Male care in a free-ranging group of Japanese macaques (*Macaca fuscata*)

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Abstract

Among the *Macaca* species, adult male Japanese macaques are the least likely to perform male care (i.e., affiliative interactions between adult males and immatures, including holding, carrying, and grooming); however, they perform male care for infants, albeit infrequently. We examined 17 cases of male care observed for the first time when the immature was younger than 1 year of age. Eleven of the 31 adult males who remained as central males during the 30-year observation period performed male care. Their age and dominance rank did not influence the occurrence of male care. Most cases were first recorded between the last part of the mating season and the first part of the birth season (January–March), whereas male care was rarely observed during the mating season (October–December). In 12 of the 17 cases, male care ceased within 6 months after the first observation, whereas in the remaining cases, it continued for at least 1 year. In 15 of the 17 cases, males tended to perform male care for matrilineally unrelated female infants of low-ranking mothers. In some cases, the male and infant mother showed grooming interactions for 6 months both before and after the start of male care, whereas such grooming interactions were never recorded either before or after the start of male care in other cases. We also examined some hypotheses on male–immature associations and the probable benefits that males and infants might acquire through male care.

Keywords Japanese macaques · Male care · Carrying · Holding · Grooming

Introduction

Associations between adult males (hereafter referred to as males) and immatures have been observed in promiscuous primate species, thus forming multi-male/multi-female groups such as those found in macaques (*Macaca* spp.) and baboons (*Papio* spp.) (Amici et al. 2019; Maestripieri 1998; Whitten 1987). There are two non-exclusive hypotheses that provide an evolutionary interpretation of male–immature associations. The paternal care hypothesis predicts that a male preferentially associates with immature(s) whom he has sired or probably sired, thus leading to an increase in the chances of survival of the offspring (Bernstain et al. 1981; Buchan et al. 2003; Busse and Hamilton 1981; Huchard et al. 2013; Kuběnová et al. 2019; Langos et al.

2013; Minge et al. 2016; Moscovice et al. 2009). The mating effort hypothesis predicts that a male provides care to an unrelated immature, thereby increasing his chance to mate with the immature's mother, and thus leading to the care-then-mate strategy (Kuběnová et al. 2019; Ménard et al. 2001; van Schaik and Paul 1996). We additionally propose two other hypotheses to explain the male–immature associations. Long-term male–female associations have been observed in some macaque and baboon species (Ostner et al. 2013; Smuts 1985; Takahata 1982), and their potential benefits such as protection against disruption of activities by other group members and protection against infanticide have been discussed (Palombit et al. 1997; Smuts 1985). A male–immature association might occur as a by-product of the male's persistent affiliative relationship with a specific female (the by-product hypothesis). This hypothesis can be included in the paternal care hypothesis if the male maintains a long-term affiliative relationship, including mating with the female, and he performs male care for an infant to whom the female gives birth. A male may mate with a specific female infant with whom the male has a close affiliative relationship when the female immature grows up, indicating

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that the male's close affiliative relationship with the female immature can lead to an increase in his mating opportunities in the future (the effort-for-future mating hypothesis).

Males and immatures can acquire temporal benefits through male–immature associations. In the cold season, when a mother holds her infant, it not only warms the infant but also warms the mother (Ueno and Nakamichi 2016); similarly, if a male holds the infant, it also warms the male. Males who hold infants may be tolerated by higher-ranking males; thus, these males can achieve more stable or higher social positions (Deag and Crook 1971; Itani 1959; Kummer 1967). Some immatures can successfully increase in rank with the protection provided by males (Itani 1959; Itoigawa 2001). Moreover, close associations with a specific male can be beneficial for the survival of orphaned immatures, particularly in infants who lose their mothers during the cold season (Hasegawa and Hiraiwa 1980).

Maestripieri (1998) categorized Barbary (*M. sylvanus*), stumptail (*M. arctoides*), Assamese (*M. assamensis*), bonnet (*M. radiata*), toque (*M. sinica*), and Tibetan macaques (*M. thibetana*) as macaque species in which males commonly have affiliative interactions with infants, such as holding and carrying them. Males belonging to these species tend to have some specific infants with whom they frequently interact, and such male-infant affiliative associations begin when infants are still in the early stages of development (Deag and Crook 1971; Estrada 1984; Kuběnová et al. 2019; Kümmerli and Martin 2008). However, little information is available on how long such affiliative associations last. In these *Macaca* species, males tend to select male infants more frequently (Dittus 1977; Estrada 1984; Ogawa 1995), and they tend to ignore infants with low-ranking mothers (Paul et al. 1996). Moreover, two males simultaneously and briefly manipulate an infant, and such triadic interactions are useful for the establishment and maintenance of bonds between males (Deag and Crook 1971; Kümmerli and Martin 2008; Kalbitz et al. 2017; Ogawa 1995).

In contrast, Japanese macaques (*M. fuscata*) are categorized as macaque species in which males are least likely to have affiliative interactions with infants younger than 1 year of age as well as triadic (male–infant–male) interactions (Maestripieri 1998). However, this does not mean that male Japanese macaques do not interact with young infants.

Some early studies and questionnaire surveys have reported that some, but not all, males have intense affiliative interactions with infants, albeit infrequently, in wild, provisioned, and captive groups of Japanese macaques (Alexander 1970; Gouzoules 1984; Hasegawa and Hiraiwa 1980; Itani 1959; Nakagawa et al. 2011; Table S1). According to Gouzoules (1984), males begin affiliating with female infants aged 3 to 4 months in four male–female infant dyads; their interactions disappear during the mating season and resume thereafter. However, detailed information on male-infant affiliative relationships is still not available.

In this study, we defined intense affiliative interactions between males and immatures that include holding, carrying, and grooming as "male care" (Fig. 1); we focused on male–immature dyads, in which we observed male care for the first time when the immatures were less than 1 year of age. Based on cases of male care recorded in the last three decades in a free-ranging, provisioned group of Japanese macaques, we aimed to examine male care in terms of the following factors: dominance ranks and ages of males, sex of infants, dominance ranks of infants' mothers, kin relation through maternal line between males and infants' mothers, season of the year in which male care started, period during which male care lasted, and presence or absence of grooming interactions between males and infants' mothers before and after the start of male care. Based on our findings, we also aimed to characterize male care in Japanese macaques and to examine the above-mentioned hypotheses for male care and the benefits that males and infants can acquire through male care.

Methods

Study group and animals

The present study was conducted in a free-ranging group of Japanese macaques at Katsuyama, Okayama Prefecture, Japan. The Katsuyama group has been artificially provisioned since 1958, and the ages and matrilineal kin relationships of all individuals born after 1958 are known. The group is usually fed wheat and soybeans a few times a day, depending on how long the group stayed in the vicinity

Fig. 1 Male care: (left) a male holding an infant (case 13); (middle) a male carrying an infant dorsally (case 11); and (right) a male grooming an infant (case 8)

of the feeding site (approximately 610 m^2) during day-time. The time that the group stayed in the vicinity usually varied between 1 and 8 h per day. When the monkeys stayed in the vicinity of the feeding site, they either ate natural food or rested. More detailed information on this group has been reported previously (Itoigawa et al. 1992; Nakamichi et al. 2020).

During the observation period of this study from November 1990 to March 2020, the numbers of adult males (6 years of age or older) and adult females (5 years of age or older) ranged from 6 to 47 and 55 to 110, respectively. Adult males were divided into two types (Kato 2001): (1) central males, who were likely to stay in the vicinity of the feeding area not only during feeding time but also during non-feeding periods (i.e., resting times), together with other central adult males, adult females, and immatures; and (2) peripheral males, who were less likely to remain near the feeding area during non-feeding periods and those that did not always eat artificially provisioned foods in the feeding area during feeding time. Given that it was not easy to observe peripheral males, we only focused on the central males. There was a clear and stable dominance rank order among the central males (Kato 2001; Nakamichi et al. 1995b), and they were dominant over all the peripheral males. The results were based on supplanting, wherein one animal changes its position when another one approaches it without a display of any obvious dominant behavior, and agonistic interactions, wherein dominant behavior such as gaze and threat posture by one animal is followed by subordinate behavior such as a grimace and gaze-avoidance by another. In the Katsuyama group, all central males were born during the 30-year observation period, and they were 6–29 years of age, while most males left upon maturity (Kato 2001). The number of central males varied between 3 and 10, and the total number of central males reached 31 during the 30-year observation period. The tenures of the central males ranged from 2 to 14 years. Most central males ended their tenures when they left the group, while at least one aged central male ended his tenure due to death. The total number of male years (i.e., the total number of years of tenure for the 31 males) reached 194. For statistical analyses of the age and dominance rank of males who performed male care, the values obtained from the male years were used as the expected values.

The birth season of the Katsuyama group was from the beginning of April to mid-July, with the peak occurring from mid-April to June, and the mating season was from the beginning of October to mid-February, with the peak appearing between mid-October and December. The number of births per year ranged from 6 to 51. The sex ratio at birth of the Katsuyama group was 0.92 for the 30-year period.

Data collection and analyses

M.N. observed the group with individual identification for 30 years from November 1990 to March 2020, with a total of 1121 observation days. He observed the group in 303 (86%) of 353 months during the 30-year period. He usually observed animals at a distance of a few to a few tens of meters, using binoculars at times when the group stayed in the vicinity of the feeding site. He mainly recorded the grooming interactions and interactions that were related to dominance relations among group members while walking around (Nakamichi et al. 1995a, b; Nakamichi and Shizawa 2003; Nakamichi and Yamada 2007; Nakamichi et al. 2020). While observing the group for his own research projects, he recorded the names of a male and an immature participating in male care, including holding, carrying, or grooming ad libitum. We are confident that the holding, carrying, and grooming of an infant less than 1 year of age by an adult male are very conspicuous actions; therefore, experienced researchers who can identify adult individuals of a group can also easily recognize such behaviors performed by males towards infants. However, males may groom yearlings or those 2 or more years old as often as they do infants, but they are less likely to hold and even more unlikely to carry them than they are infants. It is likely that we would have failed to record male grooming of yearlings or 2-year-olds, as such interactions through grooming are not as conspicuous as holding and carrying. Therefore, in this study, we focused on male–immature dyads in which male care was recorded for the first time only when the immature was younger than 1 year of age (i.e., an infant). We did not deal with male–immature dyads in which we recorded male care for the first time after the immatures were 1 year old.

M.N. identified 17 cases of male care from his field notes. Moreover, K.Y. and M.U. recorded one and three cases, respectively. K.Y. and M.U. observed the Katsuyama group with individual identification since 2000 and 2009, respectively. They usually recorded the data using focal animal sampling for their own research projects. Of the 21 cases, four were excluded because male care was recorded only for 1 day (Tables 1 and S2).

We examined 17 cases of male care in terms of the following factors: the male's age in years and infant's age in months, infant's sex, male dominance rank among central males, dominance rank of the infant's mother among adult females, presence or absence of kin relationships through maternal lines between the male and infant, the month of the year in which male care started, and presence or absence of grooming interactions between the male and infant's mother for 6 months before and after the start of male care.

The central males were divided into two groups, those from the first- to third-ranking positions and those from the fourth- to tenth-ranking positions, given that the

Table 1 Information on males and infants who formed dyads of male care and the presence or absence of grooming interactions between males and infants' mothers

| Case | Males | | | Infants | | | Male care | | | | | Grooming interactions between male and infant's mother | |
| | Name[a] | Age in years[b] | Dominance rank[b] | Name | Sex | Mother's rank | Age of infant when | | Male left the group | Duration (days)[h] | Maternal kin | Before[i] | After[i] |
							Male care started	Male care ended					
1	Ceria73'79'89	17	7th	Monia79'98'06	F	L	11 m	1 y 11 m	2 y 10 m	391	Different	Yes (25)	Yes (31)
2	Fena70	20	3rd	Terina84'90	F	L	8 m	1 y 2 m	6 y 9 m	177	Different	Yes (24)	Yes (31)
3	Fena70	21	3rd	Mara68'84'91	F	H	7 m	8 m	5 y 8 m	31	Different	No (38)	Yes (31)
4	Keriia75	15	5th	Tera68'77'90	F	L	10 m	1 y 3 m	6 y 2 m[e]	157	Different	No (38)	No (45)
5	Keriia75	17	4th	Tera68'73'92	F	L	9 m	2 y 1 m[c]	11 y 3 m	505	Different	No (31)	[d]
6	Keriia75	26	1st	Tera68'73'92'01	F	L	6 m	2 y 1 m	2 y 1 m[f]	561	Different	Yes (21)	Yes (24)
7	Beria71'79'87'92	12	5th	Elzia71'76'83'98'04	M	L	9 m	1 y 0 m	1 y 1 m	87	Different	No (25)	No (35)
8	Beria71'79'87'94	12	2nd	Tera68'73'89'97'06	F	L	2 m	4 y 11 m	5 y 2 m	1731	Different	No (25)	No (31)
9	Beria71'79'79'87'96	10	3rd	Barisa71'85'95'06	M	L	9 m	1 y 0 m	2 y 6 m	79	Different	No (28)	No (26)
10	Beria71'79'94	10	3rd	Elzia73'85'04	F	L	9 m	1 y 2 m	2 y 2 m	136	Different	Yes (28)	No (30)
11	Beria71'79'94	11	2nd	Barisa71'84'96'05	F	L	8 m	1 y 1 m	1 y 1 m	163	Different	No (28)	Yes (21)
12	Beria71'88'96'03	10	3rd	Tera68'73'89'97'06'13	F	L	9 m	10 m	6 y 11 mg	11	Different	?	?
13	Beria71'88'96'03	12	3rd	Tera68'73'89'97'06'15	F	L	9–11 m	9–11 m	4 y 9–11 mg	13	Different	?	?
14	Beria71'88'96'03	16	1st	Pet92'01'06'11'19	F	H	8 m	8 m	8 y 11 mg	19	Same	?	?
15	Beria71'92'05	8	1st	Tera68'73'92'13	F	L	8 m	8 m	5 y 1 m	4	Different	?	?
16	Tania71'80	12	5th	Lipkisa73'81'98	F	L	6 m	2 y 0 m	2 y 2 m	559	Different	Yes (24)	Yes (22)
17	Tanina69'78'87	17	7th	Elzia71'76'83'88'95'04	M	L	5 m	10 m	4 y 5 m[e]	150	Different	Yes (28)	Yes (28)

[a] Each name reveals its birth year and mother's name. For example, Beria71'79'87'92 of case 7 was born in 1992 from Beria71'79'87, who was born from her mother Beria71'79 in 1987. Beria71'79'87'94 of case 8 was born in 1974 from Beria71'79'87. Thus, these two males were brothers whose age difference was 2 years

[b] When male care was first observed

[c] It is probable that this female infant Tera68'73'92 continued receiving male care from the male Keriia75 after she was 2 years and 1 month old

[d] Directly before or after male care started, the infant's mother disappeared from the group

[e] The infant left the group while the male remained in it

[f] The male died at the feeding site

[g] When the present study finished in March 2020, the male remained in the group

[h] The period of male care that we defined operationally as the period between the first day and the last day on which we recorded male care in the field notes could be underestimated

[i] "Yes" and "no" show that grooming interactions were observed and were not observed, respectively, for 6 months before or after the start of male care. The value in parentheses shows observational days for the 6 months

F female, M male

m month, y year

H high-ranking females who belong to the top-ranking kin group or in the top 30% among all females

L low-ranking females who are females other the high-ranking females

? Data are not available

dominance rank order among the top three males was extremely stable so that almost all second- or third-ranking males rose in rank only when the first- or second-ranking males died or left the group. Females of the few highly ranked kin groups, accounting for over 30% of all females, were considered high-ranking because the dominance rank order among the females was almost linear, and they were collectively ranked within their kin group. The remaining females were considered low-ranking because the dominance rank order among them was not always linear, and they were likely to be ranked separately from members of their own kin. Supplanting episodes, agonistic interactions, and food-dominance tests were used to determine dominance relations among females (Nakamichi et al. 1995a; Nakamichi and Yamada 2010). Paternity analyses were not performed, and reliable behavioral data related to paternity, such as mating activities between adults, were not available.

To examine the month of the year in which male care was first recorded, the 14 cases recorded by M.N. were analyzed. As the number of days in which M.N. observed the group varied from month to month, the relative number of the first observed cases of male care for each month per 100 observation days was calculated. The number of observational days of M.N. per month (January–December) was 97, 68, 80, 120, 96, 82, 145, 131, 88, 56, 60, and 98, respectively.

When the group remained in the vicinity of the feeding area, M.N. recorded the grooming interactions between adults in 20-min sessions, during which he walked around to find grooming pairs (see Nakamichi and Shizawa, 2003, for the detailed recording procedure for dyadic grooming). Grooming data were collected from October 1992 to May 1994, April 1998 to July 2002, and April 2003 to September 2013. M.N. also recorded the grooming interactions ad libitum from August 1990 to September 1992.

Additionally, M.N. collected the proximity data of central males to adult group members during the 20-min sessions (see Nakamichi et al., 1995b, for the detailed recording procedure). He collected proximity data every month from November 1990 to June 1994, during which case 5 began (Table 1). He recorded both the names of adults with whom the male of case 5 showed close proximity, and whether this male engaged in male care towards the specific infant in these 20-min sessions (see legends of Fig. 4 for the number of 20-min sessions and behaviors recorded).

We performed a chi-square (X^2) test, Fisher's exact test, and binomial test to evaluate the influence of some factors such as the season, age in years, and dominance positions of the males and infant sexes on the occurrence of male care. Statistical significance was set at $P < 0.05$.

Results

Males and infants

In the 17 cases, 11 different males formed affiliative dyads with one to three different infants in the different years (Table 1); however, no males performed male care for two or more infants during the same period, and no infants received male care from two or more males during the same period. These 11 males accounted for 35% of the 31 central males throughout the 30-year observation period.

The males were 8 to 26 years old (mean [SD]: 14.5 [4.8] years old) when they started male care for their specific infants. There were four, six, five, and two males in the age classes of 6–10 years, 11–15 years, 16–20 years, and 21 years or more, respectively. The distribution of ages of males across the four age classes was not significantly different from that of the expected values (Fisher's exact test, $P = 0.543$, n.s., Table S3). The dominance ranks of the males at the time when they started male care ranged from the first- to seventh-ranking positions. The distribution of the number of males from the first- to third-ranking positions and those from the fourth- to tenth-ranking positions was not significantly different from that of the expected values ($X^2 = 1.151$, $df = 1$, n.s., Table S4). These findings revealed that male care was least likely to be influenced by the age and dominance rank of the males, at least among the central males.

Among the 17 cases, 14 were female infants (82%), and three were male infants (18%), indicating that males preferentially provided male care to female infants as compared to male infants (Table 1, binomial test, $P < 0.01$). In all but one of the 17 dyads, the males and infants belonged to different maternal kin groups (Table 1). In the remaining dyad (case 14), both the male and infant belonged to the top-ranking kin group, but their maternal relatedness was 1/256, which was so distant that the male and infant could be considered as unrelated. In these 17 cases, two mothers (12%) were high-ranking, whereas the remaining 15 (88%) were low-ranking. The distribution of infants with high- and low-ranking mothers was significantly different from that of the expected values; that is, the number of infants born from high-ranking females and that from low-ranking females during the 30-year observation period was 287 (42%) and 395 (58%), respectively (Fisher's exact test, $P = 0.012$, Table S5). These findings revealed that males were more likely to perform male care for maternally unrelated female infants from low-ranking kin groups than those from high-ranking kin groups.

Figure 2 shows the first recorded relative number of cases of male care per 100 observational days for each month of the year. The highest three values for the relative
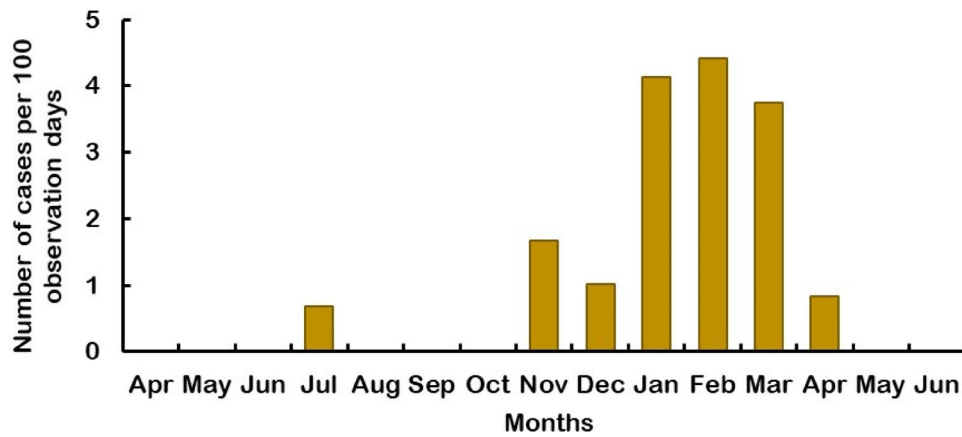
Fig. 2 First recorded relative number of cases of male care per 100 observational days for each month of the year. The numbers of cases of male care recorded by M.N. during the 30-year observation period were four, three, three, one, one, one, and one in January, February, March, April, July, November, and December, respectively. The birth season of the study group was from April to June. Therefore, the

period from April to June on the left side of the x-axis corresponds to that during which infants were in the first to third months after birth, and the period from April to June on the right side of the x-axis corresponds to that during which some infants were still in the 10th to 12th months after birth and other infants were already 1 year old

number of cases were obtained in January, February, and March, and the total value for these 3 months reached 74% of that for all months. In 12 (71%) of the 17 cases, male care was recorded last during the period from February to August of the year following the birth of each infant (8 months to 1 year and 3 months of infant age), and the length of male care in these cases was 11 to 177 days, whereas in the remaining five cases, male care continued to be recorded for up to approximately 2 years of age or more (Fig. 3 and Table 1).

Figure 4 shows one case of male care, where the fourth-ranking male started to perform male care for a female infant who lost her mother a few days before or after the female infant was orphaned at the age of 9 months (case 5). A month after the start of male care (February 1993), the male spent as much as 65% of his time being in contact with the female infant, including holding and carrying her (Fig. 4). The male continued male care towards the female infant until the infant was at least 2 years and 1 month old, without the mating season of 3.5 months. The male was also observed to provide agonistic aid to the female infant on at least two occasions. Before the female gave birth to her first infant at 6 years of age, she became dominant over her two sisters that were 2 and 7 years older than she was.

Males and infants' mothers

In 13 of the 17 cases, grooming data between the male and infant's mother for 6 months before and after the start of male care were available. Based on the presence or absence of grooming interactions between the male and infant's mother for 6 months before and after the start of male care,
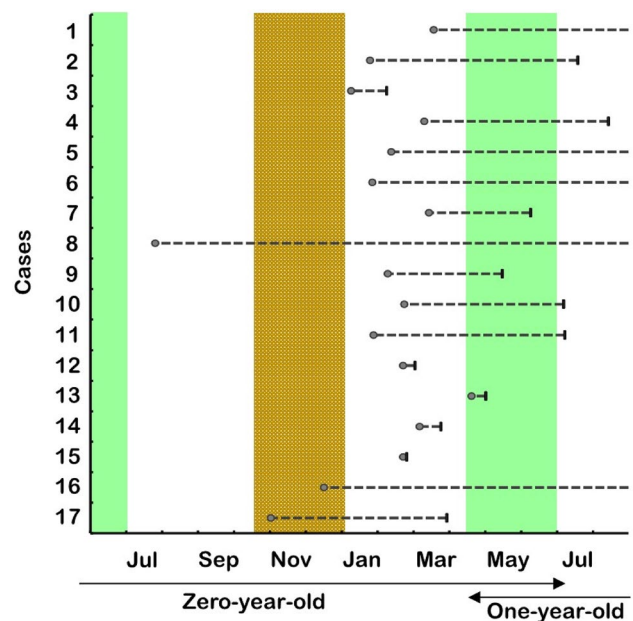

Fig. 3 Seventeen cases of male care. Circles and short vertical bars represent the time when male care was first and last observed, respectively. Dotted lines represent the period during which male care was observed. A dotted line without a vertical line indicates that male care lasted after the end of July. Dark brown squares show the peak period of mating season, and light green squares show the peak period of birth season

we classified 12 of the 13 cases into four types (Table 1). The remaining case in which the infant became an orphan (case 5) was not classified into any type. In type 1, no grooming interactions were observed between the male and infant's mother for either 6 months before or after the start of male
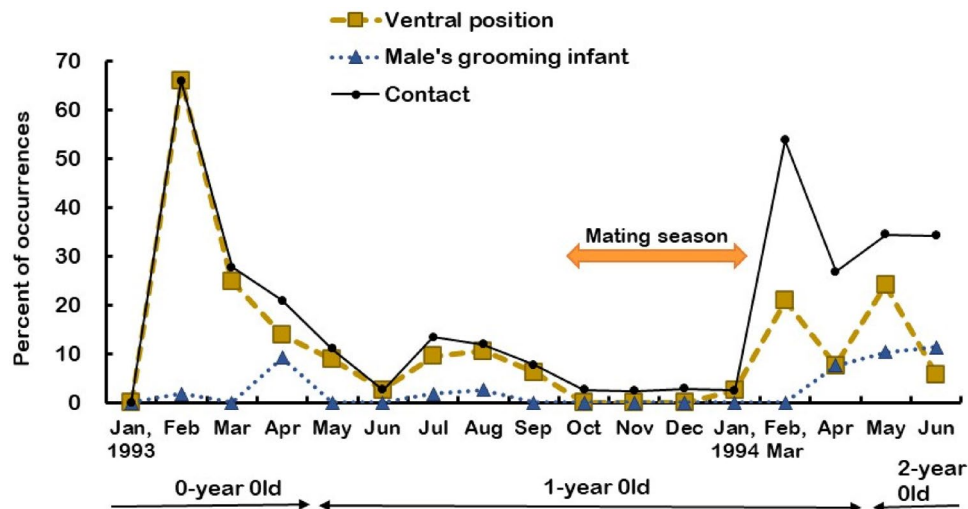
Fig. 4 Percentage of 20-min sessions during which the male *Keriia75* showed affiliative interactions with the female infant *Tera68'73'92* (case 5). *Keriia75* started his male care towards *Tera68'73'92* on February 11, 1993, when she was 9 months old. The values for February 1993 were calculated based on the data collected after the start of male care. The ventral position was recorded when the infant was sitting or lying, in contact with the male's ventral surface, and sometimes being held by him. Contact included all affiliative interactions between them that were accompanied by physical body contact such as holding, carrying, grooming, being groomed, and passive contact. The sample sizes, that is, the number of 20-min sessions in which the male was observed monthly from January 1993, were 53, 53, 36, 43, 45, 38, 52, 75, 64, 38, 42, 35, 39, 43, 26, 29, and 35, respectively. As the number of 20-min sessions in February 1994 was as small as 13, this value was combined with that of March 1994

care. In type 2, grooming interactions were observed both before and after the start of male care. In type 3, grooming interactions were not observed before the start of male care; however, they were observed after it. Type 4 was the reverse of type 3. The numbers of cases in types 1, 2, 3, and 4 were four, five, two, and one, respectively. Hence, in six of the 12 cases, the male provided male care to an infant that was the offspring of a female with whom the male had not had grooming interactions, whereas in the remaining six cases, the males began caring for an infant, wherein the mother was an individual with whom the male had grooming interactions.

Discussion

The present study confirmed that male care was infrequently observed in Japanese macaques, and it highlights some characteristics of male care. Only a small number of cases of male care started during the peak period of the mating season from October to December. Some previous studies also reported that male care was rarely observed during the mating season (Alexander 1970; Gouzoules 1984; Hasegawa and Hiraiwa 1980). On the other hand, most cases of male care started from January to March. Testosterone, an androgenic steroid hormone, is positively associated with mating activities and negatively associated with paternal behaviors in many species with seasonal breeding schedules (Onyango

et al. 2013). In fact, the testosterone levels of male Japanese macaques in a free-ranging group, which was different from that of the present study group, were the highest in the early and middle parts of the mating season, whereas they were low in the non-mating season (Muroyama et al. 2007), and they were correlated with male noncontact aggression during the mating season in the captive groups of Japanese macaques (Barrett et al. 2002). Therefore, males with high testosterone levels and those that are sexually active and aggressive could be least likely to orient their concern towards infants, and infants should avoid approaching or staying near such males. In contrast, in the final stages of the mating season (i.e., January and February), some males became sexually inactive; thus, they seemed to be calmer. It is probable that some males begin affiliative interactions with infants. Moreover, January, February, and March were the first, second, and fourth coldest months of the year, respectively, in the region inhabited by the study group (see Table S6 for the mean temperatures per month). The Japanese macaques in our study group showed increased huddling behaviors during winter for thermoregulation; however, females with young offspring are less likely to huddle with other group members than adult females without young offspring (Ueno and Nakamichi 2016). This means that holding a young offspring could be useful for mothers to warm themselves. It is probable that the sexually inactive male started male care towards the specific infant for unknown reasons, and the associations between them could have been

strengthened by holding the infant, given that holding could warm both of them during winter and early spring.

Although infant sex did not affect the male choice of infants for male care in crested macaques *M. nigra* (Kerhoas et al. 2016), studies have reported that in stump-tailed, rhesus *M. mulatta*, Tibetan *M. thibetana*, and Barbary macaques, males tend to preferentially associate with male infants or juveniles of high-ranking mothers, but the preference of males for such infants has not been discussed (Estrada 1984; Langos et al. 2013; Ogawa 1995; Paul et al. 1996). In contrast, in the present study, it was found that male care was skewed towards female infants. Moreover, it was also observed that in most cases, infants who received male care were those of low-ranking mothers. These findings could be related to the behavioral tendency that female infants prefer to stay near adult males more than male infants. In Japanese macaques, female immatures prefer relationships with females of various age classes, infants, and adult males when they are away from their mothers, whereas male immatures preferentially maintain close relationships with males of the same or similar age (Nakamichi 1989). These sex differences tend to appear in the second half of the first year of life, during which infant Japanese macaques spend less time in proximity to their mothers (Nakamichi 1989). Moreover, according to Imakawa (1988), female Japanese macaque juveniles with low-ranking mothers remained near central males more than those with high-ranking mothers, as males do not need to move around as often as low-ranking mothers, who may move around more frequently to avoid agonistic interactions or to be supplanted by higher-ranking mothers. Therefore, it is probable that, like young female juveniles with low-ranking mothers, when infants are in the second half of the first year, some female infants with low-ranking mothers tend to remain near central males more frequently than those with high-ranking mothers and male infants. Such a behavioral tendency for female infants with low-ranking mothers to remain near central males could facilitate some of them receiving male care more easily than other infants.

As most Japanese macaques who lose their mothers during the first year after birth do not survive (Hasegawa and Hiraiwa 1980), male care could be beneficial for the survival of an orphaned infant. In case 5 of this study, the 9-month-old female infant started to receive intensive and frequent care from the adult male directly before or after she lost her mother early in February, the coldest month of the year. This female infant might have barely survived without receiving his care such as holding and carrying frequently. Adult sisters commonly rank in the reverse order of age in Japanese macaques (Kawamura 1958; Nakamichi et al. 1995a), but younger sisters tend to be subordinate to their older sister(s) when they become orphaned during infancy (Takahata 1991). However, this orphaned female infant became dominant to her older sisters before she reached adulthood,

which could depend on her affiliative relationship with the fourth-ranking male. Although she and her two older sisters lost their mother when they were young immatures or a nulliparous young adult, they successfully inherited their mother's dominance rank among the adult females (Nakamichi, personal observations). These findings could also be dependent on their relatively frequent associations with the same male, including their occasional proximity to and grooming interactions with him.

The present study did not include either paternity or behavioral data on consort relationships between males and females, but some findings of this study can help us examine the extent to which the proposed hypotheses (see ''Introduction'') appropriately explain male–immature associations. Although some factors such as the dominance ranks of mothers can affect the birth sex ratio, there is no clear difference in the number of male and female births in macaques and baboons (Cheney et al. 2004; Dittus 1998; Itoigawa et al. 1992; Meikle and Vessey 1988; Paul and Kuester 1990; Silk and Strum 2010), indicating that males sire male and female infants equally. Therefore, the paternal hypothesis predicts that males provide male care to male and female infants equally. However, we found that males preferred female infants in approximately 80% of male care cases, which could hardly support the paternal care hypothesis. We also found that males had grooming interactions with mothers of their specific infants after the start of male care in only two cases. This finding does not support the mating effort hypothesis (the care-then-mate strategy). On the other hand, our finding that males showed grooming interactions with mothers before the start of male care to the mothers' infants in half of the observed cases could partly support the by-product hypothesis, which predicts that a male maintains long-term associations with a female, thereby increasing the opportunity to provide male care for her infant. Moreover, these findings could support the paternal care hypothesis if the male has maintained long-term associations with a female, including mating with her and male care towards an infant to whom she gave birth.

In the present study, female infants, but not male infants, were most likely to be selected by males as specific infants. These findings may support the effort-for-future mating hypothesis, that is, males may mate with their specific female infants when they grow up. However, in five of the 14 cases, including female infants, the male left the group or died before the infant reached the age of 4.5 years, at which time the female Japanese macaques could be pregnant (Table 1). These cases contradict the effort-for-future mating hypothesis. In the remaining nine cases, the male remained in the group when the infant grew up, but behavioral data on the presence or absence of mating activities between them were not available. Therefore, the present findings are not sufficient to refute this hypothesis.

The question remains as to why an infrequently performed behavior such as male care for infants by a relatively small number of individuals was maintained in almost all groups of Japanese macaques (see ''Introduction'' and Table S1). In future studies, more detailed behavioral data with more cases, together with paternity data, are needed to answer this question and to achieve a comprehensive understanding of male care in Japanese macaques. Given that we found that biological and social factors such as age and dominance positions of males were not related to the performance of male care and that only some central males performed male care, we may also need to focus on idiosyncratic or individual factors such as personality, based on the detailed behavioral descriptions of each case of male care.

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