Chapter 1

General introduction

1.1 Maternal investment

A newborn primate is completely dependent upon its mother (Fossey, 1979; Lee, 1995), the primary socialising agent during early infancy. At this life stage, mortality is at its highest (Eisenberg, 1981) and therefore, the mother-infant relationship in transition to independence is of utmost importance for offspring survival. Maternal investment (MI), by definition, is any form of mother's expenditure, such as time, energy and risk that benefits the offspring and as such, increases its chance of survival and reproductive success at the cost of the mother's ability to invest in other offspring (Trivers, 1972). In most mammals, parental investment is primarily provided by the mother, since gestation and lactation are provided by females, although the costs of paternal contribution to offspring survival through protection against extrinsic risks should not be underestimated (Geary, 1998; Bercovitch, 2002). A mother's reproductive success and investment strategy during and beyond infancy is also judged in fitness terms by the eventual reproductive success of her infant. Thus, the knowledge of MI during infancy and beyond, as well as mother-offspring relationships, and their determinants, is of critical importance to further the understanding of female reproductive success (FRS) and life history strategies in primates, specifically the mountain gorilla (*Gorilla beringei beringei*). Consequently, this thesis will contribute to a better understanding of mountain gorilla population dynamics in one of their last remaining natural refuges, the Virunga Conservation Area.

1.1.1 Measures of maternal investment and their challenges

Measuring MI has always challenged researchers, since the currency of costs and benefits for mother and offspring involves fitness components, such as reproductive success, survivorship, and fertility of both parties (Clutton-Brock, 1991). Empirical testing becomes particularly difficult in animals with a long life span, slow reproductive rate, and a complex social network, such as found in primates. Hence, indirect rather than direct fitness

measures are often used in MI studies, focussing on prenatal and/or postnatal life stage periods.

The most prominent measure of prenatal MI, which strongly dominates the literature on maternal investment, is the birth sex ratio (see review by Brown, 2001; Côté & Festa-Bianchet, 2001; Keller et al., 2001; Visscher & Aarde, 2004; Silk & Brown, 2008). Sex-differences in the variance of reproductive success should be reflected in a sex-biased birth ratio towards the sex that provides the highest fitness return to the parent (Trivers & Willard, 1973; Clutton-Brock, 1991). Other commonly used measures for MI during the prenatal period include foetal mortality (Brown, 2001; Roof et al., 2005) and offspring birth weight, the latter providing the average mass produced per day of gestation (Trillmich, 1986; Young et al., 1990).

MI studies that focus on the postnatal period generally incorporate three different types of measures derived from long-term demographic records, maternal behaviour, and indicators of offspring development and maternal condition. Demographic records usually provide inter-birth intervals (IBIs) (Lee & Moss, 1986; Green & Rothstein, 1991; Brown, 2001; Robbins et al., 2007a, b), indicating the length of the MI period, offspring survival (mortality rate) after birth (Clutton-Brock et al., 1985; Derocher & Stirling, 1998; Heymann & Soini, 1999; Brown, 2001; Robbins et al., 2007a, b), surviving birth rates (Trillmich, 1986), and the age of the first parturition in daughters (Robbins et al., 2007a).

Mothers can regulate resource allocation through behavioural adjustments after birth (Trivers & Willard, 1973; see review by Bercovitch, 2002), but only a minority of MI studies has focused on the postnatal period using behavioural measures. To ensure offspring survival and bodily growth and maintenance during the period of nutritional dependence, mothers support their offspring through milk provision (Fossey, 1979; Lee, 1995). In mammals with anovulatory postpartum cycles, milk transfer is one of the key measures for estimating costs and benefits, as it can directly influence the IBI and thus mother's reproductive outcome (Lee, 1987), with weaned age and suckling frequency playing a regulatory role in the anovulatory effect (Konner & Worthman, 1980; Lee, 1987; Stewart, 1988; Gomendio, 1989; Wyss & Maroni 1993; Stevenson et al., 1997). The time spent suckling (i.e. duration

of nipple contact) and milk composition have also been used to assess the amount of maternal resources diverted to the offspring (e.g. Trillmich, 1986; Clark, 1990; Gomendio, 1990). However, the true milk intake and its impact on offspring future reproductive success (Trivers, 1972) can usually only be speculated. Empirical studies on the reliability of suckling time as predictor of milk transfer have revealed conflicting results (see review by Cameron, 1998).

Similarly, other energetically costly and time consuming maternal behaviours, such as transport, grooming, and the provision of warmth and protection through body contact have been investigated (Randolph et al., 1977; Johnson, 1986; Gittleman & Thompson, 1988; Altmann & Samuel, 1992; Tardif, 1994; Muroyama, 1995; Kramer, 1998; Schino & Troisi, 1998; Hayes & Salomon, 2006). Furthermore, mother's time spent feeding has been used as an indirect measure of maternal costs, since mothers usually have to increase their food intake to meet additional costs of the growing offspring. Various studies have demonstrated that mothers do indeed feed longer with increasing age of offspring in response to costs of growing (Millar, 1977; Altmann, 1980; Dunbar & Dunbar, 1988).

Direct measures of offspring development, such as offspring weight and growth rate (Trillmich, 1986; Derocher & Stirling, 1998; Cameron, 1998), and direct measures of maternal condition, such as maternal weight and health status (Sánchez et al., 1999; Krief et al., 2005), are crucial for verifying immediate (short-term) costs and benefits of MI for both parties. Thus, their assessment should be integrated in MI studies which focus on maternal behaviour. However, this is not always feasible under field conditions, and thus indirect measurements have to suffice.

Importantly, to further understand the underlying reasons for MI decisions and ultimately female reproductive strategies, MI studies should consider 'care-dependent' sources of offspring mortality (e.g. milk transfer) in combination with 'care-independent' sources of mortality (e.g. food availability and predation), which can strongly influence the chance of offspring survival (Lycett et al., 1998).

1.1.2 Sex-biased investment models

There are several models that predict the quality and quantity of MI in each offspring sex, and they differ primarily in key factors responsible for maternal adjustments, such as dispersal patterns, maternal condition and resource competition. The Trivers & Willard hypothesis (TWH; 1973), also known as the 'male quality' hypothesis, postulates that in species where the reproductive success varies between males and females, natural selection should favour mothers who are able to adjust their investment with respect to maternal condition, with those in good condition investing more in the sex of offspring with the greatest potential fitness return (i.e. of producing grand-offspring). This hypothesis makes three assumptions. Firstly, that mothers in good condition produce offspring in good condition by the end of the MI period, and secondly, that the advantage gained through being in good condition is maintained into adulthood. Thirdly, it assumes that male and female offspring benefit differently from additional resources received from mothers in good condition, in terms of their future reproductive success.

The common application of the TWH to polygynous species, in which males are expected to have a greater variance in reproductive success than females (Clutton-Brock, 1988), reflects that mothers in good condition should invest more in sons, while those in poorer condition should invest heavily in daughters. The interpretation and measurement of the term 'condition' varies, with probably the most common being that of dominance (Brown, 2001; Grant, 2003), although maternal age, body size, parity and socioeconomic scales have been applied (e.g. Boltnev & York, 2001; see review by Keller et al., 2001; see review by Bercovitch, 2002; Weladji et al., 2003; Braza, 2004). Since TWH was published, numerous MI studies across a wide range of species, including humans, have used the model as a framework with the vast majority focusing on birth sex ratio. Their findings vary widely with some providing support such as ungulates (i.e. red deers, *Cervus elaphus*, and mountain goats, *Oreamnos armericanus*) (see review by Hewison & Gaillard, 1999; Côté & Fest-Bianchet, 2000), nonhuman primates (i.e. rhesus macaques, *Macaca mulatta*, barbary macaques, *M. sylvanus*, and Hanuman langurs, *Semnopithecus entellus*) (see review by Brown, 2001; Ostner et al.,

2005), humans (see review by Keller et al., 2001), cetaceans (i.e. Southern elephant seals, *Mirounga leonina*) (Wilkinson & Aarde, 2001), while others produce opposite results encompassing studies on ungulates (i.e. mooses, *Alces alces*, and horses, *Equus caballus*) (see review by Hewison & Gaillard, 1999), otariids (i.e. Antarctic fur seals, *Arctocephalus gazelle*) (Lunn & Arnould, 1997), primates (i.e. yellow baboons, *Papio cynocephalus*, Japanese macaques, *M. fuscata*, and white-headed langurs, *Trachypithecus leucocephalus*) (see review by Brown, 2001; Zhao et al. 2009).

While the TWH is based on maternal condition, other hypotheses take into account environmental and social parameters as crucial mechanisms in adjusting MI. Poor habitat quality, limited resources and high competition for resources may result in early termination of lactation and other 'expensive' forms of care (Dunbar, 1988). In contrast, a lack of suitable weaning foods coupled with harsh conditions has been found to lengthen the period of MI in mountain baboons (Lycett et al., 1998). The 'local resource competition' model (LRC) predicts sex-biased MI toward the dispersing sex, thus decreasing local competition between parent and their philopatric offspring (Clark, 1978; Johnson, 1988). Later, the original LRC model was modified by adding another important factor: dominance rank 'inheritance' (Simpson & Simpson, 1982; Silk, 1983). The modified model, as well as the 'advantage-daughter' model (Altmann, 1980), which is also known as 'local resource enhancement' model (LRE; Gowaty & Lennartz, 1985), state that in female philopatric societies raising daughters is more costly than raising sons because additional females in the group cause an increase in competition for limited resources. This leads to the prediction, contrary to the TWH, that mothers in better condition should invest more heavily in daughters, who 'inherit' their advantageous condition and serve as supporters against other matrilines. However, mothers in poor condition are expected to invest more in dispersing sons, since the harassment of daughters with mothers in poor condition will cause an increase in daughter mortality before reaching reproductive age. Many studies involving a wide range of species have provided evidence for both the LRC model, including birds (i.e. eastern bluebirds, *Sialia sialis*, and redheads, *Anthya americana*) (see review by Gowaty, 1993), ungulates (i.e. roe deer, *Capreolus capreolus*) (Hewison &

Gaillard, 1996), hymenoptera (i.e. ants, *Cataglyphis cursor*) (Pearcy & Aron, 2006), primates (i.e. brown greater galago, *Otolemur crassicaudatus*, and spider monkeys, *Ateles* spp.) (Clark, 1978; Johnson, 1988; Chapman et al., 1989; see review by Silk & Brown, 2008) and the LRE model, including hymenoptera (i.e. allodapine bees, *Exoneura bicolour*) (Schwarz, 1988; see review by Chapuisat & Keller, 1999), rodentia (i.e. Townsend's voles, *Microtus townsendii*) (Lambin, 1994) and primates (i.e. common marmosets, *Callithrix jacchus*, and golden lion tamarins, *Leontopithecus rosalia*) (see review by Silk & Brown, 2008).

The population adjustment hypothesis (see Bercovitch, 2002) is concerned with the level of population rather than the individual, predicting that sons and daughters receive an equal amount of MI due to their identical contribution of genes to successive generations (Fisher, 1930). Consequently, if one sex is more costly to produce, mothers are expected to allocate more resources to each individual of that sex but adjust the secondary sex birth ratio in favour of the other sex (Silk & Brown, 2004).

1.1.2.1 Application to mountain gorillas (Gorilla b. b.)

Which MI model can be best applied to mountain gorillas? The mountain gorilla is a highly sexually dimorphic species with a polygynous mating system (Taylor, 1997; Harcourt & Stewart, 2007), suggesting that males have a greater variance in reproductive success than females (Clutton-Brock, 1988), although this has not yet been empirically demonstrated for mountain gorillas. Given that a meta-analysis on long-term behavioural records from 1967-2004 (Robbins et al., 2005) suggested that female mountain gorillas develop stronger dominance relationships than previously reported (Stewart & Harcourt, 1987; Watts, 1994c), the mountain gorilla may be an appropriate species to apply the TWH.

The mountain gorilla population in the Virunga massif is highly folivorous (Watts, 1998). The majority of their herbivorous food source is abundant and relatively evenly distributed (Fossey and Harcourt, 1977; Vedder, 1984; Watts, 1984), although the food quality can vary within gorilla home ranges (Vedder, 1984). Thus, gorillas are usually not confronted with

seasonal food shortages. However, considering the increase in group size (up to 65 individuals; pers. obs.) over the last four decades, an increase in food competition and decrease in individual reproductive success might be expected (van Schaik et al., 1983b; see Robbins et al., 2007b). Watts (1988) found a direct relationship between group size and the time spent feeding in mountain gorillas. These groups were still relatively small compared to present-day group sizes. Another recent study conducted by Robbins et al. (2007b) on long-term demographic records showed that within-group scramble competition in female mountain gorillas is negligible and FRS was not affected by group size, even when groups grew larger over the years. It may be that an increase in energetic costs of foraging and feeding competition within growing groups may be compensated by a larger group spread rather than a longer travel distance (Dias & Strier, 2003; Smith et al., 2005; Robbins et al., 2007b). Nevertheless, within-group contest competition for food was evident in mountain gorillas, indicated by shorter IBIs in high-ranking females compared to low-ranking females (Robbins et al., 2007b). Although it still needs to be shown that rank-related differences in FRS are linked to food competition and socioecological factors explained only a small proportion of variance, the LRC model cannot be excluded as a potential framework when investigating sex-biased MI in mountain gorillas.

Males and females disperse in mountain gorillas (Doran & McNeilage, 2001), which makes it difficult to apply models that base assumptions on sex-specific dispersal patterns, such as the LRC or LRE model. Nevertheless, associated with the increase in the average group size (1971 - 2003: mean = 7.9 - 11.4; 1976 - 2003: 3.5% - 15.6% of social groups had >20 individuals) in mountain gorilla groups (Gray et al., 2003) have been remarkable changes in the group composition (e.g. up to 5-7 silverbacks and 21 females in a group). In mountain gorillas, 36% of groups are multimale groups (Gray et al., 2003). These large groups provide both sexes with the opportunity for reproduction in the natal group and the cohabitation of maternal relatives. Thus, both sexes may stay for a lifetime in their natal group (Harcourt et al., 1976; Watts, 1990a; Robbins, 1995). Such circumstances provide the opportunity for the development of relationships (and alliances) with extended kin (e.g. Watts, 1994b) and this could potentially influence some aspects of the mother-infant

relationship, leading to a variation in MI tactics with the demography of the group, particular with the maturity of adult male(s). When taking these social aspects into consideration, sex-biased MI in mountain gorilla may adopt patterns that correspond with the LRC and LRE models.

Inverse sex-biases in the birth ratio and in offspring mortality would favour the population adjustment model (Silk & Brown, 2004). However, long-term demographic records provided no evidence for a sex-bias in mountain gorillas either in the birth ratio or in offspring mortality (Robbins et al., 2007a).

In summary, current knowledge suggests that the TWH may provide the most appropriate framework to investigate MI in mountain gorillas and was applied throughout this thesis, aiming to provide a comprehensive update on female reproductive strategies in mountain gorillas.

1.1.3 The relative influence of mother and offspring on maternal investment patterns

The role of offspring in shaping parental investment and parent-offspring relationships has gained increasing attention during past decades (Bell, 1968; Trivers, 1974; Belsky, 1984; Lytton, 1990; Bateson, 1994). Offspring often have better 'knowledge' of their actual needs than parents and should therefore signal to the mother when they require more maternal resources (Trivers, 1974; Barrett et al., 2006). However, there is also the potential for offspring to exploit solicitation behaviours to gain advantage over the caregiver (Trivers, 1974).

Parent-offspring conflict (POC) theory (Trivers, 1974) provides a framework to understand the proximate cause of actions taken by the parent and offspring during the period of prenatal and postnatal parental investment. Trivers proposed that natural selection favours offspring who demand more investment than parents are selected to give, with a genetic conflict being the underlying cause of the different parental investment optima of the parent versus the offspring. Parents are equally related to all of their offspring, and hence should be selected to allocate their resources evenly over offspring (current and future). Offspring, however, are fully related to themselves, but will normally share only half their genes with their full siblings in

monogamous mating systems, and one-quarter with their half-siblings in promiscuous mating systems respectively (Hamilton, 1964). Thus, offspring will benefit more by maximising their investment from the parent than sharing this MI with their siblings. Parent and offspring are therefore expected to disagree over the timing, amount and termination of parental investment (Trivers, 1974; Maestripieri, 2002a), with the extent of this disparity being dependent on the coefficient of relatedness between siblings (Trivers, 1974; Parker & Macnair, 1978, 1979; Robinson, 1980).

The POC theory has inspired numerous theoretical models, which can be divided into 'battleground models' (Godfray & Parker, 1992) and 'resolution models' (Godfray, 1995). The former type (Trivers, 1974; Parker & Macnair, 1978; Godfray, 1995) primarily aims to calculate the disparity in optima of parents' and offspring's resource allocation, which defines the potential intensity (width of 'battleground' zone) of the POC. Resolution models (Trivers, 1974; Zahavi, 1977; Parker & Macnair, 1979; Eshel & Feldman, 1991; Yamamura & Higashi, 1992) incorporate assumptions about the phenotypic interactions between the parent and offspring, such as the time in contact and the weaning process, and instead seek to predict the outcome of prenatal and postnatal POCs (see Haig, 1993; Godfray, 1995).

In comparison to the vast number of theoretical models and continual development, evidence for the selective force of POC stemming from empirical studies remains negligible (Trivers & Hare, 1976; Haig & Westoby, 1989; Haig, 2000). This can be partly explained by the inherent challenges of measuring MI and its fitness consequences for both parties (see above), but is also complicated due to the enormous complexity and the dynamic element of parent-offspring interactions (Hinde-Spencer-Booth, 1971; Takada & Kigami, 1991; Godfray, 1995; Rodrígues-Gironés et al., 1998; McNamara et al., 1999), which make the formulation of unambiguous and testable predictions about the behaviour of the parent and offspring extremely challenging. This thesis aims to take into account an 'infant's eye-view' (Barrett et al., 2006) on MI patterns in mountain gorillas, using the POC theory as an explanatory framework. Despite the difficulties involved in studying POCs empirically, findings can contribute to our understanding of

the dynamics of mother-offspring relationships in great apes, our closest relatives (see also Godfray, 1995; Maestriprieri, 2002).

1.1.4 Determinants of maternal investment and the mother-offspring relationship

Apart from offspring sex, maternal condition (dominance, body size and weight, parity) and 'care-independent' factors (e.g. food shortage, disease) (e.g. Tanaka, 1997; Derocher & Stirling, 1998; Amatayakul et al., 1999; see review by Brown, 2001; Bales et al., 2002), MI and the dynamics of mother-offspring relationships may be influenced by a wide range of other factors, which should be considered within a single model when investigating MI (Brown, 2001). Such factors are offspring age, group size and composition, including the presence of similar-aged peers, adult males, siblings, and other relatives or unrelated helpers (e.g. Pusey, 1983; Fletcher, 1994; Tardif, 1994; Brent et al., 1997; Stewart, 2001; Nowell, 2005; Lloyd et al., 2009). An infant who is surrounded by similarly-aged peers and/or siblings may demand less attention from its mother than one who is raised in a group with few play partners available (e.g. Brent et al., 1997). Equally, potential helpers in infant care, such as relatives (e.g. Pusey, 1983), may enable mothers to reduce costs in terms of time and energy (see Caine, 1993; Savage et al., 1996; Schaffner & Caine, 2000) without reducing infant care and chance of survival. Furthermore, maternal experience can also influence mother-offspring interactions, with mothers who have little prior experience of raising an infant being more aggressive towards offspring (Hiraiwa, 1981, Dwyers & Lawrence, 2000) or less responsive (see Hiraiwa, 1981; Juarbe-Díaz, 1998; Maestripieri & Carroll, 1998) than multiparous mothers, while old females have been known to invest heavily in their last offspring (Kemps, et al., 1989; Fletcher 1994, 2001; Nowell, 2005). Thus, in addition to key factors required for investigating the TWH (maternal condition and offspring sex), this study considered a variety of other potential determinants of maternal-offspring relationships, such as offspring age, group size, parity as indicator of maternal experience and condition, the presence of siblings, and maternal relatives.

1.1.4.1 Personality: A neglected determinant of maternal behaviour

The importance of studying individual differences has been widely recognised (Hayes & Jenkins, 1997), including its potential role in reproductive success (Stevenson-Hinde et al., 1980; Eaves et al., 1990). In humans, parental personality can influence parental behaviour, which has particular consequences for a child's early experiences and may affect a child's development (Belsky, 1984, 1990; Belsky et al., 1995; Kochanska et al., 1997; Clark, 2000; Smith et al., 2006). It seems surprising that mother and offspring personality have not only been largely neglected as potential determinants of maternal behaviour in nonhuman primates, despite their phylogenetically close relationship to humans, but also in other animal species, which may be attributed to the methodological challenges involved in personality assessment of animals (Gosling, 2001; Uher, 2008). Considering the immense contribution of human personality to our understanding of parenting and child development, the benefit of overcoming methodological obstacles and investigating the parenting-personality link in nonhuman primates and other animals can advance the understanding of maternal behaviour in animals and help to address questions that are difficult to answer through human studies. Therefore, this thesis aims to assess gorilla personality in order to link maternal behaviour with mother and offspring personality.

1.1.5 Maternal investment in mountain gorillas and evidence for TWH

A recent study (Robbins et al., 2007a) of the sex-biased investment of 61 female mountain gorillas using long-term demographic records from 1967-2004 of the population in the Virunga massif showed that high-ranking females have shorter IBIs than low-ranking females, suggesting a higher reproductive success in high-ranking females. Sex-differences within both types of mothers provided support for the TWH (1973). After removing two outliers, IBIs of high-ranking mothers were longer after having sons, while those of subordinate mothers were longer after having daughters. Given that female mountain gorillas do not appear to regulate the sex of their offspring

at birth, findings on IBIs suggested that they may adjust their postnatal MI (Robbins et al., 2007a).

Our understanding of postnatal MI in the genus *Gorilla* is limited, with little published captive research (Hedeen, 1980; Brown, 2002), and our knowledge of the wild situation being based on research that has focused on the social and behavioural development of immature mountain gorillas (Fossey, 1979; Stewart, 1981; Fletcher, 1994, 2001) and western gorillas (*G. gorilla gorilla*) (Nowell, 2005). A few significant sex-biases emerged from studies on mountain gorillas, such as daughters receiving more maternal grooming than sons, whereas sons were carried dorsally by their mothers up to an older age than daughters (Fletcher, 1994; 2001). Sex-differences in suckling patterns and weaned age have not yet been studied conclusively due to small sample sizes in each individual study.

Apart from sex-differences, parity-related patterns have emerged in MI studies on mountain gorillas. Multiparous mothers spent more time transporting their offspring dorsally than primiparous mothers, who spent more time carrying their offspring ventrally, which is possibly more protective (Fletcher, 1994). However, the study concerned was hampered by all daughters having multiparous mothers and most sons being born to primiparous mothers during that period, thus confounding the analysis and limiting firm conclusions. Primiparous mothers also had 50% higher offspring mortality and 20% longer IBIs than multiparous mothers, indicating a reduced reproductive performance in primiparous females (Robbins et al., 2006). There is also evidence that maternal age affects fertility, with low fertility in the youngest and oldest females (Robbins et al., 2006). In addition, mother-offspring association patterns during group feeding sessions differed between groups, with offspring in larger groups spending less time in contact with their mothers than those on smaller groups (Fletcher, 1994).

None of the behavioural studies considered maternal condition as an influential factor, partly because female relationships were traditionally categorised as egalitarian (e.g. Sterck et al., 1997; Robbins et al., 2005, 2007) and because of difficulties in assessing body size and weight in wild individuals. To yield more light on previously discovered and other potential determinants of MI, and improve understanding of findings from long-term

records on MI, more behavioural data that provide direct measures, such as suckling, are needed. To achieve this, suckling data from four different field periods are combined in Chapter 3 to overcome the sample size limitations that is experienced in each individual study.

1.2 Aims

The need for more data on postnatal MI behaviours and mother-offspring interactions to expand the understanding of MI and its determinants during the period of maternal dependency in primates has been outlined. The main aim of this thesis was to extend the current body of knowledge of MI and mother-offspring relationships and to provide a detailed, thorough investigation of behavioural correlates of postnatal MI in mountain gorillas. This is crucial in furthering the understanding of FRS and life history strategies in the mountain gorilla, and *Gorilla* more generally, and consequently of mountain gorilla population dynamics in one of their last remaining natural refuges, the Virunga Conservation Area. The thesis was structured to enable the investigation of four key areas.

Chapter 2 introduces the study area and study individuals and provides detailed information about methodologies and techniques that have been employed. Further detail of specific methodologies will be contained in the chapter to which they pertain.

Chapter 3 focuses on suckling, the key measure of postnatal MI in primates without postpartum oestrus (Lee, 1987). Important aspects of suckling behaviour, including weaned age, are investigated for evidence of the TWH (1973), using several indicators of maternal condition, such as the mother's dominance strength, maternal parity and age. For this purpose, suckling data from four different field periods were combined.

Chapter 4 investigates how and to what extent mother and offspring shape MI patterns, focussing on behavioural conflicts (Trivers, 1974), that arise over the timing and amount/termination of different forms of MI, such as

milk provision, transport, grooming and body contact. Maternal rejections and offspring solicitation behaviour are explored, taking maternal experience into account. Maternal responsiveness patterns are examined for evidence of the honest signalling hypothesis (Godfray, 1991).

Chapter 5 investigates maternal feeding time and resultant efficiency, which are forms of maternal costs related to the growing offspring, for evidence of the TWH, taking into account factors that influence maternal time budgets. Furthermore, activity budgets of immature gorillas are investigated to describe variations in energetic expenditures and energetic demands upon the mother, considering age, sex, group size and weaning status.

Chapter 6 exclusively focuses on personality as a neglected determinant of maternal behaviour and is divided into two parts. The first part incorporates the first ever assessment and description of personality structure in a wild ape, while the second part aims primarily to link mountain gorilla mother and offspring personality with a view to interpreting maternal behaviour. Similarities between mother and offspring phenotypic personality, and the potential impact of the mother's personality on an offspring's early social environment were also investigated in this chapter.

Chapter 7 reviews key findings from this study and discusses how they further our understanding of MI and mother-offspring relationships in mountain gorillas, by providing a comprehensive update on female reproductive strategies. Limitations of the thesis and future directions are highlighted and discussed.