example, in vervet monkeys (*Chlorocebus aethiops*) dominant individuals of the philopatric sex are preferred demonstrators of behavior to the migrating sex, potentially causing selection of highly localized traditions (van de Waal et al. 2010). Similarly, given that Japanese macaques are female philopatric with male dispersal (Pusey and Packer 1987) and embracing is performed principally by females, emigrating males would act as poor transmitters of this behavior. Embracing variants (including its presence or absence) would therefore be more likely to remain localized to natal groups than other Japanese macaque behavior variants that were more frequently performed by both sexes.

Bernard Thierry

Centre National de la Recherche Scientifique, and Département Ecologie, Physiologie et Ethologie, Institut Pluridisciplinaire Hubert Curien, Université de Strasbourg, 23 rue Becquerel, F-67087 Strasbourg, France (bernard.thierry@iphec.cnrs.fr). 22 VIII 14

The discovery of the propagation of food washing in the Japanese macaques on Koshima islet during the fifties was the starting point for the study of animal traditions (Kawai 1965). A number of socially transmitted subsistence techniques have been since reported in various species. We had to wait a further 20 years, however, before discovering the first evidence of traditions pertaining to social behavior in chimpanzees: hand-clasp grooming (McGrew and Tutin 1978) and the leaf-clip display (Nishida 1980), present in some communities and absent in others. Given the large number of Japanese macaque groups that have been studied, it is noteworthy that to date, no such social customs have been reported with certainty in this species. The issue has however surfaced several times

through the years. Stephenson (1973) was the first to describe intergroup differences in patterns of sexual consortship, but as the data were relatively limited, these differences might have been an effect of sampling variation. Green (1975a) then identified distinctive vocal patterns in three different geographical locations, but these sites were distant from each other, meaning that it was impossible to establish whether local variations had a learned or a genetic basis. In a further case, Grewal (1981) reported an unusual behavior pattern performed as a threat, namely self-wrist biting, in half a dozen monkeys in the Arashiyama population; given the small number of individuals, however, this could have been considered a mainly idiosyncratic pattern. As these three cases were not investigated any further, the question of social customs in Japanese macaques and other monkeys has long remained an undecided issue.

In this context, the observations of Nakagawa and colleagues deserve careful scrutiny. While the embracing gesture belongs to the common repertoire of macaques, Japanese macaques performed it in a rather stereotyped form, which makes it a recognizable pattern with variants that can be readily identified. Another characteristic of embracing in Japanese macaques is that it is mainly reported in females at the mating season. It could be that embracing is especially frequent between estrus females (Wolfe 1979), but discriminating between estrus and nonestrus females is difficult in the field. This brings me to a first concern: as evidence regarding the absence of embraces in several groups came from multiple observers whose work did not focus on this behavior, it may be asked whether their reports always corresponded to the mating period. Behavior frequencies that vary according to seasons are prone to observational bias (Nishida 1987). To ensure that intergroup differences in embracing were not due to sampling variation, it would be worthwhile for the authors to provide details of the observation duration for each observer during the mating season, together with information about the subjects that were followed. A second question relates to the lifetime of different types of embrace. The survival of social customs is probably fragile if they do not have a particular purpose. Transitory social customs have been documented in white-faced capuchin monkeys: gestures are typically initiated by some individuals, propagate through social networks, then vanish some years later (Perry et al. 2003). If customs originate from idiosyncratic patterns or demographic changes (Sapolsky and Share 2004), they are likely to die out when source individuals disappear, bringing the group back to the modal repertoire of the species (Thierry 2000). It appears necessary to check whether the embracing variants of Japanese macaques are simply fads linked to certain individuals, or whether they persist over generations, qualifying them as genuine traditions. Finally, we must consider the possibility that intergroup differences are genetically determined (see Vasey and Jiskoot 2010). From the study of Nakagawa and colleagues, we understand that embraces can be present or absent in groups living in the same regions, on

both Yakushima and Kinkazan islands, thus casting doubt on the genetic hypothesis. Systematically mapping the frequencies of embracing variants would allow confirmation—on a quantitative basis—that social transmission is responsible for geographic variation patterns.

In view of the large number of socially transmitted behaviors recorded in monkeys and apes, one could believe that traditions are commonly found in primate populations. In most species, however, traditions have only been pinpointed in a minority of groups, with the additional restriction that usually no more than one case of tradition has been reported for each group. A critical, pending question is whether traditions are isolated cases or a widespread phenomenon in group-living animals such as monkeys. After all, when individuals gifted with elaborated learning abilities interact on a frequent basis, they inevitably learn from each other (Thierry 1994). Several candidates for social customs have recently been proposed (Brockett, Horwich, and Jones 2005; Laidre 2008; Falótico and Ottoni 2013; Santorelli et al. 2011), but however suggestive these cases may be, we are given little information about their underpinnings. In this respect, after more than half a century of investigating Japanese macaques, the findings of Nakagawa and colleagues have great potential. If their study of intergroup differences in embracing gestures delivers as promised, that could mean that social learning has a pervasive influence on primate behaviors, subtly coloring them to an extent that was unsuspected until recently.

Reply

As the debut scientific paper in cultural primatology for Naofumi Nakagawa—who has majored in feeding ecology (e.g., Nakagawa 1989, 2009) and socioecology (e.g., Nakagawa 1998, 2008)—it is very pleasing that five cultural primatologists, including authorities such as Professor McGrew and Professor Thierry, a leading expert on ethological studies in macaques, have acknowledged the importance of our paper on social customs.

The reviewers explained and suggested a more detailed background for the present study—Leca and Bonnie highlighted debates on the definition of culture and disputes regarding methodology, respectively; Nakamura and Thierry suggested the history of cultural primatology in Japan and on Japanese macaques, respectively; and McGrew noted the erroneous citation of his paper on ladder-and-piton use in chimpanzees. We very much appreciate these contributions and helpful, thought-provoking comments. We discuss several of these in detail below.

According to the primary method for identifying cultural behaviors in nonhuman primates that has been used throughout at least the last 15 years (Bonnie), we have centered this paper on ruling out genetic and ecological explanations

(method of exclusion) for differences in patterns of embracing behaviors. In response to Nakamura's question, we have added greater explanation of the presence/absence of these behaviors. We had originally concluded that embracing serves the function of tension reduction, although we accept McGrew's critique that there may not be enough direct evidence for this.

Embracing as a tactile signal is redundant since it accompanies lip smacking (a visual signal) and girneys (an auditory signal) that serve equivalent function. This means that the combination of redundant signals does not change the intensity of this function (for details, see Partan and Marler 1999). Some individuals in Kinkazan and Yakushima independently began to exhibit embracing. Since embracing never served a function other than tension reduction, no causal differences were found between groups with and without embracing. This same reasoning applies to explain the presumed temporal change (i.e., the disappearance and reemergence of embracing). Shimooka and Nakagawa (2014) speculated that the evolutionary history of embracing in the genus *Macaca* progressed as follows: embracing was an ancestral gesture that had become very infrequent in rhesus macaques, which are phylogenetically close to Japanese macaques. Thus, embracing may have been hidden in Japanese macaques and reemerged in the Kinkazan population. This reemergence was accompanied by lip smacking, which is also an ancestral display that has been retained among Japanese macaques. While embracing and lip smacking would have functioned as equivalent signals in ancestral macaques, lip smacking might have worked as the backup signal while embracing was hidden in Japanese macaques.

As for the differences in patterns of embracing behavior, our inappropriate use of the word "imply" invited the reasonable critique over "the use of patterns of embracing variants to speculate on potential genetic relatedness between Japanese macaques subspecies" (Santorelli). Our original intention had been to rule out the possibility that genetic differences caused the differences in embracing. Therefore, we should have stated the following: "Such a behavioral similarity between Yakushima macaques and rhesus macaques, the closest allied species to Japanese macaques, may be possibly because Yakushima macaques are genetically closer to rhesus macaques than are the macaques in Kinkazan."

As Bonnie noted, the prevalent methodology has been a point of debate. Langergraber et al. (2011) and Koops, McGrew, and Matsuzawa (2013) have revealed the difficulty of ruling out genetic and ecological explanations for intergroup differences in chimpanzee behaviors, respectively. These findings agree with Nakagawa's experience as an ecologist and socioecologist. We are venturing to raise, despite limited evidence, the possibility that rather than ecological factors, the social environment might explain the presence/absence of embracing behaviors. All three populations that exhibit embracing live in cool-temperate zones (Shimokita, Kinkazan, and Hakusan), and have experienced mass mortality due to

abnormal weather during the winter (heavy snowfall and extremely low temperature) and poor fruit crop during the preceding autumn in 1983 (Izawa 1988; personal communication). The Yakushima population also experienced mass mortality in 1998–99 (Hanya et al. 2004). Embracing occurred more frequently between non-kin grooming partners than kin partners in Kinkazan (Shimooka and Nakagawa 2014) although no clear evidence was obtained in Yakushima (as McGrew noted). The deaths of related female kin might have increased the prevalence of allogrooming between non-kin females, which consequently increased the prevalence of embracing. In this case, the combination of embracing and lip smacking might have intensified the function of these signals (enhancement, Partan and Marler 1999). At any rate, embracing has been observed for at least 29 years (Kinkazan) and 9 years (Yakushima) since the mass mortality events, and therefore can be called a tradition, rather than a fad (response to McGrew's and Thierry's comments).

Leca's intriguing hypothesis that embracing is more common in groups with a "mellow" social style is also another way in which the social environment might explain the presence/absence of embracing behaviors. However, Nakagawa's preliminary results do not support this hypothesis since Japanese macaques in Yakushima exhibited a "mellow" (or "tolerant," to use our term) but the macaques in Kinkazan did not (Nakagawa 2010). If we could find such a set of social behavioral variations linked to different social styles (e.g., "tolerant" vs. "despotic") in Japanese macaques, then this tradition would qualify as culture according to Whiten and van Schaik's (2007) definition (Nakamura).

Multiple reviewer concern centered on the limited season (mating season) of our study period, the limited sex of our study subjects (females), and their reproductive condition (in estrus) (McGrew, Santorelli, and Thierry). This is because our data were collected mainly on the mating behaviors of adult females and an alpha male. However, as we have mentioned in this paper on Yakushima, and in our previous work in Kinkazan (Shimooka and Nakagawa 2014), not only estrus but also anestrus females exhibited embracing during the mating season. Additionally, as we have described in Shimooka and Nakagawa (2014), adult females on Kinkazan exhibited embracing outside the mating season. Although the focal animals of the present study are limited to adult females, we also collected data on the embracing partner of the focal females. As a result, we can say that adult males hardly exchanged embraces with adult females not only in Yakushima but also in Kinkazan (Shimooka and Nakagawa 2014). Judging from Majolo et al.'s (2005) study on postconflict behavior among male Japanese macaques in Yakushima, immediately after aggression, males appeared to exchange mounting instead of embracing.

In the future, further work should be done on embracing and its redundant signals, such as lip smacking and girneys. This work should target all age/sex classes within each group

and should be done throughout the year across many different populations of Japanese macaques.

—Naofumi Nakagawa, Miki Matsubara, Yukiko Shimooka, and Mari Nishikawa

References Cited

- Agetsuma, Naoki, and Naofumi Nakagawa. 1998. Effects of habitat differences on feeding behaviors of Japanese monkeys: comparison between Yakushima and Kinkazan. *Primates* 39:275–289.
- Altmann, Jeanne. 1974. Observation study of behavior: sampling methods. *Behaviour* 49:227–267.
- Aunger, Robert. 1995. On ethnography: storytelling or science? *Current Anthropology* 36(1):97–130. [KEB]
- Bonnie, Kristin E., and Frans B. M. de Waal. 2006. Affiliation promotes the transmission of a social custom: handclasp grooming among captive chimpanzees. *Primates* 47:27–34.
- Brockett, Robin C., Robert H. Horwich, and Clara B. Jones. 2005. Hand-holding by Belizean black howler monkeys: intentional communication in a neotropical primate. *Folia Primatologica* 76:227–230.
- Caldwell, Christine A., and Andrew Whiten. 2006. Social learning in monkeys and apes: cultural animals? In *Primates in perspective*. Christina J. Campbell, Agustín Fuentes, Katherine C. MacKinnon, Melissa Panger, and Simon K. Bearder, eds. Pp. 652–664. Oxford: Oxford University Press.
- de Waal, Frans B. M. 2001. *The ape and the sushi master*. New York: Basic Books. [KEB]
- de Waal, Frans B. M., and Michael Sere. 1997. Propagation of handclasp grooming among captive chimpanzees. *American Journal of Primatology* 43: 399–346.
- Falótico, Tiago, and Eduardo B. Ottoni. 2013. Stone throwing as a sexual display in wild female bearded capuchin monkeys, *Sapajus libidinosus*. *Plos One* 8:e79535. [BT]
- Fragaszy, D. M., and S. Perry. 2003. *The biology of traditions: models and evidence*. Cambridge: Cambridge University Press. [J-BL]
- Green, S. 1975a. Dialects in Japanese monkeys: vocal learning and cultural transmission of locale-specific behaviour? *Zeitschrift fuer Tierpsychologie* 38: 304–314. [WCM, BT]
- . 1975b. Variation of vocal pattern with social situation in the Japanese monkey (*Macaca fuscata*): a field study. In *Primate behavior*, vol. 4. L. A. Rosenblum, ed. Pp. 1–102. New York: Academic Press.
- Grewal, Baldev S. 1981. Self-wrist biting in Arashiyama-B troop of Japanese monkeys (*Macaca fuscata fuscata*). *Primates* 22:277–280. [BT]
- Gruber, Thibaud, Kevin B. Potts, Christopher Krupenye, Maisie-Rose Byrne, Constance Mackworth-Young, William C. McGrew, Vernon Reynolds, and Klaus Zuberbühler. 2012. The influence of ecology on chimpanzee (Pan troglodytes) cultural behavior: a case study of five Ugandan chimpanzee communities. *Journal of Comparative Psychology* 126(4):446–457. [KEB]
- Hamada, Yuzuru, and Ayumi Yamamoto. 2010. Morphological characteristics, growth, and aging in Japanese macaques. In *The Japanese macaques*. Naofumi Nakagawa, Masayuki Nakamichi, and Hideki Sugiura, eds. Pp. 27–52. Tokyo: Springer.
- Hanya, Goro, Miki Matsubara, Hideki Sugiura, Sachiko Hayakawa, Shunji Goto, Toshiaki Tanaka, Joseph Soltis, and Naohiko Noma. 2004. Mass mortality of Japanese macaques in a western coastal forest of Yakushima. *Ecological Research* 19:179–188.
- Hayasaka, Kenji, Satoshi Horai, Takashi Gojobori, Takayoshi Shotake, Ken Nozawa, and Ei Matsunaga. 1988. Phylogenetic relationships among Japanese, rhesus, Formosan, and crab-eating monkeys, inferred from restriction-enzyme analysis of mitochondrial DNAs. *Molecular Biology and Evolution* 5:270–281.
- Heine, Steven J. 2011. *Cultural psychology*. 2nd edition. New York: Norton.
- Hesler, Nana, and Julia Fischer. 2007. Gestural communication in Barbary macaques (*Macaca sylvanus*): an overview. In *The gestural communications in apes and monkeys*. Josep Call and Michael Tomasello, eds. Pp. 159–196. Hillsdale, NJ: Lawrence Erlbaum Associates.
- Hill, K. 2009. Animal "culture"? In *The question of animal culture*. K. N. Laland and B. G. Galef, eds. Pp. 269–287. Cambridge, MA: Harvard University Press. [J-BL]
- Huffman, Michael A. 1984. Stone-play of *Macaca fuscata* in Arashiyama B

- troop: transmission of a non-adaptive behavior. *Journal of Human Evolution* 13:725–735.
- Huffman, Michael A., Jean-Baptiste Leca, and Chamalie A. D. Nahallage. 2010. Cultured Japanese macaques: a multidisciplinary approach to stone handling behavior and its implications for the evolution of behavioral tradition in nonhuman primates. In *Japanese macaques*. Naofumi Nakagawa, Masayuki Nakamichi, and Hideki Sugiura, eds. Pp. 191–219. Tokyo: Springer.
- Imanishi, Kinji. 1952. Evolution of humanity. In *Man*. Kinji Imanishi, ed. Pp. 36–94. Tokyo: Mainichi-Shinbunsha. [In Japanese.] [MN]
- Ingold, Tim. 2001. The use and abuse of ethnography. *Behavioral and Brain Sciences* 24:337–337. [KEB]
- Inoue-Nakamura, N., and T. Matsuzawa. 1997. Development of stone tool use by wild chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology* 111:159–173. [J-BL]
- Isaji, Mina. 2010. Rocking-embrace behavior in Kinkazan B1 group. *Japanese Monkeys in Miyagi Prefecture* 26:25–31. [In Japanese.]
- Itani, Junnichi. 1963. Vocal communication of the wild Japanese monkeys. *Primates* 4:11–66.
- Itani, Junichiro, and Akisato Nishimura. 1973. The study of infrahuman culture in Japan. In *Precultural primate behavior*. Emil W. Menzel, ed. Pp. 26–50. Basel: Karger. [MN]
- Izawa, Kosei. 1988. The ecological study of wild Japanese monkeys, living in Kinkazan Island, Miyagi Prefecture: a preliminary report. *Bulletin of Miyagi University of Education* 23:1–9. [In Japanese with English abstract.]
- . 2009. *Studies of wild Japanese monkeys*. Tokyo: Dobutsusha. [In Japanese.]
- . 2010. Rocking-embrace behavior in wild Japanese monkeys: *Japanese Monkeys in Miyagi Prefecture* 26:32–43. [In Japanese]
- Kawai, Masao. 1965. Newly acquired pre-cultural behavior of the natural troop of Japanese monkeys on Koshima Islet. *Primates* 6:1–30.
- Kawamoto, Yoshi, Takayoshi Shotake, Ken Nozawa, Sakie Kawamoto, Kenichiro Tomari, Shizuka Kawai, Kei Shirai, et al. 2007. Postgracial expansion of Japanese macaques (*Macaca fuscata*) inferred from mitochondrial DNA phylogeography. *Primates* 48:27–40.
- Kawamura, Shunzo. 1956. Culture before human: with special reference to Japanese macaques. *Shizen* 11(11):28–34. [In Japanese.] [MN]
- . 1965. Sub-culture in Japanese macaques. In *Monkey: sociological studies*. Shunzo Kawamura and Junichiro Itani, eds. Pp. 237–289. Tokyo: Chuokouoronsha. [In Japanese.]
- Koops, K., William C. McGrew, and Tetsuro Matsuzawa. 2013. Ecology of culture: do environmental factors influence foraging tool use in wild chimpanzees, *Pan troglodytes* verus? *Animal Behaviour* 85(1):175–185. [KEB]
- Krützen, Michael, Carel P. van Schaik, and Andrew Whiten. 2006. The animal culture debate: response to Laland and Janik. *Trends in Ecology and Evolution* 22:6.
- Kutsukake, Nobuyuki. 2003. Assessing relationship quality and social anxiety among wild chimpanzees using self-directed behavior. *Behaviour* 140:1153–1171.
- Laidre, Mark E. 2011. Meaningful gesture in monkeys? Investigating whether mandrills create social culture. *PLoS ONE* 6:e14610.
- . 2008. Do captive mandrills invent new gestures? *Animal Cognition* 11:179–187. [BT]
- Laland, K. 2002. Culture in nonhuman organisms. In *International encyclopedia of the social and behavioral sciences*. N. J. Smelser and P. B. Baltes, eds. Pp. 3164–3167. Oxford: Elsevier. [CS]
- Laland, K. N., and B. G. Galef. 2009. *The question of animal culture*. Cambridge, MA: Harvard University Press. [J-BL]
- Laland, Kevin N., and William Hoppitt. 2003. Do animals have culture? *Evolutionary Anthropology* 12:150–159.
- Laland, Kevin N., and Vincent M. Janik. 2006. The animal cultures debate. *Trends in Ecology and Evolution* 21(1):542–547. [KEB]
- Langergraber, Kevin E., Christophe Boesch, Eiji Inoue, Miho Inoue-Murayama, John C. Mitani, Toshisada Nishida, Anne Pusey, et al. 2011. Genetic and 'cultural' similarity in wild chimpanzees. *Proceedings of the Royal Society B: Biological Sciences* 278(1704):408–416.
- Leca, J.-B., N. Gunst, and M. A. Huffman. 2011. Complexity in object manipulation by Japanese macaques (*Macaca fuscata*): a cross-sectional analysis of manual coordination in stone handling patterns. *Journal of Comparative Psychology* 125:61–71. [J-BL]
- Leca, J.-B., N. Gunst, L. Ottenheimer Carrier, and P. L. Vasey. 2014. Inter-group variation in non-conceptive sexual activity in female Japanese macaques: could it be cultural? *Animal Behavior and Cognition* 1:387–409. [J-BL]
- Leca, Jean-Baptiste, Nöelle Gunst, and Michael A. Huffman. 2007. Japanese macaque cultures: inter- and intra-troop behavioral variability of stone handling patters across 10 troops. *Behaviour* 144:251–281.
- . 2008. Food provisioning and stone handling tradition in Japanese macaques: a comparative study of ten troops. *American Journal of Primatology* 70:803–813.
- . 2010. Indirect social influence in the maintenance of the stone-handling tradition in Japanese macaques, *Macaca fuscata*. *Animal Behaviour* 79:117–126.
- Lumsden, C. J., and E. O. Wilson. 1981. *Genes, mind and culture: the co-evolutionary process*. Cambridge, MA: Harvard University Press. [J-BL]
- Lycett, Stephen J., Mark Collard, and William C. McGrew. 2007. Phylogenetic analyses of behavior support existence of culture among wild chimpanzees. *Proceedings of the National Academy of Sciences* 104(45):17588–17592. [KEB]
- . 2009. Cladistic analyses of behavioral variation in wild *Pan troglodytes*: exploring the chimpanzee culture hypothesis. *Journal of Human Evolution* 57:337–349, doi:10.1016/j.jhevol.2009.05.015. [KEB]
- Maestripietri, Dario. 2007. Gestural communication in three species of macaques (*Macaca mulatta*, *M. nemestrina*, *M. arctoides*): Use of signals in relation to dominance and social context. In *Gestural communication in nonhuman and human primates*. Katja Liebal, Cornelia Müller, and Simone Pika, eds. Pp. 51–66. Amsterdam/Philadelphia: John Benjamins Publishing Company.
- Maestripietri, Dario, and Kim Wallen. 1997. Affiliative and submissive communication in rhesus macaques. *Primates* 38:127–138.
- Majolo, Bonaventura, Rafaella Ventura, and Nicola Koyama. 2005. Postconflict behavior among male Japanese macaques. *International Journal of Primatology* 26:321–336.
- Manson, Joseph H., and Susan Perry. 2000. Correlates of self-directed behaviour in wild white-faced capuchins. *Ethology* 106:301–317.
- Marmi, Josep, Jaume Bertranpetit, Jaume Terradas, Osamu Takenaka, and Xarier Domingo-Roura. 2004. Radiation and phylogeography in the Japanese macaque, *Macaca fuscata*: *Molecular Phylogenetics and Evolution* 30: 676–685.
- Martin, Paul, and Patrick Bateson. 1990. *Measuring behavior*. Cambridge: Cambridge University Press.
- Maruhashi, Tamaki, Chiemi Saito, and Naoki Agetsuma. 1998. Home range structure and intergroup competition for land of Japanese macaques in evergreen and deciduous forests. *Primates* 39:291–301.
- Matsusaka, Takahisa, Hitonaru Nishie, Masaki Shimada, Nobuyuki Kutsukake, Koichiro Zamma, Michio Nakamura, and Toshisada Nishida. 2006. Tool-use for drinking water by immature chimpanzees of Mahale: prevalence of an unessential behavior. *Primates* 47:113–122.
- McDougall, Petra. 2011. Scratching our heads: rethinking social anxiety in vervets (*Chlorocebus aethiops*). *International Journal of Primatology* 32:335–345.
- McGrew, W. C. 1992. *Chimpanzee material culture: Implications for human evolution*. Cambridge: Cambridge University Press. [WCM]
- . 2004. *The cultured chimpanzee: Reflections on cultural primatology*. Cambridge: Cambridge University Press. [KEB, WCM]
- McGrew, William C. 1998. Culture in nonhuman primates? *Annual Review of Anthropology* 27:301–328.
- McGrew, William C., Linda F. Marchant, S. E. Scott, and Caroline E. G. Tutin. 2001. Intergroup differences in a social custom of wild chimpanzees: the grooming hand-clasp of the Mahale Mountains. *Current Anthropology* 42: 148–153.
- McGrew, W. C., C. E. G. Tutin, and P. S. Midgett. 1975. Tool use in a group of captive chimpanzees: I. Escape. *Zeitschrift fuer Tierpsychologie* 37:145–162. [WCM]
- McGrew, William C., and Caroline E. G. Tutin. 1978. Evidence for a social custom in wild chimpanzees? *Man* 13:243–251.
- Mead, M. 1928. *Coming of age in Samoa*. New York: William and Morrow. [KEB]
- Mori, Akio. 1975. Signals found in the grooming interactions of wild Japanese monkeys of the Koshima troop. *Primates* 16:107–140.
- Moura, Antonio Christian de. 2005. Stone banging by wild capuchin monkeys: an unusual auditory display. *Folia Primatologica* 78:36–45.
- Nakagawa, N. 2013. Cultural diversity of social behaviours in Japanese macaques. In *Monkeys, apes, and humans: Primatology in Japan*. M.A. Huffman et al., eds. Pp. 1–12. Tokyo: Springer. [WCM]
- Nakagawa, Naofumi. 1989. Feeding strategies of Japanese monkeys against the deterioration of habitat quality. *Primates* 30:1–16.

- . 1998. Ecological determinants of the behavior and social structure of Japanese monkeys: a synthesis. *Primates* 39:375–383.
- . 2008. Despotic wild patas monkeys (*Erythrocebus patas*) in Kala Maloué, Cameroon. *American Journal of Primatology* 70:238–246.
- . 2009. Feeding rate as valuable information in primate feeding ecology. *Primates* 50:131–141.
- . 2010. Intraspecific differences in social structure of the Japanese macaques: a revival of lost legacy by updated knowledge and perspective. In *The Japanese macaques*. Naofumi Nakagawa, Masayuki Nakamichi, and Hideki Sugiura, eds. Pp. 271–290. Tokyo: Springer.
- Nakagawa, Naofumi, Masayuki Nakamichi, and Kazunori Yamada. 2011. Report on the questionnaire for infrequently-observed behaviors in Japanese macaques. *Primate Research* 27:111–125 [In Japanese with English summary.]
- Nakamura, Michio, William C. McGrew, Linda F. Marchant, and Toshisada Nishida. 2000. Social scratch: another custom in wild chimpanzees? *Primates* 41:237–248.
- Nakamura, Michio, and Toshisada Nishida. 2006. Subtle behavioral variation in wild chimpanzees, with special reference to Imanishi's of *kaluchua*. *Primates* 47:35–42.
- . 2013. Ontogeny of a social custom in wild chimpanzees: age changes in grooming hand-clasp at Mahale. *American Journal of Primatology* 75: 186–196.
- Nakamura, Michio, and Shigeo Uehara. 2004. Proximate factors of different types of grooming hand-clasp in Mahale chimpanzees: implications for chimpanzee social customs. *Current Anthropology* 45:108–114.
- Nishida, Toshisada. 1980. The leaf-clipping display: a newly-discovered expressive gesture in wild chimpanzees. *Journal of Human Evolution* 9:117–128. [BT]
- . 1987. Local traditions and cultural transmission. In *Primate societies*. Barbara B. Smuts, Dorothy L. Cheney, Robert M. Seyfarth, Richard W. Wrangham, and Thomas T. Struhsaker, eds. Pp. 462–474. Chicago: University of Chicago Press.
- Nishida, Toshisada, John C. Mitani, and David P. Watts. 2004. Variable grooming behaviours in wild chimpanzees. *Folia Primatologica* 75:31–36.
- Nishikawa, Mari, Mariko Suzuki, and David S. Sprague. 2014. Activity and social factors affect cohesion among individuals in female Japanese macaques: a simultaneous focal-follow study. *American Journal of Primatology* 76:694–703.
- Nozawa, Ken, Takayoshi Shotake, Yoshiko Ohkura, and Yuichi Tanabe. 1977. Genetic variations within and between species of Asian macaques. *Japan Journal of Genetics* 52:15–30.
- Panger, Melissa A., Susan Perry, Lisa Rose, Julie Gros-Luis, Erin Vogel, Katherine C. Mackinnon, and Mary Baker. 2002. Cross-site differences in foraging behavior of white-faced capuchins (*Cebus capuchinus*). *American Journal of Physical Anthropology* 119:52–56.
- Parton, Sarah, and Peter Marler. 1999. Communication goes multimodal. *Science* 283:1272–1273.
- Pavani, Silvia, Dario Maestripieri, Gabriele Schino, Pier G. Turillazzi, and Stefano Scucchi. 1991. Factors influencing scratching behavior in long-tailed macaques (*Macaca fascicularis*). *Folia Primatologica* 57:34–38.
- Perry, Susan, Mary Baker, Linda Fedigan, Julie Gros-Louis, Katherine Jack, Katherine C. MacKinnon, Joseph H. Manson, Melissa Panger, Kendra Pyle, and Lisa Rose. 2003. Social conventions in wild white-faced capuchin monkeys. *Current Anthropology* 44:241–268.
- Perry, Susan, and Joseph H. Manson. 2003. Traditions in monkeys. *Evolutionary Anthropology* 12:71–81.
- Pusey, A. E., and C. Packer. 1987. Dispersal and philopatry. In *Primate societies*. B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham and T. T. Struhsaker, eds. Pp. 250–266. Chicago: University of Chicago Press. [CS]
- Richerson, Peter J., and Robert Boyd. 2005. *Not by genes alone: how culture transformed human evolution*. Chicago: University of Chicago Press.
- Saito, Chiemi, Shizue Sato, Sigeru Suzuki, Hideki Sugiura, Naoki Agetsuma, Yukio Takahata, Chisato Sasaki, Hiroyuki Takahashi, Toshiaki Tanaka, and Juichi Yamagiwa. 1998. Aggressive intergroup encounters in two populations of Japanese macaques (*Macaca fuscata*). *Primates* 39:303–312.
- Sakura, Osamu. 1989. Variability in contact calls between troops of Japanese macaques: a possible case of neutral evolution of animal culture. *Animal Behaviour* 38:900–902.
- Santorelli, Claire J., Colleen M. Schaffner, and Filippo Aureli. 2011. Universal behaviors as candidate traditions in wild spider monkeys. *PLoS ONE* 6: e24400.
- Santorelli, Claire J., Colleen M. Schaffner, Christina J. Campbell, Hugh Notman, Mary S. Pavelka, Jennifer A. Weghorst, and Filippo Aureli. 2011. Traditions in spider monkeys are biased towards the social domain. *PLoS ONE* 6:e16863.
- Sapolsky, Robert M. 2006. Social cultures among nonhuman primates. *Current Anthropology* 47:641–656.
- Sapolsky, Robert M., and Lisa J. Share. 2004. A pacific culture among wild baboons: its emergence and transmission. *PLoS Biology* 2:534–541. [MN, BT]
- Schino, Gabriele, Stefano Scucchi, Dario Maestripieri, and Pier G. Turillazzi. 1990. Social tension in familiar and unfamiliar pairs of long-tailed macaques. *Behaviour* 113:264–272.
- Shimooka, Yukiko, and Naofumi Nakagawa. 2014. Functions of unreported “rocking-embrace” gesture between female Japanese macaques (*Macaca fuscata*) in Kinkazan Island, Japan. *Primates* 52:327–335.
- Stephenson, Gordon R. 1973. Testing for group specific communication patterns in Japanese macaques. In *Precultural primate behavior*. Emil W. Menzel, ed. Pp. 51–75. Basel: Karger.
- Takahashi, Hiroyuki, and Takeshi Furuichi. 1998. Comparative study of grooming relationships among wild Japanese macaques in Kinkazan A troop and Yakushima M troop. *Primates* 39:365–374.
- Thierry, Bernard. 1983. Clasp behavior in *Macaca tonkeana*. *Behaviour* 89: 1–28.
- . 1994. Social transmission, tradition and culture in primates: from the epiphenomenon to the phenomenon. *Techniques and Cultures* 23/24: 91–119. [BT]
- . 2000. Building elements of morality are not elements of morality. *Journal of Consciousness Studies* 7:60–62. [BT]
- Thierry, Bernard, Lenora E. Bynum, Suzanne Baker, Margaret F. Kinnaird, Shuichi Matsumura, Yasuyuki Muroyama, Timothy G. O'Brien, Odile Petit, and Kunio Watanabe. 2000. The social repertoire of Sulawesi macaques. *Primate Research* 16:203–226.
- Tomasello, Michael, Ann C. Kruger, and Hilary H. Ratner. 1993. Cultural learning. *Behavioral and Brain Sciences* 16:495–552. [MN]
- van de Waal, E., N. Renevey, C. Monique Favre, and R. Bshary. 2010. Selective attention to philopatric models causes directed social learning in wild vervet monkeys. *Proceedings of the Royal Society, B* 277:2105–2111. [CS]
- van Leeuwen, Edwin J. C., Katherine A. Cronin, and Daniel B. Haun. 2014. A group-specific arbitrary tradition in chimpanzees (Pan troglodytes). *Animal Cognition*, doi:10.1007/s10071-014-0766-8. [KEB]
- van Schaik, Carel P., Marc Ancrenaz, Gwendolyn Borgen, Birute Galdikas, Cheryl D. Knott, Ian Singleton, Akira Suzuki, Sri Suci Utami, and Michelle Merrill. 2003. Orangutan cultures and the evolution of material culture. *Science* 299:102–105.
- Vasey, Paul. L., and Hester Jiskoot. 2010. The biogeography and evolution of female homosexual behavior in Japanese macaques. *Archives of Sexual Behavior* 39:1439–1441. [BT]
- Watson, Claire F., and Christine A. Caldwell. 2009. Understanding behavioral traditions in primates: are current experimental approaches too focused on food? *International Journal of Primatology* 30(1):143–167. [KEB]
- Weinberg, Susan M., and Douglas K. Candland. 1981. Brief report: “Stone-grooming” in *Macaca fuscata*: *American Journal of Primatology* 1:465–468.
- Whiten, Andrew, Jane Goodall, William C. McGrew, Toshisada Nishida, Vernon Reynolds, Yukimaru Sugiyama, Caroline E. G. Tutin, Richard W. Wrangham, and Christophe Boesch. 1999. Cultures in chimpanzees. *Nature* 399: 682–685.
- Whiten, Andrew, and Carel P. van Schaik. 2007. The evolution of animal “cultures” and social intelligence. *Philosophical Transactions of the Royal Society of London. Series B* 362:603–620.
- Wolfe, Linda. 1979. Behavioral patterns of estrous females of the Arashiyama West troop of Japanese macaques (*Macaca fuscata*). *Primates* 20:525–534. [BT]
- Yamagiwa, Juichi, Kosei Izawa, and Tamaki Maruhashi. 1998. Long-term studies on wild Japanese macaques in natural habitats at Kinkazan and Yakushima: preface. *Primates* 39:255–256.