Chapter 7

Final discussion

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The way in which a mother distributes maternal resources to her current and future offspring is crucial for offspring survival and the reproductive success of both the mother and offspring (Trivers, 1972). However, behavioural correlates of maternal investment (MI) and mother-offspring relationships are lacking in mountain gorillas and are currently based on previous studies of social and behavioural development (Fossey, 1979; Stewart, 1981, 1988; Fletcher, 1994, 2001). This thesis has provided a comprehensive update on FRS through an in-depth investigation of four key areas of mother-offspring relationships, using a wide range of behavioural measures. Data from four field seasons have been combined and analysed to maximise potential for interpretation.

The present chapter brings together findings from the four key areas and discusses how they further our understanding of MI and mother-offspring relationships in mountain gorillas. Limitations and future directions are highlighted and discussed as well as important future research areas identified. Recommendations are provided to the authority of the ORTPN and the KRC for continuation of data collection and behavioural monitoring, which will enable further study of this vital area.

7.1 Update on female reproductive strategies in the mountain gorilla

The TWH (1973) was identified as the most appropriate framework to investigate MI in mountain gorillas (Chapter 1). Several key findings from the current research were indeed consistent with the predictions of the TWH, showing that female mountain gorillas invest in their offspring in a way which reflects their maternal condition, with mothers in good condition investing more heavily into sons and mothers in poor condition investing more into daughters. The strongest support for the TWH emerged from suckling frequency data, which supports previous findings on IBIs (Robbins et al.,

2007a), and underpins the impact of suckling frequency on anovulation in most primates (Konner & Worthman, 1980; Lee, 1987; Stewart, 1988; Taylor et al., 1991; Gordon et al., 1995; McNeilly, 1997). This is the first evidence for the TWH in suckling patterns in a nonhuman species of primate and may reflect the level of sexual dimorphism in this polygynous species.

However, using nipple contact as an indicator for milk transfer presents limitations (see review by Cameron, 1998), which cannot be ignored, including the assumption that milk quality does not vary between mothers and that milk transfer is consistent throughout all suckling bouts. Currently, there is little understanding of how these factors vary in mountain gorillas. Future studies may well alter our perception of suckling and its usefulness as a measure of MI, but for now it remains a key tool in investing MI.

Sex-biased MI consistent with the TWH was also evident in weaned age, and shared a clear decline in daughters when the mother's condition improved, whilst for sons, it remained comparatively stable across maternal condition. Current findings also support previously discovered age-related patterns in mountain gorilla female reproductive success, which have shown a relatively low fertility for young and old females (Robbins et al., 2006).

Weaned age patterns as revealed from the current research will need to be confirmed as data improve quantitatively and qualitatively. To achieve this, the recording of weaned age records in immature gorillas should be implemented immediately into the protocol for all long-term behavioural data collection. In addition, potential long-term impacts of play depression induced through early-weaning on offspring development should be further investigated (Chapter 5).

Sex-differences in weaned age, as a function of maternal condition, strongly suggest that the TWH in mountain gorillas is primarily determined through the regulation of resource allocation into daughters, as sons receive similar levels of maternal resources across varying maternal condition. Such a mechanism may evolve if the capacity to manipulate early MI in sons is limited due to higher costs of raising sons than daughters. This could occur due to neonatal sexual dimorphism, such as higher birth body mass and

faster growth rates in males than in females (Meder, 1990; Leigh & Shea, 1996).

Throughout this thesis, the importance and need for data on offspring birth weight/size and growth rate has been highlighted to further our understanding of the costs and benefits of MI decisions for the mother and the offspring. Photogrammetry, a non-invasive method to assess sexual dimorphism, has been successfully applied recently to adult western gorilla males in a bai setting (Breuer et al., 2007). The implementation of such a method to assess growth and size in wild mountain gorillas would entail various challenges, mostly related to visibility, but its feasibility should be explored in future studies.

Further support for the TWH was provided by findings on the mother's feeding activity (Chapter 5), which likely reflect maternal costs and effort to provide additional resources to the growing offspring (Millar, 1977; Altmann, 1980; Dunbar & Dunbar, 1988). Low-ranking mothers (LDS_3) fed more efficiently when they had daughters, whereas higher-ranking mothers (MDS_3) fed more efficiently when they had sons. The lack of sex-differences in the feeding efficiency within highest-ranking mothers (HDS_3) remains curious, but may be caused by aging mothers within this category who were likely to invest equally in sons and daughters as predicted by the terminal hypothesis (see Caro et al. 1995).

The sum of the key findings on suckling frequency and weaned age, as discussed so far, clearly favour the TWH from other MI models (see Chapter 1), which have also been introduced in the framework of this thesis. Both the LRC model (Clark, 1978; Silk, 1983) and LRE model (Gowaty & Lennartz, 1985) base their predictions on the dispersing sex and the level of food competition. In contrast with previous findings (Robbins et al., 2007b), this current research provided no clear evidence for contest competition over food. Although a rank-related feeding advantage of dominant mothers over middle-ranking mothers occurred, there was no equivalent feeding advantage of dominant mothers over low-ranking mothers. However, the presence of maternal relatives in the group was associated with less time spent feeding with the group in the current study nearly the entire infancy, though was unrelated to feeding efficiency. Potentially, mothers may gain an advantage

in accessing high quality food patches with the presence of relatives, who are more tolerant towards each other and support each other in contest competition (Harcourt, 1989; Watts, 1994b). In order to investigate the maternal-relative effect, further research should address the question of whether the quantity and quality of the food consumed by female mountain gorillas vary as a function of the presence of maternal relatives during synchronised feeding with the group. Such a study would also address the question of whether feeding time is a reliable indicator of energy intake in mountain gorillas (see Zinner, 1999).

Consistent with socioecological theories (Wrangham, 1980; Sterck et al., 1997), but in contrast to previous research (Robbins et al., 2007b), findings from this study suggest that mountain gorillas engage in scramble competition over food. Such theories predict a stronger scramble than contest competition in non-nepotistic species, such as the mountain gorilla, indicated by stronger group-size effects than dominance effects on measures of reproductive success (Wrangham, 1980; Sterck et al., 1997). Here, offspring living in small groups were weaned earlier than offspring living in large groups and thus strengthen the evidence. The lack of such a group-size effect on IBIs (Robbins et al., 2007b) is curious, but may indicate higher miscarriage rates in mothers who wean offspring at an early age; although groups are regularly monitored, there is a generally high uncertainty regarding the actual miscarriage rate in this population (see Robbins et al., 2007a). Further research should consider the regular use of pregnancy testing, which has already been used successfully in this population (Czekala & Robbins, 2001); this would not only detect miscarriages, but would provide more accurate data on the timing of conception in relation to weaning (Chapter 3). With recent demographic changes, including group splits and new group formation, the opportunity has now arisen to study MI in groups of varied size and composition, which would enhance understanding still further.

Group-size effects from patterns of group synchronisation did not lend support that adult mountain gorillas engage in scramble competition over food or use adjustments in the level of synchrony as a strategy to reduce food competition when groups grow larger. However, costs of living in large groups were evident in the activity budget of immature gorillas who spent

more time foraging during gR and gNR when living in large groups, although findings need to be interpreted with caution.

There is accumulating evidence from long-term records (Robbins et al., 2007b) and from this study that mountain gorillas face higher levels of within-group food competition than was previously reported (Fossey & Harcourt, 1977; Watts, 1985b; Harcourt, 1989). If this is indeed the case, a pertinent question would be to ask why mountain gorilla mothers do not adapt MI strategies such as those proposed by the LRC and LRE models. An obvious explanation might be that the level of food competition is simply not strong enough to favour such strategies in an area of food abundance with a relatively even distribution (Fossey and Harcourt, 1977; Vedder, 1984, Watts, 1984). Findings from the present study suggest that individuals are able to adequately reduce the costs of social foraging through larger group spreads (Dias & Strier, 2003; Smith et al., 2005) and lower levels of synchrony between group members during feeding (see Rands et al., 2003). In addition, male and female mountain gorillas disperse (Doran & McNeilage, 2001) or stay for a lifetime in their natal group (Harcourt et al., 1976; Watts, 1990a, b; Robbins, 1995), which makes it difficult to adopt MI strategies that base assumptions on sex-specific dispersal patterns, such as the LRC or LRE model. Female dominance studies in mountain gorillas lack evidence that offspring 'inherit' the mother's social status (Watts, 1985b; Robbins et al., 2005; Chapter 6), as assumed by the LRE model; although daughters may occasionally rank closely to their mothers in the dominance hierarchy, due to heritable dominance traits (Réale et al., 1999; also see Chapter 6). Moreover, gorilla mothers may benefit equally from the presence of sons and daughters in the group, in terms of the opportunity for alloparenting (see Silk & Brown, 2008). Both offspring sexes may offer their mother and future offspring protection, grooming and support during competitive interactions over food (Harcourt, 1989). Although allomaternal behaviour is frequently observed in the mountain gorilla research groups (pers. obs.), it is still a largely understudied research area in *Gorilla* (see Hutchinson & Fletcher, in prep.) but crucial to further our understanding of the role of maternal relatives in infant caring.

In light of the findings from long-term records and the findings from this thesis on postnatal MI in mountain gorillas (Table 7.1), there is growing evidence that females bias their postnatal investment towards the sex with the greatest potential fitness return with respect to maternal condition. Very limited evidence from the prenatal period suggests that mountain gorillas may not regulate MI through a physiological mechanism (see review by Brown, 2001; Grant, 2003) before birth, but instead adjust maternal resource allocation during the postnatal period in the manner proposed by TWH. Thus, it is proposed here that the TWH can indeed be applied to the period of postnatal MI in mountain gorillas, as has been shown for humans (see Keller et al., 2001) and other animal species (e.g. wood rat, *Neotoma floridana*, McClure, 1981; red deer, *Cervus elaphus*, Clutton-Brock et al., 1984; hamster, *Mesocricetus auratus*, Labov et al., 1986; house mice, *Mus domesticus,* Wright, 1988; Mongolian gerbil, *Meriones unguiculatus*, Clark et al., 1990).

Table 7.1 – Summary of findings (1-5) on correlates of prenatal and postnatal maternal investment (MI) and their evidence for differences between offspring sex, maternal rank, and for the Trivers & Willard hypothesis (TWH) in *Gorilla*.

MI period	Measurement	Sex	Rank	(TWH)
Prenatal	Lactation-Pregnancy overlap (subsequent offspring)[1,4,5]	NS	NS	NS
	Sex birth ratio[2]	NS	NS	NS
	Birth weight[3]	? (♀ < ♂)[3]	?	?
	Miscarriage (Foetal mortality)	?	?	?
Postnatal	Mortality[2]	NS	NS	NS
	Inter-birth interval[2] (IBI)	NS	NS	H: ♀ < ♂ L: ♀ > ♂
	Suckling[1,4]	NS	NS	H: ♀ < ♂ L: ♀ > ♂
	Milk composition	?	?	?
	Feeding time[1]	NS	gR: H < M	NS
	Feeding efficiency[1]	NS	NS	M: ♀ < ♂ L: ♀ > ♂
	Dorsal transport[4]	♀ < ♂	?	?
	Growth rate[3]	? (♀ < ♂)[2]	?	?
	Weaned age[1,4,5]	NS	NS	H: ♀ < ♂
	Lactation-Pregnancy overlap (current offspring)[1,4,5]	NS	NS	NS
	Timing of weaning in relation to subsequent conception	NS	NS	L: ♀ < ♂[5]

[1]Current study, [2]Robbins et al. 2007a, [3]neonatal sexual dimorphism shown in *Gorilla gorilla gorilla* (Leigh & Seah, 1996), [4]age at which infant were carried dorsally (Fletcher, 1994); [4]after the first year until fifth year in *Gorilla gorilla gorilla* (Leigh & Seah, 1996), [5]Stewart, 1988; '?' = no data available, NS = not significant, shaded = effect unknown, gR = group resting.

The inherent challenges in measuring MI (Clutton-Brock, 1991), in particular in long-living primates and wild populations (see Brown, 2001), should not be underestimated and, given the limitations due to the use of

proxy measures, such as nipple contact time, further studies are necessary. Ideally, MI studies should (by definition) involve measures that indicate maternal costs and offspring benefits in terms of survival chances and future reproductive success (Clutton-Brock, 1991). Future research should consider the reproductive success of mothers and offspring presented in the current study, through continued longitudinal data collection with attention to seasonality, particularly the presence of bamboo shoot as a potential weaning food (see Chapter 3).

Despite the unquestionable importance of such long-term effects of MI, the contribution of short-term effects to our understanding of costs and benefits of MI decisions should not be underestimated. Short-term effects, such as growth rates, body weight changes, and potentially health status (Krief et al., 2005; Breuer et al., 2007) do not only reflect how much a mother has invested in her offspring, but also help to understand future adjustments in the level of MI (Kilner & Hinde, 2008; see Chapter 4), and thus should be explored in future studies on MI, whenever possible, to complement findings on behavioural correlates of MI.

Taking a wider perspective on future direction, which would enhance the current research and further improve our recent understanding of MI and life-history strategies in mountain gorillas and *Gorilla*, future research should include a much needed focus on maternal care, during the later stages of ontogeny. Since mother and offspring usually maintain their relationship beyond the period of nutritional dependence, and which can even last a life-time, studies which focus on maternal care (which does not diminish reproductive output of the mother, see Clutton-Brock, 1991), are of critical importance to further our understanding of life history strategies and thus should be incorporated in future investigations. In addition, as long-term records and behavioural data on MI in the other remaining mountain gorilla population, in the Bwindi Impenetrable National Park accumulate, findings from both mountain gorilla populations should be compared. Although they are separated by only 25 km, differences are expected due to variation in the anatomy, habitat, and ecology of the populations (Sarmiento et al., 1999). Equally, growing knowledge from eastern lowland and western gorilla

populations (see Nowell, 2005) will provide further opportunities to understand determinants of MI in *Gorilla*.

7.1.1 Selection of indicators of maternal condition

There has been considerable discussion about the misleading term of 'maternal ability' in TWH (Bercovitch, 2000; Brown, 2001; Grant, 2003). Maternal ability (condition) has been interpreted in many different ways with indirect measures being used rather than direct measures. The current study suggests that a single measure applied to all behavioural correlates may not be appropriate, since correlates of MI may be affected differently by different indicators of maternal condition. For example, reduced reproductive success, measured by IBIs, in very old mothers (Robbins et al., 2006) may not reflect milk production and allocation to sons and daughters, but possibly reflect ability to resume oestrus or to successfully conceive again. Thus, very old mothers may wean sons and daughters at similar ages but provide milk less frequently to daughters than sons during the period of milk provision. The selection of indicators in MI studies should therefore also take into account potential effects of the measure of maternal condition on each of the correlates of MI under consideration.

7.2   Bidirectional   influence   of   the   mother-offspring relationship on maternal investment patterns

To fully understand MI patterns in species where mother and offspring directly interact, the offspring should be taken into account as an actor (Trivers, 1974; Barrett et al., 2006). Findings from this current study demonstrated the important role of offspring in shaping MI patterns.

7.2.1 Mother-offspring behavioural conflicts (MOBCs)

Mountain gorilla mother-offspring dyads seem to solve behavioural conflicts at a compromise level between the optima of both parties, and thus add to empirical studies that support the pro-rata models (Parker & Macnair, 1979; Altmann, 1980; Parker, 1985; Clutton-Brock, 1991; Queller, 1994; Rogowitz, 1996) rather than the *force majeure* model (Alexander, 1974). This was apparent in short- and long-term effects of maternal rejections and offspring solicitation behaviour on MI patterns, which showed that the mother won the conflicts in the long-term, although offspring did succeed in impeding changes in MI patterns (Chapter 4). Findings were further underpinned by varying maternal responsiveness patterns, which are likely to reflect strongly alternating periods of honest and deceitful solicitation behaviour of offspring, addressing several ongoing behavioural conflicts to which mothers behaviourally adjust (Hauser, 1986) based on a mutual monitoring (Altmann, 1980). Periods of low maternal responsiveness suggest that offspring employed deceitful signals to manipulate MI patterns, which mothers learn to discriminate (Trivers, 1974; Hauser, 1986). Therefore, the alternative honest signalling theory (Godfray, 1991), which proposed that offspring always signal their true condition, was not supported in this study. As expected, maternal experience affected maternal responsiveness and refusal behaviour, which may partly explain lower reproductive success in primiparous mothers compared to multiparous mothers (Robbins et al., 2006). Longitudinal studies are an exceptional resource for the study of parity-related intra-individual variation (Hayes & Jenkins, 1996) in maternal behaviour that should be used in future.

Having now identified MOBCs in mountain gorillas, which need to be interpreted in the scope of behavioural disputes (Mock & Forbes, 1992; Bateson, 1994; Kilner & Hinde, 2008), further steps must be undertaken to implement these findings into other key areas of MI study. Further research aims to develop an index for the strength of behavioural conflicts, which incorporates mother's and offspring's antagonistic effort in manipulating MI patterns, in a similar way to the proximity index developed by Hinde (Hinde & Atkinson, 1970). Such an index would provide a relative measure which

reflects the disparity of the mother and offspring optimum of MI, and thus facilitates the comparison between and within mother-offspring dyads across the period of MI. In addition, index scores could be used to investigate the Trivers & Willard (1973) effect on the strength of MOBC and also to further our understanding of bidirectional influence in mother and offspring personality.

Sibling conflicts were not considered in the current study. However, competition for the mother's resources can be high between siblings (Kilner & Hinde, 2008). Prenatal competition both through delaying a mother's resumption of oestrus (Maestripieri, 2002a) and after subsequent conception when lactation overlaps with pregnancy, and postnatal competition could each affect MI. Sibling competition is currently understudied in primates with a strong bias towards studies on sibling rivalry in birds (see review by Hudson & Trillmich, 2008), and thus future studies on MI should explore this area.

7.2.2 Mother-offspring personality

For the first time, it has demonstrated that the personality of wild mountain gorillas can be reliably assessed by human ratings, in a comparable manner to other great ape species from captive settings (orang-utan: Weiss et al., 2006; chimpanzees: Weiss et al., 2007). In addition, both mother and offspring personality could explain variation in important maternal behaviours, supporting strongly the bidirectional model (Bell, 1968; Clark et al., 2000). Most personality effects on maternal behaviour were complex, due to variation across the period of MI or potential inter-correlation with third factors, such as age, maternal parity and rank. Longitudinal studies can help to separate personality effects from interfering third factors and yield light on the question whether offspring personality truly shapes maternal behaviour or whether maternal behaviour induces offspring personality in the first place. Since personality can be affected by environmental changes (Loehlin et al., 1990), such studies should, ideally, involve reassessments of gorilla personality. This pioneering work, however, has illustrated the strong potential of personality as an important determinant of mother-offspring

relationships, but also that we are just beginning to understand the importance of personality on mother-offspring relationships in nonhuman primates. The availability of important social partners for young gorillas, such as playmates and silverbacks, was dependent on the maternal personality. Further research needs to investigate whether such variation in the mother's social environment can lead to variation in offspring behaviour, and potentially in the development of social expertise, which will ultimately affect reproductive success.

7.3 Implications for conservation

The development of effective conservation management programmes for any species depends upon an understanding of female reproductive strategies. For the highly endangered mountain gorilla, an increased knowledge of maternal investment in offspring will feed into population dynamics models and analyses of population viability, which in turn help to identify key factors that put this population at risk (Burgman et al., 1993; Beissinger & Westphal, 1998). The knowledge of factors that influence female reproductive performance and offspring development help to prioritise habitats, groups or individuals in protection programmes, for example when implementing vaccines for the Ebola virus (Sullivan et al., 2000; Swenson et al., 2008) into the Virunga mountain gorilla population.

Reintroduction programmes also benefit from studies of maternal investment, mother-offspring relationships and female reproductive performance. Identifying critical factors that differentiate reproductively successful mothers from less successful mothers is crucial for reintroduction projects. For such a project to work, a good understanding of changes in the mother-offspring relationship and the behaviour of each party throughout the period of dependency and beyond is needed. Such an understanding also aids veterinarians and conservation personnel who regularly work with the gorillas in evaluating unusual behaviour such as sudden depression or physical change in relatively young offspring after being weaned.

7.4 Conclusion

This thesis has focused on postnatal maternal investment in mountain gorillas and has provided a comprehensive update on female reproductive strategies in one of two remaining wild populations. A bidirectional investigation on mother-offspring relationships has improved our understanding of both the mother's and offspring's role in shaping maternal investment patterns. In addition, the importance of mother and offspring personality as determinants of maternal behaviour has been demonstrated. Future directions have been outlined, but emphasise the need for continued recording of mother-offspring interactions in mountain gorilla populations to enable further analysis of mother-offspring relationships and their resultant reproductive success over the long term.