PRIMATE REPORT

76

Aug. 2008

Lion-tailed macaque
Macaca silenus

Cover photo: The lion-tailed macaque (*Macaca silenus*) - a model for the study of fragmentation (Photo: W. Kaumanns).

Editor: Dr. Dr. Michael Schwibbe

Assistance: Heike Klensang

Deutsches Primatenzentrum (DPZ)
Leibniz-Institut für Primatenforschung

Subscription price: € 10,00 / issue

ISSN 0343-3528

Printed by Goltze GmbH & Co KG, 37079 Göttingen, Germany

Contents

FEMALE COUNTERSTRATEGIES TO MALE ALTERNATIVE REPRODUCTIVE BEHAVIORS IN PRIMATES AND OTHER MAMMALS

Jones CB

Key words: coercion, female counterstrategies, force, male alternative reproductive behaviors, persuasion, policing, power, reproductive biostates

Abstract

This monograph discusses female counterstrategies to male alternative reproductive behaviors (ARB) that impose a cost on the inclusive fitness of females under a variety of environmental regimes. *Ceteris paribus*, females may be viewed as host organisms exploited by male parasites, a condition that may be deleterious to females. Sometimes, however, male parasitism is beneficial to females, and the factors inducing these states are explored. It is argued that researchers should increase efforts to investigate and to explain female reproductive behaviors, including both direct and indirect types of aggression. A simple mathematical treatment is advanced to exemplify the antecedents and outcomes of social skew for individual lifetime reproductive success. Providing both novel and derived perspectives on female reproductive behavior, this monograph attempts to clarify definitions of the female state, to consider the costs and benefits of the "female problem", to deconstruct the *myths* associated with the female biostate, to consider *policing* in relation to reproductive and social skew, to evaluate the manifestations of *power* by females, to describe male ARB and their potential consequences for female targets, to delineate female counterstrategies to male ARB, and to consider outstanding questions related to female counterstrategies, including suggestions for future research. Female counterstrategies are discussed in the context of a popular schema whereby behaviors classifiable as *persuasion*, *coercion*, or *force* are expected to be employed to repress competition in groups. All of the responses designated to function as these types of behaviors are presumed to facilitate fitness if genetically correlated in contexts in which the female biostate occasions stress or other costs beyond some threshold levels optimal for survival and reproduction.

Introduction

Research on mammalian sex and reproduction (genetic interests expressed through allocation of resources into mating and parenting effort) in the Order Primates has been dominated by studies of male tactics and strategies until relatively recently (Dixson, 1998; Shahnoor and Jones, 2003). While variations in male reproductive success within groups is relatively well documented for several primate taxa (Dixson, 1998; Ellis, 1995), a comparable understanding of variations in primate female reproductive success is lacking (Dixson, 1998). Research is needed to investigate causes and consequences of within-group relative contributions of direct (selfish) reproduction by female primates ("reproductive skew") in an attempt to detect patterns and processes leading to despotic (high skew) or egalitarian (intermediate or low skew) female relationships. In some species of primates, only one or a few females breed (despotism); in others, females appear to have relatively equivalent breeding opportunities within a reproductive unit (egalitarianism). High or intermediate skew societies are generally distinguished by the presence of helpers who do not reproduce or whose reproductive rate is compromised (e.g., "allomaternal care": Hrdy, 1976; Jones, 1986; Dietz, 2004). Investigations are also required to identify primate "signatures" differentiating patterns of reproductive skew among female primates, and, possibly, other social mammals, from those of social insects, fish, and birds. These studies also have the potential to inform our understanding of reproductive skew within groups of human females by identifying for primates those features characterizing variations in individual opportunities to produce young directly.

Several recent treatments have argued that theories of reproductive skew may yield general formulations for the evolution of social behavior (e.g., Kokko and Johnstone, 1999; Shellman-Reeve and Reeve, 2000; Neff, 2001). There is some disagreement, however, about the relative utility of "transactional" models, on the one hand, and "tug of war" or "indirect control" models, on the other (see Hager, 2003 a). In the former, the presence of one or more same-sex subordinates is beneficial to the dominant extending an "incentive" (i.e., a share of total group reproductive productivity) to the subordinate. Incentives are theorized to induce the subordinate to remain in the group and, since it is the dominant who "decides" to yield or not to yield a staying incentive to a subordinate, the dominant ultimately determines group size (Reeve and Emlen, 2000; Jones, 2004). In "tug of war" models (Clutton-Brock, 1998; see Hager, 2003a), dominants have "incomplete control" over the reproduction of same-sex group members. In this condition, subordinates may have options other than leaving the reproductive unit (dispersal or colonization) if his/her interests conflict with those of the same-sex dominant (see Vehrencamp, 2000). Reproductive skew in groups with "incomplete control" by dominants is expected to be lower, on average, than reproductive skew in groups described by the classic, transactional models (Vehrencamp, 2000).

Several authors (e.g., Reeve and Emlen, 2002; Vehrencamp, 2000) point out that the degree of reproductive skew within groups is a function of three primary factors: (1) dispersal costs (see Hager, 2003 b), (2) the probability of breeding successfully (e.g., costs of reproduction: see Hager and Johnstone, 2004; Kokko and Johnstone, 1999), and (3) the coefficient of within-group relatedness. Recent treatments suggest that interbirth interval (IBI) is a good proxy for assessing relative reproductive skew in primates (e.g., Broom et al., 2004). Table 1 provides a preliminary and qualitative attempt to classify several primate species on the basis of their mating system(s), including degree of variability noted as "facultative" and/or "condition-dependent" (F/CD), effects that may be ubiquitous in primates and other social mammals, predisposing them to exhibit intermediate skew in many regimes (see Jones, 2005), unlike birds (see Vehrencamp, 2000).

One of the most neglected topics in the life sciences concerns the causes and consequences of reproductive decision rules (strategies: Gross, 1996) by females. These decisions, not necessarily conscious and aware ones, involve the allocation of time and energy into mating effort and parenting effort. It is particularly important for female mammals to assess differential costs and benefits of reproductive acts since, in this order, the female sex, compared to the male biostate, bears greater burdens of gestation, lactation, and parental care, *ceteris paribus*. Additionally, female mammals generally exhibit less resource holding potential (RHP: see Parker, 1974) than males in the same conditions, a factor placing constraints on their temporal and energetic fitness budgets (Parker, 1974) whereby resources invested in one response represent resources unavailable to other responses. For several reasons, the induction of female strategies related to mating and parenting has received less attention than the same processes for males. For example, in his classic volume on sexual selection, Charles Darwin (1871) emphasized the conditions and effects of male sexual activities, a perspective that biased the evolutionary literature for decades. Further, although Darwin (1871) proposed a role for the ability of "female choice" to bias the contribution of a subset of male alleles to future generations, this idea remained controversial primarily because his explication of "female choice" was obfuscating (Cronin, 1991) and, also, because of objections by Huxley (1938 a,b), among other prominent biologists. By the 1970s, however, robust mathematical treatments (e.g., Lande, 1981) demonstrated the realism of Darwin's proposal, and, soon afterwards, laboratory and field research provided empirical support for the evolutionary efficacy of "female choice" in a range of organisms (see Andersson, 1994).

Table 1: Preliminary and qualitative classification of primate mating systems and the degree of skew to which groups within these species may be predisposed (based on Vehrencamp, 2000). F/CD= Facultative and/or condition-dependent as a function of local regime which may lead to a high degree of variability in reproductive architecture within species. See text for further information.

		Females		
		Solitary	**Low or intermediate skew**	**High skew**
Males	**Solitary**	Some callitrichids (F/CD); titi monkeys, gibbons	Polygynous howlers (F/CD); langurs (F/CD); gorillas (F/CD)	Some cooperatively breeding callitrichids (F/CD)
	Low or intermediate skew	Some callitrichids (F/CD)	Muriqui; Moor macaque; bonobo; chimpanzee (F/CD?)	Humans? (F/CD?)
	High skew	Some callitrichids (F/CD)	Age-graded and polygynandrous howlers (F/CD); langurs (F/CD); savannah baboons; gorilla (F/CD)	Soem callitrichids (F/CD)

The present monograph advances several perspectives on female reproductive decision making, in particular, counterstrategies to male alternative reproductive behaviors (ARB). An assumption of this document is that male ARB may sometimes benefit, sometimes be deleterious to female inclusive fitness (Rice, 2000). Faced with circumstances potentially damaging to their lifetime reproductive success, females may, not necessarily consciously, adopt responses likely to decrease if not minimize the damaging genetic effects of events perpetrated by past, current, or prospective mates. These female counterstrategies to male ARB are expected to be displayed in response to some threshold of endogenous (e.g., regulatory gene activity, hormone levels) or exogenous (e.g., temperature, interaction rates) stimulation. The character states of each sex, combined with the particular genotypic and phenotypic traits of individuals, will afford members of a given species with a mix of advantageous and disadvantageous features, many of which can be combined and recombined for an individualized behavioral repertoire employed in the ubiquitous game of survival and reproduction (Darwin, 1859). This monograph will attempt, among other objectives, (1) to clarify definitions of the female state, (2) to specify the "female problem", including disadvantages inherent to this character state, (3) to delineate certain *myths* associated with treatments of the female character state, (4) to provide an overview of *policing* tactics and strategies by females and males and their relationship to reproductive and social (all genetically interested responses involving interaction with conspecifics) skew, (5) to address the notion of *power* in relation to female behavior and social organization, including the efficacy of indirect and direct aggression exhibited by this character state, (6) to describe important male ARB, their potential consequences for female targets, and (7) potential responses (counterstrategies) by females to these male action patterns. This document will conclude by (8) considering outstanding questions related to female counterstrategies, including suggestions for future research.

What is a Mammalian Female?

The most common descriptions of a mammalian female expressly or implicitly rely upon a chromosomal definition whereby females are characterized as XX, males as XY. Genetics may, also, define the female state where genetic imprinting (Szymañski and Barciszewski, 2006) is used as the defining feature identifying alleles deleterious to males, the more active character state (see Rice, 2000). Recent treatments advance the view that sex determination is a function of the ratio between X chromosomes to the number of sets of autosomes (the X : A ratio) (Salz, 2007). Feminist treatments criticize biological and binary definitions of reproductive character states, arguing that these ("female", "male") are a function of both psychosocial as well as biological factors (e.g., Strum and Fedigan, 2000). Other common treatments characterize the female sex as that phenotype bearing the greatest costs from parenting effort (Trivers, 1972; also see Penn and Smith, 2007). Additionally, females are viewed as the agents responsible for polygyny (Emlen and Oring, 1977; Bradbury and Vehrencamp, 1977; Wittenberger, 1980) because their dispersion and quality in time and space are directly dependent upon the distribution, abundance, and quality of limiting resources upon which male dispersion is mapped. This schema, termed the "socioecological model" by primatologists (Sterck et al., 1997), advances the view that male tactics and strategies are a function of those exhibited by females utilizing limiting resources (particularly food and space) available for conversion into viable offspring who, themselves, successfully reproduce (see Box 1). In other treatments found frequently in the literature, a mammalian female is defined as the character state with less resource holding potential (see review by Strum and Fedigan, 2000), a ubiquitous tendency to mate multiply during any fertile period (Jones and Cortés-Ortiz, 1998), the trait complex most likely to exhibit indirect rather than direct aggression (e.g., Archer and Coyne, 2005), the character state with certain thresholds or types of neurophysiological features (Martin, 2007; Dubé and Amireault, 2007), the energy-maximizing phenotype (Schoener, 1971), the phenotype with certain morphological (Wilson et al., 2005; Gueguen, 2007; Swami and Trovée, 2007) or behavioral (Pfefferle et al., 2007) characteristics, and the more canalized or "buffered" phenotype (Brody, 1942; Lerner, 1970; Jones, 2005a).

Several lines of evidence related to the topics discussed in the present monograph support the latter inferences. For example, Sinervo and Zamudio (2001) found that male side-blotched lizards (*Uta stansburiana*) exhibited a broader range of alternative reproductive behaviors than did females, suggesting greater genetic and development "buffering" in the latter character state. Because all of these topics have received ample attention by mammalian researchers (see, for example, Eisenberg, 1981; Andersson, 1994), the present monograph will discuss three additional behavioral traits as signature traits of mammalian females. These character states: (1) phenotypic manipulation, (2) strategic handicapping, and (3) female emancipation will be advanced as important formulations for understanding all levels of mammalian female behavior and social organization. A simple mathematical treatment will also be applied to the common element between the sexual biostates.

Studying the "Female Problem"

Male behavior and social organization has been discussed in the primate literature since its inception (Shahnoor and Jones, 2003). In general, males have been viewed as the more active and powerful sex, determining the outcome of reproductive interactions with females. Because of these assumptions, males are widely considered to be the primary targets of sexual selection (differential reproduction), particularly via the mechanism of male-male competition for mates (intrasexual selection). Clutton-Brock (2007; see Kuester and Paul, 1996) has recently reviewed the case for considering sexually selected tactics and strategies in females (i.e., mate choice and mate competition) as well as the likelihood that males exhibit mate choice. Clutton-Brock's review made three inferences: (1) that Darwin's (1871) theory remains a robust conceptual framework for the investigation of secondary sexual characteristics in males and females; (2) that sexual selection acting on female-female competition and female mate choice may explain the evolution of secondary sexual characteristics in females (Fig. 1); and, (3) that many questions remain unanswered about the action of sexual selection on females, in particular, what features of males induce female-female competition. These topics, in part, define the "female problem" as one whereby certain combinations of genetically correlated character states are associated with benefits to lifetime reproductive success. The "female problem" is related to the challenge to differentiate between a female and a male in the sense that defining differences between the sexes can be quantitatively formulated as some repeatable difference threshold between sets or combinations of character states. The "female problem" will be resolved when, as Clutton-Brock (2007) suggests, more is known about the mechanisms and functions controlling the causes and consequences of sexual selection in females.

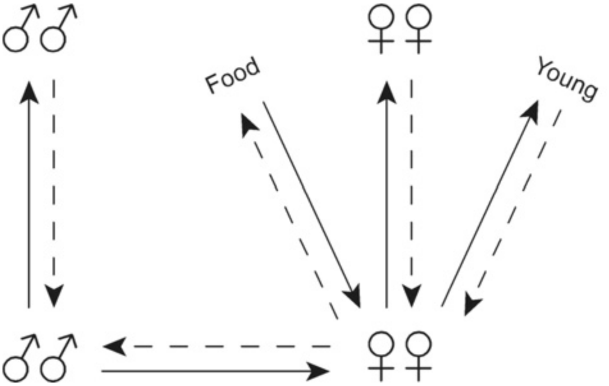

Fig. 1: Figure shows suggested directions of potential conflict(s) (differential optima) where one class or category of individuals imposes costs in inclusive fitness upon another class or category of individuals (closed arrows) to which the latter may respond adaptively (counterstrategies:broken arrows). Across taxa, the evolution of social behavior (interindividual interactions among conspecifics) is likely to reveal the significance of these patterns for complex sociality—the repression of competition by selfish, cooperative, altruistic, or spiteful behavior. © Clara B. Jones

Myths about the Female Character State

Two myths, in particular, abound about the female character state. First, in the primate literature, females are ubiquitously assumed to be more "social" (all types of genetically interested responses involving interactions between conspecifics) than males. Implicit in this assumption is the implication that cooperation and altruism are more desirable responses to conspecifics than selfish or spiteful behavior. This perspective overlooks the important observation that behaviors are expected to be exhibited where their benefits outweigh their costs. Thus, all genetically correlated behaviors, not only those benefiting the reproduction of a conspecific (*sensu* West-Eberhard, 1967), have the potential to advance a female's inclusive fitness. Future research is required to identify the particular endogenous and exogenous factors that may bias male or female behavior in favor of cooperation or altruism. If, indeed, the female character state is more likely to be so biased, then this finding would, further, assist with empirical definitions of females, on the one hand, and males, on the other.

Another myth that has helped to obscure quantitative, empirically based definitions of sexual character states is the perspective that plasticity is usually beneficial to individuals. This assumption is widespread in primatology and has retarded research into the developmental genetics and consequent phenotypic expression of female behavioral biology. Findings from both invertebrates and vertebrates, for example, suggest that females are the more canalized or buffered sex, a state which, if supported by additional evidence, would indicate that females are less plastic, *ceteris paribus*, than males in the same conditions (Lerner, 1970; Jones, 2005; also see Brody, 1942). If, as the literature suggests, it is accurate to say that females are more likely to display behavior facilitating the reproduction of conspecifics (cooperative or altruistic behaviors), perhaps this social strategy compensates for the costs of canalization. Another possibility generated by research on eusocial insects (Helms Cahan et al., 2004) is that canalization increases the likelihood that female phenogroups or biostates will rely more upon *hard-wired* (genetically induced) mechanisms (e.g., polymorphisms) than environmentally determined or switched ones (e.g., polyphenisms). In order to test these and related ideas, it will be necessary to compare and contrast the structures and functions of genetic mechanisms in males and females and to identify the endogenous and exogenous factors responsible for the resulting character states.

Social Skew and Policing in Mammals: Implications for Females

Differential reproduction is fundamental to the evolution of social behavior. Early attempts to describe lawful patterns of interindividual behavior within and between societies emphasized the direct and indirect relationships between an actor and one or more recipients of a response for the optimization of "inclusive fitness". Advances in the study of reproductive skew (the within-sex partitioning of reproduction within social groups) were presaged by early work in behavioral ecology demonstrating a relationship between dispersion and quality of food resources and variations in social behavior, social organization, and mating system(s) within and between populations (Emlen and Oring, 1977; Bradbury and Vehrencamp, 1977). Subsequent treatments incorporated fitness effects upon all individuals influenced by an actor's behavior, not only offspring and kin (see Reeve, 2001). These models differentiated, also, between local and global effects. Models of reproductive skew incorporate ecological and social as well as genetic (r) factors in an attempt to describe how individuals with selfish interests behave to increase the likelihood that total group reproductive output will be biased towards themselves. Key literature has pointed out that suppression of competition and, related to this, suppression of reproduction (by *ego* or others) are fundamental processes, in addition to kin selection, for the evolution of complex sociality (cooperative breeding or eusociality) (Frank, 1995).

Cooperative breeding or eusociality imply high skew in which one or a few individuals of a given sex are primarily responsible for group output ("despotic") while, in intermediate or low skew societies, within-group reproduction is distributed more equally ("egalitarian"). Different skew models make different predictions, and these research projects are in their early stages (Hager, 2003).On the one hand, "transactional" models emphasize stable strategies among members of the same sex in a group in the partitioning of reproduction. These schemas assume that one or more dominant individual benefits from the presence of one or more subordinate. Individuals may have different optima; however, it is assumed to be beneficial to same sex interactants to maintain stable relations. Indeed, the advantages to inclusive fitness of stable relations occasioned by energy savings may favor asymmetrical relations as commonly found in bisexual associations (i.e., males are usually dominant, females, subordinate).

Concession models of skew, on the other hand, assume that the presence of one or more same-sex subordinates is beneficial to the dominant that may extend "incentives" (i.e., one or more shares of total group reproductive productivity) to the subordinate in order to decrease the likelihood that (s)he will emigrate or escalate an interaction. Incentives are theorized to induce a subordinate to remain in the group and, since it is the dominant who "decides" to yield or not to yield incentives to a subordinate, the dominant ultimately determines group size in these models. In "tug of war" models, dominants exercise "incomplete control" over the reproduction of same-sex group members. In this condition, subordinates may have options other than leaving the reproductive unit (dispersal or colonization) if the costs of remaining outweigh the associated benefits.

An important insight into the logic of transactional models is the recognition that, at some varying threshold point, extreme selfishness among interacting individuals destabilizes a group. Individual costs, then, should increase in these conditions, a tradeoff that should, on average, occur more often for subordinates than for dominants. An extrapolation from this framework is that subordinate "decisions" may, in some regimes, be more likely to stabilize potential stochasticity within groups, *ceteris paribus*. Other recent theoretical schemas describe the conditions under which selfishness is likely to increase (Langer et al., 2004; Reeve and Shen, 2006). Still more recent theoretical work exhibits the importance of intergroup conflict for the evolution of complex social behavior and social organization (Reeve and Hölldobler, 2007).

Research on social evolution has sometimes viewed social factors and sexual/reproductive factors as effectively the same. Importantly, however, recent work demonstrates the value of treating mating systems and social systems from a coevolutionary perspective whereby costs imposed by one individual or group upon another individual or group lead the group imposed upon (e.g., subordinates, females) to adopt short-term or long-term countertactics and counterstrategies to the imposer's behaviors or displays (Crespi, 2007). Such states may exhibit significant potential for instability, a topic in need of study by researchers in the field of causes and consequences of reproductive skew. This program will prove to be a daunting task because the requisite empirical studies are lacking. Thus, for the foreseeable future, theoretical work on reproductive skew is expected to remain particularly influential.

Related to social, sexual, and reproductive tradeoffs is the growing body of evidence that energetic factors, in particular, energy savings, may provide fundamental explanations for its rise. It will be particularly interesting to investigate the potential for pathways sensitive to energy-maximization and/or energy-savings to be implicated across taxa in the evolution of complex sociality (see Toth et al., 2007). For example, most models of reproductive skew posit a role for dispersal costs, costs of reproduction, and the coefficient of within-group relatedness as fundamental to the evolution of cooperative behavior and social organization and of eusociality (e.g., Reeve and Emlen, 2000). Other factors have been advanced for their possible significance such as resource patchiness, environmental stochasticity, and alloparental care. Eventually, the differential energetics of all possible determinants of complex social behavior and social organization will need to be explored
(see **www.nescent.org/dir/sabbatical_fellow.php?id=00005**).

The database on social insects, female dominated societies, has been fundamental to research on reproductive skew and attempts to identify general principles of social behavior (Hamilton, 1964; Keller, 1995; Heinze and Keller, 2000; Reeve, 2001; West et al., 2002; Jones and Agoramoorthy, 2003). This body of literature, however, has rarely been discussed in relation to what features of each sex are more or less generic. Since males are the more derived character state, it might be expected that features of their state would contribute less to general formulations. Related to the search for general principles of social behavior is the program to identify comparisons between social insects and social vertebrates, an ongoing enterprise in the animal behavior and behavioral ecology literature for the past 30 years or more (e.g., Wilson, 1971, 1975; Jones, 1980, in preparation; Brockmann, 1997). As evidence of the latter statement, the results of research on social insects have been employed to provide research questions and a conceptual framework for the investigation of social mammals (Jones, 1996, 2000, 2005a, Jones and Agoramoorthy, 2003; Flack et al., 2005a,b).

One pattern elucidated by research on social insects holds that within-society competition may be restrained not only by high coefficients of relatedness (*r*, the "relatedness hypothesis": Hammond and Keller, 2004) but also by *policing*–the mutual maintenance of "civic order" (the "efficiency hypothesis": Hammond and Keller, 2004; also see Ratnieks and Wenseleers, 2005; Frank, 1995, 2003). In a stimulating paper, Flack and her colleagues (2005a) recently presented a model of the mechanisms and effects of policing–a term originally proposed in the insect literature to describe the control and management of selfishness within societies (Ratnieks and Wenseleers, 2005). The work by these authors suggests that the project to discover general principles of social behavior (the "Hamiltonian" project) would be advanced by a more comprehensive definition of *reproduction* than that employed in their paper and that a novel term, *social skew* might describe this broader concept of reproduction. Social skew may be a particularly important concept for the analysis of female behavior and organization in time and space since, as pointed out above, females are widely regarded as being the more *social* character state in the literature on mammals (e.g., Smuts et al., 1987; Solomon and French, 1997).

Flack et al.'s (2005a) model incorporates both adaptive and non-adaptive assumptions because of its claim that "in primates, conflicts are in many cases only indirectly tied to reproduction–contests erupt over valuable resources and status positions that group members learn are of value in their particular social system." As Mc Cleery (1978) has made clear, however, all behavioral responses, whether direct or indirect, may be assessed for their impact upon inclusive fitness. This perspective is of particular import for the evaluation of female tactics and strategies since these are often presumed in the primate literature to be the target of weak or no sexual selection compared to those of males (see discussion by Clutton-Brock, 2007). Several authors (e.g., Pigliucci, 2001; West-Eberhard, 2003; Jones, 2005a) have suggested, however, that sources of behavioral variability, including learning, may modify phenotypes even if responses are genetically uncorrelated and/or are not adaptive (fitness promoting) effects, a condition that might occur under weak sexual selection. These factors, nonetheless, have the potential to influence interindividual outcomes within societies that may have positive, negative, or zero consequences for the reproduction of group members. Since mammalian males are more likely to be the solitary character state or the sex interacting less commonly with other conspecifics as a component of a lifetime reproductive strategy, the impact of social factors for inclusive fitness maximizing is of special import for treatments of female responses, including their counterstrategies to male behavior and configurations in time and space.

Flack et al. (2005a) treat primate and insect reproduction dichotomously, contrasting the variability, complexity, and proximate causes and consequences of primate conflicts with purportedly lower-order insect responses. Such a limited view raises the possibility that a broader definition of reproduction than that envisioned by Flack et al. (2005a) is warranted. Consistent with this suggestion, Ratnieks and Wenseleers (2005) have pointed out that "more effective policing results in fewer individuals acting selfishly", suggesting that the treatment by Flack and her collaborators is related to models of reproductive skew (the within-group apportionment of reproduction: Hager, 2001; Reeve, 2001). A more comprehensive approach would hold that all variance in the apportionment of limiting resources within groups is a fundamentally social enterprise since all social responses, not only those related to the allocation of reproductive effort, entail differential within-group apportionment of limiting resources (e.g., mates, space, food, as well as offspring: see Mc Cleery, 1978). As such, the within-group variance in "the ability to do or act in a situation" (Beekman et al., 2003, p. 277) in which genetic and/or phenotypic conflicts of interest exist might be envisioned as *social skew*, a quantitatively varying term incorporating all phenomena related to differential attempts by individuals to control or to manage within group selfish behavior, including conflicts over limiting resources (e.g., a group's reproductive output).

A partial theoretical formulation of social skew is provided by West et al.'s (2002) extension of the well-known Hamilton's rule (1964), $rb - c > 0$, originally formulated to predict when altruistic behavior (behavior benefiting the reproduction of the recipient but not the actor) towards relatives (progeny and other kin) will be favored where c is the altruist's cost in fitness, b, the fitness benefit to the recipient, and r the coefficient of relatedness ("inclusive fitness"). Since all behaviors may be envisioned as occurring in response to some ratio of benefits to costs (to inclusive fitness: +, - , or 0), possibly a threshold value, Hamilton's rule provides a framework for understanding responses other than altruistic ones (e.g., policing). For example, while applications of Hamilton's rule generally assume that benefiting the reproduction of relatives is advantageous to the actor, West et al. (2002) showed that such actions may lead to increased–rather than decreased–competition among kin, "reducing or even completely removing the net selective advantage" of the original act. This insight permits Hamilton's rule to be generalized to behaviors other than altruism (e.g., policing) since West et al.'s (2002; also see Mc Cleery, 1978) extension shows that behavioral decision-making will be a function of the behavior's positive and negative influences on all organisms affected by the act. Where policing is advantageous, a *decision* to police (e.g., a decision to intervene in ongoing fights or contests) is expected to depend upon the act's consequences upon the competitive regime of the actor's direct (progeny) or indirect (other relatives) kin. This view suggests that, on average, policing may decrease local competition for limiting resources (supporting the "effectiveness hypothesis"), such as a group's reproductive or other social (e.g., grooming, play) output (see below).

West et al. (2002) show that it is helpful to consider not only the relationship between actor and recipient, as for Hamilton's rule, but also a behavior's fitness consequences for all individuals affected by an act (e.g., all individuals affected by attempts to control or manage the expression of selfishness within groups). Since male and female optima are expected to differ so that females will be primarily interested in the apportionment of food, space, and other resources convertible to offspring and males, the apportionment of females (see, for example, Trivers, 1972; Emlen and Oring, 1977), the values of parameters are expected to differ in most conditions for the sexes (see Jones and Agoramoorthy, 2003). In general, female inclusive fitness is expected to be more dependent upon those values reflecting consequences for or interactions with conspecifics since male interests should favor selfish reproduction because of the potentially deleterious effects of low paternity confidence which will dilute genetically effective factors and decrease benefits to males from indirect reproduction, *ceteris paribus*, compared to females in the same conditions.

West et al. (2002) extend Hamilton's rule so that $r_{xy} b - c - r_{xy} d > 0$, where r_{xy} is the actor's relatedness to the beneficiary of the act (thus, Hamilton's r), c and b are defined as in Hamilton's rule, r_{xe} is the actor's relatedness to individuals experiencing increased competition from the beneficiary, and d is the general decrement in fitness associated with the act. Thus, when applied to acts of policing, a decision (not necessarily conscious and aware) to act will be a function of the actor's potential benefits and costs from the consequences of policing for the inclusive fitness of relatives and non-relatives. r_{xe} will be associated with local (single patch) competition, increasing as within-patch competition for limiting resources intensifies. It is particularly important to recognize, as outlined above, that, compared to males, females are expected to be most concerned with the broad spectrum of factors discussed by West et al. (2002) since male interests will primarily concern direct reproductive (genetically interested) effects. To reiterate, the present paper holds that, in general and compared to males, female inclusive fitness is more dependent upon tradeoffs from conspecifics other than direct offspring.

The values c and d are expected to incorporate effects–genotypic and/or phenotypic–such as those imposed by learning which may be non-adaptive and may result from manipulation and/or exploitation by other group members, including kin (e.g., "phenotypic manipulation": see Jones, 2005a and below). Such effects may represent real costs (e.g., stochasticity, inaccuracy, loss of time and energy) or costs borne in the short term in expectation of future benefits (see Crespi, 2000). As a result, primates and other social mammals (e.g., many cetaceans, rodents, pinnipeds) may be especially vulnerable to "best-of-a-bad-job" outcomes (Brockmann, 2001; Jones and Agoramoorthy, 2003; see Jones, 2005c)–including intermediate or low levels of social skew–because of the condition- and situation-dependence of their tactics and strategies and the resulting variability, uncertainty, and, possibly, risk of genotypic and phenotypic effects resulting from local competition. All of these factors, combined with others (e.g., dispersal costs and the probability of breeding successfully), will influence social skew within groups, including the variance in social behavior discussed by Flack et al. (2005a) and are expected to exhibit particular import for females compared to the male character state.

Females, Power, and Policing

Power (the ability to do or act in a situation in which conflict over reproduction exists: Beekman et al., 2003) derives from the ability of individuals to repress competition in their social units, including their ability to monopolize limiting resources that can be converted into offspring (Jones, 2000). Power is ubiquitously viewed as a male attribute in the canon of the humanities (Faubion, 1994), the social and behavioral sciences (Molm, 1997), and in the biological sciences (Beekman et al., 2003). According to Frank (1995; also see Crespi and Choe, 1997), repression of competition is achieved either by self-restraint or by coercion or force (e.g., policing). The female character state is often not predisposed to repression of competition by coercion or force because their resource holding potential is generally less effective, both genetically and phenotypically, than that of males (but see Setchell et al., 2006). It appears, then, that the differential character states defined as female, on the one hand, and male, on the other, represent alternative phenotypes for allocation of time and energy into predominantly non-damaging (females) and predominantly damaging (males) (after Parker, 1974; but see Jones, 1996) phenogroups. Such differentiation is widespread in nature in the form of division of labor, role, and task and should be explored by behavioral ecologists as responses to both morphological and ecological constraints, varying coefficients of relationship (*r*), dispersal costs, and costs of reproduction. For each of these factors, mammalian males are expected to be at an advantage compared to females because of the inherent anisogamous inequality between the sexes and the consequently high costs in maintenance, gestation, lactation, and parenting incurred by mammalian females. These and related differences (e.g., the environmental potential to favor counterstrategies adaptive to females or males) are likely to explain comparisons and contrasts between the sexual character states in mammals.

Inherent in the differences between genetically correlated female and male traits is the concept of *sexual conflict* (Arnqvist and Rowe, 2005) whereby the reproductive (genetically interested) decisions and their consequent evolutionary biases differ. As Chapman (2006; also see Rice, 2000) points out, sexual conflict devolves from anisogamy and from low relatedness of mating dyads, thus, explaining its widespread distribution in organisms. As stated previously, the genetic, physiological, and phenotypic consequences of anisogamy are particularly pronounced in mammals. As a result, sexual conflict is expected to operate with strong evolutionary force in this Class. Similar to the ideas of Clutton-Brock (2007), Chapman (2006) suggests that sexual conflict is poorly defined in the literature and that little empirical evidence exists for it, primarily because it is difficult to observe. Furthermore, Chapman points out that little is known about the relationship between sexual conflict and mechanisms of reproductive isolation and speciation. Finally, as several authors have made clear, Chapman emphasizes that the distinctions, if any, between sexual conflict and sexual selection are unclear. According to her, Arnqvist and Rowe (2005) clearly identify the unique features of sexual conflict by stressing that sexual conflict represents selection upon females to reduce mating costs. Although Arnqvist and Rowe's (2005) definition is, as stated by Chapman (2006), is clear and precise, in the final analysis sexual conflict may be viewed as a mechanism leading to differential reproduction. Thus, sexual conflict, like coercion as discussed by Smuts and Smuts (1993), is best viewed as one of many mechanisms of sexual selection, all of which may be characterized as intrasexual processes (West-Eberhard, 1979; Andersson, 1994).

Chapman (2006) provided details about the non-adaptive outcomes of female reproductive decisions, making the point that mechanisms of sexual conflict are inconsistent with "good genes" models of sexual selection, specifically, Fisher's (1930) "runaway process". In this qualitative treatment, Fisher suggested that female mate biases and male traits were genetically correlated and that initial female preferences produce a positive correlation between female decisions and male characters. Fisher argued that the non-randomly generated correlation would be strengthened with each generation, causing the "runaway" evolution of female preferences and male traits. Fisher's (1930) ideas were unpopular, particularly because of Huxley's (1938a,b) opposition. However, they were vindicated by theoretical work decades later (e.g., O'donald, 1977; Lande, 1981) which showed that even when female preferences are mediated by genetically regulated sensory and neural mechanisms, a positive genetic correlation may occur between mating preferences of females and a male's phenotype. Arnqvist and Rowe (2005) showed that non-equilibrium models may be the best fit to cases of sexual conflict because of the very large number of ways that females and males may respond to costs imposed by the opposite sex.

One of these costs to mammalian females and their young is actual or potential aggression by a male. Because most mammalian females are physically compromised compared to males in the same conditions, use of damaging tactics and strategies to optimize inclusive fitness is often not an option for the female character state. As a result, it has been suggested that those alternative responses most beneficial to mammalian females will involve the expression of indirect attempts to monopolize or influence males and/or the resources that they manipulate (e.g., other males and females) or control (e.g., space or food). Brown et al. (1997) advance a useful schema for the classification and interpretation of conflict situations, including potential or actual conflict between the sexes in mammals. According to these authors, "Conflict arises whenever the outcome of an interaction yields differing optima for different individuals or classes of individuals" (Brown et al., 1997, p. 353). As discussed by Trivers (1972), conflict between males and females, particularly in mammalian species, arises due to anisogamy and the fundamentally different energetic investment in gametes between the sexes. Additionally, for mammals, there is an inherent difference in time investment between males and females whereby female mammals invest significantly more time in physical maintenance, gestation, lactation, repair and recovery after the latter two stages, and parenting. Indeed, the latter period of energetic and temporal investment may extend, at least intermittently and often unpredictably, across a lifetime. These latter comments do not take into account the additional investment females sometimes accrue in the children of their issues and so on.

Brown et al. (1997) posit that each member of an interacting dyad "will be selected to manipulate the interaction in ways that bring the outcome closer to its optimum" (p. 353). In this schema, the mechanisms of manipulation are (1) persuasion, (2) coercion, and (3) force. Persuasion is advanced to be a cooperative mechanism whereby conflict is resolved in a manner beneficial to the inclusive fitness of both parties. An interesting feature of this mechanism as described by Brown et al. (1997) is that an individual may behave selfishly while, at the same time, facilitating the genetic interests of another–the recipient of the actor's behaviors. In male–female interactions, either sex may adopt this strategy although it is likely to be exhibited primarily by females since persuasion is expected to involve costs in time to which males will be averse (Schoener, 1971).

An example of female persuasion of males occurs in mantled howler monkeys (*Alouatta palliata*) when females employ the rear-present posture to induce males to follow them to a tree bearing preferred food (e.g., flowers, new leaves, or fruit) (Jones, 1997). In this situation, optima differ between the sexes since a female's priority is to feed and to control the timing of fertilization while a male's is to monopolize some threshold optimum number of females, to intromit, and to inseminate a partner and outcompete any residual sperm in her reproductive tract (Alexander et al., 1997). By definition, these differential optima represent different tradeoffs of time and energy entailing differential allocation of resources into parenting (females) or mating (males) effort. The cooperative nature of this interaction is that, although a female behaves selfishly by utilizing the male's defensive abilities to monopolize a feeding source for her, the male may benefit by increasing his likelihood of copulation with this or other females *via* his protective and/or guarding behavior.

Coercion has been discussed by Smuts and Smuts (1983) in their classic paper delineating mechanisms and functions, causes and consequences of coercion in primates, a treatment applicable to all mammals. As Brown et al. (1997) define it, coercion involves a game between interactants in which the costs of continued time–energy investment outweigh benefits for one party, resulting in that individual's avoidance, retreat, or escape. In these conflicts or struggles, interactants assess each others' resource holding potential and, possibly, "intent" or motive (see Brown et al., 1997, p. 354), resulting in rapid settlement or struggles reaching a "give up" point for the party with the lowest threshold of response to challenges to his or her "fitness budget". Examples given by these authors are harassment, limiting access to resources, and struggles over mating initiation or termination. When male mammals attempt to coordinate or control female behavior, the latter character state may counter with any of the responses indicated by Brown et al. (1997). For example, female mantled howler monkeys may harass a courting pair or a pair *in copula*, increasing the likelihood that a successful fertilization will be denied a male (C. B. Jones, personal observation). Alternatively, mammalian males may direct females away from feeding sites until ejaculation is effected, potentially imposing nutritional, energetic, or other costs upon females. Additionally, female mantled howler monkeys may terminate mating during the pre-intromission phases of courtship or after intromission has been effected but before a successful ejaculation (Jones, 1985).

Male-male competition, a topic discussed at length by Darwin (1871), may lead to intense exhibitions of indicator behaviors and displays by males to attract, coordinate, and control females and to repel challengers. Force is expected to be more characteristic of mammalian males than of mammalian females for the reasons already stated (i.e., differential body size and fighting ability: Reichard et al., 2005; also see Darwin, 1871) and, also, because force is a "time minimizing" strategy upon which male "decisions" are primarily based (Schoener, 1971), *ceteris paribus*. As Brown et al. (1997) point out, force reduces or eliminates the benefits of control for the opponent although it may not entail costs and may be beneficial for the opponent. The differential benefits and costs of force or other alternative responses (persuasion, coercion) are expected to derive from the degree of environmental predictability and consequent resource dispersion and quality upon which female dispersion and quality will be mapped (Jones, et al., in press). Males will be more likely to employ aggressive tactics when resources are clumped and females defensible or monopolizable in time and space, and unpredictable patterns of resource dispersion may lead to "female emancipation", an environmental state likely to be costly to females if the advantages to females from coexisting with one or more males in bisexual groups (e.g., advantages derived from male defense of resources) are lost. Female emancipation may, also, be deleterious to male fitness since female, rather than male, decisions are thereby enhanced and time-minimizing strategies disfavored under these conditions. Most mammals are solitary, a condition probably related directly to the unpredictability of resources (Jones, in press).

In another scenario, both sexes may benefit from force exhibited by males. For example, female mantled howler monkeys may benefit from forced copulation ("rape" or "traumatic insemination") under some conditions, for example, when a dominant and presumably fitter male usurps a copulation attempt by a subordinate, and, presumably, less fit, male (Jones, 2002). Perhaps infanticide and the threat thereof represent the classic examples of force in the primate literature about which much has been written (e.g., Van Schaik and Janson, 2000). In this case, one sex, generally males, impose reproductive costs upon the other sex, generally females. Although it is most often assumed in the mammalian literature that the short-term reproductive (e.g., energetic, physiological) and other (e.g., possible injury) costs borne by females are deleterious to the latter's inclusive fitness, I am unaware of any theoretical or empirical attempts to demonstrate differential costs and/or benefits to females from infanticide over the course of a lifetime and beyond. Although the arguments in favor of the benefits of force to males in their intersexual relations are persuasive, researchers need to investigate, as well, the adaptive significance to mammalian males of tactics and strategies other than forceful ones (e.g., female – male cooperation).

A final perspective on force in relation to male ARB concerns force as a type of punishment (Jones, 2006; Jones, 2007b). Where female: male interactions are viewed from the perspective of host (usually females) : parasite (usually males) relations, variability in host (female) behavior may be induced by the virulence of the social parasite [pathogenic male(s)]. Responses by both host and parasite may be induced by endogenous (e.g., hormones) or exogenous (e.g., learned responses) factors, probably as a function of generation time (T) and/or reproductive value (r). All punishment is, theoretically, expected to decrease the likelihood of selfish behavior(s) and will, as well, decrease social skew, minimizing the apportionment of resources to individuals of a given sex within groups. Several topics discussed in this monograph so far are consistent with these definitions and expectations (e.g., virulence, aggression or force, policing, display, social parasitism). Table 2 is a tentative schema displaying expected outcomes favored from punishment applied by an actor (parasite or male) to a recipient (host or female), and expected costs and benefits. Future theoretical and empirical work needs to test the assumptions and other features of this qualitative treatment.

A related topic needing theoretical and empirical treatment by investigators is "resistance to being manipulated" (S. Vehrencamp, personal communication, 2007), a class of responses that should be studied within the context of conflict theory. Females and other subordinates might be particularly inclined to resist male manipulation, coordination, and control where these individuals experience deleterious costs to inclusive fitness. On the other hand, in some conditions, dominants might, also, might demonstrate resistance to manipulation, coordination, and control by other group members, especially where dominant individuals achieve only incomplete control over their group mates. In these situations, it seems likely that individuals with greater resource holding potential or fighting ability will benefit from tactics and strategies of resistance that will minimize costs to their inclusive fitness and maximize their control over less powerful members of their group. It will, then, be very important to identify when and under what conditions resistance to manipulation benefits individuals (x age, x sex, and x other factors such as *r*) and when it does not. Studying female mantled howler monkeys, I have found that females of any rank are most likely to resist control by males (e.g., terminating or rejecting sexual advances by males or terminating copulations: see Jones, 1985) and by female competitors (interrupting mates *in copula*: C.B. Jones, unpublished) where limiting food resources are unpredictable in time and space (Jones, 1995; C.B. Jones, unpublished), apparently increasing costs of monopolization by males or control by other adults. Similar acts of resistance have been described in other taxa (e.g., Arnqvist, 2006).

Table 2: Punishment by the dominant actor (parasitic male) and expected outcomes for subordinate recipient (host female).

Punishment leads to	**Costs to recipient**	**Benefits to recipient**	**Favors**
Selfishness	Recipient loses	Actor benefits	High skew
Cooperation	See Alexander, 1974	Actor gains, Recipient gains	Intermediate or low skew
Altruism	Actor loses	Recipient gains	Intermediate or Low skew
Spite	Actor loses	Recipient loses	Intermediate or low skew; dispersal (?)

Male Alternative Reproductive Behaviors (*ARB*)

Male ARB are expected to benefit the inclusive fitness of males, *ceteris paribus*, and may be deleterious to the inclusive fitness of females (Rice, 2000). Reviewing "major themes" in developmental plasticity and evolution, West-Eberhard (2003) proposed that "alternative phenotypes" represent "more than one adaptive option in a given functional context" (p. 377). West-Eberhard's (2003) treatment is primarily concerned with micro- and macroevolutionary events leading to speciation while the present paper concerns behavioral processes at the individual and interindividual levels having the potential to enhance fitness. The latter events may be precursors to the sorts of novel responses that interest West-Eberhard as raw material for Darwinian effects. In particular, the processes to be emphasized here share in common the requirement that females behave as active agents of their own inclusive fitness (lifetime reproductive success via direct and indirect descendents). West-Eberhard (2003) points out that alternative phenotypes may be polymorphisms (genotypically regulated alternative responses) or polyphenisms (environmentally switched alternatives) and that they are important sources of biological diversity.

Jones and Agoramoorthy (2003) reviewed and discussed alternative reproductive (genetically interested) behaviors (ARB) in primates, a treatment that can be applied to other mammals. Here we emphasize male ARB because it is these responses that will determine differential reproductive or genetic costs and benefits to female inclusive fitness. As Rice (2000) advanced, when costs to lifetime reproductive success of females increases beyond some threshold level(s) for individual females or, possibly, for particular female phenogroups (Jones, 2005), females may respond with one or more counterstrategies to decrease or minimize the deleterious effects of male action patterns. What are the most likely male ARB in primates?

Jones and Agoramoorthy (2003) employed Taborsky's (1998) schema to discuss ARB among male primates. In this system, two classes of male mating phenotypes were described: bourgeois and parasitic. Bourgeois males follow the decision rule: owner defends, non-owner retreats. Bourgeois males monopolize females or resources that females require for successful reproduction, including rearing of young. Parasitic males, on the other hand, exploit the investment of bourgeois males by adopting tactics and strategies other than monopolization (e.g., sneaker). Studying male Costa Rican mantled howling monkeys, Jones (1995) described five ARB including two forms of consort behavior, sneaker, appeaser, and fighter. Each of these strategies was associated with male dominance rank so that, for example, high-ranking males were the only ones observed to consort with females away from their group. Since dominance rank in this species is age-graded with younger males the highest ranking, male mantled howlers pursue a conditional strategy (Parker, 1982), initially employing consorting away from the group, switching to consorting within sight of other group members, and subsequently switching to sneaker, appeaser, and fighter modes. Recent evidence suggests that male ARB are determined by adult sex ratio and group size (Jones et al., 2008), supporting the prediction of the "socio-ecological" model (e.g., Emlen and Oring, 1977; Sterck et al., 1997) that male ARB will be a function of habitat related demographic patterns and the subsequently varying potential of males to monopolize females in heterogeneous regimes. These inferences may pertain to all vertebrate societies in which males compete directly for access to females.

Jones and Agoramoorthy (2003) argued that ARB were indicative of "best of a bad job" tactics and strategies (Brockmann, 2001) reflecting non-optimal responses resulting from environmental or other (e.g., individual quality) variations. In a more subtle treatment, Lee (2005) discussed a "status dependent model" whereby players above some level of fighting ability or resource-holding power adopt the tactic with the higher payoff, on average, while those below some threshold level demonstrate "best of a bad job" alternatives, the lower payoff tactics and strategies. The empirical results presented by Jones (1995) for mantled howler monkeys and discussed above conform to the "status dependent model" and, also, suggest that the switch point prediction made by Lee (2005) is age-dependent, at least in *Alouatta*.

An important question remaining concerns identification of those environmental features responsible for variations in male responses, including variations in limiting resources, including female quality, dispersion, and/or abundance (Alfaro, 2005; also see Kvarnemo and Simmons, 1999; Jones et al., 2008). These factors are expected to influence male behavior and organization in time and space, and increased variability of female quality, dispersion, and/or abundance is predicted to increase male allocation of resources to reproductive effort, investment of time. An inference from the "socioecological model" is that variations in female traits will depend upon variations in resources convertible to offspring, constraints upon females imposed by nutrient limitation and other resources (e.g., space) required for successful reproduction. The paper by Jones et al. (2008) provides support for the view that resources influence male ARB indirectly by influencing the operational sex ratio (Emlen and Oring, 1977) and group size, factors responsible for the ability of males to dominate fights and contests and to monopolize females.

Jones (2005) applied a parasite – host model to male (usually parasite) – female (usually host) interactions, discussing the causes and consequences of (genotypic and phenotypic) conflicts between them. In this case, May and Anderson's (in Moore, 2002) model describing the fitness of a parasite as the density-dependent value, reproductive rate, was readily applied to relations between mantled howler monkey males and females. Where males parasitize females, female sociality may best be explained by costs incurred by females from male behavior as well as costs incurred from the responses of female competitors. Where females parasitize males (Jones, 1997), including conditions in heterogeneous regimes in which females are unpredictable to males in time and space (Jones, 1995), costs in time imposed on males (see Schoener, 1971) may select for male mate selectivity (Jones, 1985) and potential benefits to females may favor "female emancipation". Contrary to the conclusions of some recent reports (e.g., Alberts et al., 2006), male "choosiness" and other exaggerated social traits displayed by male mammals are likely to be a function of costs imposed by females and by male challengers. These costs are likely to be costs in time to which males may respond with actions benefiting (e.g., parental care) or deleterious to (e.g., some forms of exploitation such as infanticide) the reproductive success of one or more females. Elaborate patterns of time-investment by male mammals (e.g., in courtship or paternal care) are, thus, a likely consequence of costs resulting from male-male and male-female interactions (e.g., Jones and Van Cantfort, 2007). Theoretical (mathematical) treatments specific to social parasitism in mammals are also required. Parasite-host models should also be helpful in analyzing other intersexual interactions characterized by dependence or asymmetry (e.g., partitioning of feeding schedules and sites; division of labor or task)

Female Counterstrategies to Male Alternative Reproductive Behaviors (ARB)

Female counterstrategies to male ARB, if adaptive, are expected to benefit the inclusive fitness of females and to be costly to the inclusive fitness of males (RICE, 2000). Following inferences from the "socioecological model", Fig. 1 advances the view that variability in the distribution, quality, and abundance of food significantly determines female dispersion and quality. Patterns of male response and dispersion, on the other hand, are expected to be a function not only of female distribution in space and time but, also, of the effects of other males. The latter influences are not incorporated into the "socioecological model", a treatment awaiting future research. As noted above, because males will usually exhibit greater fighting ability and resource-holding potential than females, the coevolutionary arms race between the sexes will be generated by male actors targeting female recipients (Table 3). Where male behaviors impose costs upon females above some threshold value(s), females may be favored who respond with counterstrategies to decrease, minimize, neutralize, or eliminate the deleterious effects of male acts (Rice, 2000). This section will discuss four female responses that may function as counterstrategies in some conditions, *ceteris paribus*: (1) multiple mating by females and (2) female-female competition.

Table 3: Preliminary list of alternative reproductive behaviors (ARB) of males and female counterstrategies. These lists are not intended to be exhaustive. + indicates "potentially beneficial to inclusive fitness of the opposite sex" while – indicates "potentially deleterious to inclusive fitness of the opposite sex". As discussed in text, the differential costs and benefits of these behaviors are likely to be a function of the distribution, abundance, and quality of group members in time and space. Thus, hypothesized advantage or disadvantage is intuitive and expected to be condition- and situation-dependent. As suggested by the work of Sinervo and Zamudio (2001), males appear to have a broader range of responses than females, supporting the view that females are more "canalized" than males (Lerner, 1970).

Male ARB	**Female Counterstrategies**
Parental care/+	Phenotypic hitchhiking/+
"Friendship"/+	Dependence/+
Cooperation/+	Exaggerated traits (e.g., genital hypertrophy)/- or +
Exaggerated traits (e.g., displays)/- or +	Appeasement/- or +
Aggression/-	Female dominance/- or +
Force/-	Deception (e.g., false estrus)/-
Coercion/-	Manipulation/-
Policing and monopolization/-	Exit threats/-
Punishment/-	Multiple mating/-
Infanticide/-	Same sex partner preference/-
Parasitism/-	Infanticide/-
Reject copulation/-	Mechanisms of "pretender punishment" (e.g., "marking", "reputation", sub-group differentiation)/-
Manipulation/-	
Strategic handicapping/-	
Deception/-	
Dominance/-	
Same sex partner preference/-	

Multiple mating by females occurs when this sex copulates with more than one reproductively active male during an estrus or menstrual period (Wolff and Macdonald, 2004). Jennions and Petrie (2000) considered "the potential benefits that females may gain from mating more than once in a single reproductive cycle" (p. 21). These authors suggest that multiple mating by females, a precopulatory mechanisms of mate choice, may evolve simply because females encounter opportunities to "trade up" genetically. In another condition, females mate multiply because precopulatory cues are weak, possibly leading to errors in decision-making when females exhibit mate choice. Finally, Jennions and Petrie (2000) advance the commonly held view that multiple mating by females promotes genetic diversity among offspring. These authors concluded that scant evidence exists to suggest that multiple mating enhances female fitness by increasing the likelihood that females will mate with genetically superior males, promoting the view, rather, that postmating mechanisms such as "cryptic" female choice (Reeder, 2003) are likely to be most profitable for females.

Wolff and Macdonald (2004), mammalogists noted especially for their studies of bison and carnivores, respectively, have argued persuasively that Hrdy's (1979) hypothesis for the evolution of multimale mating by mammalian females is correct. Hrdy's (1979) hypothesis states that "multimale mating functions to confuse paternity which, in turn, deters infanticide" (Wolff and Macdonald, 2004). Evaluating data for the 133 species of mammals in which multimale mating has been documented, Wolff and Macdonald(2004) strongly suggest that, of the nine hypotheses attempting to explain multimale mating (Wolff and Macdonald, 2004, Table 1, p. 128), Hrdy's explains most of the observed variance in the data set. Further, this paper describes infanticide as a "pacemaker" for the evolution of multimale mating based upon the "scenario" of Van Schaik and Kappeler (1997) showing "a possible transition from polygyny to promiscuity and monogamy" (Wolff and Macdonald, 2004, p. 131). Although Wolff and Macdonald do not discuss their analysis in relation to thresholds of response or operational sex ratios (also see Queller, 1997), this review and its conclusions provide a very tight case for the utility of Hrdy's (1979) treatment given available research–both theoretical and empirical.

Wolff and Macdonald (2004) argue that the *origin* of multimale mating was not sexually selected (i.e., did not occur in response to genetic or other benefits derived from mating with one male over another). Instead, these authors consider the benefits of multimale mating to be derived wholly from those gained by a female in protecting her living offspring from infanticide. Wolff and Macdonald (2004) do point out that sexually selected benefits might be obtained secondarily "once multimale mating evolved for some other purpose" (p. 130). In light of other treatments of "promiscuity" (e.g., Stacey, 1982; Neff, 2000; Andersson, 2005; Possamai et al., 2007), it will be necessary to carefully unpack the relationship, if any, between multimale mating and sexual selection. Holland and Rice (1999), for example, demonstrate a relationship between sexual selection, "promiscuity", and "intersexual antagonistic coevolution". Hrdy (1974, 1979; also see Van Schaik and Janson, 2000) originally claimed that infanticide by males was sexually selected and, consistent with Holland's and Rice's arguments, multimale mating might be viewed as a response to intersexual conflict and a male trait (infanticide) increasing male fitness at a female's expense. To quote Holland and Rice (1999, p. 5083), "Conflict between mates hinges on sexual infidelity…. [W]henever an individual has multiple mates, the lifetime reproductive success of that individual will differ from the success of its mates. Thus, promiscuity necessarily introduces the opportunity for sexual conflict through the evolution of novel traits that increase the reproductive success of members of one sex at a cost to members of the opposite sex" Multimale mating, probably a ubiquitous trait among primate females, implies, then, intersexual conflict favoring the evolution of female counterstrategies to costs imposed by males, a topic in the early stages of investigation for the Primate Order.

Other characters of the female biostate support the view that multiple mating by females is adaptive. For example, where mammalian females exhibit the capacity for multiple orgasms (i.e., short orgasmic refractory periods exhibited by human females: see Jones, 2007), the relatively brief duration of these responses will facilitate multiple mating whereas longer refractory periods would not. Female action patterns, including multiple mating, are best interpreted as behaviors selected to facilitate, coordinate, and control fertilization, the primary reproductive function of pre- and post-copulatory "female choice" (Alexander et al., 1997). Linking multiple mating to the theoretical perspectives of Alexander and his colleagues (1997) provides a perspective sufficiently different than the one provided by Wolff and Macdonald (2004) to warrant further investigation. On the other hand, multiple mating, the capacity for multiorgasmic response, as well as infanticide are unlikely to be non-adaptive or neutral phenomena because of their high energetic costs (see Jones, 2007) and, thus, are expected to benefit the inclusive fitness of females.

Following Hrdy's (1974, 1979) work, the discussion by Wolff and Macdonald (2004) as well as other scenarios to explain multiple mating by females may be viewed as transactions between potential or actual mates. Shellman-Reeve and Reeve (2000) model interactions between males and females in accord with transaction theory, a category of reproductive skew models including "concession" and "constraint" models (see Hager, 2003). In this view, promiscuity is viewed as a transaction between social mates. Females and males, then, are assumed to be in conflict over the most beneficial tradeoff of mating effort and parenting effort. Neff (2001) points out that, where males are larger than females (as for most mammals, including primates), an amended "tug of war" model may be most appropriate. This author describes Shellman-Reeve's and Reeve's (2000) treatment as showing that the evolution of infidelity requires an assessment of both female and male interests. Because Shellman-Reeve and Reeve (2000) model these states elegantly and with general import, Neff suggests that "transactional theory might provide the basis for a truly unifying theory of social evolution" (p. 175). Despite the literature documenting advantages to females from multimale mating, it is important to keep in mind that this counterstrategy to costs imposed by attempts by males to monopolize the reproductive interests of females may incur significant costs for females, as well (e.g., Muller et al., 2007).

Female-female competition may arise as a counterstrategy to reproductive costs imposed upon females by males (e.g., Su and Birky, 2007). In the primate literature, female countertactics and counterstrategies are generally discussed as responses to costs incurred from infanticidal or potentially infanticidal males (Van Schaik, 2000). Palombit et al. (2001), for example, described female-female competition for male "friends" by lactating female chacma baboons (*Papio cynocephalus ursinus*). These associations benefit females and their young by ensuring protection from infanticide, a male behavior that is assumed by most researchers to be deleterious to a female's lifetime reproductive success. It is, however, possible to imagine conditions in which females might be complicit with infanticidal males if an offspring's genetic or physical state has been compromised by being fathered by an inferior male increasing the likelihood of morbidity and mortality of the young. In such cases, termination of reproductive investment sooner rather than later would be advantageous to both maternal inclusive fitness as well as fitness of the infanticidal male.

Directions for Future Research

Several topics generated by the current treatment of female counterstrategies to male ARB arise. First, and, possibly, most significant is an extension of Frank's (1995) treatment of "repression of competition" to induce cooperation (and, possibly, altruism). It seems likely that, in addition to kin selection ("self-restraint") and coercion, reinforcement or reward may, also, facilitate the expression of cooperation (and, possibly, altruism). Indeed, any repeated stimulation of reward centers will increase the probability that attempts by an actor (say, a male) to manipulate, coordinate, and control the behavior of one or more recipients (say, females) will be successful because of the extremely influential effects of the dopaminergic systems associated with reward in mammalian brains (Gao and Horvath, 2008). Second, Shanoor and Jones (2003) discuss "the male problem", a topic of investigation for many years by scientists studying primates. A developing interest in "the female problem", as discussed above, will permit primatologists to compare and contrast features of the two reproductive biostates, both qualitatively and quantitatively, for a more thorough appreciation of sexual selection, sexual conflict, and differential intrasexual reproduction. Third, a broad array of "stealth" strategies has evolved in females, apparently without counteradaptation by males. Future studies are required to investigate the costs and benefits to both sexes of these tactics and strategies. A female may, for example, become pregnant when it is not in a male's interest for her to do so (e.g., for economic or social reasons). Another example entails females inducing a male to copulate when she is not ovulating. Possibly, males have not evolved counterstrategies to cheating by females because of the relatively inexpensive (in terms of time and energy) tactics and strategies occasioned by coercion and force.

Fourth, a large literature exists on female dominance of males, particularly among some lemuroids (Jolly, 1998). Female dominance of males in mammals requires investigation as a counterstrategy to male ARB. Fifth, several tactics and strategies characteristic of female behavior [e.g., "playing victim"; "hitchhiking" on male traits such as parasitism of resources controlled by males; same sex partner preference ("homosexuality")] may be viewed as possible responses by females to costs imposed by males (e.g., reproductive demands imposed by males beyond the threshold optimal for females). This area of investigation is likely to engage feminist primatologists seeking evolutionary explanations for psychosocial aspects of female personality, cognition, emotions, and behavior. Finally, primates (in particular, monkeys, apes, and humans) appear to be an excellent model for theoretical and empirical research on female countertactics to male ARB because of their phenotypic variability, both endogenously and exogenously induced. Nonetheless, it remains unclear how representative primates are for comparative studies. Additional work is needed to construct cross-taxa, cross-continental comparative studies, either meta-analyses or phylogenetic ones to identify both conserved and plastic features of female counterstrategies to costs imposed by males (Table 1). In the words of Clutton-Brock (2007, p. 1885), "Many important questions about the operation of sexual selection in females and the evolution of sex differences have yet to be answered. Where females compete directly with each other, it is often unclear precisely what they are competing for. Where females have developed obvious secondary sexual characters, it is often uncertain whether these are used principally to attract males or in intrasexual competition for resources, and how their development is limited is unknown." Hopefully, the present monograph will stimulate discussion, ideas, and research leading to a better understanding of females, especially their behavior and the decisions upon which their responses depend.

Acknowledgments

Discussions with the late Jasper Loftus-Hills were my first introduction to many of the ideas developed in the present monographsociobiology. Jasper's memory continues to remain an important model as well as a significant source of inspiration for my work. David Wallace, a social psychologist, has also been instrumental in stimulating my thinking about the precursors and antecedents to social responses. Our unpublished note titled "The Social Psychology of Exploitation: Social Parasitism and Social Influence" proved a good source of insight for one section of the monograph. My research on primate sexual and aggressive behavior was initiated in the 1970s and has, hopefully, matured with advances in the literature of ethology, animal behavior, sociobiology, and behavioral ecology. My understanding of female counterstrategies to male ARB was fostered, also, by developments in research methodology, including theoretical approaches to the study of behavior and social organization, especially, cooperation, competition, and conflict at all levels of organismal analysis. The Editor of *Primate Report*, Michael Schwibbe, has encouraged my contributions to his journal for more than a decade. I am grateful for his and his staff's encouragement, advice, and superior technical expertise. The author was supported by the National Evolutionary Synthesis Center (NESCent, NSF # EF-0423641).

References

Alexander RD, Marshall DC, Cooley JR (1997): Evolutionary perspectives on insect mating. In: Choe JC, Crespi BJ (ed.): *The Evolution of Mating Systems in Insects and Arachnids*. Cambridge, UK, Cambridge University Press: 4-31.

Alfaro JW (2005): Male mating strategies and reproductive constraints in a group of wild tufted capuchin monkeys (*Cebus apella nigritus*). *Am J Primatol* 67: 313-328.

Andersson M (1994): Sexual Selection. Princeton, NJ, Princeton University Press.

Andersson M (2005): : Evolution of classical polyandry: three steps to female emancipation. *Ethology* 111: 1-23.

Archer J, Coyne SM (2005): An integrated review of indirect, relational, and social aggression. *Personality and Social Psychology Review* 9: 212-230.

Arnqvist G (2006): Sensory exploitation and sexual conflict. *Philos Trans R Soc London* [*Biol*] 361: 375-386.

Arnqvist G, Rowe L (2005): Sexual Conflict. Princeton: Princeton University Press.

Beekman M, Komdeur J, Ratnieks FLW (2003): Reproductive conflicts in social animals: Who has power? *Tree* 18: 277-282.

Bradbury JW, Vehrencamp SL (1977): Social organization and foraging in emballonurid bats III: mating systems. *Behav Ecol Sociobiol* 2: 1-17.

Brockmann HJ (1997): Cooperative breeding in wasps and vertebrates: the role of ecological constraints. In: Choe JC, Crespi BJ (eds.): *The Evolution of Social Behavior in Insects and Arachnids*. Cambridge, UK, Cambridge University Press: 347-371.

Brockmann HJ (2001): The evolution of alternative strategies and tactics. *Adv Study Behav* 30: 1-51.

Brody EG (1942): Genetic basis of spontaneous activity in the albino rat. *Comparative Psychology Monographs* 17: 1-24.

Broom M, Borries C, Koenig A (2004): Infanticide and infant defence by males: modeling the conditions in primate multi-male groups. *J Theor Biol* 231: 261-270.

Brown WD, Crespi BJ, Choe JC (1997): Sexual conflict and the evolution of mating systems. In: Crespi BJ, Choe JC (eds): *The Evolution of Mating Systems in Insects and Arachnids*. Cambridge, UK, Cambridge University Press: 352-377.

Chapman T (2006): Sex and power. *Nature* 439: 537.

Clutton-Brock T (1998): Reproductive concessions and skew in vertebrates. *Trends Ecol Evolut* 13: 288-292.

Clutton-Brock T (2007): Sexual selection in males and females. *Science* 318: 1882-1885.

Crespi BJ (2000): The evolution of maladaptation. *Heredity* 84: 623-629.

Crespi BJ (2007): Comparative evolutionary ecology of social and sexual systems: water-breathing insects come of age. In: Duffy JE, Thiel M (eds.): *Evolutionary Ecology of Social and Sexual Systems: Crustaceans as Model Organisms*. Oxford, UK, Oxford University Press: 442-460.

Crespi BJ, Choe JC (1997): Explanation and evolution of social systems. In: Crespi BJ, Choe JC (eds.): *The Evolution of Social Behavior in Insects and Arachnids*. Cambridge, UK, Cambridge University Press: 499-524.

Cronin H (1991): The Ant and the Peacock: Altruism and Sexual Selection From Darwin to Today. Cambridge, UK, Cambridge University Press.

Darwin C (1859): The Origin of Species. New York: The Modern Library.

Darwin C (1871): The Descent of Man. New York: The Modern Library.

Dietz JM (2004): Kinship structure and reproductive skew in cooperatively breeding primates. In: Chapais B, Berman CM (eds.): K*inship and Behavior in Primates*. Oxford, UK, Oxford University Press: 223-241.

Dixson AF (1998): Primate Sexuality: Comparative Studies of the Prosimians, Monkeys, Apes, and Human Beings. Cambridge, UK, Cambridge University Press.

Dubé F, Amireault P (2007): Local serotonergic signaling in mammalian follicles, oocytes, and early embryos. *Life Sci* 81: 1627-1637.

Eisenberg JF (1981): The Mammalian Radiations: An Analysis of Trends in Evolution. Chicago, The University of Chicago Press.

Ellis L (1995): dominance and reproductive success among nonhuman animals: a cross-species comparison. *Ethol Sociobiol* 16: 257-333.

Emlen ST, Oring L (1977): Ecology, sexual selection and the evolution of mating systems. *Science* 197: 215-223.

Faubion JD (ed, 1994): Michel Foucault: Power, Volume 3. New York: The New Press.

Flack FC, De Waal FBM, Krakauer DC (2005a): Social structure, robustness, and policing cost in a cognitively sophisticated species. *Amer Nat* 165: E-article.

Flack FC, De Waal FBM, Krakauer DC (2005b): Robustness mechanisms in primate societies: a perturbation study. *Proc R Soc Lond* [*Biol*]: doi: 10.1098/rspb.2004.3019. (published online).

Fisher RA (1930): The genetical theory of natural selection. Oxford, UK, Clarendon Press.

Frank SA (1965): Mutual policing and repression of competition in the evolution of cooperative groups. *Nature* 377: 520-522.

Frank SA (2003): Perspective: repression of competition and the evolution of cooperation. *Evolution* 57: 693-705.

Gao Q, Horvath TL (2008): Neuronal control of energy homeostatis. *FEBS Letters* 582: 132-141.

Gross MR (1996): Alternative reproductive strategies and tactics: diversity within sexes. *Trends Ecol Evol* 11: 92-97

Gueguen N (2007): Women's bust size and men's courtship solicitation. *Body Image* 4: 386-390.

Hager R (2003a): Models of reproductive skew applied to primates. In: Jones CB (ed.): *Sexual Selection and Reproductive Competition in Primates: New Perspectives and Directions*. Norman, OK, American Society of Primatologists: 65-101.

Hager R (2003b): The effects of dispersal costs on reproductive skew and within-group aggression in primate groups. *Primate Report* 67: 85-98.

Hager R, Johnstone RA (2004): Infanticide and control of reproduction in cooperative and communal breeders. *Anim Behav* 67: 941-949.

Hamilton WD (1964): The evolution of social behavior. *J Theor Biol* 7: 1-52.

Hammond RL, Keller L (2004): Conflict over male parentage in social insects. *PLoS Biol* 2: e248, www.plosbiology.org.

Heinze J, Keller L (2000): Alternative reproductive strategies: a queen perspective in ants. *Trends Ecol Evolut* 15: 508-512.

Helms Cahan S, Julian GE, Rissing SW, Schwander T, Parker JD, Keller L (2004): Loss of phenotypic plasticity generates genotype-caste association in harvester ants. *Curr Biol* 14: 2277-2282.

Holland B, Rice WR (1999): Experimental removal of sexual selection reverses intersexual antagonistic coevolution and removes a reproductive load. *Proc Natl Acad Sci USA* 96: 5083-5088.

Hrdy SB (1974): Male-male competition and infanticide among the langurs (*Presbytis entellus*) of Abu, Rajasthan. *Folia Primat* 22: 19-58.

Hrdy SB (1976): The care and exploitation of nonhuman primate infants by conspecifics other than the mother. *Adv Stud Behav* 101-158.

Hrdy SB (1979): Infanticide among animals: a review, classification, and examination of the implications for the reproductive strategies of females. *Ethol Sociobiol* 1: 13-40.

Huxley J (1938a): Darwin's theory of sexual selection and the data subsumed by it, in the light of recent research. *Am Nat* 72: 416-433.

Huxley J (1938b): The present standing of the theory of sexual selection. In: Debeer GR (ed): *Evolution*. Oxford, UK, Oxford University Press: 11-42.

Jennions MD, Petrie M (2000): Why do females mate multiply? A review of the genetic benefits. *Biol Rev Camb Philos Soc* 75: 21-64.

Johnstone RA, Cant MA (1999): Reproductive skew and the threat of eviction: a new perspective. *Proc R Soc Lond* [*Biol*]: 275-279.

Jolly A (1998): Pair-bonding, female aggression, and the evolution of lemur societies. *Folia Primatol* 69 Supplement 1: 1-13.

Jones CB (1980): The functions of status in the mantled howler monkey (*Alouatta palliata* Gray): intraspecific competition for group membership in a folivorous Neotropical Primates. *Primates* 21: 389-405.

Jones CB (1985): Reproductive patterns in mantled howler monkeys: estrus, mate choice, and copulation. *Primates* 26: 130-142.

Jones CB (1986): Infant transfer behavior in humans: a note on the exploitation of young. *Aggressive Behavior* 12: 167-173.

Jones CB (1995): Alternative reproductive behaviors in the mantled howler monkey (*Alouatta palliata* Gray): testing Carpenter's hypothesis. *Boletin Primatologico Latinoamericano* 5: 1-5.

Jones CB (1996a): The selective advantage of patriarchal restraint. *Hum Nature* 7: 97-102.

Jones CB (1996b): Temporal division of labor in a primate: age-dependent foraging behavior. *Neotropical Primates* 4: 50-53.

Jones CB (1997): Social parasitism in the mantled howler monkey, *Alouatta palliata* Gray (Primates: Cebidae): Involuntary altruism in a mammal? *Sociobiology* 30: 51-61.

Jones CB (2000): Alouatta palliata politics: empirical and theoretical aspects of power. *Primate Report* 56: 3-21.

Jones CB (2002a): A possible example of coercive mating in mantled howling monkeys (*Alouatta palliata*) related to sperm competition. *Neotropical Primates* 10: 95-96.

Jones CB (2002b): Negative reinforcement in primate societies related to aggressive restraint. *Folia Primatol* 73: 140-143.

Jones CB (2004): The number of adult females in groups of polygynous howling monkeys (*Alouatta* spp.): theoretical inferences. *Primate Report* 68: 7-25.

Jones CB (2005): Behavioral Flexibility in Primates: Causes and Consequences. New York, Springer.

Jones CB (2006): Social parasitism in mammals with particular reference to Neotropical primates. *Mastozoología Neotropical* 12: 19-35.

Jones CB (2007a): Orgasm as a post-copulatory display. *Arch Sex Behav* 36: 633-636.

Jones CB (2007b): The evolution of exploitation in humans: "Surrounded by strangers I thought were my friends". *Ethology* 113: 499-510.

Jones CB (in press): The effects of heterogeneous regimes on reproductive skew in eutherian mammals. In: Hager R, Jones CB (eds): R*eproductive skew in vertebrates: Proximate and ultimate causes*. Cambridge, UK, Cambridge University Press.

Jones CB, Agoramoorthy G (2003): Alternative reproductive behaviors in primates: towards general principles. In: Jones CB (ed.): *Sexual selection and reproduc-*

tive competition in primates: New perspectives and directions. Norman, OK, American Society of Primatologists: 103-139.

Jones CB, Cortés-Ortiz L (1998): Facultative polyandry in the howling monkey (*Alouatta palliata*): Carpenter was correct. *Boletín Primatológico Latinoamericano* 7: 1-7.

Jones CB, Van Cantfort TE (2007): Multimodal communication by male mantled howler monkeys (*Alouatta palliata*) in sexual contexts: a descriptive analysis. *Folia Primatol* 78: 166-185.

Jones CB, Milanov V, Hager R (2008, in press): Predictors of male residence patterns in groups of black howler monkeys. *J Zool* (2008).

Keller L (1995): Social life: the paradox of multiple-queen colonies. *Trends Ecol Evol* 10: 355-360.

Kokko H, Johnstone RA (1999): Social queuing in animal societies: a dynamic model of reproductive skew. *Proc R Soc Lond* [*Biol*] 266: 571-578.

Kuester J, Paul A (1996): Female-female competition and male mate choice in Barbary macaques (*Macaca sylvanus*). *Behaviour* 133: 763-790.

Kvarnemo C, Simmons LW (1999): Variance in female quality, operational sex ratio and male mate choice in a bushcricket. *Behav Ecol Sociobiol* 45: 245-252.

Lande R (1981): Models of speciation by sexual selection on polygynous traits. *Proc Natl Acad Sci USA* 78: 3721-3725.

Langer P, Hogendoorn K, Keller L (2004): Tug-of-war over reproduction in a social bee. *Nature* 428: 844-847.

Lerner IM (1970): Genetic Homeostasis. New York, Dover.

Lindenfors P, Fröberg L, Nunn CL (2004): Females drive primate social evolution. *Proc R Soc Lond* [*Biol*] Supplement 3: S101-S103

Martin RD (2007): The evolution of human reproduction: a primatological perspective. *Am J Phys Anthropol* 45: 59-84.

Mc Cleery RG: Optimal behavior sequences and decision-making. In: Krebs JR, Davies NB (eds.): *Behaviorual Ecology: An Evolutionary Approach*. Sunderland, MA, Sinauer: 377-410.

Molm LD (1977): Coercive Power in Social Exchange. New York, Cambridge University Press.

Moore J (2002): Parasites and the Behavior of Animals. Oxford, UK, Oxford University Press.

Muller MN, Kahlenberg SM, Thompson ME, Wrangham RW (2007): Male coercion and the costs of promiscuous mating for female chimpanzees. Proc R Soc Lond [*Biol*] 274: 1009-1014.

Neff BD (2001): Infidelity as a transaction between social mates. *Trends Ecol Evol* 16: 175.

O'donald P (1977): Theoretical aspects of sexual selection. *Theor Popul Biol* 12: 298-334.

Palombit RA, Cheney DL, Seyfarth RM (2001): Female-female competition for male "friends" in wild chacma baboons, *Papio cynocephalus ursinus*. *Anim Behav* 61: 1159-1171.

Parker GA (1974): Assessment strategy and the evolution of fighting behaviour. *J Theor Biol* 47: 223-243.

Parker GA (1982): Phenotype-limited evolutionarily stable strategies. In: King's College Sociobiology Group (eds): *Current Problems in Sociobiology. Cambridge, UK, Cambridge University Press: 173-201.*

Penn DJ, Smith KR (2007): Differential fitness costs of reproduction between the sexes. *Proc Natl Acad Sci USA* 104: 553-558.

Pfefferle D, Brauch K, Heistermann M, Hodges JK, Fischer J (2008): Female Barbary macaque (*Macaca sylvanus*) copulation calls do not reveal the fertile phase but influence mating outcome.*Proc R Soc Lond* [*Biol*] 275: 571-578.

Pigliucci M (2001): Phenotypic Plasticity: Beyond Nature and Nurture. Baltimore, MD, The Johns Hopkins University Press.

Possamai CB, Young RJ, Mendes SL, Strier KB (2007): Socio-sexual behavior of female Northern muriquis (*Brachyteles hypoxanthus*). *Am J Primatol* 69: 766-776.

Queller DC (1997): Why do females care more than males? *Proc R Soc Lond* [*Biol*] 264: 1555-1557.

Ratnieks FLW, Wenseleers T (2005): Policing insect societies. *Science* 307: 54-56.

Reeder D-A M (2003): The potential for cryptic female choice in primates: behavioral, anatomical, and physiological considerations. In: Jones CB (ed.): *Sexual Selection and Reproductive Competition in Primates: New Perspectives and Directions*. Norman, OK, American Society of Primatologists: 255-303.

Reeve HK (2001): In search of unified theories in sociobiology: help from social wasps. In: Dugatkin LA (ed): *Model Systems in Behavioral Ecology: Integrating Conceptual*, *Theoretical*, *and Empirical Approaches*. Princeton, Princeton University Press: 57-71.

Reeve HK, Emlen ST (2000): Reproductive skew and group size: an *N*-person staying incentive model. *Behav Ecol* 11: 640-647.

Reeve HK, Hölldobler B (2007): The emergence of a superorganism through intergroup competition. *Proc Natl Acad Sci USA* 104: 9736-9740.

Reeve HK, Shen SF (2006): A missing model in reproductive skew theory: the bordered tug-of-war. *Proc Natl Acad Sci USA* 103: 8430-8434.

Reichard M, Bryja J, Ondrackova M, Davidova M, Kaniewska P, Smith C (2005): Sexual selection for male dominance reduces opportunities for female mate choice in the European bitterling (*Rhodeus sericeus*). *Mol Ecol* 14: 1533-1542.

Rice WR (2000): Dangerous liaisons. *Proc Natl Acad Sci USA 97: 12953-12955.*

Salz HK (2007): Male or female? The answer depends on when you ask. *PLoS Biol* 5: e335.

Schoener TW (1971): Theory of feeding strategies. *Annu Rev Ecol Syst* 2: 369-404.

Setchell JM, Knapp LA, Wickings EJ (2006): Violent coalitionary attack by female mandrills against an injured alpha male. *Am J Primatol* 68: 411-418.

Shahnoor N, Jones CB (2003): A brief history of the study of sexual selection and reproductive competition in primatology. In: Jones CB (ed). *Sexual Selection and Reproductive Competition in Primates: New Perspectives and Directions*. Norman, OK, American Society of Primatologists: 1-43.

Shellman-Reeve JS, Reeve HK (2000): Extra-pair paternity as the result of reproductive transactions between paired mates. *Proc R Soc Lond* [*Biol*] 267: 2543-2546.

Sinervo B, Zamudio KR (2001): The evolution of alternative reproductive strategies: fitness differential, heritability, and genetic correlation between the sexes. *J Hered* 92: 198-205.

Smuts BB, Smuts RW (1993): Male aggression and sexual coercion of females in nonhuman primates and other mammals: evidence and theoretical implications. *Adv Stud Behav* 22: 1-63.

Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds, 1987): Primate Societies. Chicago, The University of Chicago Press.

Solomon NG, French JA (1997): Cooperative Breeding in Mammals. Cambridge, UK, Cambridge University Press.

Stacey PB (1982): Female promiscuity and male reproductive success in social birds and mammals. *Am Nat*: 51-64.

Sterck EHM, Watts DP, Van Schaik, CP (1997).: The evolution of female social relationships in nonhuman primates. *Behav Ecol Sociobiol* 41: 291-309.

Strum SC, Fedigan LM (2000): Primate Encounters: Models of Science, Gender, and Society. Chicago, The University of Chicago Press.

Su H-H, Birky WA (2007): Within group female-female agonistic interactions in Taiwanese macaques (*Macaca cyclopis*). *Am J Primatol* 69: 199-211.

Swami V, Trovée MJ (2007): The relative contribution of profile body shape and weight to judgments of women's physical attractiveness in Britain and Malaysia. *Body Image* 4: 391-396.

Szymañski M, Barciszewski J (2006): Regulatory RNAs in mammals. *Handbook of Experimental Pharmacology* 173: 45-72.

Taborsky M (1998): Sperm competition in fish: "bourgeois" males and parasitic spawning. *Trends Ecol Evolut* 13: 222-227.

Taborsky M (2001): The evolution of bourgeois, parasitic, and cooperative reproductive behaviors in fishes. *J Hered*: 100-110.

Toth AL, Varala K, Newman TC, Miguez FE, Hutchison SK, Willoughby DA, Simons JF, Egholm M, Hunt JH, Hudson ME Robinson GE (2007): Wasp gene expression supports an evolutionary link between maternal behavior and eusociality. *Sciencexpress*, **www.sciencexpress.org,** 10.1126/science.1146647: 1-4.

Trivers RL (1972): Parental investment and sexual selection. In: CAMPBELL, B. (ed.): *Sexual Selection and the Descent of Man 1871-1971*. Chicago, Aldine: 136-179.

Van Schaik CP (2000): Social counterstrategies against infanticide by males in primates and other mammals. In: Kappeler PM (ed): *Primate Males: Causes and Consequences of Variation in Group Composition*. Cambridge, UK, Cambridge University Press: 34-52.

Van Schaik CP, Janson CH (eds, 2002)): Infanticide by Males and its Implications. Cambridge, UK, Cambridge University Press.

Van Schaik CP, Kappeler PM (1997): Infanticide risk and the evolution of male-female association in primates. *Proc R Soc Lond* [*Biol*] 264: 1687-1694.

Vehrencamp SL (2000): Evolutionary routes to joint-female nesting in birds. *Behav Ecol*: 334-344.

West M-J (1967): Foundress associations in polistine wasps: dominance hierarchies and the evolution of social behavior. *Science* 157: 1584-1585.

West SA, Pen I, Griffin AS (2002): Cooperation and competition between relatives. *Science* 296: 72-75.

West-Eberhard MJ (1979): Sexual selection, social competition, and evolution. *Proceedings of the American Philosophical Society* 123: 222-234.

Wilson EO (1971): The Insect Societies. Cambridge, MA, Belknap Press.
Wilson EO (1975): Sociobiology: The New Synthesis. Cambridge, MA, Belknap Press.
Wilson JM, Tripp DA, Boland FJ (2005): The relative contributions of subjective and objective measures of body shape and size to body image and disordered eating in women. *Body Image* 2: 233-247.
Wittenberger JF (1980): Group size and polygamy in social mammals. *Am Nat* 115: 197-222.
Wolff JO, Macdonald DW (2004): Promiscuous females protect their offspring. *Trends Ecol Evolut* 19: 127-134.

Correspondence to:
Director, Theoretical Primatology Project (TPP), 2820 North May Street, Number 3, Southern Pines, NC 28387-3500, USA; alouatta04@yahoo.com

OFFSPRING PROTECTION BY MALE MANDRILLS, *MANDRILLUS SPHINX*

Laidre ME, Yorzinski JL

Key words: paternal care, kin guarding, defensive coalition, agonistic support, *Mandrillus*

Abstract

Most mammals are characterized by a lack of parental care by the male sex. This is particularly true in highly polygynous, sexually selected species and species in which fathers remain only weakly associated with their offspring. Here we report observations suggesting the existence of male parental care in the mandrill (*Mandrillus sphinx*, Primates: Cercopithecinae), one of the most sexually dimorphic mammal species known and a species in which, in the wild, males reside in social groups solely for the breeding season. Adult males in three captive groups exhibited aggressive, protective behavior when definite or likely offspring became involved in agonistic confrontations with individuals outside of the group. Males were observed to abandon feeding opportunities, sexual consorts, and allogrooming sessions to intervene on behalf of their threatened offspring. In one of the three groups, the male was occasionally removed, leaving only his mate and their two juvenile offspring; during these periods (when support from their father was unavailable) each of the juveniles initiated significantly fewer extra-group agonistic disputes. A fourth group was studied in which the male was unrelated to the two juveniles, and in this group the male failed to protect the juveniles from outside threats. Although these observations of paternal care were detected across varying social and ecological conditions, it is unclear to what extent they apply in the wild.

Introduction

In cases where parents remain in association with their offspring the opportunity arises for adaptive molding of parental care by natural selection (Wilson, 1975). Forms of care will be selectively favored when they contribute to increased survival and reproduction of progeny while minimally decreasing a parent's ability to invest in future offspring (Trivers, 1972). For example, parents could provide assistance to offspring engaged in agonistic conflicts, thereby protecting their vulnerable progeny from outside threats. In sexually dimorphic species the cost to a parent of providing such agonistic support would be lower for the larger, competitively superior sex, translating to a greater net benefit if the larger sex performs this type of parental care. In theory, however, the larger, competitively superior sex will generally be less inclined to provide parental care: this sex's dimorphism is likely a product of strong sexual selection for maximizing opportunities for progeny production rather than progeny care (Clutton-Brock, 1991).

An extreme sexual dimorphism is known to exist in mandrills (*Mandrillus sphinx*), Old World monkeys endemic to equatorial West Africa. Adult males of this species are three times heavier than the average female (Wickings and Dixson, 1992), exhibit especially well-developed canines, and display the brightest coloration of any mammal (Darwin, 1871). A male mandrill's coloration (particularly its redness) appears to function as an intrasexual signal, communicating information about the male's current rank and resource holding potential (Setchell and Dixson, 2001). A strong history of sexual selection thus appears to have characterized mandrill evolution (Setchell et al., 2005a). Recent field observations of wild mandrills have further revealed that adult males remain only seasonally present in groups, becoming social exclusively while females are in estrous and otherwise living solitarily (Abernethy et al., 2002). The existence of paternal care (such as offspring protection by fathers) might therefore seem unlikely in mandrills, especially given adult males' weak association with groups (and hence with their progeny). As Abernethy et al. (2002, p. 136) conclude: "As most males are absent from the horde during half the year, it seems highly unlikely that they play any role in horde cohesion, protection or leadership."

We report on a series of captive studies suggesting that male mandrills may perform a valuable protective role within groups by intervening on behalf of offspring involved in extra-group agonistic encounters. We further show that this paternal protective behavior manifests itself across varying socio-ecological conditions and also in contexts where other fitness-enhancing behaviors are opportune alternatives for fathers.

Methods

Observations focused on four captive mandrill groups containing one or more adult males along with immature conspecifics. The immatures within the groups represented either offspring or non-offspring of the adult males and included juveniles and infants of both sexes. Two of the study groups were housed in zoos in NY, USA. The Syracuse group (at the Rosamond Gifford Zoo) consisted of an adult male, an adult female, and their two juvenile female offspring. The Buffalo group (at the Buffalo Zoological Gardens) consisted of an adult male, an adult female, and two juvenile females sired by a different male. Two other study groups were housed in larger, semi-free ranging colonies at the Centre International de Recherches Médicales in Franceville, Gabon. The 'Enclosure 3' group consisted of 2 adult males, 10 adult females, 5 juvenile males, 3 juvenile females, 2 infant males, and 3 infant females. The 'Enclosure 2' group consisted of 4 adult males, 10 adult females, 9 sub-adult males, 6 sub-adult females, 10 juvenile males, 12 juvenile females, 4 infant males, and 7 infant females. The observation period spanned January 2002 – May 2005 and details on enclosure habitat, feeding regimen, observation hours and sampling regimes for each group are provided in Table 1 in Laidre (2008).

The Syracuse group was the first group we studied and our general approach in this investigation was to use the behavior of the Syracuse adult male as a hypothesis for how males in other groups might behave if male mandrills protect their offspring. The groups we studied had varying housing environments and/or social compositions, allowing us to evaluate the generality of paternal protective behaviors across different conditions. If paternal protective behavior is a species-specific phenomena in mandrills then it should occur (i) across different ecological conditions (ranging from small, indoor zoo enclosures to large, outdoor naturalistic enclosures), (ii) across different social conditions (ranging from single-male harem groups to multi-male, multi-female groups), and (iii) only in groups in which males are housed with definite or likely offspring. [DNA analyses have shown that paternity is strongly positively correlated with dominance rank in mandrills and that alpha males sire the great majority (80-100 %) of offspring (Dixson et al., 1993). Accordingly, we assumed that the dominant males in the Enclosure 2 and 3 groups were the likely fathers of the majority of the immatures within their groups, since they had been alphas for several years (E.J. Wickings, pers. comm.)]. Predictions (i) and (ii) were tested by comparing the Syracuse male's behavior with that of the dominant males in the Enclosure 2 and 3 groups (the latter of whom were housed in large, outdoor naturalistic enclosures and within multi-male, multi-female groups). Prediction (iii) was tested by comparing the Syracuse male's behavior with that of the Buffalo male (the latter of whom was also housed in a zoo enclosure but with unrelated immatures).

To assay possible paternal protective behavior we focused on extra-group agonistic interactions that involved immatures, determining if males ever intervened in these interactions on behalf of their offspring. In the zoo groups, extra-group agonistic interactions began when an immature slapped the glass wall that separated the enclosure and visitor viewing area. The glass was slapped directly at one or more visitors who had approached too closely, and the performance of a glass slap appeared hostile, frequently causing the visitors to jump back (Exemplars of this behavior were filmed and have been stored in the Visual Media Collections of the Cornell Laboratory of Ornithology's Macaulay Library. These video clips can be viewed though the Laboratory's website). In the two semi-free ranging groups, extra-group agonistic interactions occurred along the chain-link fence bordering the groups' enclosures, which were adjacent. Along the border individuals frequently became involved in altercations with non-group mates, screaming when the altercation became too rough. Such screaming appeared to be the vocal equivalent of glass slapping, and both behaviors were readily detectable by other group members, providing a means of attracting agonistic aid.

In addition to evaluating behavioral changes in adult males during such extra-group agonistic interactions, we also evaluated changes in the immatures' behavior during periods when their father was unavailable to provide protection. This was possible because the adult male in the Syracuse group was occasionally separated and housed off-exhibit. If agonistic protection provided by a mandrill father is beneficial to his offspring, then when a father is absent his offspring should be less successful in extra-group agonistic confrontations, thus initiating fewer confrontations. We tested this prediction by evaluating how often the juveniles in the Syracuse group performed glass slaps when their father was present versus absent.

Finally, we also report the amount of other forms of male care that we observed in mandrills, to compare the relative level of affiliative versus aggressive, protective care by fathers. Two additional groups (see Laidre, 2008) are included in the report of this data. (These groups were not included in our analysis of extra-group agonism since extra-group interactions were not observed to occur at these zoos.) The Tampa group from the Lowry Park Zoo (FL, USA) contained 1 adult male, 1 sub-adult male, 2 adult females, 3 juvenile males, 1 juvenile female, and 1 infant female (the adult male being the father of all the immatures). And the Paignton group from the Paignton Zoo Environmental Park (UK) contained 1 adult male, 1 adult female, and an unrelated infant male.

Results

The behavior of the adult male in the Syracuse group changed dramatically in response to the performance of glass slaps by his juvenile daughters (Fig. 1). In the period after either offspring's glass slap compared to the period before their glass slap the male significantly increased how often he charged the visitors, paced alongside the length of the glass, slapped the glass, and directed threat displays at the visitors (for each behavior: Two-tailed, paired t-test, $t > 5$, $df = 118$, $p < 0.0001$). The male's behavior frequently caused the visitors to jump back from their original location.

The Syracuse male remained vigilant of his offspring's welfare even after moving out of sight into the off-exhibit enclosure. If one of his daughters performed a glass slap after the male had moved off-exhibit (and if the door between the two enclosures had been left open), the male would immediately rush into the exhibit enclosure. The male would do so even if it required (a) abandoning food (which was provided in bulk only in the off-exhibit enclosure), (b) abandoning his estrous consort (a lone female who was kept in a separate cage in the off-exhibit enclosure), and (c) terminating an allogrooming session (with either his mate or the other, lone female). The male would not rush into the exhibit enclosure, however, when visitors pounded on the glass wall, confirming that his protective response was solely motivated by his offspring.

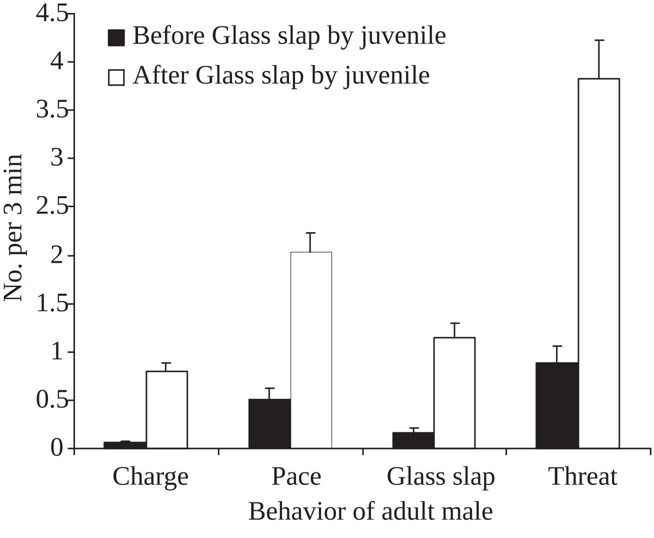

Fig. 1: Mean + SE of the number of times different aggressive behaviors were directed at visitors by the adult male in the Syracuse group 3 min before and after either of his juvenile daughters slapped the glass at the visitors. Included in the analysis are N=119 glass slaps by these juveniles. To ensure that the 3 min periods associated with different glass slaps did not overlap, glass slaps that occurred within 6 min of an earlier glass slap were not included in the analysis.

On one or more days each month, the male in the Syracuse group was removed from the rest of the group and locked in the off-exhibit enclosure for the entire day.

On days when the adult male was absent, both his juvenile daughters directed significantly fewer glass slaps toward the visitors: the younger juvenile averaged 0.67 glass slaps when her father was absent and 18.6 glass slaps when he was present (Two-tailed t-test, $t = 3.71$, $df = 18$, $p < 0.005$); the older juvenile averaged 0.67 glass slaps when her father was absent and 3.9 glass slaps when he was present (Two-tailed t-test, $t = 2.82$, $df = 18$, $p < 0.05$). These differences in the average number of glass slaps were not attributable to the number of visitors, which averaged 1596 on days when the male was present and 1539 on days when he was absent (Two-tailed t-test, $t = 0.30$, $df = 18$, $p = 0.77$).

Within the Enclosure 2 and 3 groups each dominant male consistently exhibited protective behavior when immatures from its group screamed during an extra-group agonistic confrontation. In the Enclosure 3 group, the only other adult male (the subordinate) never exhibited protective behavior, and in the Enclosure 2 group, only one of the subordinate adult males ever exhibited protective behavior. We were unable to record protective behaviors in as much detail as the Syracuse group (because the fence bordering the two Franceville enclosures faced away from our only observation point); however, on over thirty occasions across over 2 months of daily observation we observed the dominant males in each group charge the fence immediately after one of their immatures screamed. The only other context in which either of these males locomoted so rapidly was to drive off rivals (Laidre, 2005) within their group or to access newly discovered food (Laidre, 2006). Like the Syracuse male, the dominant males in each Franceville group were also observed to abandon feeding opportunities and allogrooming sessions to intervene on behalf of immatures.

In the Buffalo group (where the immatures were unrelated to the male) there was no significant increase in any form of aggressive, protective behavior by the male following a glass slap by one of the immatures. This male, however, showed a similar tendency to the Syracuse male to generally aggress against visitors, directing on average just over 7 threat displays per h at the visitors.

Across all study groups, representing over 1000 h observation (>700 for M.E.L. and > 500 for J.L.Y.), we never observed affiliative paternal care (such as carrying, holding, retrieving, embracing, or playing). In fact, virtually no non-aggressive tactile contact took place between adult males and immatures and on only one occasion (lasting under 10 sec) did we observe grooming of an immature by an adult male.

Discussion

Aside from monogamous and polyandrous species, paternal care within primates has also been reported in several Old World monkey species with a multi-male, multi-female group structure, including baboons and macaques (reviewed in Taub and Redican, 1984). Itani (1959), who first reported on paternal care in nonhuman primates, showed that male Japanese macaques safeguard infants, both by providing affiliative care (including carrying, hugging, grooming, playing, and food-access privileges) and by providing aggressive protection. This latter form of male care has been rarely reported in multi-male primate groups. As Borries et al. (1999, p. 351) note "only a few hints on protector males living in multimale groups are to be found in the primatological literature."

In this study, we found that adult male mandrills in captivity provided essentially no affiliative paternal care but were vigilant of possible threats to their offspring, exhibiting aggressive, protective behavior when offspring became involved in agonistic encounters. In some instances, a male's protective behavior even took priority over other, fitness-enhancing activities (like consorts with an estrous female, food consumption, or allogrooming), suggesting that the behavior fulfills an important function. There was also indirect evidence that offspring benefited from their father's protection, since they decreased their involvement in agonistic encounters when their father was absent. Lastly, the protective paternal care was (i) detected under varying ecological conditions (including small, indoor zoo enclosures to large, outdoor naturalistic enclosures), (ii) detected under varying social conditions (including single-male harem groups and multi-male, multi-female groups), and (iii) absent when a male was not the father of the immatures (Buffalo group) or performed rarely when a male was unlikely to have fathered the immatures (subordinates in Enclosure 2 and 3 groups). Altogether, these results suggest that male mandrills can provide beneficial paternal care by attacking potential sources of danger to their offspring (see also Yorzinski and Vehrencamp, 2008).

One explanation for these results is that male care is an artifact of captivity: fathers are forced to remain in continuous association with their offspring whereas in the wild they are only semi-permanent members of social groups. Wild male mandrills, however, could still potentially benefit from performing such care, since offspring that were protected would presumably be more likely to survive to reproductive age, thus enhancing a male's lifetime reproductive success. Also, even if a substantial portion of a male's time and energy budget is devoted to mate guarding (which has recently been shown to correlate with paternity in mandrills (Setchell et al., 2005b)), this need not preclude offspring protection: attempting to sire more offspring and caring for existing offspring are not mutually exclusive strategies (Parker and Schwagmeyer, 2005). Males could employ a 'mixed' strategy, pursuing and guarding fertile females some portion of the time while at other times (particularly when offspring are in danger) providing paternal care. The existence of such a mixed strategy would be plausible physiologically since the hypothesized form of paternal care (attacking threats to one's offspring) is hormonally compatible with aggressive mating competition, requiring no drop in a dominant male's elevated plasma testosterone level (Wickings and Dixson, 1992). Although extrapolations from captivity to the wild are necessarily tentative, our observations from zoos and semi-free ranging groups suggest the following prediction: if free ranging male mandrills tend to return to groups in which they were reproductively successful in the past, then protective care by fathers may also be detectable in wild mandrills. Detailed tests of this and other hypotheses about wild mandrill behavior will require overcoming the obstacles associated with field studies of this species (Abernethy et al., 2002).

Acknowledgements

We thank the Rosamond Gifford Zoo, especially Judy Talbot for data on the number of visitors; the Buffalo Zoological Gardens, especially Jerry Aquilina; the Centre International de Recherches Médicales, especially Jean Wickings, Bettina Salle, and

Olivier Bourry; the Lowry Park Zoo; and the Paignton Zoo Environmental Park, especially Andrew Priest, for making their animals available for study. Jeanne Altmann and Sandra Vehrencamp provided helpful discussion, and Adam Arcadi and Sandra Vehrencamp loaned video equipment. Supported by grants from the Howard Hughes Medical Foundation, the Andrew W. Mellon Fund, and the Explorers Club (M.E.L.), by the Cornell Presidential Research Scholars Program (J.L.Y.), and by support from Sandra Vehrencamp.

References

Abernethy KA, White LJT, Wickings EJ (2002): Hordes of mandrills (*Mandrillus sphinx*): extreme group size and seasonal male presence. *J Zool* 258: 131-137.

Borries C, Launhardt K, Epplen C, Epplen JT, Winkler P (1999): Males as infant protectors in Hanuman langurs (*Presbytis entellus*) living in multimale groups - defence pattern, paternity and sexual behaviour. *Behav Ecol Sociobiol* 46: 350-356.

Clutton-Brock TH (1991): The evolution of parental care. Princeton, Princeton University Press.

Darwin C (1871): The descent of man and selection in relation to sex. London, John Murray.

Dixson AF, Bossi T, Wickings EJ (1993): Male dominance and genetically determined reproductive success in the mandrill (*Mandrillus sphinx*). *Primates* 34: 525-532.

Itani J (1959): Paternal care in the wild Japanese monkey, *Macaca fuscata fuscata*. *Primates* 2: 61-93.

Laidre ME (2005): Honest signaling of intentions: the importance of performance risk, receiver response, and prior knowledge of opponents in the threat displays of mandrills. *Behaviour* 142: 455-476.

Laidre ME (2006): Manipulation without mind-reading: information suppression and leakage during food discovery by mandrills (*Mandrillus sphinx*). *Behaviour* 143: 365-392.

Laidre ME (2008): Do captive mandrills invent new gestures? *Anim Cogn* 11: 179-187.

Parker GA, Schwagmeyer PL (2005): Male "mixed" reproductive strategies in biparental species: Trivers was probably right, but why? *Amer Nat* 165: 95-106.

Setchell JM, Dixson AF (2001): Changes in the secondary sexual adornments of male mandrills are associated with gain and loss of alpha status. *Horm Behav* 39: 177-184.

Setchell JM, Charpentier M, Wickings EJ (2005a): Sexual selection and reproductive careers in mandrills (*Mandrillus sphinx*). *Behav Ecol Sociobiol* 58: 474-485.

Setchell JM, Charpentier M, Wickings EJ (2005b): Mate guarding and paternity in mandrills: factors influencing alpha male monopoly. *Anim Behav* 70: 1105-1120.

Taub DM, Redican WK (1984): Adult male-infant interactions in Old World monkeys and apes. In: Taub DM (ed): *Primate paternalism.* New York, Van Nostrand Reinhold Co.: 377-406.

Trivers RL (1972): Parental investment and sexual selection. In: Campbell B (ed): *Sexual selection and the descent of man*. Chicago, Aldine: 136-179.
Wickings EJ, Dixson AF (1992): Testicular function, secondary sexual development, and social status in male mandrills (*Mandrillus sphinx*). *Physiol Behav* 52: 909-916.
Wilson EO (1975): Sociobiology: the new synthesis. Cambridge, Harvard University Press.
Yorzinski JL, Vehrencamp SL (2008): Preliminary report: antipredator behaviors of mandrills. *Primate Report* 75: 11-18.

Authors' address:

Mark E. Laidre: Department of Ecology and Evolutionary Biology, and Program in Neuroscience, Princeton University, Princeton, NJ 08544-1003, USA, MEL23@cornell.edu
Jessica L. Yorzinski: Animal Behavior Graduate Group, University of California, Davis, One Shields Avenue, Davis, CA 95616, USA, jyorzinski@ucdavis.edu

PRIMATE POPULATIONS IN ZOOS: A CASE OF FRAGMENTATION

Kaumanns W, Singh M, Krebs E, Schwitzer C

Key words: Primates, Strepsirrhini, Platyrrhini, Cercopithecoidea, Hylobatidae, Hominidae, population development, captivity, forest fragments

Abstract

This paper reports an analysis of the development of captive primate populations under the European Endangered Species Programme (EEP) between 1990 and 2002. The 25 species included in this analysis represent the entire primate taxa from prosimians to great apes. Although each primate species under EEP constitutes a 'metapopulation', the groups of a species are located in different zoos. Such groups are usually small, do not comprise of all age-sex classes, inter-troop encounters in these groups are absent, and male exchanges between groups are rare. In their natural habitats, most primate species now live in fragmented forests. Several features of forest fragments and captive groups are similar. We, therefore, propose that the captive groups are a case of fragmentation, and an analysis of the processes of development in captive populations might help understand such processes in forest fragments. Most primate species registered growth rates far below the optimum or expected. Since proximate factors such as food supply, predation etc. are controlled in captive situations, we conjecture that the population growth is limited by the living conditions leading to a lack of expression of full range of adaptive behaviours. Such behavioural problems may also be present in forest fragments. We opine that only special management programmes that also include special emphasis on behavioural management can augment population development in forest fragments and in captive populations.

Introduction

Primates have been kept under human care for a long time. In the earlier times, wild caught animals were kept as display animals and there was no emphasis on breeding. It is only since 1950s that zoos started to maintain records for their primate colonies. It was only in the 1980s that the need for self-sustainable populations and population management above the level of a single institution was recognized. Special breeding programmes such as Species Survival Plan (SSP) in North America (Anonymous a) and European Endangered Species Programme (EEP) in Europe (Anonymous b) were initiated for many species. The most notable aspect of these breeding programmes is that the entire captive population of a species in a region has been considered as a 'metapopulation' and studbooks are maintained for all animals involved in the breeding programmes.

The breeding programmes were started for the species that are threatened in their natural habitats. Many primate species have been subjected to severe habitat loss and habitat degradation.One of the consequences of such processes has been habitat fragmentation (Marsh, 2003a).Groups of some primate species inhabiting forest fragments have become isolated and small. Forest fragmentation has been seen, and is expected, to affect animal species mainly in two ways: the local extinction of certain species, and the changes in population structure and dynamics in others. However, a species' responses to fragmentation usually are not so dramatic as to become visible in a short period of time. The ideal way to understand such responses is to track them through time, by beginning to observe a species in the pre-fragmentation forests, through the process of fragmentation, and then for a relatively long period in the forest fragments. However, in reality there are limitations to realize such a goal. Most of the existing fragments came into existence several years or decades before attention was focused on them (Laurance and Bierregaard, 1997). Nothing is known about the status of primate populations in such regions when they were parts of a continuous forest. At present, much of the data comes from field studies that usually last from a few months to a few years only. The long-term changes in the population structure of a species in fragments, therefore, are rarely analysed on a systematic basis.

The zoo populations with isolated and small groups resemble populations in fragmented habitats. The zoo populations, therefore, are a case of fragmentation. Systematic data have been maintained on population size, and birth and death rates in captive populations, especially from the beginning of the coordinated breeding programmes. The 'development' of the captive population of a species, therefore, can be discerned from such data. An analysis of population development in captive groups may help us understand what could happen to populations in forest fragments: it is mainly when comparative data on population dynamics come from different habitat types and living conditions that the potential of a species for survival and growth can be understood.

The growth of populations in their natural habitats is limited by the carrying capacity of their environment. Carrying capacity is mainly understood in terms of availability of food resources. We presume that in captivity, where the food supply is permanently ensured, the animals are no more limited by the carrying capacity and should be able to reproduce to their maximum potential. The maximum potential can be defined as the reproductive output where all females reproduce with a low variance in reproduction, and retain critical life history traits including age at first birth, inter-birth interval and longevity equal to that in the natural habitats of a species.

The European breeding programmes (EEP) for several primate species started in 1990. Over the years, more species were brought under EEP and several new institutions joined the program (Kaumanns et al., 2005). In this article, we report the data on several of them, and discuss the possible factors related to their development.

Materials and Methods

The populations under analysis comprise of zoo colonies in several European countries. Such colonies usually comprise a single group of a species with only a few individuals. The group composition changes through births and deaths, and also by occasional exchange of animals between zoos as prescribed by management decisions. Often a group comprises of an adult male, few adult females and offspring. The type and the size of enclosures vary among species and among zoos. Enclosures usually include indoor and outdoor spaces, with horizontal and vertical structures allowing a dispersal opportunity of a number of meters. Food is either available all the time, or several times a day, dispersed in the enclosure. Veterinary care is provided.

We have analysed the data on demographic development of 25 species of primates including prosimians, New World monkeys, Old World monkeys, gibbons and great apes. The present analysis is a continuation of a preliminary evaluation of these populations (KAUMANNS et al., 2000). The sources for these data are the EEP Yearbooks maintained for each species by the concerned coordinators. Although data are available on some species for several decades, the period for the main analysis for all species is from 1990 (the beginning of EEP) to 2002. In addition to the overall development in terms of population size, data on births and infant mortality are also analysed. Though there are more than 25 primate species under EEP, we have omitted analysis for the few species where there was intentional birth control, or the species that came into EEP only recently. For analysis of birth and death rates in relation to other factors, we have classified species according to their social systems and inter-birth interval categories on the basis of what is observed in these species in their natural habitats.

Results

Overall Population Development

Figures 1 to 5 show the overall population development of all species included in this analysis. The other relevant data for population development for each species are given in Table 1. Some species started with a population size of less than 50 whereas some had an initial size of more than 100. Except for Douc's langur (*Pygathrix nemaeus*), the population of all other species increased at varying rates (Table 1). The total primate population increased at an annual rate of about 7.8 %. However, this rate varied from minus and as low as less than one percent to about 33 % for different species. The mean annual birth rate (newborn to population size) was about 13.2 % and it varied from about five percent to about 32 %. The overall infant mortality was 22.3 % and it varied considerably for different species ranging from as low as zero to as high as about 46 %. For a comparative analysis on population development, we have divided the analysis according to the taxonomic units.

Strepsirrhini

The data on population development of four species of Strepsirrhini are shown in Fig. 1. Black-and white ruffed lemur (*Varecia variegata*) and Red ruffed lemur (*V. rubra*) showed a considerable growth in their populations due to a fairly high birth rate (Table 1) and due to the fact that they often have multiple births. Black lemur (*Eulemur macaco*) and Mongoose lemur (*E. mongoz*) showed only a marginal increase. Black lemur had a low birth rate and high infant mortality. Mongoose lemur, though had a low infant mortality, the birth rate was also low.

Table 1: Population development data on 25 species of primates under European Endangered Species Programme (EEP) between 1990 and 2002.

Species	**Taxa**	**Social structure**	**IBI**	**Births**	**Starting size**	**Present size***	**No. years in EEP**	**Total % Increase**	**% Annual increase**	**%Annual birth rate**	**% Infant mortality**	**%Females producing**
Eulemur macaco	Strepsirrhini	MM-MF	<1 year	Multiple	89	112	6	25.8	4.31	15.2	33.2	?
Varecia variegata	Strepsirrhini	Family	<1 year	Multiple	156	378	11	142.3	12.94	23.6	32.6	?
Varecia rubra	Strepsirrhini	Family	<1 year	Multiple	62	284	11	358.1	32.55	22.4	29.7	?
Eulemur mongoz	Strepsirrhini	Family	<1 year	Single	28	32	6	14.3	2.38	11.6	8.3	?
Saguinus imperator	Platyrrhini	OM-MF	?	Multiple	104	186	8	78.9	9.86	32.2	45.9	?
Saguinus oedipus	Platyrrhini	MM-MF	<1 year	Multiple	275	547	8	98.9	12.36	29.9	40.1	?
Callimico goeldii	Platyrrhini	Family	<1 year	Single	81	257	11	217.3	19.75	23.6	23.3	?
Ateles fuscipes	Platyrrhini	MM-MF	>2 years	Single	114	177	7	55.3	7.89	8.9	9.6	26.9
Pithecia pithecia	Platyrrhini	Family	<1 year	Single	104	160	7	51.9	7.42	17.3	23.5	58.0
Lagothrix lagotricha	Platyrrhini	MM-MF	1-2 years	Single	69	74	11	7.3	0.66	11.5	27.4	33.6
Macaca nigra	Cercopithecoidea	MM-MF	1-2 years	Single	132	180	10	36.4	3.64	10.6	4.5	28.1
Mandrillus leucophaeus	Cercopithecoidea	OM-MF	1-2 years	Single	25	47	11	88.0	8.00	10.8	9.6	29.4
Macaca silenus	Cercopithecoidea	OM-MF	>2 years	Single	85	236	11	177.6	16.15	11.5	33.7	30.3
Cercopithecus diana	Cercopithecoidea	OM-MF	<1 year	Single	60	83	11	38.3	3.48	7.9	21.0	17.7
Theropithecus gelada	Cercopithecoidea	MM-MF	1-2 years	Single	56	108	11	92.9	8.44	18.6	39.8	51.4
Colobus polykomos	Cercopithecoidea	MM-MF	1-2 years	Single	19	33	8	63.2	7.89	14.9	0	18.2
Pygathrix namaeus	Cercopithecoidea	MM-MF	1-2 years	Single	24	9	11	(-)62.5	(-)5.68	6.6	18.2	15.4
Nomascus leucogenys	Hylobatidae	Family	>2 years	Single	53	67	11	26.4	2.40	7.7	28.5	?
Nomascus gabriella	Hylobatidae	Family	>2 years	Single	31	64	11	106.5	9.68	6.7	20.9	?
Hylobates pileatus	Hylobatidae	Family	>2 years	Single	26	35	11	34.6	3.15	7.5	0	?
Nomascus siki	Hylobatidae	Family	>2 years	Single	6	9	11	50.1	4.54	8.2	11.1	?
Pongo pygmaeus	Hominidae	S/FF	>2 years	Single	101	148	11	46.5	4.23	5.1	31.8	13.0
Pongo abelii	Hominidae	S/FF	>2 years	Single	101	133	11	31.7	2.88	5.5	27.2	14.1
Gorilla gorilla gorilla	Hominidae	OM-MF	>2 years	Single	200	385	11	92.5	8.41	5.8	22.5	12.5
Pan paniscus	Hominidae	S/FF	>2 years	Single	35	68	11	94.3	8.57	7.0	16.1	18.7

MM-FF Multimale-Multifemale; S/FF Solitary Fission Fusion; OM-MF Onemale-Multifemale; IBI Inter Birth Interval; ? Numbers not available; *Last available records

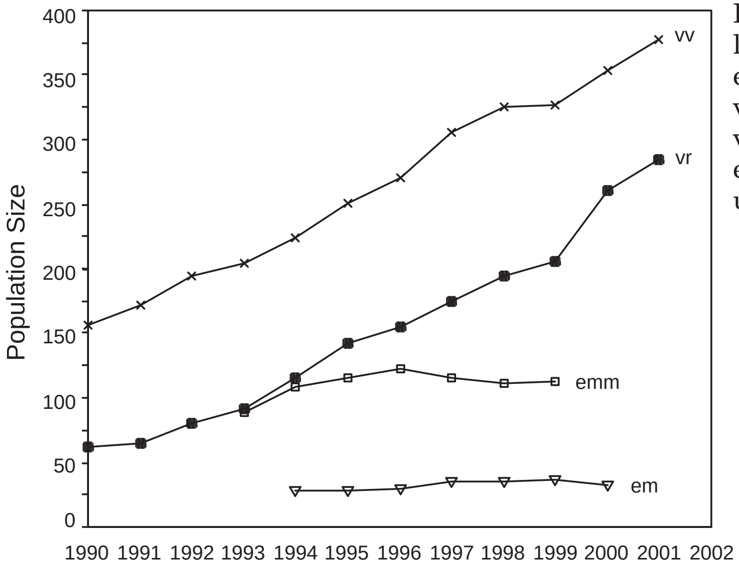

Fig. 1: Population development in emm=*Eulemur macaco*; vv=Varecia variegata; vr=*V. rubra*; em=*E. mongoz*. under EEP (1990-2002).

Platyrrhini

Fig. 2 shows the population development of several species of Platyrrhini. Only the three species of tamarins showed a considerable gain in their populations. This was due to multiple births and the fact that several new institutions joined EEP. Although the tamarins have a high birth rate, the infant mortality rate at the same time is also quite high (Table 1). The populations of the other species increased only marginally due to high infant mortality.

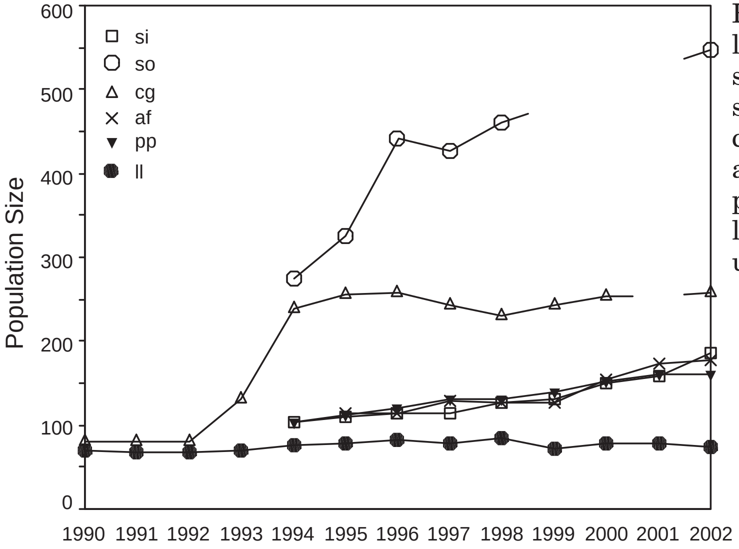

Fig. 2: Population development in si=*Saguinus imperator*; so=*S. oedipus*; cg=*Callimico goeldii*; af=*Ateles fuscipes*; pp=*Pithecia pithecia*; ll=*Lagothrix lagotricha* under EEP (1990-2002).

Cercopithecoidea

Population development over the years under EEP for Cercopithecids is shown in Fig. 3. The lion-tailed macaques (*Macaca silenus*) registered a comparatively high increase in the population, initially due to inclusion of new animal into EEP and later because of births of new infants. The population of Dschelada (*Theropithecus gelada*) also increased considerably, although the infant mortality rate was relatively high (Table 1). The populations of the species increased only little with Douc langurs showing a steady decline in their numbers.

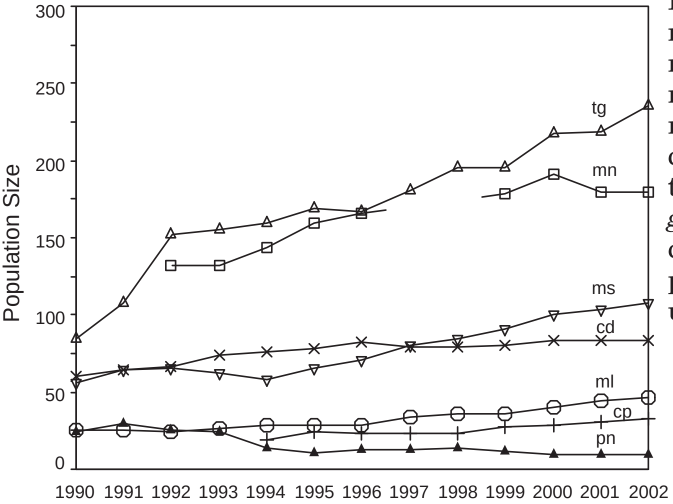

Fig. 3: Population development in mn=*Macaca nigra*; ml=*Mandrillus leucophaeus*; ms=*Macaca silenus*; cd=*Cercopithecus diana*; tg=*Theropithecus gelada*; cp=*Colobus polykomos*; pn=*Pygathrix namaeus* under EEP (1990-2002).

Hylobatidae

Fig. 4 shows the development of populations of gibbons. Despite a nearly 21 % infant mortality rate (Table 1), the population of Gabriella's gibbon (*Nomascus gabriella*) increased more than that of other species registering an overall increase of more than 100 %. The populations of the other species only marginally increased.

Hominidae

Population development of great apes is shown in Fig. 5. The population of Western lowland gorilla (*Gorilla gorilla gorilla*) considerably increased partly due to the inclusion of a large number of new EEP participants and their animals during 1993, and mainly due to birth of new infants. The population of Borneo orangutan (*Pongo pygmaeus*) has remained almost constant except the importation of some individuals during 1992. The populations of Sumatran orangutan (*Pongo abelii*) and Bonobo (*Pan paniscus*) have shown only a marginal and moderate increase respectively. Great apes showed a low birth rate and a high infant mortality (Table 1).

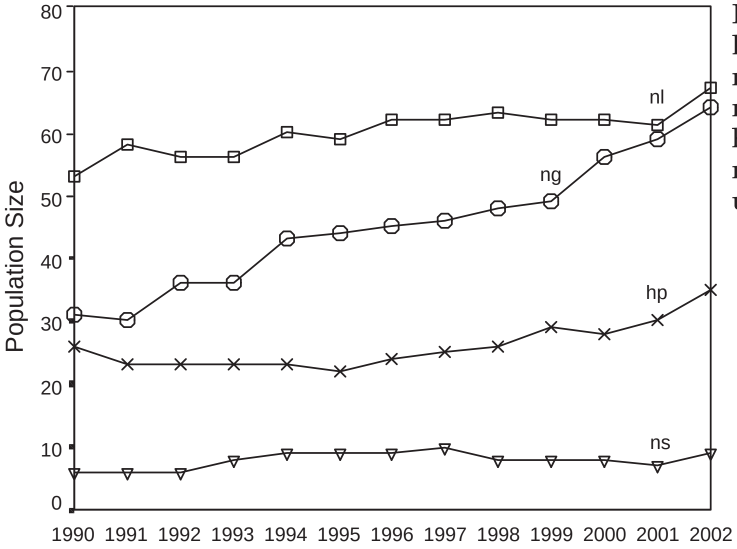

Fig. 4: Population development in ng=*Nomascus gabriella*; nl=*N. leucogenys*; hp=*Hylobates pileatus*; ns=*Nomascus siki* under EEP (1990-2002)

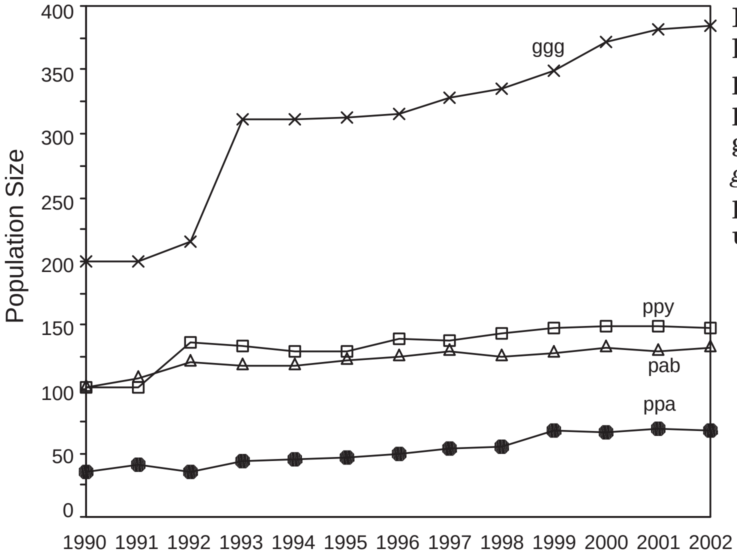

Fig. 5: Population development in ppy=*Pongo pygmaeus*; pab=*Pongo abelii*; ggg=*Gorilla gorilla gorilla*; ppa=*Pan paniscus* under EEP (1990-2002).

Birth and infant mortality rates in relation to other variables

Birth rates

Figures 6 to 9 show the percent annual birth rate in relation to several other factors. The birth rates in different taxa (Fig. 6) were significantly different with lower taxa including Strepsirrhini and Platyrrhini recording high birth rates followed by Cercopithecoidea, Hylobatidae and Hominidae (Kruskal-Wallis H χ^2=17.08; df=4;

p<.01). There was no difference (Kruskal-Wallis H χ^2=6.58; df=3; NS) in birth rates with relation to social system of the species (Fig. 7). The population size at start correlated positively with birth rate (Pearson Product Moment r=0.42; N=25; p<.05).

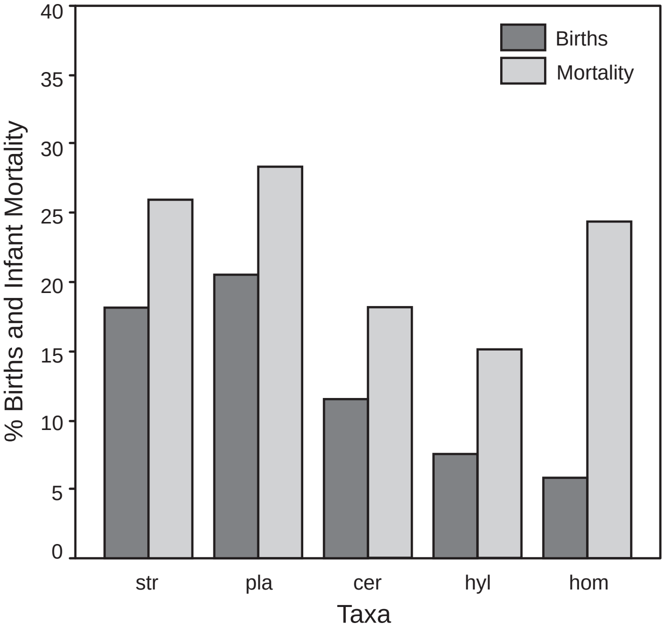

Fig. 6: Birth and infant mortality in different taxa
str=Strepsirrhini;
pla=Platyrrhini;
cer=Cercopithecoidea;
hyl=Hylobatidae;
hom=Hominidae
under EEP (1990-2002).

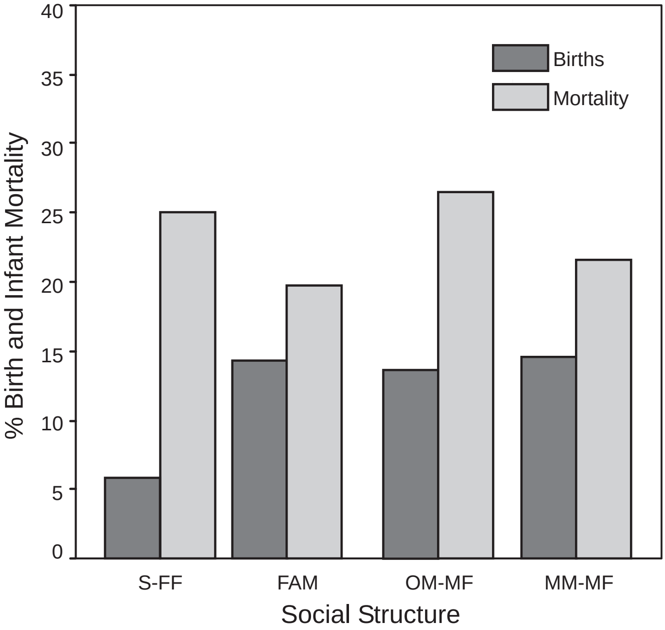

Fig. 7: Birth and infant mortality in relation to social structure in
S-FF=Solitary Fission Fusion;
FAM=Family;
OM-MF=Onemale-Multifemale;
MM-MF=Multimale-Multifemale
systems under EEP (1990-2002).

Infant mortality rates

Infant mortality did not vary among the taxa (Kruskal-Wallis H χ^2=3.68; df=4: NS), except that the Hylobates and Cercopithecids showed a slightly lower mortality rates than other taxa (Fig. 6). Infant mortality rate did not differ in relation to social system (Fig. 7) (Kruskal-Wallis H χ^2=0.79; df=3; NS). There was no effect of birth intervals on infant mortality rates (Fig. 8) (Kruskal-Wallis H χ^2=2.66; df=2; NS). Infant mortality was significantly higher in species that have multiple births than species with only one infant at a time (Fig. 9) (Mann-Whitney U=7.00; p<.01). The initial population size correlated positively with infant mortality (Pearson Product Moment r=0.46; N=25; p<.05). Birth rate and death rate were also found to be positively correlated (Pearson Product Moment r=0.54; N=25; p<.01).

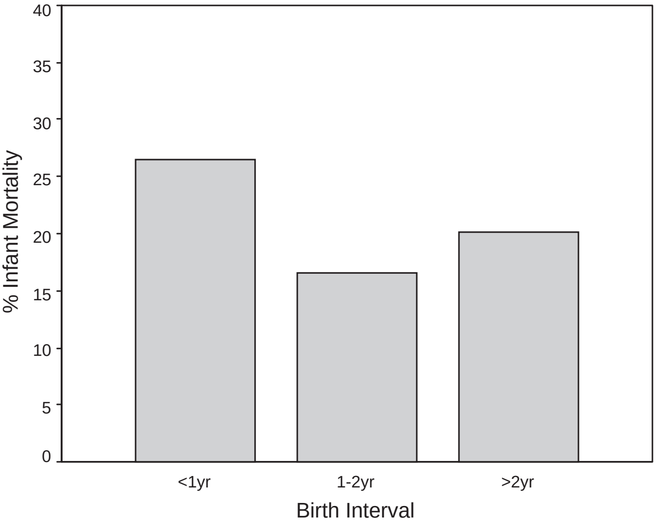

Fig. 8: Birth and infant mortality in relation to birth interval in
<1yr=less than one year;
1-2yr=one to two years;
>2yr=more than two years
under EEP (1990-2002).

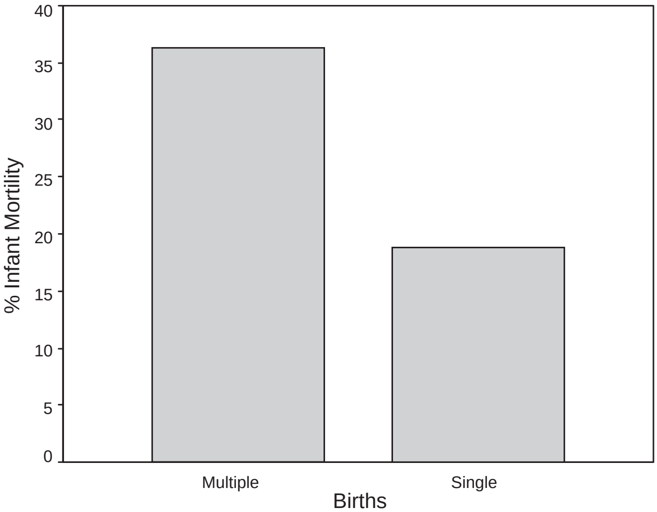

Fig. 9: Birth and infant mortality in relation to single or multiple births under EEP (1990-2002).

Number of adult females and births

Table 1 presents the mean percentage of adult females producing per year for the species on which numbers were available. In the prosimians, 27 to 58% of the females reproduced per year. In the Cercopithecoidea, the percentage of females reproducing per year varied between 15 and 51. About 12 to 18% females reproduced per year in the great apes. These percentages are far below the expected numbers. It was also observed that in some species such as lion-tailed macaque and great apes, where systematic records are available also before EEP, a fairly large percentage of adult females failed to reproduce at all throughout their lives (Kaumanns et al., 2000, 2004; Schwitzer, 2003).

Discussion

The main purpose of this study was to analyse the development of captive primate populations under EEP, discuss the factors related to this development, and to contribute to the development of a perspective for understanding population dynamics in forest fragments. Although notable growth by birth was observed in the case of some populations such as the lion-tailed macaque and species with multiple births, the primate species, by and large, registered growth rates far below the optimum or expected. The higher birth rate in some populations was countered by higher infant mortality rates. A large number of females in several species did not reproduce at all. In fact, in several species, it was observed that over the years, the production of an infant required an increasing number of female-years (Kaumanns et al., 2000, 2004 Schwitzer, 2003). The effective population size, consequently, kept decreasing. As a result, the populations did grow but not substantially.

In the natural habitats, growth rates are determined by resource availability, intra and inter-specific competition, predation and colonising ability of a species. r-selected species are not limited by the above factors, and hence, grow rapidly. On the other hand, K-selected species stabilise their populations at or close to the carrying capacity of their habitats. In captivity, food resources are not limited. Effective utilization of resources does not depend on competition. The resources available per individual are unlimited, and hence, all females could reproduce. Environmental unpredictability and seasonal variations are controlled. Colonizing ability does not limit dispersal as individuals are removed from a captive group when the group size increases. Predation is totally absent. General health status is good, and any sick and wounded individuals are medically treated. Therefore, there should be no limit on reproduction and, in principle, a population could grow exponentially. Why then the primate populations in captivity have not registered a significant increase closer to the maximum expected for a period of over a decade under EEP?

The possible explanation lies in the low reproductive output that could occur due to failure to mate, failure to conceive or early abortion. It is necessary to look for the proximate factors behind these phenomena. Since diet and veterinary care etc. are ruled out as proximate factors, the key aspect that remains to be looked at is the behaviour of individuals and the network of social relationships. At present, no detailed investigations are available on behaviour of primate species under EEP specifically focused on the above issues, and hence, the possible explanations can only be speculative or at the most inferential. Some of these are discussed below.

Due to space and other restrictions, the group size in most captive primate species is kept small with usually one adult male. In contrast to what happens in large groups with several males, the mating opportunities in small groups may be less, and depend upon the ‘personality’ of the only available adult male. In addition, in species where there is female mate choice, a behavioural incompatibility between a female and the only available male may restrict mating.In many species e.g. the lion-tailed macaques, a mating pair is often harassed by other females, and the consort pair usually moves away from the core of the group (KUMAR, 2000). The space restrictions in captivity usually do not permit such spacing out and the probability of interference in mating remains high. This may often result in failure to conceive.

It is an established fact that in primates, most behaviour patterns develop through proper socialization. The conditions for this in captivity may be limited, for instance, if there is the absence of certain age-sex classes in a group. The older juvenile males are always taken out of a captive group that results in a virtual absence of subadult males. In most primate species, the presence of subadult males in groups is critical for socialization of infants and juveniles, especially males. Other than with peers, the juveniles often indulge in social play with subadult males (SINGH et al., 1980) and avoid adult males. A demographic structure with younger siblings, peers and subadult males provides a complete social environment for the juveniles to learn to deal with various age-sex classes and to learn appropriate adult behaviour patterns. A complete absence of subadult males in captive groups may result in learning deficits in juveniles that may affect their reproductive behaviour later when they are adults. The opportunities for juvenile females to learn the skills of parental care may also be limited. Juvenile females reaching adulthood are sometimes removed to establish new groups. The juvenile females have most of their social interactions either with their mothers or with the younger siblings. In some primate species such as langurs, the juvenile females are often observed to sit in ventral contact with their younger siblings. A lack of generation overlap in captive groups deprives young members of such learning opportunities. Another condition which may influence socialisation negatively is the hand-rearing of animals. It may be specifically mentioned that in the historical European ape population which also constitutes the populations in the present study, a large proportion of the individuals are hand-reared (Kaumanns et al., 2004).

The adult males are periodically replaced to avoid mating between father and daughters. The arbitrary introduction of new males may sometimes result in behavioural incompatibilities between males and some females. However, often very little is known about the social competence of the new male. There are no quantitative data on how adult females of the group really react to the new male. A non acceptance of the male even for short periods of time may result in considerable gaps in reproductive output. In natural groups of primates, inter-troop encounters are a usual phenomenon. Such encounters not only provide opportunities for adult males to join new groups, they also trigger increased cohesion among group members. These encounters also probably increase levels of stress and general arousal that in turn influence reproductive success (Carlstead and Sheperdson, 1994).

The space limitations in captivity may force the animals for increased inter-individual interactions. The mean distance between two farthest individuals, calculated at different times when the group is engaged in different activities such as foraging or resting, in a group of primates in its natural habitat. It is possible to have an enclosure of a size that would permit such a mean distance between two farthest individuals in a captive group. However, it has been found that animals are sensitive not only to the proximity of other animals but also to the 'absolute space' that is available to them. Increased density increases aggressive interactions, but the rate of aggression in rabbits increased even when the density was kept constant but the total space occupied by a group was reduced (Myers et al., 1971). The effects of such space limitations may not always be directly observable such as increased number of aggressive episodes but could also result in non-observable conditions such as constantly heightened state of stress. It is possible that such states influence reproductive processes negatively. It is also difficult to experimentally test the effect of space on reproduction since the responses of animals are not expected to vary linearly with reduction or increase in space.

It therefore appears that in captivity, there is a risk that some aspects of social behaviour are either defectively learned and/or do not have the opportunity for expression.This may affect reproductive system such that reproductive output decreases.

Primate groups in forest fragments may be characterised by most features of the captive groups, especially those related to social and demographic structures. In addition, groups of a species that is not able to make use of the surrounding areas such as an agricultural plot, a village, a road, a pastoral grazing patch etc. ('matrix') of a fragment are more likely to suffer (Marsh, 2003b). A typical example of this are the Nilgiri langur (*Trachypithecus johnii*) and the lion-tailed macaque inhabiting rainforest fragments in the Western Ghats of southern India. The Nilgiri langur is by and large a habitat generalist and the lion-tailed macaque is a typical habitat specialist (Singh et al., 1997). A langur group makes use of several forest fragments or at least some individuals such as adult males often move between fragments making use of scattered oak trees in tea plantations or the vegetation along streams or roads (Umapathy and Kumar, 2003). On the other hand, in the same forest fragments, each group of lion-tailed macaques is completely confined to a fragment. It has been observed that the lion-tailed macaque groups inhabiting forest fragments have a lower birth rate (Umapathy and Kumar, 2004), significantly high or low group size (Singh et al., 2002) and deviant behaviour patterns (Singh et al., 2001) as compared to the groups of the species inhabiting large forest complexes. A characteristic feature of primates in fragments appears to be that due to limited dispersal opportunities, such groups would tend to have a deviant demographic structure either under-represented or over-represented by certain age-sex classes and they would also lack external stimuli provided by immigrations and inter-troop encounters. These conditions can be regarded as 'reduced living conditions'. These features in turn are bound to affect behaviour, especially social behaviour, of group members that may further affect their reproductive processes. A repeated study on the same population of black-and-white colobus showed that the birth rate of 0.405 infants per adult female reduced to only 0.026 infants per adult female in just five years due to forest fragmentation (Chapman et al., 2003). In addition, due to human proximity, certain species may also be hunted. If such species have a low reproductive output, it may become impossible for them to replenish their numbers fast enough and they may become locally extinct (Kumara and Singh, 2004).

The data presented in this article also show that primate species in captivity showed considerable variance in their reproductive output. This variation is related to the reproductive biology of a species. In their natural habitats, the species would probably show similar variation. However, it is possible that the effects of captivity and its related features are more pronounced in some species than in others.

The results of the present analysis showed that the initial population size when a species was brought into EEP influenced its birth rate, and consequently its overall growth. The species starting with low numbers grew less. Species occurring in naturally low numbers, occupying wide ranges, having low fertility and depending on patchy and unpredictable resources are specifically vulnerable to habitat fragmentation (Meffe and Carroll, 1994). The number of animals in each fragment is usually quite low. Species such as orang-utan and lion-tailed macaque are typical examples of this. Such populations by themselves, therefore, have a little chance of recovery unless management could ensure their dispersal.

The ultimate purpose of management, both in captivity and in forest fragments, is to create living conditions such that they facilitate expression of full range of adaptive behaviours and optimise life-history patterns of a species as in their more natural habitats. Only then the populations can be augmented.

References

Anonymous a: **www.aza.org/ConScience/ConScienceSSPFact**

Anonymous b: **www.eaza.net/EEP/3EEPinfo.html**

Carlstead K, Sheperdson D (1994): Effects of environmental enrichment on reproduction. *Zoo Biol* 13: 447-458.

Chapman CA, Lawes MJ, Naughton-Treves L, Gillespie T (2003): Primate survival in community-owned forest fragments: Are metapopulation models useful amidst intensive use?. In: Marsh LK (ed.): *Primates in Fragments*. New York, Kluwer Academic/Plenum Publishers: 63-78.

Kaumanns W, Krebs E, Nogge G (2004): Menschenaffen in Menschenhand. Langzeitentwicklung europäischer Menschenaffenpopulationen. *Zool Garten N.F.* 74: 217-228.

Kaumanns W, Krebs E, Schwitzer C, Singh M (2005): Primaten in Europa. *Zeitschrift des Kölner Zoo* 48: 85-96.

Kaumanns W, Schwitzer C, Klumpe K, Schmid P (2000): How are primate breeding programs doing? – An overview and preliminary analysis. In: Rietkerk F, Hiddinga B, Brouwer K, Smits S (eds.): *EEP Yearbook 1998/99*. Amsterdam, EAZA Executive Office: 448-460.

Kumar A (2000): Sexual harassment among female lion-tailed macaques (*Macaca silenus*) in the wild. *J Bombay Nat Hist Soc* 97: 42-51.

Kumara HN, Singh M (2004): Distribution and abundance of primates in rainforests of the Western Ghats, India, and the conservation of *Macaca silenus*. *Int J Primatol* 25:1001-1018.

Laurance WF, and Bierregaard RO (eds.) (1997): Tropical Forest Remnants: Ecology, Management and Conservation of Fragmented Communities. Chicago, University of Chicago Press.

Marsh LK (ed), (2003a): Primates in Fragments. New York, Kluwer Academic/Plenum Publishers.

Marsh LK (2003b): The nature of fragmentation. In: Marsh LK (ed): *Primates in Fragments.* New York, Kluwer Academic/Plenum Publishers: 1-10.

Meffe GK, Carroll CR (1994): Principles of Conservation Biology. Sunderland, Sinauer Associates.

Myers K, Hale CS, Mykytowycz R, Hughes RL (1971): The effect of varying density and space on sociality and health in animals. In: Esser AH (ed.): *Behaviour and Environment: The Use of Space by Animals and Men.* New York Plenum Press: 148-187.

Schwitzer C (2003): Energy Intake and Obesity in Captive Lemurs (Primates, Lemuridae). Munster, Schüling Verlag.

Singh M, Kumar MA, Kumara HN, Sharma AK, Kaumanns W (2002): Distribution, population structure, and conservation of lion-tailed macaques (*Macaca silenus*) in the Anaimalai Hills, Western Ghats, India. *Am J Primatol* 57: 91-102.

Singh M, Kumara HN, Kumar MA, Sharma AK (2001): Behavioural responses of lion-tailed macaques (*Macaca silenus*) to a changing habitat in a tropical rainforest fragment in the Western Ghats, India. *Folia Primatol* 72: 278-291.

Singh M, Prakash P, Pirta RS (1980): Changing patterns of behaviour during the early stages of bonnet monkey *Macaca radiata*. *Proc Indian Acad Sci* 89: 101-108.

Singh M, Singh M, Kumara HN, Kumar MA, D'Souza L (1997): Inter- and intra-specific associations of nonhuman primates in Anaimalai Hills, south India. *Mammalia* 61: 7-28.

Umapathy G, Kumar A (2003): Impacts of forest fragmentation on lion-tailed macaque and Nilgiri langur in Western Ghats, India. In: Marsh LK (ed.): *Primates in Fragments.* New York, Kluwer Academic/Plenum Publishers: 163-189.

Umapathy G, Kumar A (2004): The demography of the lion-tailed macaque (*Macaca silenus*) in the Anamalai Hills, south India. *Primates* 41:119-126.

Authors' addresses:
Kaumanns W: Eschenweg 5, 37130 Gleichen, Germany, silenus@t-online.de
Singh M: Biopsychology Laboratory, University of Myore, Mysore-570006, India, mewasingh@bsnl.in
Krebs E: Cologne Zoo, Riehler Street 173, 50735 Cologne, Germany
Schwitzer C: Bristol Zoo Gardens, Clifton, Bristol BS8 3HA, UK

A 30-YEARS HISTORY OF KAILANA-I (K-I OR B-19) BISEXUAL TROOP OF HANUMAN LANGUR, *SEMNOPITHECUS ENTELLUS* AT JODHPUR (INDIA)

Mohnot SM, Winkler P, Mohnot U, Sommer V, Agoramoorthy G, Rajpurohit LS, Srivastava A, Borries C, Ross C, Stephen D, Chhangani AK, Schülke O, Bhaker NR, Little C, Rajpurohit RS, Sharma G, Rajpurohit DS, Devilal, Vijay P, Swami B

Key words: Hanuman langur, *Semnopithecus entellus*, troop history, long-term study

Abstract

There are about 1950 langurs in and around Jodhpur comprised of 50 groups (35 bisexual troops and 15 all-male bands) within 150 sqkm area. Kailana-I is a unimale bisexual group of Hanuman langurs living on the bank of Kailana Lake 9 km. West to the Jodhpur city. The group has been regularly followed to observe different behavioural aspects for last three decades. In 1977, before splitting into two sub groups (i.e. Kailana-I & Kailana-II), there were 36 individuals comprised of one adult male, 20 adult females, one sub-adult, 5 juvenile females and 9 infants in Kailana groups. At the starting of 1978, this group has splitted into Kailana-I and Kailana-II (due to course of the invasion of all male band in between October-December 1977) carrying 14 and 12 individuals respectively.

In April 1978 there were 14 individuals (one adult male, 11 adult females, 1-1 juvenile and infant) in Kailana-I troop. After 5 years in April 1982 the group size has increased by 8 members (i.e. troop size = 22), while in next 5 years the total members of troop was 24 in April 1987, which remained 18 in April 1992 while 19 in April 1997 and there were 14 langurs in this troop in May 2002 and in May 2007 also the number of individuals found same (i.e. 14) in this study troop.

Although the whole population of Jodhpur langurs became more than double in last 30 years (i.e. 1950 in 2007 from about 900 langurs in 1977) but the size of Kailana-I group has increased in 1982 by 57 % and in 1987 by 71 % approximately, while in 2007 the group size decreased and reached back to that of 1978. The reason behind it might be due to frequent resident male changes taken place in K-I group in compare to other groups. Observations reveal that in some groups, which were more stable and resident male changed after an average tenure of 26.5 months, the group size just doubled in these 30 years.

Introduction

Studies on life histories and demographic parameters of free ranging primates are still comparatively rare. Comparable long-term data are only available for some Cercopithecine species e.g. for *Papio cynocephalus* by Altmann et al. (1977). Life histories are the key elements of population dynamics; it is through life histories that selection operates. Even the most comprehensive cross-sectional studies of demographic parameters of entire populations turn out to be inadequate substitutes for longitudinal focal animal studies to understand evolutionary processes in primate populations (Winkler et al., 1984).

This paper presents a 30 years group history of a one male bisexual troop of free-ranging population of Hanuman langurs, *Semnopithecus entellus* (Dufresne, 1797), Primates: Cercopithecide: Colobinae. This species is the most widespread of the non-human primates of the Indian sub continent and has aroused special interest because of the documentation of infanticide (Sugiyama, 1965; Hardy, 1977; Roonwal and Mohnot, 1977; Mohnot, 1971; Makwana, 1979; Agoromoorthy and Mohnot, 1988; Rajpurohit et al., 1986, 2008; Sommer and Mohnot, 1985).

A genetically isolated pocket population of about 1950 langurs is organized in 50 groups (i.e. 35 unimale groups and 15 all male bands) (Rajpurohit et al., 2006) is monitored for last three decades and regular census data available since 1967-68. An understanding of the population dynamics of langurs is essential in this context, as the genetic fitness is defined in forms of the demographic parameters of survival and fertility rates.

For last 35 years the census data on Jodhpur langurs have been published time-to-time (Mohnot, 1974; Mohnot et al, 1981, 1987; Rajpurohit, 1987; Rajpurohit et al., 1994, 2006). About 18 Ph.D's have been awarded and over 750 research articles been published on different aspects of ecobehaviour, sociobiology, demography and conservation during last 35-40 years. In other words, that the species is the best studied in nature around Jodhpur.

The present paper deals with a particular unimale bisexual group (harem) for the troop history and demographic changes occurred in this troop for the last three decades.

Material and Methods

The data of this research article are part of a long-term field study of Hanuman langurs conducted around Jodhpur located in Rajasthan at the eastern edge of the Great Indian Desert (altitude above 241m, latitude 26°18' N and longitude 73°08' E). The climate is dry with maximum temperatures 48° C in May/June and minimum around 0° C in December/January. Jodhpur receives 90 % of its scanty rainfall (average 370 mm.) during monsoon in July to September.

The habitat occupied by the langurs around Jodhpur includes open scrub forests, fields farms, orchards and ruined buildings (Mohnot, 1974; Winkler, 1981; Rajpurohit, 1987; Chhangani, 2000). The natural open scrub vegetation is dominated by xerophytes plants, including *Prosopis juliflora*, *Prosopis cineraria*, *Acacia senegal*, *Euphorbia caducifolia*, *Caparis desidua* and *Calotropis procera*. The langurs feed an about 200 natural and cultivated plants species (Mohnot, 1974; Winkler, 1981; Srivastava, 1989). Local people used to provision most of the langurs groups for religious reasons with wheat or millet preparations, vegetables, nuts and fruits.

The animals are easy to observe since they are not shy and spend most of the daytime on ground. At the time of census we do select the best time of the day for particular group, however we count the animal early morning when they leave their roosting or returning from foraging sites at evening hours. The counting has been done head to head method and the age categorization as well as infant juvenile sex identification also done simultaneously. For larger groups we do cross counting with the help of two field workers repeating two or three times.

The species exhibit clear-cut sexual dimorphism. On average, adult males weight 18.5 kg and adult females weight 11.7 kg (Sommer, 1985). The reproductive units are bisexual, one male troop (harems) with a single adult breeding male. Multimale troops are very rare here but some time a multimale situation emerged at the time of resident male change. With very few exceptions, females remain for life in their natal troop. Male emigrate-usually as juveniles-to unisexual all male bands, whose home ranges can be on large as 20 sq km. While the bisexual troop occupies its own home range of about 0.5-1.5 sq km (Rajpurohit, 1987; Rajpurohit and Sommer, 1993; Chhangani, 2000; Schülke, 2001).

The study group Kailana-I (K-I) roosts at the bank of Kailana Lake (an artificial reservoir used for the Jodhpur city drinking water) on the *Prosopis* trees regularly followed by Indian and German researcher for last 30 years (see Fig. 1 in Rajpurohit et al., 2008). Our interest for this focal group because this group members had individually identified since 1977, and besides that it contains some very old females. Some females are more than 30 year's of age, for example Female F-1 of this troop died in 1996 at the age of about 35 years (Mohnot, pers. commun. and pers. obs.).

Observation and Results

When the Jodhpur langur population was censused first time in 1977, the whole population was about 900 langurs and the bisexual group Kailana (B-25) size observed 36 individuals (Mohnot et al., 1981). In 1978 when Paul Winkler followed this study group, has splited into two subgroups (due to course of the invasion of all male band between October-December 1977). Which were later designated as Kailana-I (K-I or B-19) living at original site and Kailana-II (K-II or B-20) started living at Bijolai palace near Bijolai bisexual group, which was, displaced afterward towards Bhimbharak (Winkler, 1981 and pers. obser.). The demographic changes occurred during 1977-2007 divided into 7 times with the gap of every 5 years are presented here (see Table 1).

Discussion

A geographical isolation population of about 1950 Hanuman langur around Jodhpur that has been intensive studied by various Indian and German researchers since 1968. And it has been censused time to time for last three decades (Mohnot et al., 1981; Mohnot et al., 1987; Rajpurohit et al., 2006). There was a group fission in Kailana (B-25) bisexual group in 1978 (Winkler, 1981) and the group structure and size of this focal group observed during last 30 years suggest that group size has increased from 14 (in 1978) to 22 in 1982, 24, 18 and 19 in 1987, 1992 and 1997 respectively. But in April 2002 and May 2007 the group size decreased from 19 to 14 individuals. So the troop size of K-I is same as it was in 1978. And there is no net growth observed in K-I during last 30 years.

Table 1: A 30-Years (1978-2007) History of Kailana-I (K-I or B-19) Bisexual Troops of Hanuman Langur (*Semnopithecus entellus*) around Jodhpur (Sources: Mohnot et al., 1981, 1987, Winkler, 1981; Sommer, 1985; Rajpurohit, 1987, 1997, 2004, 2005, 2008; Borries, 1989; Srivastava, 1989; Chhangani, 2000; Bhaker, 2002; Rajpurohit et al. 2006, 2008; Sharma, 2007).

Year	**Census**		**Study group**	**Group Composition and Size**										
	Month	**Whole Popul.**		**Adult**		**Sub-Adult**		**Juvenile**		**Infant**		**Total**		
				M	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**T**
1977	Feb.	900	Kaliana*	1	20	-	1	2	3	6	3	9	27	36
1978	April	930	Kaliana-I	1	11	-	-	-	1	-	1	-	-	14
1982	April	1120	K-I	1	11	1	1	2	5	2	1	5	17	22
1987	April	1276	K-I	1	12	-	-	2	3	4	2	7	17	24
1992	April	1523	K-I	1	8	-	1	3	2	2	1	6	12	18
1997	April	1750	K-I	1	7	-	1	4	1	2	3	7	12	19
2002	May	1815	K-I	1	8	-	-	3	2	-	-	4	10	14
2007	May	1947	K-I	1	8	-	-	1	2	-	2	2	12	14
M=Male, F= Female, T=Total; *Total Population of Kailana troop before splitting in two sub troops; K-I and K-II in December, 1977 (Winkler, 1981 and pers. commun.)														

The population growth of whole langur population of Jodhpur found more than 100 % in last three decades (i.e. from 900 in 1978 to about 1950 in 2007). While the growth in study troop K-I observed only 36 % till 1997 (i.e. from 14 in 1978 to 19 in 1997). And as per 2007 census data, there were only 14 members in this troop. So there is no net growth occur in this troop in last 30 years. The population growth of particular group varied from other group and from the over all population. Feeding by local people, predation, normal or frequent male changes and the natural resources are the main factors affecting the population growth.

The study group Kailana-I had many more resident male changes in comparison to other groups in which the average resident tenure investigated 26.5 month (cf: Sommer and Rajpurohit, 1989). In other words that K-I bisexual group had resident male changed very frequently and we know generally a new resident participate in infanticide activity to kill the suckling infants sired by his predecessor. And this practice of course helps in the stability of the group size. Simultaneously, where we have groups with more stable normal residency in those the group size just doubled during last 30 years.

Acknowledgement

We are grateful to (Late) Prof. M.L. Roonwal, Former Director-Zoological Survey of India (ZSI) and later Vice-Chancellor of University of Jodhpur (India) and (Late) Prof. Christian Vogel, Former Director, Institute of Anthropology, George August University, Göttingen (Germany) for initiating and encouraging primate researches in India particularly in Jodhpur. To Prof. Y. Sugiyama (Japan), (Late) Prof. M.D. Parthasarathy (Bangalore), Prof. C. Southwick (U.S.A.), (Late) Prof. I. Prakash (Jodhpur), Prof. S.B. Hrdy (USA), Mr. D. Ferguson-USFWS (USA), Dr. Jim Moore (USA), Prof. O. Takenaka (Japan), Prof. A.S. Kapoor, Prof. N.K. Lohiya (Jaipur) and Mr. Neil Nightingle (BBC) for collaboration and admiration time to time. To all the heads of Department of Zoology, University of Jodhpur (now J.N.V. University), Jodhpur during these 3-4 decades for logistic support. Thanks are due to UGC, DST, CSIR, MAB-DOE&F, ICCR, Primate Research Centre (PRC), (India), GRF, DPZ, AvHF, DAAD (Germany), CEC (Brussels), BBC, UCL and Roehampto Inst. London (U.K.), Indo-US Primate Project (USFWS-Washington), PRI, Kyoto University (Japan), Univ. of Otago (New Zealand) for financial support to different researches in different project time to time. To the different authorities such as Ministry of Foreign Affairs, Passport Officer, CID Police, Forest Department and other local bodies for favouring and or permitting to conduct such field researches in their premises and other help of their concerned. Thanks are also due to Shri Rameshwal Lal and Shyam Singh-1978-1995 (CAZRI), Mr. Murli (ZSI), Mr. Pankaj Agarwal-1995-2001 (Indo-US Primate Project) and Mr. Bundu Khan-2002-present (PRC) for their help in typing the manuscript. And at last but not least, the langurs (study animals) are acknowledged as well.

References

Agoramoorthy G (1987): Reproductive behaviour in Hanuman langurs, *Presbytis entellus*. Ph.D. Thesis, University of Jodhpur, Jodhpur, India.

Agoramoorthy G, Mohnot SM (1988): Infanticide and juvenilicide in Hanuman langur (*Presbytis entellus*) around Jodhpur, India. *Hum Evol* 3: 279-296.

Altmann J, Altmann SA, Hausfater G, McCuskey SA (1977): Life history of yellow baboons: physical development, reproductive parameters and infant mortality. *Primates* 18: 315-330.

Bhaker NR (2002): Role of vocal communication in sociobiology of Hanuman langur, *Semnopithecus entellus* around Jodhpur (India). Ph.D. Thesis, J.N.V. University, Jodhpur, India.

Borries C (1989): Konkurrenz unter freilebenden languren-weibchen (*Semnopithecus entellus*). Ph.D. Thesis, Georg-August Universitat, Göttingen, Germany.

Chhangani AK (2000): Eco-behaviour diversity of langur, *Presbytis entellus* living in different ecosystems. Ph.D. Thesis, J.N.V. University, Jodhpur, India.

Hrdy SB (1977): The langurs of Abu: Female and male strategies of reproduction. Harvard University Press, Cambridge, Mass.

Makwana SC (1979): Infanticide and social change in two groups of the Hanuman langur *Presbytis entellus* at Jodhpur. *Primates* 20(2): 293-300.

Mohnot SM (1971): Some aspects of social change and infant killing in Hanuman langur, *Presbytis entellus* (Primates: Cercopithcidae) in western India. *Mammalia* 35(2): 175-198.

Mohnot SM (1974): Ecology and behaviour of the common Indian langur, *Presbytis entellus*. Ph.D. Thesis, University of Jodhpur, Jodhpur, India.

Mohnot SM, Gadgil M, Makwana SC (1981): The dynamics of the Hanuman langur population of Jodhpur, Rajasthan, India. *Primates* 22: 182-191.

Mohnot SM, Agoramoorthy G, Rajpurohit LS, Srivastava A (1987): Ecobehavioural studies of Hanuman langur, *Presbytis entellus*. Technical Report (1983-86) pp. IV+89. Mab Project, Department of Environment, Govt. of India, New Delhi.

Rajpurohit LS, Mohnot SM, Agoramoorthy G, Srivastava A (1986): Observation on ousted alpha males of bisexual groups of Hanuman langur (*Presbytis entellus*). *Primate Report* 14: 209.

Rajpurohit LS (1987): Male social organization in Hanuman langur (*Presbytis entellus*). Ph.D. Thesis, University of Jodhpur, Jodhpur, India.

Rajpurohit LS (1992): Origin and composition of the unisexual unit-an all-male band in Hanuman langurs, *Presbytis entellus* around Jodhpur, India. *Primate Report* 34: 47-52.

Rajpurohit LS (1997): Why do mothers carry the corpses of their infant in Hanuman langurs, *Presbytis entellus*? *J Natcon* 9(2): 183-193.

Rajpurohit RS (2004): Study the conflict and reconciliation in Hanuman langur (*Semnopithecus entellus*). Ph.D. Thesis, J.N.V. University, Jodhpur, India.

Rajpurohit DS (2005): Study the dominance Hierarchy and its role in social organization in Hanuman langur, *Semnopithecus entellus* (Dufresne, 1797). Ph.D. Thesis, J.N.V. University, Jodhpur, India.

Rajpurohit LS (2008): Male social organization-Paternal behaviour in Hanuman langur. *Final Technical Report* (2004-07)-UGC, GOI.

Rajpurohit LS, Sommer V (1991): Sex differences in mortality among langurs *Presbytis entellus* of Jodhpur, Rajasthan. *Folia Primatol* 56: 17-27.

Rajpurohit LS, Srivastava A, Mohnot SM (1994): Birth dynamics in Hanuman langur, *Presbytis entellus* of Jodhpur, India. *J Biosci* 19(3): 315-324.

Rajpurohit LS, Chhangani AK, Mohnot SM (2006): Population dynamics of Jodhpur langurs during 1995-2001. *Proc Nat Acad Sci India*, Vol. 75 B(II): 141-147.

Rajpurohit LS, Chhangani AK, Rajpurohit RS, Bhaker NR, Rajpurohit DS, Sharma G (2008): Recent observation on resident male change followed by infanticide in Hanuman langur (*Semnopithecus entellus*) around Jodhpur. *Primate Report* 75: 33-40.

Roonwal ML, Mohnot SM (eds.1977): Primates of south Asia: Ecology, sociobiology and behaviour. XVIII+ 421 pp. Cambridge, Mass. Harvard Univ. Press.

Schulke O (2001): Differential energy budget and monopolization potential of harem holders and bachelors in Hanuman langur, *Semnopithecus entellus*: Preliminary results. *Am J Primatol* 55: 57-63.

Sharma G (2007): Study on the paternal care in Hanuman langur (*Semnopithecus entellus*). Ph.D. Thesis, J.N.V. University, Jodhpur, India.

Sommer V (1985): Weibliche und mannliche reproduktionsstrategin der Hanuman – Languren (*Presbytis entellus*) von Jodhpur, Rajasthan/Indien. Ph.D. Thesis, Gerog-August Universitat, Göttingen, Germany.

Sommer V, Mohnot SM (1985): New observations on infanticide among Hanuman langur (*Presbytis entellus*) near Jodhpur (Rajasthan/India). *Behav Ecol Sociobiol* 16: 245-248.

Sommer V, Rajpurohit LS (1989): Male reproductive success in harem troops of Hanuman langurs (*Presbytis entellus*). *Int J Primatol* 10: 293-317.

Srivastava A (1989): Feeding ecology and behaviour of Hanuman langur, *Presbytis entellus*. Ph.D. Thesis, University of Jodhpur, India.

Sugiyama Y (1965): On the social change of Hanuman langurs (*Presbytis entellus*) in their natural conditions. *Primates* 6: 381-417.

Winkler P (1981): Zur Öko-Ethologie freilebender Hanuman Languren (*Presbytis entellus entellus* Dufresne, 1797) in Jodhpur (Rajasthan), Indien. Unpubl. Ph.D. Thesis, Gerog-August Universitat, Göttingen, Germany.

Winkler P, Loch H, Vogel C (1984): Life history of Hanuman langur (*Presbytis entellus*). Reproductive parameters, infant mortality and troop development. *Folia Primatol* 43: 1-23.

Corresponding Author:
Dr. L.S. Rajpurohit: Department of Zoology, J.N.V. University, Jodhpur-342001, India and Primate Research Centre, 396, 3rd C Road, Sardarpura, Jodhpur-342003, India, prcindia@sancharnet.in or lsrajpurohit@rediffmail.com

MORPHOLOGY AND DISTRIBUTION OF LESIONS ASSOCIATED WITH WASTING MARMOSET SYNDROME IN COMMON MARMOSETS (*CALLITHRIX JACCHUS*)

Zöller M, Mätz-Rensing K, Kaup F-J

Key words: *Callithrix jacchus*, chronic enteritis, common marmoset, diarrhea, hypoproteinaemia, weight loss

Abstract

Wasting Marmoset Syndrome (WMS) is a disease that affects captive callitrichids and can cause substantial problems in zoological and experimental marmoset husbandries due to high morbidity and mortality rates. Pathogenetic mechanisms and etiological factors of this complex syndrome are still under discussion. In the present study seventeen common marmosets (*Callithrix jacchus*) with clinical signs of WMS were included in postmortal investigations. In addition to chronic colitis, which has commonly been reported in WMS so far, the main pathological findings included generalized chronic and chronic active T-cell-mediated enteritis in the small and large intestine, which is regarded as the key pathogenetic process and starting point in the development of WMS by causing a malassimilation syndrome as a result of functional disorders of the intestinal barrier. However, although inflammatory respectively degenerative lesions of the liver and the kidneys are also constant findings in WMS affected marmosets, they do not seem to be directly associated with the disease, but represent distinct disease entities of callitrichids.

Introduction

Wasting Marmoset Syndrome (WMS) is a disease of captive callitrichids that may cause substantial problems in zoological and experimental marmoset livestock husbandries. Among the callitrichids the common marmoset (*Callithrix jacchus*) is the mainly affected species (Ialeggio and Baker, 1995).

WMS is characterized by progressive weight loss despite of normal food intake and a deteriorating general condition. Further clinical signs of the disease include chronic intermittent diarrhea, multifocal alopecia and muscle atrophy leading to movement disorders (McNees et al., 1983; Potkay, 1992). At post mortem examination chronic colitis as well as inflammatory and degenerative alterations of liver and kidneys represent typical findings (Sainsbury et al., 1992; Logan and Khan, 1996). WMS is a fatal disease with a high mortality (60 - 100 %). Death often occurs a few weeks after the onset of clinical symptoms due to severe emaciation and energetic insufficiency of affected animals (Shimwell et al., 1979; Chalifoux et al., 1982). The incidence of WMS in callitrichid colonies varies between 4 and 6 % (Morin, 1983; Sainsbury et al., 1992; Quohs, 2003). Since the first description by King (1976) in Jersey Zoo, a number of reports have been published about WMS in marmosets, but so far pathogenetic mechanisms and etiological factors of this complex syndrome could not be clearly identified. As there are no uniform descriptions of the disease pattern or evidences of etiologic influences, a consistent definition of this syndrome has not been postulated to date. Because of the nonspecific etiology an effective therapeutic concept is not available (Shimwell et al., 1979; Chalifoux et al., 1982; Sainsbury et al., 1992).

Recent studies about the WMS indicate that inflammatory intestinal changes play a decisive role in the pathogenesis of the disease (Quohs, 2003; Bongard, 2005). Therefore, seventeen common marmosets from the German Primate Center, Göttingen, Germany that developed clinical signs of WMS during a time period of two years were examined in the present study. Light microscopic and immunohistochemical investigations with main focus on the intestinal tract were carried out to systematically characterize the pathomorphologic picture of the disease. Additionally, microbial examinations were performed to determine the influence of bacterial and parasitological organisms on the disease.

Materials and methods

Animals and housing conditions

The common marmosets (*Callithrix jacchus*) from the German Primate Center, 11 females and 6 males, aged 1 - 9 years and weighing 202 - 330 g at the time of euthanasia, were housed in indoor facilities in male-female pairings or small family groups for both breeding and experimental purposes. Marmosets from the breeding colony were housed in groups in either accessible (250 cm in height, 100 cm in width, 100 cm in depth) or non-accessible (127 cm in height, 50 cm in width, 80 cm in depth) cages. Marmosets from the experimental animal unit were housed in pairs in cages measuring 100 cm in height, 50 cm in width and 70 cm in depth. All cage types were equipped with wooden or metal nest boxes and trunks and branches for environmental enrichment. Animal rooms were maintained at 25° C with 50 - 60 % relative humidity on a 12 h light/dark cycle with 30 min ‘dawn’ and ‘dusk’ periods. The room light level during the light phase was 350 - 400 lux at 1 m above the floor. Animals were fed twice a day from Monday to Saturday. Morning feeding consisted of a mash on the basis of a pap (Milupa GmbH & Co, 61381 Friedrichsdorf, Germany) or rice gruel with added vitamins and minerals. A varying mixture of fruits, vegetables, eggs, rice, pasta, zwieback, cat food, chicken and pellets for marmosets (Ssniff Spezialdiäten-GmbH, 59494 Soest, Germany) was offered for midday feeding. On Sunday there was a change of feeding regimen with only one feeding consisting of bananas, vegetables, cottage cheese and mealworms. Animals had free access to water at all times.

Identification of WMS affected animals was carried out on the basis of weight development and responsiveness to treatment. All marmosets were weighed at regular time intervals to monitor body weight development. Therapeutic measures in affected animals included application of additional food, paramunity inducers (Baypamune®, Bayer HealthCare AG, 51373 Leverkusen, Germany, 2 x 0,5 ml/animal/day, subcutaneous injection) and a mixture of vitamins, minerals and amino acids (Amynin®, 85399 Merial, Hallbergmoos, Germany, 2 ml/animal/day, subcutaneous

injection). Enrofloxacin (Baytril®, Bayer HealthCare AG, 51373 Leverkusen, Germany, 0,004 ml/animal/day, intramuscular injection) was used for treatment of animals with watery or bloody diarrhea.
Marmosets were regarded as 'wasters' when they met all criteria listed in Table 1.

Table 1: Clinical criteria for identification of WMS affected marmosets.

Weight development	weight loss: - more than 50 g within a few days or - slowly progressive (weeks/months) with final body weights of less than 300 g
Responsiveness to treatment	unresponsiveness to common antibiotic therapy or evidence of relapse after short-term therapeutic success
Food intake	normal

Post mortem examination and collection of samples

All animals of the present study had to be euthanized in advanced stages of disease for ethical reasons due to increasing weakness and weight loss. Previous to the necropsy blood samples for hematological and serological examinations collected by heart puncture under a standardized ketamine/xylazine anesthesia with Göttinger Mixture II (0,1 ml/kg body weight). 10 ml Göttinger Mixture II consist of 5 ml ketamine (100 mg/kg, Ketavet®, Pfizer Pharma GmbH, 76139 Karlsruhe, Germany), 1 ml xylazine (10 %, Rompun®, Bayer HealthCare, 51373 Leverkusen, Germany), 0,1 ml atropin (1 %, Atropin, Wirtschaftsgenossenschaft Deutscher Tierärzte (WDT) eG, 30827 Garbsen, Germany) and 3,9 ml aqua ad injectionem. Blood for hematology was collected in calcium ethylene diaminetetraacetic - treated tubes (BD Vacutainer Systems, Roborough, Plymouth, PL6 7BPP, UK) and analyzed in an automated blood count analyzer with integrated software for data management (CELL-DYN 4000 blood count analyzer, Abbott Laboratories, Illinois 60064-3500, USA). Tubes containing an inert gel barrier and a double clot activator were used for serum chemistry (BD Vacutainer Systems, Roborough, Plymouth, PL6 7BPP, UK). Serum was obtained by centrifugation at 2500 g at room temperature for 20 min and analysed in an automated chemical analyser (MODULAR ANALYTICS, P-Modul, Roche Diagnostics, 68305 Mannheim, Germany). Euthanasia was performed by intracardial injection of pentobarbital (Narcoren®, 85399 Merial, Hallbergmoos, Germany, 1ml/ kg body weight). A complete necropsy was performed in all animals with clinical symptoms of WMS. Tissue samples for pathomorphologic investigations were taken routinely from the organ systems including each gut section and were immediately fixed in 10 % phosphate-buffered formaldehyde for histological examinations and in 4 % phosphate-buffered formaldehyde for immunohistochemical examinations.

Preparation for histology and immunohistochemistry

Following fixation in 10 % phosphate-buffered formaldehyde for at least 24 h, tissue samples were automatically paraffin-embedded (Hypercenter XP, Thermo Shandon, 60437 Frankfurt am Main, Germany), sectioned at 3 μm and stained with hematoxylin and eosin (H&E). For verification of hemosiderosis a Berlin-blue reaction of liver, kidney and spleen was made for every marmoset.

Immunohistochemical investigations were carried out on paraffin-embedded sections of the intestine fixed in 4 % phosphate-buffered formaldehyde using the SABC-method (streptavidin-biotin-complex) and the chromogene DAB (diaminobenzidine tetrahydrochloride, *i*View^{TM} DAB detection kit, Ventana, BP 30144, F-67404 Illkirch CEDEX, France). Primary antibodies were anti-CD3 antibody (rabbit anti-human T cell, DakoCytomation GmbH, 22083 Hamburg, Germany), anti-CD20 antibody (monoclonal mouse anti-human CD20cy, Clone 26, DakoCytomation GmbH, 22083 Hamburg, Germany) and anti-MAC antibody (monoclonal mouse anti-human myeloid/histiocyte antigen, Clone MAC387, DakoCytomation GmbH, 22083 Hamburg, Germany). Subsequent to an appropriate pretreatment, the slides (18/cycle) were placed in the NEXES-immunostaining-module (Ventana, BP 30144, F-67404 Illkirch CEDEX, France) with one positive (lymph node tissue from *Callithrix jacchus* and one negative control (PBS) in each cycle.

Data collection, documentation and statistics

The histopathological findings were recorded in an examination protocol for each marmoset. A detailed comparative histological examination was performed on the tissue samples from the six gut sections with the objective to classify and gradually categorize the inflammatory changes of the intestine according to the studies of Chalifoux et al. (1982) and Clapp et al. (1988). Therefore, every intestinal site of each animal was examined for mononuclear and polymorphnuclear cells in the propria, crypt abscesses, GALT hyperplasia and ulceration at 400-times magnification. Grading of these parameters was performed according to the criteria listed in Table 2. In addition to the semi quantitative evaluation, a descriptive characterization and documentation of epithelial atypia (epithelial degeneration and regeneration), villous-/crypt morphology and further findings not included in the examination parameters was performed.

Table 2: Evaluation scheme for the semi quantitative assessment of the intestinal inflammatory reaction.

grade	**mononuclear cells in the *Lamina propria***	**polymorphnuclear cells in the *Lamina propria***	**crypt abscesses**	**GALT-hyperplasia**	**ulceration**
negative	no or sporadic (< 10) mononuclear cells in the *L. propria*	no polymorphnuclear cells in the *L. propria*	no crypt abscesses	no hyperplasia or activation of GALT	no ulceration
minimal	few (>10) mononuclear cells in the *L. propria*	few polymorphnuclear cells in the *L. propria*	1-2 crypt abscesses	mild follikular hyperplasia without follicular centre activation	focal ulceration without inflammatory reaction

grade	**mononuclear cells in the *Lamina propria***	**polymorphnuclear cells in the *Lamina propria***	**crypt abscesses**	**GALT-hyperplasia**	**ulceration**
mild	sparse infiltration of mononuclear cells in the *L. propria*	sparse infiltration of polymorphnuclear cells in the *L. propria*	moderate number of crypt abscesses	moderate hyperplasia with indicated follicular centre activation	focal ulceration with inflammatory reaction
moderate	dense infiltration of mononuclear cells in the *L. propria*	dense infiltration of polymorphnuclear cells in the *L. propria*	numerous crypt abscesses	distinct hyperplasia with obvious follicular centres	multifocal ulceration with moderate inflammatory reaction
severe	myriad mononuclear cells in the *L. propria*	myriad polymorphnuclear cells in the *L. propria*	crypt abscesses in almost all crypt lumina	massive hyperplasia with distinct follicular centres and narrow marginal zone	multifocal ulceration with distinct inflammatory reaction

Classification of the enteritis included severity code and time dependence and was carried out for the respective gut sections in all marmosets. Time dependence was determined in accordance with the composition of the inflammatory cell infiltrate in the propria and included acute, chronic active (chronic with an acute component) and chronic enteritis.

To determine statistical differences in severity between the various intestinal segments and to correlate the intestinal lesions with the severity of kidney alterations, a Spearman Rank-order correlation analysis was performed ($n = 17$). Therefore, the severity grades of intestinal and renal lesions were converted into ordinal data with a ranking from 1 to 4 (no lesion = 0, minimal = 1, mild = 2, moderate = 3, severe = 4). Statistical significance was set at $P < 0.05$. Sample pairs with positive correlation coefficients tend to increase together. For pairs with negative correlation coefficients, one variable tends to decrease while the other increases.

Bacteriological and parasitological examination

A bacteriological examination of small and large intestine, liver, spleen, kidney, heart and lung and a parasitological examination of small and large intestine was performed in each marmoset at the time of necropsy. Bacterial culture of the organ spectrum was performed on blood agar plates incubated at 37° C for 24 h (Columbia-Agar Basis®, Merck KG aA, 64293 Darmstadt). In addition, feces material was incubated on salmonella agar (Merck KG aA, 64293 Darmstadt, Germany), Mac Conkey agar (Merck KG aA, 64293 Darmstadt, Germany) at 37° C for 24 h and on campylobacter agar at 42° C for 48 h under microaerophilic conditions (CampyPak Plus®, Becton Dickinson GmbH, 69126 Heidelberg, Germany). For specific detection of enteropathogenic clostridia an ELISA (enzyme-linked immunosorbent assay) was available (ProSpecT® II *Clostridium difficile* Toxin A Microplate Assay, Remel Inc, Lenexa KS 66215, USA). Establishment of *E. coli* culture was followed by strain typing by the national reference centre for salmonella and other enteric pathogens (Robert-Koch-Institut, 38855 Wernigerode, Germany).

Parasitology of fecal samples was performed by light microscopic examination of native feces preparations. All marmosets were tested for *Entamoeba histolytica*, *Cryptosporidium* sp. and *Giardia lamblia* using a specific ELISA (ProSpecT Cryptosporidium Microplate Assay, ProSpecT *Entamoeba histolytica* Microplate Assay, ProSpecT Giardia Microplate Assay, Alexon-Trend Inc, Ramsey Minnesota 553039115, USA).

Results

Hematology and serum chemistry

Blood analyses revealed variations of different hematological and serological parameters. Substantial findings included anemia in five animals and a decrease of the serum albumin level accompanied by decreased total protein levels in all marmosets of the investigation group. An increase of the serum enzymes lactate dehydrogenase (LDH), aspartate aminotransferase (AST), creatine kinase (CK) and alkaline phosphatase (AP) was evident in most of the tested marmosets. Increased blood urea nitrogen (BUN) levels indicating concomitant renal disease were observed in the serum of three marmosets with WMS (Table 3).

Macroscopic examinations

At necropsy, ten marmosets showed main pathological changes that were located in the digestive tract, the urinary tract and the bones. Macroscopically, pathological changes of the intestinal tract were observed only in two animals and were represented by watery feces, increased thickness of the intestinal wall, segmental dilatation and follicular hyperplasia of the mesenteric lymph nodes. Lesions of the urinary tract affected the kidneys of two animals and were characterized by enlargement, elucidation, compact consistency and a grained surface. Five marmosets showed an increased elasticity and fragile consistency of various bones, whereas the cranial bones and ribs were primarily affected. All marmosets of the investigation group showed cachexia and severe dehydration.

Light microscopic and immunohistochemical examinations of the intestine

Contrary to the macroscopic findings, detailed histological examination of the tissue samples from the six gut sections revealed inflammatory changes of the small and large intestinal mucosa in all marmosets of the present study. The inflammatory cells predominantly consisted of mononuclear cells that were graded as minimal to moderate in most gut sections. Only the colon showed an increased number of neutrophils in the mucosa. Crypt abscesses were a rare finding and were mainly graded as minimal to mild. Mild to moderate hyperplasia of the GALT-system was correlated with the amount of inflammatory cells in the propria. Ulceration of the mucosa with penetration of the basal lamina was only observed in two animals with WMS. Epithelial atypia was a rather uncommon finding and included the presence

Table 3: Clinicochemical results of the WMS affected marmosets with indication of reference values for common marmosets according to Fortman et al. (2001) and Pryce et al. (1997).

parameter	**reference**	**animal (G)-number**																
	value	**6634**	**6650**	**6687**	**6688**	**6694**	**6787**	**6795**	**6821**	**6859**	**6869**	**6905**	**6931**	**6940**	**7035**	**7079**	**7092**	**7096**
albumin (g/dl)	4,4-5,8	3,35	3,84	3,01	3,31	3,03	*	3,82	2,94	4,19	3,44	3,47	1,25	2,15	2,97	*	2,45	2,88
alkaline phosphatase (U/l)	34-88	56	101	49	48	92	*	112	158	94	200	332	95	67	276	*	150	589
amylase (U/l)	337-1523	781,8	779,5	545,5	774,1	1363	*	1148	999,2	639,9	865,7	643,9	591,1	479,2	575,1	*	589,4	728
total bilirubin (mg/dl)	0-1,02	0,06	0,08	0,07	0,09	0,15	*	0,09	0,09	0,09	0,22	0,07	0,1	0,04	0,14	*	0,14	0,18
calcium (mmol/l)	2,3-2,9	3,77	2,31	2,25	2,91	2,9	*	3,98	2,95	2,5	2,03	1,62	2,3	2,28	2,2	*	1,9	2,22
cholesterol (mg/dl)	136-234	114	142	73	102	139	*	135	115	114	173	108	197	126	57	*	99	77
creatin kinase (U/l)	920-2410	1635	4468	4674	3859	3349	*	47	5656	2078	7335	2614	32654	21098	1144	*	1274	2283
creatinin (mg/dl)	0,25-1,9	0,33	0,23	0,19	0,29	0,57	*	0,26	0,065	0,24	0,3	0,24	0,07	0,14	0,12	*	0,28	0,15
total protein (g/dl)	6,4-8,0	5,38	6,05	4,93	5,48	6,43	*	6,33	5,51	6,21	6,52	5,14	3,07	4,9	4,56	*	4,98	5,13
glucose (mg/dl)	124-220	145	106	159	169	250	*	121	199	87	149	138	190	105	184	*	210	253
AST (U/l)	106-196	122,1	360,3	172	148,5	207,8	*	59,6	468,7	175,3	82,6	236	1105	3905	286,4	*	197,1	585,4
ALT (U/l)	38-72	0,1	10,9	8,8	2	9,3	*	2	36,8	13,3	5,6	15,4	45,8	39,8	2,5	*	11,5	9
GGT (U/l)	5,8-15,3	< 4	1,2	1,3	0,1	< 4	*	1,4	2,5	1	3	3,2	5,2	2,3	3,8	*	4,1	4
uric acid (mg/dl)	0,02-8	0,97	1,06	1,27	1,47	2,47	*	0,67	2,31	2,35	1,13	1,73	1,14	0,78	0,53	*	1,33	1,37
BUN (mg/dl)	15-29	9,5	35,9	12,9	10	40,5	*	4,7	18,9	18,5	13	10,9	49,6	21,6	13,3	*	25,6	9
iron (?mol/l)	6-45	21,4	21,7	27,8	27,2	11,5	*	16	36	23,5	20,6	10,4	19	9	27,6	*	13,6	42,2
LDH (U/l)	108-328	571	582	292	121	558	*	83	594	351	1310	306	3352	4065	249	*	317	174
triglycerids (mg/dl)	63-209	66	62	43	57	236	*	183	151	50	82	57	97	225	93	*	83	45
phosphore (mmol/l)	1,4-2,3	1,58	2,33	2,9	2,29	5,31	*	1,69	3,24	2,53	0,88	1,49	1,21	2,05	0,42	*	1,35	1,21
sodium (mmol/l)	153-169	150,1	152,3	152,8	148,7	125,7	*	156,8	137	152,9	150,6	158,4	152	155,8	149,3	*	147,5	141,6
potassium (mmol/l)	3,5-4,7	3,65	4,12	4,38	3,08	5,24	*	4,93	7,19	4,52	3,77	5,18	4,1	2,46	7,85	*	3,91	5,12
chloride (mmol/l)	93-121	106,2	112,6	124	114,6	80,3	*	107	108,6	116,3	108,7	118	111,8	123,8	119	*	116,9	104,7
* not examine																		

of necrotic epithelial cells, vacuolation and thinning of the epithelium and intraepithelial microabscesses. Variations of crypt and villous morphology were characterized by villous atrophy and fusion and crypt dilatation in the small intestine and crypt atrophy, branching of crypts and crypt dilatation in the large intestine (Figures 1, 2). Further findings included hyperemic villi, submucosal inflammatory cell infiltration and dilatation of duodenal glands in individual animals. A common finding was attaching bacteria at the epithelial surface and within the intestinal lumen of the duodenum and the colon.

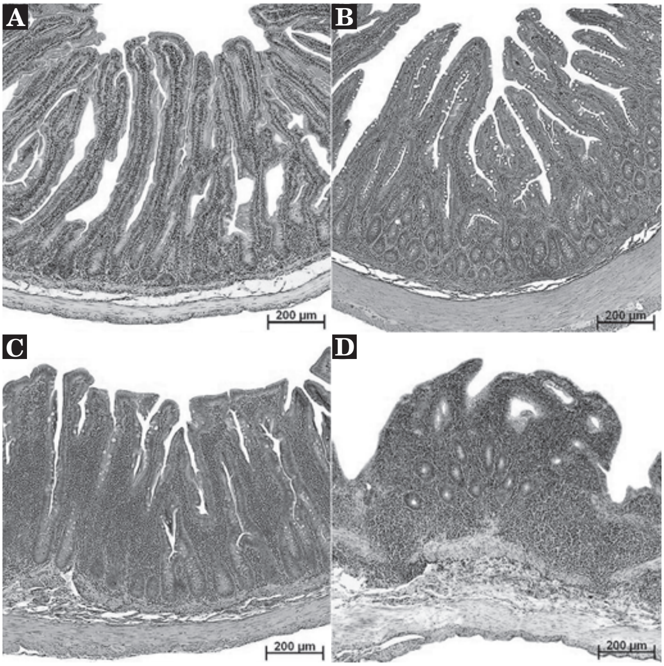

Fig. 1: Grading of the intestinal inflammation on the basis of the severity code in the small intestine (H&E, Scalebar = 200 µm). A: Enteritis, minimal with few inflammatory cells in the propria and intact villous architecture, jejunum. B: Enteritis, mild with few inflammatory cells in the propria and beginning villous atrophy and fusion, duodenum. C: Enteritis, moderate with a dense inflammatory cell infiltrate in the propria and increasing shortening and fusing of villi, jejunum. D: Enteritis, severe with a dense inflammatory infiltrate in the propria. Villi almost disappeared, ileum.

Evaluation of the chronicity of inflammatory lesions almost exclusively revealed chronic and chronic active enteritis. Acute inflammatory lesions were only detected in the jejunum of one animal. Except for the colon chronic enteritis was the most prevalent finding in all gut sections. Distribution of severity codes showed distinct accentuation within the cranial parts of the intestine. A high incidence of mild to moderate enteritis was observed in the cranial parts of the intestine, whereas minimal inflammatory reactions were mainly present in the colon and the rectum (Figure 3). Statistical analysis revealed no significant relationship of severity grades between the small and large intestinal sites ($P > 0.05$). However, a significant correlation of severity of enteritis was present between Caecum, Colon and Rectum (positive correlation coefficient, $P < 0.05$).

Immunohistochemical examinations showed that the mononuclear cell infiltration predominantly consisted of T lymphocytes in all gut sections (Figure 4). In contrast to the T cells, B lymphocytes and macrophages were only sporadically observed in the intestinal propria.

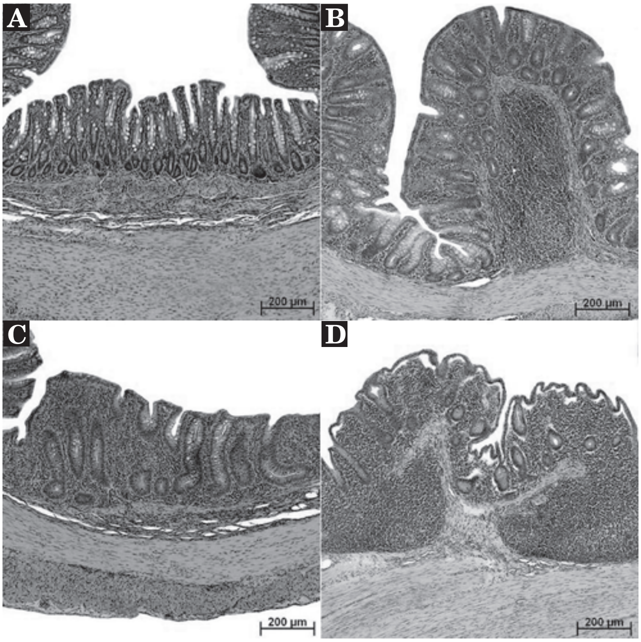

Fig. 2: Grading of the intestinal inflammation on the basis of the severity code in the large intestine (H&E, Scalebar = 200 µm). A: Enteritis, minimal with few inflammatory cells in the propria and intact crypt architecture, rectum. B: Enteritis, mild with few inflammatory cells, beginning crypt atrophy and mild GALT hyperplasia, colon. C: Enteritis, moderate with a dense inflammatory cell infiltrate within the propria and distinct atrophy and branching of crypts, caecum. D: Enteritis, severe with a dense inflammatory cell infiltrate within the propria. Normal crypt architecture disappeared, rectum.

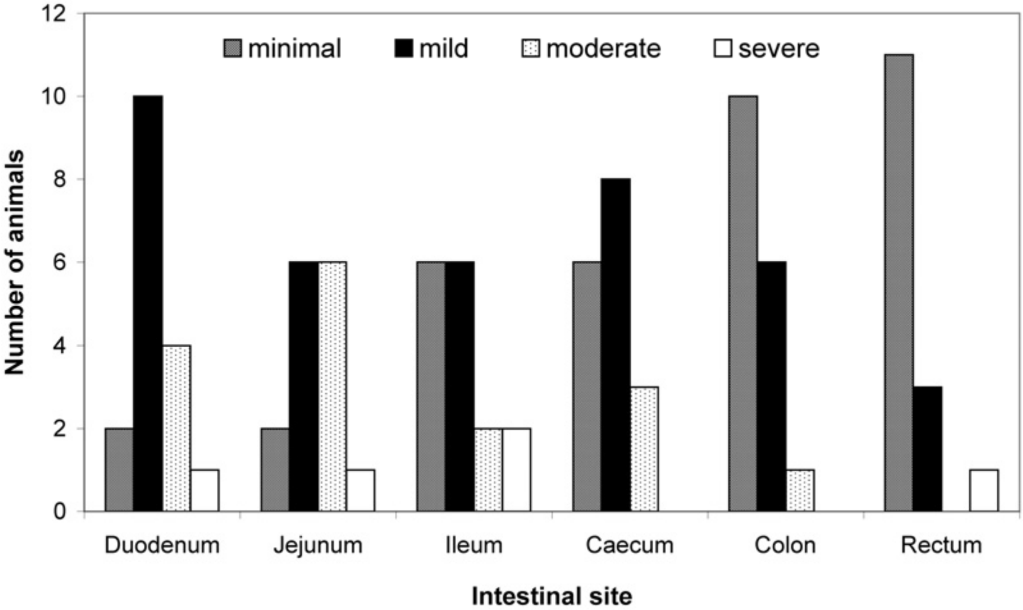

Fig. 3: Distribution of severity codes of chronic and chronic active enteritis depending on the intestinal localization in marmosets with WMS.

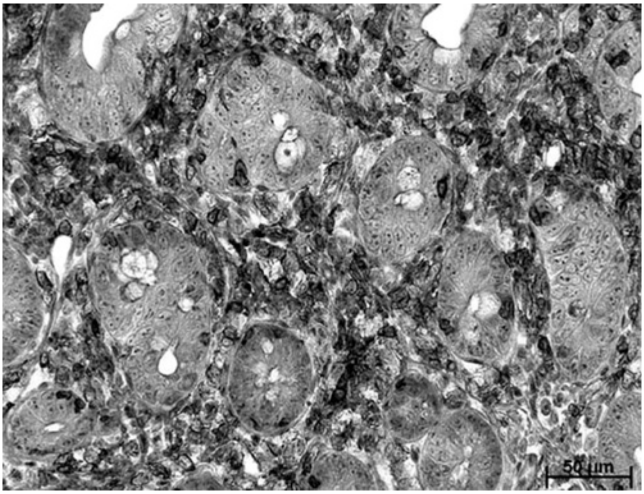

Fig. 4: Enteritis, chronic active, moderate in the jejunum of a common marmoset affected with WMS. Most of the inflammatory cells are consistent with T lymphocytes (IHC-SABC, CD3, Scalebar = 50 µm).

Light microscopic examinations of other organs

At microscopic examination, pathohistological findings were frequently observed within the kidneys and the liver of WMS affected marmosets.

Pathological changes of the kidneys were characterized by minimal to moderate chronic interstitial nephritis (Figure 5) in eleven marmosets. In addition, there was glomerular mesangial proliferation of variable severity (minimal to moderate) in all examined animals. Both interstitial and glomerular lesions were statistically independent of the intestinal lesions ($P > 0.05$).

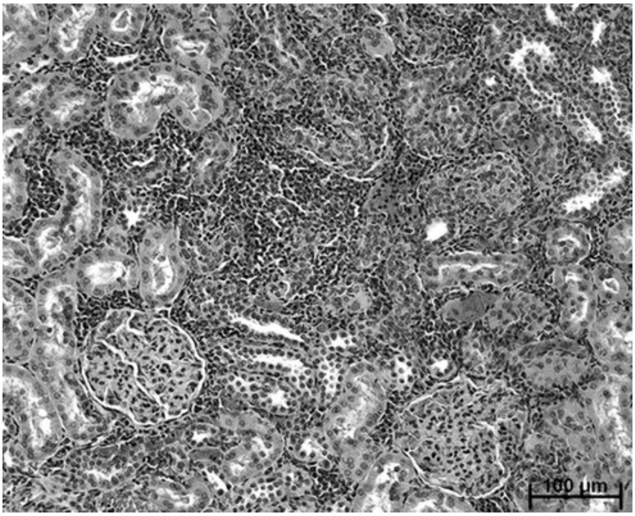

Fig. 5: Moderate interstitial nephritis in a marmoset affected with WMS (H&E, Scalebar = 100 µm).

Pathohistological changes of the liver were detected in all marmosets of the investigation group and were represented by mild chronic hepatitis with evidence of microgranuloma, vacuolar degeneration of centrolobular hepatocytes and moderate to severe hemosiderosis (Figure 6).

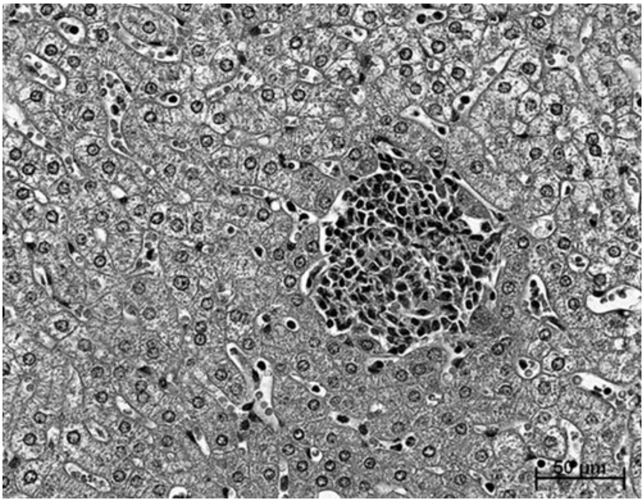

Fig. 6: Liver of a WMS affected marmoset with diffuse vacuolation of hepatocytes and focal microgranuloma (H&E, Scalebar = 50 µm).

Microbiological examinations and pedigree analyses

Bacterial agents were exclusively isolated from the small and large intestine. An overview about the presence of bacteria within the intestinal tract is provided in table 4. The ELISA for specific identification of *Clostridium difficile* was negative in all tested marmosets. Typing of haemolytic *E. coli* strains revealed the serovars O6:

Table 4: Incidence of bacterial isolates in the intestinal tract of the marmosets.

small intestine	**incidence**
mono infectious	
E. coli	1
haemolytic *E. coli*	1
Streptococcus sp.	1
double infections	
E. coli + *Streptococcus* sp.	1
E. coli + *Acinetobacter* sp.	1
E. coli + *Klebsiella* sp.	1
triple infections	
E. coli + *Streptococcus* sp.+ *Klebsiella* sp.	1
E. coli + *Streptococcus* sp.+ *Campylobacter* sp.	1
large intestine	**incidence**
mono infections	
E. coli	8
Streptococcus sp.	1

double infections	
E. coli + *Streptococcus sp.*	2
E. coli + haemolytic *E. coli*	2
Campylobacter sp. + *Klebsiella ozeaneae*	1
triple infections	
E. coli + *Klebsiella* sp. + *Proteus* sp.	1
fourfold infections	
E. coli + haemolytic *E. coli* + *Campylobacter* sp. + *Klebsiella* sp.	1
fivefold infections	
E. coli + *Klebsiella* sp. + *Streptococcus* sp. + *Campylobacter* sp. + *Citrobacter freundii*	1

Parasitological examinations on small and large intestinal feces at the time of necropsy revealed *Giardia lamblia* in four animals.

Comparative investigations of marmoset pedigrees with distinct composition regarding the characteristic (WMS) were not indicative of a monogenetic defect in animals with WMS as there was no accumulation of WMS cases in the offspring of couples with one or two WMS affected marmosets.

Discussion

In the present study clinical criteria for the identification of potential ‘wasters’ were established in consideration of physiological animal weights and published data about WMS pathology and therapeutic success. Definition of these criteria was essential as WMS is a heterogeneously described disease with a variable clinical picture. The choice of animals for the present study was primarily based on the condition of severe weight loss during normal food intake which is a repeatedly reported characteristic of WMS affected adult marmosets (Tribe, 1978; Morin, 1983; Logan and Khan, 1996). To exclude bacterial infections as the cause of weight loss and deteriorating general condition for the marmosets of the present study unresponsiveness to common antibiotics represented a further criterion for the intravital diagnosis of WMS. The marmosets that were chosen in accordance with these criteria were between one and nine years old and included both male and female animals indicating that WMS is a disease entity occurring irrespectively of sex and age.

Hematology and serology represented additional clinical laboratory diagnostic methods for the identification of WMS affected marmosets. Anemia that is regularly described in association with WMS was only detected in five marmosets and probably resulted from hypoproteinaemia (Wixson and Griffith, 1986; Pritzker and Kessler, 1998; Juan-Salles et al., 2003). In all marmosets hypoproteinemia was characterized by decreased levels of the major globulin fraction, the albumin (Shinwell et al., 1979; Logan and Khan, 1996; Miller et al., 1997). Hypalbuminemia is a well known feature of WMS, but its pathogenesis is still unknown. Decreased serum albumin levels can be caused by several conditions such as nutritional protein deficiency, malassimilation, protein loosing enteropathy, nephropathy (nephrotic syndrome) and chronic hepatopathy. In consideration of the histological results it is hypothesized that the enteritis is responsible for a malassimilation syndrome leading to malabsorption of different nutrients such as proteins, vitamins and minerals. Provided that the inflammatory lesions in the small intestine are associated with malfunction of the intestinal barrier, a malassimilation syndrome most likely represents the pathogenetic mechanism in WMS.

Chronic enteritis is a commonly reported histological finding in WMS affected marmosets and was observed in all marmosets of the present study (Chalifoux et al., 1982; Quohs, 2003). However, distribution of inflammatory lesions differed from the literature. While most authors report on chronic colitis in WMS affected animals (Chalifoux et al., 1982; Sainsbury et al., 1992; Iallegio and Baker, 1995), enteritis was found throughout all parts of the intestine in the marmosets of the present study. In the large intestine, chronic active colitis represented a typical finding. The acute component represented by neutrophilic infiltration argues for a recurrent injurious factor leading to recidivating activation of the chronic mucosal inflammation. The results of the statistical analysis, which showed no significant relationship between the inflammatory lesions of the large intestine segments and the small intestine segments, but a positive correlation between the severity grades of the three large intestine segments, raises the question of the diagnostic relevance of rectal biopsies in WMS. Although the morphology of the enteric lesions in the biopsy may be exemplarily for the other large intestine segments, it does no reflect the inflammatory conditions of the small intestine, which are considered to be of main importance in the development of WMS.

WMS associated lesions of the kidneys included chronic interstitial nephritis and glomerular lesions causing uraemia in three animals. Chronic inflammation of the kidneys has often been reported in marmosets with WMS, but the etiology of this lesions is still unknown (Potkay, 1992; Sainsbury et al., 1992). As the statistical analysis shows no correlation between the renal and intestinal lesions, it must be assumed that the kidney lesions represent an independent disease entity, which is not directly associated with WMS.

Histological changes of the liver included chronic hepatitis, degeneration and hemosiderosis. Non purulent mild hepatitis has also been reported in WMS affected marmosets and is probably a secondary reaction to degenerative cell loss (Chalifoux et al., 1982). According to Quohs (2003) hepatocyte degeneration is the result of intracellular pigment deposition. Hepatic alterations did obviously not lead to functional restriction as the liver specific enzyme ALT was not increased in any of the tested marmosets with WMS. AP, AST and LDH are not regarded as liver specific and can also result from bone and muscular disease. Hemosiderosis is a common finding in New World monkeys and has also been reported regularly in association with WMS (Brack and Rothe, 1981; Chalifoux et al., 1982; Quohs, 2003). Potential causes of hepatic iron storage include dietary iron overload and a lack of chelating agents such as tannins in the diet of captive callitrichids (Miller et al., 1997; Claus et al., 2002).

Macroscopic and serological examinations indicated the presence of bone disease in WMS affected marmosets. Disorders in bone metabolism are a common finding in captive marmosets and are attributed to vitamin D or calcium deficiency leading to insufficient mineralization of bones (Sainsbury et al., 1992; Hatt and Sainsbury, 1998). It remains unknown whether this symptom represents an individual disease entity (metabolic bone disease, MBD) or an WMS associated lesion (Iallegio and Baker, 1995). Causes of decreased availability of vitamin D or calcium include nutritional deficiency, malabsorption due to intestinal infections and insufficient renal production of the active vitamin D metabolite due to nephropathy (Fowler, 1986; Sainsbury et al., 1992;Hatt and Sainsbury, 1998). The pathohistological findings support the hypothesis that decreased intestinal absorption of vitamin D and/ or insufficient renal production of active vitamin D metabolites are potential causative factors of bone metabolism disorders in WMS affected marmosets.

Immunohistochemical examinations of the intestinal inflammatory cell infiltrate have not been performed in WMS affected marmosets yet. The differentiation of the mononuclear cell infiltrate represents a first step into the investigation of immunopathological processes in WMS. In all parts of the intestine there was a T cell mediated immune response. Further differentiation of T lymphocytes between CD 4+ and CD 8+ T cells was not possible as there was no cross reaction between the corresponding antibodies and the cellular antigens of the paraffin-embedded marmoset tissue. In human medicine, T cell dominated chronic enteritis represents the histopathologic picture of inflammatory bowel disease (IBD: Crohn´s disease and ulcerative colitis), whose characteristic, but non-specific pathological features may resemble the enteric lesions of WMS affected marmosets. However, in human patients suffering from IBD the inflammatory reaction is most commonly limited to the large intestine and is often accompanied by ulceration and granulomatous reactions (Yantiss and Odze, 2006).

Postmortal microbiological examinations were unsuggestive of bacterial causes for the WMS. Although obligatory enteropathogens such as *Campylobacter* sp. and hemolytic *E. coli* strains were isolated in individual animals, the microbial flora of WMS affected marmosets mainly consisted of rather non pathogenic or facultative pathogenic bacteria and parasites (Gibson, 1998; Toft and Eberhard, 1992; Johnson and Russo, 2002). The results indicate that the isolated bacteria and parasites do not represent causative agents for WMS, but may play a role in the maintenance of the intestinal inflammation and therefore may influence the progression of the disease.

The results of the present study provide evidence to suggest that a malassimilation syndrome represents the central pathogenetic pathway in the development of WMS. The etiology of the underlying unspecific enteritis still remains unclear. Currently it is assumed that the WMS is a multifactorial disease with exogenous and endogenous contributing factors including stress, allergenic reactions to dietary components, a deregulation of the intestinal immune system as stated for human IBD and hereditary effects in terms of a multigenetic disease (Chalifoux et al., 1982; Morin, 1983; Tucker, 1984; Barnard et al., 1988). Because of the nonspecific etiology of WMS, therapeutic approaches can only target the symptoms of the disease. Treatment with antibiotics to prevent secondary infections as well as application of paramunity inducers, minerals, and vitamins has been reported to improve the condition of affected animals. However, the effects of therapeutic measures are often only temporary and are regularly followed by relapses (Chalifoux et al., 1982; Sainsbury et al., 1992; Iallegio and Baker, 1995).

In conclusion, clinical as well as postmortal criteria have to be considered for the diagnosis of WMS in common marmosets. Clinical evaluation is based on weight development, feeding behaviour and therapeutic success. In addition, hypalbuminemia represents a reliable serological marker. Infectious causes should be excluded. Chronic or chronic active T cell dominated enteritis represent the cardinal pathogenetic process leading to a malassimilation syndrome with decreased nutrient utilization. Further clinical symptoms and pathologic organ changes may occur in the course of disease depending on the constitution of the corresponding animal.

Acknowledgments

This work was supported by the Deutsche Forschungsgemeinschaft (DFG Graduate Training Program - GRK 289, 'Perspectives of primatology': Integration of genetic, neurobiological and ethological approaches). The authors thank Dr. Annette Schrod and Dr. Tamara Becker for veterinary care and Wolfgang Henkel, Elke Lischka, Hafiza Zuri, Nadine Knöchelmann and Karin Kaiser-Jarry for technical assistance and laboratory work.

References

Barnard D, Knapka J, Renquist D (1988): The apparent reversal of a wasting syndrome by nutritional intervention in *Saguinus mystax*. *Lab Anim Sci* 38: 282-288.

Bongard O (2005): Contribution à l'étude du syndrome de dépérissement du oustiti: comparaison avec la maladie coeliaque humaine. Dissertation, Ecole Nationale Vétérinaire, Toulouse.

Brack M, Rothe H (1981): Chronic tubulointerstitial nephritis and wasting disease in marmosets (*Callithrix jacchus*). *Vet Pathol* 18: 45-54.

Chalifoux LV, Bronson RT, Escajadillo A, McKenna S (1982): An analysis of the association of gastroenteric lesions with chronic wasting syndrome of marmosets. *Vet Pathol* 19: 141-162.

Clapp NK, Henke ML, Lushbaugh CC, Humason GL, Gangaware BL (1988): Effect of various biological factors on spontaneous marmoset and tamarin colitis. A retrospective histopathologic study. *Dig Dis Sci* 33: 1013-1019.

Claus M, Lechner-Dol M, Hänichen T, Hat JM (2002): Excessive iron storage in captive mammalian herbivores - a hypothesis for its evolutionary etiopathology. Proc Eur Assoc Zoo Wildl Vet, 4th scientific meeting: 123-129.

Fortman JD, Hewett TA, Bennett BT (2001): The laboratory nonhuman primate. CRC Press, Boca Raton.

Fowler ME (1986): Zoo and Wild Animal Medicine. Saunders, Philadelphia.

Gibson SV (1998): Bacterial and mycotic diseases. In: Bennett BT, Abee CR, Hendrickson R (eds.). Nonhuman primates in biomedical research: Diseases. Academic Press, San Diego: 59-110.

Hatt JM, Sainsbury AW (1998): Unusual case of metabolic bone disease in a common marmoset (*Callithrix jacchus*). *Vet Rec* 143: 78-80.

Ialeggio DM, Baker AJ (1995): Results of a preliminary survey into wasting marmoset syndrome in callitrichid collections. *Proc Ann Conf Nutr Adv Group* 1: 148-158.

Johnson JR, Russo TA (2002): Extraintestinal pathogenic *Escherichia coli*: "The other bad *E. coli*". *J Lab Clin Med* 139: 155-162.

Juan-Salles C, Prats N, Resendes A, Domingo M, Hilton D, Ruiz JM, Garner MM, Valls X, Marco AJ (2003): Anemia, myopathy and pansteatitis in Vitamin E-deficient captive marmosets (*Callithrix* spp.). *Vet Pathol* 40: 540-547.

King GJ (1976): An investigation into „Wasting Marmoset Syndrome“ at Jersey Zoo. *Ann Rep Jersey Wildl Preserv Trust* 13: 97-107.

Logan AC, Khan KNM (1996): Clinical pathologic changes in two marmosets with wasting syndrome. *Toxicol Pathol* 24: 707-709.

McNees DW, Lewis RW, Ponzio BJ, Stein FJ, Sis RF (1983): Carbohydrate tolerance, serum albumin and protein values of normal and "waster" marmosets. *Primates* 24: 537-545.

Miller GF, Barnard DE, Woodward RA, Flynn BM, Bulte JW (1997). Hepatic hemosiderosis in common marmosets, *Callithrix jacchus*: effect of diet on incidence and severity. *Lab Anim Sci* 47: 138-142.

Morin ML (1983): A different approach in examining a wasting syndrome. *Lab Anim* 12: 36-41.

Potkay S (1992): Diseases of the *Callitrichidae:* a review. *J Med Primatol* 21: 189-236.

Pritzker KPH, Kessler MJ (1998): Diseases of the musculoskeletal system. In: Bennett BT, Abee CR, Hendrickson R (eds.). Nonhuman primates in biomedical research: Diseases. Academic Press, San Diego: 415-460.

Pryce C, Scott L, Schnell C (1997): Marmosets and tamarins in biomedical research: proceedings of a workshop. DSSD Imagery, Salisbury.

Quohs A (2003): Retrospective investigation on the occurence of diseases in a colony of common marmosets considering particularly the Wasting Marmoset Syndrome [German]. Dissertation, School of Veterinary Medicine, Hannover.

Sainsbury AW, Cunningham AA, Hawkey CM, Garden OA (1992): Conditions causing loss of weight in marmosets. *Proc Symp Assoc Brit Wild Anim Keepers* 17: 16-22.

Shimwell M, Warrington BF, Fowler JSL (1979): Dietary habits relating to ‘wasting marmoset syndrome’ (WMS). *Lab Anim* 13: 13.

Toft JD, Eberhard ML (1998): Parasitic diseases. In: Bennett BT, Abee CR, Hendrickson R (eds.). Nonhuman primates in biomedical research: Diseases. Academic Press, San Diego.

Tribe GW (1978): Wasting syndrome in primates. *Primate Supply* 4: 15-17.

Tucker M (1984): A survey of the pathology of marmosets (*Callithrix jacchus*) under experiment. *Lab Anim* 18: 351-358.

Wixson SK, Griffith JW (1986): Nutritial deficiency anemias in nonhuman primates. *Lab Anim Sci* 36: 231-236.

Yantiss RK, Odze RD (2006): Diagnostic difficulties in inflammatory bowel disease pathology. *Histopathology* 48: 116-132.

Corresponding author:

Dr. Martina Zöller, German Primate Center, Department of Infection Pathology, Kellnerweg 4, 37077 Göttingen, Germany, mzoeller@gmx.de.

GUIDELINES FOR AUTHORS

In General: The Primate Report publishes original papers, abstracts and contributions from the meetings of national and international primatological societies, from symposia as well as book reviews. Special issues like surveys on primatological activities in habitat countries and census of captive primates in the Old World countries complete the spectrum.
Original papers written in English can be accepted from any area of primatology, including breeding and husbandry, behaviour, evolutionary biology, morphology, physiology and palaeontology.

Arrangement

Title page: The first page of each paper should indicate the title (main title underlined), a short title for use as running head, the authors' names, and the name of the institute where the work was conducted.

Full address: The postal address of the author to whom correspondence should be sent must be given at the bottom of the page. Please also supply phone and fax and E-mail numbers.

Key words: For indexing purposes, a list of 6-10 key words in English is essential.

Abstract: Each paper needs an abstract of up to 10 lines in English, an additional one in French, Spanish, Portugese or German is optional.

Tables and illustrations: Tables and illustrations (both numbered in Arabic numerals) should be prepared on separate sheets. Tables require a heading and figures a legend, also prepared on a separate sheet. On the back of each illustration, indicate its number, the author's name, and 'top'. Colour illustrations are reproduced only at special agreement.

References: The list of references in alphabetic order should include only those publications which are cited in the text. Examples:

Papers published in periodicals: Birkebak TA, Wang NP, Weyrich J (1996): Uterine epitheloid leiomyosarcoma in a pig-tailed macaque. *J Med Primatol* 25: 367-369.

Monographs: Kappeler PM, Pereira ME (eds, 2003): Primate Life History and Socioecology. Chicago, University Press.

Edited books: Charles-Dominique P (1974): Aggression and territoriality in nocturnal prosimians. In: Holloway RL (ed): *Primate Aggression, Territoriality and Xenophobia: A Comparative Perspective*. New York, Academic Press: 31-48.

Reprints: 20 sample copies of the contribution are free of charge to the first author.

Disk Submission: We welcome the submission of manuscripts, graphs and drawings on disk. The preferred storage medium is a 3.5-inch disk in MS-DOS format. Macintosh is also acceptable. The preferred word processing package is Microsoft Word. Other commonly used PC text programs are also accepted, as well as ASCII format. Graphs and drawings can be accepted as bitmap files (tif, pcx, bmp etc.), but vectorized data (cgm, wmf, eps, etc.) or cdr-data files are preferred.

Publication data: The Primate Report is published 3 times annually, including the annual scientific report of the German Primate Center (DPZ), which is free of charge for subscribers.

Editor's address:

Dr. Dr. M.H. Schwibbe, Deutsches Primatenzentrum GmbH (DPZ), Kellnerweg 4, D-37077 Göttingen, Germany; E-mail: mschwib2@gwdg.de or klensang@dpz.eu