What I learned throughout behavioral observations on Japanese macaques

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My duties as Editor-in-Chief of *Primates* started on January 1st, 2021. I'm very happy and honored to get the baton from immediate-past Editor-in-Chief, Dr. Tetsuro Matsuzawa, and to work in collaboration with two vice Editors-in-Chief, Drs. Jim Anderson and Satoshi Hirata, as well as Associate Editors, Advisory Board members and the many contributors to *Primates*. I hope to draw upon my experiences of long-term behavioral observations on Japanese macaques (*Macaca fuscata*) as well as ring-tailed lemurs (*Lemur catta*), gorillas (*Gorilla gorilla gorilla*) and some other primate species both in the wild and in captivity, and some herbivorous nonprimates such as giraffes (*Giraffa camelopardalis*) and black rhinoceros (*Diceros bicornis*) in zoos, to guide my efforts as Editor-in-Chief. My aim is to work to make our journal better and stronger. Taking the opportunity of writing this editorial, I want to introduce myself to the readers. The following paragraphs describe some of my experiences with Japanese macaques.

Japanese macaques with congenital limb malformations

An encounter with some particular monkeys 43 years ago in the Awajishima free-ranging, provisioned group of Japanese macaques strongly influenced my direction toward primatology. Those were young Japanese macaques with congenital limb malformations. When I visited the Awajishima Monkey Park for the first time to do my graduation research together with my seniors, I was very surprised to see such malformed monkeys living in the group. Some—the most severe cases—had no hands or feet, while others had hands or feet with distorted fingers or toes. The precise deformities varied from monkey to monkey (Fig. 1).

Fig. 1 Young Japanese macaques with congenital limb-malformations in the Awajishima group. (Top) A few-months-old infant with malformed fingers and toes. (Bottom) A 1-year-old male infant with no hands

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Like other primate infants, Japanese macaque infants are born with a grasping reflex. They can cling to their mothers' belly immediately after birth using their four limbs, without any support from their mother. By contrast, as newborns they cannot walk any far distance. An early study hypothesized that the clinging of infants to their mothers was important for eliciting maternal care (Hansen 1966), but the fact that some congenitally malformed infants who cannot perform normal clinging behavior can survive in the wild indicates that mothers must provide extra maternal care toward such disabled infants, despite the absence of any stimulation from infant clinging. Therefore, when I saw these disabled infants and their mothers at the feeding site, I decided to enter graduate school to study them.

I first started following a severely malformed male infant (“*Tanago*”), who had no hands and distorted feet, with the aim of describing his mother’s caretaking and his behavioral development during the first year of life. His mother continued providing maternal behaviors that accommodated *Tanago*’s disabilities. She carried him in one hand and walked on her other three limbs. She also held him against her ventrum with one or both forearms when nursing (Fig. 2). Without her cradling, *Tanago* could not have kept his mother’s nipple in his mouth in the early period of his development, as he had no hands. In fact, there were no clear differences in time spent in contact with the mother, suckling and being groomed by her, between *Tanago* and nondisabled infants. *Tanago* developed locomotor patterns adapted to his limb deformities: he first used quadrupedal walking on elbows and his malformed feet, and then acquired bipedal walking, although his locomotor ability was clearly inferior than that of nondisabled infants. Like the latter, with increasing age he spent less time with his mother and more time with other group members. Nondisabled infants are very likely to interact with same- or similar-aged infants or juveniles for social play and while traveling, not only on the ground but

Fig. 2 A severely malformed male infant “*Tanago*” who had no hands and distorted feet. His mother uses one hand to support him in the ventral position. (The photo was taken in July 1979)

also in trees. *Tanago* played with nondisabled infants, but because of his restricted locomotor abilities he had difficulty following them when they ran away or climbed up a tree. Instead, he often approached and stayed near or in contact with adults, who were less active than infants and juveniles around the feeding site, and adults behaved tolerantly toward him, with no signs of rejection. My first paper describing these observations on *Tanago*’s development was limited by short focal observation times and the small number of nondisabled infants observed, but I’m pleased that it was published in *Primates* (Nakamichi et al. 1983a).

Some other studies on immature Japanese macaques with limb malformations gave results similar to those of my debut paper (Nakamichi 1986; Nakamichi et al. 1983b; Turner et al. 2005, 2008, 2012). The survival rate of such infants during the first year after birth was 72%, much lower than the 90% for nondisabled infants (Nakamichi et al. 1997). However, I consider it unlikely that as many as 72% of disabled infants could have survived in the free-ranging group without compensatory maternal care for their disabilities, along with the infants acquiring their own locomotor patterns, and social tolerance by other group members.

The occurrence of congenital limb malformations in provisioned groups of Japanese macaques was known as early as the 1950s. In fact, monkeys with limb malformations were found not only in provisioned groups but also in wild groups across Japan, and their frequency of occurrence was high during the 1960s and 1970s (Yoshihiro et al. 1979; Sugiyama et al. 2014). In recent years, the incidence appears to have decreased to around zero. The causes of congenital limb malformations in Japanese macaques are largely unknown. Agrochemicals attached to provisioned food are the main suspected cause, but monkeys with congenital malformations were also found in wild groups (Sugiyama et al. 2014). The phenomenon is also reported in crop-raiding wild baboons and chimpanzees (Krief et al. 2017).

When I submitted my first article on the topic, one reviewer commented that this was a case of “an unfortunate experiment of nature.” I completely agree with this comment even now. Several other cases of nonhuman primate mothers continuing to take care of their disabled infants are known. A chimpanzee mother adjusted her behavior to cope with her severely disabled infant, who exhibited symptoms resembling Down syndrome, and who survived for 23 months in the wild (Matsumoto et al. 2016). Individuals with severe congenital disabilities may even survive to adulthood in the wild. Struhsaker et al. (2011) reported that a female baboon with no upper jaw was a healthy, well-integrated member of her group, who raised her own offspring. Turner et al. (2014) investigated the relationships between physical impairment caused by congenital limb malformations and social behavior among adult individuals in the Awajishima group, and concluded

that a socially neutral response, consisting of acceptance of disabled individuals by nondisabled ones without active assistance toward them, could contribute to disabled individuals' survival in the group. Studies on primates with disabilities following accidents or injuries have also provided useful information on overcoming disabilities and nondisabled individuals' responses to them (e.g., Chapman and Chapman 1987; Cibot et al. 2016; Campbell 2019). Individuals with congenital and acquired disabilities can provide us with opportunities to observe the behavioral complexity, flexibility, and adaptive capabilities of non-human primates (Fig. 3), as shown by the behavioral repertoires of nondisabled monkeys. This also applies to disabled individuals in captivity (Hayashi, et al. 2013; Sakuraba et al. 2016). For example, one captive chimpanzee with Down syndrome survived to 27 years of age and routinely interacted with some conspecifics, supported by a dedicated keeper (Hirata et al. 2017; Hirata 2020).

Our knowledge about social responses to severely disabled nonhuman primates can also contribute to the debate about the evolutionary emergence of prosocial or altruistic behavior, based on deformities found in ancestral hominids (DeGusta 2002; Lodkipanidze et al. 2005). Moreover, the ways disabled nonhuman primates live in social groups could have implications for modern humans.

Fig. 3 A 20-year-old female with no hands nurses her nondisabled infant in the Awajishima group. She has experience in taking care of her congenitally malformed infants

The Katsuyama group of Japanese macaques

After finishing observations on malformed monkeys in the Awajishima group, I observed long-tailed macaques (*M. fascicularis*) at the Tsukuba Primate Center (TPC), a center for breeding and rearing monkeys to be used as laboratory animals (Honjo 1985). My interest was in describing changes in maternal behavior which might appear in the process of domestication. F1 mothers who were born from wild-born females at TPC and who grew up in captivity exhibited a relatively passive maternal style compared with wild-born mothers, and I considered that such a passive maternal style might be the first behavioral indication of domestication (Nakamichi et al. 1996b). I wanted to continue observing F2 mothers and successive generations, but ceased when I took a post as assistant professor in the laboratory where I had been a graduate student. I again started to observe Japanese macaques, but a different group: the Katsuyama group.

Primatology in Japan is known to date from 1948, and in the early 1950s, provisioning of several groups of Japanese macaques including Koshima, Takasakiyama, Arasiyama and Mino started, with the purpose of attracting tourists and for research (for the history of research on wild Japanese macaques, see Matsuzawa and Yamagiwa 2017; Sugiyama 2020; Yamagiwa 2010). Provisioning of the Katsuyama group started in 1958, several years after those groups, in a collaboration between the local government of Katsuyama Town (now Maniwa city) and Osaka University. Now, the kin relations through maternal lines and the ages of all group members born in the Katsuyama group after 1958 are known. Naosuke Itoigawa led continuous observations on the Katsuyama group for the first 40 years, and he was my mentor. He started collecting quantitative data to describe sex differences in the context of mother–infant relationships, adopting the focal sampling method in the early 1960s (Itoigawa 1973). At around the same time, Struhsaker (1971) was conducting quantitative observations on wild vervet monkey (*Cercopithecus aethiops*) mothers and infants in Kenya. Focal sampling is now widely used in observational studies of various animal species both in the wild and in captivity, but the studies by Itoigawa and Struhsaker may be the first to have used quantitative focal sampling on mother–infant relationships in wild nonhuman primates. Based on his long-term observations on the Katsuyama group in collaboration with his colleagues and students, Itoigawa reported on topics including infant development, aging, adult male relationships, male–female relationships, group fission, reproduction and demography, among others (Itoigawa 1973, 1982, 1993, 1997, 2001; Itoigawa et al. 1992).

In 1990, I started to identify monkeys in the Katsuyama group, without any particular research projects (Fig. 4).

Fig. 4 The Katsuyama group of Japanese macaques. (Left) The feeding site. Tourists visit here to enjoy seeing monkeys and the waterfall, named *Kanbanotaki*. (Right, top) Two 14-year-old unrelated females sunbathe in the morning after a snowfall during the night. (Right, bottom) Adult females of three generations: A grandmother aged 27 (right) grooms her granddaughter aged 6 (middle), who grooms her daughter aged 14 (left). The grandmother is probably farsighted given the distance between her eyes and fingers—much greater than when she was younger and compared to her granddaughter (from Nakamichi 2019)

At that time, approximately 40 years had passed since the start of wild Japanese macaque research, and various behaviors had already been studied not only at Katsuyama and other provisioned sites, but also in wild, non-provisioned ones. Therefore, it seemed to me that it was not easy for people to come up with original research themes. However, while I focused on identifying adult individuals in the Katsuyama group, I noticed that dominance relationships between adult females did not necessarily follow Kawamura's two rules, which were that (1) females acquire the social rank just below that of their mothers, and (2) sisters rank in inverse order of age. Kawamura established these two rules by observing 13 adult and young adult females of the Mino provisioned group, and his article was published in the first volume of *Primates*, in 1958 (Kawamura 1958). His work is the milestone of the early period of primatology in Japan.

In comparison to the Mino group, the Katsuyama group was a large one, with up to 76 adult females each belonging to one of 17 kin groups. In high-ranking kin groups, dominance relations among females followed Kawamura's rules perfectly, and all females in one kin group were collectively ranked above or below those in other kin groups. In middle- and low-ranking kin groups, however, there were some dyads whose dominance relations did not adhere to Kawamura's rules, and some females were ranked separately from other members of their kin group. I suggested that these differences in dominance relations between high-ranking and middle- or low-ranking kin groups might reflect differences in the degree of social cohesiveness among kin groups

(Nakamichi et al. 1995a). My subsequent observations on grooming interactions between adult females revealed why females of high-ranking kin groups formed a highly cohesive matrilineal unit (Nakamichi and Shizawa 2003). It is because female grooming interactions in high-ranking kin groups are more evenly spread among almost all related females, whereas females in middle- or low-ranking kin groups tend to concentrate their grooming on only a small subset of their relatives (Nakamichi and Shizawa 2003).

My colleagues and I have been observing the Katsuyama group for the past 30 years, working on our own projects and in collaboration with each other. Mainly, we have described various aspects of social relationships such as long-term affiliations between the alpha male and alpha female, which can help him maintain the alpha position until immediately before his death due to old age (Nakamichi et al. 1995b), stability and changes in grooming and proximity relationships with increasing age (Kato 1999; Nakamichi 2003; Nakamichi and Yamada 2007; Fig. 5), triadic grooming among adult females, which is relatively rare in Japanese macaques (Nakamichi et al. 2020, Fig. 6), social relations among immatures (Imakawa 1988, 1990), social grooming of adolescent orphans (Yamada et al. 2005), processes of leaving the group by young adult and adult males (Kato et al. 1999; Kato 2001), and so on. We also studied the effect of solicitations on grooming exchanges (Ueno et al. 2014), the self-rewarding nature of grooming for affiliated partners but not unaffiliated ones (Ueno et al. 2015), how grooming can facilitate huddling formation for thermoregulation (Ueno and Nakamichi 2018), and social rank-related differences

Fig. 5 Long-term grooming relationship. These two 22-year-old unrelated females born in 1984 were observed to groom in 1993 and were still seen to do so between 2003 and 2006, when grooming interactions were systematically recorded. They seemed to maintain an affiliative relationship for years

Fig. 7 A grandmother taking care of her young granddaughter. A 23-year-old female with no young offspring of her own (left) allowed her 1-year-old granddaughter to adopt a suckling posture including nipple contact, even though she did not produce milk. One month earlier, her 12-year-old daughter (right) gave birth, and no longer allowed the 1-year-old to suckle. However, the grandmother started to produce milk within 1 month after the granddaughter started to suckle

Fig. 6 Triadic grooming among three adult females. The 24-year-old female on the left and her granddaughter aged 6 (right) groom the older female's niece, aged 13. Triadic grooming is observed infrequently in the Katsuyama group

in maternal monitoring of infants (Onisi and Nakamichi 2010). We were able to record a live birth (Nakamichi et al. 1992) and a very rare fatal attack on an unweaned infant by a non-resident male (Yamada and Nakamichi 2006). We also described two cases supporting the grandmother hypothesis: old grandmothers without dependent offspring provided essential care toward their dependent grandchildren (Nakamichi et al. 2010 Fig. 7). Based on our long history of observing the Katsuyama group, my colleagues have been developing a new approach to study the group, involving new technology: automatically detecting and tracking in video recordings with deep learning and particle filter (Ueno et al. 2019).

Fig. 8 A 23-year-old female has dug up grass root and carried it several meters to the edge of the river, where she washes a piece to eat

Comparisons among groups of Japanese macaques

From the beginning of studies on macaque groups across Japan, some researchers were interested in intraspecific differences in social structure (for a review, see Nakagawa 2010). Koyama and his colleagues compared the Katsuyama group with six other provisioned groups, using quantitative data on social tension and gregariousness (Koyama et al. 1981). They recorded the number of monkeys who remained within a circle of 8 m diameter containing scattered provisioned foods, and the frequencies of agonistic vocalizations they emitted. These two values were used as the measure of gregariousness and social tension, respectively. There was a positive correlation between the measures in six of the seven groups: the higher the gregariousness of the group, the higher the level of social tension. The Katsuyama group showed the lowest levels of social tension and gregariousness. In contrast to the other six groups, the Awajishima group showed high gregariousness, but a low level of social tension. In other words, Katsuyama group members were not tolerant of other individuals' proximity when social tension was high, as in a feeding situation, whereas Awajishima group members were so tolerant that they could forage in close proximity to each other. The social tolerance of the Awajishima group might contribute toward so many congenitally malformed individuals being able to survive in the group. Moreover, when the two groups were compared using a task which required two macaques to pull the two ends of a single rope simultaneously to obtain food rewards, some individuals in the tolerant Awajishima group successfully solved the task and allowed the partner to stay nearby and get food, but individuals in the less tolerant Katsuyama group rarely succeeded (Kaigaishi et al. 2019). This field experiment clearly shows that Japanese macaques possess the ability to cooperate with conspecifics to get food, but that a tendency toward tolerance is important for cooperation to emerge.

As some Japanese macaque groups have been observed for many years, a few comparative studies have been conducted, leading to new findings and perspectives (see Yamagiwa et al. 1998 and Special Issue of *Primates* 39 (3) in 1998; Leca et al. 2007; and “*The Japanese Macaques*” edited by Nakagawa et al. 2010). Although it may be tough for a single researcher to conduct such comparative studies, it can be valuable to visit other field sites to see the animals firsthand. The late Dr. Hans Kummer taught me the importance of visiting other researchers' field sites when I met him for the first time at an IPS meeting almost 30 years ago (the XIV International Primatological Society Congress, held in Strasbourg, France, 1992). We can

recognize similarities and identify differences when we visit other groups. For example, a behavior which is habitually seen in one group might be seen never or only rarely in another group. I became more aware of this through visiting different groups of Japanese macaques. Moreover, it is also true for seeing different species.

Observations on prosimian species and apes

I had the opportunity to observe wild ring-tailed lemurs in Madagascar, albeit for only 4 months. During that period, I happened to find six dead infants. I saw that the mothers were unable to pick up and carry their dead infant, but they moved back and forth between their dead infant and their group. These observations showed that ring-tailed lemur mothers are less able than simian mothers to carry their dead infants, although their maternal affectional systems appear highly similar (Nakamichi et al. 1996b).

Over the past 20 years, in parallel with studying Japanese macaques, I have continued observing a group of gorillas at San Diego Zoo Safari Park, California, USA. The apes sometimes surprised me with their behaviors. A good example is baby-transfer between a young mother and her experienced mother: when a young mother put her 1-day-old baby on the ground just in front of her own mother, the latter quickly picked it up and handed it back to the young mother, which seemed like very unusual behavior in nonhuman primates. But thereafter, these baby-transfer acts between the older female and her daughter happened sometimes, and through such interactions the young mother's maternal behaviors improved (Nakamichi et al. 2004). I realized that my accumulated experiences with Japanese macaques were useful for observing the lemurs and gorillas, and my experiences with prosimians and apes have in turn stimulated my research on Japanese macaques at Katsuyama.

Conflict between people and Japanese macaques—mostly caused by monkeys' crop-raiding—continues to be an issue in Japan. When we conduct studies on Japanese macaques, we have to be aware of this problem. When we observe animals in captivity, we have to pay attention to their well-being and enrichment. When I observed wild ring-tailed lemurs, I was at an eco-tourism site, and had to consider conservation. When I observe the gorilla group at the zoo, I also consider enrichment and conservation issues for this endangered species. All of the animals I have observed have given me wonderful opportunities to learn about not only their lives, but also their surroundings, and ourselves, that is, humans. Therefore, I consider such opportunities as gifts from nature to me. It is with these experiences in mind that I look forward to performing my duties as Editor-in-Chief of *Primates*.

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