

**Inequality in nature: Patterns of reproductive skew
among male redfronted lemurs
(*Eulemur fulvus rufus*)**

Dissertation

zur Erlangung des mathematisch-naturwissenschaftlichen Doktorgrades

„Doctor rerum naturalium“

der Georg-August-Universität Göttingen

vorgelegt von

Markus Port

aus

Kassel

Göttingen 2008

Referent: Prof. Dr. Peter M. Kappeler

Korreferent: Prof. Dr. Eckhard W. Heymann

Tag der mündlichen Prüfung: 22.10.2008

PREFACE

The present study is part of the project “Geschlechterverhältnis und reproductive skew bei gruppenlebenden Lemuren” (Sex ratios and reproductive skew in gregarious lemurs), funded by the German Research Council (DFG). As an overall goal, this project aimed at illuminating the factors shaping the evolution of the unusual social organizations of two sympatrically living gregarious lemur species, redfronted lemurs (*Eulemur fulvus rufus*) and Verreaux’ sifakas (*Propithecus verreauxi verreauxi*). While the sifaka-part of the project is treated by the Diploma thesis of Livia Schäffler (Schäffler 2005, Kappeler and Schäffler 2008) as well as by the PhD thesis of Vanessa Mass (in preparation), my research focused on reproductive skew and social power among male redfronted lemurs as well as on a general evaluation of the applicability of reproductive skew theory to primates and other mammals.

Except for Chapter 1, which provides a general introduction to reproductive skew theory, the chapters of this thesis have been submitted to different refereed scientific journals. Chapters 2 and 4 have already been published (Kappeler and Port 2008, Port et al. 2009), while chapter 4 is currently under revision. I carried out all practical work involved in this thesis myself, including the paternity analyses conducted for Chapter 2, as well as the behavioural observations conducted for Chapter 4, the latter with the indispensable help of Jean-Pierre Ratolojanahary, a Malagasy field assistant, who also kept the observations going during my absence from the field. I also wrote all chapters of this thesis. My co-author Dagmar Clough contributed valuable observational data to Chapter 4, and Peter Kappeler was responsible for the general project supervision. He contributed to each of the manuscripts in exactly the way it should be expected from an attentive and responsible supervisor. Furthermore, Peter Kappeler is first author of Chapter 2, as he provided the necessary samples and demographic data from 10 years of research at the Kirindy field station, Madagascar.

Only with this extensive data set it was possible to conduct one of the most comprehensive studies of reproductive skew in a primate.

The chapters of this thesis appear as in the published or submitted versions, however, with one notable exception: Table 1.1 and Figure 1.1 have been submitted together with Chapter 3, but in this thesis they have been incorporated into Chapter 1. For the present thesis, this is more convenient, as both the table and the figure refer to a description of reproductive skew theory, which is provided in Chapter 1 in most detail.

CONTENTS

GENERAL INTRODUCTION	1
CHAPTER 1:.....	6
An introduction to reproductive skew theory	
CHAPTER 2:.....	15
Mutual tolerance or reproductive competition? Patterns of reproductive skew among male redfronted lemurs (<i>Eulemur fulvus rufus</i>)	
With Peter M. Kappeler	
CHAPTER 3:.....	39
The utility of reproductive skew theory in the study of male primates - a review	
With Peter M. Kappeler	
CHAPTER 4:.....	59
Market effects offset the reciprocation of grooming in free-ranging redfronted lemurs (<i>Eulemur fulvus rufus</i>)	
With Dagmar Clough and Peter M. Kappeler	
GENERAL DISCUSSION.....	83
SUMMARY	94
REFERENCES.....	95
ACKNOWLEDGMENTS.....	109
APPENDIX.....	111

GENERAL INTRODUCTION

Male reproductive strategies and the unusual adult sex ratios of gregarious lemurs

The adaptive basis of group-living has always been a major focus of socioecological research (e.g., Hamilton 1964, Alexander 1974, van Schaik 1983, Emlen 1995, Nonacs 2001). Group-living should be selected for whenever individuals gain benefits from an association with conspecifics, such as improved protection from predators (Hamilton 1971, van Schaik 1983), joint defence of resources or territories (van Schaik 1989, Packer et al. 1988) or assistance in infant care (Brown 1987, Goldizen 1987). However, group-living may also be associated with a significant disadvantage: Reproductive competition between same-sexed group members frequently results in a high variation in their reproductive success (Ellis 1995), commonly referred to as reproductive skew. Therefore, it is to be expected that stable groups will form only if the benefits provided by an association compensate for the disadvantages imposed by reproductive competition.

In mammals, males have a higher potential rate of reproduction than females (Clutton-Brock and Parker 1992) and thus, a male's reproductive success is mainly limited by the access to mates (Bateman 1948, Trivers 1972). As a consequence, males compete more intensely for mates than females, which in many species led to the evolution of dimorphism in body size and secondary sexual characters (Darwin 1871, Clutton-Brock 2007). In relation to group-living, competition among males should result in the attempt to exclude rivals from groups of females (Clutton-Brock 1989, Kappeler 1999). It has therefore been predicted that where females form groups that are small enough to be defended by a single male, uni-male groups should be the predominant form of social organization (Emlen and Oring 1977, Clutton-Brock 1989).

Among gregarious primates this prediction has been tested and confirmed in cercopithecine monkeys, in which groups of less than six females are usually monopolized by a single male (Andelman 1986). In contrast, the gregarious lemurs of Madagascar markedly differ from this prediction. Even though groups do on average not contain more than five females, the number of adult males usually equals or exceeds the number of females (Kappeler 2000a), hence, lemur males do not monopolize small groups of females. This form of social organization is unusual among primates and other mammals, and has not yet been explained satisfactorily (but see van Schaik and Kappeler 1996, Wright 1999). However, previous studies of primate social organization have mainly focused on male-male competition, but little emphasis has yet been laid on possible benefits that males could gain from an association with other males. For instance, males are more vigilant than females in some species (van Schaik and van Noordwijk 1989, van Schaik and Hörstermann 1994) and a higher number of males may be more effective in defending a group of females (Packer et al. 1988, Ortega and Arita 2002, Ostner and Kappeler 2004). Given these benefits, selection may favour increased tolerance among males. However, as each male should nevertheless seek to maximize its reproductive success, it requires an explanation how the conflict over reproduction is resolved, and hence, the stability of a group maintained.

Reproductive skew theory

Vehrencamp (1983a, b) first integrated the benefits of sociality into a theoretical model aimed at explaining how within-group conflict over the division of reproduction can be overcome. Accordingly, selection acts on stronger, dominant group members to secure more reproduction for themselves, but at the same time at subordinate individuals to leave the group if the prospects of reproduction are better elsewhere. Thus, if dominants profit from the presence of subordinates, i.e., if it is in their interest to maintain group stability, the level of

skew they can impose on subordinates is limited by the latter's options outside the group. Vehrencamp's model was later extended by Reeve and Ratniecks (1993); their so-called 'concession model' initially aimed at explaining cooperative nest foundation in polistine wasps, but was soon applied to vertebrate taxa as well (e.g., MacRae 1996, Jamieson 1997). It finally led to a rapid spread of reproductive skew theory and a still ongoing development of new models (see Chapter 1). A central assumption of the concession model and its successors is that a dominant group member completely controls all reproductive opportunities within the group, but voluntarily concedes a share of reproduction to subordinates as an incentive to stay in the group. In contrast, in the 'restraint model' the subordinate is in control (the model is restricted to a two person association, Johnstone and Cant 1999a), but voluntarily exercises a reproductive restraint to avoid being evicted from the group by the dominant. However, it has been criticised that the assumption of one group member completely controlling reproduction within the group is unlikely to hold for the vast majority of vertebrate taxa (Clutton-Brock 1998). Therefore, models have been developed which do not assume, that group members voluntarily share fertilizations, but in which the division of reproduction is the consequence of forcible competition between them (tug-of-war models: Reeve et al. 1998, Nonacs 2007). A common feature of all reproductive skew models is to predict an evolutionarily stable level of reproductive skew, which depends on various environmental and demographic variables (see Chapter 1). In this way, reproductive skew theory provides testable predictions regarding the involvement of cooperative forces (or a lack thereof) in the evolution of group-living.

It must be noted that the term 'reproductive skew' is not necessarily restricted to reproductive skew theory, but more generally refers to any unequal distribution of reproductive success. It has therefore been studied by primatologists (e.g., Altmann et al. 1996, Alberts et al. 2003, Huck et al. 2005) as well as by students of other mammals (e.g., Campagna and LeBoeuf 1988, Say et al. 2001, Dugdale et al. 2007) without referring to reproductive skew theory. Instead, considerable attention has been paid to the priority of

access model (Altmann 1962, Alberts et al. 2003), according to which high ranking males are able to monopolize fertilizations as long as females are receptive asynchronously, whereas low-ranking males get to mate as the number of synchronously receptive females increases. Due to this lack of control on the dominant's part, it has been argued that the priority of access model has similarities to tug-of-war models (Kutsukake and Nunn 2006, in press). However, whereas the mechanism by which dominants lose control is specified in the former (increase in female number), this is not the case in the latter (see Chapter 3). Moreover, as the priority of access model merely examines the proximate mechanisms of reproductive competition, it is not a suitable tool to illuminate the ultimate reasons for group formation.

Contents of the thesis

The overall aim of this study was to test models of reproductive skew in redfronted lemurs (*Eulemur fulvus rufus*). These lemurs are representative of gregarious lemurs as they live in small groups with even or male-biased adult sex ratios (Overdorff 1998, Wimmer and Kappeler 2002). Males apparently profit from an association with other males, as larger groups are less likely to be taken over by intruders (Ostner and Kappeler 2004). In addition, in each group, one male is clearly dominant over all other males and monopolizes the majority of social contacts and matings with females (Ostner and Kappeler 1999). These features make redfronted lemurs ideal candidates for tests of the concession- and restraint model. Evidence in favour of either of these models would indicate the importance of male-male cooperation in the evolution of group-living in this species, and thus, provide a possible explanation for the unusual adult sex ratios of redfronted lemur groups.

While **Chapter 1** provides a brief introduction to reproductive skew theory, in **Chapter 2**, I use demographic and paternity data obtained from a redfronted lemur population in western Madagascar to empirically test the three most influential reproductive skew models (the concession, the restraint, and the tug-of-war model), as well as the priority of access

model. In **Chapter 3**, I review the applicability of current reproductive skew theory to the study of male primates. It has been argued that reproductive skew theory provides a general framework to explain the evolution of sociality across animal taxa (Keller and Reeve 1994, Johnstone 2000). However, most of the early models were developed to explain the partitioning of reproduction among hymenopteran queens, and it has been largely ignored that primates and other mammals differ markedly from social insects in both their life histories and social organizations. Moreover, different mechanisms are involved in the division of reproduction among males and females, which are not sufficiently accounted for by the existing models. I therefore highlight these shortcomings and discuss possible extensions needed to meet the requirements of primate social organization and male reproductive biology.

In **Chapter 4**, the focus turns back to redfronted lemurs. Using biological market theory (Noë and Hammerstein 1994, 1995), I examine agonistic interactions and the exchange of grooming in groups of redfronted lemurs. In relation to this thesis, male-male relationships are of particular interest. The elements of the social structure analyzed in this chapter provide valuable information about the social power among males, which may in turn help to assess their roles in the possible exchange of reproduction. In particular, if dominant males are selected to give reproductive concessions to subordinates, it should be expected that they also behave tolerantly towards them on a social level. In contrast, if subordinates are selected to exercise reproductive restraint to avoid being evicted from their group, it should be expected that they provide dominants with (additional) social services as well.

Finally, I summarize the major findings of this thesis and discuss their relevance in relation to the evolution of the unusual group compositions of redfronted lemurs.

CHAPTER 1:

An introduction to reproductive skew theory

Markus Port

Introduction

The first reproductive skew models were built upon the assumption that a dominant individual (or breeder) not only competes with, but also profits from the presence of same-sexed subordinates within its group (Vehrencamp 1983a, b). Accordingly, there is selection on the dominant not to expel the subordinate as a competitor, but to accept it within the group and even to tolerate some of its reproductive efforts. This reproductive incentive is required because selection simultaneously acts on the subordinate to leave the group if it can do better elsewhere. This assumption is implicit in *transactional models* of reproductive skew theory, according to which reproductive skew is the outcome of reproductive transactions between dominant and subordinate group members, mediated either by the subordinates' threat to leave the group (concession-based models) or by the dominant's threat to evict the subordinate (the restraint model). In contrast, *compromise models* assume that reproductive skew is the outcome of a struggle over reproduction between group members, the intensity of which is only mediated by the detrimental effects it imposes on group productivity.

Here, I provide a simple verbal description of the major developments in reproductive skew theory. For details concerning the mathematical features of the models see, e.g., Reeve and Ratniecks (1993), Johnstone (2000), Johnstone and Cant (in press). A critical evaluation of the assumptions underlying the models as well as of the variables incorporated in them is provided in Chapter 3.

Transactional models

The concession model and its extensions

Reeve and Ratniecks' (1993) concession model assumes that a dominant *completely controls* all reproductive opportunities within its group, but *voluntarily* concedes a share of it to a

subordinate as an incentive to stay (the model was limited to two person associations). The magnitude of this staying incentive can be found by seeking the *minimum* share of reproduction required by the subordinate to make staying more favourable than leaving the group (but see Cant (2006) for an alternative approach). This minimum share, in turn, is a function of the subordinate's prospects of breeding independently outside the dominant's territory, its contribution to the group's productivity, its relatedness to the dominant, and, in an extension of the basic model, its fighting ability (Table 1.1). Because a subordinate's prospects of successful breeding outside the dominant's territory ultimately determine the minimum fitness it requires in its current group, the staying incentive is predicted to increase as the constraints on solitary breeding relax. It is also predicted to increase with the subordinate's fighting ability, because stronger subordinates are more likely to challenge the dominant. Conversely, the subordinate's share is predicted to decrease as its relatedness to the dominant increases, because subordinates related to the dominant profit from indirect fitness and, thus, require less of an incentive to stay. The subordinate's share is also predicted to decrease when it contributes more to the group's productivity. This latter prediction seems to be counterintuitive at first glance, but it results from the fact that a lower relative share of an absolutely higher group output is required to meet the expected subordinate's fitness by leaving the group.

If the *minimum* share required by the subordinate falls below the *maximum* share the dominant would accept, the subordinate is expected to receive its minimum share and the group will be stable. Otherwise, the model assumes that the dominant withholds the share required by the subordinate, which in turn forces the latter to leave. The difference between the minimum share required by the subordinate and the maximum share the dominant is willing to tolerate has previously been called the 'window of selfishness' (Reeve 2000, see Fig. 1.1). But since the dominant controls the allocation of reproduction, i.e. the power in the concession model is with the dominant, the dominant is selected to seek its own maximum

within the window of selfishness by reducing the subordinate's share to the minimum required by the latter. Hence, the evolutionary stable level of skew is found by seeking the subordinate's minimum.

First extensions of the concession model stressed the importance of distinguishing between symmetrical and asymmetrical relatedness (Reeve and Keller 1995, 1996). This distinction is of particular importance in nuclear families in which helpers are mainly recruited from adult offspring and in which a subordinate's *effective* relatedness to the dominant's offspring may be different from the dominant's *effective* relatedness to the subordinate's offspring. This distinction can have far reaching consequences for the level of skew and is of importance not only to the concession model, but to all reproductive skew models in which indirect fitness benefits are estimated.

In its original form, the concession model is restricted to two person associations that reproduce in a single breeding season, and in which reproductive allocation takes place once at the beginning of this period. Later extensions allowed subordinates to choose among several dominants (the bidding-game, Reeve 1998), examined the level of skew in larger associations (Johnstone et al. 1999, Reeve and Emlen 2000, see Appendix C), and incorporated future fitness benefits through queuing for breeding positions (Kokko and Johnstone 1999, Kokko et al. 2001, Cant and English 2006) as well as skew adjustments over a prolonged period of time (Zink and Reeve 2005). However, all these models assume that a social contract is arranged between same-sexed group members only, and only two models have so far accounted for the fact that the opposite sex may also exert control over the allocation of reproduction (Cant and Reeve 2002, Hamilton and Heg 2007).

Table 1.1: Relationship between various variables and the subordinate's share of reproduction as predicted by the major reproductive skew models. Note that the predicted effect of each variable assumes that all other variables are held constant.

Variable	Transactional models			Compromise models	Synthetic models
	Concession	Bidding Game	Restraint	Tug-of-war	BTOW
x	+	0	-	0	+
k	-	+	+	0	0
r	-	0	+	0	0
f	+		+ ¹	+	+

Abbreviations: BTOW= bordered tug-of-war (Reeve and Shen 2006); x= constraints on solitary breeding (the lower x the harsher the constraints); k= subordinate's contribution to group productivity (note that this variable becomes a function, of the number of males in larger associations); r= relatedness between subordinate and dominant, f= subordinate's fighting ability, N= number of subordinates, + = positive relationship, - = negative relationship, 0= no relationship. ¹This prediction follows from the assumption that subordinates with a higher fighting ability impose higher eviction costs.

The restraint model

This model assumes that the subordinate controls reproduction, yet the dominant still controls group membership (i.e., it has the power to evict the subordinate). Therefore, the subordinate voluntarily exercises reproductive restraint in order to avoid being evicted (Johnstone and Cant 1999a). As compared to the concession model, power over the allocation of reproduction in the restraint model is transferred to the subordinate. As a result, it is the subordinate who is selected to seek its maximum within the window of selfishness by claiming exactly as much reproduction as the dominant would tolerate before it pays the latter to evict the subordinate. Hence, the evolutionary stable level of skew is obtained from the *maximum* share of reproduction tolerated by the dominant (Fig. 1.1). As a result, the predictions relating the level of skew to the variables incorporated in the model are exactly opposite to those derived from the concession model (Table 1.1). Furthermore, the share of reproduction the subordinate can claim unsanctioned, is also determined by the dominant's costs of evicting the subordinate.

Buston et al. (2007) recently synthesized the concession and the restraint model by defining the individual in control of reproduction as ‘the allocator’, irrespective of whether it is the dominant or the subordinate, and the remaining individual as ‘the partner’. They show that with these new definitions, both models are identical and their predictions equivalent to those of the concession model. This is because according to their new definitions, the individual formerly known as the subordinate in the restraint model, is now supposed to *actively* concede a share of reproduction to its partner instead of (merely *passively*) exercising a reproductive restraint. Even though this approach may largely simplify the transactional framework, it appears to be somewhat arbitrary. In ‘the real world’ it is usually hard to decide whether an animal actively concedes reproduction to its partner or whether it simply refrains from reproducing although, in ‘the mathematical world’, this distinction completely changes the predictions of the model.

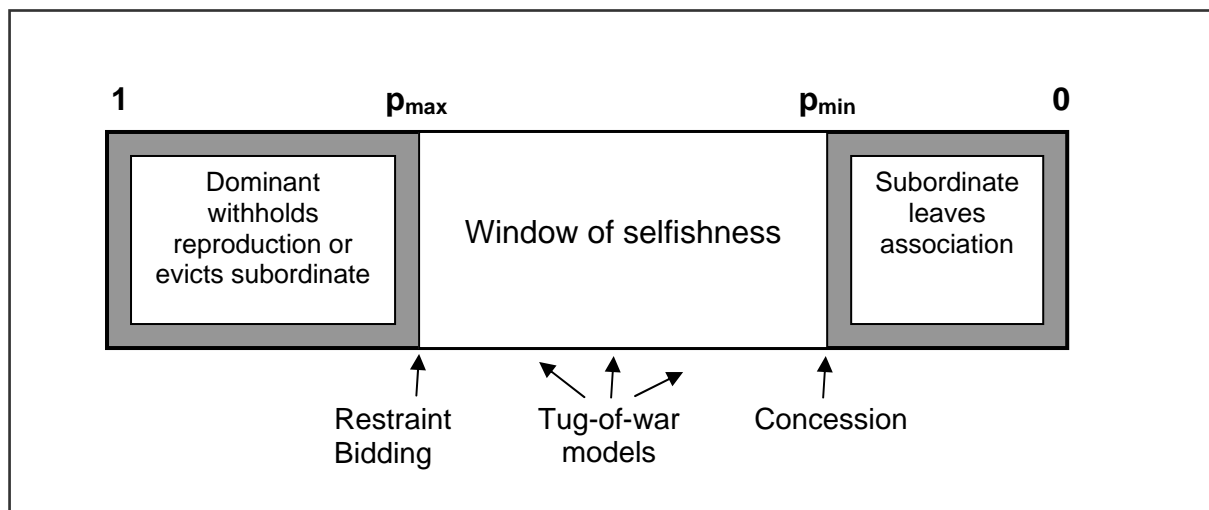


Figure 1.1: The reproductive skew continuum shown as the subordinate’s share of reproduction. p_{\max} indicates the maximum share the dominant is willing to tolerate before it pays to evict the subordinate, p_{\min} indicates the minimum share the subordinate needs to make staying more favorable than leaving. Arrows show the level of skew according to the models indicated. Note that in the BTOW, the subordinate’s share is constrained to lie between p_{\max} and p_{\min} , in the classic tug-of-war model it is bordered to its right through p_{\min} , whereas in Nonac’s (2007) escalating version it is not constrained at all.

Compromise models

It has been argued that the assumption that one individual completely controls the division of reproduction within the group is unlikely to hold in the majority of animal societies (Clutton-Brock 1998). In a second class of models, this assumption has therefore been relaxed, and the division of reproduction is assumed to represent a compromise between the optima of dominant and subordinate(s). Even though a number of models are available, some of them only concern reproductive sharing among females (Cant 1998, Johnstone and Cant 1999b, Hager and Johnstone 2004), and are therefore not considered in any more detail here. Tug-of-war models (Reeve et al. 1998, Nonacs 2007) are the most widely applied compromise models and are also most relevant to reproductive sharing among male primates.

Tug-of-war models

According to tug-of-war models (Reeve et al. 1998 provided two models, but usually their ‘subordinate inefficiency’ model is referred to as *the* tug-of-war model), the division of reproduction is the outcome of a struggle over reproduction between a dominant and a subordinate in which both parties freely decide how much energy they invest into the contest. However, the amount of energy is limited by the fact that energy invested into the struggle over reproduction is at the expense of group productivity. At the evolutionarily stable equilibrium the subordinate’s share of reproduction only increases as its competitive ability increases, but (in contrast to transactional models) is virtually insensitive to relatedness (Table 2), because relatives are both thought to reduce their competitive effort, with the result that the level of reproductive skew does not change. Moreover, if the model is extended to arbitrary group sizes, the dominant is predicted to lose more reproduction to subordinates as their number increases, because a higher number of competitors means that their ‘pull’ in the tug-of-war will be stronger.

Thus, in contrast to transactional models, the level of reproductive skew in the tug-of-war model does not result from a social contract between individuals, but from of a compromise between pursuing an egoistic strategy and the costs this strategy imposes on group productivity. But even this model considers issues of group stability, because it assumes that the dominant will not push the subordinate's share of reproduction below its minimum lest it forces the subordinate to leave and loses the benefits of association (Fig. 1.1). Therefore, Nonacs (2006) argued that the original tug-of-war model lies well within the transactional framework and demonstrated that once the animals are given the option to sequentially adjust their level of aggression to the actions of their partner (i.e., to escalate in conflict), any border restricting the tug-of-war is unlikely to be stable (Nonacs 2007). This is not surprising, however, as Nonacs' analysis excludes the possibility for either individual to leave the group, leaving an escalation in the tug-of-war as the only option (see Johnstone and Cant, in press).

Synthetic models

This brief outline illustrates that the broad application of both transactional and tug-of-war models suffers from weaknesses: transactional models are built upon the unrealistic assumption that one individual completely controls reproduction, and tug-of-war models do not sufficiently incorporate the individuals' options outside the group. Thus, a realistic model of reproductive skew needs to explain how the conflict over reproduction within groups is resolved in the absence of complete control (the tug-of-war approach), and at the same time how the incentive of either group member to dissolve the group (by eviction or voluntary departure) is overcome (the transactional approach). Based on this idea, Johnstone (2000) and Reeve and Shen (2006) attempted to synthesize both classes of models by restricting the tug-of-war to the 'window of selfishness' (Fig. 1.1). However, both approaches have been criticized as they are based on several unrealistic assumptions (for details see Nonacs 2006,

2007, Johnstone and Cant, in press). Recently, Johnstone and Cant (in press) corrected the weaknesses of these earlier syntheses by developing a model in which the division of reproduction is basically decided in a tug-of-war but each individual is given the option to ‘ease off’ its competitive effort in response to being evicted or deserted by its partner. Thus, this model allows for negotiations about the level of competition within a group, which is different from the allocation of reproductive incentives assumed by most other models, including previous syntheses.

CHAPTER 2:

Mutual tolerance or reproductive competition? Patterns of reproductive skew among male redfronted lemurs

(Eulemur fulvus rufus)

Peter M. Kappeler & Markus Port

Abstract

The social organization of gregarious lemurs significantly deviates from predictions of the socioecological model, as they form small groups in which the number of males approximately equals the number of females. This study uses models of reproductive skew theory as a new approach to explain this unusual group composition, in particular the high number of males, in a representative of these lemurs, the redfronted lemur (*Eulemur fulvus rufus*). We tested two central predictions of ‘concession’ models of reproductive skew theory, which assume that subordinates may be allowed limited reproduction by dominant group members as an incentive to remain in the group, thereby increasing the group’s overall productivity. Accordingly, relatives are predicted to receive less reproduction than non-relatives, and the overall amount of reproductive concessions given to subordinates is predicted to increase as the number of subordinates increases. In addition, we tested whether the number of females in a group, a variable not previously incorporated in reproductive skew theory, affected reproductive skew among males. Using microsatellite analyses of tissue DNA, we determined paternities of 49 offspring born into our study population in Kirindy forest (western Madagascar) since 1996 to determine patterns of male reproductive skew to test these predictions. Our analyses revealed remarkable reproductive skew, with 71% of all infants being sired by dominant males, but both predictions of reproductive skew models could not be supported. Instead, the number of females best predicted the apportionment of reproduction among the males in this species, suggesting that current reproductive skew models need to incorporate this factor to predict reproductive partitioning among male primates and perhaps other group-living mammals.

Keywords sexual selection, reproductive skew, primates, paternity, *Eulemur fulvus*

Introduction

The adaptive basis of variation among mammalian social systems has been a major focus of socioecological research from its inception (Crook and Gartlan 1966, Clutton-Brock 1989). According to the socioecological model, the distribution of females is primarily determined by the distribution of risks and resources in the environment, whereas males distribute themselves in response to the spatio-temporal distribution of receptive females (Emlen and Oring 1977). From a male's perspective, reproductive success is mainly limited by access to mates (Bateman 1948, Trivers 1972). Therefore, whenever females form social units that are small enough to be defended by a single male, males should try to monopolize females via the exclusion of rivals (Kappeler 1999). As a consequence, small groups of females are expected to be monopolized by one adult male (Clutton-Brock 1989).

Among gregarious primates this prediction was supported by studies of cercopithecine monkeys, in which groups of less than six females are usually monopolized by a single male (Andelman 1986). In contrast, the gregarious lemurs of Madagascar markedly differ from this prediction as they usually form groups with even or male-biased sex ratios, even though groups do on average not contain more than five females (Kappeler 2000a). This deviation from predictions of the socioecological model has not yet been explained in a satisfactory manner (but see e.g. van Schaik and Kappeler 1996). However, previous studies of the evolution of primate social systems focused on male-male competition for mates, whereas little emphasis has yet been laid on male behavior beyond competition. In fact, dominant males could also profit from the presence of additional males via group augmentation benefits (e.g. van Schaik and van Noordwijk 1989, Packer et al. 1988), so that the benefits derived from the presence of additional males may exceed the costs the latter impose due to lost paternity. Therefore, selection may favor increased mutual tolerance among males.

Vehrencamp (1983a, b) first integrated this assumption into a quantitative model of group-living. This model was later extended by Reeve and Ratniecks (1993), who assumed

that the dominant group member completely controls the reproductive opportunities within a group but voluntarily gives a share of reproduction to subordinates as an incentive to remain in the group, as the latter's presence increases the dominant's fitness. Accordingly, a subordinate's share of reproduction is determined by its prospects for solitary breeding outside the dominant's territory, its contribution to the group's productivity, its relatedness to the dominant and its relative fighting-ability. This theoretical framework allowed for quantitative tests of the evolution of group-living that considered not only competition among same-sexed group members but also their benefits from peaceful association.

During the last decade, Reeve and Ratnieck's "concession" model passed through several extensions, some of which allowed subordinates to choose among several dominants (the "bidding game", Reeve 1998), or to queue for dominant-status (Kokko and Johnstone 1999), and the original two-player version was extended to larger associations (Johnstone et al. 1999, Reeve and Emlen 2000). However, it has been criticized that the most eminent assumption of the concession model, the dominant's ability to monopolize reproduction, is unlikely to hold for the majority of animal societies (Clutton-Brock 1998). Therefore, alternative models have been developed in which the dominant lacks control over the allocation of reproduction. Instead, reproductive skew within groups is either a consequence of direct competition (the "tug-of-war model", Reeve et al. 1998), which decreases group-productivity, or a consequence of the subordinate's restraint from reproduction due to the threat of being evicted from the group (the "restraint" model, Johnstone and Cant 1999). In terms of the variables thought to affect reproductive skew, these latter models make predictions that are different from, or even opposite to, those derived from the concession model. Finally, Johnstone (2000) and Reeve and Shen (2006) reconciled the mainstream models, but their synthetic approaches remain to be tested and continue to be debated (e.g., Nonacs 2006, 2007).

Most tests of reproductive skew theory were conducted with small colonies of social insects (reviewed in Reeve and Keller 2001) but an increasing number of studies have used vertebrate model organisms (fish: e.g. Stiver et al. 2005, Heg et al. 2006; birds: e.g. Jamieson 1997, Haydock and Koenig 2003, Williams 2004; mammals: e.g. Clutton-Brock et al. 2001, Widdig et al. 2004, Kutsukake and Nunn 2006). Most of these vertebrate studies concluded that a “limited control” scenario best explains the apportionment of reproduction whereas only a few studies supported the concession model in vertebrates (McRae 1996, Jamieson 1997).

The aim of this study is to test models of reproductive skew theory in redfronted lemurs (*Eulemur fulvus rufus*) to illuminate the evolution of group size and composition in this species. In particular, evidence in support of the concession model would indicate the importance of male-male cooperation as an ultimate reason for the unusual social organization of these lemurs. Their small groups with even sex ratios make redfronted lemurs a particularly appropriate species for tests of reproductive skew theory. In addition, one male clearly dominates all other males and monopolizes the majority of social contacts and matings with females (Ostner and Kappeler 1999) but also benefits from the presence of subordinates as groups with more males are less likely to be taken over by potentially infanticidal intruders (Ostner and Kappeler 2004). Therefore, an important assumption of the concession model seems to be fulfilled in this species. Preliminary parentage analyses revealed that 6 out of 9 infants were sired by dominant males (Wimmer and Kappeler 2002), the question remains whether the observed skew is the consequence of concessions given by the dominant or his inability to prevent subordinates from mating.

Using demographic and paternity data, we test two of the predictions of reproductive skew theory (summarized in Table 2.1): First, according to the concession model, relatives of a dominant are expected to gain less reproduction than non-relatives (because relatives profit from inclusive fitness), whereas, according to the restraint model, relatives are predicted to

gain more reproduction (because the eviction of relatives is costlier to the dominant). The tug-of-war model, in contrast, predicts skew to be insensitive to relatedness. Second, according to the tug-of-war model, an increase in the number of males within a group translates into an increase in the number of competitors. Therefore, the dominant's share of reproduction is predicted to decrease with an increasing number of males. Unfortunately, predictions of the concession model are not that straightforward and depend on within-group relatedness (Johnstone et al. 1999, Reeve and Emlen 2000) as well as on the chosen measure of skew (Port, unpubl. data). In this study we measured skew as the total proportion of reproduction obtained by all subordinates within a group (see Methods). If we assume group productivity to be a decelerating function of group size, we predict this measure of skew to increase as the number of subordinates increases, even though the concessions required by a single subordinate may decrease in some cases (Reeve and Emlen 2000). For instance, due to the concave curvature of the productivity function, two subordinates together will require a larger share of reproduction than one alone, although each of them may be satisfied with a yet lower personal share in an association of three, as compared to an association of two subordinates.

Using demographic data also enabled us to measure the impact of the number of females in a group on male reproductive skew. This variable has not yet been incorporated in reproductive skew theory even though several primate studies revealed that the number of females in a group may set a limit to a dominants' ability to monopolize matings, especially if female receptive periods overlap (e.g. Andelman 1986, Nunn 1999, Cords 2000). Accordingly, the "priority-of-access" model (Altmann 1962) predicts that more low-ranking males get to mate as the number of synchronously receptive females increases (see Alberts et al 2003). We can not directly measure reproductive synchrony in this study, but as redfronted lemurs are highly seasonal breeders, we predict reproductive skew to decrease with an increasing number of females within groups. Note that in contrast to the tug-of-war model, which focuses on the energy allocated by males to their struggle over reproduction, the

priority-of-access model reflects a dominant's inability to monopolize several females at the same time.

Table 2.1: Predicted and observed relationships between the number of males, the number of females and relatedness (between dominant and subordinates) and the subordinates' fraction of reproduction according to three reproductive skew models and the priority of access model.

Variable	Concession	Restraint	Tug-of-war	Priority of access	Observed
Number of Males	+ ^a	No prediction	+	No prediction	0
Number of Females	No prediction	No prediction	No prediction	+ ^b	+
Relatedness	-	+	0	No prediction	0

+: positive relationship, -: negative relationship, 0: no relationship predicted.

^aNote that this prediction is based on the measure of skew used in this study, the proportion of reproduction obtained by all subordinates, and the assumption that group productivity is a decelerating function of group size.

^bThis prediction assumes reproductive synchrony to increase with female number (note that redfronted lemurs are highly seasonal breeders).

Material and methods

Study population and data collection

This study is part of an ongoing long-term study conducted in Kirindy Forest, a dry deciduous forest located within a forestry concession operated by the Centre Formation Professionnelle Forestière (CFPF) Morondava, approximately 60 km northeast of Morondava, western Madagascar. For a detailed description of the forest see Sorg et al. (2003).

All study animals belonged to one of five groups (A, B, F, I, J) living in a 60-ha study-area, which is part of the German Primate Center field site at Kirindy. Unmarked individuals that were either born into or that have migrated into our study population have been regularly captured since 1996 and marked with unique nylon collars or radio collars. In addition, small tissue-samples (2-3 mm²) from the ear were taken from anaesthetized animals and transferred

to 70-90% ethanol for later DNA extraction. All groups have also been subjected to daily or at least weekly demographic censuses since 1996 by local field assistants. Dominance relationships among males were assessed on the basis of decided agonistic interactions during behavioral observations carried out in 1997 (Ostner and Kappeler 1999), 1999-2000 (Ostner 2004), and 2004-2006 (Port, unpubl. data).

Group size (excl. newborn offspring) of the five study groups ranged between 4 and 11 individuals (mean= 6.73), including 2-5 (mean= 3.37) adult males and 1-3 (mean 2.26) adult females (Table 2.1). Redfronted lemur groups usually consist of a core of related females (Wimmer and Kappeler 2002); adult males are either natal males that delayed their dispersal (the number of which ranged in our study between 0 and 2; mean= 0.52), or immigrants (range 2-4; mean= 2.85). Reproduction in redfronted lemurs is highly seasonal. Mating behavior is largely restricted to a few weeks in May/ June (Ostner and Kappeler 2004), during which a female's fertile period is limited to 1-3 days (Boskoff 1978).

Paternity analyses

Sixty-nine infants were born into our study population between 1996 and 2004, 49 of which survived until they were old enough (about 5 months) to be captured. DNA was extracted from tissue samples using QIAamp[®] tissue kits (Quiagen) and analyzed at 11 nuclear markers (microsatellites): Efr 05, Efr 08, Efr 24, Efr 30, Efr 37, Efr 56, Efr 80 (for details see Jekielek and Strobeck 1999), I3, L2, Efr 02 and Efr F9 (for details see Wimmer and Kappeler 2002). The mean number of alleles per locus was 9.6 (range 5-17), and the mean observed heterozygosity was 0.79 (+/- 0.07). Because mothers of offspring were usually known, the total exclusionary power of the 11 markers was 0.99996.

Paternity analyses were performed using the program CERVUS 2.0 (Marshall et al. 1998). Candidate males were excluded from paternity if they showed at least one heterozygous mismatch with a given mother-offspring pair. In addition, CERVUS calculates

log-likelihood ratios (LOD-scores), which represent the likelihood of paternity of a candidate male relative to a randomly chosen male. The difference between the LOD-scores of the most likely and the second most likely male is expressed as the Δ -statistic. Confidence intervals of this statistic are assessed in a large number of paternity test simulations that require locus-specific allele frequency data for the population of interest and some additional population parameters, which were defined as follows: For each group and each year, we considered the probability that, in addition to the resident males, one unsampled male could have sired offspring. This in turn translates to a proportion of sampled candidate males of 0.77. The mean number of candidate fathers per group and year was set to five (mean number of resident males plus one unsampled male, rounded up), the mean proportion of loci typed was 0.97. Error rate, estimated from known mother-offspring pairs, was 0.002, and was set to 0.01. A total of 50,000 simulation cycles were performed.

Relatedness analyses

Pair-wise relatedness coefficients were calculated with RELATEDNESS 5.0.8 (based on a method of Queller and Goodnight 1989), using the same microsatellite data. If, according to the concession or restraint model, individuals treat relatives and non-relatives differentially, individuals have to be able to perceive each other's relatedness. Relatedness coefficients are continuous measures of the proportion of alleles identical by descent that are shared between pairs of individuals (Blouin 2003). However, it is unlikely that animals perceive relatedness on a continuous scale. Instead, they are more likely to distinguish discrete relatedness classes dependent on the social system in which they live. Redfronted lemurs are probably not able to distinguish full sibs from maternal half sibs or paternal half sibs from animals that simply originate from the same group. But they should be able to discriminate individuals that stem from the same group (and are thus likely to be related) from individuals that stem from a different group (and are likely to be unrelated).

In order to account for the animals' inability to perceive relatedness on a continuous scale, we created the following discrete relatedness classes for our analyses: Parent-Offspring (PO), Full Sib (FS), Half Sib (HF), Same Origin (SO; animals that have no shared parent but originate from the same group), and Unrelated (UR). We used relatedness information derived from pedigrees and previous analyses of mitochondrial haplotypes (Wimmer 2000, Wimmer and Kappeler 2002) as well as from our paternity analyses to calculate relatedness coefficients of 90 known PO-pairs, 21 known FS-pairs, 72 known HS-pairs, 37 known SO-pairs and 100 randomly drawn pairs of individuals that were supposed to be unrelated. By this means, we obtained the distribution of relatedness coefficients within each class and, as suggested by Blouin et al. (1996), used the midpoint between two distributions as the cut-off value for the classification of unknown pairs based solely on their relatedness coefficients.

However, due to high variance in marker-based relatedness estimates (van de Castele et al. 2001), a high misclassification rate is to be expected (Blouin et al. 1996). For every r -value that entered our analysis we therefore estimated the probability that it belonged to another distribution than the one it was assigned to by the method of Blouin et al. (1996), using the following procedure: Relatedness coefficients within all classes (except for FS, where sample size was too small) were normally distributed (goodness of fit- χ^2 : PO: $\chi^2= 4.15$, $df= 4$, $p= 0.39$; HS: $\chi^2= 3.82$ $df= 4$, $p= 0.43$; SO: $\chi^2= 3.74$; $df= 1$; $p= 0.06$; UR: $\chi^2= 4.11$, $df= 2$, $p= 0.13$). For every r -value in question we therefore obtained a corresponding z -score for each of the five distributions, hence the cumulative probabilities of this r belonging to each class. Specifically, for r -values classified as "unrelated" we were interested in the probability p that these coefficients belonged to the adjacent (higher) SO-distribution, and for r -values assigned to one of the "related"-classes we were interested in the probability $1-p$ that these coefficients belonged to the (lower) UR-distribution. This way, we effectively restricted our analysis to a comparison of related vs. unrelated animals. We did so because we believe that

this is the most basic distinction that the animals are able to make, and because our sample size precluded a more detailed analysis (see results).

Measures of reproductive skew

More than 20 indices to measure reproductive skew have been proposed in the literature (e.g. Kokko et al. 1999, Nonacs 2003). In order to test the relationship between both male and female group size and skew, our aim was to measure skew in each group for each reproductive season. However, since the number of offspring born in a given season was very small, the calculation of such an index would be highly susceptible to chance effects in male reproductive success (see Kokko et al. 1999). Instead, using the statistics described below, we tested whether the probability that offspring was sired by subordinates was affected by either male or female group size. Our measure of reproductive skew was the relative share of reproduction obtained by *all* subordinates, which is equivalent to the dominant's proportion of reproduction. This measure of skew has been used in some previous studies (e.g. Hannonen and Sundström 2003, Kutsukake and Nunn 2006), and the predictions of most N-person models are based on it (Reeve et al 1998, Reeve and Emlen 2000, but see Johnstone et al. 1999). However, it has the disadvantage that it does not describe the distribution of reproduction *among* subordinates and does therefore not capture all aspects of reproductive skew.

Statistical analyses

We analyzed the relationship between the subordinates' proportion of reproduction and group size using an ordered logistic regression model. This is an extension of standard logistic regression in which the dependent variable is allowed to be ordinally scaled (Long 1997). The dependent variable was the proportion of reproduction attributable to subordinates, the value of which depended on the number of infants born in a given season (range 1-3), yielding the

corresponding discrete values of 0, $\frac{1}{3}$, $\frac{1}{2}$, $\frac{2}{3}$, and 1. Given the rarity of some values ($\frac{1}{3}$, $\frac{2}{3}$) and the fact that not all values ($\frac{1}{3}$, $\frac{1}{2}$, $\frac{2}{3}$) could be obtained every season, we classified the subordinates' reproductive success as "low" if none of the infants of a given season were sired by them, as "medium" if $\frac{1}{3}$, $\frac{1}{2}$, or $\frac{2}{3}$ of the infants were sired by them, and as "high" if all infants were sired by subordinates. Hence, we obtained an ordinaly scaled dependent variable with three classes. The number of females and the number of adult males present during the mating season entered our model as predictor variables. In a first model we did not distinguish between natal males and immigrants because natal males were also observed to copulate with females other than their mothers (e.g. their aunts). In a second model, we excluded natal males from the analysis. Because both models yielded very similar results, only the results of the model including natal males are reported here. The models were calculated using SPSS 12.0.

While significance testing of the overall model as well as of the regression coefficients is straightforward, a more detailed interpretation of the regression coefficients is complicated by the non-linearity of the model and its ordinaly scaled dependent variable. We therefore provide a more detailed description of the model in the appendix and stress that the quantitative impact of a regression coefficient on the dependent variable can not directly be estimated from the magnitude of this coefficient. Instead, equation 2 (see appendix) has to be used to calculate the probability of the dependent variable to be of one of the three classes (e.g. subordinates having "high" reproductive success), given the appearance of the independent variables incorporated in the model.

Finally, in order to test the relationship between reproductive skew and relatedness, we tested for all offspring sired by subordinates whether subordinates related with the dominant were more likely to sire offspring than non-relatives. This analysis was performed using a binomial test in which the expected probability that infants are sired by relatives was derived from the proportion of relatives present in the respective groups.

Results

Paternities

Paternity analyses were carried out for 49 infants born between 1996 and 2004. Paternity could be assigned to 47 of them; in all these cases, all but one male showed at least one heterozygous mismatch with a given mother-offspring dyad. According to the CERVUS Δ -criterion, 45 paternities could be assigned with 98% confidence and two paternities with 95%. In two cases, paternity could not be assigned. Both infants were born in the same group in the same year (F3, see Table 2.2), in which male group-composition was unstable. None of the males present before or after the change in group composition could be assigned paternity; hence, both infants were probably sired by extra-group males. One infant was sired by a natal male (group F4); an older brother of the infant's mother. This group contained no immigrant males during that mating season. A detailed table of all paternities is available in the Appendix.

Of the 47 cases in which paternity could be assigned, dominance relationships between males could be determined in 38 cases. 27 (71%) of these 38 infants were sired by dominants, whereas only 11 (29%) were sired by subordinates. Given the fact that over all mating seasons the number of subordinates was on average 2.57 times higher than the number of dominants, the observed distribution of paternities between both classes of males was significantly different from random mating ($\chi^2 = 34.94$, $df=1$, $p < 0.001$). On an individual level, dominants sired 6.31 times as many offspring per individual and season as did subordinates (Fig. 1.1).

Table 2.1: Group composition, number of offspring born, and subordinates' share of reproduction in five redfronted lemur-groups from 1996 to 2004. Only group-years in which at least one infant survived until capture are shown; only group-years indicated in bold letters entered the analysis of reproductive skew (see notes below).

Group ^a	Year	Number offspring	Number males	Number females	Subordinates share ^b	Subordinates share (class)
A1	1996	2	3	2	$\frac{1}{2}$	medium
A1	1997	2	3	2	0	low
A1	1998	1	4	2	0	low
A1	1999	2	4	2	0	low
A2	2002	1	5	2	0	low
A2	2003	2	5	2	0	low
A2	2004	2	4	2	$\frac{1}{2}$	medium
B1	1996	3	4	3	$\frac{2}{3}$	medium
B1	1997	2	3	3	0	low
B1	1998	2	4	2	0	low
B1	1999	1	4	3	1	high
B2	2001	1	4	2	0	low
B2	2002	3	3	3	0	low
B2	2003	2	3	3	1	high
B2	2004	3	4	3	$\frac{2}{3}$	medium
F1	1997	1	3	2	?	?
F2	1999	2	3	2	0	low
F2	2000	2	4	2	0	low
F2	2001	1	3	2	0	low
F2	2002	1	4	3	1	high
F3	2003	2	?	?	2x EGP ^c	?
F4	2004	1	2	1	?	?
I1	1996	1	?	?	?	?
I1	1997	1	?	?	?	?
J1	1997	1	?	?	?	?
J1	1999	2	4	2	?	?
J2	2001	1	3	2	?	?
J2	2002	1	2	2	?	?
J3	2003	1	2	3	1	high
J3	2004	2	2	2	0	low

^aNumbers indicate tenures of different dominants (or groups of males, if dominance relationships were not known).

^bThe subordinates' share of reproduction could only be determined if dominance relationships could be inferred from behavioral observations. If in a given year the animals were not observed, we assumed that the male that was dominant in the year of observation was also dominant in the year before. In some years, however, information about dominance relationships was too sparse to reliably classify individuals as dominant or subordinate.

^cExtra-group paternity.

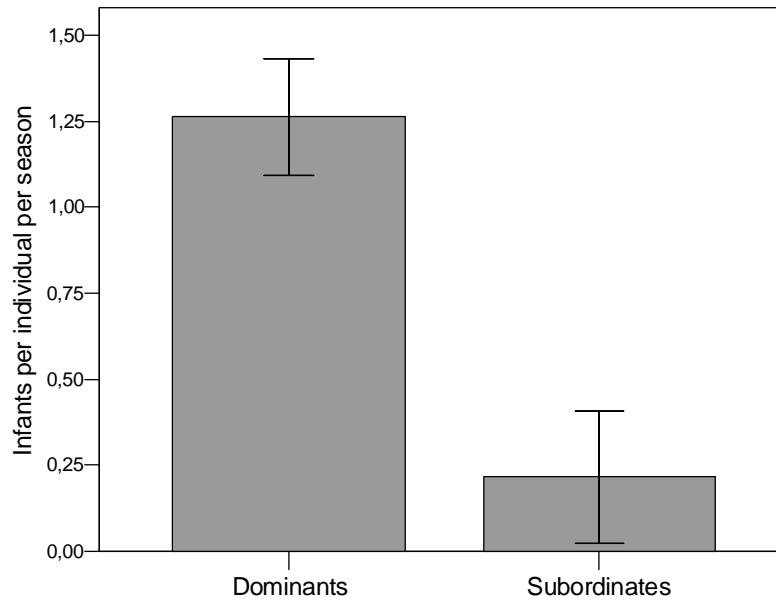


Figure 2.1: Reproductive success of dominants and subordinates: Mean \pm 95% Conf. Interval number of infants sired per season per individual.

Reproductive skew and group size

Table 2.2 shows the number of adult males and females for each group and each year of the study, along with the proportion of offspring sired by subordinates. The overall ordered logit model with both the number of males and the number of females as continuous predictor variables was significant (log likelihood = -8.52, $G = 9.83$, $df = 2$, $p = 0.007$), but only the number of females affected the proportion of offspring sired by subordinates significantly ($\hat{\beta}_f = 3.11$, $W = 7.51$, $df = 1$, $p = 0.006$). Thus, as the number of females increased, subordinates were more likely to sire a larger proportion of offspring. The number of males had no significant effect (Table 2.3). Because the number of males was also not correlated with the number of females ($r_s = -0.2$, $p = 0.4$), multicollinearity among independent variables had presumably no effect on our model.

A more detailed impression of the magnitude that an increase in the number of females had on the subordinates' reproductive success can be gained from equation 2 (see appendix).

Using the parameters derived from the model and setting the number of males at its mean (3.57 for the group years tested in the model), the probabilities of subordinates having low, medium or high reproductive success given various numbers of females can be calculated (Table 2.4). Results indicate that subordinates had virtually no chance of siring offspring if there is only one female in the group. The probability to father offspring remained low as the number of females increased to two (P= 0.11 to sire one, P= 0.04 to sire two infants) but increased substantially as the number of females rose to three. The very high chance of subordinates to father all offspring if the number of females is three (P= 0.46) is approximately what would be expected under random mating.

Table 2.3: Results of the ordered logit model: $\hat{\tau}_1$ and $\hat{\tau}_2$ represent threshold values in the ordinally scaled dependent variable (see appendix), $\hat{\beta}_m$ and $\hat{\beta}_f$ are maximum likelihood estimates of the regression coefficients relating the number of males, and the number of females, respectively, to the proportion of offspring obtained by subordinates.

	Estimate	SE	Wald	df	p	-95% CI (estimate)	+95% CI (estimate)
$\hat{\tau}_1$	7.34	3.92	3.51	1	0.06	-0.34	15.03
$\hat{\tau}_2$	8.86	4.13	4.61	1	0.03	0.77	16.96
$\hat{\beta}_m$	-0.17	0.67	0.06	1	0.8	-1.49	1.15
$\hat{\beta}_f$	3.11	1.13	7.51	1	0.006	0.89	5.33

Table 2.4: Probabilities of subordinates to have low, medium, or high reproductive success given various numbers of females. The number of males is set to its mean (3.57). Probabilities are calculated from the parameters derived from the ordered logit model using equation 2 (appendix).

	$x_f = 1$	$x_f = 2$	$x_f = 3$
Pr (y= "low" \bar{x}_m, x_f)	0.99	0.85	0.20
Pr (y= "medium" \bar{x}_m, x_f)	---	0.11	0.34
Pr (y= "high" \bar{x}_m, x_f)	0.01	0.04	0.46

Allowing for an interaction of the number of males and the number of females did not significantly change the model (log likelihood= -8.49, $G= 0.06$, $df= 1$, $p= 0.81$). The most important conclusion of this result is that the subordinates' reproductive success remained unaffected by the number of males, irrespective of the number of females.

Reproductive skew and relatedness

To test the relationship between reproductive skew and relatedness, we were interested in the relatedness between dominant males and all subordinates present during the corresponding dominant's tenure. Since these males were usually immigrants, their relatedness had to be estimated from relatedness coefficients. Table 2.5 summarizes all relevant dominant/subordinate-pairs along with their corresponding relatedness estimates. For a first classification we assigned all pairs to one of our discrete relatedness classes using the method suggested by Blouin et al. (1996). In addition, we calculated z-scores to obtain an estimate of each coefficient's probability to belong to a different relatedness class. If pairs were classified as unrelated based on the method of Blouin et al., z-scores were calculated for the probability that the relatedness coefficients were drawn from the adjacent, lowest relatedness distribution, the SO-distribution; if pairs were classified as related (irrespective of the class), z-scores were calculated for the probability that the coefficients were drawn from the UR-distribution. In ambiguous cases, where possible, we also used information about the males' haplotypes to reach a final assessment of the relatedness of all relevant dominant/ subordinate-pairs (see footnotes of Table 2.5 for details).

After having classified all subordinates as being either related or unrelated to the corresponding dominant, we identified three of the 11 infants sired by subordinates as being sired by subordinates related with the dominant. The remaining eight infants were fathered by unrelated subordinates. However, during the different mating seasons the number of subordinates not related with the dominant was exactly three times as high as the number of

Table 2.5: Pairwise relatedness estimates for dominant males with all subordinate males present during their tenures.

Group	Male ^a	Estimated r with dominant	Relatedness with dominant ^b	z ^c	p(z) or 1-p(z)	haplotype ^d	Corrected Relatedness ^e
A1	KRK	***	***	***	***	7	***
	<i>Rho</i>	- 0.07	UR	- 1.25	0.11	2	UR
	<i>Zyp</i>	0.07	SO	0.92	0.18	2	UR ^f
	<i>Lem</i>	0.02	UR	- 0.69	0.25	1	UR
	<i>Nig</i>	0	UR	- 0.81	0.21	10	UR
	<i>Vul</i>	-0.26	UR	---	---	1	UR
	<i>Str</i>	0.46	PO/FS	---	---	1	Son
A2	GIG	***	***	***	***	?	***
	<i>Kos</i>	0.73	PO/FS	6.0	<0.001	?	PO/FS
	<i>Bal</i>	0.04	UR	- 0.56	0.29	11	UR
	<i>Tim</i>	0.02	UR	---	---	3	UR
	<i>Cap</i>	-0.07	UR	---	---	1	UR
B1	BAL	***	***	***	***	11	***
	<i>Sin</i>	0.22	HS	2.08	0.02	6	related ^g
	<i>Kom</i>	0.12	SO	1.31	0.1	4	UR ^h
	<i>Sul</i>	0.09	SO	1.08	0.14	10	UR ^h
	<i>Lom</i>	0.1	SO	1.15	0.13	3	UR ^h
	<i>Bor</i>	0.5	PO/FS	---	---	3	Son
	<i>Hon</i>	0.1	SO	1.15	0.13	5	UR ^h
B2	ALO	***	***	***	***	?	***
	<i>Tha</i>	- 0.03	UR	- 1.0	0.16	?	UR
	<i>Obi</i>	- 0.08	UR	- 1.31	0.1	?	UR
	<i>Lao</i>	- 0.12	UR	- 1.56	0.06	?	UR
	<i>But</i>	- 0.08	UR	- 1.31	0.16	?	UR
	<i>Tim</i>	0.06	SO	---	---	3	UR
F2	LAR	***	***	***	***	12	***
	<i>Wes</i>	0.46	PO/FS	3.92	<0.001	11	Son ⁱ
	<i>Key</i>	0.1	SO	1.15	0.13	11	UR ^j
	<i>Bar</i>	- 0.07	UR	---	---	1	UR
	<i>Vin</i>	0.44	PO/FS	---	---	1	Son
J3	CAN	***	***	***	***	?	***
	<i>Kir</i>	0.59	PO/FS	4.92	<0.001	?	PO/FS

^aDominant males in capital letters, subordinates that sired offspring in italic.

^bClassification based on the method of Blouin et al. (1996).

^cCalculation of z-scores see main text. z-scores were not calculated, if true relatedness was known from pedigrees.

^dHaplotypes taken from Wimmer and Kappeler (2002) and Wimmer (2000), therefore not available for all males.

^eReclassification based on pedigree information or on assessments described below.

^fHigh probability that r was drawn from UR-distribution, different haplotype than dominant, therefore probably unrelated.

^gVery low probability that r was drawn from UR-distribution, albeit different haplotype than dominant. Rare case of paternal half sibs with unrelated mothers?

^hDominant male BAL had high relatedness coefficients with all subordinates, probably due to BAL possessing some rare alleles. However, all subordinates had different haplotypes than BAL, thus probably all unrelated.

ⁱVery high r , suggesting either brothers or father/ son, however, different haplotypes. Therefore, Wes probably LARs son.

^jDifferent haplotype than dominant, at the same time highly related with Wes (not shown). Thus, Wes and Key probably brothers, but Key not sired by LAR, therefore unrelated.

relatives. Therefore, under the assumption that all subordinates had equal probabilities of siring offspring, relatedness with the dominant had no significant effect on reproductive success of subordinates (Binomial-test: exact $p= 0.71$). If we used the relatedness classification derived solely by relatedness coefficients, the number of infants fathered by relatives was slightly higher (five), but in this case the number of relatives present during the corresponding mating seasons was also higher (approximately equal to the number of non-relatives). Therefore, in this case as well, the reproductive success of both classes was not different from chance (Binomial-test: exact $p= 0.5$).

Discussion

Redfronted lemurs live in small groups, in which the number of males equals or exceeds the number of females. Although males are mostly unrelated to each other, our study revealed that reproductive success is not equally distributed among them, but instead skewed towards dominants. However, the distribution of reproduction within groups could not be explained by models of reproductive skew theory. First, a subordinate's relatedness to the dominant did not affect its reproductive success. Relatives were neither less likely nor more likely to sire offspring than non-relatives (as predicted by the concession and restraint model, respectively). Note, however, that this result is based on small sample size and should therefore only be viewed as preliminary evidence. Second, the number of males in a group did not affect

reproductive skew. This result clearly contradicts the tug-of-war model and, based on the way skew was measured in this study, the concession model as well. Instead, the number of females in a group best predicted the subordinates' probability of siring offspring, which supports the priority-of-access model (Altmann 1962). A summary of the results in relation to our predictions is provided in Table 2.1.

According to the priority-of-access model, it is not the mere number of females within a group, but the number of synchronously receptive females that predict a subordinate male's prospects to mate. In support of this prediction, Charpentier et al. (2005) found that the probability of dominant male mandrills (*Mandrillus sphinx*) to sire offspring indeed decreased as the number of simultaneously tumescent females increased (but see Engh et al. 2002, Kutsukake and Nunn 2006). In our study, detailed data on female mating synchrony were not available, but, given the highly seasonal reproduction of redfronted lemurs, some degree of estrous overlap between females seems likely (see Ostner and Kappeler 2004). In contrast, in red howler monkeys (*Alouatta seniculus*), which exhibit a similar social organization, but in which reproduction is asynchronous, reproductive skew among males is very high with dominant males fathering all offspring (Pope 1990).

In addition to the number of synchronously receptive females, the priority-of-access model also predicts that a subordinate's rank influences its reproductive success. Detailed data on subordinate rank were not available for all group years; in addition, the low number of infants born per birth-season and the low probability of subordinates to sire offspring precluded a test of this prediction at the reproductive level. For a more complete understanding of the proximate mechanisms underlying the observed pattern of reproductive skew, it may therefore be more promising to test this prediction of the priority-of-access model with data on mating skew.

In accordance with the priority-of-access model, our statistical model estimated that subordinates had roughly zero probability of siring offspring if only one female was present in

the group. This probability remained low if groups contained two females, but markedly increased as the number of females increased to three, reaching a level that would be expected if all males (including the dominant) had equal probabilities of siring offspring. We believe that this estimate is an overestimation by our model, because in three cases where groups comprised three females, only one infant survived until a tissue sample could be taken, and in each case, this infant was sired by a subordinate, resulting in “high” reproductive success of subordinates in the respective group-years. It is unlikely, however, that the infants conceived by the remaining females (but that did not survive) were also sired by subordinates, in which case “medium” reproductive success of subordinates would have been a more realistic classification. This example illustrates the high susceptibility to chance effects of small sample sizes in the study of reproductive skew. This problem is probably relevant whenever studies aim to measure reproductive skew on a year-by-year basis in species with low reproductive rates. The positive relationship between the number of females and the subordinates’ reproductive success, however, remained unchanged by this finding (as confirmed by a “standard” logistic regression, in which the subordinates’ reproductive success was dichotomous instead of ordinally scaled; unpubl. results).

Compared to the priority-of-access model, reproductive skew theory performed rather poorly in explaining variation in male reproductive success in redfronted lemurs. In accordance with our study, most tests of reproductive skew theory previously conducted with vertebrates concluded that dominants usually lack control over the allocation of reproduction (e.g. Clutton-Brock 2001, Williams 2003). Some studies reported that female estrous overlap (Charpentier et al. 2005) or female choice (Engh et al. 2002, Widdig et al. 2004) affected reproductive skew among males, which led the authors to conclude that “limited control” models best account for the observed pattern of the partition of reproduction. However, it remained unclear which *models* these authors mean, because rejection of the concession model does not necessarily mean acceptance of an alternative reproductive skew model, and if

empirical results point to a different direction (e.g. the priority-of-access model), they should not be used to evaluate reproductive skew theory. For example, the finding that a dominant lacks control does not necessarily provide support for the “limited control” models of reproductive skew theory (cf. Kappeler and Schaffler 2008). Moreover, as this term summarizes models as different as the restraint- and the tug-of-war model, we recommend avoiding it at all and sticking more closely to the original models instead of using some oversimplifying dichotomy.

Clearly, however, the concession model failed to provide an explanation for the partition of reproduction among male redfronted lemurs. But as these lemurs are long-lived animals, it could be argued that this partition takes place over several breeding seasons (Zink and Reeve 2005). Although we were not able to formally test this assumption, it is unlikely to hold in our population, however, because variation in the subordinates’ reproductive success was rather high, which is not consistent with the assumption of a dominant allocating some share of reproduction to all of his subordinates. Thus, based on the results of this study, cooperative forces among males are unlikely to provide an explanation for the evolution of small groups with equal sex ratios in this species. Yet, if the same proximate mechanisms seem to determine male reproductive success in both lemurs and in Old World monkeys, this leaves us with the question of why they differ so strikingly in their social organization? The most parsimonious explanation is probably linked to the highly seasonal reproduction of lemurs. Given a sufficient abundance of resources during most of the year, a surplus of males creates almost no costs to a dominant. But if these males contribute to the prolongation of a dominant’s tenure (Ostner and Kappeler 2004), it may benefit the dominant to accept a short phase of high competition during which some reproductive opportunities may even be lost. In another lemur species (*Propithecus verreauxi*), these losses are even less than 10% (Kappeler and Schaffler 2008). Importantly, combining the results of Ostner and Kappeler (2004) and this study, the net number of males seems to increase the dominant’s tenure length but

imposes few costs on its reproductive success. Thus, if one-male groups are not stable, a surplus in the number of males beyond a two-male association first and foremost provides benefits but imposes few costs. This is the case whenever access to fertile females, but not the tug-of-war between males, determines male reproductive success, which, in turn, could explain the even or slightly male-biased adult sex ratios.

At this point it is still premature to completely dismiss reproductive skew theory as an explanatory framework for idiosyncrasies of lemur sociality because by far not all reproductive skew models could be tested by our study. The finding, however, that a variable incorporated in none of these models, namely the number of females in a group, best predicted the apportionment of reproduction among male redfronted lemurs, casts doubt on the applicability of existing reproductive skew theory to this species. This is probably not only the case for redfronted lemurs, but applies to primates in general, as the social organizations of primates strikingly differ from those of the social insects for which most of these models were originally developed. For example, hymenopteran queens usually mate once at the beginning of their life, when sperm of one or several males is stored for later breeding (Thornhill and Alcock 1983, Reeve 1991). Therefore, once an association between queens is formed, the conflict over who lays how many eggs is decided between the queens only. In contrast, in primates the opposite sex also becomes involved in this conflict. Thus, if reproductive skew among male primates is the focus of interest, the role of females is to be considered as well.

The priority of access model accounts for the role of both sexes better than current reproductive skew theory (but see Cant and Reeve 2002), but some recent empirical evidence also pointed towards the importance of the number of males in the distribution of reproduction, hence, supporting the tug-of-war model (Kutsukake and Nunn 2006), or a combination of both the priority of access and the tug-of-war model (Boesch et al. 2006). Thus, as neither model alone seems sufficient to explain the pattern of reproductive skew

among male primates, their synthesis could help to improve our understanding of sociality and reproductive sharing within this taxon. Kutsukake and Nunn (in press) recently proposed such a synthesis by incorporating the number of males into the priority of access model. Their extended priority of access model therefore provides a valuable first step in the development of models that more closely fit the requirements and realities of primate social organizations.

Acknowledgements We thank the Malagasy Ministère de l'Environnement et des Eaux et Forêts, the Département Biologie Animale de l'Université d'Antanannarivo and the Centre de Formation Professionnelle Forestière Morondava for authorising and supporting our long-term research in Kirindy and the late Berthe Rakotosamimanana, Olga Ramilijaona, Daniel Rakotondravony and Joel Ratsirarson for their support. The equipe DPZ at Kirindy, in particular Tiana Andrianjanahary, Mamitiana Razafindrasamba, Jean-Pierre Ratolojanahary, Nielsen Rabarijaona, Rodin Rasoloarison and Léonard Razafimanantsoa as well as Edidier and Enafa from Project Beza Mahafaly made indispensable contributions to gidro capture and monitoring. We are also grateful to Manfred Eberle and Christina Oberdieck for their support in the lab, to Vanessa Mass for useful discussions, as well as to Jörg Schmidt for his suggestions concerning the ordered logit model. Finally, we would like to thank Charles Nunn, Nobuyuki Kutsukake and one anonymous referee for constructive comments on a previous version of the manuscript. Funding was provided by the German Research Council (DFG: Ka 1082/1-3 and Ka 1082/9).

CHAPTER 3:

The utility of reproductive skew theory in the study of male primates – a review

Markus Port & Peter M. Kappeler

In review, *Evolutionary Anthropology*

Introduction

The number of adult males in a primate group is the most variable aspect of primate social organization. The causes for this variation have constituted a long-standing major research focus in primatology (Kappeler 2000b, Kappeler and van Schaik 2002). As a male's reproductive success is mainly limited by the access to females (Trivers 1972, Clutton-Brock and Parker 1992), competition among males should result in the exclusion of rivals from groups of females (Clutton-Brock 1989, Kappeler 1999). Yet, a great number of primate species live in groups with several adult males. To explain this coexistence of males and its consequences, primatologists recently began applying the framework of reproductive skew theory (Hager 2003, Kutsukake and Nunn, in press). This body of theory was developed to examine variation in reproductive skew within and across populations and species, to explain the preconditions for stable associations as well as how reproduction should be distributed therein (Vehrencamp 1983a, b, Keller and Reeve 1994, Johnstone 2000). Here, we summarize the main aspects of this theory, review its application in studies of male primates and identify a number of pitfalls of this approach.

Most of the original reproductive skew models were developed to explain the division of reproduction among queens in small colonies of social insects (Reeve and Ratniecks 1993, Reeve and Keller 2001), but they were quickly extended to female birds and mammals (e.g. McRae 1997, Jamieson 1997, Clutton-Brock et al. 2001), and subsequently also applied to investigate patterns of reproductive skew among males in various species (e.g. Haydock and Koenig 2003, Heg et al. 2006, Dugdale et al. 2008), including primates (see table 3.1). However, most studies of primates found at best equivocal support for the predictions of reproductive skew theory. Even though it has been argued that models of reproductive skew may provide a unifying theory for the evolution of sociality (Keller and Reeve 1994, Johnstone 2000), we believe that the lack of support in primates is due to fundamental

Table 3.1: Summary of studies investigating reproductive skew in male primates. Only the indicated studies were carried out as tests of reproductive skew theory; the remaining studies discussed (parts of) their results in the context of reproductive skew theory.

Species	Major results	Refs
Verreaux's sifakas (<i>Propithecus verreauxi</i>)	Extremely high reproductive skew. Results attributed to tug-of-war model; Perhaps a case of queuing with almost complete control by dominants.	1
Redfronted lemurs (<i>Eulemur fulvus rufus</i>) [Test]	Subordinates more likely to sire offspring as number of females, but not number of males increased. Relatives of dominant not more likely to sire offspring than non-relatives.	2
Moustached tamarins (<i>Saguinus mystax</i>)	High reproductive skew in this cooperatively breeding neotropical primate. High monopolization potential of dominant male due to effective mate-guarding.	3
Rhesus macaques (<i>Macaca mulatta</i>) [Test]	High percentage of extra-group paternities; heterozygosity of MHC-genes best predictor of male reproductive success. Both results taken as evidence for female choice/ 'limited control'.	4
Long-tailed macaques (<i>Macaca fascicularis</i>)	Male rank best predictor of consort time and reproductive success. Lack of complete monopolization despite highly asynchronous reproduction attributed to energy constraints on mate-guarding; possibly indicating tug-of-war.	5
Mandrills (<i>Mandrillus sphinx</i>)	Good fit of observed distributions of mate guarding and paternity to priority-of-access model, but alpha male's monopoly of mate guarding and paternity decreased as number of males increased.	6
Mandrills (<i>Mandrillus sphinx</i>) [Test]	Dominants more likely to sire offspring as number of adult males increased, but less likely as number of simultaneously tumescent females and mean relatedness with subordinates increased	7
Mountain gorillas (<i>Gorilla b. beringei</i>)	Moderate reproductive skew attributed to tug-of-war model	8
Mountain gorillas (<i>Gorilla b. beringei</i>)	Agent based model using demographic parameters from mountain gorilla population. Subordinates should exercise reproductive restraint; queuing better strategy than leaving the group, consistent with queuing model of reproductive skew	9
Chimpanzees (<i>Pan troglodytes</i>)	Distribution of paternities accords with priority-of-access model. Rank good predictor of male's reproductive success, alpha male's share lower when higher number of estrous females, but also lower when higher number of competitors.	10

Meta analysis of mating skew (31 primate species) [Test]	Mating skew decreased as number of males increased, but was not influenced by measures of female reproductive synchrony or pattern of male dispersal (used as proxy of relatedness).	11
Meta analysis of reproductive skew (19 primate species) [Test]	Dominant's share of reproduction decreased as female reproductive synchrony increased, but was less consistently related with number of males. Threat of paternity losses to extra-group males did not affect skew within groups	12

References: 1 Kappeler and Sch affler (2008); 2 Kappeler and Port (2008); 3 Huck (2004) 4 Widdig et al. (2004); 5 Engelhardt et al. (2006); 6 Setchell et al. (2005); 7 Charpentier et al. (2005); 8 Bradley et al. (2005); 9 Robbins and Robins (2005) 10 Boesch et al. (2006); 11 Kutsukake and Nunn (2006); 12 Ostner et al. (in review).

differences in the social organizations and life histories of primates (and other mammals) and the social insects for which most of the early models were developed. It seems therefore indicated to critically review the utility of this theory to the study of male primates. We will do so by first providing a short summary of the main developments within reproductive skew theory, before examining the assumptions underlying the relevant models, as well as the variables predicted to affect skew. Finally, we will consider features of primate social organization and reproductive biology that may play a role in the division of reproduction among males, but which are not sufficiently incorporated into existing reproductive skew theory.

A brief introduction to reproductive skew theory

Reproductive skew theory is commonly divided into two broad categories: *Transactional models* assume that reproductive skew is the outcome of reproductive transactions between dominant and subordinate group members, mediated either by the subordinate's threat to leave the group (concession-based models: Reeve and Ratniecks 1993, Reeve 1998, Kokko and Johnstone 1999, Reeve and Emlen 2000, Zink and Reeve 2005) or by the dominant's

threat to evict the subordinate (the restraint model: Johnstone and Cant 1999a). Transactional models are distinguished from *compromise models*, basically tug-of-war models (Reeve et al. 1998, Reeve and Shen 2006, Nonacs 2007, but see Cant 1998, Johnstone and Cant 1999b), which assume that reproductive skew is the outcome of a costly struggle over reproduction between group members. In two-person associations reproductive skew can be described as a continuum, in which the subordinate's share can be qualitatively categorized according to the model in question (Fig. 1.1): In concession-based models dominants are thought to control reproduction. Therefore, they are predicted to concede just enough reproduction to subordinates to entice them to stay, hence, subordinates will receive their minimum share required to make the association more profitable than leaving the group. In contrast, according to the restraint model, subordinates are assumed to control reproduction, and are therefore predicted to reap off the maximum share that the dominant is just willing to tolerate before it pays the latter to evict the subordinate (but see Buston et al. 2007 for recent modeling). Finally, in tug-of-war models, the subordinate's share lies either to the left of the subordinate's minimum (the 'original' tug-of-war model: Reeve et al. 1998), between the optima of dominant and subordinate, i.e. within the 'window of selfishness' (Reeve 2000; the bordered tug-of-war [BTOW]: Reeve and Shen 2006), or is not restricted by the requirements of either dominant or subordinate (Nonacs's [2007] escalating tug-of-war). For a more detailed description of reproductive skew theory we refer to the excellent reviews by Johnstone (2000) and Magrath et al. (2004), and for more recent discussion regarding tug-of-war models to Reeve and Shen (2006), as well as to Nonacs (2006, 2007).

Despite attempts to synthesize the mainstream models (Johnstone 2000, Reeve and Shen 2006, Buston et al. 2007), research in reproductive skew theory has remained oriented towards the aforementioned dichotomy. It is further noteworthy that apart from this common classification the term '*limited control models*' is sometimes used to refer to models in which the dominant lacks control over the allocation of reproduction (Widdig et al. 2004, Engelhardt

et al. 2006, Ostner et al., in review). However, this term appears to be misleading as it summarizes models as different as restraint and tug-of-war models, as well as concepts not related to reproductive skew theory (see below). We therefore suggest avoiding this term and sticking more closely to the original models instead of using some oversimplifying dichotomy.

When to apply reproductive skew theory? Assumptions underlying the models

Every optimality model is built upon a set of assumptions which describe the situation and ‘goals’ of the model organisms (Vehrencamp 1983a). Every test of a model should ideally be preceded by a careful evaluation of its assumptions. In practice, this is not always possible. However, the predictions of a model can only be met if its assumptions are not violated. If they are, any test of the model becomes meaningless.

Subordinates contribute to group productivity

Most transactional models assume that dominants profit from the presence of subordinates, usually in the form of increased group productivity, i.e. increased egg-output or number of surviving offspring. Whereas in many taxa it is feasible to check this assumption (e.g. Queller et al. 2000, Haydock and Koenig 2003, Langer et al. 2004), its inspection is hampered in primates due to their low reproductive rates, and, where possible, requires an analysis of survival probabilities rather than offspring production. This is necessary, however, as dominants can generally only be expected to give reproductive concessions if they profit from the association with subordinates. On the other hand, primates are relatively long-lived animals, and their fitness is not only determined by their immediate reproductive output, but also by their prospects for future reproduction. By incorporating survival probability as an

additional component of fitness in reproductive skew theory, queuing models revealed that groups can be stable without the subordinates' contribution to group productivity, and that dominants even accept slightly detrimental effects on current reproduction if the subordinate's presence increases their probability to keep their breeding position in the future (Kokko and Johnstone 1999). However, it must be recognized that in such a situation the 'classic' concession model and its predictions do not necessarily apply. Instead, complete skew (as possibly realized in Verreaux' sifakas, Kappeler and Schaffler 2008) can be the model's solution. Thus, any test of reproductive skew models in primates should be preceded by an analysis of whether and how subordinate males benefit the dominant, and the appropriate models should be chosen accordingly.

The dominant controls reproduction

Most previous studies on reproductive skew in male primates concluded that dominant males lack control over the division of reproduction within their groups (see table 3.1). This conclusion was usually derived from a careful examination of the observed pattern of skew in relation to reproductive skew models. However, in many primate species the dominant's lack of control may be evident without a test of reproductive skew models, e.g., in cases where the dominant is constraint in its ability to mate-guard fertile females (see below) and/ or females are regularly observed to engage in sneak copulations with subordinate males.

The constraints which dominant male primates face in controlling reproduction can best be illustrated through a comparison with the queens of eusocial insects for which the concession model was originally developed (see Reeve and Ratniecks 1993): Hymenopteran queens usually mate at the beginning of their life cycle and store sperm of one or several males for later breeding (Thornhill and Alcock 1983, Reeve 1991), but once an association is formed, the question who lays how many eggs is decided only between the queens. In this context, it is reasonable to assume that dominant queens exert control over the allocation of

reproduction, because they may destroy any eggs laid by subordinates, in particular as they are able to discriminate their own eggs from those of other queens (Röseler 1991). Females in some mammalian species are also able to exert control over the reproduction of subordinates, either by suppression of their reproductive physiology (French 1997, Faulkes and Bennett 2001, Young et al. 2006), or by infanticide (Clutton-Brock et al. 1998, Saltzmann et al. 2008). However, this is unlikely to be the case in males (where selective infanticide is usually hampered by paternity uncertainties).

But even in cases in which males are able to exercise some control over access to females, concessions are unlikely to be evolutionary stable: Dominants may exhibit some behavioral tolerance towards subordinates (Duffy et al. 2007), or subordinates may refrain to a certain degree from matings, but as paternity is determined inside the female's reproductive tract they can never be 'sure' about the outcome of their (behavioral) strategy. Kokko (2003) analyzed the evolutionary stability of the concession model under such circumstances and concluded that if subordinates lack the ability to accurately assess the value of reproductive benefits dominants may concede to them, the latter are selected to act increasingly selfishly by offering increasingly less concessions, which will ultimately lead to the breakdown of group stability. Kokko did not explicitly examine the restraint model, but we suggest that if the dominant is unable to accurately monitor restraint by the subordinate, the latter will be selected to cheat, in which case the dominant will ultimately do better evicting it.

It is evident from these reflections that the concession model (and possibly the restraint model) does not apply to the study of reproductive skew in male primates. However, the conclusion that a dominant lacks control is not necessarily the confirmation of the compromise branch of reproductive skew theory or any so-called 'limited control' model. It rather uncovers the violation of an assumption and defines the set of models that are left to explain the observed skew, i.e. the models which do not assume dominant control. Having identified these models, strict tests of their predictions can be performed.

What can we measure? Variables incorporated in reproductive skew models

Reproductive skew

Ironically, one of the most challenging tasks in testing reproductive skew theory in primates is to measure reproductive skew. Several indices have been proposed in the literature (reviewed in Kokko et al. 1999, Nonacs 2003), but their use in tests of reproductive skew theory is problematic: Indices of reproductive skew are usually sensitive to group size (i.e., the number of competitors), as well as to the number of group benefits to be divided (e.g., paternities or matings) (for a discussion see Tsuji and Tsuji 1998, Tsuji and Kasuya 2001, Nonacs 2003). Thus, in any comparison of reproductive skew between groups, different index-values may be obtained merely as a consequence of different group sizes or productivities (number of infants born), even though the relative share or reproduction obtained by dominants can be quite similar. Therefore, if the focus of interest lies on the share of reproduction dominants lose or concede to subordinates in groups of different size, the dominant's share of reproduction may in many cases be a more convenient proxy for skew. This is particularly true as the predictions of most models in relation to larger associations are also based on the dominant's share (Reeve et al. 1998, Reeve and Emlen 2000). On the other hand, it needs to be stressed that the dominant's share does not capture the whole dimension of reproductive skew. It merely describes the amount of reproduction monopolized by the dominant, but, in larger groups, does not consider the division of reproduction *among* subordinates. Thus, if the focus of interest lies on judging whether an observed distribution of reproduction can be attributed to chance (e.g., as a consequence of random mating) or not, the use of an appropriate index is highly recommended (see Kokko et al. 1999, Nonacs 2003).

A further problem in the measurement of reproductive skew in primates is linked to their low reproductive rates. In particular if skew is measured within one breeding season,

researchers may face the problem that the number of offspring to be divided is very low. In such cases, instead of summarizing the level of inequality by any measure, a probabilistic approach, such as the probability of either dominant or subordinate(s) to sire offspring could be a worthwhile alternative (see Charpentier et al. 2005, Kappeler and Port 2008).

Students of primates and other mammals are often able to measure skew not only at the reproductive but also at the behavioral level, i.e., as mating skew (Cant 2000, Kutsukake and Nunn 2006). However, an important distinction has to be made between mating skew and reproductive skew: While at the reproductive level, any share gained by a subordinate directly goes at the expense of the dominant (i.e., the game is zero-sum), matings by a subordinate do not per se diminish the dominant's mating frequency (hence, the game is *not* zero-sum). At this point it is again worthwhile to consider the 'female case', because reproductive sharing among females is also not necessarily zero-sum, in particular in mammals, in which females are constrained regarding the magnitude of their reproductive output. Thus, offspring produced by a subordinate does not directly go at the expense of the dominant, although secondary fitness costs are likely to arise due to resource competition between the females' offspring. In contrast, due to their higher reproductive potential, reproductive sharing among males always is zero-sum at the reproductive level, but not the behavioral (mating-) level. This reflection not only illustrates another difference in the division of reproduction between males and females, but also suggests that it could be worthwhile to pay more attention to mating skew in the study of male primates. However, to what extent the partitioning of reproduction based on mating concessions can be evolutionary stable is a question to be answered by theoreticians.

Variables predicted to affect reproductive skew

According to reproductive skew models, several demographic and environmental variables are predicted to affect the division of reproduction (Table 1.2). In the next section, we briefly

review these variables and discuss their relevance, but also the challenges to measure them in the study of primates. A key feature of any test of reproductive skew models is to look for a relationship between one or more of these variables and the level of skew, assuming that all other variables remain constant. If tests are conducted within a single population, constancy of some variables across groups (e.g., constraints on solitary breeding) seems to be a realistic assumption, but it is less likely to hold if such tests are conducted across populations or species.

Relatedness

Due to the ease of measuring relatedness based on genetic markers (Queller and Goodnight 1989) relatedness has become the most widely analyzed variable in reproductive skew studies (e.g. Queller et al. 2000, Haydock and Koenig 2003, Charpentier et al. 2005). Marker-based relatedness coefficients are continuous measures of the proportion of alleles identical by descent that are shared between pairs of individuals (Blouin 2003). Consequently, most studies treated relatedness coefficients as a continuous variable, usually in correlation analyses with a (continuous) measure of skew (e.g. Reeve et al. 2000, Hannonen and Sundström 2003). We do not attempt to judge the perceptive abilities of insects (see Gamboa 2004), but we believe that it is unlikely that primates and other mammals perceive relatedness on a continuous scale, but instead are more likely to distinguish discrete relatedness classes depending on the social system in which they live.

Whereas maternal relatedness is likely to be perceived via familiarity, the perception of paternal relatedness is in many cases less feasible and depends on male tenure and reproductive skew (Widdig 2007). As we can not expect animals to adjust the level of concessions (or restraint) according to a distinction which they are probably not able to make, we suggest that tests of relatedness should focus on discrete classes that animals are likely to perceive (see also Field et al. 1998, Magrath et al. 2004, Kappeler and Port 2008). In addition,

correlation or regression analyses in larger associations are usually forced to test the overall level of skew against the mean relatedness within groups (e.g., Charpentier et al. 2005), but skew adjustments are more likely to be based on dyadic relatedness (Johnstone et al. 1999). Thus, in this respect as well, a comparison of the reproductive success of several discrete classes seems to be more promising.

Constraints on solitary breeding

According to transactional skew theory, a subordinate's prospects of successful breeding outside the dominant's territory ultimately determine the minimum fitness it requires to make staying the more favorable option than leaving the group. However, these constraints on independent breeding are difficult to estimate in primates, and would ideally require an experimental setting (Langer et al. 2004, Heg et al. 2006). Furthermore, it is questionable whether a simple definition of 'outside' accurately defines a subordinate primate's breeding options (Kokko and Lundberg 2001). As in most species, all suitable habitat is likely to be saturated to some degree, the predominant option of a dispersing subordinate is not the formation of a new group but joining another group with supposedly better breeding conditions or trying to take over a group from an established resident. Leaving this latter option out of consideration, the bidding game (Reeve 1998) describes this situation more appropriately than the classic concession model. Accordingly, subordinates are given the option of choosing among several dominants and consequently associate with the one offering the highest reproductive bet. This case of partner choice resembles the concept of biological markets (Noë and Hammerstein 1994, see also Johnstone 2000), and clearly introduces a higher level of flexibility into reproductive skew theory. However, it is still based on the (probably unrealistic) concept of reproductive concessions. It would therefore be interesting to consider a scenario, in which dominants compete for the help of subordinates but at the same time lack control over the division of reproduction within their groups.

In addition, primates are relatively long-lived animals and from a subordinate's point of view, their fitness may not predominantly depend on immediate reproductive opportunities, but also on future fitness benefits. Therefore, if survival prospects are sufficiently enhanced, subordinates may benefit from staying, regardless of ecological constraints (Kokko et al. 2001, Kokko and Ekman 2002), even in the absence of own reproduction (Kokko and Johnstone 1999), but eventually depending on the length of the breeding queue (Cant and English 2006). Most of these models focus on the evolution of group size instead of the reproductive skew therein, but they may provide the framework necessary to extend reproductive skew theory to the complex life histories of primates. To more accurately fit these life history traits, a subordinate's options should not simply be defined by an environmentally determined constant (Kokko and Lundberg 2001), but should also consider survival prospects and competition associated with different dispersal strategies, including both queuing and take-over. Queuing models may in many cases be suitable to describe reproductive division and group formation in primates, but their test is challenging (e.g., Kappeler and Schädler 2008): Although they release researchers from the task of estimating an abstractly defined environmental constant, they require empirical measures equally hard to obtain, such as survival probabilities, take-over rates, and habitat saturation.

The subordinate's contribution to group productivity

Transactional models of reproductive skew predict that the subordinate's share of reproduction depends on its contribution to group productivity, according to the concession model, for instance, it is predicted to decrease with increasing subordinate contribution. This prediction seems to be counterintuitive at first glance, but it results from the fact that a lower relative share of an absolutely higher group output is required to meet the expected subordinate's fitness by leaving the group. Hence, the dominant is assumed to behave strictly despotically by pushing down the subordinate's fitness to its minimum, regardless of its

contribution to group productivity. On a theoretical level, however, such a form of strict despotism is to be expected only if the dominant has perfect information about the subordinate's prospects of independent breeding. This reflection illustrates a further possible flaw in the concession model. In contrast, imperfect information would strengthen the subordinate's position and eventually open up the model to the possibility of 'negotiation'.

However, this discussion is probably bound to remain academic in the study of primates because fine-scaled adjustments of skew, both from the dominant's and from the subordinate's perspective, are hardly feasible due to the low reproductive rates of primates. Whereas it is technically possible to precisely adjust the evolutionary stable level of skew over a large brood size (as is common in insects or fish), this may in many cases be impossible if only a handful of infants are to be divided (see also Magrath et al 2004). For instance, if the number of males exceeds the number of offspring, it is technically impossible to yield the minimum staying incentive to each subordinate. For the same reasons, it is in many cases impossible that all subordinates exercise their reproductive restraint without sacrificing their minimum fitness requirements. Thus, constraints on the partitioning of reproduction cast doubt on the evolutionary stability of transactional models in primates, at least if skew is to be adjusted within one breeding bout and if the reproductive level is considered.

It is possible that reproductive allocation takes place over a prolonged period of time (see Zink and Reeve 2005), but for such a type of reproductive sharing to be stable uncertainties associated with future reproduction need to be overcome. If the allocation of reproduction is extended over several breeding seasons, this requires book-keeping by the dominant and, if the number of subordinates is large relative to the dominant's tenure, does still not completely solve the problems associated with the concession of full offspring 'units'. It could therefore be worthwhile to explore whether selection in primates might act at the

level of mating concessions (i.e. the probability to sire offspring) rather than at the reproductive level.

Group size

With the exception of the tug-of-war model, most original models of reproductive skew theory focused on associations consisting of one dominant and only one subordinate. In an extension of the concession model to arbitrary group sizes, Reeve and Emlen (2000) found that the classic model can be generalized to larger groups, but their analysis was restricted to subordinates who are equally related both among themselves and to the dominant (see Johnstone et al. 1999 for problems arising from this assumption). But apart from the issue of generalization, group size provides reproductive skew theory with a notable opportunity, namely as a variable predicting skew. Although this has been recognized by empiricists (e.g. Field et al. 1998, Kutsukake and Nunn 2006), theoreticians have so far made little effort to elaborate on this possible relationship.

In the tug-of-war model, the dominant's share of reproduction is predicted to decrease as the number of subordinates increases (Reeve et al. 1998), and the same is true in the concession model in the case of non-related subordinates (Reeve and Emlen 2000). More generally, if a staying incentive is required by subordinates and if dominants are willing to concede it (i.e., under the conditions a group is predicted to be stable), the dominant's relative share will always decrease in the concession model as long as group productivity is a decelerating function of group size and irrespective of relatedness or other parameters (see appendix C). We emphasize that the dominant's absolute share (i.e., its fitness) can nevertheless increase as long as the productivity benefit provided by an additional subordinate compensates for the incentive it needs.

Fighting ability

Reeve and Ratniecks (1993) extended their concession model to the case where a dominant offers peace incentives to the subordinate in order to induce it to cooperate peacefully instead of risking a fight for the dominant position, resulting in the prediction that the magnitude of the peace incentive increases as the subordinate's fighting ability increases (Table 2). Similar predictions are derived in other reproductive skew models, e.g., in the tug-of-war model or in the restraint model (via the cost of evicting the subordinate), and also in models developed outside the framework of reproductive skew theory, such as the priority-of-access model (Altmann 1962, Alberts et al. 2003). Thus, even though fighting ability is a variable relatively easy to measure in primates by means of body mass or rank, it hardly sheds light on the mechanisms underlying the division of reproduction because all models predict the same qualitative relationship between fighting ability and skew.

Tug-of-war models and the role of females in primate social organization

Throughout the previous sections, we listed a number of reasons why we believe that transactional skew theory does not apply to the study of male primates. One of these reasons was that due to the bisexual associations of primates, it is highly unlikely that dominant males control the division of reproduction. But even if transactional models can be excluded, reproductive skew theory still provides an alternative framework: Tug-of-war models (Reeve et al. 1998, Nonacs 2007) do not assume the allocation of reproduction by either group member and are not affected by the aforementioned concerns. But are they really suitable to describe the division of reproduction among male primates? When researchers concluded that 'limited control' models best describe the patterns of reproductive skew (Widdig et al. 2004, Charpentier et al. 2005, Setchell et al. 2005, Engelhardt et al. 2006, Ostner et al., in review), they may have implicitly referred to tug-of-war models. These authors also listed several

factors that led them to their conclusion, such as the number of males in the group (Charpentier et al. 2005, Setchell et al. 2005, Kutsukake and Nunn 2006), temporal overlap of female receptive periods (Charpentier et al. 2005, Ostner et al., in review), or female choice (Widdig et al. 2004). Strictly speaking, however, only the number of males, but none of the other factors is predicted to affect skew according to tug-of-war models (but see Kutsukake and Nunn, in press). The solutions of these models result from the amount of energy allocated by males to their tug-of-war over reproduction, but we emphasize that the number of receptive females or their partner preferences do not directly play a role in these models.

Thus far, only two models (Cant and Reeve 2002, Hamilton and Heg 2007) have been developed to investigate reproductive sharing in bi-sexual groups and to explicitly predict reproductive skew among males. However, both models focus on associations of two males and only one female. But apart from having their own reproductive interests (as assumed by both models), females also constitute a resource males have to compete for; a fact that has yet completely been neglected by existing reproductive skew theory, and that is much better accounted for by the priority-of-access model (Altmann 1962, Alberts et al. 2003), a verbal model which has found wide application and some support among primates and other mammals (e.g. Say et al. 2001, Alberts et al. 2003, Setchell et al. 2005, Boesch et al. 2006, Kappeler and Port 2008). Accordingly, dominant males are able to monopolize access to females as long as there is only one female receptive at a time, but as the number of simultaneously receptive females increases, lower ranking males get to mate as well. Authors referring to ‘limited control’ models may have also had this model in mind, but we stress that it is built upon a very different theoretical background, hence, it is not a reproductive skew model in the strict sense. However, the classification ‘limited control’ is correct insofar as recent empirical evidence suggests that neither tug-of-war models nor the priority-of-access model alone sufficiently explain the distribution of reproduction among male primates (Bradley et al. 2005, Kutsukake and Nunn 2006, Engelhardt et al. 2006). Therefore,

Kutsukake and Nunn (in press) recently suggested to synthesize both models and to incorporate the number of males in an extension of the priority-of-access model. Their suggestion provides a valuable first step towards the understanding of the factors shaping reproductive skew among male primates, yet it is so far a verbal extension, and a theoretical model incorporating both the number of males and the number of simultaneously receptive females is still lacking.

Moreover, the priority-of-access model is only suitable to describe the proximate patterns of skew, but not the ultimate reasons for group formation and stability. Even (or especially) if the dominant lacks control over the division of reproduction, the presence of subordinates in a group requires an explanation. Just like in transactional skew theory, such an explanation would have to consider both the dominant's and the subordinates' perspective: The dominant's perspective would have to involve an evaluation of the costs and benefits associated with subordinates, and the subordinates' perspective would have to consider their prospects of staying in a group versus dispersing (and possibly queuing elsewhere). From this perspective, the priority-of-access model shares some features with queuing models of reproductive skew theory (Kokko and Johnstone 1999, Kokko et al. 2001, Cant and English 2006). As these models may best acknowledge the social organization and life histories of primates, and given the success of the priority-of-access model in the study of primates (Alberts et al. 2003, Setchell et al. 2005, Boesch et al. 2006), we encourage any attempt to synthesize these still very different approaches. Such a synthesis could eventually estimate the fitness of a given position in the queue from the reproductive success expected for that rank under the priority-of-access assumption. Combining the probability to reach a certain rank with the expected fitness at this rank could improve our understanding of stable group sizes, dispersal decisions, and eventually reproductive sharing among male primates.

Conclusions

We provided a brief review of current reproductive skew models and high-lighted some problems in their application to male primates. We stressed the need to carefully evaluate the assumptions underlying the models and to choose the appropriate models accordingly. But we also discussed life history traits and aspects of primate social organization that are not in agreement with, or not even included in, current reproductive skew theory. Due to their low reproductive rates, primates are limited in their opportunities to divide reproduction adequately to meet the requirements of transactional models. Due to sperm competition, males lack the ability to accurately assess the value of reproductive benefits that are being exchanged, which calls into question the evolutionary stability of these models. These concerns most likely exclude transactional skew theory as an explanatory basis for the evolution of multi-male associations in primates, which is consistent with empirical data (see table 3.1). However, tug-of-war models do not describe the scenario underlying the division of reproduction among male primates either, because just like most transactional models, they consider unisexual associations in which the number of females or their receptive overlap are not incorporated as predictors affecting the level of skew. In most cases, the priority-of-access model better than tug-of-war models predicts pattern of male reproductive skew, but some variation is likely to be accounted for by tug-of-war models as well. Thus, a synthesis of these models could help to improve our understanding of the (proximate) patterns of reproductive skew among male primates.

The evolution of group-living and the associated division of reproduction have always been among the most fundamental problems in behavioral ecology (Hamilton 1964, Alexander 1974, Emlen 1995). The ideas underlying reproductive skew theory were therefore not new, but the development of these models formalized existing ideas and concepts and allowed for more precise tests of hypotheses. However, skew models could not live up to the hopes of a unifying theory because they did not account for crucial aspects of vertebrate

behavior and biology (Clutton-Brock 1998, Magrath et al. 2004), and they could so far also not greatly enhance our understanding of reproductive skew in primates. The aim of this review was to identify and to discuss several shortcomings of the existing models. This way, we do not call for an end of reproductive skew research in primates, but for the development of theoretical models which are more suitable to describe reproductive skew and the evolution of sociality in this taxon.

Acknowledgments

We thank Hanna Kokko for her constructive comments on an earlier version of this article. Financial support was granted by the German Research Council (Ka 1082/9).

CHAPTER 4:

Market effects offset the reciprocation of grooming in free-ranging redfronted lemurs (*Eulemur fulvus rufus*)

Markus Port, Dagmar Clough and Peter M. Kappeler

Abstract

Social grooming is a commonly observed affiliative behaviour in primates. Grooming has been suggested to represent a service in a biological marketplace, exchanged either for grooming or for other social commodities or services. Accordingly, grooming is predicted to be approximately reciprocated within a dyad when no other services are being exchanged, but it should be more asymmetrical if partners have different quantities of other services to offer. We analysed 412 grooming bouts observed in four groups of free-ranging redfronted lemurs to test this prediction. Grooming in this species seems to take place in a highly reciprocal manner because partners usually alternate in the roles of groomer and gromee within a grooming bout. However, within dyads there were asymmetries in the duration of grooming given and received. In both sexes, more grooming was directed from low-ranking towards high-ranking individuals than *vice versa*, and in males this asymmetry became more pronounced as the number of subordinates per group increased. Grooming in bisexual dyads was generally skewed in favour of males, but patterns of grooming between the sexes were less clear than within the sexes. In addition, aggression occurred at high frequencies between classes of individuals that were characterized by nonreciprocal grooming, suggesting that grooming may serve as a means to reduce aggression in dyads with a high potential for conflicts. Taken together, our results indicate that a strict reciprocation of grooming can be offset by power differentials between partners, where grooming appears to be traded by subordinates in exchange for the tolerance of dominants.

Keywords aggression, biological market, *Eulemur fulvus rufus*, grooming, reciprocal altruism, redfronted lemur

Introduction

Cleaning another individual's fur (allogrooming, hereafter grooming) constitutes a common form of affiliative behaviour in primates (Sparks 1967; Goosen 1987), and has also been observed in a number of other mammalian species (e.g. impalas, *Aepicerops melampus*: Hart & Hart 1992; wood mice, *Apodemus sylvaticus*: Stopka & Macdonald 1999; meerkats, *Suricata suricata*: Kutsukake & Clutton-Brock 2006). Grooming is beneficial for the recipient as dirt and ectoparasites are removed (Hutchins & Barash 1976; Barton 1985); yet this behaviour is likely to be associated with costs for the individual performing it, for example, in the form of decreased vigilance (Maestriperi 1993; Mooring & Hart 1995) or decreased time available for other activities (Dunbar 1992; Henzi et al. 1997). It has therefore been suggested that grooming represents a form of altruism (Seyfarth and Cheney 1984).

Across primate species, many grooming interactions take place among relatives (Schino 2001), where altruism can be attributed to kin selection (Hamilton 1964). However, grooming also occurs among nonkin. Altruism among nonkin is assumed to be favoured by natural selection if the altruist later receives a significant benefit from the recipient of the initial altruistic act (reciprocal altruism: Trivers 1971). It has therefore been suggested that grooming within pairs of individuals should be reciprocated over time, or exchanged for other beneficial acts (Hemelrijk & Ek 1991). Because the first theoretical model to predict grooming relationships in primates considered grooming to be the means by which individuals maintain social bonds (Seyfarth 1977), much emphasis concerning an interchange with other forms of altruism has traditionally been laid on support in conflicts (e.g. Seyfarth & Cheney 1984; Hemelrijk 1994). However, whereas several studies revealed that grooming itself is usually reciprocated (e.g. Hemelrijk & Ek 1991; Leinfelder et al. 2001; Ventura et al. 2006), evidence suggesting an exchange for coalitionary support is rare (Henzi & Barrett 1999; but see Schino 2007 for a recent meta-analysis).

Henzi & Barrett (1999) extended the traditional reciprocal altruism approach of social grooming by attributing a more flexible function to this behaviour. Following biological market theory (Noë & Hammerstein 1995), they proposed that grooming represents a service in a biological marketplace, which can be exchanged for grooming (reciprocated) or for other services or commodities in the market. Accordingly, grooming is predicted to be reciprocated in dyads where no other services are being exchanged, but to be asymmetrical if it is traded as a commodity to obtain a different service from the partner. Coalitionary support represents only one possible service; further services or commodities are, for instance, tolerance (Kapsalis & Berman 1996; Kutsukake & Clutton-Brock 2006), food (de Waal 1997) or matings (Gumert 2007a). Thus, individuals can be divided into different trader classes, depending on what they have to offer. The concept of trader classes has found wide application within the biological market framework, not only in the study of grooming behaviour or other forms of intraspecific cooperation, but also in interspecific mutualism (Noë 2001). The exchange of commodities between members of different trader classes is predicted to be influenced by supply and demand in the market, such that individuals offering a rare commodity are expected to increase their demands from trading partners. Asymmetries in supply and demand usually result from different numbers of individuals within classes, for example from different numbers of males and receptive females (Gumert 2007a) or cleaner fish and their clients (Soares et al. 2008), but may also be the consequence of the seasonal appearance of commodities, such as contested food resources (Barrett et al. 2002).

The market model has successfully been applied to explain grooming patterns in both Old World monkeys (e.g. Barrett et al. 1999; Henzi & Barrett 2002; Gumert 2007a, b) and New World monkeys (Lazaro-Perea et al. 2004), but to our knowledge this is the first study to apply it to a group-living strepsirrhine, the redfronted lemur. Like all strepsirrhines, these lemurs use a tooth-comb in the lower jaw for grooming, which, in a sequence of upward movements of the head, is stroked through the partner's fur (Barton 1987). After having

performed such an episode of upward movements, the former groomer is then typically groomed by its partner. Afterwards, the roles are reversed again, and several episodes are exchanged this way before one partner terminates the grooming bout. Therefore, redfronted lemurs provide an excellent opportunity to study grooming in a species in which it is always reciprocated within a bout. Hence, our study is not subject to a problem frequently encountered by previous studies, which is the absence of immediate reciprocation (*cf.* Barrett & Henzi 2001, Schino et al. 2003).

We examined grooming reciprocity in redfronted lemurs by analysing both the number of grooming episodes of each partner and the total duration of grooming exchanged within a bout. As we expected market forces to offset grooming reciprocity in some dyads, we did not predict grooming to be completely reciprocal. Instead, we derived the following predictions:

- (1) Among females, we predicted more grooming to be directed from low-ranking females towards high-ranking ones than *vice versa*. This prediction is based on the observation that the former are often targets of aggression by the latter (Vick and Pereira 1989), often leading to evictions from their groups (see Methods). Hence, we predicted grooming to be used by low-ranking females mainly as a currency exchanged for the tolerance of high-ranking females.
- (2) Although Henzi & Barrett (1999) originally developed their market model to explain grooming relationships among females, they later argued that grooming is likely to be exchanged for mating opportunities between the sexes (Barrett & Henzi 2001; see also Gumert 2007a). As females are generally the limiting resource for males (Trivers 1972), we predicted grooming to be asymmetric in male-female dyads, with more grooming directed from males to females than *vice versa*. In addition, we predicted the level of asymmetry to increase when the value of the commodity exchanged was particularly high, that is, during the mating season.

(3) Only a few studies have examined grooming relationships among males (Hemelrijk & Ek 1991), possibly because grooming is relatively rare among males in most species (Goosen 1987; van Hooff & van Schaik 1994). Redfronted lemurs represent an ideal study species to examine this behaviour in males, not only because it is common (Kappeler 1993a), but also because males in this species can effectively be divided into two trader classes owing to their unique social system (Ostner & Kappeler 1999): in each group one male is clearly dominant over all other males, whereas subordinates cannot be ranked further in a linear hierarchy. We therefore predicted grooming to be reciprocal between subordinates (which can exchange grooming only for itself), whereas more grooming should be directed from subordinates to dominants in exchange for the latter's tolerance, in particular with regard to group membership, but possibly also in the context of mating (see Duffy et al. 2007). In addition, according to the law of supply and demand, we expected dominants to increase their demands if they were given the opportunity to pay off competing subordinates. As a consequence, the level of asymmetry in dominant-subordinate dyads should increase with increasing number of subordinates, in particular as the threat of eviction should also be more pronounced as group size increases.

Finally, we were interested in whether patterns of aggression in redfronted lemurs correspond to patterns of grooming. We therefore analysed aggressive interactions between individuals assigned to the same trader classes as defined in our analysis of grooming.

Methods

Redfronted Lemurs

Redfronted lemurs are 2 kg, sexually monomorphic, cathemeral Malagasy primates living in groups of 5-16 individuals with an even or male-biased sex ratio (Overdorff et al. 1999, Ostner & Kappeler 2004). Groups usually consist of a core of related females, whereas males

migrate, sometimes delaying dispersal beyond sexual maturity (Wimmer & Kappeler 2002). Male dispersal is not usually associated with prior aggression, but male eviction can occasionally occur in unusually large groups (Vick & Pereira 1989; M. Port, pers. observation). Females, in contrast, are more frequently evicted as group size increases, typically by members of their own sex. One male per group, the so-called 'central male' (Ostner & Kappeler 1999), clearly dominates all other males, whereas the remaining subordinates cannot be ranked along a linear hierarchy. Central males interact affiliatively with females more frequently than subordinate males (Ostner & Kappeler 1999) and father the majority of offspring born in their groups (Kappeler & Port 2008). Reproduction in redfronted lemurs is highly seasonal. Mating behaviour is largely restricted to a few weeks in May-June (Ostner and Kappeler 2004), during which a female's fertile period is limited to 1-3 days (Boskoff 1978).

Study Population and Data Collection

The study was conducted in Kirindy Forest, a dry deciduous forest located within a forestry concession operated by the Centre Formation Professionnelle Forestière (CFPF), approximately 60 km northeast of Morondava, western Madagascar. For a detailed description of the forest see Sorg et al. (2003). Study animals belonged to one of four groups (A, B, F, J) living in a 60 ha study area (CS7), which is part of the German Primate Centre field site. As part of an ongoing long-term study, all individuals were habituated to human presence and have been regularly captured and marked with unique nylon collars (weight 10 g, equivalent to 0.005-0.01% (mean= 0.007%) of an animal's body weight) or radiocollars (Biotrack, Wareham, Dorset, UK weight: 32 g, equivalent to 0.015-0.021% (mean= 0.016%) of an animal's body weight). Animals were equipped with the collars during brief anaesthesia (induced by applying 0.2 ml GMII; Rensing 1999) after blow-pipe darting by an experienced Malagasy technician. Individuals are returned to their social groups within 1 h and we have

not observed any injuries or adverse effects on behaviour as a result of the capture procedure or the collars. Our research was approved by the Malagasy Ministère de l'Environnement et des Eaux et Forêts.

Behavioural observations were conducted from March to September 2005 and from April to July in 2006 and 2007. Group compositions in the respective years are presented in Table 4.1. Focal animal observations were carried out on all adult individuals (> 2.5 years) in an alternating order for 3.5 h in the morning (between 0700 and 1100 hours) and 3 h in the afternoon (between 1400 and 1730 hours). For each focal animal, both periods together (i.e. 6.5 h of observation) made up one statistical day. We recorded all affiliative and agonistic interactions of the focal animal following Pereira & Kappeler (1997), noting who initiated and who terminated the interaction. As spontaneous submission (i.e. agonistic interactions in which one animal showed submissive behaviour without prior aggression by its partner) was very rare (see also Kappeler 1993b), this form of agonism was not included in our analysis. Thus, for the present study, an agonistic interaction always consisted of either an aggressive act (cuff, bite, etc.) or signal (certain vocalizations), and was defined as decided if the target showed submissive behaviour, and as not decided if the target showed no perceptible signs of submission. In addition, during focal animal observations one of us (M.P.) recorded grooming behaviour using a handheld computer (PsionWorkabout, Psion PLC, London, U.K.). A grooming bout was defined to begin when one animal initiated the first grooming episode, and to end if either one animal left, or the partners remained in social contact, but did not exchange grooming for at least 5 min. This way, a total of 412 complete grooming bouts between either adult or subadult (1-2.5 years) individuals were recorded. Although subadults were not included in the focal animal observations, they were included in the analysis of grooming reciprocity because the threat of group eviction is most pronounced for this class of individuals. We did not include infants in this analysis, however, as we did not expect infants to possess fully developed grooming skills.

Table 4.1. Group composition of the four study groups

Group	Year	Adult males	Subadult males	Adult females	Subadult females	Infants
A	2005	3	0	2	2	1
	2006	3	0	2	1	0
	2007	4	0	2	1	2
B	2005	6	1	2	0	2
	2006	4	1	3	0	0
	2007	4	1	3	0	3
F	2005	2	0	1	2	1
	2006	2	0	3	0	0
	2007	3	0	3	0	0
J	2005	3	1	2	0	1
	2006	4	0	2	0	0
	2007	2	0	2	0	1

Adults: > 2.5 years; Subadults: 1 – 2.5 years; Infants: < 1 year. If group compositions changed within years, compositions that prevailed over most of the time are presented.

Data Analyses

Each of the 412 grooming bouts was analysed separately, using the Observer software package (Noldus Information Technology, Wageningen, The Netherlands). This way, we obtained both the number of grooming episodes of two interacting animals within a bout as well as the precise duration of grooming exchanged between the partners. In 6% of episodes (accounting for 9% of the total time spent grooming) both partners groomed simultaneously. Because these episodes represented a relatively small fraction of overall grooming and as they were not relevant for assessing the level of reciprocity, they were excluded from further analyses, which then proceeded at two levels.

First, to determine whether grooming was reciprocated within bouts, we were interested in whether the animals performed and received the same number of episodes, and whether both partners groomed for approximately the same total duration. We used linear mixed-effects models, in which the performance of an animal (i.e. either episodes or duration) was regressed against the performance of its partner. For each bout, the performances of the grooming partners were randomly assigned as the response and explanatory variable in the

regression model (i.e. grooming received and grooming given). Thus, each dyad, which represents the independent unit in studies of social behaviour, could yield two ‘clusters’ (cf. Manson et al. 2004): bouts in which the performance of animal A was assigned the response and the performance of animal B the explanatory variable, and *vice versa*. To avoid pseudoreplication of clusters containing the same animals, ‘cluster’ (as defined above) was included in the model as a random effect. The model was fitted using maximum likelihood estimation. To allow for a direct comparison between the number of episodes exchanged and the duration of grooming, both measures were standardized using z-transformation. Owing to a right-tailed skew in the distribution of grooming durations, we used a Box-Cox transformation (Box & Cox 1964) to achieve normality before the data were standardized. For further comparisons, we report the deviance ($D = -2 \text{ Log Likelihood}$ of the fitted model) of each model.

Second, to test whether power asymmetries between partners are responsible for grooming asymmetries within dyads, we calculated an index of reciprocity R (Payne et al. 2003; see Löttker et al. 2007 for a similar approach):

$$R = \frac{(G_A - G_B)}{(G_A + G_B)},$$

in which G_A is the amount (episodes or time) animal A, and G_B the amount animal B spent grooming. The R index can range from -1 to 1, where a value of 0 represents complete reciprocity, negative values indicate that individual A received more grooming than it gave, and positive values indicate that individual B received more grooming than it gave. Note that, in contrast to the regression analysis, partners within a dyad were assigned the roles of A or B according to the trader classes to which they belonged to in the lemurs’ grooming market rather than randomly (Table 4.2).

We calculated R indices for all available grooming bouts, but as most dyads were observed in more than one bout, means across bouts were calculated within each dyad. We

Table 4.2. Categories to which dyads of redfronted lemurs were assigned according to their membership to different “trader” classes, and the number of dyads obtained in each category

Category	Role A	Role B	Dyads
CI	Central males	Immigrant subordinates	6
CN	Central males	Natal subordinates	9
SS	Subordinates ^a	Subordinates ^a	14
FC	Females	Central males	13
FRP	Females	Reproductive Subordinates ^b	22
FRL	Females	Relatives ^c	9
HH	High ranking females ^a	High ranking females ^a	4
HL	High ranking females	Low ranking females	6

^aNo further distinctions were made within these classes; roles were assigned randomly but consistently within dyads.

^bSubordinates which were not or distantly related with the female they groomed with; generally immigrants, but also a few natal subordinates.

^cSubordinates which were closely related (brothers, sons) with the female they groomed with. Relatedness for all dyads relevant to this study could be derived from pedigrees.

then assigned dyads to one of eight categories, according to the different trader classes to which each animal belonged (Table 4.2). We defined three categories of male-male dyads, three categories of male-female dyads and two categories of female-female dyads. In male-male dyads, males were classified as either central or subordinate male (see Introduction), and subordinates were further divided into natal subordinates and immigrants. In male-female dyads, males were also classified as central and subordinate male, but in this case subordinates were further divided into reproductive males (i.e. subordinates not or distantly related to their female dyadic partner) and relatives (i.e. close relatives of their female dyadic partner). Note that the classification of subordinates within male-male dyads does not match the classification of subordinates within male-female dyads. Although immigrants could be classified as reproductive males without exception, some subordinates were observed mating with females of their natal groups (e.g. their aunts or cousins); these natal males were therefore classified as reproductive males in male-female dyads. Finally, females were ranked based on decided agonistic interactions (see above): however, each group contained

two females that almost never interacted agonistically and which we therefore both classified as high ranking. If groups consisted of more than two females, the remaining females regularly received aggression from, and showed submission to, either one or both of the high ranking females and could therefore be classified as low ranking. A dyad of low ranking females existed only once (group A, 2005), but as these individuals were not included in the focal animal observations during that time, no grooming was observed in this dyad.

We defined grooming to be nonreciprocal if the 95% confidence intervals of the mean R values within categories did not include 0; in addition, we tested for differences between categories using analysis of variance (ANOVA). In the case of grooming between females, we used nonparametric statistics because of the low number of available dyads.

Frequencies of aggressive interactions across categories were compared using chi-square tests; by calculating the expected frequencies we took into account both the different numbers of dyads within categories and the different observation times of individuals within dyads. The analysis of aggressive interactions did not include the mating season, as the dominance relationships between males can temporarily collapse during this time (Ostner & Kappeler 1999). Statistical analyses were performed with R version 2.5.1 (R Foundation for Statistical Computing, Vienna, Austria). All tests were two tailed.

Results

Grooming Reciprocity within Bouts

The linear mixed-effects model for the number of episodes exchanged within a bout revealed a highly significant relationship between the number of episodes redfronted lemurs spent grooming their partners and the number of episodes they were groomed by them ($F_{1,254} = 2228.94$, $p < 0.001$). The overall slope of the regression was positive, and close to 1 ($b \pm SE = 0.91 \pm 0.02$), that is, close to the predicted relationship if grooming was completely reciprocal (Fig. 4.1a). The same analysis performed on the total duration of grooming exchanged within

a bout revealed an apparently similar result. The amount of time the animals spent grooming their partners was significantly related to the amount of time they received grooming ($F_{1,254} = 261.56$, $p < 0.001$); hence, grooming was time matched within bouts. However, in contrast to the analysis of episodes, the slope of the regression strongly deviated from perfect reciprocity ($b \pm SE = 0.62 \pm 0.04$, Fig. 4.1b), indicating that factors other than strict reciprocity affected the distribution of grooming duration within a bout. Moreover, the deviance of the model containing grooming durations was much higher ($D = 950.35$) than the deviance of the model containing episodes ($D = 385.37$).

In summary, grooming appeared to be highly reciprocal with regard to an exchange of episodes, but reciprocity was much weaker for the time both partners spent grooming. We therefore restricted the following analyses of possible market effects on the symmetry of grooming to the analysis of grooming durations.

Grooming Reciprocity and Trader Classes

Male-male dyads

Grooming among male redfronted lemurs was only reciprocal in dyads consisting of subordinates (mean $R \pm 95\%$ confidence interval = 0.03 ± 0.1), whereas central males received more grooming from both immigrants and natal males than they gave in return (mean $R \pm 95\%$ confidence interval = -0.26 ± 0.21 and -0.29 ± 0.13 , respectively, Fig. 4.2). The symmetry of grooming was different across the three male categories (one-way ANOVA: $F_{2,26} = 11.14$, $p < 0.001$), where dyads consisting of subordinates differed significantly from both other categories (Scheffé Test: SS versus CI: $p = 0.009$, SS versus CN: $p = 0.001$; see table 4.2 for categories). Moreover, throughout the study 10 subordinates were observed grooming with both a central male and another subordinate. These subordinates spent

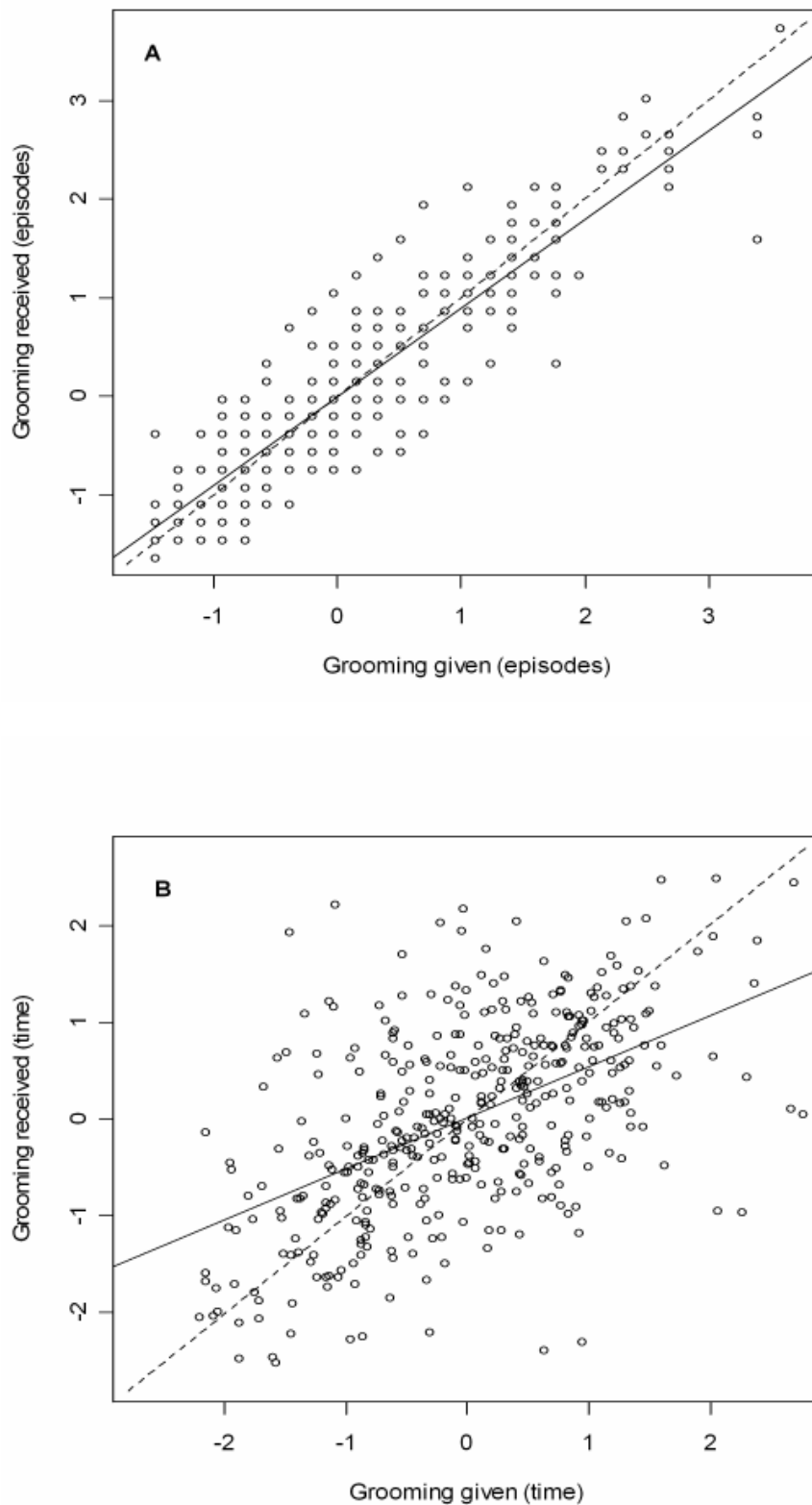


Figure 4.1. Grooming reciprocity within bouts. Panel A shows the number of episodes each animal performed grooming within a bout, panel B the total grooming durations. The solid lines indicates the estimated slope of the regression, the dashed lines represent the line of complete reciprocity. Both measures are standardized (z-transformed), grooming durations were Box-Cox transformed before standardization.

on average more time grooming the central male (mean $R \pm 95\%$ confidence interval = -0.29 ± 0.14) than they spent grooming the subordinate (mean $R \pm 95\%$ confidence interval = -0.06 ± 0.13). This difference was statistically significant (Paired t test: $t_9 = -2.54$, $p = 0.03$).

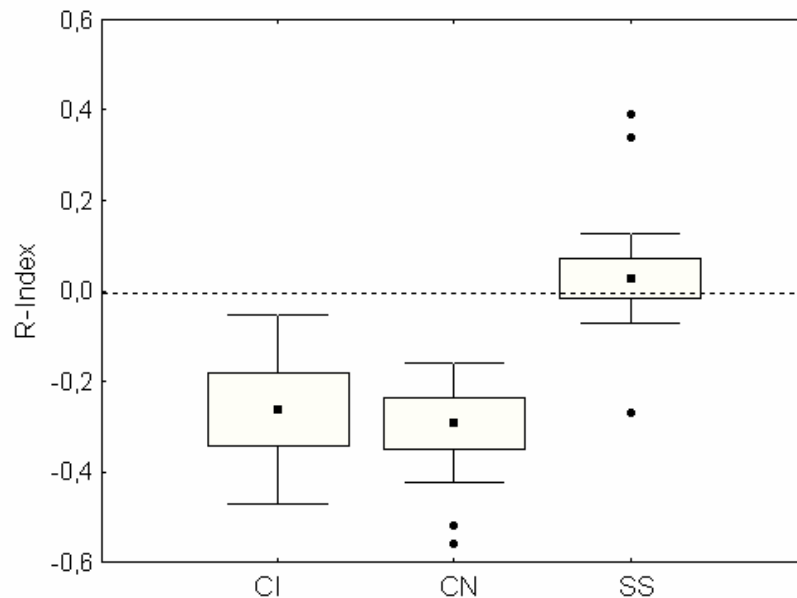


Figure 4.2. Mean \pm SE (boxes) R-indices within the three male categories. Whiskers indicate the 95% confidence interval of the means, outliers are given as dots. The dashed line indicates complete reciprocity. CI= dyads consisting of central males and immigrants, CN= dyads consisting of central males and natal males, SS= dyads consisting of subordinates only.

Because no difference in grooming reciprocity was found between dyads consisting of central males and immigrants and dyads consisting of central males and natal males (Scheffé Test: CI versus CN: $p = 0.95$), we pooled the data from both categories and analysed whether the level of reciprocity changed as a function of male group size. Data were split into different study periods (years) if male group composition changed between years. We found a negative correlation between the level of reciprocity and the number of subordinates ($r_{14} = -0.67$, $p = 0.005$), indicating that central males received most grooming from subordinates when the number of competing subordinates was highest. One dyad entered the analysis twice: the

central male of group B was observed grooming with the same subordinate in 2005 and in 2006. Removing either data point from the correlation did not alter the results, however.

Aggressive interactions outside the mating season occurred at a rate of 0.43, 0.16 and 0.21 events per statistical day between central males and immigrants, central males and natal males, and among subordinates, respectively. Central males initiated all agonistic interactions with both immigrants and natal males, and won 55% of encounters ($N = 53$) with immigrants and 94% of encounters ($N = 16$) with natal males. The remaining conflicts were undecided; generally central males displayed aggressive behaviour towards subordinates but the latter showed no perceptible reaction. In no case did a subordinate win an agonistic interaction with the central male. The frequencies of aggression were not equally distributed across the three male categories ($\chi^2_2 = 37.36$, $p < 0.001$). Central males directed significantly more aggression towards immigrants ($\chi^2_1 = 23.29$, $p < 0.001$), whereas aggression was less frequent than expected among subordinates ($\chi^2_1 = 14.02$, $p < 0.001$).

Female-Male Dyads

Opposite to the direction expected under the grooming for sex scenario, females groomed both central males and reproductive subordinates longer than *vice versa* (Fig. 4.3). The level of asymmetry was strongest in the central male category (mean $R \pm 95\%$ confidence interval = 0.3 ± 0.12), but grooming was also slightly biased in favour of males in the reproductive male category (mean $R \pm 95\%$ confidence interval = 0.11 ± 0.1). In contrast, grooming was reciprocal between females and males that were closely related to them (mean $R \pm 95\%$ confidence interval = 0.03 ± 0.1). However, the level of symmetry did not differ significantly between categories (one-way ANOVA: $F_{2,41} = 1.74$, $p = 0.19$). To check for the possibility that the direction of grooming was reversed during the mating season, we performed a repeated measures ANOVA for the subset of dyads ($N = 14$) with both central and reproductive males for which repeated measures during and outside the mating season were available. Male class

was included in the model as the between-subject factor. We did not find any significant effect in this model (season: $F_{1,12} = 0.22$, $p = 0.65$; season*category: $F_{1,12} = 0.66$, $p = 0.43$), indicating that neither central males nor reproductive males increased their grooming effort during the mating season.

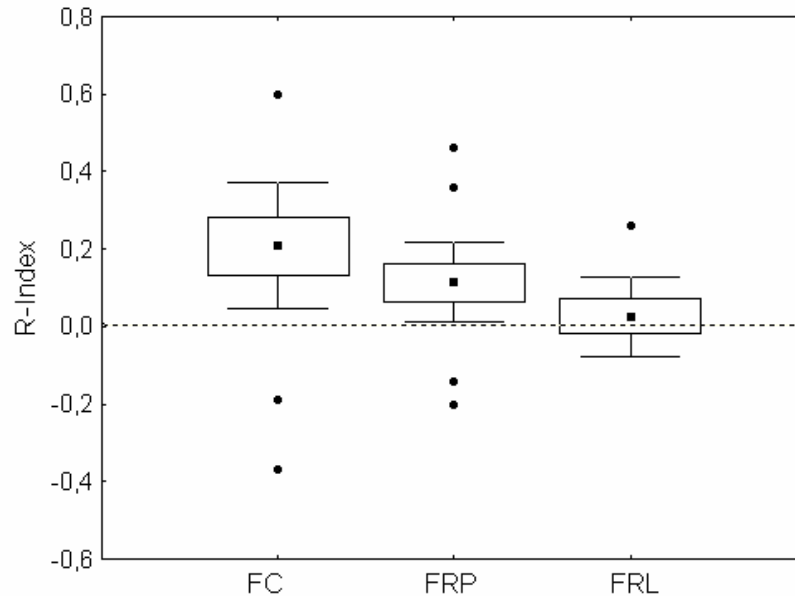


Figure 4.3. Mean \pm SE (boxes) R-indices within the three female/male categories. Whiskers indicate the 95% confidence interval of the means, outliers are given as dots. The dashed line indicates complete reciprocity. FC= dyads consisting of females and central males, FRP= dyads consisting of females and reproductive males, FRL= dyads consisting of females and males with which they are closely related.

Conflicts between females and males occurred at a rate of 0.2, 0.36 and 0.1 events per statistical day with central males, reproductive males and relatives, respectively. Aggression was generally initiated by males, who also won the vast majority of encounters. Females showed submission to central males in 92% ($N = 64$), to reproductive males in 71% ($N = 74$), and to relatives in 74% ($N = 23$) of encounters. Females won agonistic interactions with males in 8% of encounters with reproductive males, and in 4% of encounters with relatives, but they were never observed winning a conflict against a central male. Aggression was not equally

distributed across the three female-male categories ($\chi^2_2 = 11.96$, $p = 0.002$), but only central males and females interacted aggressively more often than expected ($\chi^2_1 = 8.0$, $p = 0.005$).

Female-female dyads

In dyads of high-ranking females, both partners spent approximately the same amount of time grooming each other. Within the category of high-ranking females R indices ranged from 0.12 to -0.15 (median = 0). In contrast, a very high asymmetry of grooming was found in dyads consisting of high- and low-ranking females: R indices within this category ranged from -0.23 to -0.58 (median = -0.41), indicating that low-ranking females groomed higher-ranking females longer than *vice versa*. The level of symmetry was significantly different between the two categories (Mann-Whitney U test: $U = 0$, $N_1 = 4$, $N_2 = 6$, $p = 0.01$, Fig. 4.4). The bias in favour of high-ranking females in dyads consisting of high- and low-ranking females represents the strongest asymmetry in grooming observed across all eight categories.

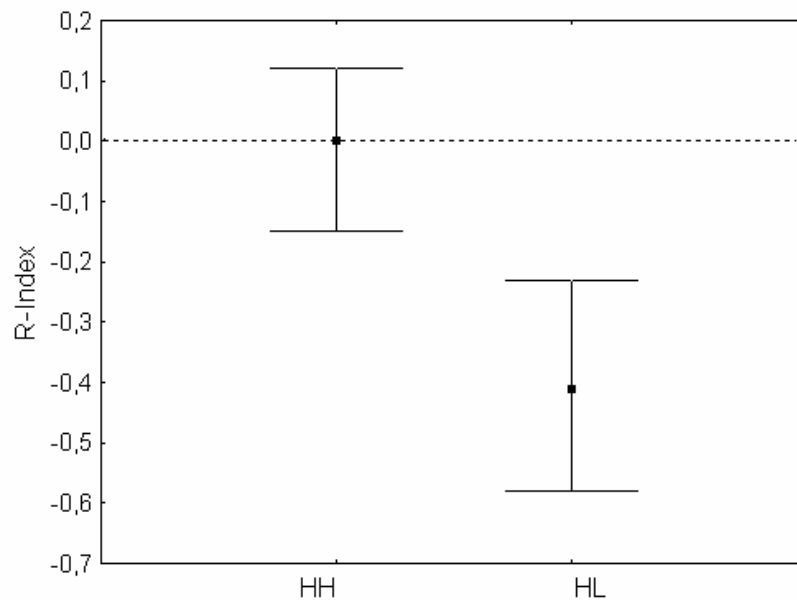


Figure 4.4. Medians of R-Indices within the two female categories. Whiskers indicate the overall data range (min-max). The dashed line represents the line of complete reciprocity. HH= Dyads consisting of high-ranking females, HL= Dyads consisting of high- and low-ranking females.

Agonistic interactions between high-ranking females occurred at a very low rate. In 923 h of focal animal observations we could only observe four such conflicts. In contrast, aggression between high- and low-ranking females occurred at the highest rate observed across categories (0.66 encounters per statistical day). Consequently, the frequencies of aggression differed significantly between the two female categories ($\chi^2_1 = 59.48$, $p < 0.001$). Except for two cases, aggression was always initiated by high-ranking females, who also won the majority (86%, $N = 58$) of conflicts with low-ranking females.

Discussion

Grooming and Social Power

Our analyses revealed that grooming between redfronted lemurs was highly reciprocal if the exchange of roles between partners within a grooming bout was considered, but that reciprocity was less pronounced with respect to the total duration that members of a dyad spent grooming each other. Instead, power differentials between grooming partners belonging to different trader classes in a biological marketplace seem to offset the strict reciprocation of grooming in some dyads. As predicted, grooming was reciprocal in dyads of animals belonging to the same trader class, namely among subordinate males and among high-ranking females, which had no other services or commodities but grooming to offer each other. In contrast, in both sexes, grooming was directed up the social hierarchy, that is, more grooming was given by low-ranking individuals towards high-ranking ones than *vice versa*. These patterns of grooming are comparable to results obtained in a number of studies on Old World monkeys (e.g. Barrett et al. 2002, Schino et al 2003, Ventura et al. 2006, but see Leinfelder et al. 2001) and a cooperatively breeding carnivore, the meerkat (Kutsukake & Clutton-Brock 2006). In redfronted lemurs, low-ranking females, the individuals most threatened by eviction from their groups, gave the largest amount of grooming relative to what they received. Similar results were obtained in meerkats (Kutsukake & Clutton-Brock

2006), suggesting that in both species subordinates exchange grooming for the tolerance of dominants.

The patterns of agonistic interactions between different classes of individuals corresponded to the patterns of grooming in that a pronounced level of grooming asymmetry was associated with high rates of agonism. A notable exception was found in males: central males directed significantly more aggression than expected towards immigrants, but not towards natal males, even though the level of grooming asymmetry did not differ between the two subordinate classes. In contrast, the patterns of grooming *between* the sexes were in accordance with the aforementioned trend: adult males were generally dominant over females, directed more aggression towards females than *vice versa*, and also received more grooming from females than they gave in return. Moreover, in the female-male category in which grooming was most asymmetric, namely in dyads with central males, the frequencies of aggression were also higher than expected. However, even though more grooming was directed by females towards males, its mean duration was not significantly different between the three female-male categories. We cannot therefore unequivocally explain the functional significance of grooming between the sexes, but as grooming in dyads of females and males unrelated to them was consistently skewed in favour of the latter, both across dyads and over time, we can reject the prediction that males trade grooming for future mating opportunities. Given the fact that males won most agonistic interactions with females, it is possible, but remains to be examined in more detail, that females may trade grooming for access to resources.

A positive relationship between grooming and the level of aggression was also found in chacma baboons, *Papio cynocephalus* (Barrett et al. 2002), Japanese macaques, *Macaca fuscata* (Schino et al. 2005) and meerkats (Kutsukake & Clutton-Brock 2006). It could be argued that it appears to be maladaptive that individuals directing more grooming to others are 'rewarded' with higher levels of aggression. Such an argument, however, would imply a

causal relationship between aggression and grooming, with higher levels of grooming resulting in reduced aggression, but causality in this relationship could also be the other way around: aggression could result in a higher investment in grooming by subordinates to appease potential aggressors (Silk 1982, Schino et al. 2005). A clear distinction between the two processes becomes difficult as they are likely to operate simultaneously (Schino et al. 2005). Neither relationship would weaken the assumption that grooming is exchanged for the tolerance of higher-ranking individuals, but the adaptive significance of this behaviour can hardly be estimated without a baseline rate of aggression (i.e. the level of aggression in the absence of grooming). The fact, however, that in three primate species and one social carnivore grooming was found to be more reciprocal when aggression was low, but asymmetrical when aggression was common, together with the tension-reducing function of this behaviour (Schino et al. 1988, Aureli et al. 1999) strengthens the suggestion that it serves as a means to reduce aggression in dyads with a high potential for conflicts.

Alternative Explanations

The first theoretical model to examine grooming relationships in primates (Seyfarth 1977) already predicted grooming to be skewed in favour of dominants, hence basically in the direction observed in our study. It could therefore be asked whether the concept of biological markets adds something new to the explanation of patterns of grooming in redfronted lemurs. According to Seyfarth's (1977) model, an unequal distribution of grooming among group members results from the assumptions that the time available for grooming is limited and that, therefore, access to high-ranking grooming partners is restricted. Both assumptions do not seem to be met in redfronted lemurs, however, because these cathemeral animals spend considerable amounts of time resting, with ample opportunities for grooming. Moreover, at least among females, it does not seem that low-rankers are excluded from access to high-rankers: low-ranking females were observed grooming with high-ranking females as often as

high-ranking females groomed among themselves (unpublished data), yet the symmetry of grooming was very different between these categories. Similar results were obtained for chacma baboons (Henzi et al. 2003).

On the other hand, the mere finding that grooming is directed up the social hierarchy does not necessarily provide support for a biological market. To provide more conclusive evidence, it needs to be shown that commodities are exchanged and/ or that the outcome of an exchange is affected by the availability of traders or commodities in the market. For instance, Henzi & Barrett (2002) and Gumert (2007b) showed that newborn infants may serve as ‘commodities’ in a grooming market and that their mothers obtained grooming from other females for permission to handle the infants. As a further example, as the supply of cleaners in a cleaner fish market increased, individual fish provided a better service to their clients (Soares et al. 2008). A very similar effect was found among the males in our study: subordinates increased their investment in grooming the dominant as the number of competitors increased, presumably because they became more vulnerable to eviction. Thus, market forces seem to affect the exchange of grooming in redfronted lemurs beyond the mere effect of dominance.

To our knowledge, our study is the first to investigate grooming in a primate in which the exchange of grooming is divided into several small parcels. A very similar form of grooming in impalas has been considered one of the ‘classic’ examples of reciprocal altruism (Hart & Hart 1992; but see Connor 1995a, b), and has been assigned to its predominant model, the tit-for-tat strategy (Axelrod & Hamilton 1981). Looking merely at the number of grooming episodes exchanged within a bout indeed gives the impression of high reciprocity and a tit-for-tat like exchange. However, a closer examination of the grooming durations revealed that, in contrast to impalas, strict reciprocation can be offset by power differentials between individuals. Such power differentials are a common element of many primate societies, probably distinguish redfronted lemurs from impalas, and may thus be responsible

for the lower degree of reciprocity in this species. Moreover, reciprocity is not hindered by the fact that redfronted lemurs cannot accurately assess the values of the benefits exchanged (Stevens & Hauser 2004), because reciprocation of grooming occurs in some dyads, and if it does not occur, both individuals firmly distribute grooming according to their standing in the marketplace.

Conclusions

In summary, even though grooming between redfronted lemurs takes place in an apparently highly reciprocal manner, and the prerequisites for reciprocal altruism are likely to be met (see Stevens & Hauser 2004), reciprocal altruism cannot explain all dimensions of this behaviour. Instead, as predicted by the biological market approach (Henzi & Barrett 1999), some degree of time matching occurred, but market effects accounted for the break-up of strict reciprocity. However, to dismiss reciprocal altruism completely as an explanation for the exchange of grooming in redfronted lemurs, one must show that grooming is not reciprocated on a larger timescale (functional reciprocation versus immediate reciprocation, Schino et al. 2003). As we focused on the exchange of grooming within bouts, our data are not sufficient to rule out this possibility completely.

Our study is the first to carry out a formal test of the biological market approach of social grooming in a group-living strepsirrhine primate. We could show that this behaviour serves a social function in redfronted lemurs by providing evidence of market effects in this species. Because, unlike in anthropoid primates, grooming in lemurs is *always* reciprocal, but may differ in the *degree* of reciprocity, these animals represent an ideal model system to investigate further the biological market approach of grooming in primates. Experimental studies, in particular, would provide researchers with the opportunity to manipulate power differentials between individuals, for example by provisioning food resources that can or

cannot be monopolized by dominants, which should translate into shifts in grooming reciprocity.

Acknowledgements We thank the Malagasy Ministère de l'Environnement et des Eaux et Forêts, the Département Biologie Animale de l'Université d'Antananarivo and the Centre de Formation Professionnelle Forestière de Morondava for authorizing and supporting our research in Kirindy. We are also grateful to Jean-Pierre Ratolojanahary, Janna Etz, Fabian Nürnberger, Lantonirina Ratovonjanahary, Jessica Schäckermann, Annette Schneider and Friederike Scholz for their contributions to data collection. Finally, thank Peter Henzi and an anonymous referee for their constructive comments on the paper. Funding was provided by the German Research Council (DFG: Ka 1082/9).

GENERAL DISCUSSION

Redfronted lemurs live in small groups with even or male-biased adult sex ratios. This group composition is unusual among primates and other mammals in that socioecological models predict that small groups of females should be monopolized by a single male (Emlen and Oring 1977, Clutton-Brock 1989). However, this pattern of group composition is predominant among gregarious lemurs (Kappeler 2000a) and has not yet been explained in a satisfactory manner. The major aim of this thesis was to use models of reproductive skew to examine whether selection could have favoured an increased level of tolerance among male redfronted lemurs, ultimately explaining the coexistence of several males associated with small groups of females. In addition, using biological market theory, I examined elements of the social structure within groups of redfronted lemurs to further illuminate the relationships among the males in this species.

Major findings: Reproductive concessions as a route to group-living?

The results presented in Chapter 2 revealed that although male redfronted lemurs are generally not related to the females in their groups, reproduction is not equally distributed but skewed towards dominants, who fathered 71% of the offspring analysed in our study. The distribution of paternities was used to test predictions derived from the three most prominent models of reproductive skew theory, the concession, the restraint, and the tug-of-war model. However, none of the predictions of these models could be confirmed by our analyses: First, subordinates related to the dominant were neither less likely nor were they more likely to sire offspring than non-relatives, as predicted by the concession and the restraint model, respectively. Second, the number of subordinates present in a group did not affect the dominant's share of reproduction, as predicted by both the concession and the tug-of-war

model. Finally, as a third piece of evidence against the concession model we found a high variation in reproductive success among subordinates which is inconsistent with the assumption of a dominant conceding equal shares of reproduction to each of its subordinates. Thus, based on these results, it seems unlikely that dominant male redfronted lemurs give reproductive concessions to subordinates as an incentive to remain in the group.

The results presented in Chapter 4 add further evidence to this suggestion because dominant males directed relatively high levels of aggression towards immigrant males, the class of subordinates they compete with most intensely for the fertilization of females. Moreover, grooming between dominants and subordinates (irrespective of their class) was asymmetric, in that subordinates directed more grooming towards dominants than *vice versa*. In accordance with previous studies on grooming behaviour in primates and other mammals (Barrett et al. 2002, Schino et al. 2005, Kutsukake and Clutton-Brock 2006), we interpreted this asymmetry in the way that grooming is used by subordinates as a social service to appease dominants and to possibly prevent being evicted from their groups. This latter suggestion was supported by the finding that subordinates increased their effort in grooming the dominant as the number of subordinates in a group, and presumably each subordinate's risk of eviction, increased. Thus, subordinates seem to exchange grooming for the dominant's tolerance, possibly to be allowed to remain in the group. Although the exchange of benefits takes place at different levels, the patterns of grooming observed among male redfronted lemurs are more consistent with the restraint approach of reproductive skew theory than with the concession approach. If social services are directed from subordinates towards dominants, there is no reason to assume that reproductive benefits are exchanged the other way around. In contrast, among females in cooperatively breeding common marmosets, it was found that dominants directed more grooming towards subordinates as an incentive to stay and help raising the dominants offspring (Lazaro-Perea et al. 2004).

The empirical results of this thesis therefore do not support the hypothesis that a dominant gives reproductive concessions to subordinates as an incentive to remain in the group. This is in line with theoretical objections raised against the applicability of the concession model to male primates (Chapter 3). First, as the success of a fertilization attempt is subject to sperm competition, the value of possible reproductive transactions can not adequately be assessed by their receivers, which ultimately questions their evolutionary stability (see Kokko 2003 for details). Second, the number of infants to be divided within a group is relatively small, both within one mating season and over the duration of a dominant's tenure. This questions whether the allocation of full infant 'units' is suitable to meet either group member's fitness requirements. For instance, if the number of males exceeds the number of offspring to be divided, it is technically impossible to yield the minimum staying incentive to each subordinate (see Chapter 3 for a more detailed discussion). Thus, based on both empirical and theoretical results of this thesis, it appears to be highly unlikely that reproductive concessions constituted a route to the evolution of group living in redfronted lemurs.

Alternative explanations

Mating skew

The rejection of the concession model in Chapter 2 is based on an analysis of paternities, i.e. an analysis of reproductive skew. However, it is possible that an analysis of mating skew would yield a different result. For instance, Duffy et al. (2007) recently found that subordinate male chimpanzees that supported the dominant more often in agonistic interactions with rivals, had a higher mating success. Matings do not suffer from the problem of indivisibility (outlined above and in Chapter 3) but as long as it can not be ascertained that animals are able to adequately assess the chances of fertilization, it is questionable whether the rules of reproductive skew models apply. It is possible that dominants tolerate matings of

subordinates, and, from a subordinate's point of view, it is further possible that any non-zero chance of fertilization is enough an incentive to remain in the group. However, a scenario in which dominants tolerate matings, and hence, grant subordinates the *chance* to sire offspring, is different from a scenario in which dominants concede discrete pieces of reproduction to subordinates. Whether or not the former scenario can be evolutionary stable, is a question that remains to be answered by theoreticians.

Moreover, from a researcher's point of view, an analysis of mating skew is hampered by the researcher's inability to assess the chance of fertilization associated with an observed mating. One is therefore forced to treat every mating equally in any quantitative analysis of mating skew, which is probably not sufficient to describe the reality of reproduction in redfronted lemurs. Males in this species can mate several times over short periods of time, thereby presumably not substantially increasing their chance of fertilization. In contrast, a single mating at a more important time of the female's receptive period can yield a much higher chance of fertilization. Preliminary data on mating skew (Port, unpubl. data) from four groups of redfronted lemurs obtained between 2005–2007 revealed that the distribution of matings was significantly different from random in only six of nine cases analyzed (in only four of nine cases if only immigrant males are considered). Moreover, in three of these nine cases, a subordinate male and not the dominant obtained the highest number of matings observed in the group. Even though different periods of time are analyzed, these data barely accord with the data on reproductive skew presented in Chapter 2, indicating that the mere frequency of matings is a bad predictor of reproductive success. Thus, given both theoretical and empirical problems involved in the analysis of mating skew, any further quantitative test of reproductive skew models based on mating skew appears to be fruitless in redfronted lemurs.

Reproductive restraint

In Chapter 4, we suggested that subordinate male redfronted lemurs exchange grooming for the dominant's tolerance, presumably to be allowed to remain in the group. If subordinates face the threat of eviction, they are also predicted to exercise reproductive restraint, in that they leave the dominant with just enough reproduction to make the association favourable over dissolving the group (Johnstone and Cant 1999a). In Chapter 2 we rejected the restraint model but this rejection was based on a small sample size. In addition, we were only able to test one variable (relatedness) pertaining to this model. A more complete test of the model is hampered by the fact that further variables incorporated into the model, e.g., the subordinate's prospects of breeding independently, are difficult to estimate.

Nonetheless, two lines of evidence make the restraint model an implausible explanation for the division of reproduction in redfronted lemurs either: First, the level of aggression among males dramatically increases during the mating season, when the dominance hierarchy can collapse temporarily (Ostner and Kappeler 1999, pers. observations). This, however, is not in accordance with the idea of subordinates exercising reproductive restraint. Second, as a transactional model, the restraint model presumably suffers from the same theoretical objections raised against the concession model (see Chapter 3). For instance, if the number of subordinates equals or exceeds the number of infants to be divided, it is technically impossible that all subordinates exercise their reproductive restraint without sacrificing their minimum fitness requirements. Moreover, in multi-member associations a collective action problem (Olson 1965, Nunn 1999b) is likely to arise among subordinates about who exercises how much restraint.

Reproductive competition and the benefits of grouping

It appears to be unlikely that cooperative forces are involved in the division of reproduction among males in groups of redfronted lemurs. Dominants do not give reproductive concessions

to subordinates and it does also not seem that subordinates voluntarily refrain from reproducing. Thus, the division of reproduction appears to be the result of competition among males. Within the framework of reproductive skew theory, the issue of male-male competition is addressed by the tug-of-war model. However, in Chapter 2 we concluded that the predictions of this model are also not met, as the number of males in a group had no significant impact on the dominant's loss of reproduction. Instead, the share of reproduction obtained by subordinates was best predicted by the number of females. Given the highly seasonal reproduction of redfronted lemurs, this result was best accounted for by the priority of access model (Altmann 1962, Alberts et al. 2003), which assumes that high-ranking males are able to monopolize access to females as long as only one female is receptive at the same time, but that lower ranking males get to mate as the number of simultaneously receptive females increases. We therefore concluded in Chapter 3, that a realistic model of reproductive skew in male mammals has to include the number of females as a predictor variable. This does not necessarily imply that females exercise their own reproductive interests (which they probably do, see below), but that females constitute a resource that males have to compete for. So far, this issue has not been addressed by reproductive skew theory.

However, having identified competition for access to fertile females as the proximate mechanism involved in the division of reproduction among male redfronted lemurs does not speak to the evolution of even adult sex ratios in this species. Comparative analyses across primate taxa revealed that apart from the number of females, measures of breeding seasonality had an impact on the number of males in a group (Ridley 1986, Nunn 1999a). It is evident that the number of simultaneously receptive females sets a limit on the dominant's ability to monopolize fertilizations (Chapter 2), but it needs to be stressed that the decision over group membership may be independent from the mechanisms involved in the division of reproduction. Thus, it remains unclear why dominants do not evict subordinates in the face of reproductive competition, a question which is not sufficiently addressed by comparative

analyses. The most parsimonious explanation may be that dominants are not able to evict subordinates or that an eviction (or an attempt thereof) is too costly. For instance, in the groups of redfronted lemurs observed from 2005-2007, in one case the dominant male and an immigrant subordinate engaged in intense agonistic interactions that lasted over several days of the mating season (pers. observation). As a result, both males were rarely observed mating, but the females of their group mated repeatedly with males from neighbouring groups. However, this is at best anecdotic evidence, and it does not sufficiently answer the question why males in non-seasonal breeders (like cercopithecines, Andelman 1986) are apparently able to evict rivals from small groups of females, whereas males in seasonal breeders (like lemurs, Kappeler 2000a) are not. Moreover, despite the fact that breeding is seasonal, not all gregarious lemurs are also characterized by high oestrous synchrony (Pereira 1991, Mass et al., in press).

As an alternative explanation, dominants may indeed tolerate the presence of subordinates. Even though the latter may not exercise reproductive restraint, it may still pay the dominant to tolerate them in the group as long as the benefits they provide throughout the year outweigh the costs they impose through the loss of some reproduction. Thus, allowing subordinates to stay can be an evolutionarily stable solution, even in the absence of voluntary reproductive transactions (see below). As an important benefit, subordinates reduce the risk of a group take-over (Ostner and Kappeler 2004), and by doing so significantly increase the dominant's fitness. The fitness costs of reproductive sharing can roughly be estimated from the paternity analyses presented in Chapter 2. However, to better assess the benefits of a reduced take-over risk, and hence, to more directly compare the fitness costs and benefits of subordinate males in redfronted lemurs, more data on take-overs are required.

In an attempt to explain the association of males in the cooperatively breeding communal pukeko (*Porphyrio porphyrio*), a gallinule bird from New Zealand, Craig (1984) proposed that territory owners are caught in a prisoner's dilemma game (Luce and Raiffa

1957). I believe that Craig's approach can also be applied to redfronted lemurs. Imagine two dominant males faced with the decision whether or not to accept a subordinate. If both dominants reject the subordinate, both will reap all reproduction within their groups and face the same take-over risk. However, if one dominant 'defects' by accepting the subordinate, it will have to share reproduction with the latter but may ultimately be better off than its partner, who, as a consequence of the defection, suffers from a relatively higher take-over risk. As a consequence, the partner will have to accept a subordinate as well, hence, mutual defection leading to multi-male groups is the only stable solution in the game. To show whether the payoff conditions of a prisoner's dilemma are fulfilled in redfronted lemurs (see Axelrod and Hamilton 1981, Craig 1984), requires an estimate of the take-over risk (as a function of the number of males), which is currently not available. However, I believe this to be a promising route for future research on the evolution of even sex ratios in this species, and possibly other gregarious lemurs.

The female perspective

The major aim of this thesis was to test models of reproductive skew theory. Most of these models were developed to explain the partitioning of reproduction in unisexual associations (see Chapter 3). Thus, applied to male mammals, they do not address the reproductive interests of females (but see Cant and Reeve 2002). However, there can be no doubt that females pursue their own reproductive strategies at the ultimate level and the corresponding mating tactics at the proximate level. The benefits of group-living addressed throughout this thesis apply to females as well (see Ostner 2004 for a discussion). Moreover, females profit from the association with multiple males as this may offer them the opportunity for mate choice, which in turn may increase the genetic diversity of their offspring (Jennions and Petrie 2000). A possible strategy for females to achieve this goal is the synchronization of their fertile periods which effectively lowers male monopolization potential (Ims 1990). The

majority of lemurs are seasonal breeders (Richard 1987) and a high degree of oestrous synchrony among females within a group is very likely in redfronted lemurs (Ostner and Kappeler 2004), but this does not seem to be a general pattern among gregarious lemurs (Pereira 1991, Mass et al., in press). Moreover, oestrous synchrony is only the first step towards the evolution of even adult sex ratios. Apart from offering females the opportunity for mate choice, it offers subordinate males the possibility to mate and makes joining a group a favourable option. But, as outlined above, the fact that dominant males are not able to monopolize reproduction does not necessarily imply that they also lack control over group membership. Thus, to explain the even adult sex ratios in lemurs, the male's perspective has to be taken into account as well. Breeding seasonality alone does not completely explain the lack of convergence in the group compositions of lemurs and anthropoid primates.

At the proximate level, female mating tactics may significantly influence the distribution of reproduction among males. Females may avoid certain males but prefer to mate with others (Sauther 1991, Matsumoto-Oda 1999), and even engage in sneak copulations to achieve this goal (Davies and Hatchwell 1992). It has been suggested that females (instead of dominant males) allocate some share of reproduction to subordinate males to induce them to remain in the group, if their presence increases the group's productivity (Cant and Reeve 2002) and some evidence from birds seems to support this suggestion (Davies et al. 1996). Furthermore, females gain from mating with multiple males because this confuses paternity among males and may prevent them from engaging in infanticide (Hrdy 1979). But even though females may exercise some choice about with whom to mate, they do not completely control the division of reproduction either. In group-living species, males have developed mate guarding as an effective counter-strategy, which prevents rivals from mating (e.g., Alberts et al. 2003, Huck et al. 2004, Setchell et al. 2005) and greatly reduces the potential for female choice, even in species with female dominance (Sauther 1991, Mass et al., in press).

In summary, it is evident that in gregarious species in which several females are receptive at the same time, neither sex completely controls the allocation of reproduction. Instead, the level of reproductive skew is very likely the outcome of an interaction of the competing mating tactics of males and females, in which the degree of reproductive monopolization of the dominant male is mainly determined by the number of simultaneously receptive females.

Conclusions

The empirical and theoretical results of this thesis revealed that dominant male redfronted lemurs do not give reproductive concessions to subordinates as an incentive to remain in the group. Thus, voluntary sharing of reproduction from the dominant's part can be excluded as an explanation for the evolution of groups with even adult sex ratios in this species. Some evidence suggests that subordinates offer social services to dominants as a 'payment' to remain in the group but it seems unlikely that they also exercise reproductive restraint to avoid being evicted. Due to a high degree of overlap of the females' receptive periods, no single group member completely controls the allocation of reproduction in groups of redfronted lemurs. This is not necessarily true for other gregarious lemurs: For instance, in Verreaux' sifakas (*Propithecus verreauxi verreauxi*) it was found that the degree of oestrus synchrony is low, resulting in a high monopolization potential of dominant males (Mass et al., in press) and, consequently, in a very high level of reproductive skew among resident males (Kappeler and Schöffler 2008). However, where control over reproduction is absent, models focusing on voluntary sharing of reproduction are unlikely to provide an explanation for the evolution of stable groups. More realistic models should shift their attention from reproductive skew to the decision over group membership. From a dominant's perspective, this decision should be based on the costs and benefits of subordinates. Whereas costs mainly arise from the expected loss of reproduction and, from a researcher's point of view, can be

estimated from the level of reproductive skew, more research is required to better understand the benefits of subordinates. Furthermore, more realistic models should go beyond the interaction between members of the same group and should pay more attention to the demands of a flexible environment. A behavioural strategy can only prove to be evolutionarily stable (*sensu* Maynard-Smith 1974), if it succeeds against competing strategies in the population as a whole.

SUMMARY

Due to male-male competition over access to fertile females, small groups of female primates are predicted to contain only one adult male. The gregarious lemurs of Madagascar significantly deviate from this prediction because they live in small groups with even adult sex ratios. In this thesis, I examined whether models of reproductive skew theory can provide an explanation for the evolution of this unusual group composition in redfronted lemurs (*Eulemur fulvus rufus*). These models assume that individuals profit from an association with same-sexed conspecifics, and that the conflict over reproduction is resolved based on an evolutionarily stable equilibrium between the competing forces of cooperation and competition.

Using a combination of demographic, molecular, and behavioural data, I empirically tested predictions of three major reproductive skew models and examined the social structure in four groups of redfronted lemurs to illuminate the distribution of social power among males. Even though reproduction is remarkably skewed in favour of dominant males, the overall division of reproduction does not support the predictions of either reproductive skew model. Furthermore, the patterns of aggression and grooming obtained from the behavioural observations do not support the assumption that dominant males tolerate the reproductive effort of subordinates. Instead, it seems that social services are provided by subordinates towards dominants, possibly to avoid eviction from the group. These results suggest that voluntary sharing of reproduction among males did not provide a route to the evolution of groups with even adult sex ratios in redfronted lemurs. Dominant males in this species are apparently not able to monopolize reproduction, and the subordinates' prospects of siring offspring are mainly determined by the number of females in a group. To become a more powerful tool to explain reproductive sharing and the evolution of sociality in male primates, future theoretical models need to incorporate the number of simultaneously receptive females as a predictor of reproductive skew at the proximate level and should pay more attention to the decision over group membership at the ultimate level.

REFERENCES

- Alberts, S.C., Watts, H.E. and Altmann, J. (2003) Queuing and queue-jumping: long-term patterns of reproductive skew in male savannah baboons, *Papio cynocephalus*. *Anim Behav* 65: 821-840.
- Alexander, R.D. (1974) The evolution of social behavior. *Annu Rev Ecol Syst* 5: 325-383.
- Altmann, S.A. (1962) A field study of the sociobiology of the rhesus monkey, *Macaca mulatta*. *Ann N Y Acad Sci* 102: 338-435.
- Andelman, S.J. (1986) Ecological and social determinants of cercopithecine mating patterns. In: Rubenstein, D.I. and Wrangham, R.W. (eds) *Ecological aspects of social evolution*. Princeton University Press, Princeton, pp. 201-216.
- Aureli, F., Preston, S.D. and de Waal, F.B.M (1999) Heart rate responses to social interactions in free-moving rhesus macaques (*Macaca mulatta*): a pilot study. *J Comp Psychol* 113: 59-65.
- Axelrod, R. and Hamilton W.D. (1981) The evolution of cooperation. *Science* 211: 1390-1396.
- Barrett, L. and Henzi, S.P. (2001) The utility of grooming in baboon troops. In: Noë, R., Hammerstein, P., and van Hooff, J.A.R.A.M. (eds) *Economics in Nature: Social Dilemmas, Mate Choice, and Biological Markets*. Cambridge University Press, Cambridge, pp. 119-145.
- Barrett, L., Gaynor, D. and Henzi, S.P. (2002) A dynamic interaction between aggression and grooming reciprocity among female chacma baboons. *Anim Behav* 63: 1047-1053.
- Barrett, L., Henzi, S.P., Weingrill, T., Lycett, J.E. and Hill, R.A. (1999) Market forces predict grooming reciprocity in female baboons. *Proc Roy Soc Lond B* 266: 665-670.
- Barton, R. A. (1985) Grooming site preferences in primates and their functional implications. *Int J Primatol* 6: 519-532.
- Barton, R.A. (1987) Allogrooming as mutualism in diurnal lemurs. *Primates* 28: 539-542.
- Bateman, A.J. (1948) Intra-sexual selection in *Drosophila*. *Heredity* 2: 349-368.
- Blouin, M.S. (2003) DNA-based methods for pedigree reconstruction and kinship analysis in natural populations. *Trends Ecol Evol* 18: 503-511.
- Blouin, M.S., Parsons, M., Lacaille, V. and Lotz, S. (1996) Use of microsatellite loci to classify individuals by relatedness. *Mol Ecol* 5: 393-401.

- Boesch, C., Kohou, G., Néné, H. and Vigilant, L. (2006) Male competition and paternity in wild chimpanzees of Taï forest. *Am J Phys Anthropol* 130: 103-115.
- Boskoff, K.J. (1978) The oestrus cycle of the brown lemur, *Lemur fulvus*. *J Reprod Fertil* 54: 313-318.
- Box, G.E.P. and Cox, D.R. 1964. An analysis of transformations. *J Roy Stat Soc B* 26: 211-246.
- Bradley, B.J., Robbins, M.M., Williamson, E.A., Steklis, H.D., Steklis, N.G., Eckhardt, N., Boesch, C., Vigilant, L. (2005) Mountain gorilla tug-of-war: Silverbacks have limited control over reproduction in multimale groups. *Proc Natl Acad Sci USA* 102: 9418-9423.
- Buston, P.M., H.K. Reeve, M.A. Cant, S.L. Vehrencamp, and S.T. Emlen. (2007) Reproductive skew and the evolution of group dissolution tactics: a synthesis of concession and restraint models. *Anim Behav* 74: 1643-1654.
- Campagna, C. and LeBoeuf, B.J. (1988) Reproductive behaviour of southern sea lions. *Behaviour* 104: 233-260.
- Cant, M.A. (1998) A model for the evolution of reproductive skew without reproductive suppression. *Anim Behav* 55: 163-169.
- Cant, M.A. (2000) Social control of reproduction in banded mongooses. *Anim Behav* 59: 147-158.
- Cant, M.A. (2006) A tale of two theories: parent-offspring conflict and reproductive skew. *Anim Behav* 71:255-263.
- Cant, M.A. and Reeve, H.K. (2002) Female control of the distribution of paternity in cooperative breeders. *Am Nat* 160: 602-611.
- Cant, M.A. and English, S. (2006) Stable group size in cooperative breeders: the role of inheritance and reproductive skew. *Behav Ecol* 17:560-568.
- Charpentier, M., Peignot, P., Hossart-McKey, M., Gimenez, O., Setchell, J.M. and Wickings, E.J. (2005) Constraints on control: factors influencing reproductive success in male mandrills (*Mandrillus sphinx*). *Behav Ecol* 16: 614-623.
- Clutton-Brock, T.H. (1989) Mammalian mating systems. *Proc R Soc Lond B* 236: 339-372.
- Clutton-Brock, T.H. (1998) Reproductive skew, concessions and limited control. *Trends Ecol Evol* 13: 288-292.
- Clutton-Brock, T.H. (2007) Sexual selection in males and females. *Science* 318:1882-1885
- Clutton-Brock, T.H. and Parker, G.A. (1992) Potential reproductive rates and the operation of sexual selection. *Q Rev Biol* 67: 437-456.

- Clutton-Brock, T.H., Brotherton, P.N.M., Russell, A.F., O'Riain, M.J., Gaynor, D., Kansky, R., Griffin, A., Manser, M., Sharpe, L., McIlrath, G.M., Small, T., Moss, A. and Monfort, S. (2001) Cooperation, control, and concession in meerkat groups. *Science* 291: 478-481.
- Clutton-Brock, T.H., Brotherton, P.N.M., Smith, R., McIlrath, G.M., Kansky, R., Gaynor, D., O'Riain, M.J., Skinner, J.D. (1998) Infanticide and expulsion of females in a cooperative mammal. *Proc R Soc Lond B* 265: 2291-2295.
- Connor, R.C. (1995a) Impala allogrooming and the parcelling model of reciprocity. *Anim Behav* 49: 528-530.
- Connor, R.C. (1995b) Altruism among non-relatives: alternatives to the 'Prisoner's Dilemma'. *Trends Ecol Evol* 10: 84-86.
- Cords, M. (2000) The number of males in guenon groups. In: Kappeler, P.M. (ed) *Primate males: Causes and consequences of group composition*. Cambridge University Press, Cambridge, pp 84-96.
- Craig, J.L. (1984) Are communal pukeko caught in the prisoner's dilemma? *Behav Ecol Sociobiol* 14:147-150.
- Crook, J.H. and Gartlan, J.C. (1966) Evolution of primate societies. *Nature* 210:1200-1203.
- Darwin, C. (1871) *The descent of man and selection in relation to sex*. Murray, London.
- Davies, N.B. and Hatchwell, B.J. (1992) The value of male parental care and its influence on reproductive allocation by male and female dunnocks. *J Anim Ecol* 61:259-272.
- Davies, N.B., Hartley, I.R., Hatchwell, B.J. and Langmore, N.E. (1996) Female control of copulations to maximize male help: a comparison of polygynandrous alpine accentors *Prunella collaris* and dunnocks *P. modularis*. *Anim Behav* 51, 27-47.
- de Waal, F.B.M. (1997) The chimpanzee's service economy: food for grooming. *Evol Hum Behav* 18: 375-386.
- Duffy, K.G., Wrangham, R.W. and Silk, J.B. (2007) Male chimpanzees exchange political support for mating opportunities. *Curr Biol* 17: R586-R587.
- Dugdale, H.L., MacDonald, D.W., Pope, L.C. and Burke, T. (2007) Polygynandry, extra group paternity and multiple paternity litters in European badger (*Meles meles*) social groups. *Mol Ecol* 16: 5294-5306.
- Dugdale, H.L., MacDonald, D.W., Pope, L.C., Johnson, P.L. and Burke, T. (2008) Reproductive skew and relatedness in social groups of European badgers, *Meles meles*. *Molec Ecol* 17: 1815-1827.

- Dunbar, R.I.M. (1992) Time: a hidden constraint on the behavioural ecology of baboons. *Behav Ecol Sociobiol* 33: 35-49.
- Emlen, S.T. (1995) An evolutionary theory of the family. *Proc Natl Acad Sci USA* 92: 8092-8099.
- Emlen, S.T. and Oring, L.W. (1977) Ecology, sexual selection, and the evolution of mating systems. *Science* 197: 215-223.
- Engelhardt, A., Heisterman, M., Hodges, J.K., Nürnberg, P. and Niemitz, C. (2006) Determinants of male reproductive success in wild long-tailed macaques (*Macaca fascicularis*) – male monopolization, female mate choice or post-copulatory mechanisms? *Behav Ecol Sociobiol* 59: 740-752.
- Engh, A.L., Funk, S.M., van Horn, R.C., Scribner, K.T., Bruford, M.W., Libants, S., Szykman, M., Smale, L. and Holekamp, K.E. (2002) Reproductive skew among males in a female dominated mammalian society. *Behav Ecol* 13: 193-200.
- Faulkes, C.G. and Bennett, N.C. (2001) Family values: group dynamics and social control of reproduction in African mole-rats. *Trends Ecol Evol* 16: 184-190.
- Field, J., Solis, C.R., Queller, D.C. and Strassmann, J.E. (1998) Social and genetic structure of paper wasp cofoundress associations: tests of reproductive skew models. *Am Nat* 151: 545-563.
- French, J.A. (1997) Proximate regulation of singular breeding in callitrichid primates. In: Solomon, N.G. and French, J.A. (eds) *Cooperative breeding in mammals*. Cambridge University Press, Cambridge, pp. 34-75.
- Gamboa, G.J. (2004) Kin recognition in eusocial wasps. *Ann Zool Fennici* 41: 789-808.
- Goosen, C. (1987) Social grooming in primates. In: Mitchell, G. and Erwin, J. (eds) *Comparative Primate Biology, Volume 2B: Behavior, Cognition, and Motivation*. Alan R. Liss Inc., New York, pp. 107-131.
- Gumert, M.D. (2007a) Payment for sex in a macaque mating market. *Anim Behav* 74: 1655-1667.
- Gumert, M.D. (2007b) Grooming and infant handling interchange in *Macaca fascicularis*: the relationship between infant supply and grooming payment. *Int J Primatol* 28: 1059-1074.
- Hager, R. (2003) Models of reproductive skew applied to primates. In: Jones, C. (ed) *Special topics in primatology*. American Society of Primatologists, Norman, Oklahoma, pp. 65-101.

- Hager, R. and Johnstone, R.A. (2004) Infanticide and control of reproduction in cooperative and communal breeders. *Anim Behav* 67: 941-949.
- Hamilton, I.M. and Heg, D. (2007) Clutch-size adjustments and skew models: effects on reproductive partitioning and group stability. *Behav Ecol* 18: 467-476.
- Hamilton, W.D. (1964) The genetical evolution of social behaviour I&II. *J Theor Biol* 7: 1-52.
- Hannonen, M. and Sundström, L. (2003) Reproductive sharing among queens in the ant *Formica fusca*. *Behav Ecol* 14: 870-875.
- Hart, B.J., and Hart, L.A. (1992) Reciprocal allogrooming in impala, *Aepycerops melampus*. *Anim Behav* 44: 1073-1083.
- Haydock, J. and Koenig, W.D. (2003) Patterns of reproductive skew in the polygynandrous Acorn Woodpecker. *Am Nat* 162: 277-289.
- Heg, D., Bergmüller, R., Bonfils, D., Otti, O., Bachar, Z., Burri, Z., Heckel, G. and Taborsky, M. (2006) Cichlids do not adjust reproductive skew to the availability of independent breeding options. *Behav Ecol* 17:419-429.
- Hemelrijk, C.K. (1994) Support for being groomed in long-tailed macaques, *Macaca fascicularis*. *Anim Behav* 48: 479-481.
- Hemelrijk, C.K. and Ek, A. (1991) Reciprocity and interchange of grooming and 'support' in captive chimpanzees. *Anim Behav* 41: 923-935.
- Henzi, S.P. and Barrett, L. (1999) The value of grooming to female primates. *Primates* 40: 47-59.
- Henzi, S.P. and Barrett, L. (2002) Infants as a commodity in a baboon market. *Anim Behav* 63: 915-921.
- Henzi, S.P., Barrett, L., Gaynor, D., Greeff, J., Weingrill, T. and Hill, R.A. (2003) Effect of resource competition on the long-term allocation of grooming by female baboons: evaluating Seyfarth's model. *Anim Behav* 66: 931-938.
- Henzi, S.P., Lycett, J.E. and Weingrill, T. (1997) Cohort size and the allocation of social effort by female mountain baboons. *Anim Behav* 54: 1235-1243.
- Hrdy, S.B. (1979) Infanticide among animals: a review, classification, and examination of the implications for the reproductive strategies of females. *Ethol Sociobiol* 1:13-40.
- Huck, M. (2004) All males are equal but some are more equal: Proximate mechanisms and genetic consequences of the social- and mating system of moustached tamarins, *Saguinus mystax mystax* (Spix, 1823). PhD Thesis, University of Bielefeld, Bielefeld.

- Huck, M., Löttker, P. and Heymann, E.W. (2004) Proximate mechanisms of reproductive monopolization in male moustached tamarins (*Saguinus mystax*). *Am J Primatol* 64: 39-56.
- Huck, M., Löttker, P., Böhle, U.-R., and Heymann, E.W. (2005) Paternity and kinship patterns in polyandrous moustached tamarins (*Saguinus mystax*). *Am J Phys Anthropol* 127: 449-464.
- Hutchins, M. and Barash, D.P. (1976) Grooming in primates: implications for its utilitarian function. *Primates* 17: 145-150.
- Ims, R.A. (1990) The ecology and evolution of reproductive synchrony. *Trends Ecol Evol* 5:135-140.
- Jamieson, I.G. (1997) Testing reproductive skew models in a communally breeding bird, the pukeko, *Porphyrio porphyrio*. *Proc R Soc Lond B* 264: 335-340.
- Jekielek, J. and Strobeck, C. (1999) Characterization of polymorphic brown lemur (*Eulemur fulvus*) microsatellite loci and their amplification in the family Lemuridae. *Mol Ecol* 8: 895-906.
- Jennions, M.C. and Petrie, M. (2000) Why do females mate multiply? A review of the genetic benefits. *Biol Rev* 75:21-64.
- Johnstone, R.A. (2000) Models of reproductive skew: A review and synthesis. *Ethology* 106: 5-26.
- Johnstone, R.A. and Cant, M.A. (1999a) Reproductive skew and the threat of eviction: a new perspective. *Proc R Soc Lond B* 266: 275-279.
- Johnstone, R.A. and Cant, M.A. (1999b) Reproductive skew and indiscriminate infanticide. *Anim Behav* 57: 243-249.
- Johnstone, R.A. and Cant, M.A. (in press) Models of reproductive skew – outside options and the resolution of reproductive conflict. In: Hager, R. and Jones, C.B. (eds) *Reproductive skew in vertebrates: Proximate mechanisms and ultimate factors*. Cambridge University Press, Cambridge, in press.
- Johnstone, R.A., Woodroffe, R., Cant, M.A. and Wrigth, J. (1999) Reproductive skew in multimember groups. *Am Nat* 153: 315-331.
- Kappeler, P.M. (1993a) Variation in social structure: the effects of sex and kinship on social interactions in three lemur species. *Ethology* 93: 125-145.
- Kappeler, P.M. (1993b) Reconciliation and post-conflict behaviour in ringtailed lemurs, *Lemur catta* and redfronted lemurs, *Eulemur fulvus rufus*. *Anim Behav* 45: 901-915.

- Kappeler, P.M. (1999) Primate socioecology: new insights from males. *Naturwissenschaften* 85: 18-29.
- Kappeler, P.M. (2000a) Causes and consequences of unusual sex ratios among lemurs. In: Kappeler PM (ed) *Primate males: Causes and consequences of group composition*. Cambridge University Press, Cambridge, pp 55-63.
- Kappeler, P.M. (2000b) *Primate males. Causes and consequences of variation in group composition*. Cambridge, Cambridge University Press.
- Kappeler, P.M. and van Schaik, C. (2002) Evolution of primate social systems. *Int J Primatol* 23: 707-740.
- Kappeler, P.M. and Port, M. (2008) Mutual tolerance or reproductive competition? Patterns of reproductive skew among male redfronted lemurs (*Eulemur fulvus rufus*). *Behav Ecol Sociobiol* 62: 1477-1488.
- Kappeler, P.M. and Schäßler, L. (2008) The lemur syndrome unresolved: extreme male reproductive skew in sifakas (*Propithecus verreauxi*), a sexually monomorphic primate with female dominance. *Behav Ecol Sociobiol* 62: 1007-1015.
- Kapsalis, E. and Berman, C.M. (1996) Models of affiliative relationships among free-ranging rhesus monkeys (*Macacca mulatta*) II. Testing predictions for three hypothesized organizing principles. *Behaviour* 133: 1235-1263.
- Keller, L. and Reeve, H.K. (1994) Partitioning of reproduction in animal societies. *Trends Ecol Evol* 9: 98-102.
- Kokko, H. (2003) Are models of reproductive skew evolutionary stable? *Proc R Soc Lond B* 270: 265-270.
- Kokko, H. and Johnstone, R.A. (1999) Social queuing in animal societies: a dynamic model of reproductive skew. *Proc R Soc Lond B* 265: 571-578.
- Kokko, H. and Lundberg, P. (2001) Dispersal, migration, and offspring retention in saturated habitats. *Am Nat* 157: 188-202.
- Kokko, H. and Ekman, J. (2002) Delayed dispersal as a route to breeding: territorial inheritance, safe havens, and ecological constraints. *Am Nat* 160: 468-484.
- Kokko, H., Mackenzie, A., Reynolds, J.D., Lindström, J. and Sutherland, W.J. (1999) Measures of inequality are not equal. *Am Nat* 72:358-382.
- Kokko, H., Johnstone, R.A. and Clutton-Brock, T.H. (2001) The evolution of cooperative breeding through group augmentation. *Proc R Soc Lond B* 268: 187-196.
- Kutsukake, N. and Clutton-Brock, T.H. (2006) Social function of allogrooming in cooperatively breeding meerkats. *Anim Behav* 72: 1059-1068.

- Kutsukake, N. and Nunn, C.L. (2006) Comparative tests of reproductive skew in male primates: the role of demographic factors and incomplete control. *Behav Ecol Sociobiol* 60: 695-706.
- Kutsukake, N. and Nunn, C.L. (in press) The causes and consequences of reproductive skew in male primates. In: Hager, R. and Jones, C.B. (eds) *Reproductive skew in vertebrates: proximate and ultimate factors*. Cambridge University Press, Cambridge
- Langer, P., Hogendoorn, K. and Keller, L. (2004) Tug-of-war over reproduction in a social bee. *Nature* 428: 844-847.
- Lazaro-Perea, C., de Fatima Arruda, M. and Snowdon, C.T. (2004) Grooming as a reward? Social function of grooming between females in cooperatively breeding marmosets. *Anim Behav* 67: 627-636.
- Leinfelder, I., De Vries, H., Deleu, R. and Nelissen, M. (2001) Rank and grooming reciprocity among females in a mixed-sex group of captive hamadryas baboons. *Am J Primatol* 55: 25-42.
- Long, J.S. (1997) *Regression models for categorical and limited dependent variables*. Sage Publications, Thousand Oaks
- Löttker, P., Huck, M., Zinner, D.P. and Heymann E.W. (2007) Grooming relationships between breeding females and adult group members in cooperatively breeding moustached tamarins (*Saguinus mystax*). *Am J Primatol* 69: 1159-1172.
- Luce, R.D. and Raiffa, H. (1957) *Games and Decisions*. Wiley, New York.
- Maestriperi, D. (1993) Vigilance costs of allogrooming in macaque mothers. *Am Nat* 141: 744-753.
- Magrath, R.D., Heinsohn, R.G. and Johnstone, R.A. (2004) Reproductive skew. In: Koenig, W.D. and Dickinson, J.L. (eds) *Ecology and evolution of cooperative breeding in birds*. Cambridge University Press, Cambridge, pp. 157-176.
- Manson, J.H., Navarrete, C.D., Silk, J.B. and Perry, S. (2004) Time-matched grooming in female primates? New analyses from two species. *Anim Behav* 67: 493-500.
- Marshall, T.C., Slate, J., Kruuk, L.E.B. and Pemberton, J.M. (1998) Statistical confidence for likelihood-based paternity inference in natural populations. *Mol Ecol* 7: 639-655.
- Mass, V., Heisterman, M., and Kappeler, P.M. (in press) Mate guarding as a male reproductive tactic in Verreaux's sifakas (*Propithecus verreauxi*). *Int J Primatol*, in press.
- Matsumoto-Oda, A. (1999) Female choice in the opportunistic mating of wild chimpanzees (*Pan troglodytes schweinfurthii*) at Mahale. *Behav Ecol Sociobiol* 46: 258-266.

- Maynard-Smith, J. (1974) The theory of games and the evolution of animal conflict. *J Theor Biol* 47:209-221.
- McRae, S.B. (1996) Family values: costs and benefits of communal nesting in the moorhen. *Anim Behav* 52: 225-245.
- Mooring, M.S. and Hart, B.L. (1995) Costs of allogrooming in impala: distraction from vigilance. *Anim Behav* 49: 1414-1416.
- Noë, R. (2001) Biological markets: partner choice as the driving force behind the evolution of mutualism. In: Noë, R., Hammerstein, P. and van Hooff, J.A.R.A.M. (eds) *Economics in Nature: Social Dilemmas, Mate Choice, and Biological Markets*. Cambridge University Press, Cambridge, pp. 119-145.
- Noë, R. and Hammerstein, P. (1994) Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating. *Behav Ecol Sociobiol* 35: 1-11.
- Noë, R. and Hammerstein, P. (1995) Biological markets. *Trends Ecol Evol* 10: 336-340.
- Nonacs, P. (2001) A life-history approach to group living and social contracts between individuals. *Ann Zool Fennici* 38: 239-254.
- Nonacs, P. (2003) Measuring the reliability of skew indices: is there one best index? *Anim Behav* 65: 615-627.
- Nonacs, P. (2006) The rise and fall of transactional skew theory in the model genus *Polistes*. *Ann Zool Fennici* 43: 443-45.
- Nonacs, P. (2007) Tug-of-war has no borders: it is the missing model in reproductive skew theory. *Evolution* 61: 1244-1250.
- Nunn, C.L. (1999a) The number of males in primate groups: a comparative test of the socioecological model. *Behav Ecol Sociobiol* 46:1-13.
- Nunn, C.L. (1999b) Collective benefits, free-riders, and male extra-group conflict. In: Kappeler, P.M. (ed) *Primate males. Causes and Consequences of variation in group composition*. Cambridge University Press, Cambridge.
- Olson, M. (1965) *The logic of collective action*. Harvard University Press, Cambridge.
- Ortega, J. and Arita, H.T. (2002) Subordinate males in harem groups of Jamaican fruit-eating bats (*Artibeus jamaicensis*): Sattelites or sneaks. *Ethology* 108: 1077-1091.
- Ostner, J. (2004) Sex-specific reproductive strategies of redfronted lemurs (*Eulemur fulvus rufus*, Primates, Lemuridae). PhD, University of Würzburg, Würzburg.
- Ostner, J. and Kappeler, P.M. (1999) Central males instead of multiple pairs in redfronted lemurs, *Eulemur fulvus rufus* (Primates, Lemuridae)? *Anim Behav* 58: 1069-1078.

- Ostner, J. and Kappeler, P.M. (2004) Male life history and the unusual sex ratios of redfronted lemur (*Eulemur fulvus rufus*) groups. *Anim Behav* 67: 249-259.
- Ostner, J., Nunn, C.L. and Schülke, O. (in review). Female reproductive synchrony predicts skewed paternity across primates. In review, *Behav Ecol*.
- Overdorff, D.J., Merenlender, A.M., Talata, P., Telo, A. and Forward, Z.E. (1999) Life history of *Eulemur fulvus rufus* from 1988 – 1998 in southeastern Madagascar. *Am J Phys Anthropol* 108: 295-310.
- Packer, C.R., Herbst, L., Pusey, A.E., Bygott, J.D., Hanby, J.P., Cairns, S.J. and Borgerhoff-Mulder, M. (1988) Reproductive success in lions. In: Clutton-Brock, T.H. (ed.) *Reproductive success*. University of Chicago Press, Chicago, pp 363-383.
- Payne, H.F.P., Lawes, M.J. & Henzi, S.P. (2003) Competition and exchange of grooming among female samango monkeys (*Cercopithecus mitis erythrarchus*). *Behaviour* 140: 453-471.
- Pereira, M.E. (1991) Asynchrony within estrous synchrony among ringtailed lemurs (Primates: Lemuridae). *Physiol Behav* 49:47-52.
- Pereira, M. E. and Kappeler, P. M. (1997) Divergent systems of agonistic relationship in lemurid primates. *Behaviour* 134: 225-274.
- Pope, T. (1990) The reproductive consequences of male cooperation in the red howler monkey: paternity exclusion in multi-male and single-male troops using genetic markers. *Behav Ecol Sociobiol* 27: 439-446.
- Port, M., Clough, D. and Kappeler, P.M. (2009) Market effects offset the reciprocation of grooming in free-ranging redfronted lemurs (*Eulemur fulvus rufus*). *Anim Behav* 77: 29-36.
- Queller, D.C. and Goodnight, K.F. (1989) Estimating relatedness using genetic markers. *Evolution* 43: 258-275.
- Queller, D.C., Zacchi, F., Cervo, R., Turillazi, S., Henshaw, M.T., Santarelli, L.A. and Strassmann, J.E. (2000) Unrelated helpers in a social insect. *Nature* 405:784-787.
- Reeve, H.K. (1991) *Polistes*. In: Ross, K.G. and Matthews, R.W. (eds): *The social biology of wasps*. Cornell University Press, Ithaca, pp. 99-148.
- Reeve, H.K. (1998) Game theory, reproductive skew, and nepotism. In: Dugatkin, L., Reeve, H.K. (eds) *Game theory and animal behaviour*. Oxford University Press, Oxford, pp. 118-145.
- Reeve, H.K. (2000) A transactional theory of within group conflict. *Am Nat* 155: 365-382.

- Reeve, H.K. and Ratnieks, F.L.W. (1993) Queen-queen conflict in polygynous societies: Mutual tolerance and reproductive skew. In: Keller, L (ed): Queen number and sociality in insects. Oxford University Press, Oxford, 45-85.
- Reeve, H.K. and Keller, L. (1995) Partitioning of reproduction in mother-daughter versus sibling associations: a test of optimal skew theory. *Am Nat* 145: 119-132.
- Reeve, H.K. and Keller, L. (1996) Relatedness asymmetry and reproductive sharing in animal societies. *Am Nat* 148: 764-769
- Reeve, H.K. and Emlen, S.T. (2000) Reproductive skew and group size: an N-person staying incentive model. *Behav Ecol* 11: 640-647.
- Reeve, H.K. and Keller, L. (2001) Tests of reproductive skew models in social insects. *Ann Rev Entomol* 46: 347-385.
- Reeve, H.K. and Shen, S.F. (2006) A missing model in reproductive skew theory: The bordered tug-of-war. *Proc Natl Acad Sci USA* 103: 8430-8434.
- Reeve, H.K., Emlen, S.T. and Keller, L. (1998) Reproductive sharings in animal societies: reproductive incentives or incomplete control by dominant breeders? *Behav Ecol* 9: 267-278.
- Reeve, H.K., Starks, P.T., Peters, J.M. and Nonacs, P. (2000) Genetic support for the evolutionary theory of reproductive transactions in social wasps. *Proc R Soc Lond B* 267: 75-79.
- Rensing, S. (1999) Immobilization and anesthesia of nonhuman primates. *Primate Report* 55: 33-38.
- Richard, A.F. (1987) Malagasy prosimians: female dominance. In: Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Wrangham, R.W. and Strushaker, T.T. (eds.) *Primate Societies*. University of Chicago Press, Chicago, pp. 25-33.
- Ridley, M. (1986) The number of males in a primate troop. *Anim Behav* 34: 1848-1858.
- Robbins, A.M. and Robbins, M.M. (2005) Fitness consequences of dispersal decisions for male mountain gorillas (*Gorilla beringei beringei*). *Behav Ecol Sociobiol* 58: 295-309.
- Röseler, P.F. (1991) Reproductive competition during colony establishment. In: Ross, K.G. and Matthews, R.W. (eds) *The social biology of wasps*. Cornell University Press, Ithaca, pp. 309-335.
- Saltzman, W., Liedl, K.J., Salper, O.J., Pick, R.R. and Abbott, D.H. (2008) Post-conception reproductive competition in cooperatively breeding common marmosets. *Horm Behav* 53: 274-286.

- Sauther, M.L. (1991) Reproductive behaviour of free-ranging *Lemur catta* at Beza Mahafaly Special Reserve, Madagascar. *Am J Phys Anthropol* 84: 463-477.
- Say, L., Pontier, D., and Natoli, E. (2001) Influence of oestrus synchrony on male reproductive success in the domestic cat (*Felix catus* L.). *Proc Roy Soc Lond B* 268: 1049-1053.
- Schäffler, L. (2005) Das genetische Paarungssystem von *Propithecus verreauxi verreauxi* im Forêt de Kirindy, West Madagaskar. Diploma Thesis, University of Würzburg, Würzburg.
- Schino, G. (2001) Grooming, competition and social rank among female primates: a meta-analysis. *Anim Behav* 62: 265-271.
- Schino, G. (2007) Grooming and agonistic support: a meta-analysis of primate reciprocal altruism. *Behav Ecol* 18: 115-120.
- Schino, G., Scucchi, S., Maestripieri, D. and Turillazzi, P.G. (1988) Allogrooming as a tension-reduction mechanism: a behavioral approach. *Am J Primatol* 16: 43-50.
- Schino, G., Ventura, R. and Troisi, A. (2003) Grooming among female Japanese macaques: distinguishing between reciprocation and interchange. *Behav Ecol* 14: 887-891
- Schino, G., Ventura, R. and Troisi, A. (2005) Grooming and aggression in captive Japanese macaques. *Primates* 46: 207-209.
- Setchell, J.M., Charpentier, M. and Wickings, J. (2005) Mate guarding and paternity in mandrills: factors influencing alpha male monopoly. *Anim Behav* 70: 1105-1120.
- Seyfarth, R.M. (1977) A model of social grooming among adult female monkeys. *J Theor Biol* 65: 671-698.
- Seyfarth, R.M. and Cheney, D.L. (1984) Grooming, alliances and reciprocal altruism in vervet monkeys. *Nature* 308: 541-542.
- Silk, J.B. (1982) Altruism among female *Macaca radiata*: explanations and analysis of patterns of grooming and coalition formation. *Behaviour* 79: 162-188.
- Soares, M.C., Bshary, R., Cardoso, S.C. and Côté, I.M. (2008) Does competition for clients increase service quality in cleaning gobies? *Ethology* 114: 625-632.
- Sorg, J., Ganzhorn, J. and Kappeler, P.M. (2003) Forestry and research in the Kirindy Forest/ Centre de Formation Professionnelle Forestière. In: Goodman, S. and Benstead, J. (eds) *The Natural History of Madagascar*. University of Chicago Press, Chicago, pp 1512-1519.
- Sparks, J. (1967) Allogrooming in primates: a review. In: Morris, D. (ed) *Primate Ethology*. Aldine Publishing Company, Chicago, pp. 148-174.

- Stevens, J.R. and Hauser, M.D. (2004) Why be nice? Psychological constraints on the evolution of cooperation. *Trends Cogn Sci* 8: 60-65.
- Stiver, K.A., Dierkes, P., Taborsky, M., Gibbs, H.L. and Balshine, S. (2005) Relatedness and helping in fish: examining the theoretical predictions. *Proc R Soc Lond B* 272: 1593-1599.
- Stopka, P. and Macdonald, D.W. (1999) The market effect in the wood mouse, *Apodemus sylvaticus*: selling information on reproductive status. *Ethology* 105: 969-982.
- Thornhill, R. and Alcock, J. (1983) *The evolution of insect mating systems*. Harvard University Press, Cambridge.
- Trivers, R.L. (1971) The evolution of reciprocal altruism. *Q Rev Biol* 46: 35-57.
- Trivers, R.L. (1972) Parental investment and sexual selection. In: Campbell, B. (ed) *Sexual selection and the descent of man, 1871-1971*. Heinemann, London, pp. 136-179.
- Tsuji, K. and Tsuji, N. (1998) Indices of reproductive skew depend on average reproductive success. *Evol Ecol* 12: 141-152.
- Tsuji, K. and Kasuya, E. (2001) What do indices of reproductive skew measure? *Am Nat* 158: 155-165.
- van de Castele, T., Galbusera, P. and Matthysen, E. (2001) A comparison of microsatellite-based pairwise relatedness estimators. *Mol Ecol* 10: 1539-1549.
- van Hooff, J. A. R. A. M. and van Schaik, C. P. (1994) Male bonds: affiliative relationships among nonhuman primate males. *Behaviour* 130: 309-337.
- van Schaik, C.P. and van Noordwijk, M.A. (1989) The special role of *Cebus* monkeys in predation avoidance and its effect on group composition. *Behav Ecol Sociobiol* 24: 265-276.
- van Schaik, C.P. and Hörstermann, M. (1994) Predation risk and the number of adult males in a primate group: a comparative test. *Behav Ecol Sociobiol* 35: 261-271.
- van Schaik, C.P. and Kappeler, P.M. (1996) The social systems of gregarious lemurs : lack of convergence with anthropoids due to evolutionary disequilibrium? *Ethology* 102: 915-941.
- Vehrencamp, S.L. (1983a) Optimal degree of skew in cooperative societies. *American Zoologist* 23: 327-335.
- Vehrencamp, S.L. (1983b) A model for the evolution of despotic versus egalitarian societies. *Animal Behaviour* 31: 667-682.

- Ventura, R., Majolo, B., Koyama, N.F., Hardie, S. and Schino, G. (2006) Reciprocation and interchange in wild Japanese macaques: grooming, cofeeding, and agonistic support. *Am J Primatol* 68: 1138-1149.
- Vick, L.G. and Pereira, M.E. (1989) Episodic targeting aggression and the histories of *Lemur* social groups. *Behav Ecol Sociobiol* 25: 3-12.
- Widdig, A. (2007) Paternal kin discrimination: the evidence and likely mechanisms. *Biol Rev* 82: 319-334.
- Widdig, A., Bercovitch, F.B., Streich, W.J., Saueremann, U., Nuernberg, P., Krawczak, M. (2004) A longitudinal analysis of reproductive skew in male macaques. *Proc R Soc Lond B* 271: 819-826.
- Williams, D.A. (2004) Female control of reproductive skew in cooperatively breeding brown jays (*Cyanocorax morio*). *Behav Ecol Sociobiol* 55: 370-380.
- Wimmer, B. (2000) Untersuchungen der Paarungssysteme und der Populationsstruktur von Lemuren an Coquerels Zwergmaki (*Mirza coquereli*), dem grauen Mausmaki (*Microcebus murinus*), dem Rotstirnmaki (*Eulemur fulvus rufus*) und dem Larvensifaka (*Propithecus verreauxi verreauxi*). PhD, University of Würzburg, Würzburg.
- Wimmer, B. and Kappeler, P.M. (2002) The effects of sexual selection and life history on the genetic structure of redfronted lemur, *Eulemur fulvus rufus*, groups. *Anim Behav* 64: 557-568.
- Wright, P.C. (1999) Lemur traits and Madagascar ecology: Coping with an island environment. *Yearbook of Physical Anthropology* 42: 31-72.
- Young, A.J., Carlson, A.A., Monfort, S.L., Russell, A.F., Bennett, N.C. and Clutton-Brock, T.H. (2006) Stress and the suppression of subordinate reproduction in cooperatively breeding meerkats. *Proc Natl Acad Sci USA* 103: 12005-12010.
- Zink, A.G. and Reeve, H.K. (2005) Predicting the temporal dynamics of reproductive skew and group membership in communal breeders. *Behav Ecol* 16: 880-888.

ACKNOWLEDGMENTS

Scientists love to talk about significance, and I can not deny that this PhD as well as the people involved in it had a significant impact on my life. Over the many years I spent with it, there are quite a lot of people (and institutions) I would like to thank:

First of all I would like to thank my supervisor Peter Kappeler, who always let me the necessary freedom to develop my own thoughts and ideas, but who never failed to guide them in the right direction and whose constructive discussions greatly improved my work during all phases of this PhD. I am also grateful to Eckhard Heymann for his support as a referee of this thesis.

The field work in Madagascar would have been impossible without the invaluable help and logistic support of the Equipe DPZ at Kirindy. I am particularly grateful to Léon Razafimanantsoa, Rodin Rasoloarison, Tiana Andrianjanahary, as well as (as a passionate eater) to Adrien, Tati and Fanja, who sometimes did more than just their job to provide hungry vazaha with delicious food. I also thank all the people who, over the course of the field work, contributed to data collection: Thanks to Lantonirina Ratovonjanahary, Friederike Scholz, Jessica Schäckermann, Annette Schneider, Janna Etz and Fabian Nürnberger. My warmest thanks, however, go to Jean-Pierre Ratolojanahary, who helped observing gidros for more than two years and who always stayed cheerful and patient despite this sometimes hard and boring work.

I am much obliged to Christina Oberdieck who introduced me to the secrets of the genetic lab, as well as to Manfred Eberle who provided indispensable help during the preparation of the paternity analyses. I thank Vanessa Mass for polishing up the English in several chapters of this thesis and Jörg Schmidt for his ongoing “economic” interest in lemur social behaviour. Furthermore, I would like to thank all my (ex-) colleagues who I shared an office with over the course of this PhD (in order of [dis-] appearance): Petra, Britta, Vanessa,

Yvan, Mojca, Silvia, Christian and Katrin. I thank all of you as well as Dagmar, Linn, Moritz, Lennart, Julia, Dirk, Susanne, Janna, Guni, Christina, Matze, José and Livia for inspiring discussions, interesting chats, but in particular for a very pleasant working atmosphere and for all the good times in Kirindy, at Jean Le Rasta's, at Europic, at Tequilla Night, and at every other place we had fun.

I think the end of this PhD is a good opportunity to thank another person I feel very obliged to: Thanks to Oliver Schülke who taught a naïve volunteer how to hunt phantoms in the night and who greatly encouraged my further interests in primatology. Moreover, together with Julia Ostner, Ole contributed lots of valuable ideas during the early planning phase of this PhD.

My greatest thanks, however, are to Anja. It is certainly not easy to be together with an odd primatologist who spends much time of the year at the other end of the world. Thanks for still being there when I came home! At this point, I am probably also supposed to thank Anja for sharing with me all the ups and downs of my PhD. However, there were no (not many!) downs. I liked this PhD from the very first beginning till the end! And I would – therefore – like to thank “the other love of my life”: I would like to thank science! I think we had a good time so far and I always tried to treat you well!

Funding for this project was provided by the German Research Council (Ka 1082/9). The field work in Madagascar would have been impossible without the permission of the Malagasy Ministère de l'Environnement et des Eaux et Forêts, and the support of the Département Biologie Animale de l'Université d'Antananarivo as well as the Centre de Formation Professionnelle Forestière de Morondava.

APPENDIX

Contents:

Appendix A: Table of all paternities	112
Appendix B: The ordered logit model	114
Appendix C: Reproductive skew and group size in the concession model	116

Appendix A: Table of all paternities

Table A1: Table of all paternities. LOD-scores represent the likelihood of paternity of a candidate male relative to a randomly chosen male. The difference between the LOD-scores of the most likely and the second most likely male is expressed as Delta. Confidence levels of Delta are assessed in a large number of paternity test simulations (see main text for details): ** 98%, * 95%. Only lines indicated in bold letters entered the analysis of reproductive skew.

Group	Year	Offspring	Offspring ID	Mother	Mother ID	Father	Father ID	O-M-F mismatches ¹	LOD	Delta	mismatch ²
A1	1996	Vulcano	7	Elba	3	Rhodos	5	0	8.53	8.53 **	
A1	1996	Stromboli	8	Corsica	2	Krk	1	0	8.84	8.84 **	
A1	1997	Sardegna	53	Elba	3	Krk	1	0	9.79	9.79 **	
A1	1997	Sicilia	54	Corsica	2	Krk	1	0	7.9	7.9 **	
A1	1998	Split	65	Elba	3	Krk	1	0	7.49	7.49 **	
A1	1999	Capri	72	Elba	3	Krk	1	0	8.56	8.56 **	
A1	1999	Kreta	73	Corsica	2	Krk	1	0	10.05	3.76 **	
A2	2002	Levanzo	106	Corsica	2	Giglio	83	0	7.77	3.57 **	
A2	2003	Ischia	120	Sardegna	53	Giglio	83	0	7.49	3.64 **	
A2	2003	Pianosa	121	Corsica	2	Giglio	83	0	9.73	7.39 **	
A2	2004	Ibiza	125	Corsica	2	Giglio	83	0	6.45	2.57 **	
A2	2004	Malta	126	Sardegna	53	Bali	15	0	8.63	4.25 **	
B1	1996	Guinea	19	Java	12	Singapur	16	0	6.58	6.58 **	
B1	1996	Papua	20	Tonga	14	Bali	15	0	7.22	7.22 **	
B1	1996	Sum Baby	21	Sumatra	13	Sulawesi	9	1	3.51	2.11 **	heterozyeous O-M
B1	1997	Pagai	55	Java	12	Bali	15	0	5.89	5.66 **	
B1	1997	Sipora	103	Tonga	14	Bali	15	0	6.09	6.09 **	
B1	1998	Timor	60	Tonga	14	Bali	15	0	8.06	2.87 **	
B1	1998	Flores	61	Java	12	Bali	15	0	7.79	2.93 **	
B1	1999	Linnga	84	Papua	20	Hong Kong	18	0	11.05	11.05 **	
B2	2001	Kuta	102	Papua	20	Alor	88	0	7.1	7.1 **	
B2	2002	Batu	107	Papua	20	Alor	88	0	7.18	7.18 **	
B2	2002	Mindanao	108	Sipora	103	Alor	88	0	6.35	6.35 **	

B2	2002	Manila	109	Linnga	84	Alor	88	0	8.1	8.1 **	
B2	2003	Camorra	118	Linnga	84	Laos	67	0	8.19	5.61 **	
B2	2003	Sentinel	119	Papua	20	Laos	67	0	8.88	8.88 **	
B2	2004	Narcondan	128	Sipora	103	Alor	88	0	10	10 **	
B2	2004	Cinque	131	Papua	20	Laos	67	0	11.03	9.47 **	
B2	2004	Kl. Scheißer	133	Linnga	84	Laos	67	0	7.25	6.43 **	
F1	1997	Barbados	57	Cuba	37	Puerto	35	0	8.4	8.4 **	
F2	1999	Lucia	75	Cuba	37	Largo	63	0	7.85	5.32 **	
F2	1999	Vincent	93	Grenada	39	Largo	63	0	9.17	7.55 **	
F2	2000	Montigo	96	Cuba	37	Largo	63	0	9.12	3.01 **	
F2	2000	St. Thomas	97	Grenada	39	Largo	63	0	7.12	5.48 **	
F2	2001	Fidel	105	Cuba	37	Largo	63	0	6.83	1.74 *	
F2	2002	Curacao	111	Cuba	37	West	62	0	7.25	5.61 **	
F3	2003	Jamaica	123	Cuba	37	?					
F3	2003	Dominica	124	Lucia	75	?					
F4	2004	Antigua	130	Lucia	75	Barbados	57	0	8.12	8.12 **	
I1	1996	Malawi	44	Namibia	47	Sudan	43	1	6.97	3.95 **	homozygeous
I1	1997	Angola	58	Namibia	47	Congo	52	0	9.05	2.97 **	
J1	1997	Burma	81			Vietnam	70	0	6.24	6.24 **	
J1	1999	Lanka	71	India	66	Laos	67	0	5.63	4.89 **	
J1	1999	Korea	85	China	80	Laos	67	0	8.86	6.58 **	
J2	2001	Cambodia	104	China	80	Nicobar	90	1	9.2	5.04 **	homozygeous
J2	2002	Irak	110	China	80	Nicobar	90	0	9.52	9.52 **	
J3	2003	Yemen	122	Cambodia	104	Kirgis	113	0	7.08	7.08 **	
J3	2004	Libanon	127	Cambodia	104	Cancun	114	0	9.64	5.41 **	
J3	2004	Lesotho	132	Burma	81	Cancun	114	0	9.58	0.88 *	

- 1) Mismatches between offspring, mothers and candidate fathers. If mothers were not known, only mismatches between offspring and candidate fathers are indicated.
- 2) Classification of mismatches. One homozygeous mismatch was not a criterion for paternity exclusion, as homozygeous mismatches are likely to occur as a result of null alleles.

Appendix B: The ordered logit model

The ordered logit model assumes that a latent variable y^* , ranging from $-\infty$ to ∞ , underlies the observed dependent variable y . With regard to the models tested in this study, in the tug-of-war or priority-of-access model, y^* can be interpreted as the dominant's inability to monopolize reproduction. As this inability increases, subordinates are more likely to gain a higher proportion of the group's overall reproduction. More precisely, the dependent variable y will switch from a lower (discrete) level to the next higher level if a certain threshold-value τ in y^* is reached. A single observation will be of class k in y according to the following equation (Long 1997):

$$y_i = k \quad \text{if} \quad \tau_{k-1} \leq y_i^* \leq \tau_k \quad \text{for} \quad k=1 \text{ to } j$$

The extreme categories 1 and j are defined by open-ended intervals with $\tau_0 = -\infty$ and $\tau_j = \infty$. In terms of our dependent variable,

$$y_i = \text{"low"} \quad \text{if} \quad -\infty \leq y_i^* \leq \tau_1$$

$$y_i = \text{"medium"} \quad \text{if} \quad \tau_1 \leq y_i^* \leq \tau_2$$

$$y_i = \text{"high"} \quad \text{if} \quad \tau_2 \leq y_i^* \leq \infty$$

Having defined the thresholds, the probability of observing k in the i th observation, conditional on the independent variables "number of males" (x_m) and "number of females" (x_f), can be calculated as follows (for a derivation of this equation see Long [1997], pp. 120-122):

$$\Pr(y_i = k | x_{mi}, x_{fi}) = G(\tau_k - x_{mi}\beta_m - x_{fi}\beta_f) - G(\tau_{k-1} - x_{mi}\beta_m - x_{fi}\beta_f) \quad [\text{Equation 1}]$$

Estimates of the threshold values and the regression coefficients (β_m and β_f) are obtained from all observations using maximum likelihood estimation. Further, assuming that the error distribution of this estimation is logistic, G can be substituted with the cumulative density function of the standard logistic distribution,

$$G(q) = \frac{\exp(q)}{1 + \exp(q)},$$

and thus,

$$\Pr(y = k | x_m, x_f) = \frac{\exp(\hat{\tau}_m - x_m \hat{\beta}_m - x_f \hat{\beta}_f)}{1 + \exp(\hat{\tau}_m - x_m \hat{\beta}_m - x_f \hat{\beta}_f)} - \frac{\exp(\hat{\tau}_{m-1} - x_m \hat{\beta}_m - x_f \hat{\beta}_f)}{1 + \exp(\hat{\tau}_{m-1} - x_m \hat{\beta}_m - x_f \hat{\beta}_f)},$$

[Equation 2]

in which $\hat{\tau}$ and $\hat{\beta}$ are maximum likelihood estimates of τ and β (see equation 1).

Appendix C: Reproductive skew and group size in the concession model

In a group of size N , each of the $N-1$ subordinates requires an individual staying incentive, which is obtained from equation (4) in Reeve and Emlen (2000):

$$p_s[N] = \frac{xg[1] - r(g[N] - g[N-1])}{g[N](1-r)},$$

in which p_s is an individual subordinate's staying incentive (which is a function of group size), x is a subordinate's constraints on solitary breeding, $g[1]$, $g[N]$, $g[N-1]$ is the productivity of a group of size 1, N , and $N-1$, respectively, and r is the coefficient of relatedness. Note that relatedness is assumed to be symmetric and that all subordinates are assumed to be equally related both among themselves and to the dominant.

Figures A1 A and B depict the individual staying incentive as a function of the number of subordinates for various levels of relatedness and constraints on solitary breeding. Group productivity is assumed to be a decelerating function of group size of the form $g[N] = aN/b + N$, in which a and b are constants. As noted by Reeve and Emlen (2000), the staying incentive either increases or decreases with group size, depending on the level of relatedness and ecological constraints. In contrast, the dominant's share of reproduction (which is often used as a measure of reproductive skew) either remains the same (if all subordinates stay without concessions), but in most cases decreases as group size increases (Figure A2 A,B). Figures A1 and A2 only show the range of group sizes under which associations are stable. For a group of size N to be stable, it is required that the dominant is willing to concede the staying incentive to all of its $N-1$ subordinates. In this case, the dominant receives $g[N]\{1-(N-1)p_s[N]\}$ offspring (Reeve and Emlen 2000), whereas the $N-1$ subordinates together receive $(N-1)g[N]p_s[N]$ offspring. If the dominant withholds the staying incentive from one of the

subordinates (forcing the latter to leave), the dominant receives $g[N-1]\{1-(N-2)p_s[N-1]\}$ offspring, the $N-2$ subordinates within the group together receive $(N-2)g[N-1]p_s[N-1]$ offspring, and the evicted subordinate receives $xg[1]$ offspring. Thus, it pays the dominant to accept all $N-1$ subordinates vs. evicting one of them if the following inequality holds (inequality (5), Reeve and Emlen (2000), modified):

$$\begin{aligned} g[N]\{1-(N-1)p_s[N]\} + r(N-1)p_s[N]g[N] &\geq \\ g[N-1]\{1-(N-2)p_s[N-1]\} + r(N-2)g[N-1]p_s[N-1] + rxg[1] & \end{aligned} \quad [1]$$

The left-hand side of inequality [1] indicates the dominant's inclusive fitness in a group of size N . As long as the association is stable, i.e., as long as inequality [1] is satisfied, the dominant's inclusive fitness increases as group size increases (Figure A3 A,B), despite the fact that its relative share of reproduction generally decreases (Figure A2 A,B).

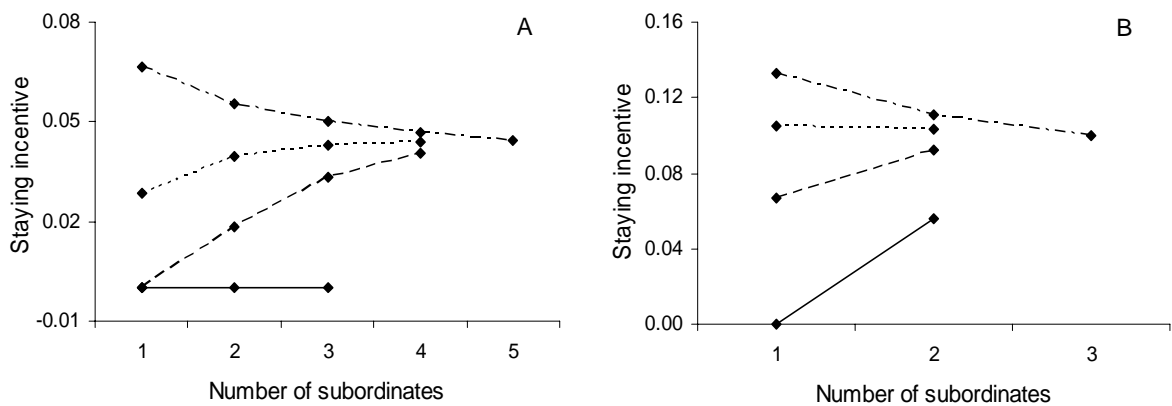


Figure A1: An individual subordinate's staying incentive as a function of group size for various levels of relatedness: $\text{---}\blacklozenge\text{---}$ $r = 0.5$; $\text{--}\blacklozenge\text{--}$ $r = 0.25$; $\text{-}\blacklozenge\text{-}$ $r = 0.125$; $\text{-}\blacklozenge\text{-}$ $r = 0$ under harsh ($x = 0.1$; Panel A) and more relaxed ($x = 0.2$; Panel B) constraints on solitary breeding. Group productivity is assumed to be a decelerating function of group size of the form $g[N] = aN/b + N$ in which N is group size, and a and b are constants set to 3 and 2, respectively. Depicted is the range of group sizes under which associations are stable.

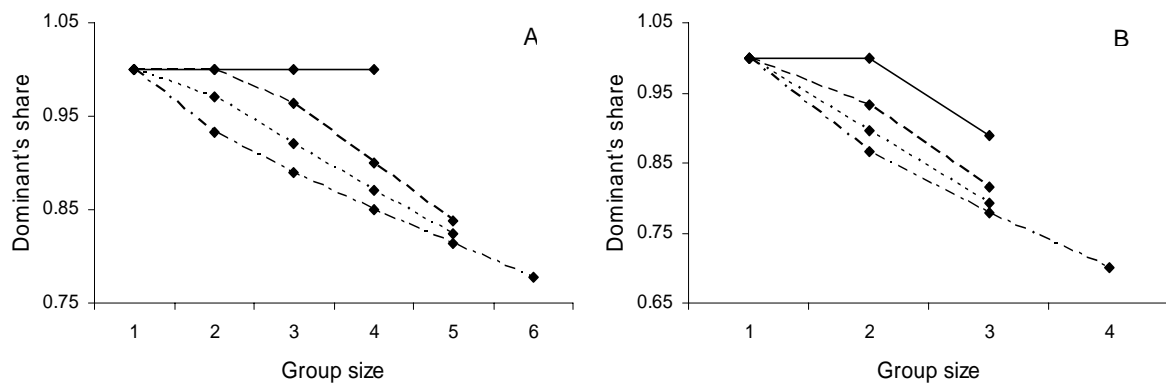


Figure A2: The dominant's share of reproduction as a function of group size for various levels of relatedness: $\text{—}\blacklozenge\text{—}$ $r = 0.5$; $\text{-}\blacklozenge\text{-}$ $r = 0.25$; $\text{-}\cdot\blacklozenge\cdot\text{-}$ $r = 0.125$; $\text{-}\blacklozenge\text{-}$ $r = 0$ under harsh ($x = 0.1$; Panel A) and more relaxed ($x = 0.2$; Panel B) constraints on solitary breeding. Group productivity is assumed to be a decelerating function of group size of the form $g[N] = aN/b+N$ in which N is group size, and a and b are constants set to 3 and 2, respectively. Depicted is the range of group sizes under which associations are stable.

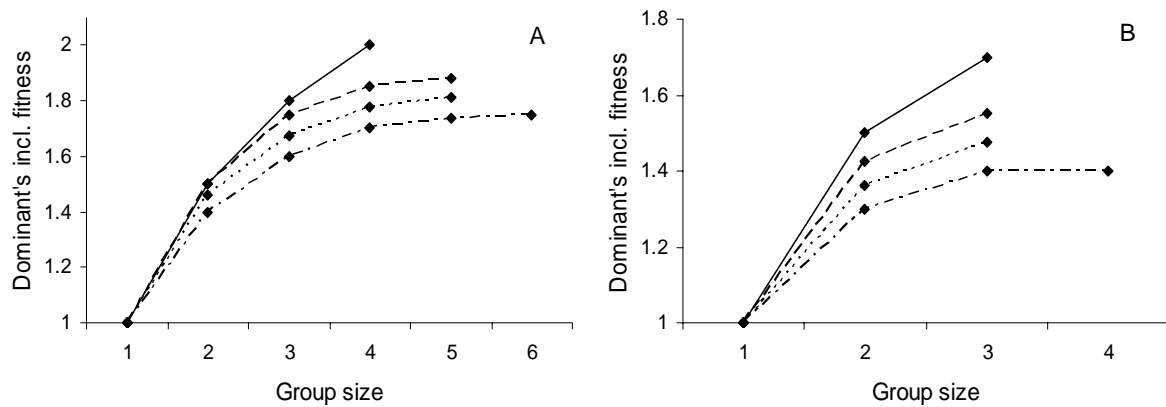


Figure A3: The dominant's inclusive fitness as a function of group size for various levels of relatedness: $\text{—}\blacklozenge\text{—}$ $r = 0.5$; $\text{-}\blacklozenge\text{-}$ $r = 0.25$; $\text{-}\cdot\blacklozenge\cdot\text{-}$ $r = 0.125$; $\text{-}\blacklozenge\text{-}$ $r = 0$ under harsh ($x = 0.1$; Panel A) and more relaxed ($x = 0.2$; Panel B) constraints on solitary breeding. Group productivity is assumed to be a decelerating function of group size of the form $g[N] = aN/b+N$ in which N is group size, and a and b are constants set to 3 and 2, respectively. Depicted is the range of group sizes under which associations are stable.

Curriculum vitae

Personal

Date of birth:	November 13, 1974	Place of birth:	Kassel, Germany
Marital status:	Single, one daughter	Nationality:	German

Education

11.2008	PhD in Biology
08.2006	Summer school in Evolutionary Anthropology, Hanse-Wissenschaftskolleg, Delmenhorst, Germany
10.2005 – 02.2006	Courses in Evolutionary Game Theory, Humboldt University, Berlin, Germany
10.2004 – 11.2008	PhD student, University of Göttingen, Germany
04.2003 – 09.2004	Preparation and planning of PhD; application for funding; Studies of History, University of Kassel, Germany
10.1996 – 03.2003	Studies of Biology, University of Göttingen, Germany, Diploma in Biology
07.1994	Abitur (High School Degree), Freiherr-vom-Stein school; Hess. Lichtenau, Germany

Work Experience

03.2008 – present	Guest scientist, German Primate Center, Göttingen, Germany
01.2005 – present	PhD Position, German Primate Center, Göttingen, Germany
01.1996 – 04.2005	Part time employment as Paramedic, Arbeiter Samariter Bund, Lohfelden, Germany
07.2001 – 09.2001	Research assistant, Ethologische Station Sennickerode, Germany
06.2000 – 08.2000	Voluntary research assistant, Forêt de Kirindy, Madagascar
05.1999 – 06.1999	Research assistant, Institute of Zoology and Anthropology, University of Göttingen, Germany

Community service

10.1994 – 12.1995	Traineeship as paramedic, Arbeiter Samariter Bund, Lohfelden, Germany
-------------------	---