Chapter 4

Mother-offspring behavioural conflicts

(MOBCs)

4.1 Introduction

Resolution models of POC (see Chapter 1; Trivers, 1974; Zahavi, 1977; Parker & Macnair, 1979; Eshel & Feldman, 1991; Yamamura & Higashi, 1992) incorporate assumptions about the phenotypic interactions between parents and offspring. One of the key questions addressed by resolution models relates to who wins the conflict. This could be the parent, the offspring, both parties by engaging in compromises, or a resulting situation where neither party retains the upper hand for long in continuums of unstable coevolutionary 'arms races' (Haig, 1993). Considering the advantage that parents have over the offspring in terms of body size (Cant, 2006) and experience, the resolution is usually expected to be at the parental optimum (Trivers, 1974) through *force majeure* (Alexander, 1974). Nevertheless, offspring may adopt subtle strategies ('psychological tactics') to gain greater PI than parents are selected to give (Trivers, 1974). The selfishness of offspring should, however, be limited since offspring share genes with parents and siblings (Hamilton, 1964). Therefore, the most common conflict resolution is PI at a compromise level between parents' and offspring' optima, so-called 'pro rata' models (Parker & Macnair, 1979; Altmann, 1980; Parker, 1985; see review Clutton-Brock, 1991).

In general, feedback mechanisms can be beneficial for parents and offspring, as offspring often have a better 'knowledge' of their actual need and state than parents, but such mechanisms can also be exploited by the offspring in order to gain advantage over parents (Trivers, 1974). Offspring could manipulate parents by exaggerating their true needs (Trivers, 1974) or even threatening ('blackmailing') parents with their own self-destruction (Zahavi, 1977; Godfray, 1995) through costly solicitation behaviour in terms of energy and attraction of potential predators (Parker & Macnair, 1979; Eshel & Feldman, 1991). Offspring could also advertise disinformation instead of exaggerating truth (Trivers, 1974), as do interspecific brood parasites which mimic solicitation signals of their host brood (Davies et al., 1998; Kilner et al., 1999). Withholding information from caregivers can be another effective manipulation strategy of offspring to gain the upper hand in

the POC (Johnstone, 1997; Kilner & Johnstone, 1997). For example, nestlings of the same brood who are sired by more than one male hide information about their paternity to force the father to feed them all (Davies et al., 1992). Overall, natural selection should favour parental ability to recognise signals that reflect offspring condition and to discriminate honest signals from deceitful signals. These abilities are expected to improve with parental experience (Trivers, 1974).

The honest signalling hypothesis, in contrast, predicts that offspring signals should be true reflections of their current state and need, and are used by the parent to allocate resources accordingly, to restore PI to their optimum (Godfray, 1991). It was proposed initially that honest signals can only evolve, if signals incorporate costs, resulting in the reduced fitness of offspring (Zahavi, 1977; Grafen, 1990). Subsequent models (see review by Wells, 2003) demonstrated, however, that honest signals do not need to be costly and that infrequent dishonesty can occur in evolutionary signalling mechanisms providing that most signals are honest.

One of the main aims of this chapter was to investigate whether offspring distress signals in mountain gorillas reflect their true need (Godfray, 1991) or whether offspring learn to employ deceitful signals to gain advantage over parents (Trivers, 1974). The latter case implies that the proportion of honest distress signals is highest during early infancy and declines with offspring age. However, if offspring provide mostly honest signals, mothers should be highly responsive throughout the period of MI. Conversely, if offspring increasingly employ deceitful signals, which mothers learn to distinguish from honest signals, maternal responsiveness to offspring distress signals should decline with time, and thus with offspring age. In this case, multiparous mothers, who would be expected to be more experienced in discriminating honest from deceitful signals (Trivers, 1974), should show a greater decline in responsiveness with increasing offspring age than primiparous mothers.

Postnatal POCs are assumed to be primarily behavioural in nature (Trivers, 1974), and MOBCs have been documented in numerous primate species, within various contexts (examples see Table 4.1), although compelling evidence supporting the POC theory is rare. This is partly due to

inherent difficulties involved in measuring PI and fitness consequences for mother and offspring (see Chapter 1). POC studies that do not take fitness consequences into account should be interpreted within the scope of behavioural squabbles or disputes rather than evolutionary conflicts (Mock & Forbes, 1992; Bateson, 1994; Kilner & Hinde, 2008).

Table 4.1 – Examples of primate studies reporting behavioural conflicts between parent and offspring in various contexts.

Context	Primates	References
Suckling (weaning)	Baboons	Nash, 1978; Altmann, 1980; Barrett & Henzi, 2000
	Chimpanzees	Van de Rijt-Pooij & Pooij, 1987
	Macaques	Gomendio 1991; Berman et al., 1993
	Humans	Wells, 2003; Fouts et al., 2005
Travelling	Baboons	Johnson, 1986
	Macaques	Nash, 1978; Altmann, 1980; Altmann & Samuel, 1992
Mating (Copulation)	Baboons	Nash, 1978; Barrett et al., 1995
	Macaques	Worlein et al., 1983; Gore, 1986; Collinge, 1987; Schino et al., 2001; Berman et al., 1993; Gomendio, 1991
	Review	Niemeyer & Anderson, 1983; Maestripieri, 2002a
Association (contact and thermoregulation)	Baboons	Barrett et al., 1995; Hauser & Fairbanks, 1988
	Chimpanzees	Van de Rijt-Pooij & Pooij, 1987
	Macaques	Johnson, 1986; Maestripieri, 1994b
Grooming	Chimpanzees	Pusey, 1983; van de Rijt-Pooij & Pooij, 1987
Feeding (except suckling)	Chimpanzees	Clark, 1977; Rosenblum & Sunderland, 1982
Night nesting	Macaques	Hammerschmidt et al., 1994

Weaning conflict has been interpreted to reflect a POC over the termination of milk supply by the mother, which can affect infant survival (McNeilly, 1979) and the mother's and offspring's future reproductive success (see review by Maestripieri, 2002a). Mother and offspring can both potentially influence the length of lactational anovulation through suckling frequency (see Chapter 3; McNeilly, 1979, 1994, 1997; Stewart, 1988; Gordon et al., 1992). Offspring may also be able to delay the mother's subsequent

conception and reproduction through harassment during copulation (Niemeyer & Anderson, 1983).

Infant transportation is the most energetically costly form of MI in primates beside lactation (Altmann & Samuels, 1992; Kramer, 1998), with costs being directly related to infant body weight (Givoni & Goldman, 1971). After birth, offspring are completely dependent upon their mother during travel (Fossey, 1979; Lee, 1995). When offspring gain body weight and have acquired motor and feeding skills, a mother's energetic costs through infant transportation may exceed the benefits (Altmann, 1980; Altmann & Samuels, 1992; Kramer, 1998). A conflict would then be expected when mothers try to reduce infant transportation, whilst offspring, on the other hand, try to prolong maternal effort during travelling to reduce their own energetic expenses and conserve energy reserves for growth and other activities such as playing (Kramer, 1998).

Whilst in physical contact with the mother, offspring may benefit from nipple access, transport, warmth, grooming and protection from predators or harassment from conspecifics (Altmann, 1980). Thus, physical contact can be crucial for effective maternal investment and may therefore be a factor about which mother and offspring disagree. A disagreement over physical contact may also reflect a conflict over the *scheduling* of PI, rather than over the *amount* of PI. Physical contact during the mother's main feeding activities may reduce the mother's foraging efficiency (Altmann, 1980; Whitten, 1982; Karrsemeijer et al., 1990; Barrett et al., 1995), affecting maternal condition and future reproductive success. Consequently, mothers may try to reduce physical contact during their feeding times and reschedule PI such as suckling, to convenient times such as resting, resulting in a restructuring of activities (Altmann, 1980; Barrett et al., 1995).

The second aim of this chapter is to apply the POC theory to behavioural conflicts occurring in mountain gorilla mother-offspring dyads. As fitness consequences of behavioural conflicts for mother and offspring could not be measured within the framework of the current study, the term 'conflict' will henceforth be used, with the understanding of the limitations involved when studying conflicts within the scope of behavioural disputes rather than evolutionary conflicts (Mock & Forbes, 1982).

Maternal rejection behaviour and offspring distress signals, which are common indicators of behavioural conflicts (Johnson, 1986; Berman et al., 1993; Barrett et al., 1995; Devinney et al., 2001; see review by Maestripieri, 2002a; Maestripieri et al., 2009), were used to identify and describe behavioural conflicts as well as changes in their occurrence over the period of MI. Variation in the strength and severity of maternal rejections as a function of offspring age and maternal experience will be investigated. The strength and severity of maternal rejection behaviour was expected to increase with offspring age, since offspring physical strength and the intensity of conflicts over the termination of maternal investment should increase with age. In general, if mother and offspring disagree over the termination of MI, mother-offspring behavioural conflicts (MOBCs) are expected to increase with time, and thus with offspring age. This should be reflected in an overall increase in the occurrence of maternal rejection behaviours and offspring distress signals over infancy by definition, while the offspring is still dependent on the mother. The main focus of attention was on behavioural conflicts arising in the context of physical contact, suckling, travelling, and grooming. The question of whether only the mother shapes MI patterns through *force majeure* (Alexander, 1974), or whether the mother and offspring both have a stake on MI patterns (pro-rata model: Parker & Macnair, 1979) within any of the behavioural conflicts were addressed by testing the predictions outlined below.

4.1.1 Predictions relating to physical contact and suckling MOBC

Two different types of physical contact and suckling MOBCs were predicted to occur (see Altmann, 1980; Barrett et al., 1995). The first conflict was expected to occur during early infancy when mothers should be trying to reduce physical contact and suckling during their main feeding times when the offspring is likely to be a hindrance, reflecting a conflict primarily over the *scheduling* of MI. A mother's main feeding period is usually during gNR when the majority of group members spent their time on feeding activities (see Chapter 5). Thus, a rescheduling of suckling events from gNR to gR would be expected, and therefore would lead to a greater reduction of physical

contact during gNR than during gR. Equally, the occurrence of maternal rejection would be expected to be higher during gNR than during gR.

The second conflict was expected to occur at a later stage, arising during the critical weaning period (see Chapter 3) when mothers try to reduce and then terminate milk provision and reduce other maternal support, such as protection, reflecting a conflict mainly over the *amount/termination* of MI. In such cases, mothers are predicted to refuse physical contact and suckling attempts irrespective of the current group activity, unless an early conflict over the *scheduling* of MI had already strongly reduced MI during gNR, which may lead to a bias in maternal rejections towards gR.

If the mother alone shapes physical contact patterns, maternal rejection of contact attempts made by the offspring should be negatively associated with time in physical contact. Conversely, if the offspring also manages to influence patterns of physical contact, the frequency of attempts to make contact by the offspring should also be positively related to the actual time spent in physical contact. Equally, if opposing behaviour is cancelling out the other effect, neither maternal rejection nor contact making by the offspring would be clearly related to physical contact.

In terms of suckling patterns, if the mother alone controls milk provision, maternal rejection of suckling attempts by offspring should be negatively associated with the actual suckling frequency. Whereas, if offspring also have a stake in controlling suckling patterns, suckling attempts by offspring should be positively associated with suckling occurrences, or a cancelling out of opposite effects would mean that neither maternal rejection nor suckling attempts by the offspring are related with the occurrence of suckling patterns.

4.1.2 Predictions relating to transport MOBC

If the mother alone controls transport patterns, the occurrence of transport should be negatively affected by maternal rejection of attempts by the offspring to be transported. If both the mother and the offspring influence transport patterns, offspring distress signals in a moving context and attempts by the offspring to be transported should also be positively

associated with the occurrence of transport. In addition, neither maternal rejection nor offspring solicitation behaviours should be related to transport patterns, if the influence is equal for offspring and mothers.

4.1.3 Predictions relating to grooming MOBC

Ectoparasite removal is one function of grooming in primates (Schaller, 1963; Freeland, 1981; Gilbert, 1997) and consequently, maternal grooming may be crucial to maintain offspring health. Another function of grooming behaviour is the establishment and maintenance of social relationships (Dunbar, 1991; Cheney, 1992; Lazaro-Perea et al., 2004). Although in mountain gorilla both sexes disperse, they may also be philopatric for a lifetime (Harcourt, 1978b; Robbins, 1995), and thus it is proposed that grooming provided by the mother may strengthen long-term social relationships between the mother and the offspring.

Field observations previous to the current study (pers. obs.) gave the impression that the grooming MOBC was controlled primarily by the offspring, who tried either to reduce or to reschedule MI (grooming) by refusing the mother's grooming attempts; the mother's response was often to discipline the offspring. If grooming patterns are mainly influenced by mothers, maternal disciplining should be directly related to the grooming occurrence. However, if offspring manage to manipulate grooming patterns, there should also be an inverse relationship between the grooming occurrence and offspring refusal behaviour or distress signals in a grooming context. Equally, if the opposing behaviour is cancelling out other effects, neither maternal disciplining, offspring refusal behaviour, or distress signalling would show an association with grooming patterns. It was also expected that the MOBC over grooming time would increase initially with age, but would diminish again when mothers tried to terminate the nutritional support. At this stage, offspring often seek the mother's attention and tend to cling on their mothers while showing infantile behaviour (Clark, 1977; pers. obs.) and the nipple access may be facilitated while being groomed by the mother.

Previous field observations also gave the impression that grooming activities were *rescheduled* to suckling periods with increasing offspring age. Three underlying causes for such a reschedule process were considered: (1) Mothers may try to provide grooming more efficiently during resting times in order to compensate for a decline in resting time spent together with increasing offspring age. In this case, grooming during suckling bouts should increase as the time mothers spend resting in association with offspring declines. (2) The reschedule process may reflect a maternal strategy to bargain nipple access for grooming, since offspring willingness to tolerate grooming should be enhanced during suckling events. In this case, grooming during suckling events should increase as offspring rejection of grooming increases. (3) Finally, rescheduling of grooming to suckling periods may also reflect an offspring-led strategy to enhance the development of future skills, through maintaining time for activities such as social play (Poirier & Smith, 1974) which requires association with similar aged peers (Fletcher, 1994). Similar to (2) overlapping grooming and suckling periods should be increasingly positively correlated with offspring rejection of grooming.

4.2 Aims

- To investigate whether offspring distress signalling in mountain gorillas supports either the honest signalling hypothesis (Godfray, 1991) or the alternative theory that offspring exploit distress signals to manipulate the mother's resource allocation (Trivers, 1974).
- Identifying potential MOBCs in mountain gorilla mother-offspring dyads using offspring distress signals and maternal rejection behaviour.
- To examine changes in maternal responsiveness to offspring distress signalling and in maternal rejection behaviours, as a function of parity through the transition to independence.

- To apply POC theory to behavioural conflicts occurring in mountain gorilla mother-offspring dyads, focusing on conflicts arising in the context of physical contact, suckling, travelling, and grooming.

- To address the question of whether the mother alone shapes maternal investment patterns through *force majeure* (Alexander, 1974) or whether the offspring also has a stake in maternal investment patterns.

4.3 Methods

All behaviours were extracted from focal samples of the mother and offspring, using continuous recording for presenting frequencies and count data and instantaneous sampling (1-min intervals) (see Chapter 2) for presenting proportions of time spent in various behaviours (e.g. in body contact, transporting and grooming). Short time intervals between time-samplings can provide accurate estimates of durations (see Martin & Bateson, 1993, pp. 91, 96). It is also important to clarify that the dataset used in this Chapter 4 differed from the dataset used in Chapter 3, since only data which were collected between 2006 and 2007 could be used for the purpose of the current investigation.

4.3.1 Maternal rejection and offspring signals of need

Maternal rejection and offspring distress data were used to identify and explore behavioural disputes. Maternal rejection behaviour (see definitions in Chapter 2) was divided into three main categories, according to level of strength and severity:

1. Level-1 (*mild*) included soft rejection behaviour (e.g. pushing see Table 4.2), without an aggressive element (see level-2 and level-3). This category also contained various behaviour apparently used to prevent behavioural disputes, such as initiation of playing and grooming by the mother to prevent suckling, only if they occurred after a suckling attempt.

2. Level-2 (*moderate*) described weak aggressive maternal behaviour, such as a single pig-grunt or shoving, which seemed to function mainly as a warning or to discipline.

3. Level-3 (*strong*) encompassed more severe maternal aggression, which was usually accompanied by physical contact and seemed to function as punishment rather than just a warning or to discipline. However, mothers were never observed carrying out serious acts of aggression towards their offspring (leading to obvious wounds).

All maternal rejection behaviour was summarised by the context in which it occurred (Table 4.2). Overall, five major contexts could be distinguished.

Table 4.2 – Maternal rejection behaviours categorised into levels of strength and severity presented by the context of occurrence. Bold = short-cuts defined below table, other abbreviations in ethogram (Table 2.7, Chapter 2).

Context	Level 1	Level 2	Level 3
1. Suckling	PLA, **CHT**, **CHP**, **COB**, TCH, B, **PSH**,	OMT, VPG1, VPG, **SHV**	**BIT**
2. Moving	B, **CHT**	OMT, VPG1, VPG2, **SHV**	**BIT**
3. Feeding (non-lactational)	**PSH**, FST	OMT, VPG1, VPG2, **SHV**, **GRB**	**BIT, CHA**
4. In contact with offspring / offspring makes contact	B, **PSH**	OMT, VPG1, VPG2, **SHV**, **GRB**	**BIT, SLP**
5. Grooming	RST	OMT, **PSH**	**BIT**

CHT = changing transport style (ventral to dorsal), CHP = changing position of offspring, COB = covering breast, PSH = pushing, SHV = shoving, GRB = grabbing, BIT = biting, SLP = slapping, V = vocalisation.

All types of offspring distress behaviour (see definitions in ethogram, Table 2.7, Chapter 2) and maternal responses to distress behaviours were summarised by the context of occurrence and type of maternal responses, which were subdivided into three response categories (Table 4.3):

1. *Positive* maternal responses to distress comprised reassuring and encouraging behaviour as well as the provision of MI (e.g. nipple access, protection, grooming and transport), although a positive response did not necessarily mean that an offspring was successful in receiving the particular MI which it tried to induce.
2. *Negative* maternal responses to distress could be of an aggressive nature, and basically encompassed maternal rejection and disciplining behaviours.
3. A mother could also *ignore* the offspring signals and show no response. In such cases, a mother usually continued her current activity without giving any attention to her offspring.

Contexts in which offspring showed distress behaviours (Table 4.3) overlapped greatly with contexts of maternal rejection.

Table 4.3 – Contexts of offspring distress behaviours and mother's positive and negative responses (see definitions in ethogram Chapter 2, Table 2.7). A third potential response, ignore and continue current activity, is not shown. Bold = short-cuts defined below table, other abbreviations in ethogram.

Context	Offspring distress behaviour	Positive response from mother	Negative response from mother
1. Offspring in physical contact with mother	VHO, VSC, VW	GRM,NC, **SCA**, TSV, VBL	B, OMT, RFS(NC), RST, VPG1, VPG2
2. Mother increases distance from the offspring	TAN, VHO, VSC, VW	NC, GRM, RTR, TCH, TRA, VBL, WAI	OMT
3. Offspring decreases distance to the mother	VHO, VW	EMB, GRM, NC, RTR, **VRP**	B, L, RFS(C)
4. In proximity to mother (not in physical contact)	VW	A, C, EMB, GRM, NC, MNT, RTR, TCH, VBL, **VRP**	L, VPG1, VPG2
5. Travel (transport, following, rump-cling)	TAN, VHO, VSC, VW	**CHT**, EMB, NC, RTR, **TRA**,VBL, **VFS**, WAI,	AGC, B, L, RFS(**CHT**) RFS(RCL), RFS(TRA), VPG1, VPG2
6. Grooming	VSC, VW	**CHP**, NC, TGRM, VPG1, VPG2,	RFS(NC), RST, VPG1, VPG2
7. Suckling	TAN, VHO, VSC, VW	**CHP**, EMB, GRM, MNT, NC, TCH, **TRA**, WAI, VBL	AGC, B, L, OMT, RFS(**CHN**), RFS(NC), VPG1, VPG2

H = hooting, S = screaming, T = tantrum, W = whimpering, SCA = scratching slightly with fingertips, CHT = changing transport style (ventral to dorsal), TRA = transport, CHN = changing nipple side, CHP = changing position, TGRM = terminated grooming, VRP = rumple-like vocalisation, VFS = singing

4.3.2 Data analysis

GLMMs (see Chapter 2) were used to investigate MOBCs as well as changes in the maternal responsiveness to offspring distress signals, maternal rejection behaviours and offspring distress signals over the period of MI.

4.3.2.1 Maternal rejection behaviours

The influence of offspring age and parity on the occurrence of maternal rejection was examined in an initial GLMM (Table 4.4). To investigate whether maternal rejection behaviour varied in the level of strength and severity with offspring age and parity, three additional GLMMs (Table 4.4) were developed, one for each of the three defined levels (see section 4.3.1). Two-way interactions were tested in each GLMM.

Table 4.4 – Structure of GLMMs for the examination of maternal rejection behaviour.

Model structure	Occurrence of maternal rejections	Strength and severity of maternal rejections
Response variable	# of maternal rejections	# of maternal rejections of level 1-3[a]
Random-effects	Mother, Group	Level 1: Mother, Group Level 2/3: Mother
Fixed-effects	Offspring age (cnt) Parity (cat: P/M)	Offspring age (cnt) Parity (cat: P/M)
Offset terms (x)	Length of observation time	# of maternal rejections
Collinearity	No	No
Overdispersion	Yes	Yes
Link function	Quasi-poisson	Quasi-poisson
Estimation method	Laplace approximation	Laplace approximation

[a]each level of maternal rejection strength and severity was tested in a separate GLMM, cnt = continuous, cat = categorical, P = primiparous, M = multiparous.

4.3.2.2 Offspring distress signals and maternal responsiveness

Variation occurring in offspring distress signals and in maternal responsiveness to offspring distress signals with offspring age and parity were investigated in separate GLMMs (Table 4.5). Focal samples which lasted less than 30 min were excluded from the GLMM for the examination of offspring distress signals. Two-way interactions were tested in each GLMM.

Table 4.5 – Structure of the GLMM for the examination of offspring distress signals and maternal responsiveness.

Model structure	Occurrence of offspring distress signal	Maternal responsiveness
Response variable	# offspring distress signals	Proportion of positive responses [a]
Random-effects	Mother Group	Mother
Fixed-effects	Offspring age (cnt) Parity (cat: P/M)	Offspring age (cnt) Parity (cat: P/M)
Offset terms	Length of observation time	-
Collinearity	No	No
Overdispersion	Yes	-
Link function	Quasi-Poisson	Gaussian
Estimation method	Laplace approximation	REML

[a]arcsine-transformed, cnt = continuous, cat = categorical, P = primiparous, M = multiparous.

4.3.2.3 Physical contact and suckling MOBCs

For the purpose of testing the physical contact and suckling MOBC, the dataset was divided by offspring age into two subsets. The first subset was used to investigate MOBCs arising from the scheduling of both of these MI measures and included mothers with offspring who were two years old or less. The second subset was used to investigate MOBCs arising due to the amount (as frequency and proportion of observation time) of both of the MI measures and included mothers with offspring who were older than two years. The cut-off point at two years was chosen due to the findings on weaned age (see Chapter 3): apart from one exception, all offspring were weaned when over the age of two years.

To find out whether the physical contact and suckling MOBCs occurred mainly over the *scheduling* or *amount/termination* of MI, the occurrence of maternal rejections, depending on the predominant group activity, was investigated initially for both datasets (Table 4.6), considering

the two-way interaction of both fixed-effects in the GLMM. The question of whether the mother alone or both the mother and offspring shape physical contact patterns and suckling occurrences was addressed in a separate GLMM for each measure of MI (Table 4.6). In those models, three-way interactions involving offspring age and the group activity were taken into account. Count data were standardised to frequencies (per 30 minutes observation time) when being fixed-effects. Observation periods from focal samples which lasted less than 30 minutes were excluded from the analysis, to ensure that frequency and proportion values were representative of mother-offspring interactions.

Table 4.6 – Structure of GLMMs for the examination of physical contact and suckling MOBCs occurring ≤ 2 years and > 2 years.

Model structure	Physical contact		Suckling events	
	Maternal rejection	Who shapes MI patterns?	Maternal rejection	Who shapes MI patterns?
Response variable	# maternal rejections	Proportion of contact time[a]	# maternal rejections	# suckling events
Random-effects	Mother Group	Mother	Mother	Mother
Fixed-effects	Offspring age (cnt) Group activity (cat: gNR/R)	Offspring age (cnt) Group activity (cat: gNR/R) F maternal rejection (cnt) F contacts made by offspring (cnt)	Offspring age (cnt) Group activity (cat: gNR/R)	Offspring age (cnt) Group activity (cat: gNR/R) F maternal rejection (cnt) F suckling attempts by offspring (cnt)
Offset terms	Length of observation time # contacts made by offspring	-	Length of observation time # suckling attempts by offspring	Length of observation time
Collinearity	No	No	No	No
Overdispersion	Yes	-	Yes	No
Link function	Quasi-Poisson	Gaussian	Quasi-Poisson	Poisson
Estimation method	Laplace approximation	REML	Laplace approximation	Laplace approximation

[a] arcsine-transformed, gNR = group non-resting, gR = group resting, cnt = continuous, cat = categorical, F = frequency.

4.3.2.5 Grooming MOBC

To examine the influence of the mother and the offspring on maternal grooming and whether mothers rescheduled grooming activities to coincide with suckling periods, three separate GLMMs were developed (Table 4.7). Two-way interactions involving offspring age were tested in GLMMs containing fixed-effects other than offspring age. The duration of time mothers spent grooming their offspring was standardised as proportion of the total time mothers spent in association with their offspring ($\leq$5m distance between mother and offspring). Focal samples during which mothers spent less than 30 min in a resting activity in association with the offspring were found to be unrepresentative of the overall occurrence of grooming behaviour, and thus were excluded from further analyses. Maternal grooming time during suckling events was standardised as a proportion of total time spent suckling.

Table 4.7 – Structure of GLMMs for the examination of a) grooming MOBCs and b) proportion of time spent grooming during suckling events and mothers' resting time in association.

Model structure	Who shapes grooming patterns?	Grooming during suckling	Maternal resting in association with offspring
Response variable	Grooming time as proportion of time that mothers spent resting in association with offspring [a]	Time spent grooming during suckling events as a proportion of total grooming time [a]	Time spent resting in association with offspring as a proportion of total observation time [a]
Random-effects	Mother Group	Mother	Mother
Fixed-effects	Offspring age (cnt) F maternal disciplining (cnt) F offspring refusal (cnt) F whimper signals (cnt)	Offspring age (cnt) F offspring refusal (cnt) Proportion of maternal resting time that is spent in association with offspring (cnt)	Offspring age (cnt)
Offset terms	-	-	-
Collinearity	No	No	-
Overdispersion	-	-	-
Link function	Gaussian	Gaussian	Gaussian
Estimation method	REML	REML	REML

[a]arcsine-transformed, F = frequency, cnt = continuous.

4.3.2.6 Transport MOBC

Four different modes of travel by offspring were distinguished: being transported by the mother; rump-clinging on the mother; following the mother; and moving independently of the mother while the mother was also travelling. The last mode included any following of other group members, apart from the mother. Being transported by other group members was excluded from the analysis.

Two GLMMs were developed (Table 4.8) to examine the transport MOBC. Transport was standardised as a proportion of the total time during which mother and offspring were travelling (per observation day rather than per transport bout) that provides a relative measure of daily energy costs to the mother and offspring during travelling. Two-way interactions involving offspring age were considered in the GLMM, which addressed the question of who shaped transport patterns (Table 4.8). Rates represent standardised frequencies per 10 min that offspring spent in any travel mode. Focal samples containing less than 10 min of offspring travel were not used in the analysis.

Table 4.8 – Structure of the GLMMs for the examination of transport MOBC.

Model structure	Maternal rejection	Who shapes transport patterns?
Response variable	# maternal rejections in moving context	Transport time as a proportion of total time spent in all travel mode [a]
Random-effects	Mother Group	Mother
Fixed-effects	Offspring age (cnt)	Offspring age (cnt) F maternal rejection (cnt) F whimper signals in moving context (cnt) F contacts made in moving contexts (cnt)
Offset terms	Total observation time	-
Collinearity	-	No
Overdispersion	Yes	-
Link function	Quasi-poisson	Gaussian
Estimation method	Laplace approximation	REML

[a] arcsine-transformed, F = frequency, cnt = continuous.

4.4 Results

4.4.1 Maternal rejection

The earliest maternal rejection occurred at the age of two months during a suckling attempt by the offspring while the (primiparous) mother was feeding. The occurrence of maternal rejections with offspring age followed a quadratic relationship (b ± SE = -0.263 ± 0.088, t = -3.005, p = 0.003) rather than a linear relationship (AIC_{Age} = 722.9, AIC_{Age2} = 692.6, df = 1, X^2 = 32.18, p < 0.001). Alongside strong variation throughout the first two years, maternal rejection peaked at 12 months and was followed by a relatively gradual decline (Figure 4.1). Beyond the second year, the level of maternal rejection remained relatively low. This indicates that behavioural conflicts were more intense before the critical weaning period (see Chapter 3) and thus were related to issues other than the termination of milk provision. Mother's parity, a measure of maternal experience, had no effect on the overall occurrence of maternal rejection.
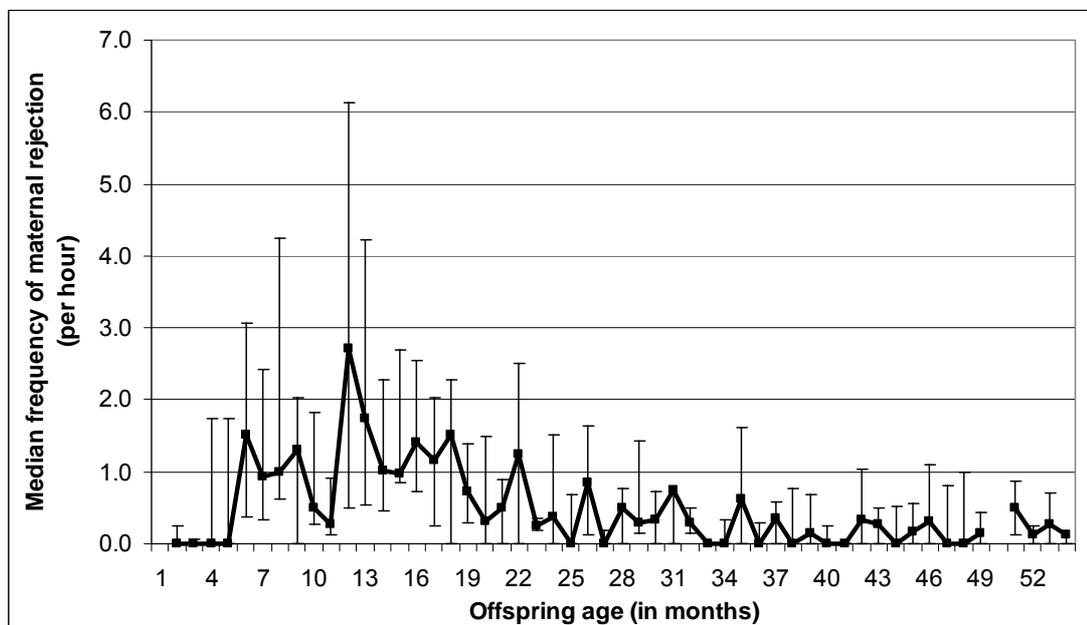
Figure 4.1 – Median frequency of maternal rejections per offspring age. Vertical lines represent IQR.

The percentage of maternal rejections observed in each behavioural context varied throughout the first four years of MI (Figure 4.2), indicating a shift in the reason for behavioural conflicts. Most maternal rejections during the first year occurred in the context of initiating contact or remaining in physical contact but rejections in this context were less important compared to other conflicts over the following years. During the second and third year, the majority of maternal rejections occurred in a moving context. Feeding-related rejections were at their highest level in years three and four. Maternal rejections within a suckling context declined from year one to year two but became the predominant context for maternal rejections during the fourth year. Disciplining during grooming increased as a proportion with increasing age.
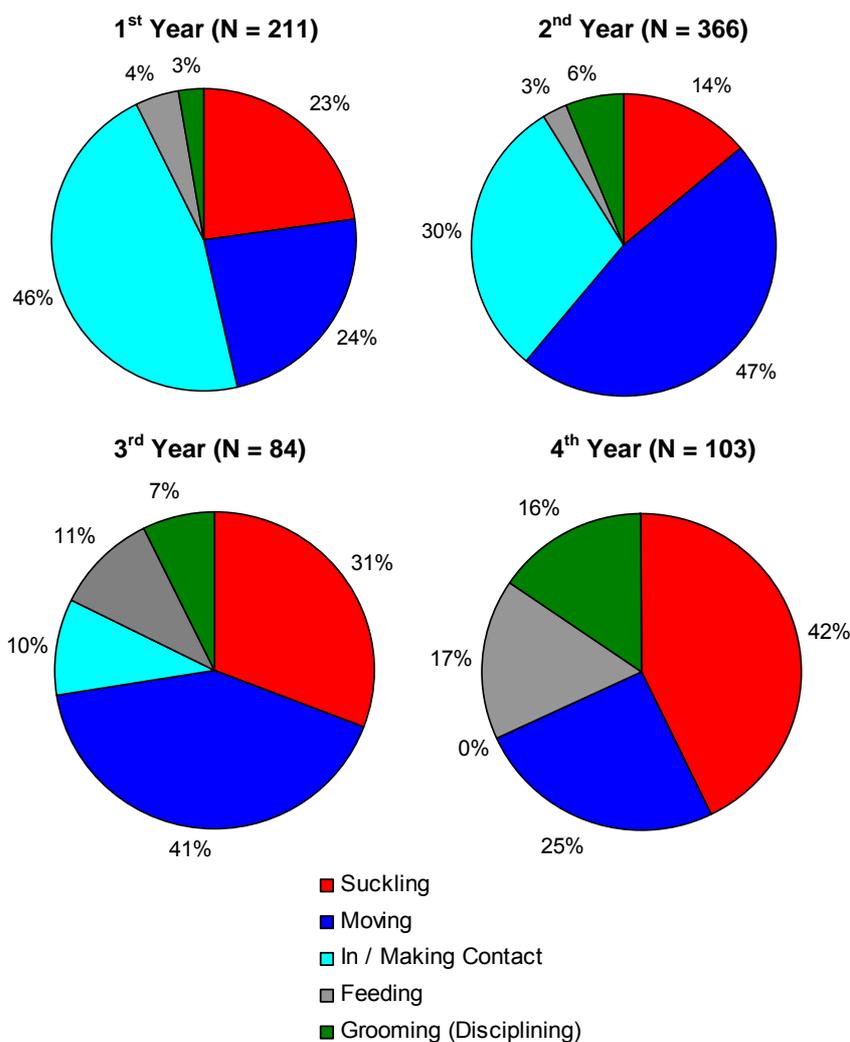
Figure 4.2 – Distribution of maternal rejections (%) over contexts of occurrence throughout the first four years of maternal investment.

The strength and severity of maternal rejection behaviour varied strongly over infancy (Figure 4.3). Mothers most commonly used a *moderate* level. In comparison, *mild* and *strong* maternal rejections occurred less consistently and at lower proportions than *moderate* rejections during most age-months.
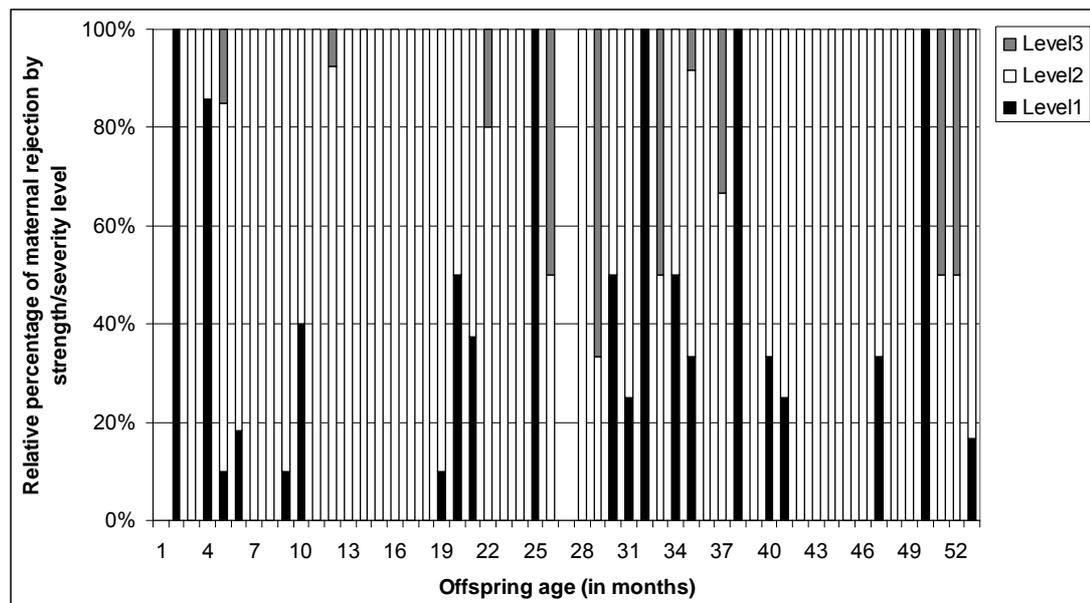

Figure 4.3 – Median levels of strength and severity (1-3) of maternal rejection behaviour presented by offspring age.

GLMMs (Table 4.9a-c) were used to examine the effect of offspring age and maternal parity on the strength and severity of maternal rejections. Data showed that multiparous mothers used *moderate* rejections at relatively constant levels during the period of MI (Table 4.9b) and reduced *mild* maternal rejections with increasing offspring age, as predicted. Primiparous mothers, however, increased *mild* maternal rejections (Table 4.9a; b = 0.047 = -0.028 + 0.075) and reduced *moderate* rejections with increasing offspring age (Table 4.9b, P3: b = -0.015 = -0.001 – 0.014). First-time mothers also tended to increase *strong* rejections at greater proportions with offspring age than multiparous mothers, who kept the proportion of *strong* rejections relatively constant (Table 4.9c). Furthermore, post hoc tests revealed that primiparous mothers employed more *strong* rejections (post-hoc test: b ± SE = 0.416 ± 0.170, t = 2.44, p = 0.015) during the period of MI, whereas no

main parity effects were found in the occurrence of *mild* (b ± SE = 0.012 ± 0.212, t = 0.06, p = 0.955) and *moderate* (b ± SE = -0.038 ± 0.075, t = -0.51, p = 0.610) maternal rejections.

Table 4.9 – GLMM showing parameter estimates of fixed-effects on the (a-c) strength and severity of maternal rejections (N = 135).

a) *Mild*. (N $_{mother}$ = 15, N $_{Group}$ = 5, d.f. = 4).

Predictor	b	SE	t value	P	
Intercept	-2.865	0.202	-14.16	**<0.001**	***
cOff_Age	-0.028	0.008	-3.35	**<0.001**	***
Parity-P	0.082	0.179	0.46	0.648	
cOff_Age~Parity-P	0.075	0.012	6.36	**<0.001**	***

b) *Moderate*. (N $_{mother}$ = 15, d.f. = 3).

Predictor	b	SE	t value	P	
Intercept	-0.188	0.050	-3.73	**<0.001**	***
cOff_Age	-0.001	0.004	-0.16	0.871	
Parity-P	-0.114	0.084	-1.37	0.171	
cOff_Age~Parity-P	-0.014	0.007	-2.11	**0.035**	*

c) *Strong*. (N $_{mother}$ = 18, d.f. = 3).

Predictor	b	SE	t value	P	
Intercept	-2.884	0.121	-23.93	**<0.001**	***
cOff_Age	0.011	0.009	1.27	0.205	
Parity-P	0.415	0.172	2.41	**0.016**	*
cOff_Age~Parity-P	0.022	0.012	1.83	**0.068**	.

Off_Age = offspring age, c = centred variable, P = primiparous.

4.4.2 Offspring distress signals

Offspring usually used three acoustically distinguishable vocalisations and tantrum displays to signal their needs to the mother. Whimpering was the most frequently recorded distress signal (N = 2197, 96.8%). The remaining vocalisations and tantrum displays were used comparatively rarely (hooting: N = 49, 2.2%; screaming: N = 39, 1.7%; tantrum: N = 15, 0.7%) and generally occurred in combination with whimper signals when the mother either did not react to a series of whimpers or when the offspring was in a stage of panic, e.g. when it suddenly recognised that the mother was out visual contact. Mother's response patterns (negative, positive, none) to the

vocalisation signals did not differ greatly (Figure 4.4). Only hooting never led to a negative response by the mother. In comparison to the majority of vocalisations, the mother rarely ignored tantrum displays and mainly responded positively.
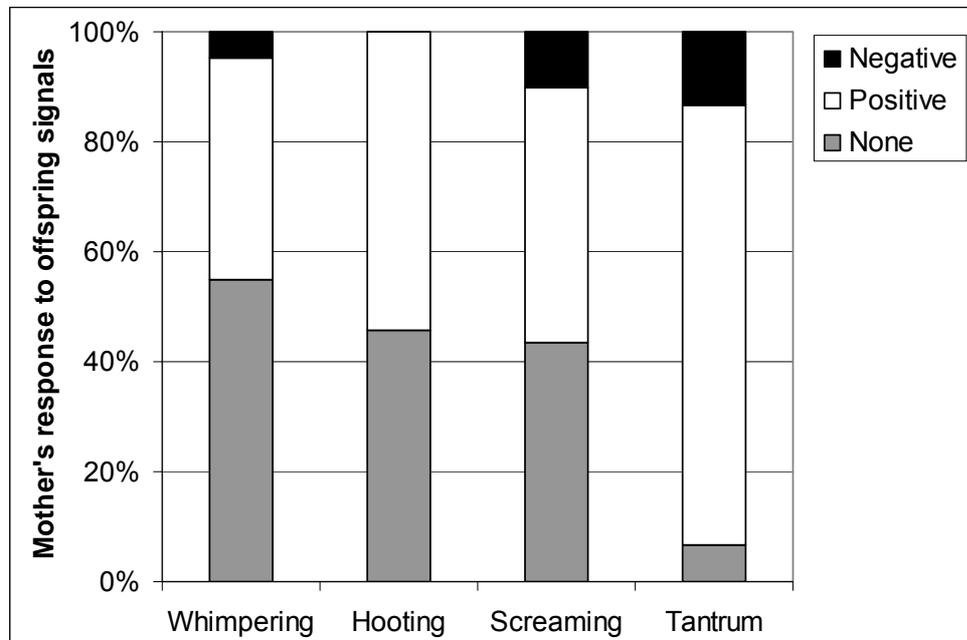

Figure 4.4 – Percentage of mothers' responses to four different offspring distress signals.

Since offspring primarily employed whimper signals, the impact of offspring age and maternal parity was only analysed for whimper signals (GLMM: N = 325, N_{Mother} = 26, d.f. = 3). Neither offspring age (b ± SE = -0.002 ± 0.015, t = -0.14, p = 0.890) nor mother's parity (b ± SE = -0.165 ± 0.940, t = -0.18, p = 0.861) had a significant effect on the occurrence of whimper signals, although strong fluctuations occurred across age-months (Figure 4.5).
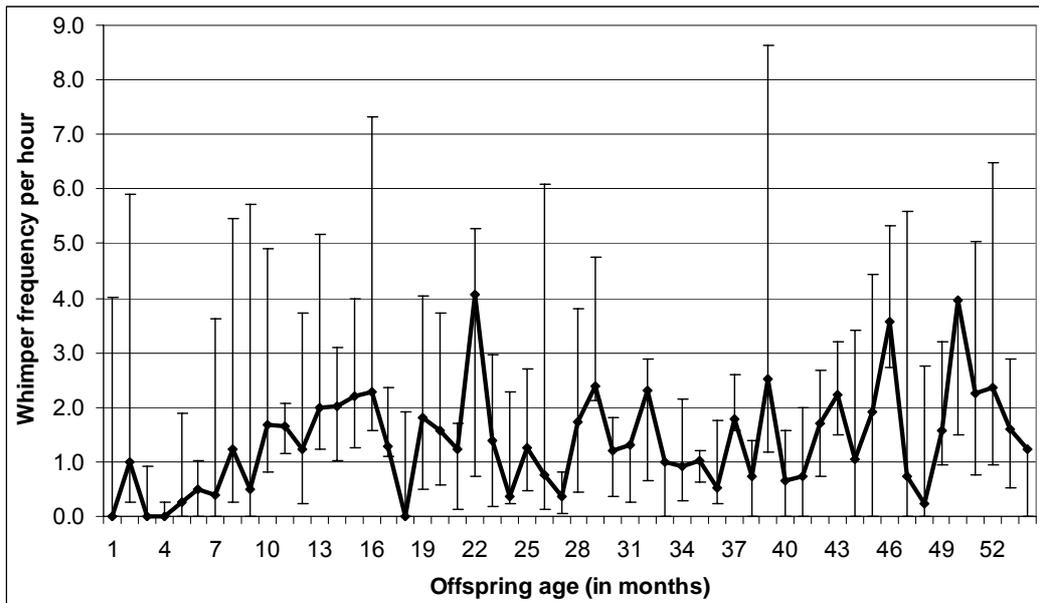
Figure 4.5 – Median frequency of offspring whimper signals by offspring age. Vertical lines = IQR.

As with maternal rejections, the percentage of whimper signals in each context strongly varied throughout the first four years of MI (Figure 4.6). Whimper signals associated with travelling clearly dominated across the years, in particular during the second and third year when the proportion of rejections (Figure 4.2) also increased and offspring became independent from their mothers during travelling (see section 4.4.7). The percentage of whimper signals in a suckling context was relatively low compared to whimper signals observed during travelling, but became more important across the years towards the weaning peak similarly to maternal rejections (Figure 4.2). Nevertheless, it remains unclear to what extent whimper signals, which were elicited in contact with the mother, in close proximity (≤5m) to the mother or while decreasing the distance to the mother also function as begging signals for nipple access, or a result directly from maternal rejection.
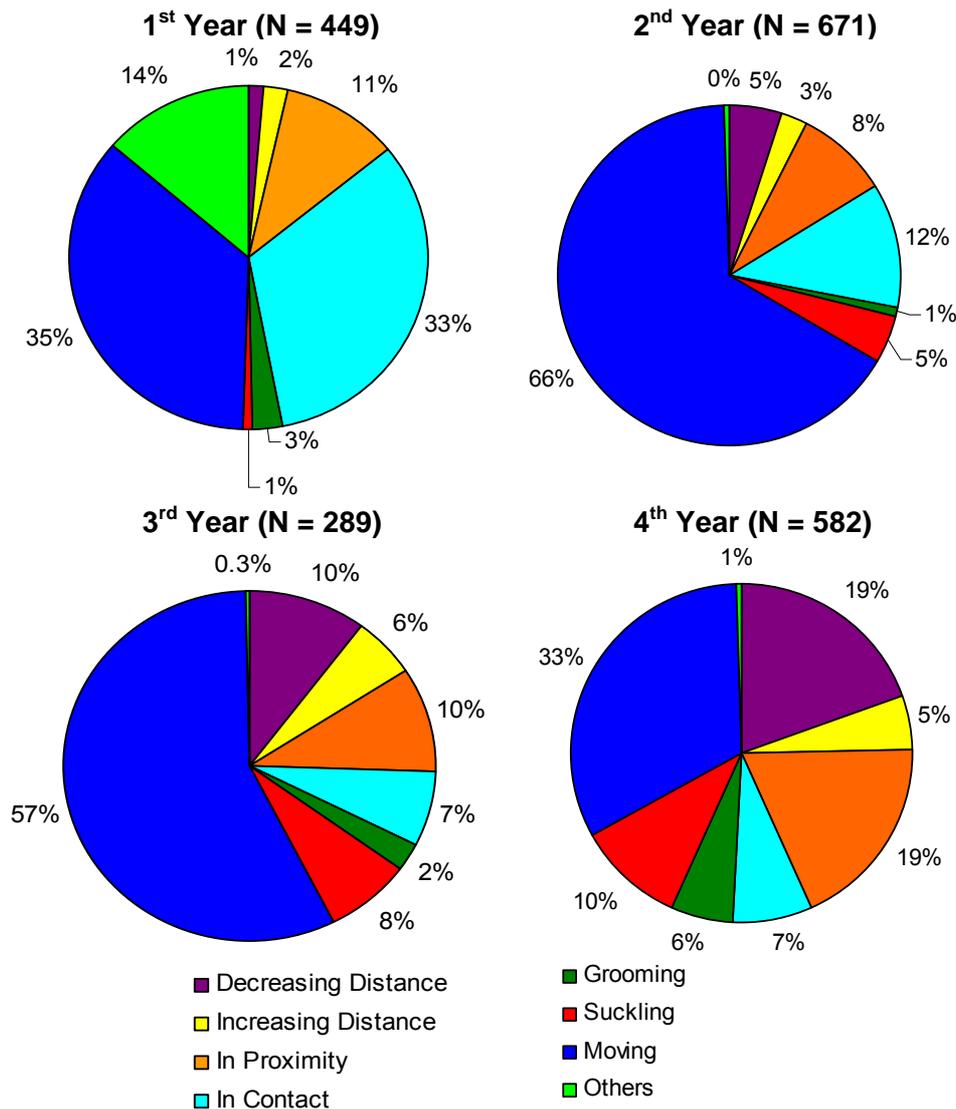
1st Year (N = 449)

2nd Year (N = 671)

3rd Year (N = 289)

4th Year (N = 582)

■ Decreasing Distance   ■ Grooming
□ Increasing Distance   ■ Suckling
■ In Proximity   ■ Moving
□ In Contact   ■ Others

Figure 4.6 – Distribution of whimper signals (%) by context across the first four years of offspring life.

4.4.3 Maternal responsiveness

The dynamics of the mother's response were also only examined for whimper signals, due to the low sample size for the remaining types of distress signals. Maternal responsiveness to whimper signals alternated strongly over the initial four years of MI, which can be divided into two phases (Figure 4.7). During the first 30 months of infancy, mothers responded increasingly positively to offspring whimper signals, showing a peak of responsiveness at the age of 27 and 30 months, concurrently with a decrease in the proportion of whimper signals that were ignored by the

mother. Beyond the age of 30 months, during the core of the critical weaning period, those patterns reversed: mothers increasingly ignored whimper signals while the proportion of positive responses to whimper signals decreased. Negative responses remained negligible over the entire period of MI. Overall, maternal responsiveness was lowest in the first three months after birth when offspring were continually in contact with the mother and at later stages of the MI period (>43 months) when most offspring were weaned (Table 3.11, Chapter 3).
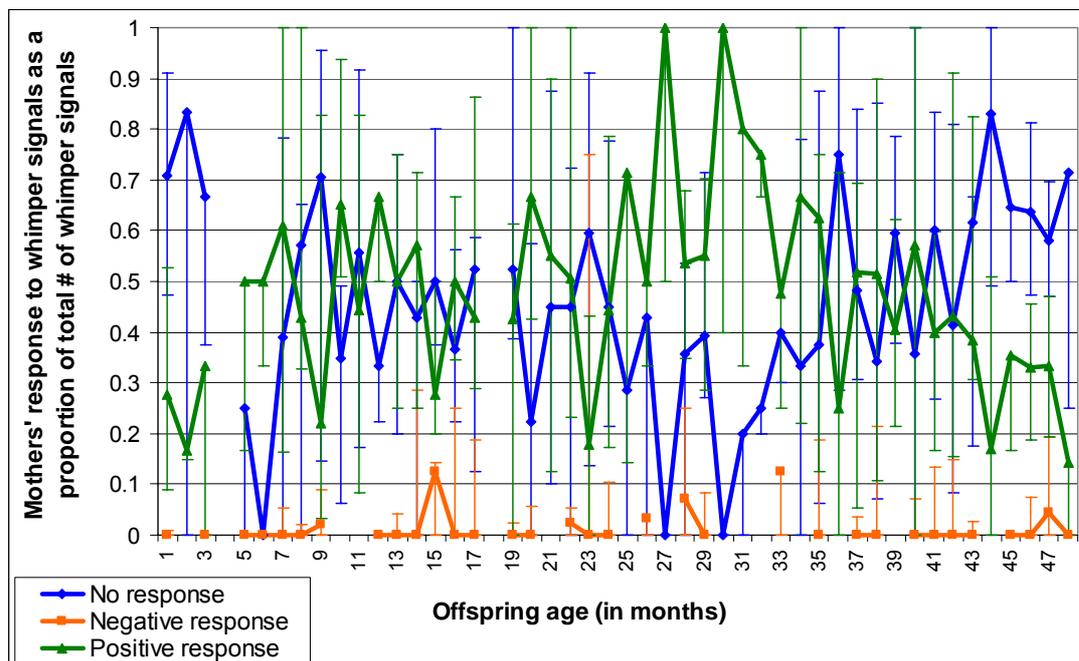
Figure 4.7 – Dynamics of mothers' response patterns to offspring whimper signals during the period of maternal investment. Vertical lines = IQR.

When adding the quadratic term of offspring age to the GLMM (Table 4.10) for the examination of maternal responsiveness, the overall fit did not improve (AIC_{Age} = 280.0, AIC_{Age2} = 280.7, d.f = 1, X^2 = 1.322, p = 0.250). Contrary to the prediction, primiparous mothers tended to reduce their responsiveness to offspring whimper signals with increasing offspring age, while the responsiveness of multiparous mothers did not show a linear change with offspring age. A post-hoc test revealed that parity had no main effect on maternal responsiveness (b ± SE = -0.038 ± 0.093, t = -0.40, p = 0.686).

Table 4.10 – GLMM showing parameter estimates of fixed-effects on the proportion of positive responses to offspring whimper signals. (N = 232, N $_{mother}$ = 20, d.f. = 3).

Predictor	b	SE	t value	P	
Intercept	0.777	0.055	13.99	**<0.001**	***
cOff_Age	-0.014	0.042	-0.34	0.733	
Parity-P	-0.049	0.088	-0.56	0.576	
cOff_Age~Parity-P	-0.118	0.064	-1.85	**0.065**	.

Off_Age = offspring age, c = centred variable, P = primiparous.

4.4.4 Physical contact MOBC

During the first three months, mother and offspring rarely broke physical contact. After this initial period, the spatial relationship between the mother and the offspring underwent major changes (Figure 4.8). The contact time during gNR declined steeply to low rates until the age of 20 months, beyond which it remained at very low levels with median rates clearly below those observed during gR (Figure 4.8). The contact time during gR also declined over the initial 17 months, the only period at which offspring spent generally less time in contact during gR than during gNR.
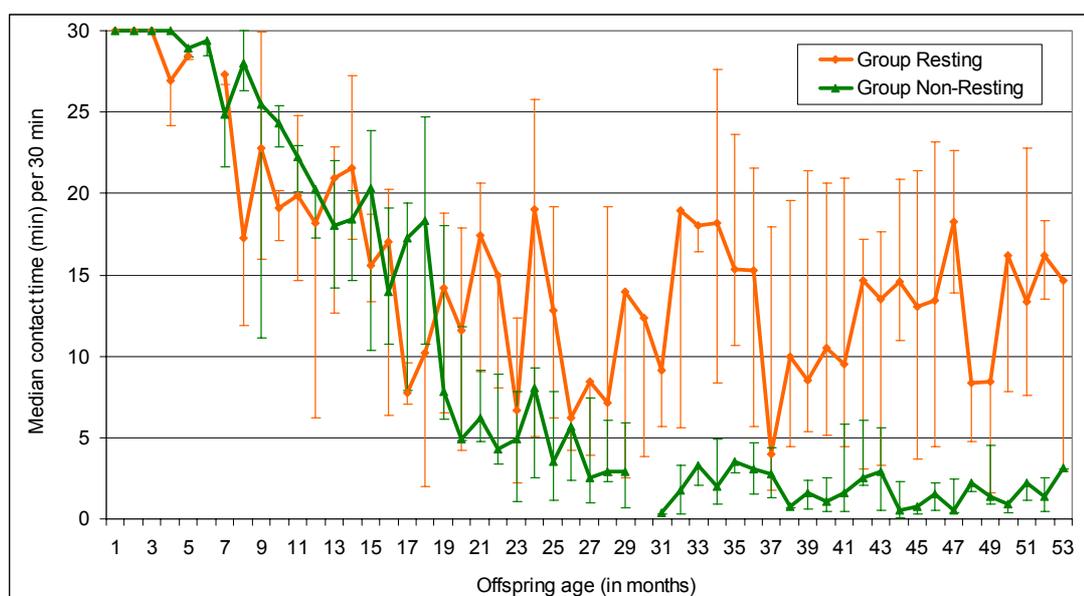

Figure 4.8 – Median contact time between mother and offspring presented by group activity and offspring age. Vertical lines = IQR.

It was primarily the offspring who initiated a reduction in contact with the mother (Figure 4.9a, b). To increase clarity, interquartile ranges are not shown in Figures 4.9a and b. Mothers made contact with offspring at relatively high rates until the age of 10 months, compared to later stages of infancy. This indicates that offspring were mainly responsible for the early decline in contact rates during gR and gNR, a developmental stage at which mothers showed the strongest levels of contact maintenance with offspring. Overall, offspring broke and made contact more frequently than mothers at nearly each stage of infancy (Figure 4.9a, b). The extent of this difference was greatly diminished beyond 36 months. During gR, offspring rates of making and breaking contact varied largely over the first three years, while rates increased rather steadily during gNR until the age of 18 months followed by a decline. At the age of three years, offspring rates of making and breaking contact remained at low levels with only minor fluctuations during both group activities. The mothers' rates of breaking contact during gNR were highest during the first 26 months, when offspring usually increase their intake of solid food (Schaller, 1963; Fossey, 1979). In contrast, mothers' rates of breaking contact during gR increased after the second year of infancy when offspring reached the critical weaning period. Maternal rejections of contacts made by offspring were generally low throughout the period of MI (Figure 4.9a, b).
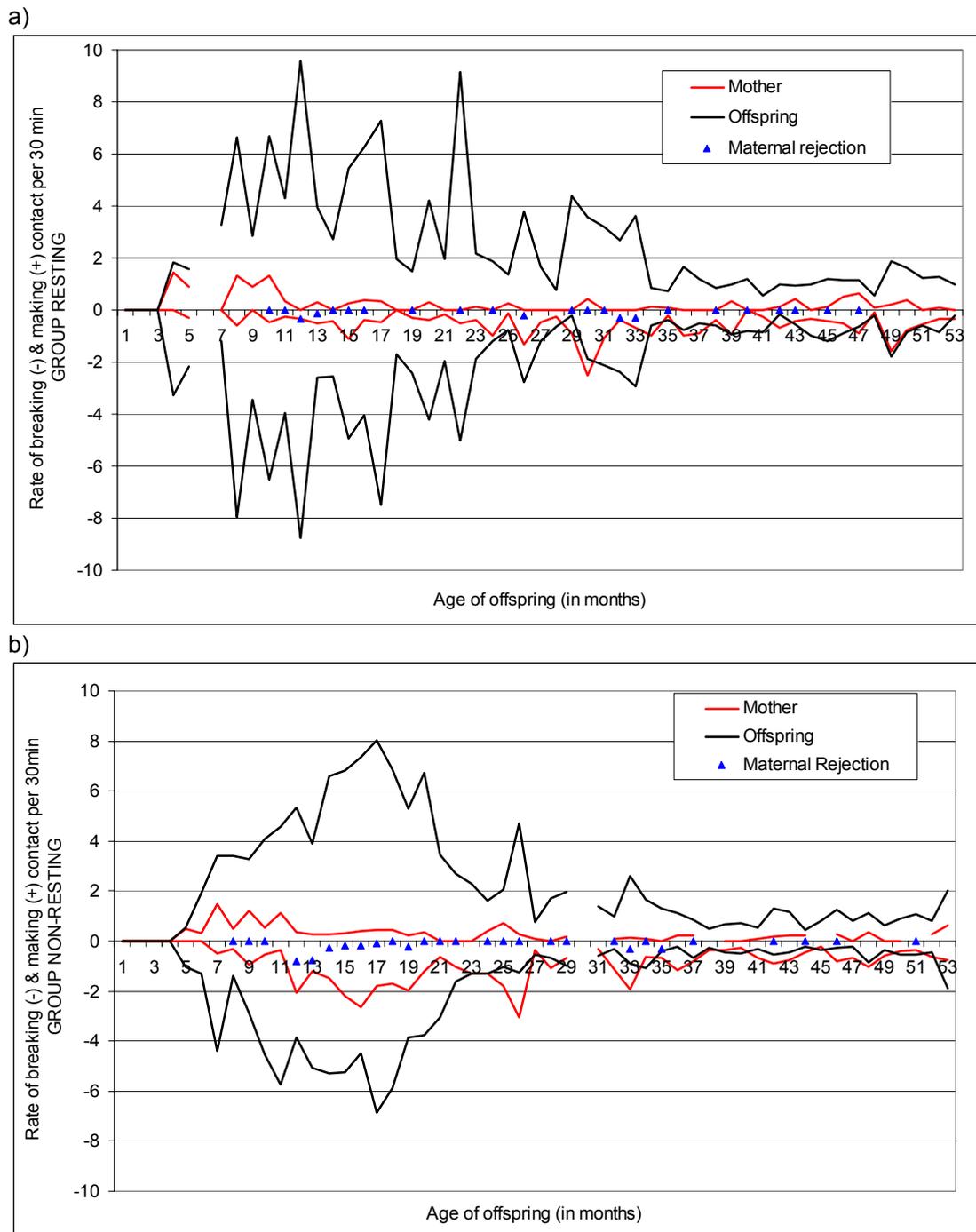
a)

b)

Figure 4.9 – Median frequency of making (positive values) and breaking (negative values) contact by mother and offspring with median frequency of maternal rejection during (a) group resting and (b) group non-resting presented by offspring age.

4.4.4.1 Scheduling of contact (offspring ≤2 years old)

In an initial GLMM (Table 4.11), the effect of offspring age and the predominant group activity on the occurrence of maternal rejections was investigated to find out if physical contact MOBC was mainly over the *scheduling* of MI during the initial two years. Mothers rejected significantly fewer contacts made by offspring during gR than gNR at the age of 15 months (centred value of offspring age) (Table 4.11). When running the GLMM without the interaction in a *post hoc* test, the main group activity effect was also significant (b ± SE = -0.952 ± 0.081, t = -11.71, p <0.001), supporting the fact that mothers tried to reduce contact primarily during gNR during the first two years. Increasing age of offspring led to an increase in maternal rejections during gR, which was not evident during gNR periods.

Table 4.11 – GLMM showing parameter estimates of fixed-effects on maternal rejections of physical contact, including offspring ≤2 years old. N = 184, N_{Mother} = 12, N_{Group} = 5, d.f. = 4.

Fixed-effect	b	SE	t value	p	
Intercept	-8.113	0.166	-48.78	**<0.001**	***
cOff_Age	0.007	0.010	0.65	0.516	
GrpAct-R	-0.911	0.066	-13.82	**<0.001**	***
cOff_Age~GrpAct-R	0.041	0.016	2.55	**0.011**	**

Off_Age = offspring age, GrpAct-R = group resting, c = centred variable.

A separate GLMM (Table 4.12) addressed the question of whether the mother, or both the mother and the offspring influenced contact patterns. The parameter estimates showed that contact time between mothers and offspring declined less strongly during gR than gNR during the first two years. The impact of contact attempts by offspring on contact time also depended on the group activity, showing that offspring succeeded in influencing contact time during gNR (b = 0.015), which was not the case during gR (b = -0.017 = 0.015 – 0.032). Irrespective of the group activity, offspring increased their influence on contact patterns as indicated by a positive interaction between contact initiation and offspring age. However, the mother also shaped the contact pattern through rejection behaviours during gNR (b = - 0.016), which was not found during gR (b = 0.259 = -0.016 + 0.275).

Table 4.12 – GLMM showing parameter estimates of fixed-effects on contact time for offspring ≤2 years old. (N = 200, N_{Mother} = 11, d.f. = 8).

Predictor	b	SE	z value	p	
Intercept	-0.941	0.034	27.51	**<0.001**	***
cOff_Age	-0.054	0.004	-13.98	**<0.001**	***
GrpAct-R	-0.029	0.032	-0.93	0.353	
cMakOff	0.015	0.005	2.86	**0.004**	**
MatRej	-0.016	0.065	-2.52	**0.012**	*
cOff_Age~GrpAct-R	0.016	0.005	3.34	**<0.001**	***
cMakOff~GrpAct-R	-0.032	0.008	-4.22	**<0.001**	***
cMakOff~cOff_Age	0.002	0.001	2.58	**0.010**	**
cMatRej~GrpAct-R	0.275	0.140	1.97	**0.049**	*

Off_Age = offspring age, GrpAct-R = group resting, MakOff = contact attempts of offspring, MatRej = maternal rejections, c = centred variable.

4.4.4.2 Amount of contact (offspring >2 years old)

In contrast to the initial two years, the GLMM (N = 219, N_{Mother} = 13, d.f. = 2) that examined maternal rejections beyond the second year showed that mothers rejected contacts made by their offspring slightly (n.s.) more during gR (b ± SE = 0.149 ± 0.078, t = 1.91, p = 0.057) than during gNR and that mothers reduced rejections of contact with increasing age (b ± SE = -0.057 ± 0.006, t = -8.89, p <0.001). This indicates that the physical contact MOBC declined during the critical weaning period and was slightly stronger during gR when most suckling events took place.

The GLMM (N = 261, N_{Mother} = 13, d.f. = 5) for the investigation of mother and offspring contribution to contact patterns revealed that mainly the offspring shaped contact patterns during the critical weaning period. This was indicated by a positive effect of contact initiation by offspring on the total time spent in contact (b ± SE = 0.058 ± 0.012, t = 4.71, p <0.001), which was stronger the older the offspring (b ± SE = 0.003 ± 0.001, t = 2.41, p = 0.016). Consistent with Figure 4.8, the model showed that mother and offspring spent more time in contact during gR than gNR (b ± SE = 0.370 ± 0.031, t = 11.91, p < 0.001).

4.4.5 Suckling MOBC

Although suckling frequencies fluctuated greatly during the period of nutritional dependence (Figure 4.10), it is clear that most suckling bouts took place during gR beyond the age of 13 months.
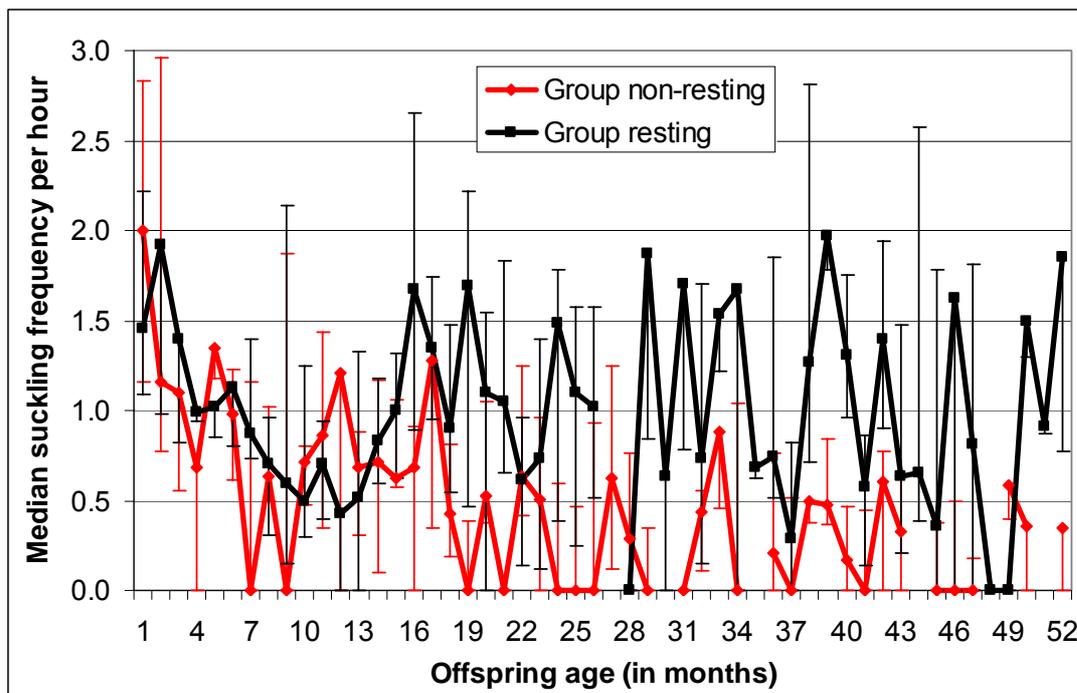

Figure 4.10 – Median suckling frequency presented by group activity and offspring age. Vertical lines = IQR.

The frequency of suckling attempts by offspring during gNR appeared to decline over infancy and drop below gR frequencies beyond the age of 17 months (Figure 4.11a, b). Maternal rejections during gNR occurred more frequently during the initial 17 months of infancy, beyond which their occurrence was rather sporadic. In comparison, maternal rejections during gR still occurred relatively regularly beyond the age of 17 months.
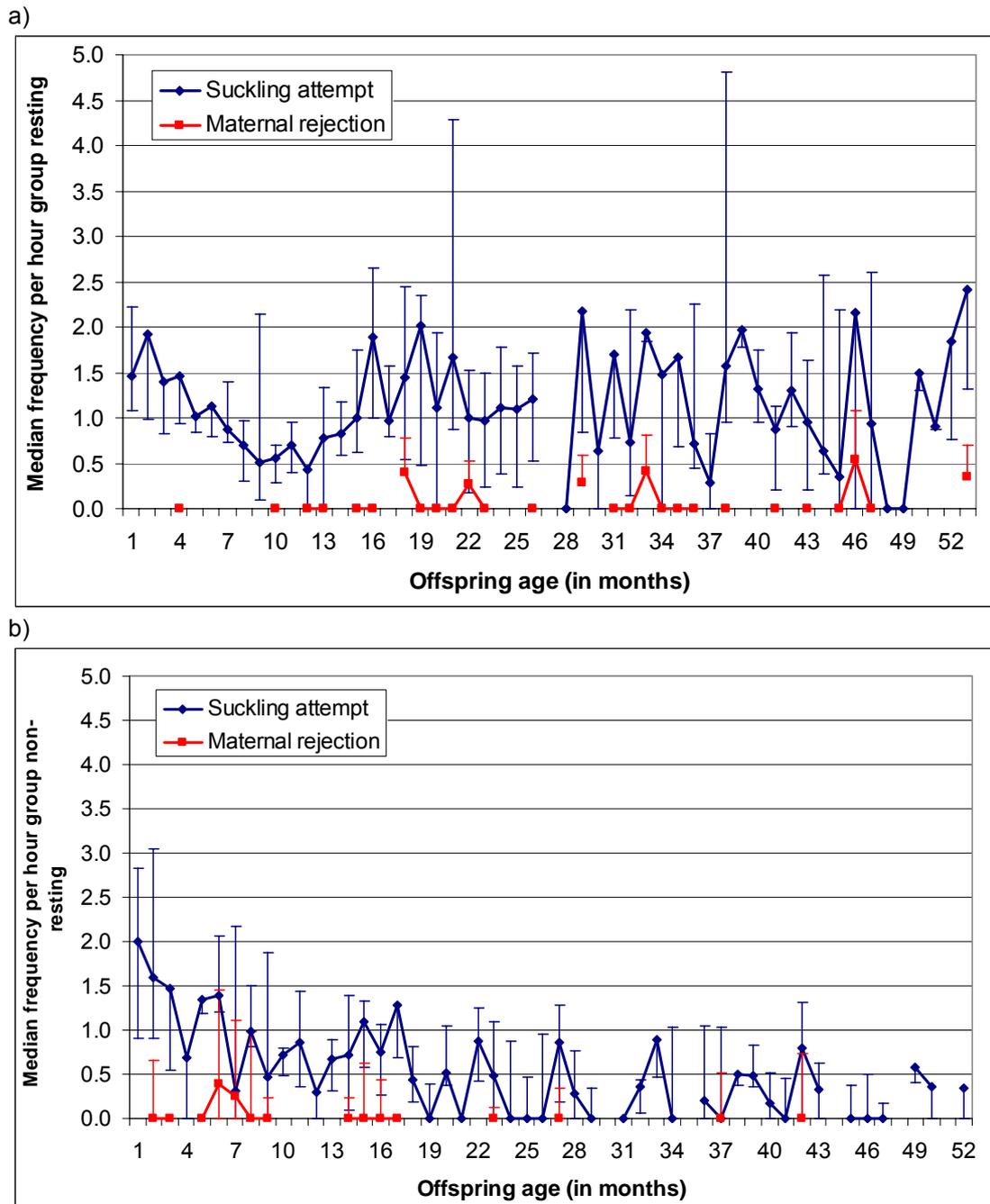
a)

b)

Figure 4.11 – Median frequency of suckling attempts and maternal rejections during (a) group resting and (b) group non-resting presented by offspring age. Vertical lines = IQR.

4.4.5.1 Scheduling of suckling (offspring ≤2 years old)

The effect of offspring age and group activity on the occurrence of maternal rejections was initially tested to see whether the suckling MOBC was mainly due to the scheduling of MI (Table 4.13). On average, mothers rejected fewer suckling attempts during gR, although this applies only to 13

month-old offspring (centred value of offspring age). However, there was also a main group activity effect when running the GLMM without the interaction term, indicating that mothers tolerated nipple access less overall during gNR during the first two years (b ± SE = -0.247 ± 0.117, t = -2.12, p = 0.034). The model (Table 4.13) also showed that the older the offspring, the lower the likelihood that a mother would reject suckling attempts during gNR (b = -0.086), while a reversed age effect was found during gR (b = 0.091 = -0.086 + 0.177), indicating that the intensity of the suckling MOBC declined during gNR but increased during gR towards the critical weaning period.

Table 4.13 – GLMM showing parameter estimates of fixed-effects on maternal rejections of suckling attempts for offspring ≤2 years old. N = 176; N_{Mother} = 14; d.f. = 3.

Fixed-effect	b	SE	t value	p	
Intercept	-7.009	0.075	-94.01	**<0.001**	***
cOff_Age	-0.086	0.009	9.21	**<0.001**	***
GrpAct-R	-0.387	0.104	-3.71	**<0.001**	***
cOff_Age~GrpAct-R	0.177	0.016	11.10	**<0.001**	***

Off_Age = offspring age, GrpAct-R = group resting, c = centred variable.

The GLMM (Table 4.14) examining mothers' and offsprings' influence on the suckling occurrence provided evidence that both parties had a stake in suckling patterns during the first two years of MI. This was indicated by both a negative effect of maternal rejections and a positive effect of suckling attempts on suckling occurrences. The latter effect was stronger the older the offspring.

Table 4.14 – GLMM showing parameter estimates of fixed-effects on suckling frequency for offspring ≤2 years old. (N = 199, N_{Mother} = 12, d.f. = 10).

Predictor	b	SE	z value	p	
Intercept	-4.643	0.090	-51.36	**<0.001**	***
cOff_Age	-0.020	0.011	-1.81	**0.070**	.
GrpAct-R	0.206	0.126	1.64	0.101	
cSuckAttempt	0.430	0.035	12.15	**<0.001**	***
MatRej	-0.332	0.074	-4.45	**<0.001**	***
cOff_Age~cSuckAttempt	0.010	0.004	2.26	**0.024**	*

Off_Age = offspring age, GrpAct-R = group resting, SuckAttempt = suckling attempts of offspring, MatRej = maternal rejections, c = centred variable.

4.4.5.2 Amount of suckling (offspring >2 years old)

The GLMM (N = 131, N_{Mother} = 14, d.f. = 2) which addressed the question of whether the suckling MOBC concerned mainly the *amount* of MI during the critical weaning period revealed that mothers rejected more suckling attempts by offspring during gR (b ± SE = 0.660 ± 0.135, t = 4.91, p < 0.001).

When examining which party shaped suckling patterns beyond the second year (Table 4.15), findings were similar to those during the first two years. Mother and offspring both shaped suckling patterns, indicated by a negative effect of maternal rejections on suckling occurrences, while suckling attempts by offspring had a positive effect on suckling occurrences. The latter effect was stronger during gNR (b = 1.152) than during gR (b = 0.296 = 1.152 – 0.856), indicating that offspring were more likely to succeed in getting nipple access per suckling attempt during gNR than during gR. However, it must be noted that fewer suckling attempts occurred during gNR beyond the second year (Figure 4.11a, b). A post hoc test without interactions showed a main group activity effect, indicating a higher occurrence of suckling bouts during gR than during gNR during the critical weaning period (b ± SE = 0.583 ± 0.179, t = 3.26, p = 0.001).

Table 4.15 – GLMM showing parameter estimates of fixed-effects on suckling frequency for offspring >2 years old. N = 174, N_{Mother} = 10, d.f. = 5.

Fixed-effect	b	SE	z value	p	
Intercept	-4.988	0.137	-36.46	**<0.001**	***
Off_Age	-0.001	0.010	-0.08	0.935	
GrpAct-R	0.550	0.172	3.20	**0.001**	**
cSuckAttempt	1.152	0.142	8.10	**<0.001**	***
MatRej	-0.380	0.110	-3.45	**<0.001**	***
GrpAct-R~cSuckAttempt	-0.856	0.148	-5.77	**<0.001**	***

Off_Age = offspring age, GrpAct-R = group resting, SuckAttempt = suckling attempts of offspring, MatRej = maternal rejections, c = centred variable.

4.4.6 Grooming MOBC

Maternal grooming, as a proportion of time in association with the offspring, fluctuated strongly over infancy (Figure 4.12). The highest level of grooming activity occurred within the first six months of infancy and later, from the end of the second year to the beginning of the third year of infancy.
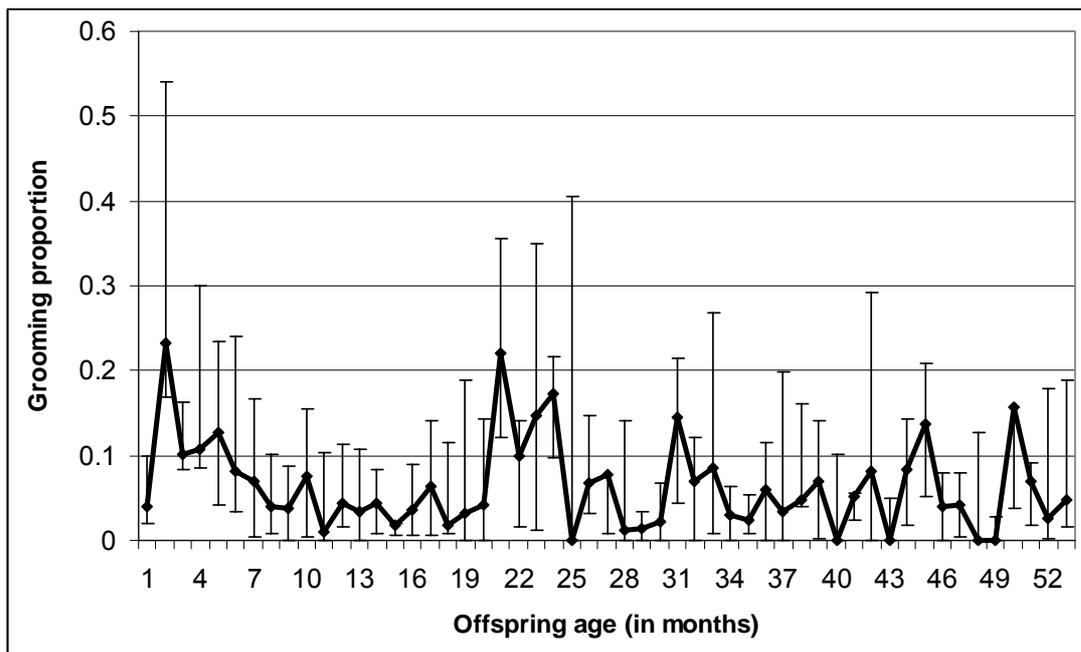

Figure 4.12 – Median time mothers spent grooming as a proportion of mother's total resting time in association (≤5m) with offspring presented by age. Vertical lines = IQR.

Offspring refused maternal grooming most frequently when they were younger than 28 months (Figure 4.13). Beyond that age, refusal behaviour of offspring generally decreased and occurred more sporadically, in particular between 45-49 months.
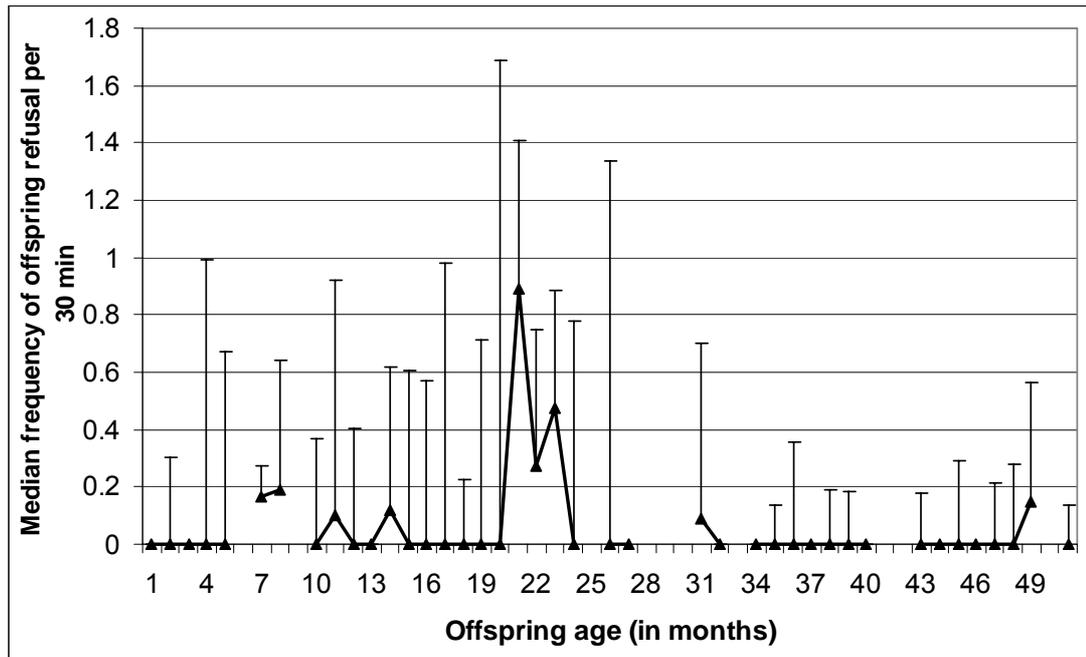
Figure 4.13 – Median frequency of grooming refusal by the offspring per 30 min of mothers' resting time in association (≤5m) with offspring represented by age. Vertical lines = IQR.

The frequency of maternal disciplining during grooming sessions was generally very low and occurred more frequently and at higher proportions within the first 28 months of infancy (Figure 4.14). Beyond that age, mothers only rarely disciplined their offspring although, simultaneously with the occurrence of offspring refusal, maternal disciplining increased temporarily at the age of 46 months, before it dropped again after the age of 51 months. Whimper signals elicited by offspring in a grooming context were mainly recorded beyond the age of 30 months (Figure 4.15), after offspring had entered the critical weaning period.
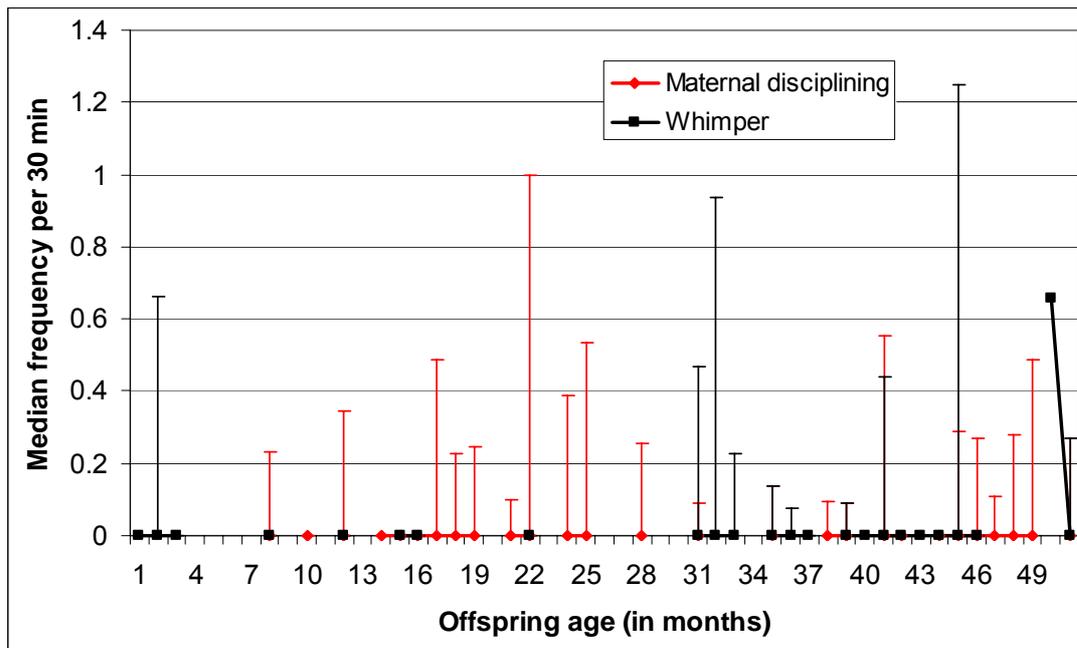
Figure 4.14 – Median frequency of maternal disciplining and offspring whimper in a grooming context per 30 min mothers' resting time in association (≤5m) with offspring represented by offspring age. Asterisks represent extreme outliers; open circles, outlier. Vertical lines = IQR.

Parameter estimates of the GLMM (N = 178; N_{Mother} = 19; N_{Group} = 6; d.f. = 5) which examined whether the mother alone or the mother and the offspring together shape grooming patterns, revealed that the more offspring refused grooming, the more the mother actually groomed (b ± SE = 0.091 ± 0.024, t = 3.87, p < 0.001). Thus, offspring were not successful in reducing grooming through refusal behaviour.

The model also confirmed that grooming as a proportion of the total time that mothers spent resting in association with their offspring was not affected by offspring age (b ± SE = -0.001 ± 0.001, t = -1.36, p = 0.173). Taking into account that mothers' resting time in association with offspring declined with offspring age (b ± SE = -0.004 ± 0.001, t = -4.02, p < 0.001), which was estimated by a separate GLMM (N = 155, N_{Mother} = 19, d.f. = 1), the overall time that mothers spent grooming their offspring also declined with age.

To examine changes in the scheduling of grooming in coordination with suckling bouts, a separated GLMM (N = 160, N_{Mother} = 19, d.f. = 5) was conducted. The parameter estimates showed that mothers rescheduled

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grooming to coincide with suckling more often with increasing offspring age (b ± SE = 0.009 ± 0.003, t = 3.51, p <0.001). This rescheduling process was inversely associated with the proportion of resting time which mothers and offspring spent in association (b ± SE = -0.293 ± 0.091, t = -3.21, p = 0.001). Offspring refusal of grooming attempts by mothers was unrelated to the rescheduling process. These findings suggest that mothers rescheduled grooming to provide maternal care more efficiently when the time spent resting in association with offspring reduced, rather than simply to bargain nipple access for permission to groom or as a direct response to offspring refusal behaviour of grooming attempts.

4.4.7 Transport MOBC

With increasing age, the proportion of travel time that offspring were transported by their mothers decreased, accompanied by an increase in the proportion of time following the mother and moving independently from the mother (Figure 4.15). Rump-cling was a rare mode of locomotion. Beyond an offspring age of 28 months, mothers were rarely seen carrying their offspring.
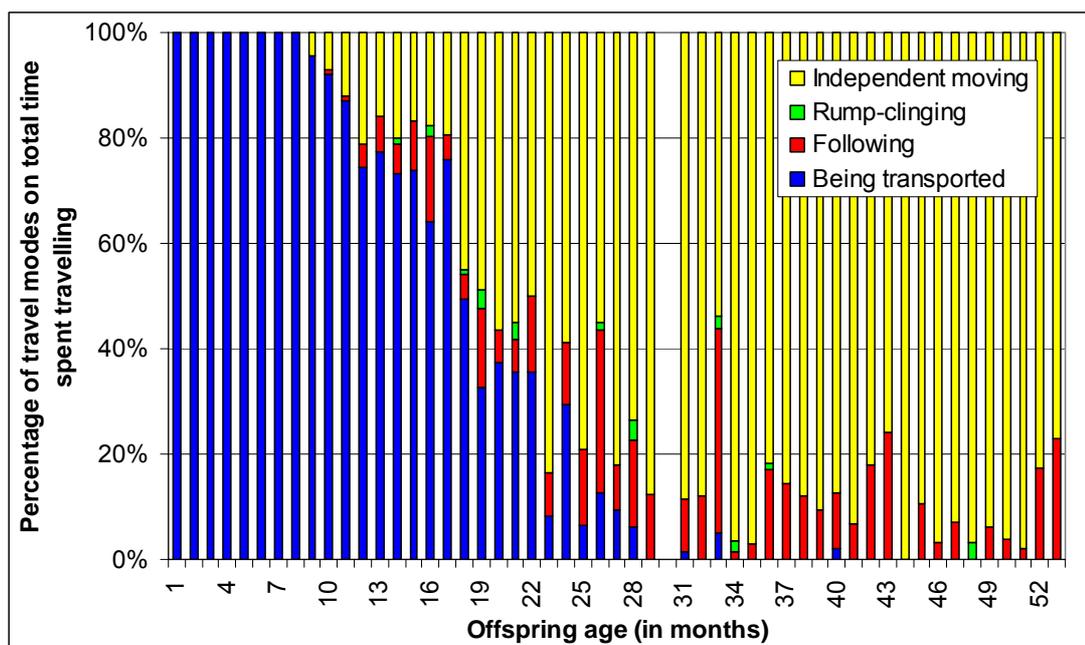

Figure 4.15 – Distribution of offspring travelling time (%) over four modes of travel presented by offspring age.

Whimper signals in moving contexts occurred throughout infancy and beyond (Figure 4.16). During the first year of infancy, maternal rejection of transport attempts by the offspring was relatively rare and occurred mainly when the mother moved very short distances and the offspring tried to climb up the mother's back. The occurrence of maternal rejection and whimper signals (Figure 4.16) suggest that the transport MOBC was strongest between the ages of 12-29 months, a period during which the proportion of time that the offspring was transported dropped from approximately 70% to zero. Maternal rejection of transport followed a quadratic relationship with offspring age (GLMM: N = 136, $N_{Mothers}$ = 24, N_{Group} = 7, b ± SE = -0.165 ± 0.069, t = -2.4, p = 0.016).
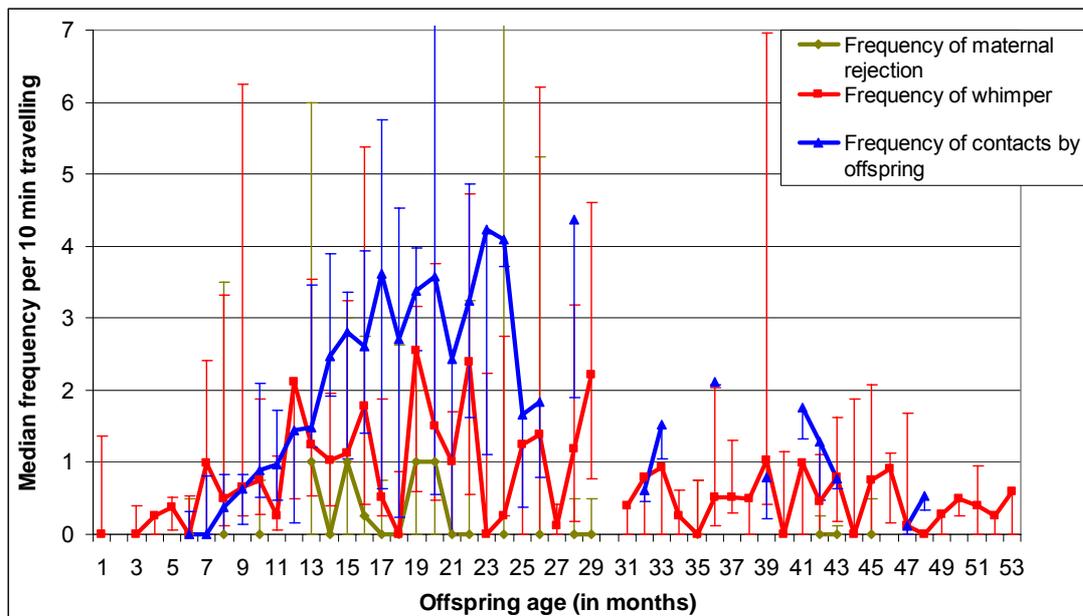

Figure 4.16 – Median frequency of contacts, made by offspring, which were rejected by mothers during travelling and median frequency of offspring whimper signals during travelling presented by offspring age. Vertical lines = IQR.

The parameter estimates of the GLMM which addressed the question of the extent to which mothers and offspring influenced transport patterns (N = 112, N_{Mother} = 12, d.f. = 4) revealed an negative effect of offspring whimper signals on transport time (b ± SE = -0.026 ± 0.011, t = -2.37, p = 0.018), indicating that offspring did not manage to increase transport by employing distress signals. Although maternal rejections of transport attempts had no

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significant effect on transport either, the estimate was negative (b ± SE = -0.046 ± 0.032, t = -1.45, p = 0.148). The model also confirmed a decline in the proportion of time that offspring were transported by their mothers with increasing offspring age (b ± SE = -0.421 ± 0.046, t = -9.17, p <0.001).

4.5 Discussion

4.5.1 Maternal rejection

It has been widely recognised that conflicts between mother and offspring can arise at stages other than weaning (Altmann, 1980; Bateson, 1994; Maestripieri, 2002a), and the results of the current study suggest that mountain gorillas are no exception. The occurrence of maternal rejection, which is commonly used to identify behavioural conflicts (Maestripieri et al., 2009), was highest before the critical weaning period when offspring were learning to travel independently, starting supplementing milk with solid food and when mother-offspring association patterns were undergoing major changes.

Maternal experience can affect the occurrence of maternal rejection (cotton-top tamarins, *Saguinus oedipus*, Johnson et al., 1991; vervet monkeys, *Cercopithecus aethiops sabaeus*, Fairbanks & McGuire, 1995; sheep, *Oris aries*, Dwyer & Lawrence, 2000). Although no such evidence emerged from this study, maternal experience may have influenced the strength and severity of rejections. Primiparous mothers employed more aggressive rejections in behavioural conflicts than multiparious mothers. High aggressiveness in first-hand mothers towards infants was also found in sheep (Dwyers & Lawrence, 2000) and Japanese macaques (*Macaca fuscata*) (Hiraiwa, 1981), and this may reflect a relatively high intensity of MOBCs (Reeve & Kellner, 1997). Parity-related differences in MI, such as lower milk secretion in primiparous mothers compared to multiparous mothers (cows, *Bos taurus*, Obara, 1992; Japanese macaques, Tanaka, 1997; human, Amatayakul et al. 1999; sheep, Sevi et al., 2000), may place

offspring of primiparous mothers further away from their optimal level of MI than offspring of multiparous mothers, leading to higher disparity in optima of mother and offspring resource allocation (Trivers, 1974; Parker & Macnair, 1978; Godfray, 1995). This disparity may increase still further, taking into account that primiparous females have often not yet reached their full adult size (Silk, 1987; Muruthi et al., 1991) and may therefore need to divert additional resources to their own growth which then cannot be available for offspring.

Primiparous mothers also increased mild and preventive rejection behaviours with offspring age which contrasted with multiparous mothers who decreased mild and preventive rejection behaviours. Differences in the use of more extreme (*mild* or *strong*) behaviours in controlling offspring behaviour between primiparous and multiparous mothers may indicate that the former are less competent and less experienced in providing appropriate maternal care, so lacking alternative rearing strategies. This is supported by long-term demographic records on the Virunga mountain gorillas; primiparous mothers have 50% higher offspring mortality and 20% longer inter-birth intervals than multiparous mothers (Robbins et al., 2006). However, other primate studies suggest the opposite: that primparous mothers provide maternal care equally as well as multiparous mothers (rhesus macaques, *M. mulatta*, Seay, 1966). To address the question of whether the disparity in optima of mother's and offspring's resource allocation is affected by parity requires measures of both the mother's and offspring's physical condition, and fitness consequences of decisions in the MOBC; it is imperative therefore that these data are collected over the long term.

4.5.2 Signalling of offspring distress

Consistent with previous observations (Fossey, 1979; Stewart, 1981; Fletcher, 2001), mountain gorilla offspring predominantly used whimper signals in interaction with their mothers, rather than tantrum displays, hooting or screaming, which may function as signals of a higher intensity of alertness. This was also supported by higher rates of positive responses from mothers to those signals compared to whimper signals. A relatively high proportion of

whimpers compared to the alternative distress signals suggest that whimper signals are relatively cheap for young mountain gorillas in terms of energy and increased risk of predation. Although mountain gorillas are not exposed to any non-human predators (Schaller, 1963), acoustic signals may attract external silverbacks and thus, increase the risk of infanticide, which accounts for 37% of infant mortality (Watts, 1989). Whimper signals in mountain gorillas are classified as 'close'-calls (Harcourt et al., 1993), which describe vocalisations audible only within the group. Hooting, in comparison, counts as a 'long'-call, which is audible at long distances (Fossey, 1972; Harcourt et al., 1993). Screaming has been described as a 'shrill and prolonged emission of extremely loud sound' (Fossey, 1972). Although classified as 'close'-calls, screams have the potential to be audible at very long distances (>1.5 km; personal observation). Therefore, whimpers may be less costly in terms of increased infanticide risk than screaming, hooting and tantrum displays, which usually occurred in combination with screaming. In terms of the metabolic costs of distress signals, there is a lack of nonhuman mammalian studies (Wells, 2003). Without information about direct fitness consequences of offspring signalling, costs of offspring distress signals can only be guessed at.

The relatively high proportion of offspring distress signalling, which was either ignored or led to negative reactions by mothers, does not support the honest signalling theory (Godfray, 1991), rather findings suggest that offspring also used distress signals to manipulate mothers, who learned to discriminate between honest and deceitful signals (see Trivers, 1974; Hauser, 1986). Reliable indicators for mothers to differentiate honest signals of need from deceitful signals may be both the offspring age and the signal rate (Maestripieri & Call, 1996). The type and combination of different distress signals could also play a role in indicating to mothers whether distress signals are true reflection of need or not. This is seen in humans, where, for a newborn, the health status correlates negatively with the crying pitch level, which parents use intuitively to detect health problems (Wells, 2003).

Maternal responsiveness in mountain gorillas varied strongly during the period of MI. This could be explained by an alternating cycle of honest

and deceitful signalling in offspring, possibly reflecting several ongoing behavioural conflicts in various contexts at different developmental stages, to which mothers and offspring behaviourally adjust (Hauser, 1986) based on a mutual monitoring (Altmann, 1980). Concurrent with an increase in deceitful signalling, maternal responsiveness was expected to decline during infancy as shown in other primate studies (vervet monkeys, Hauser, 1986; stump-tailed macaques, Maestripieri & Call, 1996). In this study, a decline in maternal responsiveness occurred only tentatively in primiparous mothers but not in multiparous mothers. Lower maternal responsiveness in first-hand mothers is a phenomenon that has been reported across species (sheep, Dwyer & Lawrence, 2000; Arabian horses, *Equus ferus caballus,* Juarbe-Díaz, 1998; Japanese macaques, Hiraiwa, 1981; cynomolgus macaques, *M. fasciculiaris*, Timmermans & Vossen, 1996; rhesus macaques, Maestripieri & Carrol, 1998; gorillas, *Gorilla gorilla gorilla*, Nakamichi et al., 2004). Assuming that the mother's ability to discriminate between honest and deceitful signals should improve with maternal experience (Trivers, 1974), a slightly stronger decline in the responsiveness of primiparous compared to multiparous mothers suggest that primiparous mothers responded slightly less to honest signals with offspring age. Alternatively, offspring of first-time mothers may employ slightly more deceitful signals than offspring of experienced mothers. Parity-related differences in the mother-offspring communication need to be studied more closely in future, if possible, integrating measures of offspring physical condition, such as health status. In particular, captive studies may help to provide more insight into the question of whether young gorillas use distress signals to manipulate mothers.

4.5.3 Mother-offspring behavioural conflicts (MOBCs)

4.5.3.1 Physical contact and suckling MOBC

Findings from behavioural conflicts over physical contact and suckling provided some evidence that mothers and offspring disagree over both the *scheduling* and the *amount* of MI during the transition to offspring independence (Altmann, 1980). Similarly to observations in other primates

(yellow baboons, *Papio cynocephalus*, Altmann, 1980; gelada baboons, *Theropithecus gelada*, Barrett et al., 1995; rhesus macaques, Johnson, 1986; Gomendio, 1991; long-tailed macaques, Karssemeijer et al., 1990), mountain gorilla mothers tried primarily to reduce physical contact during their main feeding activities, such as during gNR, when the presence of growing offspring probably became a hindrance, and to reschedule suckling events from gNR to gR. This is consistent with the scheduling hypothesis (Barrett et al., 1995). This rescheduling process during early infancy provides further support that the interference of physical contact and suckling with mothers' main feeding time can be extremely disadvantageous to mothers. During nutritional dependence of the infant, mothers have to cope with additional energetic expenses to meet maternal and offspring requirements (Randolph et al., 1977; Oftedal 1984; Gittleman & Thompson, 1988). Thus, maternal time budgets may be strongly constrained by the need for additional feeding time which requires that offspring demands are synchronised to mothers' activities (Altmann, 1980; Dunbar & Dunbar, 1988).

Although mothers managed to influence contact patterns during gNR through rejection of contact attempts by offspring, higher maternal rejection rates during gNR compared to gR did not result in lower contact times during gNR before the age of 18 months. This can be explained by the positive impact of offspring initiations on contact patterns during gNR; offspring often react to frequent maternal rejections with a temporary intensification of contacts before a long-term decline in contact (Nash, 1978; van de Rijt-Plooij & Plooij, 1987; Maestripieri, 2002a). Similar to the conflict over the scheduling the contact time, mothers rejected suckling attempts at higher rates during gNR compared to gR and succeeded in reducing the number of suckling bouts during gNR. This suggests that mothers additionally controlled the conflict over the scheduling of suckling bouts directly through the regulation of contact times (see Karssmeijer et al., 1990; Barrett et al., 1995). However, deferred changes in MI patterns were also found in the conflict over the scheduling of suckling. No clear bias of suckling events towards gR occurred before the age of 18 months, due to offspring counteracting rejections by adjusting suckling attempts, which occurs in Japanese macaques (Collinge, 1987). A similar lack of immediate effect on milk

suckling patterns at the peak of behavioural conflicts was also reported in rhesus macaques (Gomendio, 1991). Therefore, although long-term effects of the conflict over the contact time and suckling suggest that mothers finally succeeded in achieving their aims, findings also suggest that offspring managed to impede and slow down the reduction in MI during gNR. Overall, patterns of physical contact and suckling MOBCs showed strong similarities, suggesting that both conflicts were interlinked.

Mothers and offspring were involved in several behavioural conflicts at every age as shown in rhesus macaques (Simpson et al., 1986). Concurrently with the conflict over *scheduling* of contact and suckling, the conflict over the *amount* of contact and suckling started intensifying and dominated over *scheduling* conflicts during the critical weaning period (>24 months; see Chapter 3). At this time, mothers rejected contacts and suckling attempts predominantly during gR when contact time and suckling activities were highest as a result of the earlier rescheduling process. Offspring still managed to influence contact and suckling patterns through attempts to initiate contact and suckling during the critical weaning period, whereas a direct impact of maternal rejections was only evident in the suckling pattern but not in contact patterns. The general decline in maternal rejections of contact during the critical weaning period may indicate that the physical contact MOBC was eventually mediated along with the completion of weaning.

The fact that mothers were more likely to tolerate suckling attempts by offspring during gNR beyond the second year may appear paradoxical and surprising. Offspring may have learnt to cooperate with their mothers and demand nipple contact during gNR only under particular circumstances, such as during extended periods without gR. In such cases, mothers may have been more tolerant to suckling attempts. It may be that during the critical weaning period, offspring may try to exploit this form of compromise between mother and offspring and increase the demand for nipple contact during gNR to a more infantile level (Clark, 1977), which in return may lead to a temporary rise in maternal rejections.

Overall, findings from the contact and suckling MOBCs suggest that offspring managed to influence both forms of MI through counteracting

mother's rejection with contact initiation and suckling attempts during infancy and beyond. Such behaviour supports conflict mediation at a compromise level between parents' and offsprings' optima, as suggested in pro-rata models (Parker & Macnair, 1979; Altmann, 1980; Parker, 1985; Queller, 1994). Such a strategy could be effective for offspring in delaying the weaning process and increasing fat reserves, and thus effective also for mothers through improved chance of offspring survival and reproductive success.

4.5.3.2 Grooming MOBC

Evidence suggested that mothers rescheduled grooming activities to coincide with suckling events as offspring became older to provide both forms of MI more efficiently, concurrent with the reduction of resting time in association with the offspring. No previous reports of such a rescheduling process could be found in the literature. Nevertheless, the total time which mothers spent grooming their offspring declined with age, which corresponds with previous findings in gorillas (Stewart, 1981; Fletcher, 1994).

If it is assumed that grooming is an important component of maternal investment in mountain gorillas; the POC theory (Trivers, 1974) predicts that offspring should try to increase the grooming time provided by their mothers. In this study, the opposite was observed, with offspring trying to reduce grooming time, for example when playmates were around and when they were distracted by their environment. Findings suggest, however, that offspring were not very successful in manipulating grooming patterns through their refusal behaviour and whimper signals. Mothers often restrained their offspring when they tried to break away. Equally, the occurrence of grooming was not determined through maternal disciplining. It may be that the conflict was gradually resolved in progression of the rescheduling process of grooming activities to coincide with suckling events when offspring were likely to be more willing to tolerate grooming by mothers and less easily distracted.

An obvious question to ask may be why offspring seem to prefer activities, such as playing and explorative behaviour to being groomed by the mother. Playing is a fundamental behaviour for the development of future

skills which are crucial for offspring survival in primates (Poirier & Smith, 1974), such as social and motor skills. Equally, explorative behaviour may function as a preliminary stage of foraging (see Chapter 5) and thus, be an important practice for young offspring during transition to nutritional independence. Therefore, devoting time to play and exploring may be more important for offspring than being groomed. With increasing independence during travel periods, offspring can take a greater role in influencing play opportunities than previously and thus compensate lost play opportunities after completion of maternal grooming, which may explain the decline in offspring refusal of grooming beyond 21 months.

The temporary recurrence of the grooming conflict over grooming at a very late stage of MI (46-51 months) was notable. A high percentage (38%) of offspring in this study (see Chapter 3) was weaned within this age-period. Considering that grooming and suckling activities became increasingly synchronised as offspring aged, the underlying reason for the 'recurred' conflict may differ from the original reason for conflict during early infancy. During the weaning peak when mothers cease nipple access but not grooming, offspring may still associate a bout of grooming with suckling. Thus, whimper signals during grooming bouts may have functioned as begging signals for nipple access. Equally, maternal disciplining during grooming sessions may have addressed attempts by the offspring to get closer to the nipple rather than to break away, although, it was often impossible to distinguish such movements in the field.

4.5.3.3 Transport MOBC

The relative occurrence of maternal rejections and offspring whimper signals showed that behavioural conflict over transport dominated conflicts during the second and third years. Apart from lactation, transport is the most costly MI in terms of energy expenditure (Altmann & Samuels, 1992), however, independent locomotion is costlier in infants than in adults and increases nutritional demands from the young (Altmann, 1980; Altmann & Samuel, 1992) and thus, transport was a maternal investment about which mother and offspring were expected to disagree. Previous primate studies

suggest that mothers have the ability to weigh costs and benefits of carrying the offspring at any stage of MI, depending on offspring size, maternal condition, travel distance and velocity (Altmann & Samuels, 1992; Kramer, 1998). In this study, offspring were usually carried by mothers during all travel until the age of eight months similar to that observed by Fossey (1979) and Fletcher (1994). Beyond that age, transport patterns changed dramatically, suggesting that energetic costs for mothers in transporting their youngsters increasingly outweighed the benefits.

Results suggest that offspring did not manage to increase maternal transport by distress signalling; the more offspring whimpered, the less they were carried by their mothers. It may be difficult for offspring to manipulate transport patterns through exaggerations of true needs, since mothers have not only information about offspring physical condition, size and weight but also about the distance and velocity of the current travel session. After all, this is often dictated by the mother during bouts of travel. Offspring, in comparison, are less able to predict how far and fast their mothers will travel at the point which the mother starts moving away, although they may become more experienced in predicting when the speed and distance of travel alters the mother's travel behaviour with age.

Yellow baboon mothers carried older offspring disproportionally during rapid travel, resulting in greater travel distances per unit of transport time (Altmann & Samuels, 1992). This coincides with field observations in the present study: when mothers were foraging only a few metres between food patches, young offspring's (≤18 months) attempts to be transported were rejected, whereas mothers who travelled rapidly and/or over long distances were extremely rarely seen to refuse transport. It has been proposed that independent travel, during slow to moderate moving may not only be important for developing motor skills but also for developing foraging skills essential for nutritional independence and may compensate for some of the immediate energetic costs (Altmann & Samuels, 1992). In contrast, during inter-group interactions or interactions with external silverbacks, when the risk of infanticide rises (Watts, 1989) and the likelihood that the group would have to flee rapidly was high, mothers were observed to allow offspring who were even older than three years to be transported.

Actual maternal rejections of offspring transport attempts did not clearly affect transport patterns, however. Field observations suggest that mothers were able to partly control transport patterns by commencing travel while out of physical contact with the offspring. Mothers could then control whether the offspring is able to catch up for a ride or has to follow independently through regulating speed of travel. An alternative explanation for the lack of an association between achieved transport time and frequency of maternal rejection may be that offspring managed to mediate the effect of maternal rejections by succeeding, at least occasionally, in transport attempts.

4.5.4 Summary and conclusion

Findings on various behavioural conflicts in mountain gorilla mother-offspring dyads suggest that both parties engage in conflicts over the *scheduling* and the *amount* (quantity) of MI (Altmann, 1980; Barrett et al., 1995), which can temporarily overlap (Simpson et al., 1986) and may be interlinked. The impact of mother and offspring on the mediation of behavioural conflicts depended on the context and offspring age, with short-term effects of maternal rejection on offspring behaviour often being different from long-term effects, which makes the assessment of MOBCs difficult (Fairbanks, 1996). Long-term effects of the MOBCs revealed from this study suggest that mothers succeeded in achieving their aims, although offspring managed to impede and slow down the reduction in MI. Thus, the findings provide some support that pro-rata models, with conflict resolutions at a compromise level between the optima of both parties (Parker & Macnair, 1979; Altmann, 1980; Parker, 1985; Queller, 1994), apply to behavioural conflict mediation in mountain gorilla mother-offspring dyads rather than supporting the alternative hypothesis that behavioural conflict outcomes are always on mother's optimum through *force majeure* (Alexander, 1974).

Patterns of maternal responsiveness to offspring signals during the period of offspring transition to independence support the POC theory (Trivers, 1974) rather than the honest signalling hypothesis (Godfray, 1991). Offspring whimper signals appeared to be relatively cheap and to be used to

manipulate MI. Previous maternal experience had only a very slight effect on maternal responsiveness to offspring signals, whereas parity affected the strength and severity of maternal rejections, suggesting that primiparious mothers may be less competent and provide maternal care less well than multiparous mothers (Hiraiwa, 1981).

As in any prospective study, where future fitness consequences cannot be assessed, results have to be interpreted with caution. Direct antagonistic fitness consequences for mothers and offspring were not assessable within the framework of this study, due to difficulties in measuring future reproductive success and physical condition, such body weight, in a wild population.

It also remains an open question as to whether behavioural conflicts in the present study also reflect underlying genetic conflicts. More recently, cross-fostering study approaches have demonstrated genetic correlations between mother and offspring conflict-related behaviours (great tits, *Parus major*, Kölliker et al., 2000; mice, *Muss* spp., Hager & Johnstone, 2003; rhesus macaques, Maestripieri, 2004). Comparing the intensity of MOBCs in one-male and multi-male groups may be one way to approach this question in a wild gorilla population, if genetic data are also available. Maternal siblings in one-male groups are usually full-siblings, compared to multi-male groups, where it is more likely that siblings were sired by more than one male (see Bradley et al., 2005). If the disparity of optima in MI between the mother and offspring mainly depends on the coefficient of relatedness between offspring and its siblings (Trivers, 1974; Parker & Macnair, 1978; Robinson, 1980), behavioural conflicts over MI in mountain gorillas should be less severe in one-male groups, providing that a mechanism evolved that links offspring demand for MI with group characteristics (Long, 2005).