

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



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

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PREFACE

This study is part of the project "Proximate Mechanisms and Genetic Consequences of the Mating System of Polyandrous Tamarins (*Saguinus mystax*; Callitrichidae; Primates)" aimed at elucidating factors shaping the evolution of primate mating systems and reproductive strategies in general, and enlightening the ultimate causes of the extremely rare polyandrous mating system in particular. Studying such questions in primates is generally difficult, and one main problem when choosing primates as model species is the limited sample size due to small groups (which is particularly true for callitrichid primates). Additionally, when intending to study reproductive strategies, groups have to be observed frequently on a (nearly) daily basis and over an extended period of time since crucial and rare events (e.g. migrations) may go unnoticed with a less intensive observation schedule. This makes it even more difficult to observe a large number of groups without sufficient (wo)men-power (see below). Studying reproductive strategies also requires knowledge of physiological parameters (reproductive endocrinology) and genetic relationships (relatedness, maternities, paternities). Recent developments of non-invasive endocrine and genetic analyses have offered new and exciting opportunities to achieve reliable data on reproductive processes even under natural conditions. The development of genetic analyses based on the use of small amounts of hypervariable DNA (microsatellites) from faecal samples nowadays allows to reliably determine paternities and general relatedness in wild populations and has already been used successfully in a number of field studies across all primate taxa (reviewed in Woodruff 2004). Faecal samples also contain hormonal metabolites, and their measurement has been shown to accurately reflect both female and male reproductive status as well as levels of stress in wild mammals including primates (reviewed in Schwarzenberger et al. 1996; Touma & Palme in press). The use of faecal samples for genetic and endocrine analyses offers the additional advantage of frequent sampling without disturbing or stressing the animals. This is particularly important if behavioural observations shall be carried out since such observations require habituated and more or less tame animals that behave in a normal manner.

Our project combined detailed long-term behavioural observations in the natural ecological context with non-invasive monitoring of reproductive status and genetic analyses using faecal samples. In order to handle the amount of work and the different methods used, the study was a decidedly cooperative one that involved three departments of the German Primate Centre: Behavioural Ecology and Sociobiology (formerly Sociobiology), Reproductive Biology, and Primate Genetics. Data collection in the field comprised the work of two PhD-students from

the Department of Behavioural Ecology and Sociobiology, Maren Huck and me. In Peru we had the additional help of four Peruvian field assistants and two Peruvian students. Only through this relatively large number of observers was it possible to study two groups of moustached tamarins intensively on a nearly daily basis over a one-year period. The development of specific hormone assays and microsatellites for moustached tamarins was done by Michael Heistermann and Uta-Regina Böhle, respectively, from the departments of Reproductive Biology and Primate Genetics, respectively. The subsequent genetic analyses were then performed again cooperatively by Maren Huck and me. The hormone analyses were done separately: Maren Huck measured testosterone and cortisol levels in males (Huck et al. 2005b), while I measured oestrogens and gestagens in females. This followed the partitioning of the project into two different parts: the males' perspective was addressed in the doctoral thesis of Maren Huck (Huck 2004), and the females' perspective is addressed in the present thesis.

The chapters of this thesis are written in a manner that each can be read and understood separately, but they are closely connected by the underlying general question about female reproductive strategies in wild moustached tamarins. The chapters have been submitted beforehand to different refereed scientific journals. Two of them (chapters 3 and 4) have already been published, while chapter 5 is under revision. Being the first author and writer of all three manuscripts, I am fully responsible for their content (which does not deny helpful comments and criticism by the co-authors and others). My co-authors have participated insofar as Maren Huck and I collected data in the field and worked together in the lab (see above). Eckhard W. Heymann was responsible for the general project supervision; Michael Heistermann was advisor of the hormonal analyses, and Dietmar P. Zinner was advisor for statistical matters. They have been involved in the development of the separate manuscripts not more and not less than should be expected from attentive and responsible supervisors. I did not change the chapters compared to the published or submitted versions except for standardizing the layout, changing the spelling to British English throughout, correcting typing errors, and standardizing the taxonomy (see footnote 5, page 7).

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)¹. 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 sex², 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

¹ 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).

² 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 models³ 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"⁴). 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"⁴ (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

³ 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.

⁴ 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").