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**Group Dynamics and Proximate Mechanisms of  
Female Reproductive Monopolization in a  
Cooperatively Breeding Primate, the Moustached  
Tamarin (*Sanguinus mystax*)**

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## Chapter 1:

# GENERAL INTRODUCTION

### Cooperative Breeding Systems

Systems in which adult individuals aid regularly with the rearing of young in addition to the genetic parents are referred to as cooperative breeding systems (Emlen 1993)<sup>1</sup>. Cooperative breeding systems are generally characterized by (1) delayed offspring dispersal from the natal group, (2) reproductive monopolization by one or a few adults from each sex<sup>2</sup>, and (3) care for others' offspring (Solomon & French 1997b; Russell 2004). The individuals engaging in care of young are usually called helpers, auxiliaries or alloparents. They can either be non-breeding adults (in singular breeding species) or parents (in plural breeders; see below). Helping behaviour in general consists of costly acts that have the potential to improve the condition and survival of recipient breeders and/or non-descendant offspring, and may include behaviours such as feeding pregnant or lactating females and young, carrying young, vigilance/alarm calling, grooming, and assistance in thermoregulation (Jennions & Macdonald 1994; Russell 2004). While the occurrence of cooperative breeding is puzzling against the background that each individual should maximize its own reproductive success, the adaptive significance of alloparental behaviour is now generally accepted, and helpers are likely to benefit in several complementary ways both via direct and indirect mechanisms (Hamilton 1963, 1964; reviewed in Emlen et al. 1991; Jennions & Macdonald 1994).

Cooperative breeding evolved independently many times among mammalian and non-mammalian species, and has been described in approximately 220 species of birds and 120 species of mammals (see Emlen 1993, Jennions & Macdonald 1994). Among mammals it is

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<sup>1</sup> I use the term "cooperative breeding" in a neutral manner not implying that the cooperating individuals benefit in terms of fitness (see Price & Evans 1991; Solomon & French 1997b). "Cooperative breeding" as I use it, refers to shared rearing of infants (not shared parentage). Since individuals exhibit parent-like behaviour towards offspring that are not their own, "cooperative breeding" in the literature is also referred to as "alloparental care". Some authors chose the term "communal breeding". This term, however, implies the strong likelihood of shared parentage, so that following Solomon & French (1997b) it should not be used to refer to singular breeding species where non-breeding group members assist with the care of young (see below).

<sup>2</sup> In the literature the most commonly found terms are "reproductive suppression" and "reproductive inhibition". These terms, however, imply that an inability to reproduce is being imposed upon an individual by a parent or more dominant individual, and thus that control lies in the hands of the dominant individual. It is possible, though, that the non-reproducing individual may be assessing its options and refraining from reproduction when it detects the presence of a certain individual, age class of individuals, or cues from these individuals (see below). Other authors have used the term "reproductive delay". Delay, though, carries with it an ontogenetic implication, namely that reproduction may be prevented as a consequence of a time lag in the neuroendocrine maturation of the hypothalamic-pituitary-gonadal system. Yet it is clear that puberty delay is only one potential manifestation of altered endocrine status that can affect reproductive potential (see below). In my thesis I chose the term "reproductive monopolization" since it does not imply that limitations on reproduction are imposed upon an individual by another group member (see Solomon & French 1997b).

most prevalent in rodents, mongooses, canids, and callitrichid primates (Solomon & French 1997a; Russell 2004). Despite the presence of cooperative breeding in birds and mammals, studies on cooperative breeding are markedly bird-biased, and theory on the evolution of cooperative breeding has primarily been developed for birds (see Russell 2004). However, mammals differ from birds in the form of primary parental care (suckling in mammals versus provisioning in birds), which may have a major impact on the incidence and expression of cooperative breeding (Solomon & French 1997b). Information on mechanisms (physiology, behaviour) may provide insights into the functional significance of the respective physiological or behavioural trait and vice versa. Thus, examination of the proximate as well as ultimate factors that contribute to the expression of cooperative breeding in mammals is needed to understand mammalian cooperative breeding in general, but also to figure out similarities and differences to avian cooperative breeding (Solomon & French 1997b).

Cooperative breeding occurs in many types of social organization, and cooperative breeders exhibit a variety of mating systems (Emlen 1993). One can distinguish between groups in which more than one pair breeds simultaneously (plural breeders; e.g. banded mongoose, *Mungos mungo*), and groups in which only one female usually breeds (singular breeders; e.g. black-backed jackal, *Canis mesomelas*; Emlen 1993). In the latter form, helpers are usually younger individuals that delay dispersal, and remain with and aid their parents in the rearing of younger siblings. This "helper-at-the-nest" system is the most common form of cooperative breeding in both birds and mammals (Emlen 1993; Solomon & French 1997a).

Females in singular breeding species can mate either monogamously or polyandrously (Emlen 1993; Russell 2004). Polyandry arises when a single female copulates with multiple males. From an evolutionary standpoint it is difficult to understand why these males forego mating opportunities with other females (and in the extreme case even help raising offspring that might not be their own) since males usually maximize their reproductive success by mating with as many females as possible (parental investment theory: Trivers 1972). Especially in mammals where females not only invest highly in the production of nutritious oocytes but additionally bear the costs of gestation and lactation, males could easily abandon their partners and seek further matings, leaving the major burden of raising the infants to the females (which is the habitual situation in mammals). Accordingly, polyandry is the rarest mating system in mammals, and has only been reported from cooperatively breeding mammals (naked mole-rats, *Heterocephalus glaber*; dwarf mongooses, *Helogale parvula*; African wild dogs, *Lycaon pictus*; callitrichid primates), and a few human populations (Emlen 1993; Schaffner & French 2004; Crook & Crook 1988). Polyandry further implies

strong female-female competition for the breeding position. Hence, a few females have high reproductive success while the majority of females has low reproductive success or does not reproduce at all (see Emlen & Oring 1977; Clutton-Brock & Vincent 1991).

### **Female Reproductive Monopolization**

The distribution of reproduction within a group is referred to as reproductive skew (Vehrenkamp 1983a, b; Hager 2003). Groups where one or a few individuals are able to monopolize breeding show high reproductive skew, whereas those where breeding is more equally distributed show low reproductive skew (Clutton-Brock 1998; Johnstone 2000). Reproductive monopolization by one or a few (dominant) females can be expected when there are costs of subordinate females' reproduction in terms of reduced offspring survival due to limited resources (Hager 2003). For cooperatively breeding females, one limiting resource is the availability of helpers. A reduction in the helper/offspring ratio generally leads to a reduction in fitness of both dominant and subordinate females (Dietz & Baker 1993; Russell 2004).

As yet, not only the causes for the occurrence of cooperative breeding from an evolutionary perspective are poorly understood, but also the mechanisms causing and maintaining female reproductive monopolization (i.e. high reproductive skew) remain puzzling. Different models of reproductive skew make divergent predictions, depending on whether dominants are assumed to have control over the reproduction of subordinates, or whether subordinates are assumed to control their reproduction themselves. In the following I will briefly introduce four models insofar as they are relevant for the present thesis.

Concession models assume that dominants have complete control over the allocation of reproductive opportunities in the group and are able to suppress reproduction in subordinates (dominant suppression; Johnstone 2000; Hager 2003). However, when dominants benefit from the presence or actions of subordinates, dominants may concede subordinates a share of reproduction as an incentive for the latter to remain peaceably in the group ("staying incentive"; reviewed in Johnstone 2000; Hager 2003). When the staying incentive required by subordinates is low, monopolization of reproduction becomes possible. According to concession models, this should be the case when (1) relatedness between dominants and subordinates is high, leading to increased indirect benefits for subordinates, (2) the costs of dispersal are high (high "ecological constraints" for independent breeding), and (3) the presence of subordinates greatly increases the dominants' reproductive success, so that both

dominants and related subordinates profit (Keller & Reeve 1994; Clutton-Brock 1998; reviewed in Hager 2003).

As an antipode to concession models, restraint models<sup>3</sup> assume that subordinates are able to claim as much reproduction as they want, being restrained in doing so only by the dominants' tolerance limit of evicting subordinates (reviewed in Johnstone 2000; Hager 2003). Restraint models depend on the same parameters as concession models but yield opposite predictions (i.e. reproductive monopolization will be most probable when relatedness is lower, chances for independent breeding are higher, and the influence of subordinates on dominants' reproductive success are lower). This is because the same factors that make association profitable for subordinates, and thus reduce their required staying incentive, also make association profitable for dominants, and thus increase the tolerated amount of subordinates' reproduction (Johnstone 2000).

As an alternative to concession models, Hamilton (2004) developed a "commitment model of reproductive inhibition" for cooperatively breeding groups. Like restraint models, it assumes that the inability of subordinates to reproduce does not result from stress or manipulation by dominants against the interests of the subordinates, but that subordinates choose whether or not to restrain their own reproduction ("self-inhibition"<sup>4</sup>). The "self-inhibition"-model partly depends on the same parameters as concession and restraint models, and yields similar predictions as concession models: self-restraint and thus reproductive monopolization is most probable when (1) group members are closely related, (2) opportunities for independent breeding are poor, (3) eviction is costly, and (4) the chance of being detected when cheating (i.e. when reproducing) is high (Hamilton 2004).

The "reproductive suppression model"<sup>4</sup> (Wasser & Barash 1983) is a third model assuming that subordinate females control their reproduction themselves. Its predictions, however, depend on other parameters than those in the previous models. According to the "reproductive suppression model", the decision of a subordinate female to reproduce depends on the relationship of present to future reproductive conditions. Mammalian reproduction typically involves considerable investment from females, and tradeoffs exist between an individual's

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<sup>3</sup> In the literature restraint models are sometimes also referred to as "limited or incomplete control" models, according to the fact that dominants do not have control over the allocation of reproduction within the group. The term "limited / incomplete control", however, is occasionally also used as an equivalent for "tug of war" models in which neither dominants nor subordinates are assumed to have control over reproduction, and individuals struggle over reproduction (Hager 2003). Since "tug of war" models seem less appropriate for explaining reproductive monopolization in cooperatively breeding species (c.f. Hager 2003; Dietz 2004), these models are not considered here. In order to avoid confusions with terminology, I avoid the term "limited / incomplete control" in this thesis.

<sup>4</sup> Note that in these models the terms "self-inhibition" and "reproductive suppression" mean that subordinates restrain themselves from reproduction. In the following, I will standardize terminology and use the term "self-restraint" to refer to this situation.

current reproductive efforts and her future reproductive prospects (the "residual reproductive value"). Hence, females can sometimes increase their lifetime reproductive success by deferring reproduction until prevailing conditions improve. This should be the case when subordinate females face the risk of (1) inbreeding-depression due to the absence of unrelated males as mating partners, (2) infanticide by dominant females, and (3) decreased availability of helpers (Wasser & Barash 1983; Saltzman 2003). One prediction arising from the reproductive suppression model is that, in order to minimize investment in reproductive attempts that are not likely to succeed, females should terminate these attempts as early as possible in the reproductive process (Saltzman 2003).

Of the four models presented above, three seem appropriate for predicting reproductive monopolization in cooperatively breeding species. Both concession and self-inhibition models predict reproductive monopolization when relatedness between dominants and subordinates and dispersal costs are high, which is usually the case in cooperatively breeding species (see above). The reproductive suppression model emphasizes the importance of constraints of inbreeding-depression, infanticide, and decreased availability of helpers for the occurrence of reproductive monopolization. Taken together, conceding or claiming a reproductive share as staying incentive in general might not be an optimal solution for females in cooperative breeders. Instead, it is more reasonable to assume that dominant females concede a share of a contested resource (e.g. food) instead of conceding a share of reproduction (Hager 2003), or offer alternative staying incentives (e.g. social comforts like allogrooming) to subordinate individuals.

A relatively new approach incorporating this insight is the biological market theory (Noë & Hammerstein 1994, 1995). In this theory, dominant and subordinate individuals represent two distinct classes that can offer each other commodities that are either under the exclusive control of one class or can only be obtained from alternative sources at high costs (Noë & Hammerstein 1994, 1995). In the case of cooperatively breeding mammals dominant individuals (breeders) can offer subordinates (helpers) a place in the group, and helpers can offer breeders services in infant care. The exchange rate of commodities on biological markets is determined by the law of supply and demand, and in many cases a commodity in high demand (e.g. helping) will be exchanged for one in low demand (e.g. grooming; Noë & Hammerstein 1994, 1995). When helpers considerably outnumber breeders, one can predict that the former have to work harder in order to be allowed to remain in the group ("pay to stay"). In contrast, when the number of available helpers is relatively low, one can predict that they need a higher incentive to stay in the group and help ("pay for help").

In sum, in cooperatively breeding species it generally seems to be in the interest of both dominant and subordinate females to confine breeding to the dominant female, and reproductive monopolization seems to be a product of both dominant suppression and subordinate self-restraint (Wasser & Barash 1983; French 1997; Russell 2004). Empirical evidence suggests that the onset of reproductive activity in subordinate females requires both release from suppression by the dominant female and direct contact to or stimulation from an unrelated male: subordinate females not only fail to reproduce in the presence of a dominant female but also in the absence of a dominant female if unrelated males are also lacking (e.g. Widowski et al. 1990).

On the proximate level, dominant suppression and subordinate self-restraint can manifest behaviourally and/or physiologically, and can cause either the prevention of ovulation and/or conception in non-breeding females (preconception mechanisms), or reduced postnatal survivorship in the offspring of secondary breeding females (postconception mechanisms) (reviewed in French 1997). Preconception behavioural mechanisms include intrasexual aggression, reduced attractiveness or reduced sexual initiative; preconception physiological mechanisms include puberty delay and impaired ovulation (Wasser & Barash 1983; French 1997). Infanticide, inadequate maternal care, poor provisioning, and inadequate alloparental resources are possible postconception behavioural mechanisms of regulating singular female breeding, while failure of implantation, spontaneous abortion, impaired foetal growth, early post-partum mortality and depressed lactation are examples for postconception physiological mechanisms (Wasser & Barash 1983; French 1997). Regardless of which of these mechanisms actually work, all of them ultimately lead to the monopolization of reproduction by one female.

Among primates, female reproductive monopolization reaches its most extreme forms in the callitrichids, the only primate family whose members are characterized by a cooperative breeding system with only one, rarely two breeding female(s) per group, polyandrous matings, dizygotic twin offspring with high neonatal body mass, delayed offspring dispersal, and intensive helping behaviour shown by all group members (Heymann 2003a). This makes them ideal for investigating possible physiological and behavioural mechanisms that might be involved in the establishment and maintenance of female reproductive monopolization and the cooperative breeding system.

### Callitrichid Idiosyncrasies

The Neotropical primate family Callitrichidae<sup>5</sup> (callitrichids) comprises the genera *Callimico*, *Callithrix*, *Mico*, *Callibella*, *Cebuella*, *Leontopithecus*, and *Saguinus* (classification following Rylands et al. 2000, and van Roosmalen & van Roosmalen 2003). The genera *Mico* and *Callibella* were traditionally included in the genus *Callithrix*. *Callimico*, *Callithrix*, *Mico*, *Callibella*, and *Cebuella* are commonly referred to as marmosets, *Leontopithecus* and *Saguinus* are tamarins. Marmosets (except *Callimico*) differ from tamarins in their gum-feeding specializations (enlarged incisors enabling them to gouge holes in trees thereby initiating the flow of exudates).

Callitrichids generally live in small groups containing multiple adults of each sex with the sex ratio usually biased in favour of the males (Heymann 2000). Group composition is rather flexible (Heymann 2003a). Both sexes can delay dispersal and remain with their natal group, or can migrate (see Saltzman 2003). In the past, the frequency of such migratory events was used to infer group composition (Ferrari & Lopes Ferrari 1989): stability of groups was regarded as evidence for family groups composed of parents and their (adult) offspring (as proposed for marmosets). In contrast, frequent turnover of group constituents was regarded as evidence for groups composed of rather unrelated individuals (as proposed for tamarins). Due to the recent availability of genetic methods, determination of group composition became more exact, yet the pattern remained ambiguous: Nievergelt et al. (2000) found evidence for relatively stable extended family groups of closely related individuals in wild *Callithrix jacchus*, while Faulkes et al. (2003) described a more heterogeneous genetic structure in the same species with unrelated individuals commonly occurring in groups. Since the degree of relatedness between group members is an important parameter for predicting the degree of reproductive skew within a group (see above), it will be crucial to investigate true group compositions in further wild tamarin and marmoset species, by using genetic methods.

Regardless of the number of adult females in a callitrichid group, reproduction is usually restricted to a single female (Snowdon & Soini 1988; Stevenson & Rylands 1988). Mating patterns are again rather flexible (Goldizen 1987; Heymann 2003a). Although polygynous mating has been reported as well, the most common mating systems seem to be either

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<sup>5</sup> Classifications differ in whether to give this taxon the status of a family (Callitrichidae) or of a subfamily (Callitrichinae) within the family Cebidae. This is a mere academic question since the monophyly of the taxon is well documented (Rylands et al. 2000; Schneider 2000). Marmosets of the genus *Callimico* were traditionally not included in the family Callitrichidae since they differ from the other genera in tooth number (36 vs. 32: third molar still present) and the occurrence of singleton births. Recent molecular data, however, revealed their status as a sister group to the other marmoset genera (Schneider 2000). In my thesis I use the term of the family Callitrichidae (including the genus *Callimico*) following the consensus of Rylands et al. (2000). Note, however, that when citing the callitrichid characteristics of twin births, reproductive monopolization etc. I exclude *Callimico* without explicitly stating that I do so.



monogamy or polyandry. Polyandrous matings appear to provide the potential for all adult group males to sire offspring (e.g. Schaffner & French 2004). Given that callitrichids regularly produce dizygotic twins, this provides an opportunity for multiple paternities (i.e. two different fathers, each siring an offspring in the same litter). However, males may be able to monopolize reproduction through mate-guarding behaviour during fertile phases of the reproductive female (e.g. Huck et al. 2004a; Dietz 2004).

Irrespective of maternity and paternity, infants are raised cooperatively by all group members and generally no clear kin-biased patterns of the distribution of care are found (e.g. Huck et al. 2004b; Dietz 2004). Callitrichid infants are rather heavy, and neonatal twins together may comprise 14-23 % of maternal body mass (for comparison, in humans the neonatal body mass averages 5.5 % of maternal body mass; Leutenegger 1973, 1979; Garber & Leigh 1997). Helping behaviour mainly consists of carrying these heavy and rapidly developing young as the group moves through the forest canopy, which imposes high energy costs and can lead to considerable weight loss of carriers even in captivity (e.g. Sánchez et al. 1999; Achenbach & Snowdon 2002). As proposed by Goldizen (1987) helpers are essential for the successful rearing of the young, and the number of helpers may positively affect the probability of offspring survival (Garber et al. 1984; Koenig 1995; but see Heymann & Soini 1999). Given that in captivity callitrichid females exhibit a post-partum oestrus, usually 2–4 weeks after birth (French et al. 2002)<sup>6</sup>, the costly phases of pregnancy, lactation and infant-carrying can occur simultaneously. The energetic burden imposed by these unusual characteristics in the reproductive biology of callitrichids plays a key role in discussions about the evolution of polyandrous mating systems and alloparental care (e.g. Caine 1993; Eisenberg 1977; Goldizen 1990; Tardif et al. 1993).

### **Proximate Mechanisms of Reproductive Monopolization in Female Callitrichids**

Breeding females play a central and mediating role in callitrichid groups. By adapting their degree of aggressiveness, they seem to be able to promote immigrations in small groups and to cause evictions in large groups and thus to control group composition (Schaffner & French 1997; McGrew & McLuckie 1986). The proximate mechanisms assuring their reproductive monopoly include behavioural and physiological factors that may differ between species, demographic and social context, reproductive/physical status of the dominant female,

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<sup>6</sup> Unlike in rodents, where the term "post-partum oestrus" usually refers to periods immediately after the birth of infants and means that females engage in sexual behaviour and come into oestrus within a few hours after delivery, in the callitrichid literature, the term "post-partum oestrus" is generally used when an oestrus occurs within 2-4 weeks after the birth of infants. Since primate females are usually characterized by a lactational amenorrhoea, the occurrence of an oestrus in this early phase soon after delivery is in fact exceptional.

subordinates' age, and environment (captive versus wild; reviewed in Abbott et al. 1993; French 1997; Saltzman 2003). Subordinate females may be unovulatory (marmosets and genus *Saguinus*) and/or they may remain sexually inactive (all genera). Both factors seem to be influenced by the presence of a dominant female as well as by the access to an unrelated male. The inhibition of ovulation in subordinate females may be mediated through the exposition to olfactory and visual cues from the breeding female (Epple & Katz 1984; Barrett et al. 1993), but females may also remain unovulatory in the absence of a dominant female when unrelated males are absent as well (Ziegler et al. 1987a). The lack of sexual behaviour in subordinate females may be caused by dominant female harassment (genus *Leontopithecus*: French & Inglett 1989; Inglett et al. 1989) and/or by mechanisms of inbreeding-avoidance with related males (Saltzman et al. 2004). The likelihood of a daughter showing ovulatory cycles in the natal family may be affected by the reproductive/physical status of the breeding female as well as by the daughter's age: with decreasing condition of the breeding female and increasing age of subordinates, subordinate females are more likely to ovulate (Saltzman et al. 1997). In the wild, ovulations in secondary females seem to occur regularly (Savage et al. 1997; Albuquerque et al. 2001; French et al. 2003). This ovulatory activity in wild subordinates might be influenced by the less strict contact to inhibitory cues of the dominant female as well as by the contact to unrelated males, e.g. during intergroup encounters.

Breeding attempts by secondary females have been documented in a variety of callitrichid species (reviewed in Dietz 2004; Arruda et al. 2005). Breeding by two females usually involved related females and generally took place when groups contained males unrelated to the subordinate females (Dietz & Baker 1993; Goldizen et al. 1996; Savage et al. 1996a; Nievergelt et al. 2000; Saltzman et al. 2004). As suggested by Dietz and Baker (1993) and Goldizen et al. (1996), simultaneous breeding by two related females might increase the inclusive fitness of both if inbreeding does not threaten offspring survival. Yet even in the absence of unrelated males, the incidence of daughters that became pregnant in their natal groups increased with their age (see Dietz 2004). This is in line with the "reproductive suppression model" under which females should sometimes attempt to reproduce even under inauspicious conditions, if circumstances are unlikely to improve (see above). Despite the regular occurrence of two breeding females in a group, polygynous or polygynandrous situations are rarely stable. In *Leontopithecus rosalia* polygynous relationships did not exceed two years (Dietz & Baker 1993). Arruda et al. (2005) report seven incidences of subordinate female *Callithrix jacchus* that bred simultaneously with the dominant female: all but one of these females left the group after having lost their offspring. Although the actual cause of