Accessibility is a determinant of infant handling in wild Japanese macaques (*Macaca fuscata*)

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Accessibility is a determinant of infant handling in wild Japanese macaques (*Macaca fuscata*)

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Summary

In group-living primates, individuals other than mother are often attracted by infants and access to infants. This interaction is called "infant handling" and non-mother individuals are called "handler". Previous studies have examined functions of infant handling, an influence of mother-infant relationship, and behavioural processes that result in infant handling. However, these phenomena have been studied independently and inter-relationship between these topics remained unclear. Infant handling is consisted of three interactants: mother, infant, and handler. To fully understand the processes and functions of infant handling, it is necessary to consider social relationships among interactants. Also, most of previous studies on infant handling have been conducted in captive or free-ranging provisioned groups whose social characteristics (e.g., group size, group composition and intensity of competition) differ from those in wild groups. Since these differences could affect the pattern or frequency of infant handling, it is necessary to study infant handling in the wild. So, I studied determinants of pattern and frequency of infant handling in wild Japanese macaques by considering social relationships among infant, mother and handler. I collected behavioural data of infant handling, interactions between mother and infant, and grooming from handler to mother before infant handling for three years in Kinkazan Island, Japan.

In the first study (chapter 3), I examined the influence of mother-infant relationship on the frequency of infant handling by using data of infant handling and mother-infant interactions. I found that mother-infant relationship was characterised by three principal components: infant activity, rejection, and non-protectiveness. Infants who were less active and whose mothers were less protective received more frequent handling by unrelated, higher-ranked, and unrelated higher-ranked handlers, which means that those handlers have a low accessibility to infant. Low-activity infants and infants with less protective mothers were thought to be more accessible to handlers because less active infants interact with their mothers less frequently and because mothers who are less protective are unlikely to interfere with their own infants. So, handlers with less access to infants may concentrate their attentions on more accessible infants. These results suggest that a specific component of mother-infant relationship is negatively associated with the occurrence of infant handling, and raise a necessity of considering a triadic relationship to understand this complex interaction.

In the second study (chapter 4), I focused on a behavioral process before infant handling by examining grooming interactions by handler to mother. Particularly, I tested predictions of the biological market theory in the context of infant handling, which postulate that provision of grooming before infant handling is determined by value of infant. More specifically, the value of infants is predicted to be lower as the number of infant increases. I found that the occurrence and duration of grooming before infant handling was not affected by a number of infants. Its occurrence was affected by the rank difference between handler and mother and the physical distance between mother and infant. The handlers groomed a mother for long duration when their relatedness was low. These results indicated that grooming had no function of a currency as predicted by the biological market theory. Rather handlers needed to provide grooming to mother for increasing maternal tolerance and for accessing an infant when maternal tolerance was supposed to be low.

In the third study (chapter 5), I examined functions of infant handling by testing predictions from five functional hypotheses, i.e., learning-to-mother, kin selection, reproductive competition among females, coalition formation, and by-product. I found that handling by males rare occurred, infants were handled by nulliparous females more frequently than parous females, and infants were handled positively in the most cases. These results best fit predictions of learning-to-mother hypothesis, which proposes that handlers can learn how to treat infants by infant handling and enhance their future reproductive success. In addition, I found partial support for other hypotheses, indicating that functions of infant handling varied with attribute of handlers.

From these results, I concluded that determinants of pattern and frequency of infant handling in wild Japanese macaques was “accessibilities” to infant and mother for handlers. Based on characteristics of social relationship between mother and themselves and an opportunistic availability of an infant, handlers seemed to select an accessible infant that handlers can handle with low cost. These accessibilities reflect social characteristics of female-female relationships in Japanese macaques, nepotism and despotism. This study concludes that infant handling is a complex behavior involving all participants’ social relationship.

Contents

Chapter 1

General introduction

1.1. Infant handling in primates

In group-living primates, individuals other than mother are often attracted by infants. This results in frequent social interactions between infant and non-mother individuals (Maestripieri, 1994a). This behaviour has been labeled in various ways, such as “allomothering”, “aunting”, and “babysitting”. These terms imply a meaning of costly caregiving of an infant (Maestripieri, 1994a). However, it has been observed that non-mothers treat an infant with not only affiliative (e.g. holding, carrying, grooming) or neutral behaviour (e.g. touching an infant) but also with rough and negative ones (e.g., pulling, grabbing or attacking) (Maestripieri, 1994a; Schino et al., 2003). Also, those interactions *per se* do not appear to be costly for non-mother individuals, which contrast to “helping” behaviour by helpers such as food sharing or delaying breeding of themselves in cooperatively breeding species (Paul & Kuester, 1996). Based on these, a neutral term, “infant handling”, has been used to denote an interaction between infant and non-mother individual, and non-mother individuals are called “handler” (Wasser & Barash, 1981; Maestripieri, 1994a; Paul & Kuester, 1996).

Costs and benefits of infant handling

Functions of infant handling have been discussed by analysing its cost and benefits for its interactants (handlers, mother, and infant). By infant handling, it has been proposed that handlers can have several non-mutually exclusive benefits such as improving their maternal skill (vervet monkey *Cercopithecus aethiops*: Lancaster, 1971; Fairbanks, 1990; Meaney, 1990; blue monkey *Cercopithecus mitis stuhlmanni*: Föster et al., 2005; ursine colobus *Colobus vellerosus*: Bădescu et al., 2015; white-headed langurs *Trachypithecus leucocephalus* Jin et al., 2015), increasing their indirect fitness (reviewed in Riedman, 1982), acquiring a partner of alliance (chacma baboon *Papio cynocephalus ursinus*: Cheney, 1987; Formason macaques *Macaca cyclopis*: Hsu et al., 2015), and/or giving an advantage to its own offspring by harming infants of other females that can be a potential rival (Hrdy, 1976; bonnet macaques *Macaca radiata*: Silk, 1980; comment in Wasser and Barash, 1981; yellow baboon *Papio cynocephalus*: Kleindorfer & Wasser, 2004). On the other hand, handlers incur cost by infant handling such as being attacked and injured by the mother of infant (Japanese macaques *Macaca fuscata*: Schino et al., 2003).

For mothers, infant handling could be beneficial by increasing their feeding time (reviewed in Hrdy, 1976; vervet monkey: Fairbanks, 1990; capped langur *Prebytis pileate*: Stanford, 1992) and possibly accelerating infant's weaning (ursine colobus: Bădescu et al., 2016). For infants, infant handling could result in acquiring a higher status, improving social skills, increasing a possibility of adoption if the mother dies, (reviewed in Hrdy, 1976), and enhancing social bonds (rhesus macaque *Macaca mulatta*: Dunayer & Berman, 2017). However, infant handling could be costly for both mother and infant as infant handling occasionally results in harming infants and its death (macaques: McKenna, 1979; rhesus macaque: Quiatt, 1979; Japanese macaques: Schino et al., 1993).

1.2. Determinants of the pattern and frequency of infant handling

Previous studies showed that the frequency and contents of infant handling varied both between and within species in primates (reviewed in Maestripieri, 1994a). Maestripieri (1994a) suggested that the inter- and intra-specific variation is associated to the species-specific dominance style among females (i.e., a steepness of dominance relationships, which affects the direction and intensity of aggression; Thierry, 2000) and maternal style (i.e., a mother's behavioral tendency towards an infant; see Chapter 3). In despotic species, which can experience intense competition among females (Thierry, 2000), infants are likely to be harassed frequently by non-related females (Maestripieri, 1994a). This is because handlers can improve the relative competitive position of their own offspring by having a negative effect on the infants of non-relatives by harassing them (Silk, 1980; Wasser & Barash, 1981). In response to this threat, a mother and relatives of an infant may employ a protective maternal style and provide agonistic support to an infant (reviewed in Silk, 2002). As a result, it is expected that maternal style become more protective and infants receive more handling in despotic than in egalitarian species (Maestripieri, 1994a). In egalitarian species, in contrast, competition among females is believed to be moderate, and the frequency of infant harassment should therefore be lower than in despotic species (Maestripieri, 1994a).

Based on a different payoff of infant handling for handlers according to their attribute (see above), it is not surprising that the frequencies and contents of infant handling vary among females in a single species. Indeed, social relationships between handler and mother, whose characteristics were determined by many factors such as relatedness and relative dominance rank between those individuals, have been shown to affect the frequency and patterns of infant handling (Paul, 1999).

1.3. Aims of this study

As such, previous studies have examined the function of infant handling (reviewed in Maestripieri, 1994a), maternal style, and behavioural processes that result in infant handling (e.g., grooming interaction between mother and handler as payment for infant handling) (reviewed in Sánchez-Amaro & Amici, 2015). However, these phenomena have been studied independently and inter-relationship between these topics remained unclear. Infant handling is consisted of three interactants: mother, infant, and handler. To fully understand the processes involved in infant handling, it is necessary to consider the relationships among three interactants, i.e., mother, handler and infant. For example, previous studies testing the function of infant handling assumed that all infants can be freely accessible. This may not be true as the formation of social relationships is strongly affected by relatedness, dominance relationship, and other factors (Thierry, 2000). By considering relationships among three interactants, it is possible to know roles of social constraints affecting the occurrence of infant handling.

Also, most of previous studies on infant handling have been conducted in captive or free-ranging provisioned groups. It is pointed out that those groups are different from wild groups in terms of the group compositions, intensity of feeding competition, and the steepness of dominance relationships and so on (Hill 1999). As these differences are highly likely to affect the pattern or frequency of infant handling, it is essential to study infant handling in the wild.

In this thesis, I aimed to clarify the determinants of the pattern and frequency of infant handling in a wild, non-provisioned group of Japanese macaques. This is the first study to integrate components that could affect the pattern and frequency such as social relationship between mother and handler, maternal style, and a process in which infant handling occurred. I report three studies in this thesis.

In chapter 2, I report the general methods of this thesis as the following three studies are based on the same observational dataset.

In chapter 3, I examined the influence of mother-infant relationship on the frequency of infant handling. First, I characterized the mother-infant relationship by principal component analysis. Second, I analyzed the relationship between principal component score of each principal component and handling frequency.

In chapter 4, I focused on a process reaching to infant handling by examining grooming interaction by handler to mother. By doing so, I tested the biological market theory regarding infant handling.

In chapter 5, I examined functions of infant handling by testing predictions from five functional hypotheses. Particularly, I investigated effects of attribute of handlers and social relationship between handler and mother on frequency and content of infant handling.

In chapter 6, I discussed the determinants of pattern and frequency of infant handling in wild Japanese macaques from the results of each chapter. Particularly, I emphasize an importance of accessibility of an infant and a mother, overlooked components in the previous studies of infant handling.

Chapter 2

General methods

2.1. Study species

My study species is Japanese macaques (*Macaca fuscata*), an endemic species of Japan. Socioecological features of Japanese macaques are summarized in Nakagawa et al (2010). Japanese macaques form a multi-male multi-female group. Females stay in their natal group throughout life. On the other hands, males emigrate from their natal group before they matured. Their social behaviour is nepotistic and strongly affected by maternal relatedness, with related females showing higher frequency of affiliative behaviour (proximity, grooming, cofeeding) than unrelated ones. Adult males are dominant to females, and females have form a strict and despotic linear dominance hierarchy based on matrilineal groups. Their mating season is from autumn to winter, and females give birth an infant in spring to summer of the next year. There mating system is promiscuous. Females mate with multiple males during the estrus period. The paternity of an infant cannot be known from behavioral observation.

2.2. Study site and subjects

This study was conducted from April to August 2014–2016 (a total of 211 days) on Kinkazan Island, Miyagi Prefecture, northern Japan (N38° 17′ 43″, E141° 34′ 00″). During the study period, six groups of wild Japanese macaques were present at the study site; these groups have never been provisioned by humans. I selected group A, which has been habituated to human presence since 1982 (Yamagiwa & Hill, 1998), for observation. All individuals were identified by appearance and morphological features. The matrilineal genealogy and parity of all females have been recorded since 1983. Paternity of infants are not known.

During the study period, the number of individuals in group A ranged from 52 to 60 (see Table 2.1 for details). The change of group size was caused by individual death, male emigration and immigration. Adult females were defined as 7 years of age or older; I treated four 6-year-old females that gave birth as an adult. Adult males were defined as 10 years old or older, sub-adult females as 5–6 years old, sub-adult males as 5–9 years old. Juveniles were defined as 1–4 years old, and infants as younger than 1 year old. A total of 30 live births occurred during the 3 years (2014: 17 infants; 2015: 2 infants; 2016: 11 infants). There were no stillbirths. The exact dates of 12 births (50%) are known by observation. I estimated the dates of birth of the other infants from their developmental condition.

In this group, mothers start leaving from an infant about one week after birth. Infants gradually start walking about one month after the birth. By around this timing, infants start playing with each other. Infants start including food items of adults in their mouth at about 3 months of age. It takes about one year to wean completely.

2.3. Behavioural observations

I conducted all behavioural observations between sunrise and sunset. I selected 24 mother–infant pairs as targets for focal observation (Altmann, 1974). I chose observation targets to represent group composition in terms of factors such as maternal rank and infant sex (Table 2.2). This inevitably limited the sample size in terms of parity (only two primiparous females were included in our dataset). I observed each focal pair for a maximum of 2 hours per observation day. I observed each focal pair both morning and afternoon to avoid any bias from the observation of a specific pair in either the morning or the afternoon. During focal observations (total 519 sessions), I continuously recorded all infant handling (regardless of whether the handling was aggressive or affiliative) and other types of social interaction (grooming, embracing, mounting) involving the focal infant, mother, and its interaction partner. I also recorded whether a focal infant made continuous physical contact with its mother. In 519 focal sessions, infant handling continued till the end of the focal observation period, we extended our observation for 10 minutes, regardless of whether the bout of infant handling ended during that time. (32 sessions). If I lost sight of a focal pair, I terminated the focal observation session and started a new session with another mother–infant pair. When a mother and infant separated and it was not possible to observe both individuals at the same time, I observed the infant. Data for observation periods shorter than 1 hour were excluded. I collected observational data from the birth until infants were 12 weeks old. The total observation time was approximately 1,007 hours (approximately 29–97 hours per focal pair; mean, 42 hours).

To determine the dominance ranks among all the adults, I also recorded dyadic aggression (threatening, chasing, biting), submission (bared teeth facial expression), and avoidance behaviour by ad libitum sampling during focal observation.

2.4. Definition of infant handling

Following the method of Schino et al (2003), my definition of infant handling included eight behavioural types: holding, carrying, grooming, touching by hand, mouth, or nose, grasping, pulling, threating, and aggression (Table 2.3).

2.5. Statistical analyses

All statistical analyses were conducted using the R v. 3.4.1 (R Core Team 2017). Unless otherwise noted, I used a general linear mixed model (LMM) or a generalized linear mixed model (GLMM). The model with the lowest AIC was selected as the final model.

Table 2.1. Group composition in each year during the study period.

Year	2014	2015	2016
Adult male	4	3	2
Adult female (nulliparous)	18 (0)	18 (2)	19 (0)
Sub-adult male	1	1	3
Sub-adult female (all nulliparous)	3	2	6
Juvenile (male, female)	11 (4, 7)	26 (13, 13)	19 (12, 7)
Infant (male, female)	17 (11, 6)	2 (2, 0)	11 (7, 4)
Total	54	52	60

Table 2.2. Information of each focal pair. *An asterisk shows estimated date of birth.

year	mother	infant		mother			observation	
		birth day	sex	rank	age	parity	bout	Total time (hr:min:sec)
2014	RN	3/17*	male	1	11	3	21	39:27:09
	NN	3/17*	male	10	13	4	22	42:50:56
	KN	3/19*	male	9	11	2	22	42:30:47
	RR	3/21	male	3	16	5	23	45:06:42
	MO	3/22	female	18	10	1	22	42:53:46
	OP	3/29*	male	16	18	3	22	43:56:43
	KM	4/1	male	13	20	5	22	44:00:42
	AR	4/3	female	6	16	5	21	40:11:27
	OT	4/5	female	15	13	2	21	41:32:20
	RB	4/6	male	5	11	1	19	36:54:37
	RU	4/11	male	2	6	0	18	36:00:00
	FK	4/14*	male	12	16	3	17	34:00:00
2015	SM	4/8	male	7	12	2	70	134:40:28
	FP	5/9	male	11	20	5	43	80:58:25
2016	KN	3/27	female	10	13	3	27	51:26:27
	RN	3/28*	male	1	13	4	27	53:22:50
	RR	3/28*	female	3	18	6	27	53:09:47
	IS	3/28*	male	9	7	0	28	55:31:05
	NN	3/28*	female	11	15	5	27	52:14:57
	MO	3/28*	female	19	12	2	29	55:29:31
	RB	4/8	female	5	13	2	26	50:47:51
	KT	4/8	male	15	8	1	27	52:03:20
	IZ	4/15*	male	8	10	2	23	44:28:06
	RU	5/8	female	2	8	1	19	35:38:51

Table 2.3. Definition of infant handling (after Schino et al., 2003).

Content	Behavioural definition
Holding	The infant is in ventral contact with the handler
Carrying	The infant is carried on the dorsal or ventral side of the handler
Grooming	The handler plucks the infant's hair, pinches, and picks material from the infant
Touching	The infant is gently touched by the handler using its hand, leg, or nose
Grasping	The handler roughly grasps part of the infant's body
Pulling	After being grasped, the infant is roughly dragged closer by the handler
Threatening	The infant is threatened by the handler (i.e. eyes wide open and mouth widely opened without showing teeth)
Aggression	The infant is chased, bitten, or struck directly by the handler

Chapter 3

Maternal protectiveness is negatively associated with infant handling in wild Japanese macaques

3.1. Introduction

In group-living primates, maternal style varies among and within species (Maestripieri, 2018), and it has been proposed that differences in maternal style among species affect the occurrence and frequency of infant handling (Maestripieri, 1994a; Paul, 1999; see Chapter 1). To date, tests of this idea have provided mixed results, leading Paul (1999) to propose that further studies of the relationship between infant handling and maternal style are necessary.

Previous studies have often analysed mother–infant relationships using principal component analysis (PCA) to characterise maternal style by classifying related behaviours into various categories (Fairbanks & McGuire, 1988; Tanaka, 1989; Schino et al., 1995; Fairbanks, 1996; Maestripieri, 1998, 2006; Bardi et al, 2001; Bardi & Huffman, 2002, 2006; De Lathouwers & Van Elsacker, 2004). Studies of cercopithecine monkeys often extract two principal components, "protectiveness" and "rejection" (reviewed in Maestripieri, 2018); they occasionally identify a third component, either "warmth" (Maestripieri, 1998) or "infant activity" (Schino, et al., 1995). Protective mothers frequently initiate and maintain contact with their infants and also restrict their infants. Rejecting mothers frequently avoid and/or reject contact with their infants, resulting in short contact times (Hinde, 1974; Rosenblum & Youngstein, 1974; Simpson, 1985;

Altmann, 1980; Fairbanks & McGuire, 1988; Maestripieri, 1994b; Fairbanks, 1996; Bardi & Huffman, 2002).

As the occurrence of infant handling can be affected by the ease of access for the handler, maternal style may be associated with infant handling. For example, infants of protective mothers would be expected to be handled less frequently than those of non-protective mothers, as the former have been shown to be less tolerant than the latter of other individuals approaching their infants (Altmann, 1980; Fairbanks & McGuire, 1988; Maestripieri, 1994a; Fairbanks, 1996). It is also possible that a mother employs protective maternal behaviour when its infant is likely to be a target of infant handling that would cause a negative outcome. Only one study examined the relationship between maternal style and the frequency of infants' receiving handling (Maestripieri, 1998). Maestripieri (1998) showed that maternal style was mainly characterised by variations in the dimensions of protectiveness, rejection, and warmth and that these variations did not influence the frequency of infant harassment in captive pig-tailed macaques (*Macaca nemestrina*; Maestripieri, 1998). However, that study examined handling only in terms of harassment and did not explore protective behaviour (e.g. carrying, holding, or grooming), which can also result in infant death if the handling period was excessive (McKenna, 1979; Quiatt, 1979; Schino et al., 1993).

In this study, I investigated the relationship between infant handling by females and maternal style in the wild Japanese macaque, *Macaca fuscata.* Previous studies have found variations in the maternal style of captive and provisioned free-ranging groups (Tanaka, 1989; Schino et al., 1995; Bardi & Huffman, 2002; 2006). However, there have been no studies regarding maternal style in wild non-provisioned groups. Therefore, whether these results reflect maternal style under natural conditions remains unknown.

In this study, I conducted principal component analysis (PCA) of mothering style and examined the influence of maternal dominance, parity (primiparous: first birth experience; multiparous: birth after the first birth), age, matrilineal size, and infant sex. I then examined the hypothesis that these components affect the frequency of infant handling. More specifically, I tested predictions that handling frequency would be higher in mother–infant pairs with low protectiveness scores. I also explored how the effects of maternal style varied in response to the social relationship between the mother and the handler. I predicted that when handlers were individuals who were tolerated by the mother (e.g. relatives) or were less threatening to the mother (e.g. lower-ranked individuals), the mother's protectiveness would not affect the frequency of infant handling. In contrast, when the handlers were not tolerated or when they presented a potential threat to the mother (e.g. non-relatives and/or higher-ranked individuals), the infant would be handled more frequently if the mother was less protective.

3.2. Methods

Study site and behavioural observation

See Chapter 2.

Differences in maternal style

I analysed eight types of mother–infant interaction: infant access, infant leave, maternal access, maternal leave, maternal restriction, maternal rejection, contact, and grooming (Table 3.1). I calculated the frequency of each behavioural type by dividing the number of bouts by the focal observation time in each focal session. I calculated the frequencies of contact and grooming by dividing the total duration of these behaviours by the focal observation time in each focal session. I then calculated the means of these frequencies or durations for each behavioural type.

I treated each mother–infant pair independently and explored maternal style in 24 mother–infant pairs using PCA. I used a correlation matrix to standardise each explanatory variable (Crawley, 2013). I adopted principal components with eigenvalues >1 and then calculated principal component scores for each pair.

Determinants of maternal style

To test the determinants of maternal style, I ran separate linear mixed models (LMMs) using the lme4 package (R Core Team, 2017). Each extracted principal component score was set as a response variable. Matrilineal size, which could affect maternal style (rhesus macaques: Berman et al., 1997; Japanese macaques: Schino et al., 1995), was defined as the number of kin individuals present in the group. Maternal dominance was defined as the absolute rank among adult females in each year. The explanatory variables were maternal dominance, age, parity, matrilineal size, and infant sex. I set the mother's identity and study year as random effects.

Relationship between maternal style and frequency of infant handling

See Chapter 2 for handling classification. When infant handling was interrupted but resumed within 5 seconds, it was regarded as the same bout of infant handling.

I analysed the relationship between the principal component scores of the protective properties and the frequency with which each infant was handled using LMMs.

Infant handling by males was extremely rare (2014: 1/934; 2015: 9/805; 2016: 24/720 bouts). Therefore, I performed separate analyses of infant handling by all handlers and by female handlers. The explanatory variables included all extracted principal components. The response variable was the mean frequency of receiving handling in each focal observation period. This frequency was calculated by averaging the frequency of infant handling among focal sessions.

As mentioned above, it is likely that the effect of maternal style on the frequency of infant handling differs according to the relationship between the mother and the handler. To test this hypothesis, I calculated the frequency of infant handling by relatives, non-relatives, and non-relatives ranked higher and lower than the mother and relatives ranked lower than the mother. I then ran separate LMMs for each category, with frequency of infant handling as a response variable. In addition to the principal component scores, I controlled for the effects of two variables that could affect the frequency of infant handling. First, I controlled for the number of potential handlers by setting it as an additional explanatory variable. For example, when I analysed the frequency of infant handling by relatives, I controlled for the number of relatives (maternal relatedness was 0.25 or larger) that each individual mother had. As paternity was not known for this group, I used maternal relatedness; thus, the relatedness of mother–infant pairs was 0.5.

Individuals whose relatedness with the focal mother was 0.25 or more were defined as kin (mother–offspring, grandmother–grand-offspring, maternal siblings).

I also included maternal dominance rank as an explanatory variable to control for the possible influence of social context on the frequency of infant handling. Infant handling may be more likely to occur for mother–infant pairs that have many opportunities to interact with group members. This study focused on a timescale through early infant development (i.e. 12 weeks) but did not consider those elements of the social context that could change on the order of seconds or minutes (e.g. number of proximate individuals for a mother–infant pair). Therefore, this study was not designed to test how these social contexts affect infant handling. Maternal dominance rank could be a proxy for these opportunities. In Japanese macaques, dominant females are usually at the center of a group and receive more grooming than subordinate females (Nakamichi & Yamada, 2010). Therefore, it is predicted that the infants of dominant females would have more opportunities to be handled than would those of subordinate females if these social contexts affected the frequency of infant handling.

I excluded data for mothers without relatives from analyses of relatives and excluded data for mothers with no higher-ranked handlers from analyses involving higher-ranked handlers. I did not analyse infant handling by higher-ranked relatives because it did not occur in 20 focal individuals when the handler was female. All models contained the mother's identity and the study year as random variables.

3.3. Results

Differences in maternal style

Three principal components with eigenvalues greater than 1 were extracted by PCA. These components accounted for 27%, 24%, and 17% of the variance in maternal style, with a cumulative proportion of 68%. The first component was highly positively correlated with the frequencies of infant leave and infant access, and the second was highly positively correlated with the frequencies of maternal rejection and maternal leave. The third component was highly negatively correlated with the frequencies of maternal access and contact (Table 3.2). Based on these correlations, I labelled the first principal component "infant activity", the second "rejection", and the third "non-protectiveness" (Fig 3.1).

Determinants of maternal style

None of the factors was included as an explanatory variable in the final model of infant activity (Table 3.3). In the analysis of rejection, infant's sex remained in the final model.

Mothers with male infants showed a significantly higher rejection score than those with female infants (b±SE = 0.905±0.302, df = 19.177, t = 2.996, p = 0.007) (Table 3.3; Fig. 3.2). Maternal age was included as an explanatory variable for the non-protectiveness score (Table 3.3; Fig 3.3).

Relationship between differences in maternal style and frequency of infant handling

The results of our analysis of all handlers suggested that each principal component score did not affect the frequency of infant handling (Table 3.4). Non-protectiveness was included in the final model, and it positively predicted the frequency of infant handling (Table 3.4).

The results of separate analyses of relatedness and rank among handlers showed that non-protectiveness by the mother affected the handling behaviour by non-relative, higher-ranked, and higher-ranked non-relative handlers. The frequency of infant handling increased with the increasing non-protectiveness of the mother (Table 3.4, Fig. 3.4a, b, c). This result indicated that infants of mothers with low protectiveness scores were handled frequently when handlers were non-relative, higher-ranked and unrelated higher-ranked ones. In contrast, non-protectiveness did not affect the frequency of infant handling by relatives, lower-ranked individuals, or lower-ranked non-relatives (Table 3.4). Infant activity also affected infant handling frequency, with infant handling frequency decreasing as the infant activity score increased when handlers were higher-ranked individuals and higher-ranked non-relatives (Fig 3.4d, e). These results indicated that low-activity infants were handled more frequently.

Next, I analysed infant handling by female handlers. Similar to the results of the overall analysis, non-protectiveness was included in the final model, and infants with non-protective mothers tended to be handled more frequently (Table 3.5). The positive effect of non-protectiveness in mothers was significant when female handlers were non-relatives, higher-ranked, and higher-ranked non-relative individuals (Table 3.5; Fig. 3.5d, e), indicating that infants whose mothers were less protective were handled more frequently. Infant activity negatively affected the frequency of infant handling by higher-ranked females and higher-ranked non-relatives (Table 3.5; Fig. 3.5d, e). These results indicated that less active infants were handled more frequently.

3.4. Discussion

Three principal components of maternal style were extracted for the first time in a non-provisioned group of Japanese macaques: "infant activity", "rejection", and "non-protectiveness". These results were consistent with those of previous studies in Japanese macaques (provisioned free-ranging group: Tanaka, 1989; captive groups: Schino et al., 1995; Bardi & Huffman, 2002, 2006), suggesting that maternal style is not dependent on living environment. Rejection scores were affected by infant sex. Mothers of male infants had higher rejection scores than those of female infants. This indicated that mothers of male infants refused or broke physical contact more frequently than mothers of female infants. This tendency has been widely confirmed in the genus Macaca (Mitchell, 1968; Itoigawa, 1973; White & Hinde, 1975; Berman, 1984; Eaton et al., 1985). Schino et al. (2001) reported that high levels of maternal rejection promoted infant independence and reduced indications of anxiety. For example, maternal style and behavioural response were correlated in adolescent male captive vervet monkeys meeting unfamiliar adult males (Fairbanks & McGuire, 1987). That is, adolescent males who had experienced rejecting maternal care during infancy and had less contact with their mothers were bolder when meeting a strange adult male (Fairbanks & McGuire, 1987). Such effects may be adaptive in species whose males disperse from their natal group, as such males must form new social relationships with unfamiliar individuals in non-natal groups. Therefore, high levels of maternal rejection or non-protectiveness during infancy may be helpful for males during their eventual emigration.

The determinants of maternal style identified in the present study differ from those reported previously. Several researchers reported that interactions between mothers and infants differ according to maternal parity, with primiparous mothers generally being more protective than multiparous mothers (Mitchell & Stevens, 1968; Holley & Simpson, 1981; Negayama et al., 1986). In the present study, there was no difference in the protectiveness between primiparous and multiparous mothers. One reason that parity did not affect the principal components identified in the present study was that only two primiparous individuals were included in our focal observations. Schino et al. (1995) reported that protectiveness decreased with increasing maternal age and that rejection increased as the number of maternal relatives increased in captive Japanese macaques. In the present study, the number of relatives did not affect any components of maternal style, suggesting that the determinants of maternal style differ among living environments.

The results of this analysis supported our predictions and provided the first quantitative evidence that the frequency with which infants receive handling is influenced by maternal style, non-protectiveness, and infant activity. These results did not differ when considering handling by all individuals and handling by females only, which was unsurprising because most of the handlers were female (see Methods and also Maestripieri & Pelka, 2002). As predicted, infants whose mothers were less protective were handled frequently when handlers were non-relatives, higher-ranked individuals, and higher-ranked non-relatives. Additionally, infants who were less active were handled frequently when handlers were non-relatives and higher-ranked non-relatives. It has been suggested that non-relatives and/or higher-ranked handlers have less access to mothers of infants in Japanese macaque groups characterised by nepotism and despotic dominance. Infants with less protective mothers and low-activity infants were thought to be more accessible by handlers because mothers who are less protective are unlikely to interfere with their own infants and because less active infants interact with their mothers less frequently. As a result, handlers with less access to mothers of infants may concentrate their attention on more accessible infants. A non-mutually exclusive explanation is that the maternal style was shaped by the presence of group members such that a mother protected its infant more frequently and the infant became less active because potential handlers sought opportunities to gain access to the infant. This study was not designed to test this possibility directly because our analyses focused on the period through early infant development and not on each infant handling event. However, our analyses controlled for maternal dominance rank, which is commonly associated with opportunities for social interactions in Japanese macaques (Nakamichi & Yamada, 2010), and the number of potential handlers (Table 3.4, 3.5). Therefore, I suppose that the above possibility is weak at the timescale through early infant development. To test this possibility in depth, further studies involving event-level analyses will be necessary.

The results of this study demonstrate the importance of considering the influence of maternal style in studies of infant handling and other social interactions involving infants. Although previous studies of infant handling have focused on the process and function of infant handling, these studies implicitly assumed that the infants were freely accessible. However, it may be misleading to draw conclusions about the function of infant handling solely from observed infant handling events, as maternal style may be negatively associated with the attempts of potential handlers. It is possible that a specific maternal style could affect the processes underlying infant handling; for example, handlers may need to provide longer grooming bouts to protective than to non-protective mothers.

Table 3.1. Definition of mother-infant interaction.

Behaviour	**Definition**
Infant access	The frequency with which an infant approaches and initiates contact with its mother
Infant leave	The frequency with which an infant separates from its mother
Maternal access	The frequency with which a mother approaches and initiates contact with its infant
Maternal leave	The frequency with which a mother separates from its infant
Maternal restriction	The frequency with which a mother restricts the infant's movement by grasping part of the infant's body
Maternal rejection	The frequency with which a mother rejects the infant's contact or detaches the infant from the mother
Contact	The duration of physical contact between mother and infant
Grooming	The duration of grooming (plucking the hair, pinching, and picking) an infant by the mother

Table 3.2. Principal components analysis (PCA) results (n = 24). Values shown are the correlation coefficients for each behaviour. Bold numbers indicate highly correlated components.

Behaviour	PC1	PC2	PC3
Infant leave	**0.91**	0.30	0.16
Infant access	**0.72**	0.43	0.47
Maternal rejection	-0.31	**0.83**	-0.03
Maternal leave	-0.42	**0.78**	-0.04
Maternal restriction	0.21	0.25	-0.11
Grooming	0.58	-0.36	-0.29
Maternal access	0.41	0.38	**-0.61**
Contact	0.10	-0.05	**-0.80**
Eigenvalue	2.18	1.91	1.35
Proportion of variance	0.27	0.24	0.17
Cumulative proportion	0.27	0.51	0.68

Table 3.3. Relationships between principal component scores and mother–infant characteristics (n = 24). *Explanatory variable that was retained in the final model.

	b±SE	df	t	P
Infant activity				
(Intercept)	0.253±1.596	16.622	0.158	0.876
Dominance	-0.024±0.083	11.569	-0.292	0.776
Age	-0.040±0.083	17.510	-0.485	0.634
Parity	-0.036±1.240	14.069	-0.029	0.977
Matrilineal size	0.293±0.156	15.061	1.882	0.079
Infant's sex	-0.275±0.570	15.584	-0.483	0.636
Rejection				
(Intercept)	-0.488±1.253	6.729	-0.389	0.709
Dominance	0.000±0.046	11.291	-0.003	0.998
Age	0.036±0.044	17.959	0.816	0.425
Parity	-0.158±0.567	10.696	-0.293	0.775
Matrilineal size	-0.035±0.098	12.743	-0.359	0.726
Infant's sex	0.905±0.302	19.177	2.996	0.007*
Non-protectiveness				
(Intercept)	-1.893±1.134	17.000	-1.668	0.114
Dominance	-0.019±0.050	9.624	-0.379	0.713
Age	0.115±0.058	21.543	1.995	0.059*
Parity	-0.936±0.816	12.328	-1.146	0.273
Matrilineal size	-0.033±0.159	13.680	-0.211	0.836
Infant's sex	0.799±0.410	16.139	1.950	0.069

Table 3.4. Relationships between principal component scores and infant handling frequency by all handers. *Explanatory variable that was retained in the final model with the lowest AIC.

	b±SE	df	t	P
All (n = 24)				
(Intercept)	3.299±0.829	1.931	3.981	0.061
Infant activity	-0.130±0.132	18.260	-0.979	0.341
Rejection	-0.020±0.225	15.950	-0.091	0.929
Non-protectiveness	0.279±0.148	10.770	1.880	0.087
Maternal rank	-0.071±0.042	14.009	-1.696	0.112
Relative (n = 20)				
(Intercept)	-0.645±0.504	6.632	-1.279	0.244
Infant activity	-0.175±0.100	13.878	-1.752	0.102
Rejection	0.113±0.136	7.808	0.827	0.433
Non-protectiveness	0.148±0.123	14.507	1.206	0.247
Number of individuals	0.291±0.074	9.790	3.952	0.003*
Maternal rank	0.091±0.027	8.963	3.378	0.008*
Non-relative (n = 24)				
(Intercept)	1.272±3.169	1.545	0.401	0.737
Infant activity	-0.210±0.131	19.349	-1.605	0.125
Rejection	-0.035±0.259	15.670	-0.136	0.894
Non-protectiveness	0.397±0.169	19.042	2.343	0.030*
Number of individuals	0.217±0.589	0.838	0.369	0.784
Maternal rank	-0.096±0.044	12.736	-2.158	0.051
Higher-ranked (n = 24)				
(Intercept)	0.496±0.438	11.491	1.132	0.281
Infant activity	-0.250±0.084	20.108	-2.962	0.008*
Rejection	-0.035±0.094	18.852	-0.367	0.718
Non-protectiveness	0.321±0.106	19.733	3.204	0.007*
Number of individuals	0.007±0.014	17.144	0.484	0.635
Maternal rank	-0.009±0.111	13.611	-0.081	0.937
Lower-ranked (n = 24)				
(Intercept)	0.056±2.809	11.096	0.020	0.984

Infant activity	0.046±0.142	17.523	0.324	0.750
Rejection	-0.072±0.227	17.481	-0.316	0.755
Non-protectiveness	0.171±0.158	18.892	1.084	0.292
Number of individuals	0.044±0.171	16.173	2.569	0.021*
Maternal rank	0.0457±0.131	13.186	0.348	0.734
Lower-ranked relative (n = 19)				
(Intercept)	1.888±0.948	10.382	1.991	0.074
Infant activity	-0.060±0.241	14.242	-0.251	0.806
Rejection	-0.352±0.234	18.000	-1.504	0.150
Non-protectiveness	0.390±0.277	18.190	1.408	0.176
Number of individuals	-0.116±0.201	11.989	-0.577	0.575
Maternal rank	-0.045±0.065	10.386	-0.689	0.506
Higher-ranked non-relative (n =24)				
(Intercept)	0.361±0.318	10.216	1.135	0.282
Infant activity	-0.248±0.084	19.915	-2.942	0.008*
Rejection	-0.031±0.094	18.760	-0.328	0.746
Non-protectiveness	0.327±0.106	19.500	3.082	0.006*
Number of individuals	0.007±0.013	16.527	0.574	0.574
Maternal rank	-0.032±0.099	14.162	-0.326	0.749
Lower-ranked non-relative (n = 22)				
(Intercept)	-0.629±2.509	15.561	-0.251	0.805
Infant activity	0.108±0.108	16.886	0.999	0.332
Rejection	-0.039±0.197	16.057	-0.196	0.847
Non-protectiveness	0.005±0.150	14.181	0.030	0.976
Number of individuals	0.067±0.017	16.191	3.910	0.001*
Maternal rank	0.008±0.116	16.700	0.070	0.945

Table 3.5. Relationships between principal component scores and infant handling frequency by female handlers. *Explanatory variable that was retained in the final model with the lowest AIC.

	b±SE	df	t	P
All (n = 24)				
(Intercept)	2.631±0.811	1.234	3.246	0.151
Infant activity	-0.120±0.142	19.397	-0.848	0.407
Rejection	-0.014±0.247	16.980	-0.055	0.956
Non-protectiveness	0.301±0.163	12.787	1.847	0.088
Relative (n = 20)				
(Intercept)	0.335±0.402	3.458	0.833	0.458
Number of individuals	0.267±0.113	9.080	2.362	0.042*
Infant activity	-0.235±0.111	15.709	-2.116	0.051
Rejection	0.065±0.156	5.049	0.414	0.696
Non-protectiveness	0.149±0.135	15.080	1.108	0.285
Non-relative (n = 24)				
(Intercept)	-0.085±3.817	6.601	-0.022	0.983
Number of individuals	0.051±0.113	1.924	0.447	0.700
Infant activity	-0.152±0.124	17.381	-1.220	0.239
Rejection	-0.009±0.247	16.932	-0.036	0.972
Non-protectiveness	0.420±0.158	15.537	2.668	0.017*
Higher-ranked (n = 22)				
(Intercept)	0.403±0.346	11.18	1.163	0.269
Number of individuals	0.009±0.022	11.851	0.409	0.690
Infant activity	-0.239±0.092	16.871	-2.605	0.019*
Rejection	-0.042±0.100	17.663	-0.419	0.680
Non-protectiveness	0.337±0.113	17.350	2.976	0.008*
Lower-ranked (n = 24)				
(Intercept)	1.196±0.802	2.247	1.492	0.261
Number of individuals	0.056±0.025	13.971	2.270	0.040*
Infant activity	0.042±0.139	19.649	0.301	0.767
Rejection	0.014±0.218	13.929	0.064	0.950
Non-protectiveness	0.193±0.165	19.596	1.171	0.256

Lower-ranked relative (n = 19)				
(Intercept)	1.178±0.720	8.811	1.634	0.137
Number of individuals	0.006±0.345	7.665	0.018	0.986
Infant activity	-0.110±0.232	15.000	-0.475	0.642
Rejection	-0.326±0.255	17.000	-1.276	0.219
Non-protectiveness	0.395±0.291	16.000	1.360	0.193
Higher-ranked non-relative (n = 18)				
(Intercept)	0.721±0.476	10.550	1.513	0.160
Number of individuals	-0.010±0.027	10.977	-0.348	0.734
Infant activity	-0.271±0.115	14.755	-2.356	0.033*
Rejection	-0.093±0.129	13.803	-0.724	0.481
Non-protectiveness	0.310±0.133	13.265	2.324	0.037*
Lower-ranked non-relative (n = 22)				
(Intercept)	-0.289±0.532	3.431	-0.543	0.621
Number of individuals	0.087±0.023	15.141	3.889	0.001*
Infant activity	0.115±0.104	15.853	1.112	0.283
Rejection	0.027±0.159	8.778	0.168	0.870
Non-protectiveness	0.059±0.123	16.058	0.478	0.639

Figure 3.1. Distribution of principal component scores. Each point indicates a mother–infant pair.

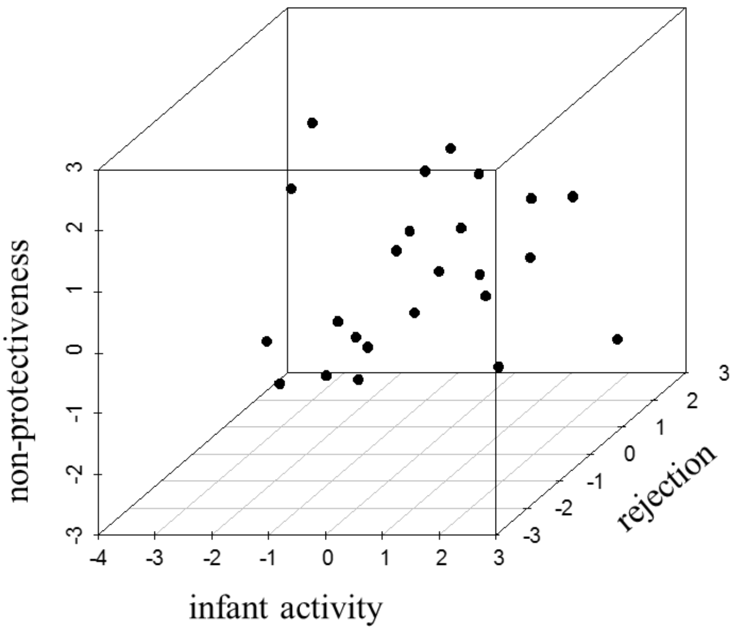


Figure 3.2. Relationship between infant sex and rejection score.

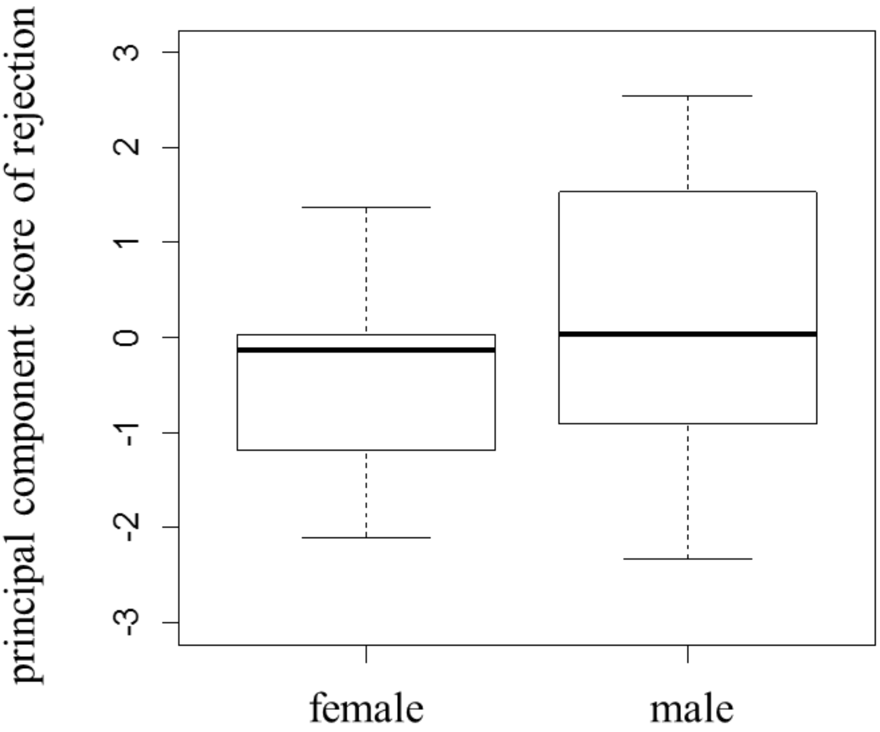


Figure 3.3. Relationship between maternal age and non-protectiveness score.

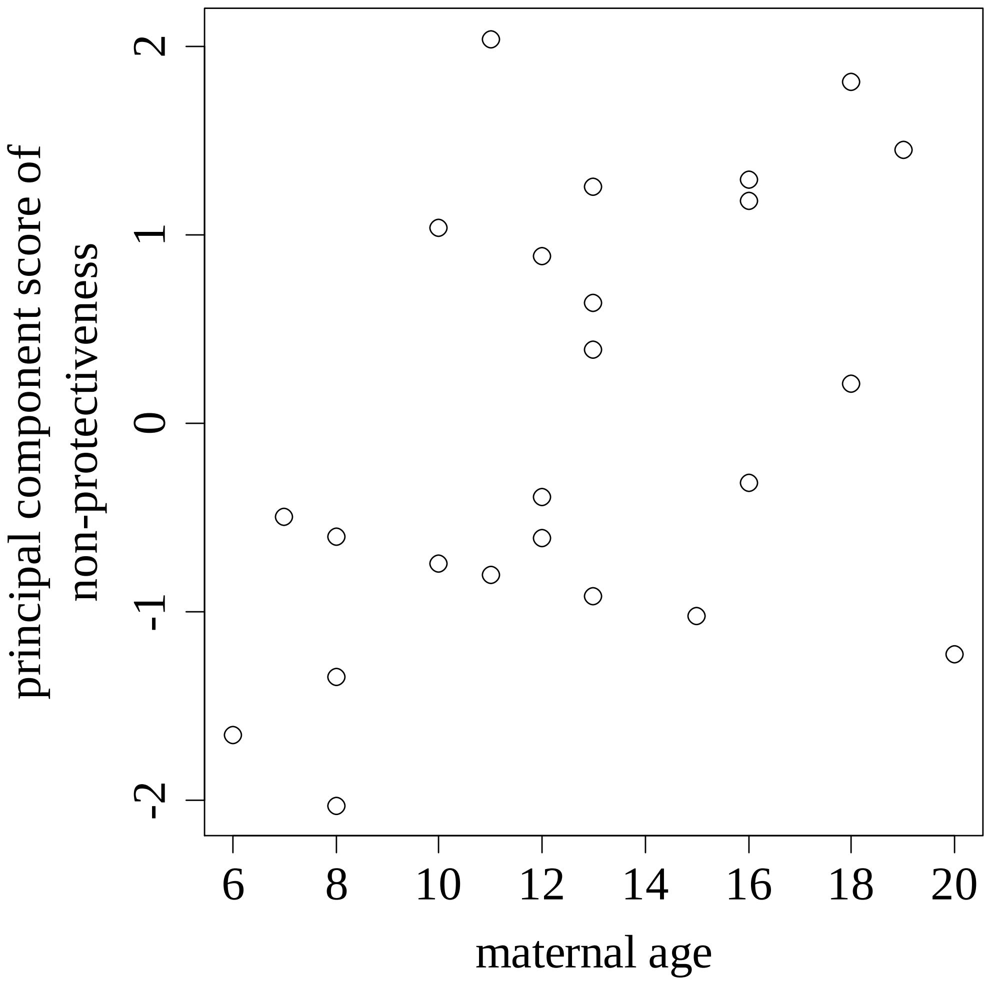


Figure 3.4. Relationships of the frequency of receiving infant handling from any type of handler with non-protectiveness scores (a, b, c) and infant activity (d, e). Each point indicates a mother–infant pair. (a) Non-relatives; (b) higher-ranked handlers; (c) higher-ranked non-relatives; (d) higher-ranked handlers; (e) higher-ranked non-relatives.

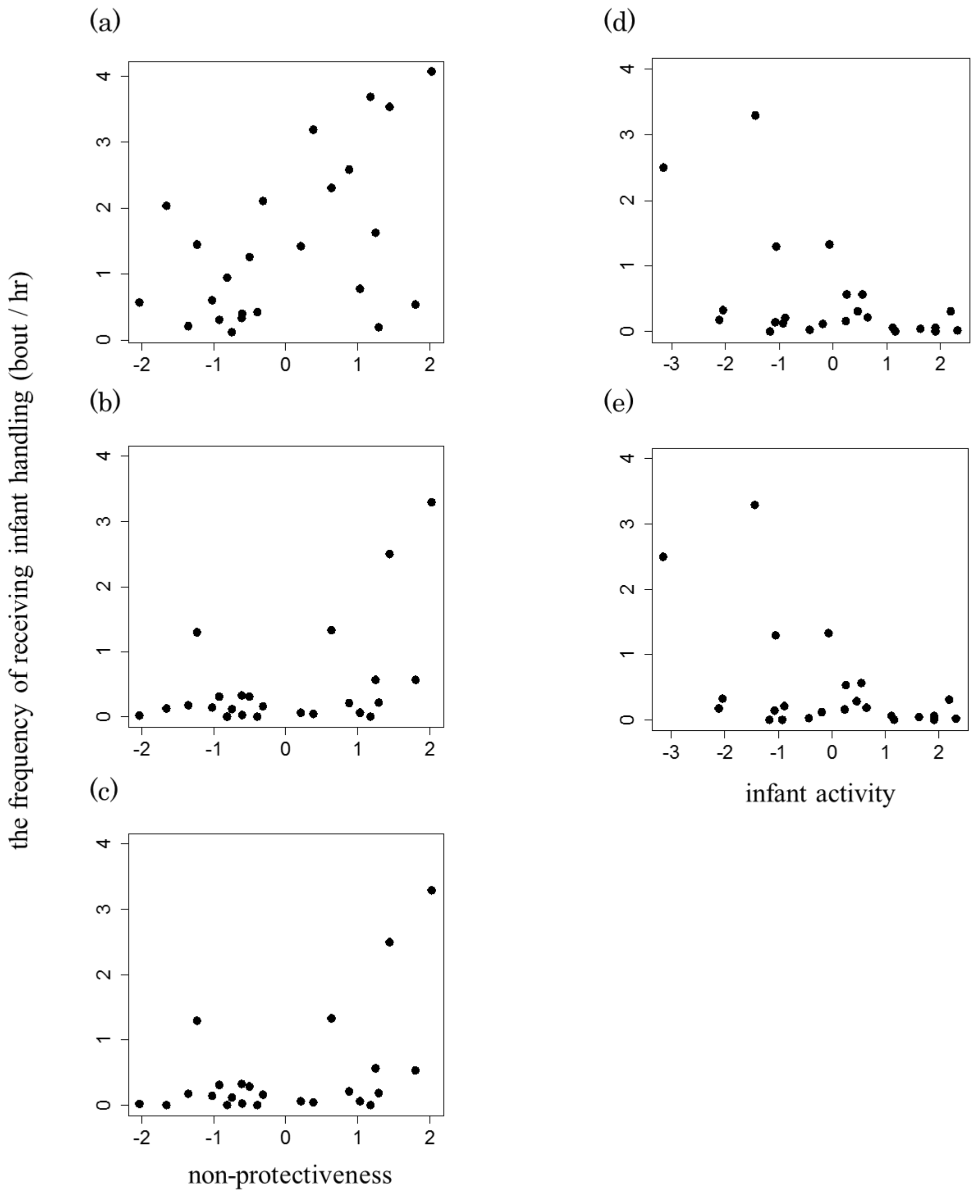
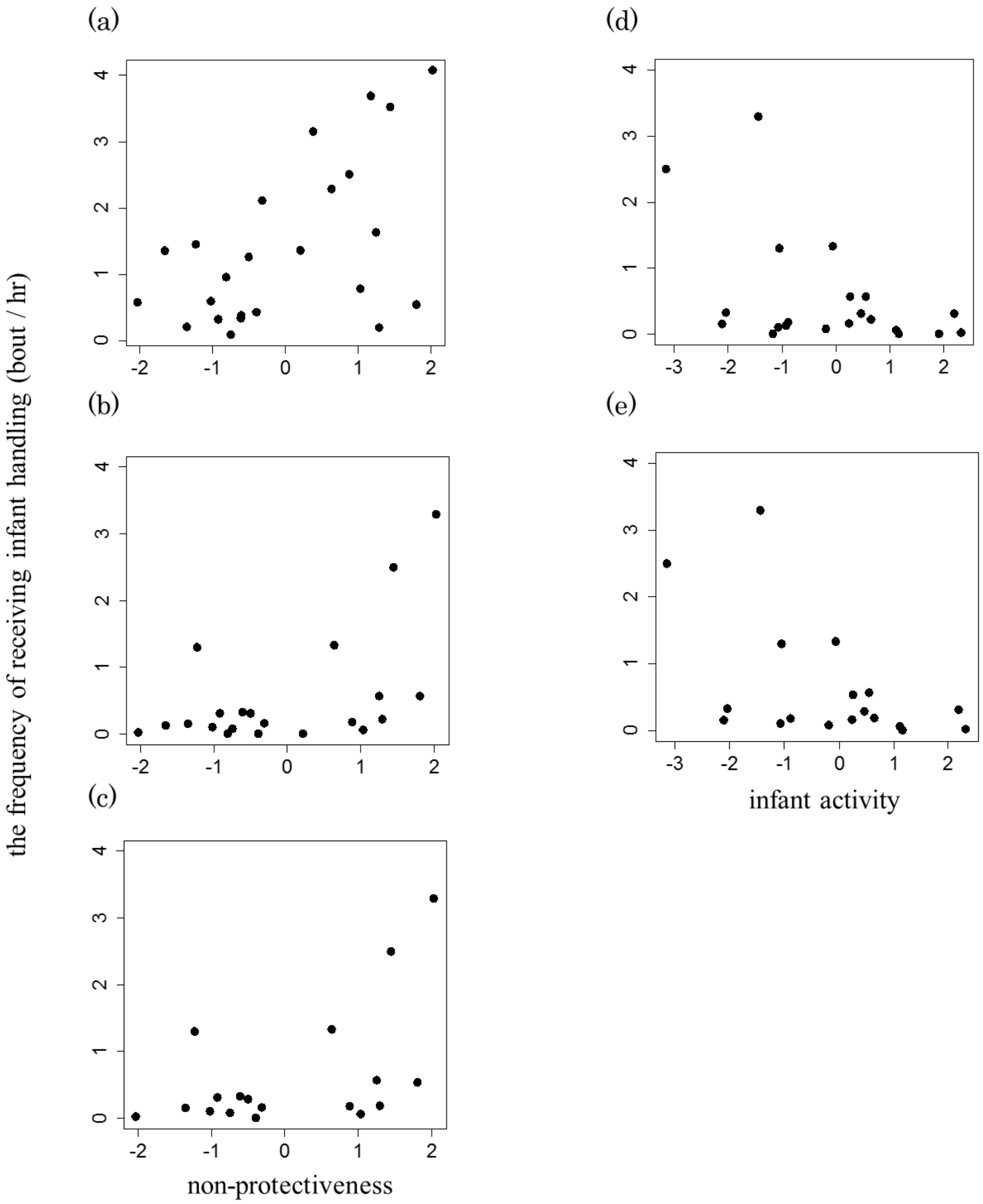


Figure 3.5. Relationships of the frequency of receiving infant handling from female handlers with non-protectiveness scores (a, b, c) and infant activity (d, e). Each point indicates a mother–infant pair. (a) Non-relatives; (b) higher-ranked handlers; (c) higher-ranked non-relatives; (d) higher-ranked handlers; (e) higher-ranked non-relatives.



Chapter 4

Payment of grooming is not always necessary for infant handling in wild Japanese macaques

4.1. Introduction

Biological market theory (BMT) has been proposed for negotiations during an exchange of “commodity” and “service” between asymmetric interactants (Noë & Hammerstein, 1994; 1995). Under BMT, the value of commodity and the amount of service paid to obtain the commodity are determined by the economical market balance of its supply and demand. In other words, in order to obtain rare commodity, it is predicted that individuals need to pay a large amount of services to the owners.

In the context of infant handling, it has been also believed that biological market is formed (Henzi & Barrett, 2002). In this market, so called “baby market”, infants are considered as "commodities", and grooming from handler to mother is considered as "services" (Henzi & Barrett, 2002). The handler’s access to infant may be costly for its mother (Henzi & Barrett, 2002) because handlers sometimes injure or kill the infant (Maestripieri, 1994a; Schino et al, 2003).

Grooming has a function of reducing social tension of its recipient (e.g., Boccia et al, 1989; Schino et al, 1998) and increasing the tolerance of partner on grooming (Gumert & Ho, 2008). So, it is thought that grooming by a handler to an infant’s mother can increase tolerance of mother and a possibility that the handler can handle the infant (Muroyama, 1994; Jiang et al., 2018). If a main purpose of handlers’ grooming is to increase maternal tolerance, it is feasible that social relationship between mother and handler would affect the occurrence and duration of grooming. It is predicted that handlers groom to mother when maternal tolerance is supposed to be low (e.g., when handlers are non-relatives).

In the interchange between grooming and infant handling, the amount of grooming that handlers need to pay to a mother has also been predicted to reflect the value of the infant, which could be determined by multiple factors. The first factor is the balance between supply and demand as the BMT predicts. Given that the value of infants is thought to decrease as a number of infants in a group increases, it is predicted that the amount of grooming by handlers would decrease as the number of infants increases (Henzi & Barrett, 2002; Fruteau et al., 2011; Gumert, 2007; Wei et al., 2013). The second factor that could affect the infant value is the rank distance between mother and handler. In a species with a despotic dominance style among females, for example, there is a possibility that handler is supported during a conflict when a handler forms a friendly relationship with a relatively high-ranked individual (Cheney, 1987; but this hypothesis was not supported in this species; see Chapter 5).

Therefore, the BMT predicts that infants of higher-ranked females are supposed to be more valuable for handlers than those of low-ranked ones. The idea of maternal tolerance also leads the same prediction. Females subordinate to a mother may need to gain tolerance by grooming. If true, it is predicted that rank difference between mother and handler is positively associated with the amount of grooming that handlers need to provide. More specifically, handlers subordinate to a mother should provide grooming more intensively than the one dominant to the mother. This prediction was supported in several (chacma baboons *Papio cynocephalus ursinus*: Henzi & Barrett, 2002; sooty mangabey *Cercocebus atys*: Fruteau et al., 2011; long-tiled monkey *Macaca fascicularis*: Gumert, 2007; Golden Snub-Nosed Monkey *Rhinopithecus roxellana*: Wei et al., 2013), but not all studies (olive baboons *Papio anubis*: Frank & Silk, 2009; tufted capuchin monkey *Cebus apella nigritus*: Tiddi et al, 2009).

As such, previous studies examined the determinants of the grooming before infant handling (Henzi & Barrett, 2002; Frank & Silk, 2009; Tiddi et al, 2009; Gumert, 2007; Fruteau et al., 2011; Wei et al., 2013). For doing so, those studies focused on a situation in which potential handlers provided grooming to mother for an access to infant. However, it remains unclear whether grooming is always necessary for infant handling. Given that grooming is a costly behavior for its actor (e.g., reduction of vigilance, Maestripieri, 1993; Cords, 1995; Ohnishi & Nakamichi, 2011), it would be preferable for handers not to provide grooming for handling an infant if possible. If correct, the physical distance between mother and infant could be a key factor for predicting the occurrence of grooming because handlers can approach an infant without providing grooming to its mother. In line with this idea, Sekizawa and Kutsukake (in press, Chapter 3) showed that infants of “non-protectiveness” mothers, which is characterized by long separation of mother and infant, received infant handling by unrelated and high-ranked (relative to mother) females frequently.

In this chapter, I investigated roles of grooming in infant handling by examining four points.

Relationship between frequency of infant handling and mother-infant distance

First, I examined a relationship between the occurrence of infant handling and physical distance between infant and mother. Given that grooming is costly (Maestripieri, 1993; Cords, 1995; Ohnishi & Nakamichi, 2011) and that mothers may restrict an attempt of infant handling by handlers (Sekizawa & Kutsukake, in press), it is predicted that handlers would be more likely to handle an infant that had been separated from its mother than the one that had been with its mother.

Determinants of grooming occurrence before infant handling

Second, I examined four factors that could affect the occurrence of grooming by handlers before infant handling.

The number of infants: infant’s value is predicted to increase as the number of infants decreases from the BMT. So, it is predicted that grooming is more likely to occur when the number of infants is small in the group.

Relative dominance relationship between handler and mother: from both BMT and maternal tolerance, it is predicted that grooming is likely to occur when the maternal rank is higher than the handler's rank. If the handler is higher-ranked than infant’s mother, mother cannot behave aggressively against the handler. In such case, it is predicted that handlers can handle an infant without grooming.

Relatedness between mother and handler: if the handler is a non-relative of a mother, maternal tolerance to a handler is supposed to be low. So, it is predicted that grooming is more likely to occur when the relatedness between mother and handler is low.

Physical distance between mother and infant: Since mothers are less likely to interfere with an attempt of infant handling by a handler as the distance between the mother and the infant increased, it is predicted that the handlers do not need to provide grooming for increasing maternal tolerance.

In addition, the effects of relatedness, dominance, and the number of infants may interact to the physical distance as it is impossible for handlers to provide grooming to a mother when an infant was distant from its mother. Therefore, we also examined two-way interactions between physical distance and those variables.

Determinants of grooming duration before infant handling

Thirdly, I analyzed the determinants of the amount of grooming before infant handling by using data in which grooming occurred before infant handling. Similar to the predictions on the occurrence of grooming, it is predicted that duration of grooming would increase when the number of infants is small, maternal rank is higher than the handler's rank, handlers are non-relatives of mothers, and a mother and an infant were in contact.

Relationship between the amount of grooming and duration of infant handling

Lastly, I tested whether the durable grooming would result in durable infant handling. If the value of infant is constant, BMT predicts that handling duration would be longer according to the amount of grooming served by a handler to mother.

4.2. Methods

Study site and behavioural observations

See chapter 2.

Data analysis

I excluded the data in which I could not observe all maternal behavior for 10 minutes before the bout of infant handling. I focused on the maternal behavior for 10 minutes immediately before infant handling and calculated duration of grooming by a handler to a mother.

I calculated a possible number of infants that each handler could approach by dividing a number of infants by the number of "potential" handlers. Here, I defined potential handlers as females other than a mother of an infant.

I classified the physical distance between mother and its infant when a handler approached within 1 m of an infant into three categories; "contact", "close", and "distant". When a mother and an infant were in contact (at least a part of their bodies), it was classified as "contact". When the physical distance between a mother and an infant was 1m or less, I classified as "close"; otherwise it was classified as "distant". When a handler interrupted infant handling but resumed within 5 minutes, I regarded these bouts as the same bout of infant handling.

Statistical analysis

In all analyses, the identity of focal pair, the identity of handler, and the study year were included as random terms.

Relationship between frequency of infant handling and mother-infant distance

I analyzed the relationship between frequencies of infant handling and whether mother and infant were in contact by GLMMs. In 44/1038 focal sessions, a focal mother-infant pair kept contact or separated (close and distant) throughout the focal observation. I excluded these sessions from the analysis. I set the frequency (the number of bouts) that the focal infant received infant handling as a response variable in GLMM with Poisson error structure. I controlled for the effects of a separate/contact time by including it as an offset (after log-transformed). I set whether mothers and infants were in contact as an explanatory variable.

Determinants of grooming occurrence before infant handling

In order to examine the necessity of grooming before infant handling, I calculated the proportion that grooming occurred before infant handling in each study year.

To examine the determinants of grooming occurrence, I ran GLMM with binomial error structure. The occurrence of grooming before infant handling was set as a response variable. Explanatory variables included the number of infants, relatedness between mother and handler, rank difference between mother and handler, and physical distance between mother and infant. In addition, I included two-way interactions between the physical distance and the other three variables.

Determinants of grooming duration before infant handling

In this analysis, I used the data subset in which grooming occurred before infant handling. Grooming duration before infant handling was set as a response variable in a (Gaussian) general linear mixed model. Explanatory variables included the number of infants, relatedness between mother and handler, rank difference between mother and handler, and physical distance between mother and infant.

Relationship between the amount of grooming and duration of infant handling

Similar to the preceding analysis, I used the data in which grooming occurred before infant handling and run a (Gaussian) general linear mixed model. In the model, a response variable was the duration of infant handling. Explanatory variables were duration of grooming and random terms were the same as the preceding model.

4.3. Results

Relationship between frequency of infant handling and mother-infant distance

The frequency of infant handling was larger when infants were separated from their mother than when infants and mothers were in contact (b±SE = 3.008±0.065, z=46.290, $p < 0.01$; Fig 4.1). This indicated that infants were handled more frequently when they separated from their mother than when they contacted with their mother.

Determinants of grooming occurrence before infant handling

Grooming was not frequent before infant handling throughout three study years. Grooming occurred in 13.7% (38/278) in 2014, 14.1% (28/198) in 2015, 21.1% (60/285) in 2016 (Fig 4.2). This result indicated that grooming was not necessarily a prerequisite behavior for infant handling.

No two-way interactions involving the physical distance were included in the final model (data not shown). As predicted, grooming was more likely to occur when the rank difference between mother and handler was large (Fig 4.3a; Table 4.1). Also, grooming was less likely to occur as the physical distance between mother and infant increased (Fig 4.3b; Table 4.1), indicating that handlers did infant handling without grooming when an infant was separated from its mother. Other factors did not affect the occurrence of grooming before infant handling (Table 4.1).

Determinants of grooming duration before infant handling

Only the relatedness between mother and handler affected the duration of grooming (Table 4.2). The duration of grooming by handler before infant handling decreased as the relatedness increased (Fig 4.4). Against the prediction from the baby market, the number of infants in the group did not affect the duration of grooming by handler to mother (Table 4.2).

Relationship between the amount of grooming and duration of infant handling

Duration of infant handling was not affected by the amount of grooming before infant handling ($b \pm SE = -0.104 \pm 0.142$, $df = 756.060$, $t = -0.731$, $p = 0.465$; Fig 4.5).

4.4. Discussion

In this paper, we examined a role of grooming before infant handling in wild Japanese macaques by investigating four points.

Relationship between frequency of infant handling and mother-infant distance

I found that infants were handled more frequently when they separated from their mother than when they were in contact with their mother. This result raises a possibility that handlers selected a situation in which grooming was not required. When infants were separated from their mothers, it must be easy for handlers to access infants because mothers may be less likely to interfere with the handler’s attempt.

Determinants of grooming occurrence before infant handling

I found that the occurrence of grooming before infant handling was not frequent throughout three years. This result indicates that grooming before infant handling is not a prerequisite factor for handling an infant for handlers. That is, it is likely that handlers selected an infant that could be handled with low costs (i.e., without providing grooming to a mother). This is reasonable as grooming is a costly behaviour for handlers (see Chap 4.1), and also as a mother may attack a handler that attempts to handle its infant.

By GLMMs, I found that grooming occurred frequently as the rank distance between mother and handler increased. This result supports the prediction from both BMT and maternal tolerance, but a non-significant effect of infant number indicates that the maternal tolerance might be a more suitable explanation than BMT (though these two ideas are not mutually exclusive). Because females form a despotic dominance hierarchy in Japanese macaques, handlers might not be able to approach infants safely as maternal rank was higher than their own. Grooming has a function of reducing social tension of its recipient (e.g., Boccia et al, 1989; Schino et al, 1998). So, grooming before infant handling may have increased the maternal tolerance, by which handlers could access the mother and infant.

Independently of the rank distance, grooming occurred frequently when the physical distance between mother and infant was small. In other words, handlers could access an infant without grooming to a mother when mother and infant were separated. Since it is difficult for a mother to interfere with the contact between infant and handler as the physical distance between the mother and infant is large, it must be easier for handlers to contact an infant. In fact, as I showed above, infants were handled more frequently when they separated from their mother than when they contacted with their mother. Therefore, the pre-handling grooming was not necessary for handlers to increase the maternal tolerance when an infant was separated from its mother.

Determinants of grooming duration before infant handling

Infant number did not affect the grooming duration before infant handling, which disagreed with the prediction from BMT. Also, rank distance between mother and handler did not affect the grooming duration before infant handling. This result again indicated that infant's value was not determined by dominance relationship between mother and infant and disagreed with the prediction of BMT. These non-significant results may not be surprising as functional analyses provided no support for coalition formation hypothesis (Chapter 5). Similarly, the distance between mother and infant did not affect the grooming duration before infant handling. This indicates that a handler groomed a mother to some extent even if that handler attempted to handle an infant that was separated from a mother. There was a possibility that whether handlers could handle an infant was determined by other factors, not by grooming duration. For example, the infant in contact to mother may separate from the mother while the handler was grooming the mother. Also, when other higher-ranked individuals were handling the infant, it is difficult for the handler to handle infants. In these cases, handlers have to wait for an opportunity to handle an infant, until when the handler may need to groom the mother to calm her and to signal the non-agonistic intention to an infant.

The duration of grooming increased as the relatedness between handler and mother decreased. From this result, it was suggested that handlers performed long grooming when the maternal tolerance was supposed to be low. Female-female social relationship of Japanese macaques is nepotistic and maternal tolerance to individuals of low relatedness is lower than individuals of high relatedness (Thierry, 2000).

Relationship between the amount of grooming and duration of infant handling

I found that there was no relationship between handling duration and grooming duration before infant handling, indicating that grooming duration before infant handling was not a determinant of handling duration. Handling duration would be influenced by how infant handling finished. When infant handling was terminated by a handler, the handling duration might reflect the amount of grooming before infant handling. In contrast, when infant handling was terminated by retrieval of an infant by its mother or by infant separation from a handler, the handling duration might not reflect the amount of grooming before infant handling.

Conclusion and implications

From these results, I conclude that grooming before infant handling did not reflect the value of infant because the predicted demand of infant did not affect the grooming occurrence and duration. Grooming occurrence and duration before infant handling changed depending on the social relationship between mother and handler. When maternal tolerance was low, grooming occurrence and duration increased. As grooming can increase the tolerance of partner (Gumert & Ho, 2008), grooming before infant handling may have the function of increasing the maternal tolerance and accessibility to infants.

Table 4.1. Determinants of the occurrence of grooming before infant handling (the number of focal mother-infant pairs was 24. n= 753).

	b±SE	Z	P
(Intercept)	-1.637±0.232	-7.047	<0.001
Number of infants	-0.936±0.622	-1.501	0.133
Relatedness	0.328±0.591	0.554	0.579
Rank difference	-0.024±0.011	-2.302	0.021
Physical distance (χ^2 = 69.713, df = 2, P < 0.001)			
Contact > Close	0.897±0.241	3.719	<0.001
Distant < Close	-1.385±0.286	-4.841	<0.001
Distant < Contact	-2.282±0.289	-7.887	<0.001

Table 4.2. Determinants of grooming duration before infant handling (the number of focal mother-infant pairs was 24. n=126).

	b±SE	df	t	P
(Intercept)	200.220±17.870	24.780	11.231	<0.001
Number of infants	-11.561±66.887	119.649	-0.173	0.863
Relatedness	-196.70±51.150	117.880	-3.846	<0.001
Rank difference	0.893±1.277	91.572	0.699	0.486
Physical distance (χ^2 = 1.062, df = 2, P = 0.588)				
Contact > Close	21.821±26.304	113.260	0.830	0.686
Distant > Contact	6.052±33.058	99.860	0.183	0.982
Distant > Close	27.873±34.105	113.440	0.817	0.693

Figure 4.1. Relationship between frequency of infant handling and whether infants were in contact with their mothers (n = 950). The number of focal mother-infant pair was 24.

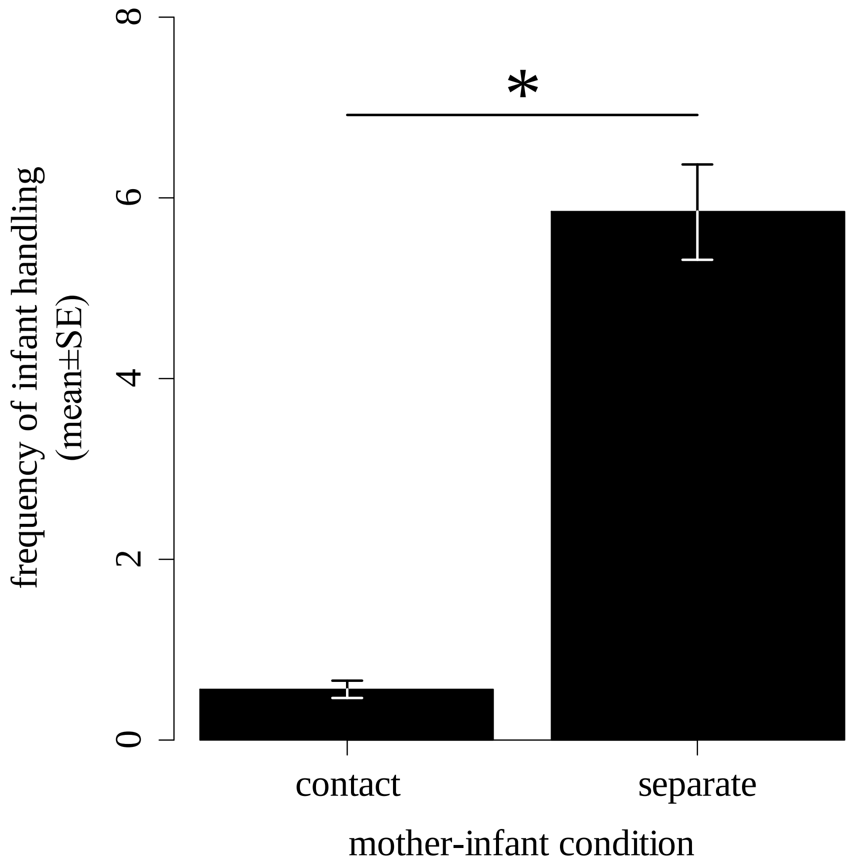


Figure 4.2. Proporiton of grooming occurrence before infant handling in three study-years (n=278 in 2014, 198 in 2015, 285 in 2016). The number of focal mother-infant pair was 12 in 2014, 2 in 2015, and 10 in 2016.

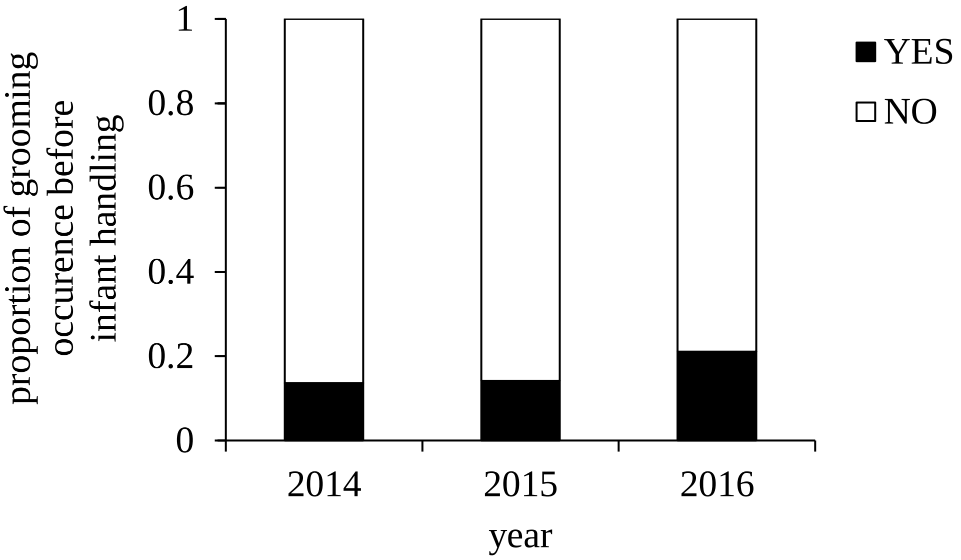
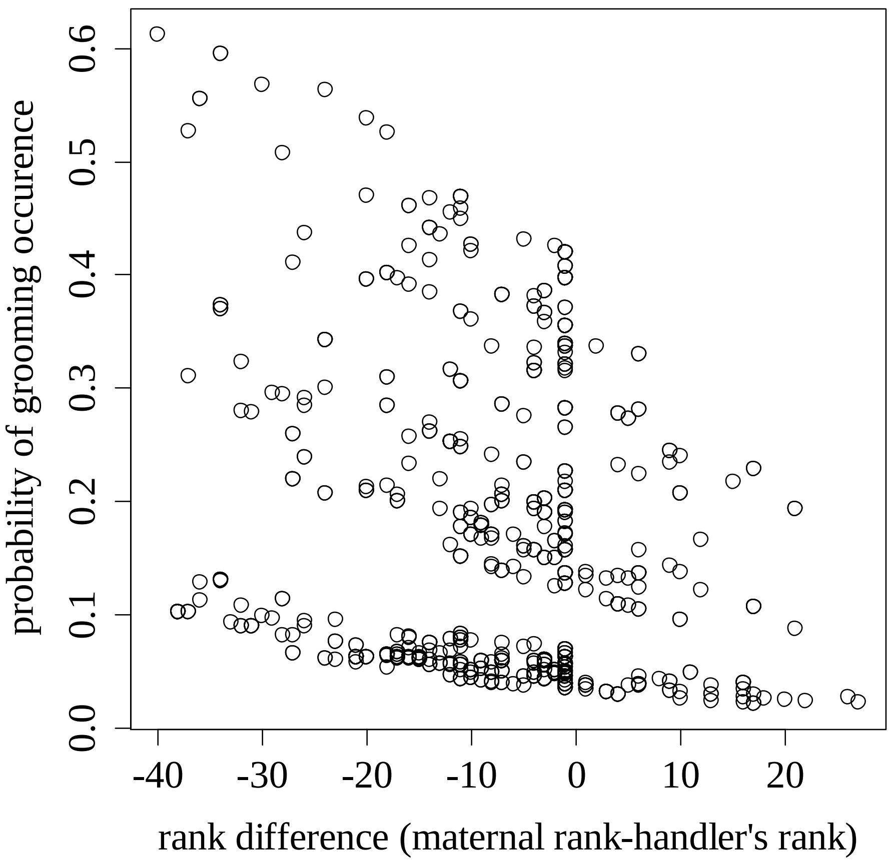
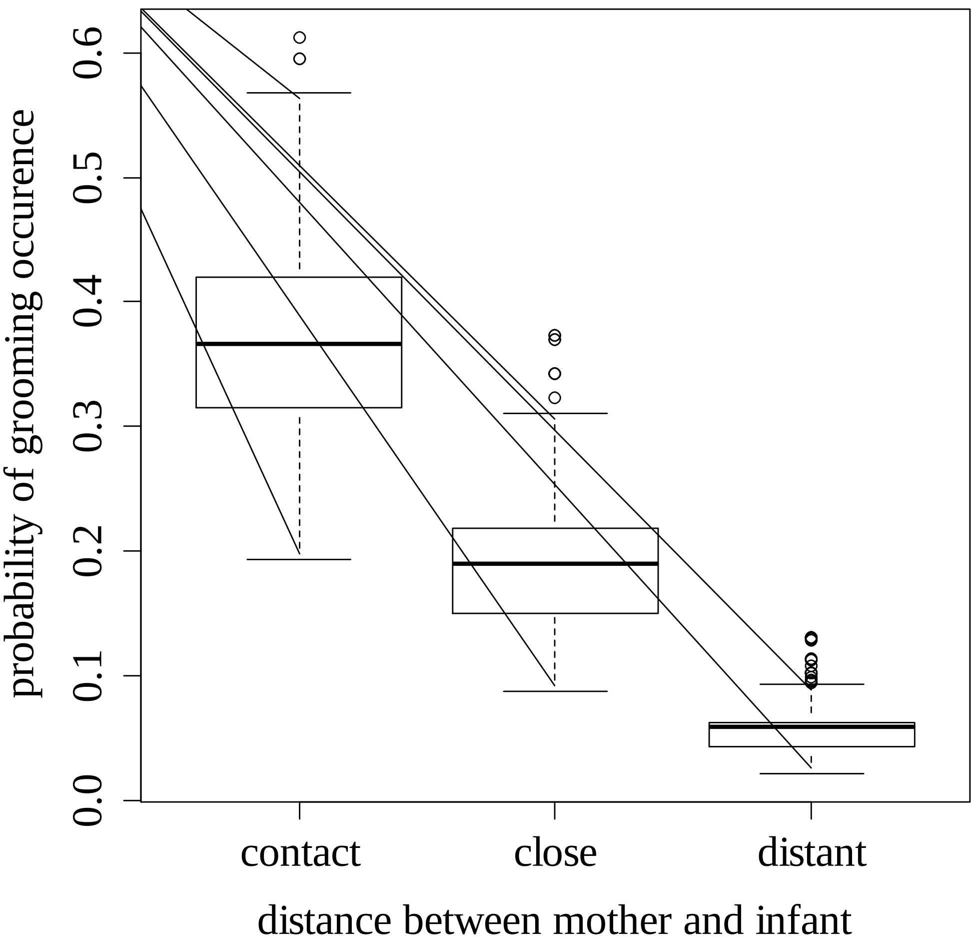


Figure 4.3. A relationship between the occurrence of grooming before infant handling and (a) rank difference between mother and handler or (b) physical distance between mother and infant (n = 753). In (a), a positive value of rank difference (horizontal axis) indicates that a mother was dominant over a handler. In (b), boxplots indicate data for each category. The number of focal mother-infant pair was 24.

(a)



(b)



probability of grooming occurence
0.0
0.1
0.2
0.3
0.4
0.5
0.6
contact
close
distant
distance between mother and infant

Fig 4.4. A relationship between grooming duration before infant handling and maternal relatedness between mother and handler (n = 126). For each category, a boxplot is shown.

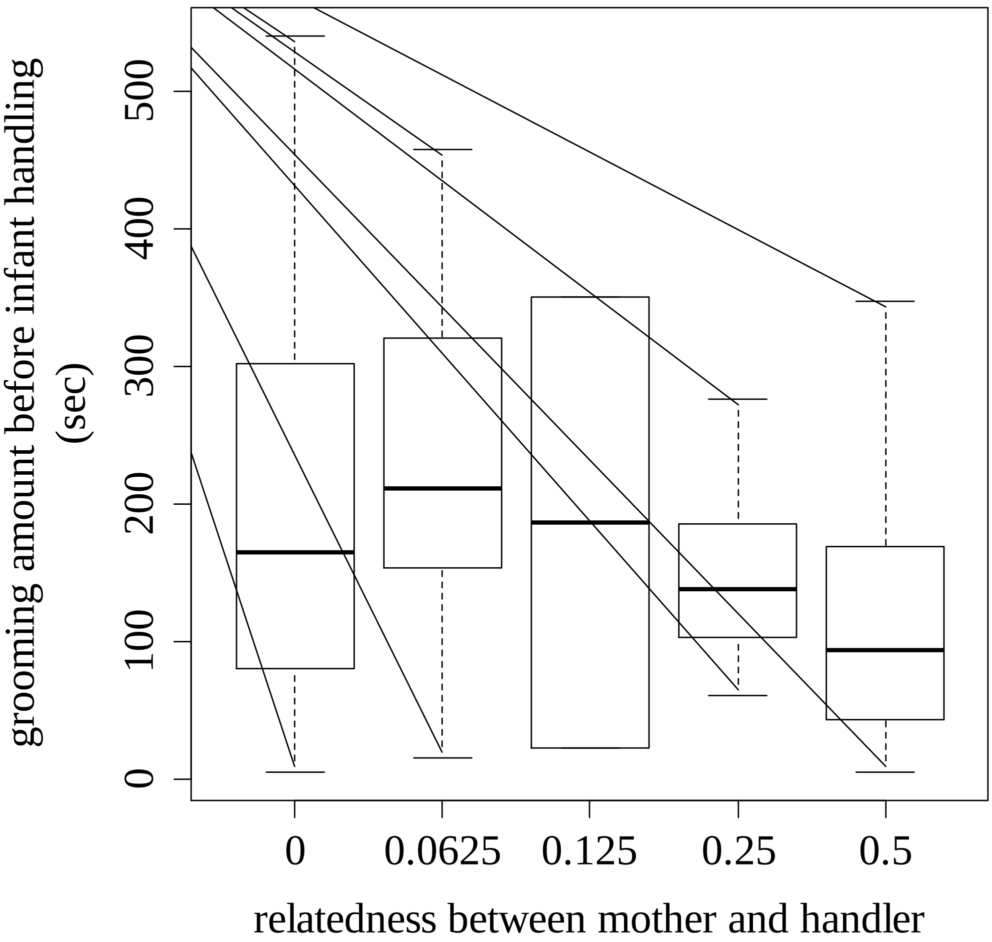
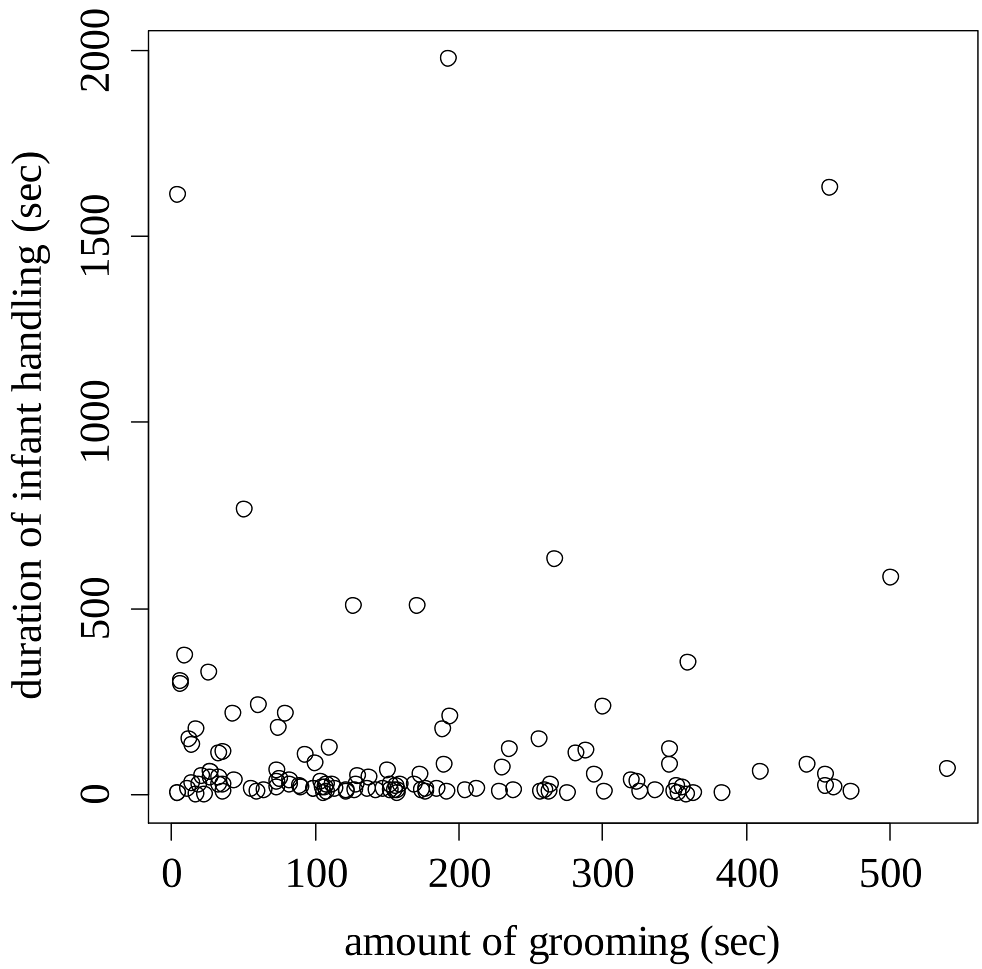


Figure 4.5. A relationship between the duration of infant handling and the amount of grooming before infant handling. Each plot shows one bout of infant handling that occurred after grooming (n = 126). The number of focal mother-infant pair was 24.



Chapter 5

Function of infant handling in wild Japanese macaques

5.1. Introduction

In group-living primates, individuals other than mothers are often attracted by infants (Chapter 1). Why are handlers interested in infants? In previous studies, researchers tested its function by investigating its possible benefits (see Chapter 1) (reviewed in Maestripieri, 1994a) and suggested that an integrated explanation that fits to various species was impossible. Maestripieri (1994a) proposed that functions of infant handling differ not only among species but also within species (Chapter 1).

Previous studies in Japanese macaques reported the occurrence of infant handling (e.g. Hiraiwa, 1981; Schino et al, 2003), but its functional test has not been done. Hiraiwa (1981) speculated that females that had performed handling an infant became better mothers but provided no quantitative data. Schino et al (2003) showed that females without maternal experience mainly performed infant handling and that infant handling by relatives of mother were more tolerated than that by non-relatives. In addition to the lack of quantitative tests, it should be noted that these studies were conducted in free-ranging provisioned or captive groups; no studies were conducted in the wild. For testing hypotheses that consider costs and benefits of infant handling, it is important to study infant handling in a wild group (see Chapter 1).

In this chapter, I tested following five functional hypotheses that are relevant to social characteristics of Japanese macaques. For doing so, I analyzed how characteristics of social relationship between handler and infant or mother affect the frequency and content of infant handling. Note that these hypotheses are not mutually exclusive. Therefore, the results should be carefully interpreted as the opposite predictions from two different hypotheses could cancel out each effect. For example, one category of females (e.g., related females or nulliparous females) and the other ones (e.g., unrelated females or parous females) may perform infant handling for different and each own purpose. If both hypotheses are correct, it is not possible to predict that one category of females perform infant handling more frequently than the other. In other words, it is possible to conclude that one hypothesis is supported only when the other hypothesis was rejected.

Hypothesis 1: Learning-to-mother

This hypothesis proposes that handlers can learn how to treat and rear an infant by infant handling and increase their reproductive success in the future (Lancaster, 1971). This hypothesis predicts that infants are handled by females more frequently than by males (prediction 1a). In addition, it is also predicted that infants are handled by nulliparous females more frequently than by parous ones because it is thought that a necessity of practice for motherhood is higher in nulliparous females than in parous females (prediction 1b), and that nulliparous females may not handle infant roughly (prediction 1c).

Hypothesis 2: Kin selection

This hypothesis proposes that handlers handle related infants and increase a survival rate of relative infants (Riedman, 1982). By doing so, handlers can gain indirect fitness benefits. This hypothesis predicted that infants are handled by relatives more frequently than by non-relatives (prediction 2a), related handlers handle infants positively (prediction 2b), and that proportion of positive handling by relatives are higher than that by non-relatives (prediction 2c).

Hypothesis 3: Reproductive competition among females

Handlers can damage an infant of other females that can be a rival of own offspring by roughly handling. Therefore, infant handling may be a behavioral tactics of reproductive competition among females (Hrdy, 1976). If so, it is predicted that infants are handled by females more frequently than males (prediction 3a); infants are handled by parous females more frequently than nulliparous females (prediction 3b); female infants are handled by parous females more frequently than male infants because females stay in their natal group throughout their life and are likely to become rivals for own offspring (prediction 3c); infants are handled by unrelated parous females more frequently than related parous females (prediction 3d); infants are handled roughly by parous females (prediction 3e); the proportion of negative handling by unrelated parous females is higher than that by related parous females (prediction 3f).

Hypothesis 4: Coalition formation

By handling an infant of a female that can be a preferable social partner, handlers may be able to acquire coalitionary support by that female when conflict occurred (Cheney, 1987). Given that related females often support each other (Thierry, 2000), this hypothesis predicted that infants are handled by handlers unrelated to a mother more frequently than relatives of mother because affiliation between non-relatives is less frequent than between relatives (Chapter 2) (prediction 4a). Also, it is predicted that infants are handled by unrelated lower-ranked handlers than higher-ranked ones because higher-ranked individuals are attractive as coalition partners for lower-ranked ones (prediction 4b); infants are handled positively by lower-ranked handlers (prediction 4c); the proportion of positive handling by lower-ranked individuals is higher than that by higher-ranked ones (prediction 4d).

Hypothesis 5: By-product

This hypothesis presumes that infant handling has no adaptive function but is simply a by-product of a proximate factor such as female's responsiveness induced by the presence of an infant (Quiatt, 1979). This hypothesis predicts that infants are handled by females more frequently than males (prediction 5a); frequencies of infant handling by nulliparous females and parous females do not differ (prediction 5b); infants are more likely to be handled positively than negatively (prediction 5c).

5.2. Methods

Study site and Behavioural observation

See Chapter 2.

Classification of infant handling

Following Schino et al (2003), the contents of infant handling (Table 2.3) was classified into three categories (positive, negative, and neutral) according to possible effects on infant, each of which included behaviors listed below.

Positive: carrying, holding, and grooming.

Neutral: gentle touching by handler's hand, nose, and mouth.

Negative: pulling, graspbing, threating, and aggression.

When the handler restarted the infant handling of the same kind of the category after interruption of the preceding bout within 5 seconds, I regarded these bouts as a single bout of infant handling.

Statistical analysis

For three years, most of infant handling was conducted by females and handling by males was extremely rare (2014: 1/1160, 2015: 10/1233, 2016: 28/1220; Fig 5.1). In addition, functional hypotheses tested in this study mainly focused on benefits of females (see Introduction). So, I excluded the handling by males.

It was not possible to test all predictions by a single analysis. Therefore, we generated a subset of data and ran separate GLMMs for testing each prediction. For example, I excluded data of infant handling by non-relatives when we tested predictions regarding infant handling by relatives. Also, I excluded the data of a focal pair that did not have potential handlers, such as focal pairs that did not have relatives being excluded when testing kin selection hypothesis.

The analyses could be broadly classified into two types according to a response variable. In the first type, I examined the predictors of the frequency of infant handling that each focal infant received in one focal observation. I set that frequency as a response variable in GLMMs with Poisson error structure. Since it is likely that the frequency of infant handling increases as the observational session was long and/or there were many potential handlers, I controlled for those effects by including as an offset (after log-transformed). In the second type, I examined the content of infant handling that each focal infant received in one focal observation. In this type of analysis, I calculated the proportion of each content category out of the total cases of infant handling in one focal observation. For example, the proportion of positive handling in a given focal session was calculated by dividing the number of positive handling by the total cases (i.e., positive + neutral + negative) of infant handling in that focal session. I set the proportion of each type of infant handling as a response term in GLMMs with binomial error structure.

In these GLMMs, the identity of focal individual, focal observation, and the study year were included as random terms.

Explanatory variables used for testing each prediction were listed below. All variables were categorical.

Infant sex: male or female

Handler's parity: parous (females that experienced giving birth) or nulliparous (females with no experience of giving birth)

Dominance: classified into high or low according to relative dominance ranks of a mother and a handler.

Kinship: classified into kin (maternal relatedness is 0.25 or greater) or non-kin (maternal relatedness is less than 0.25). For testing kin selection hypothesis (prediction 2b), I used the kinship between a handler and an infant. For testing reproductive competition among females hypothesis (prediction 3d and 3e) and coalition formation hypothesis (prediction 4a and 4b), I used the kinship between a mother and a handler.

Content of infant handling: positive, negative, or neutral. As this variable had three levels, I examined this effect by comparing the AICs of statistical models including and excluding this variable.

5.3. Results

I summarized predictions and results in Table 5.1. As reported above, the fact that males performed infant handling rarely supported prediction 1a, 3a, and 5a.

1. Learning-to-mother

Infants were handled by nulliparous females more frequently than parous females (Table 5.2; Fig 2.2a). This result supported the prediction 1b. Nulliparous females handled infants positively at the higher rate than neutrally or negatively (Table 5.2; Fig 5.2b). This result supported the prediction 1c.

2. Kin selection

Infants were handled by relatives of infants more frequently than non-relatives (Table 5.2; Fig 5.3a). This result supported the prediction 2a. The proportion of positive infant handling by relatives was higher than those of neutral and negative infant handling (Table 5.2), which supported the prediction 2b.

There was two-way interaction between kinship and content of infant handling, but the proportion of positive handling did not differ between kin and non-kin (Table 5.2; Fig 5.3b). This result did not support the prediction 2c.

3. Reproductive competition among females

As noted above, prediction 3a was supported because infant handling by males were rare. Infants were handled by nulliparous females more frequently than parous females (see the result of prediction 1b), which did not support the prediction 3b. Male infants were handled more frequently by parous females than female infants, but the infant's sex did not remain in the final model (Table 5.2), which disagreed with the prediction 3c. When I analyzed infant handling by parous females, I found that infants were handled by related parous females more frequently than unrelated ones (Table 5.2; Fig 5.4a). This result did not support the prediction 3d. Infants were handled by parous females positively (Table 5.2). This result did not support the prediction 3e.

There was a two-way interaction between content and kinship (Table 5.2). In the analysis of contents, I found no difference in the proportion of negative handling between related parous females and non-related ones (Table 5.2; Fig 2.4b). This result did not support the prediction 3f.

4. Coalition formation

Infants were handled by relatives of mothers more frequently than by non-relatives of mothers (Table 5.2; Fig 5.5a). This result did not support the prediction 4a. When I analyzed infant handling by non-relatives, however, I found that infants were handled by higher-ranked non-relatives more frequently than lower-ranked ones (Table 5.2; Fig 5.5b). This result did not support the prediction 4b. Lower-ranked handlers handled infants positively at the highest rate, which supported prediction 4c (Table 5.2).

There was a two-way interaction between dominance and content of infant handling (Table 5.2). In the analysis of contents, the proportion of positive handling by unrelated lower-ranked handlers was higher than that of unrelated higher-ranked ones (Table 5.3; Fig 5.5c). This result supported the prediction 4d.

5. By-product

Infants were handled by nulliparous females more frequently than parous females (see the result of prediction 1b). This result did not support the prediction 5b. The content of infant handling was more likely to be positive than others (Table 5.2; Fig 5.6). This result supported the prediction 5c.

5.4. Discussion

This study best supported the learning-to-mother hypothesis which proposes that handlers can learn how to handle an infant and can increase their future reproductive success.

Handlers were mostly females (prediction 1a; Fig 5.1) and infants were handled by nulliparous females more frequently than parous females (prediction 1b; Table 5.2, Fig 5.2a). Infant handling by nulliparous females was most likely to be positive (prediction 1c; Table 5.2, Fig 5.2b).

We also found a partial support for the kin selection hypothesis. Supporting prediction 2a, infants were handled by related handlers more frequently than unrelated handlers (Table5.2, Fig 5.3a). Related handlers handled infants positive in most cases (Table 5.2). However, the proportion of positive handling by relatives did not differ from that by non-relatives, which did not support prediction 2c (Table 5.2, Fig 5.3b). This indicated that handlers handled infants positively regardless of whether or not infants were kin or non-kin. This result could be caused by the characteristics of inter-female relationships in Japanese macaque societies, i.e., despotism and nepotism (Chapter 2). In these societies, unrelated handlers might be difficult to approach unrelated infant because of low tolerance by a mother of an infant (Sekizawa and Kutsukake, 2019; Chapter 3), resulting in the frequent handling by related handlers compared to by unrelated handlers.

Other three hypotheses were not supported. Reproductive competition among females hypothesis was not supported because this study did not find the predicted effects of female parity (prediction 3b), infant sex (3c; note that male infants were handled more frequently than females, which is the opposite direction from the prediction), and kinship (3d). It should be noted that the opposite effects of parity and kinship were predicted from other hypotheses (1b and 2a), and were supported (see above). Also, prediction 3e was not supported, as the proportion of negative handling did not differ between related and unrelated parous females. During the observation, I observed neither wounds that could affect the motor ability of infants nor attack by handler to infants. This observation suggests that handlers do not intend to hurt an infant directly.

Coalition formation hypothesis was not supported. Infants were handled by relatives of a mother more frequently than non-relatives of mother, which did not support the prediction 4a. The frequency of infant handling by individuals who were dominant to a mother was significantly higher than by the ones who were subordinate to the mother, disagreeing with prediction 4b. A proportion of positive handling by higher-ranked non-relatives was significantly higher than that by lower-ranked non-relatives. This indicated that handlers lower-ranked than a mother did not selectively perform a positive handling, which did not support the prediction of coalition (prediction 4c). Therefore, it seems that infant handling had no effect of improving affinity with higher individuals that may support during conflict.

Finally, the by-product hypothesis was not supported. Infants were handled positively (prediction 5c), but infants were handled by nulliparous females more frequently than parous females (prediction 5d). These indicated that the degree of interest to infant was higher for nulliparous females than for parous females.

Overall, this chapter showed that the pattern of infant handling best matched to the learning-to-mother hypothesis, i.e., females learned how to treat an infant and increase their future reproductive success. Since the first-born female is unfamiliar with mothering, an infant often died (Sugiyama & Ohsawa, 1982; Itoigawa et al., 1992; Koyama et al., 1992). So, infant handling can be an adaptive behavior to learn how to handle infants for handlers. A previous study proposed that infant handling improve a handler's maternal skill (Hiraiwa, 1981; see Introduction). Still, it is necessary to examine whether handlers really improved their maternal skill and increased their reproductive success by comparing handler's future maternal behaviour and mortality rate of handler's infant with those females that did not perform infant handling or performed infant handling less frequently. There is a necessity of investigating a long-term effect for the kin selection hypothesis that this study partially supported. In this study group, however, infants never died during the observation period. So, it was not possible to test whether infant handling by relatives actually increased survival rate of the infant. This study was not designed to examine the longitudinal positive effects of infant handling on both handlers and infants, again suggesting that longitudinal observation is necessary. Still, it is hard to believe that survival of infants handled during the early development and the handlers' future success of rearing an infant solely depend on whether that handler performed infant handling or not. If so, a low degree to which infant handling contributed to an increase of fitness component, which remains to be studied, indicates an intrinsic difficulty of testing the function of infant handling. Also, it may be premature to conclude that infant handling by parous females or unrelated females, which occurred less frequently, had no purpose although this study did not find supports for the hypotheses. One possibility is that a subtle function that this study did not test is present for infant handling by those individuals. Another possibility is that the function, if any, was hard to detect because whether handlers could access to an infant depends on maternal style (Chapter 3) and opportunistic factors such as the distance between mother and infant (Chapter 4). Further, this chapter showed that the kin and dominance relationship between handler and mother affected the occurrence of infant handling, implying that infant handling by unrelated and/or low-ranked (relative to a mother) handlers were restricted by a mother. These suggest that the occurrence of infant handling at behavioral level is prevented by several social constraints such as “accessibilities” to infant and mother, and may not always reflect handlers’ motivation to access infants.

Table 5.1. Summary of predictions and results of each hypothesis (check mark: supported; cross: not supported).

Hypotheses	Predictions	Results
Learning-to-mother	1a. infants are handled by females more frequently than by males	✔
	1b. infants are handled by nulliparous females more frequently than parous ones	✔
	1c. nulliparous females may handle infant not roughly	✔
Kin selection	2a. infants are handled by relatives more frequently than by non-relatives	✔
	2b. related handlers handle infants positively	✔
	2c. proportion of positive handling by relatives are higher than that by non-relatives	X
Reproductive competition	3a. infants are handled by females more frequently than males	✔
	3b. infants are handled by parous females more frequently than nulliparous females	X
	3c. female infants are handled by parous females more frequently than male infants	X
	3d. infants are handled by unrelated parous females more frequently than related parous females	X
	3e. infants are handled roughly by parous females	X
	3f. proportion of negative handling by unrelated parous females is higher than that by related parous females	X
Coalition formation	4a. infants are handled by handlers unrelated to a mother more frequently than relatives of mother	X
	4b. infants are handled by unrelated lower-ranked handlers than higher-ranked ones	X
	4c. infants are handled positively by lower-ranked handlers	✔
	4d. proportion of positive handling by lower-ranked non-relatives is higher than that by higher-ranked ones	✔

By-product	5a. infants are handled by females more frequently than males 5b. frequency of infant handling by nulliparous females and parous females do not differ 5c. infants are more likely to be handled positively than negatively	✔ X ✔

Table 5.2. Results of analysis for each prediction.

	b±SE	z	P
Learning-to-mother			
Prediction 1b: Handler's parity			
(Intercept)	-2.759±0.377	-7.320	<0.001
Handler's parity (nulliparous > parous)	-2.254±0.051	-43.870	<0.001
Prediction 1c: proportion of content of infant handling by nulliparous female			
(Intercept)	-1.405±0.045	-31.375	<0.001
Content ($\chi^2 = 1160.3$, df = 2, $p < 0.001$)			
Positive > Neutral	1.453±0.055	26.280	<0.001
Positive > Negative	1.678±0.057	29.223	<0.001
Neutral > Negative	0.225±0.061	3.669	<0.001
Kin selection			
Prediction 2a: Kinship			
(Intercept)	-1.505±0.344	-4.380	<0.001
Kinship (kin > non-kin)	-2.285±0.042	-54.410	<0.001
Prediction 2b: Proportion of content of infant handling by relatives			
(Intercept)	-1.271±0.085	-15.026	<0.01
Content ($\chi^2 = 362$, df = 2, $p < 0.001$)			
Positive > Neutral	1.821±0.114	15.952	<0.001
Positive > Negative	1.639±0.111	14.835.	<0.001
Neutral < Negative	-0.181±0.123	-1.471	0.141
Prediction 2c: Difference between kinship in proportion of content of infant handling			
(Intercept)	-1.271±0.085	-15.026	<0.001
Kinship × Content ($\chi^2 = 18.231$, df = 2, $p < 0.001$)			
(Intercept)	0.279±0.153	1.821	0.069
Positive (kin > non-kin)	-0.066±0.122	-0.538	0.591
(Intercept)	-1.421±0.345	-4.118	<0.001
Neutral (kin < non-kin)	0.203±0.159	1.272	0.203
(Intercept)	-1.862±0.364	-5.115	<0.001
Negative (kin > non-kin)	0.093±0.156	0.591	0.555

Reproductive competition among females			
Prediction 3c: infant's sex			
(Intercept)	-3.627±0.637	-5.699	<0.01
Infant's sex (male > female)	0.789±0.420	1.880	0.060
Prediction 3d: kinship between parous females and mother			
(Intercept)	-5.519±0.819	-6.740	<0.01
Kinship (kin > non-kin)	-1.105±0.131	-8.430	<0.01
Prediction 3e: Proportion of content of infant handling by parous females			
(Intercept)	-1.054±0.112	-9.437	<0.001
Content ($\chi^2 = 47.682$, df = 2, p < 0.001)			
Positive > Neutral	0.813±0.147	5.538	<0.001
Positive > Negative	0.912±0.149	6.125.	<0.001
Neutral > Negative	0.098±0.156	0.625	0.532
Prediction 3f: Difference between kinship in proportion of content of infant handling by parous females			
(Intercept)	-2.041±0.336	-6.073	<0.001
Content ($\chi^2 = 66.944$, df = 2, p < 0.001)			
(Intercept)	-0.718±0.780	-0.920	0.357
Positive (kin > non-kin)	-0.592±0.547	-1.083	0.279
(Intercept)	-1.900±0.584	-3.254	0.001
Neutral (kin < non-kin)	0.694±0.619	1.121	0.262
(Intercept)	0.494±1.626	0.304	0.761
Negative (kin > non-kin)	-0.913±1.063	-0.859	0.390
Coalition formation			
Prediction 4a: Kinship between handler and mother			
(Intercept)	-1.588±0.341	-4.660	<0.001
Kinship (kin > non-kin)	-2.460±0.040	-61.700	<0.001
Prediction 4b: Frequency of infant handling by non-relatives			
(Intercept)	-4.881±0.488	-10.002	<0.001
Dominance (higher > lower)	-0.174±0.052	-3.331	<0.001

Prediction 4c: Proportion of content of infant handling by lower-ranked handlers			
(Intercept)	-1.349±0.063	-21.408	<0.01
Content ($\chi^2 = 512.5$, df = 2, $p < 0.001$)			
Positive > Neutral	1.397±0.079	17.703	<0.001
Positive > Negative	1.578±0.081	19.412.	<0.001
Neutral > Negative	0.181±0.087	2.082	0.038
Prediction 4d: Difference between dominance in proportion of content of infant handling by non-relatives			
(Intercept)	-0.967±0.081	-12.008	<0.01
Content ($\chi^2 = 110.5$, df = 2, $p < 0.001$)			
(Intercept)	-0.080±0.189	-0.424	0.672
Positive (higher < lower)	0.449±0.196	2.296	0.022
(Intercept)	-1.451±0.343	-4.235	<0.001
Neutral (higher < lower)	0.462±0.220	2.098	0.036
(Intercept)	-1.212±0.319	-3.796	<0.001
Negative (higher > lower)	-1.256±0.274	-4.581	<0.001
By-product			
Prediction 5b: Proportion of content of infant handling			
(Intercept)	-1.360±0.042	-32.763	<0.001
Content ($\chi^2 = 1180.3$, df = 2, $p < 0.001$)			
Positive > Neutral	1.376±0.052	26.635	<0.001
Positive > Negative	1.584±0.053	29.631	<0.001
Neutral > Negative	0.208±0.057	3.641	<0.001

Figure 5.1. Proportions of infant handling by male and female handlers in each year. 2014: 0.09%, 2015: 0.81%, 2016: 2.30%. "n" indicates the number of focal mother-infant pairs. 2014: 1160 bouts, 2015: 1233 bouts, 2016: 1220 bouts.

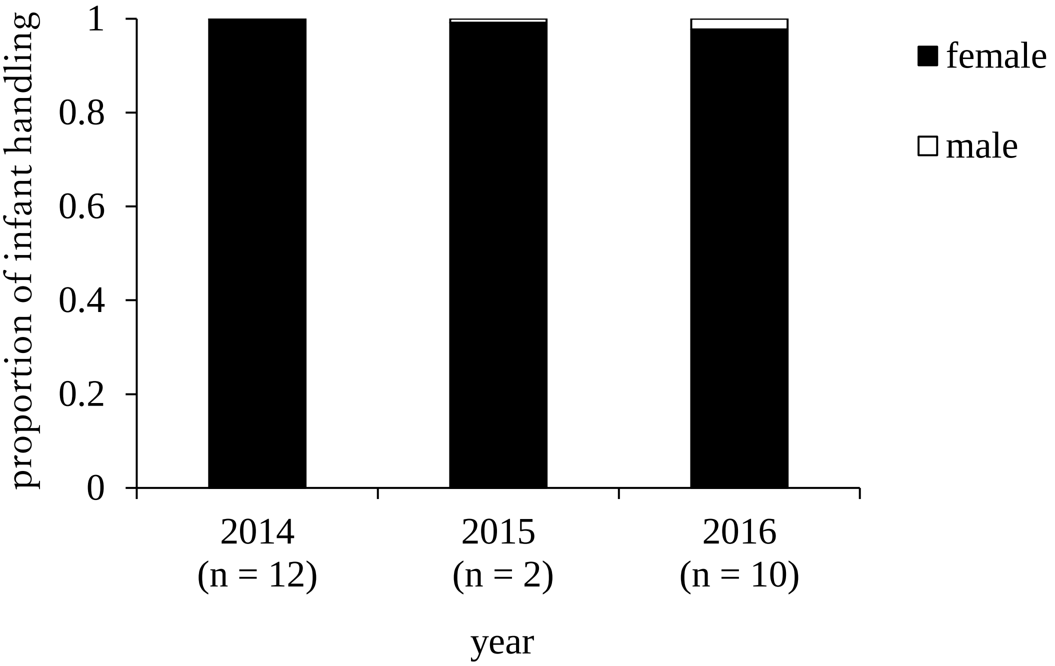
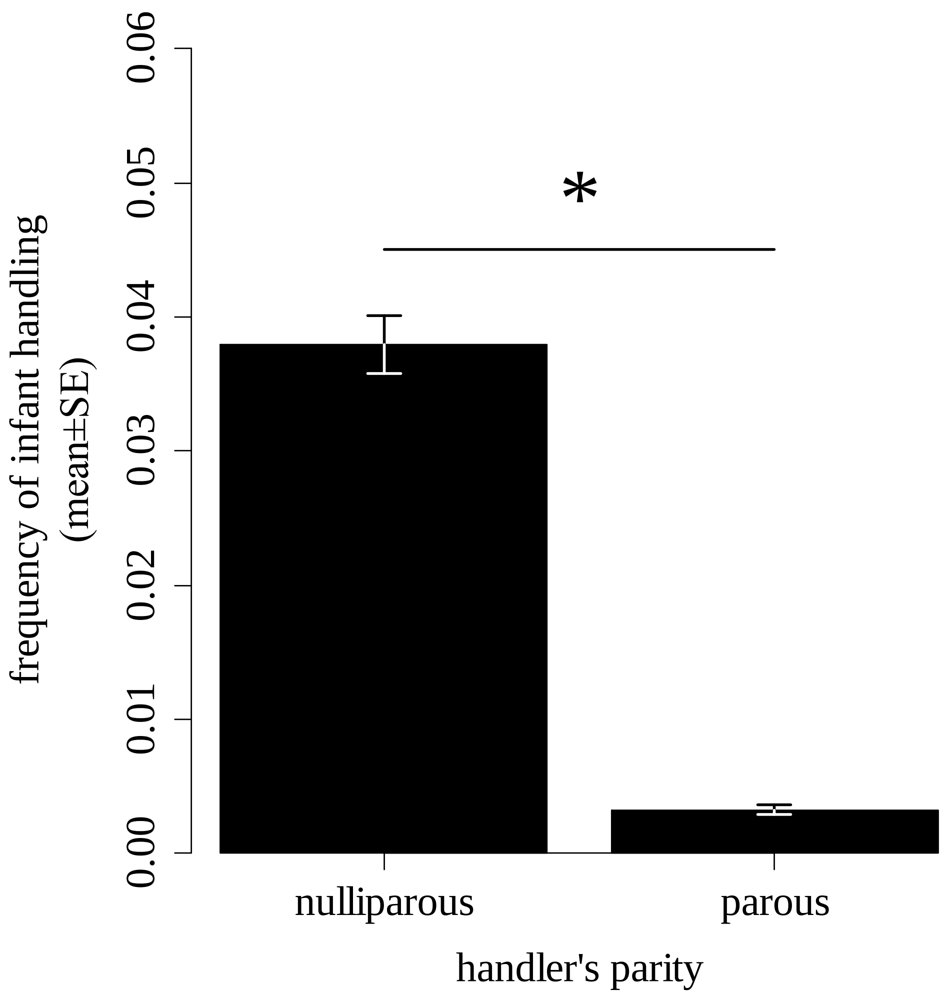


Figure 5.2. (a) Frequency of infant handling by nulliparous and parous females. Mean (+SE) values per one potential handler per one hour are shown (n = 519). (b) Proportion of infant handling in each handling content by nulliparous females (n = 3152). An asterisk indicated a statistical difference. The number of focal individuals was 24.

(a)



(b)

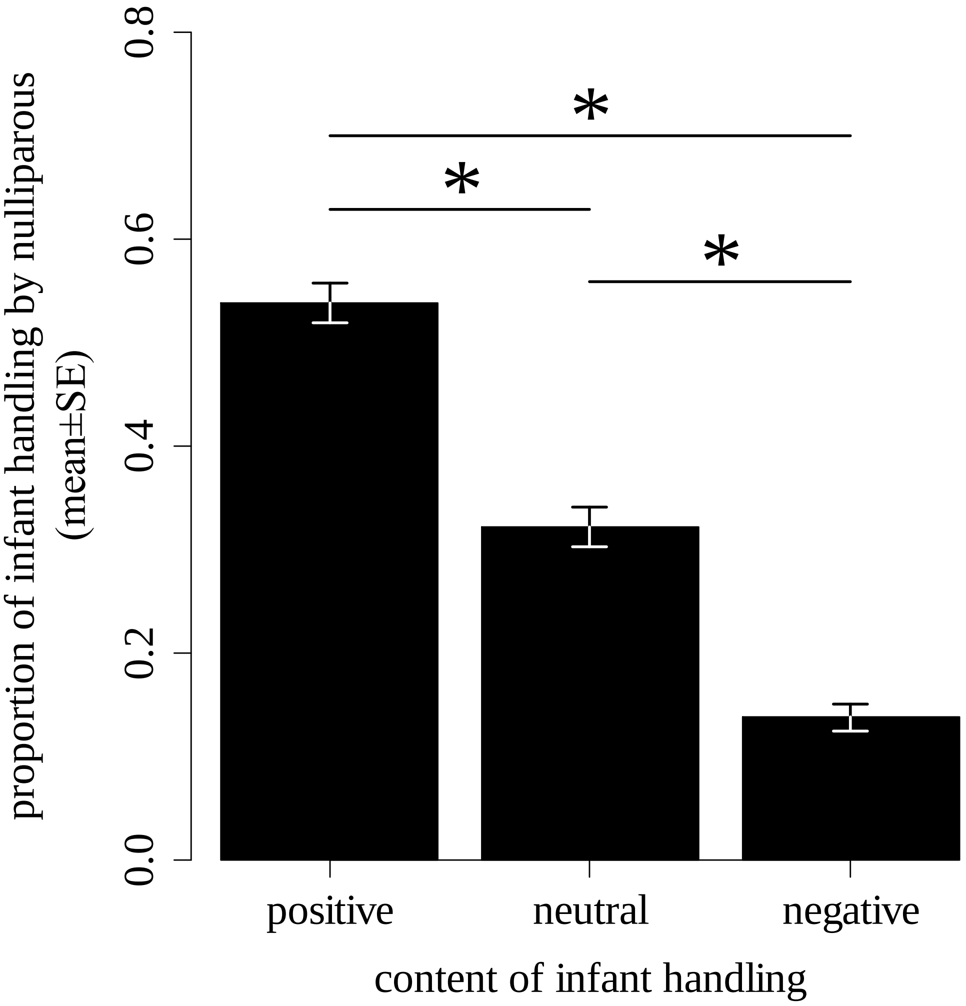
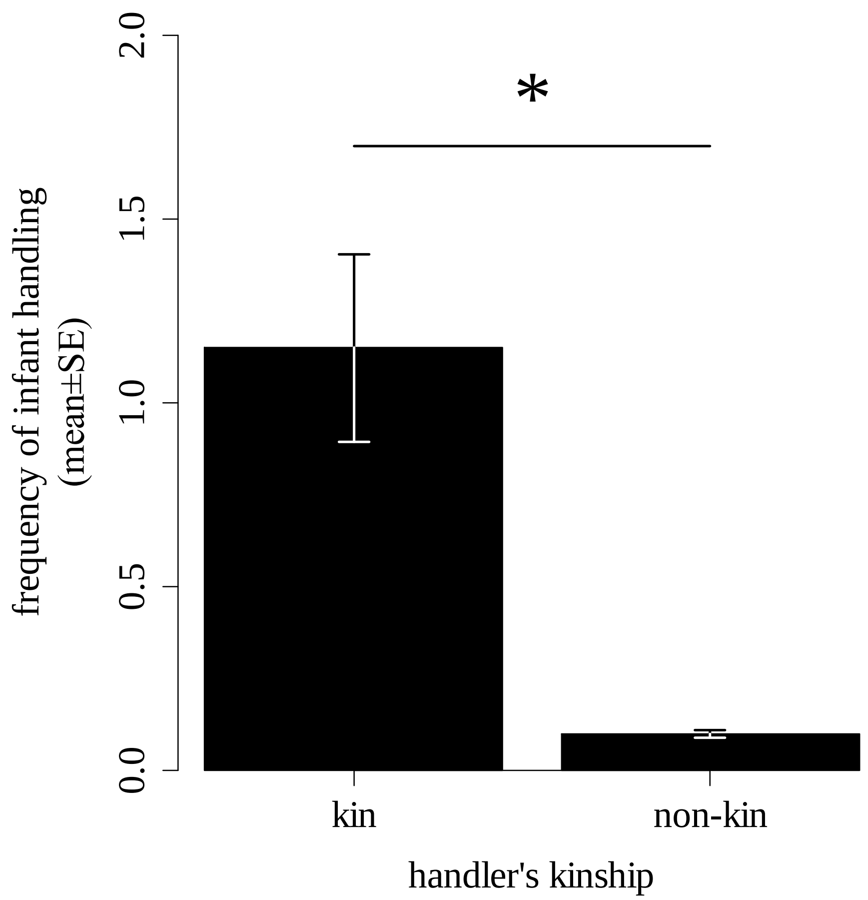
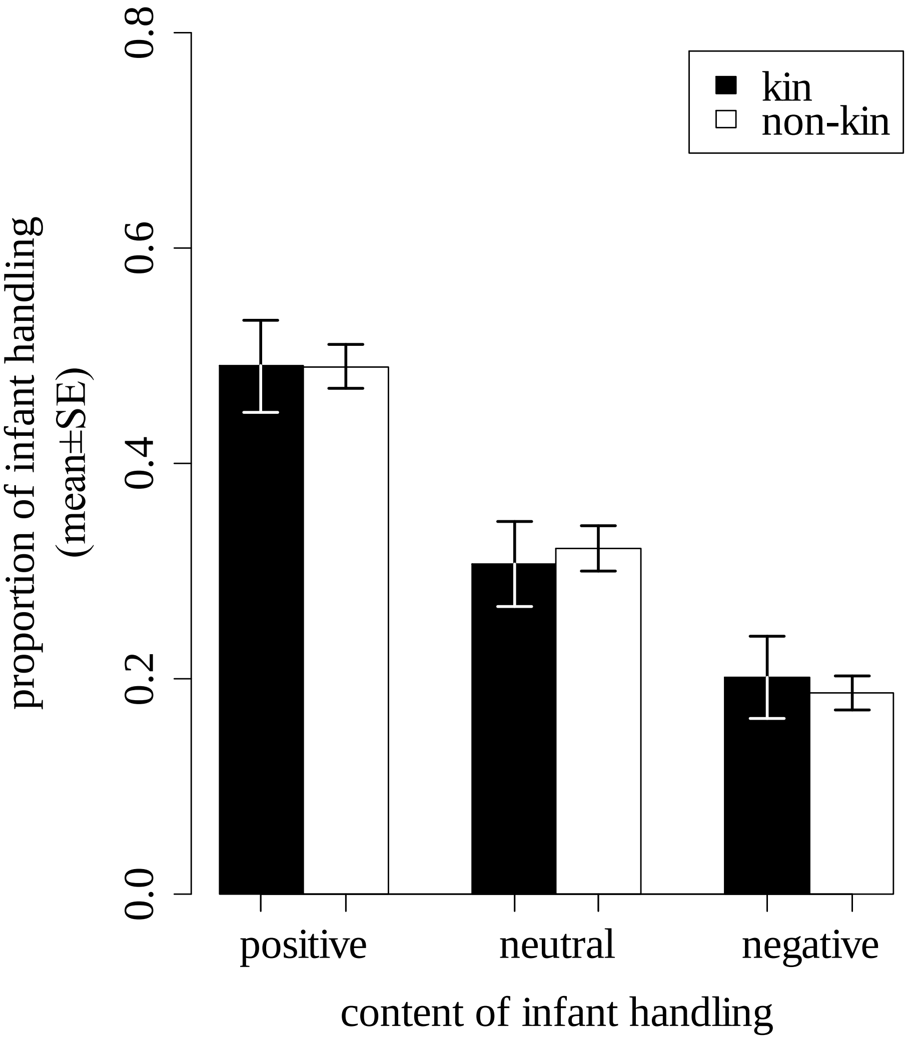

proportion of infant handling by nulliparous
(mean±SE)
0.0
0.2
0.4
0.6
0.8
*
*
*
positive
neutral
negative
content of infant handling

Figure 5.3. (a) Frequency of infant handling by kin and non-kin handlers. Mean (+SE) values per one potential handler per one hour are shown (n = 339). (b) Relationship between proportion of positive or non-positive handling and kinship (n = 3314). In both analyses, the number of focal individuals was 15. An asterisk indicated a statistical difference.

(a)



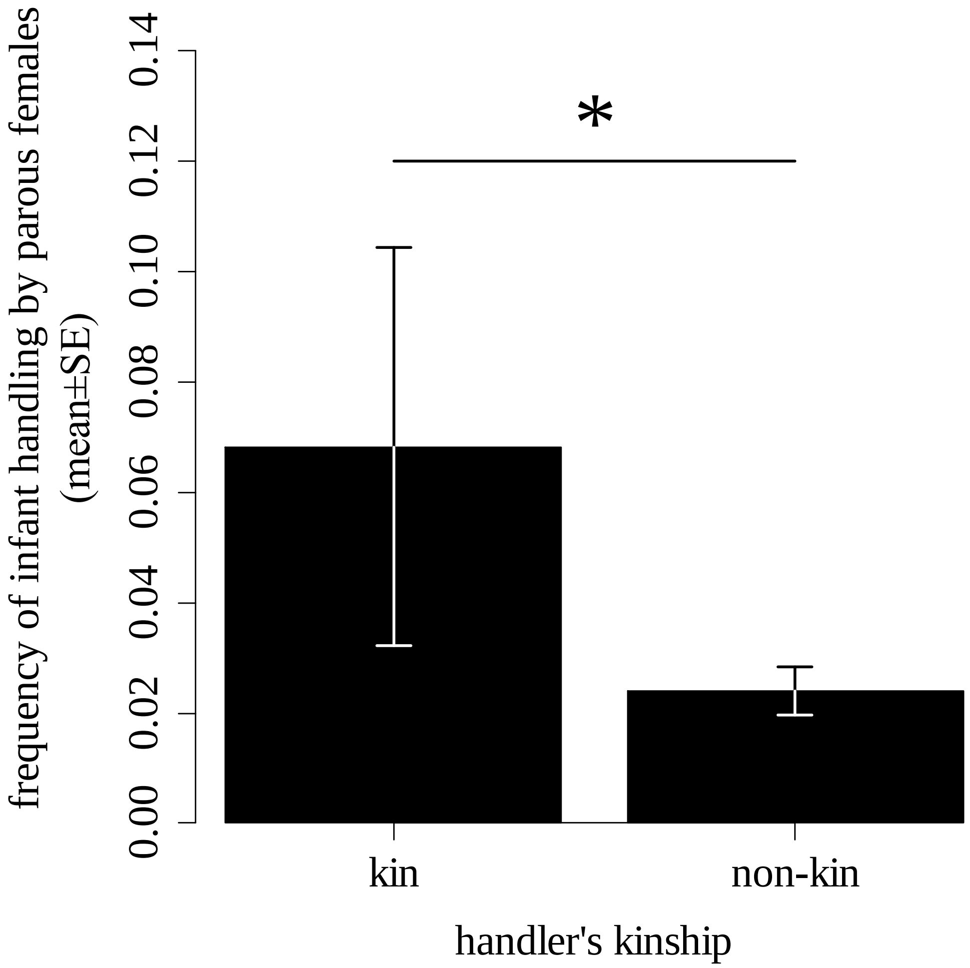
(b)



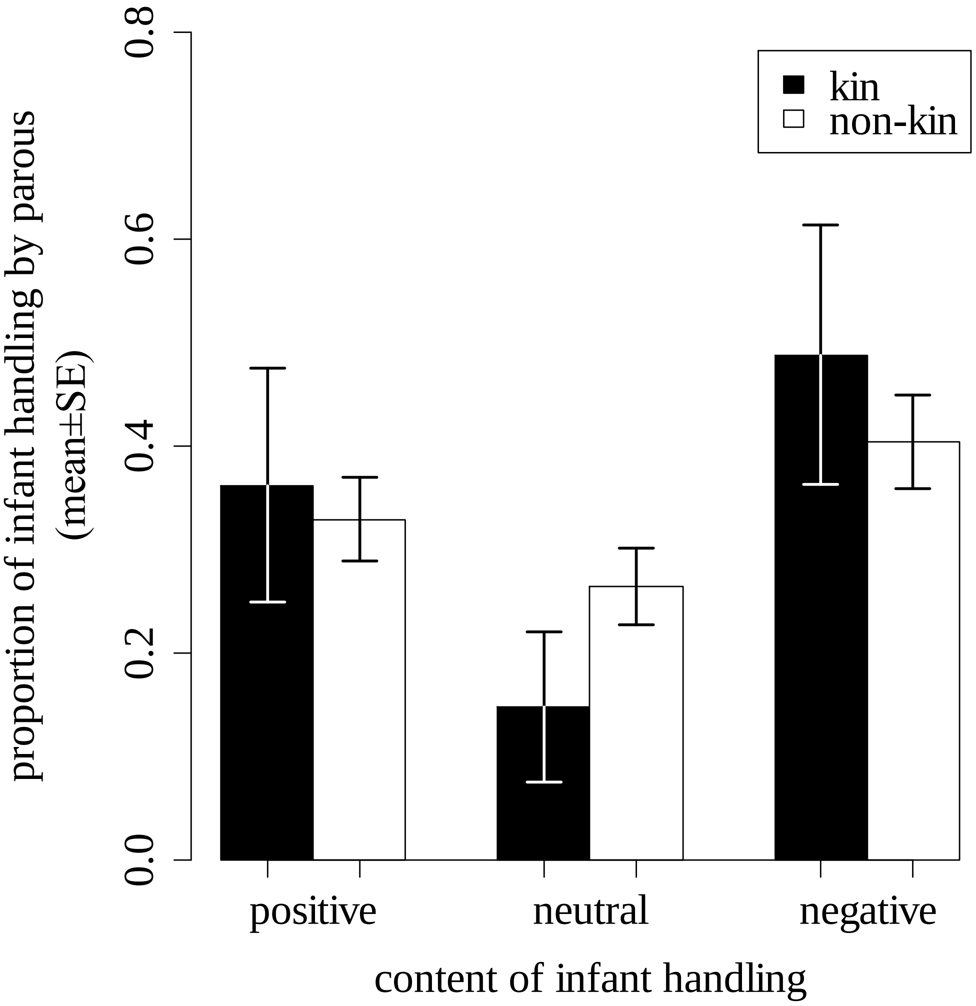
0.0
0.2
0.4
0.6
0.8
proportion of infant handling
(mean±SE)
kin
non-kin
positive
neutral
negative
content of infant handling

Figure 5.4. (a) Relationship between frequency of infant handling by parous females and kinship between mother and handler (n = 306). Mean (+SE) values per one potential handler per one hour are shown. (b) Relationship between proportion of content of infant handling by parous females and kinship between mother and handler (n = 418). In (a) and (b), the number of focal individuals was 15. An asterisk indicated a statistical difference.

(a)



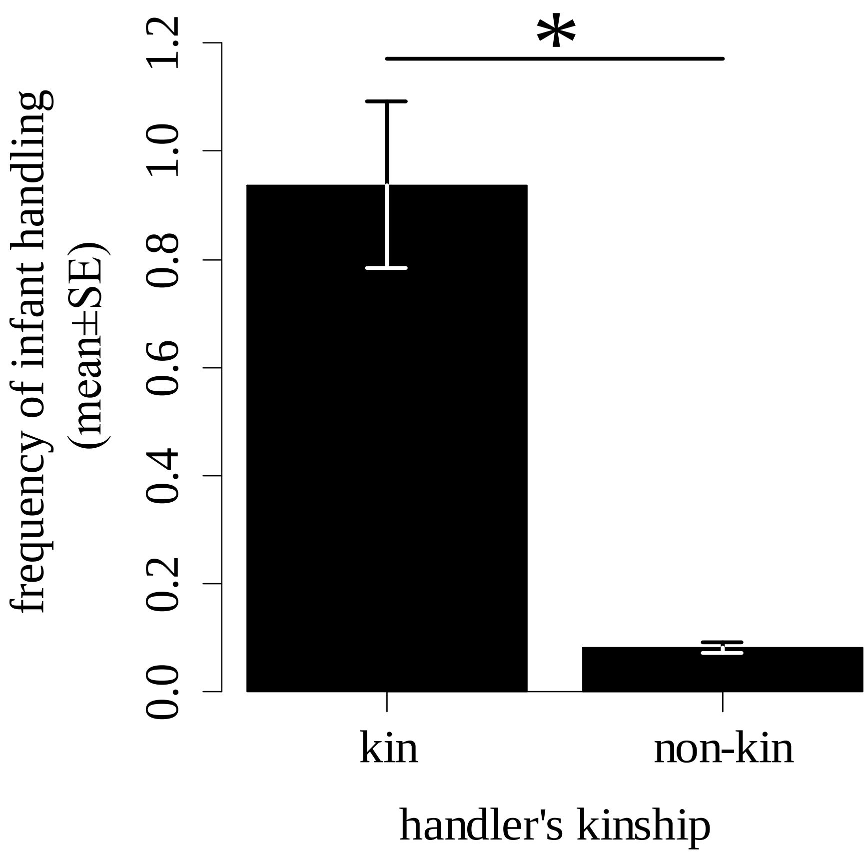
(b)



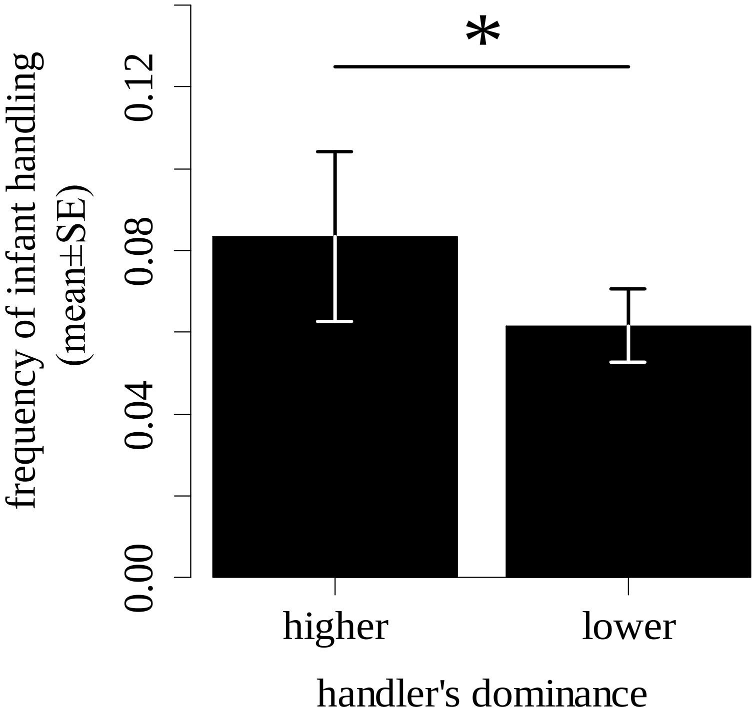
0.8
0.6
0.4
0.2
0.0
proportion of infant handling by parous
(mean±SE)
kin
non-kin
positive
neutral
negative
content of infant handling

Figure 5.5. (a) Frequency of infant handling by kin and non-kin (n = 356 for 20 focal individuals). (b) Frequency of infant handling by non-related handlers (n = 362 for 16 focal individuals). In (a) and (b), mean (+SE) values per one potential handler per one hour are shown. (c) proportions of handling content by higher or lower handlers (n = 1539 for 16 focal individuals). An asterisk indicated a statistical difference.

(a)



(b)


*
0.00
0.04
0.08
0.12
frequency of infant handling
(mean±SE)
higher
lower
handler's dominance

(c)

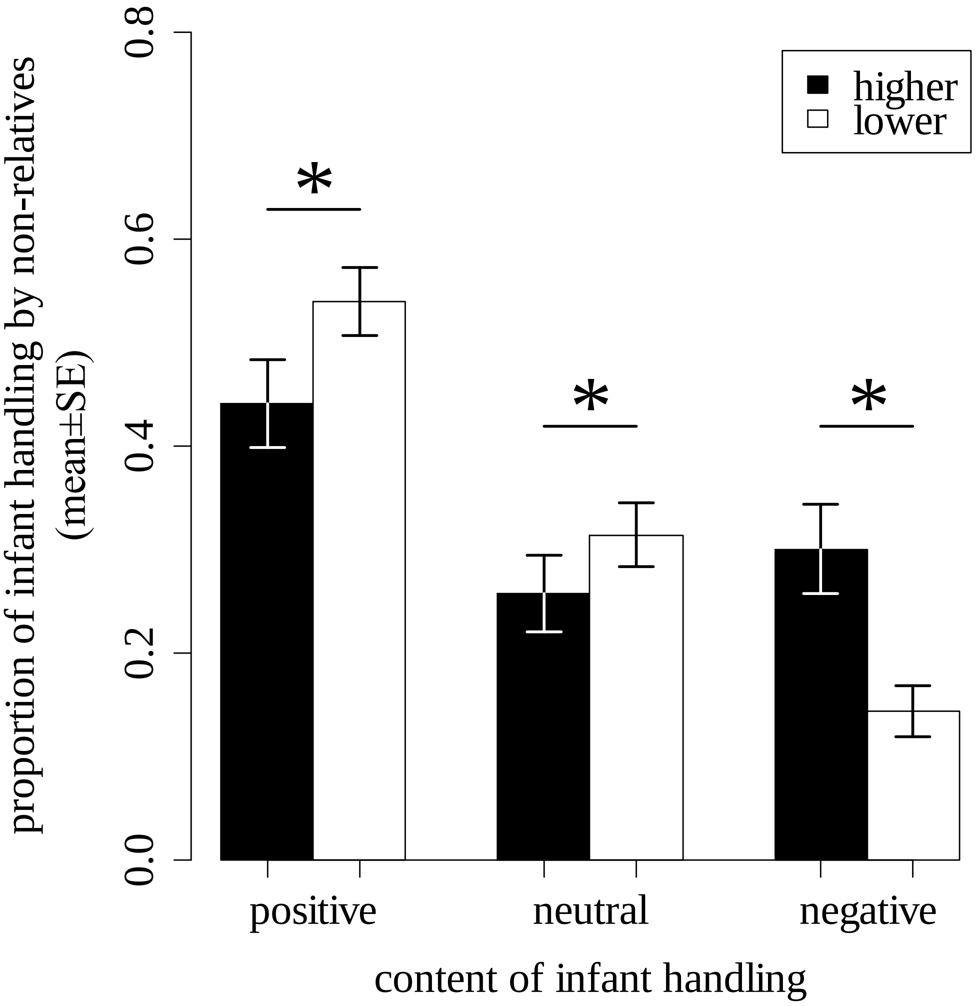
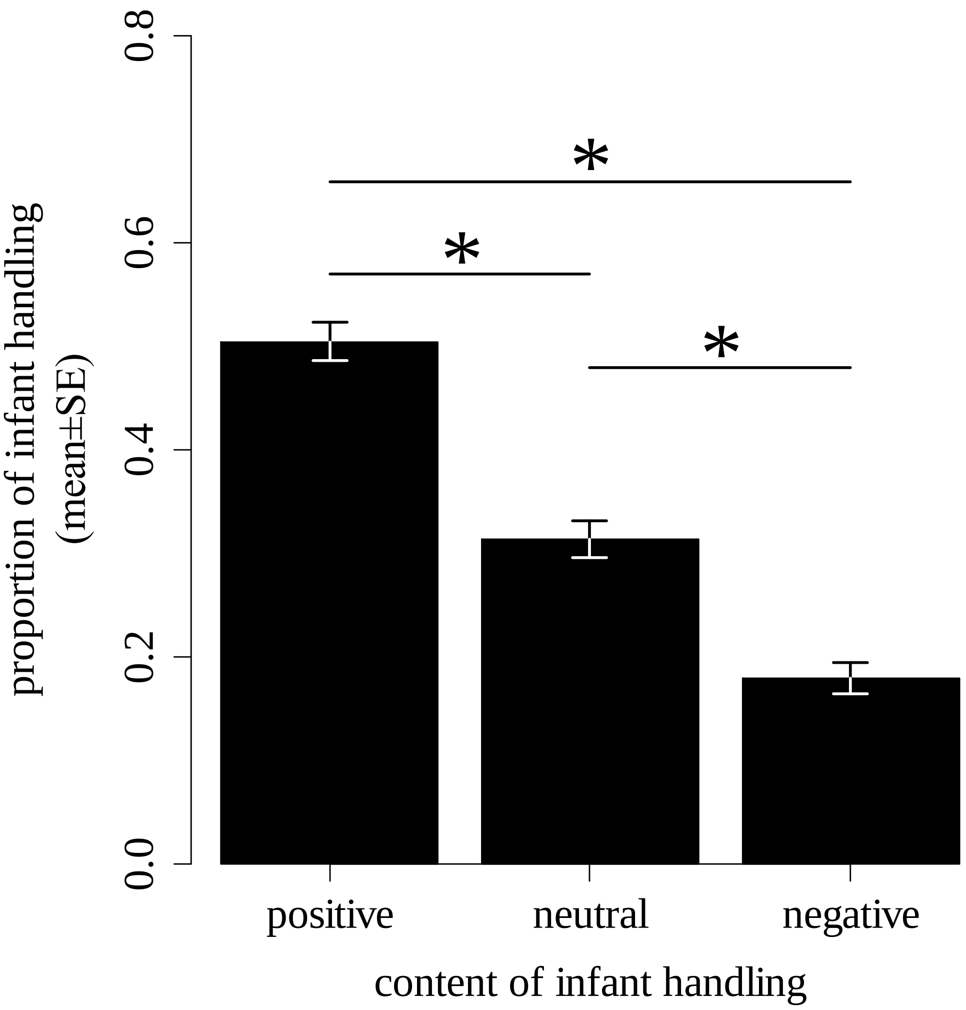

proportion of infant handling by non-relatives (mean±SE)
0.0
0.2
0.4
0.6
0.8
higher
lower
*
*
*
positive
neutral
negative
content of infant handling

Figure 5.6. Proportion of infant handling in each content (n = 3570 for 24 focal individuals).



Chapter 6

General discussion

In this thesis, I examined the determinants of pattern and frequency of infant handling in wild Japanese macaques, particularly by considering social relationships among three participants; handler, mother and infant. These studies are the first attempt to integrate maternal style, process, and function of infant handling in group-living primates. Also, my studies are the first to investigate infant handling in wild Japanese macaques.

In chapter 3, I examined an influence of a mother-infant relationship on the frequency of infant handling. I extracted three principal components using principal component analysis; infant activity, rejection, and non-protectiveness. These components affected the infant handling as the frequencies of infant handling by non-relatives, higher-ranked individuals, and non-related higher-ranked individuals were negatively associated with infant activity and non-protectiveness.

In chapter 4, I examined the role of grooming before infant handling by using concept of biological market theory. Biological market theory in the context of infant handling predicts that the occurrence and amount of grooming increases as the number of infant decreases. However, I found that the occurrence and amount of grooming were not affected by the number of infants. This suggests that grooming before infant handling by handler does not function as a currency. Rather, grooming had a function to enhance maternal tolerance because handlers groomed mother when the rank difference from mother was large, and the relatedness with mother was low. Again, I found the distance between mother and infant was important as handlers did not groom mother when the mother and infant were separated.

In chapter 5, I examined the function of infant handling by testing predictions from 5 functional hypotheses. Of those, “learning-to-mother” hypothesis best fits to my results because (i) infants were handled by nulliparous females more frequently than parous females and (ii) infants were handled in a positive way most frequently.

These results showed that pattern and frequency of infant handling in wild Japanese macaques were affected by social relationship among all interactants. More importantly, my studies suggest that the “accessibilities” to infant and mother determines the pattern and frequency of infant handling. As I explained in chapter 1, a society of Japanese macaques is characterized by nepotism and despotism among females, i.e., kin relationships, so dominance hierarchy is strict. In such social structure, it is predicted that maternal tolerance depends on social relationship among group members. Maternal tolerance to relatives is higher than non-relatives. Also, mothers may not avoid lower-ranked non-relatives who are not social threat for themselves. In contrast, dominant individuals could be social threat for mothers. When those handlers attempt to access to an infant, mothers may prevent the attempt by a handler by retrieving the infant. Also, maternal tolerance might be affected by partner's age. Generally, most of nulliparous females are relatively young (Chapter 2) and they are not considered to be social threat to mother compared to parous adult females. So, handlers need to select the situation where the maternal interference is not likely to occur or a handler is not attacked by mother, or to behave to increase the maternal tolerance. In chapter 3, I showed that infant of non-protective mother received handling more frequently than infant of protective mother when maternal tolerance to handlers is supposed to be low. In chapter 4, I found that the infants were handled more frequently when infants separated from its mother than when infants contacted with their mothers. Also, handlers did not groom mother when the distance between mother and infant (hence, handler) was large. There is a possibility that the handler was seeking a situation in which handlers can access to infant easily, in other words, when the "accessibility" to infant is high. If accessibility to infants is low, the handlers will be able to increase accessibility to infant by grooming the mother because grooming decreases the social tension of mother. Therefore, it seems that handlers reckon social relationship between themselves and mothers and select the less costly situation to handle the infant.

Handler's parity also affected the frequency of infant handling. Nulliparous females handled infant more frequently than parous females and they handled infant not negatively. Although predictions of learning-to-mother hypothesis fits the results for nulliparous females, the function of infant handling by parous females is still unknown. It is possible that the function of infant handling changes according to stages of handlers' life history such as female reproductive experience. Since parous females have already experienced giving birth, there is no need to learn how to treat infants. However, parous females handled infants, even though their frequencies were less than those by nulliparous females. From this, the function of infant handling for parous females seems to be different from that for nulliparous females. In this study, I could not clarify the function for parous females because reproductive competition hypothesis was not supported. Therefore, further studies are necessary. Also, my analyses showed that handlers might not be able to handle infants that they really attempt to handle because of low accessibilities; in other words, handlers might have forced to select an accessible infant as a target of infant handling. For example, my finding that infants were handled by relatives more frequently than non-relatives, which could have increased the inclusive fitness as the kin selection hypothesis predicts (Chapter 5), might have been a result of maternal tolerance; i.e., maternal tolerance to relatives was higher than non-relatives and relatives could access an infant easier than non-relatives. As such, this behavioural constraint could have prevented us from elucidating the function of infant handling shaped by an evolutionary process.

From these, I conclude that infant handling is a complex phenomenon involving social relationship of all interactants. Future studies of infant handling should consider this point. Also, in order to understand the long-term effects of infant handling, longitudinal observation is necessary.

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