



Battle of the sexes: cost asymmetry explains female dominance in lemurs

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(Received 25 May 2008; initial acceptance 5 June 2008;
final acceptance 10 June 2008; published online 9 August 2008; MS. number: AS-08-00346)

Keywords: asymmetrical game; bird; cost asymmetry; female dominance; intersexual contests; lemur; primate; sexual selection; sexual size dimorphism; strepsirrhine

Female dominance over males is a rare trait among mammalian social systems and within primates (Ralls 1976; Kappeler 1993), but is the norm among lemurs of Madagascar, occurring in all lemur families regardless of mating system (Kappeler 1991, 1993). Despite 23 years of discussing the mechanism of female dominance in lemurs, including hundreds of publications (based on Web of Science; <http://apps.isiknowledge.com>), consensus does not yet exist. Current theories have remained unsatisfactory among researchers and empirical tests have contradicted expectations. Uncovering the reasons for female dominance in lemurs has even recently been hailed as the 'holy grail' of lemur research (Pochron & Wright 2005). Here I present a simple explanation for the occurrence of female dominance in lemurs and suggest an evolutionary mechanism for its prevalence.

The predominant explanation in the current literature is that female dominance is an adaptation to high reproductive costs and scarcity of food in comparison to other primates due to a resource-poor and highly variable island environment (Jolly 1984; Wright 1999; Pochron et al. 2003). Female dominance is considered advantageous to females and their offspring in this case because it provides females priority of access to resources critical to their high cost of reproduction. However, in quantitative comparisons with anthropoid primates, no unusual reproductive or energetic costs for lemur females have been shown (Kappeler 1996). Additionally, if one looks beyond the primate literature to other taxa, species can be found with typical male

dominance patterns living in environments that are substantially poorer in resources and more extreme in seasonality (e.g. Mooring et al. 2003).

An alternative hypothesis is that most of the unusual social and morphological features of lemurs, including female dominance and lack of sexual dimorphism, that show lack of convergence with anthropoid primates may be a result of evolutionary disequilibrium after the extinction of large predatory eagles and large-bodied lemur species in Madagascar's recent history (van Schaik & Kappeler 1996; Kappeler 1999). The hypothesis proposes that the ancestors of the lemurs were nocturnal and pair-living and only recently became diurnal and polygamous (Kappeler 1999) after these sudden ecological changes brought about by the arrival of humans. Characteristics such as monomorphism and female dominance, they suggested, are adaptations not to current situation but to ecological pressures present before the Holocene.

The idea of phylogenetic inertia has resulted in much controversy, and genetic and physiological studies have shown little support for this theory (Roos et al. 2004; Tan et al. 2005; Kirk, 2006). Although one should certainly not consider all traits as adaptive or at evolutionary equilibrium, highly variable traits such as body size and behaviour are expected to show a quick evolutionary response to new selective pressures.

Asymmetric Payoffs in Intersexual Contests

I suggest a more parsimonious explanation to the enigma of female dominance in lemurs, which exploits their unusual sexual size monomorphism (Weckerly 1998). Simply stated, sexual size monomorphism can

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result in social dominance of one sex, if size symmetry is offset by asymmetric valuation of resources. Game theory predicts that when the fighting abilities of two contestants are comparable, the outcome will depend on the value of the resources to be won for each contestant (Parker & Rubenstein 1981). A contestant that has a higher need for a resource is likely to devote more energy into fighting for it. So, individual 1 is likely to win a contest over individual 2 when $V_1/K_1 > V_2/K_2$, where V is the value of the resource to the contestant in terms of fitness and K is the fighting capacity measured as a rate of fitness loss (Parker & Rubenstein 1981). Given sexual size monomorphism in lemurs, the fighting capacity of males and females should not differ (i.e. $K_{\text{female}} = K_{\text{male}}$), thus a contest between a male and a female lemur will most likely be decided by the higher resource need of the female (i.e. $V_{\text{female}} > V_{\text{male}}$). The nutritional demands of breeding are expected to be low for lemur males due to the short and highly seasonal mating periods of lemur taxa (Wright 1999). Thus, despite the similarity in size of the sexes, female lemurs, with their added reproductive costs (i.e. pregnancy, lactation, maternal care, etc.), are expected to have substantially higher nutritional demands overall than males. As such, a female has more to lose in terms of fitness by not attaining the resource and is therefore more likely to win a contest with a male.

Because physical fighting is costly and dangerous, it is expected that assessment of competitors will generally be used to settle contests peacefully (Parker 1974). If the expected outcome of a contest can be predicted by sex, then a *conditional* evolutionarily stable strategy is expected where the behavioural response to a conflict is affected by the respective sex of the contestants (Maynard Smith 1982). Males that defer to females may have a fitness advantage because it may be more efficient to search out new food resources than to fight with females in a contest they will more often than not lose. In other words, for lemur males, escalation of a fight is costly, assessment of a contestant is cheap, and sex is a good predictor of defeat. Thus, evolution has likely favoured female dominance over males to avoid aggression between similar-sized sexes.

This explanation requires no altruistic or kin-selected behaviour by the male nor androgenization of females. It also does not require extremes in resource limitation or reproductive requirements of lemur females. Thus, sexual monomorphism present in lemurs and asymmetrical costs of reproduction among sexes provide a simple, parsimonious explanation for female dominance. The strepsirrhine primates (including lemurs) show a sexual size ratio amongst the lowest found in mammals (Weckerly 1998), which could thus explain the prevalence of female dominance in this taxon group.

Patterns in Other Primate Taxa

For the 'cost-asymmetry hypothesis' presented here to be upheld, monomorphic nonlemur primates should follow a similar pattern of dominance based on resource need. Many monomorphic haplorrhines show little

intersexual agonistic behaviour over food resources, making dominance determinations difficult, and intensive studies have been few. However, a thorough review of the literature shows that for species in which the adult females clearly invest more into reproduction than males, female dominance is apparent (Table 1). In cooperatively breeding primates, in which one breeding female produces the majority of offspring in the group, the alpha female is often dominant over the other group members (male and female). Strict female dominance across all group members as found in lemurs is not expected in this case because non-breeding females do not invest more in reproduction than males and dominance still appears to be correlated with higher resource needs. Additionally, in cooperatively breeding species, the paternal investment in the offspring may vary greatly with group size (Santos et al. 1997), which may be a reason for the differing reports of intrasexual dominance behaviour of the alpha pair in the same species (codominant versus alpha female dominant). The presence of seasonal changes in male and female resource needs and dominance behaviours of these species should be investigated. Further support for my hypothesis is that female dominance is absent from monomorphic species in which male reproductive investment may be greater than that of females, such as in *Aotus* and *Callicebus*, the males of which consistently carry infants from birth to independence (Wright 1990; Table 1). The strict female dominance found in monomorphic lemurs may be a result of the low male reproductive investment relative to the average female of these species, resulting in strong payoff asymmetries during contests over resources.

Female Dominance in Nonprimate Mammals and Birds

Contrary to common conceptions portrayed in the literature, female dominance over males appears to be widespread among mammals and birds showing sexual size monomorphism. Female dominance has been reported for several nonprimate mammals with similar-sized sexes, including the hyrax (*Procavia capensis*; Koren et al. 2006), spotted hyena (East et al. 1993), rufous elephant shrew (*Elephantulus rufescens*; Rathbun 1979), velvet-furred swamp rat (*Rattus lutreolus*; Monamy 1997), brush-tailed possum (*Trichosurus vulpecula*; Jolly & Spurr 1996), and nutria (*Myocastor coypus*; Warkentin 1968). In the latter two examples, females maintain dominance despite being slightly smaller than males; this is also true for Peruvian squirrel monkeys (*Saimiri boliviensis peruviansis*; Boinski 1999), not listed in Table 1. In Columbian ground squirrels, *Spermophilus columbianus*, males and females show no consistent patterns of dominance until after the mating season, when females have high resource needs and become dominant over males until late in lactation (Murie & Harris 1988). During lactation, when females are most energetically stressed, female ground squirrels show greater dominance over males than those females who are not lactating. There is a similar pattern in snowshoe hares, *Lepus americanus*, the females of which become dominant over males during the summer season when breeding occurs (Graf 1981). Dall's sheep, *Ovis dalli*,

Table 1. The mating system, paternal investment, and sexual dominance of various taxa

Taxon	Mating system	Males carry offspring	Intersexual dominance bias
Haplorrhini			
<i>Ateles geoffroyi</i>	Multi-♂/♀ groups	No	Female
<i>Brachyteles arachnoides</i>	Multi-♂/♀ groups	No	Female
<i>Aotus trivigatus</i>	Pair living	Yes (carry from first week to independence)	Male
<i>Callicebus</i> sp.	Pair living	Yes (carry from first week to independence)	Egalitarian
<i>Callithrix jacchus</i>	Cooperative breeding	Yes (cooperative group care)	Females/alphas codominant*
<i>Cebuella pygmaea</i>	Cooperative breeding	Yes (cooperative group care)	Alpha female dominant
<i>Saimiri oerstedii</i>	Multi-♂/♀ groups	No	Female/egalitarian*
<i>Saguinus oedipus</i>	Cooperative breeding	Yes (cooperative group care)	Alpha female dominant
<i>Saguinus mystax</i>	Cooperative breeding	Yes (cooperative group care)	Alpha female dominant
<i>Saguinus geoffroyii</i>	Cooperative breeding	Yes (cooperative group care)	Alpha female dominant
<i>Hylobates lar</i>	Pair living	No	Female
<i>Symphalangus syndactylus</i>	Pair living	Yes (carry during year 2 over large tree gaps)	Female
Strepsirrhini			
<i>Otolemur garnettii</i>	Dispersed/polygamy	No	Female
<i>Loris lydekkerianus</i>	Dispersed/polygamy	No	Female
<i>Microcebus murinus</i> †	Dispersed/polygamy	No	Female
<i>Microcebus rufus</i> †	Dispersed/polygamy	No	Female
<i>Phaner furcifer</i> †	Dispersed/polygamy	No	Female
<i>Daubentonia</i> †	Dispersed/polygamy	No	Female
<i>Indri indri</i> †	Pair living	No	Female
<i>Propithecus coquerelli</i> †	Multi-♂/♀ groups	No	Female
<i>Propithecus diadema</i> †	Multi-♂/♀ groups	No	Female
<i>Propithecus edwardsi</i> †	Multi-♂/♀ groups	No	Female
<i>Propithecus verreauxi</i> †	Multi-♂/♀ groups	No	Female
<i>Eulemur coronatus</i> †	Multi-♂/♀ groups	No	Female
<i>Eulemur fulvus</i> †	Multi-♂/♀ groups	No	Unclear structure
<i>Eulemur macaco</i> †	Multi-♂/♀ groups	No	Female
<i>Eulemur mongozi</i> †	Multi-♂/♀ groups	Yes? (limited carrying while group resting)	Female
<i>Eulemur rubriventer</i> †	Pair living	Yes (occasionally while female is feeding or resting)	Female
<i>Hapalemur griseus</i> †	Pair living	Yes (carry infants 20% of time after 3 weeks)	Female
<i>Lemur catta</i> †	Multi-♂/♀ groups	No	Female
<i>Varecia variegata</i> †	Multi-♂/♀ groups	No	Female

Information on intrasexual dominance (Christen 1974; Tardif & Richter 1981; Strier 1990; Young et al. 1990; Baldwin 1992; Digby 1995; Palombit 1996; Garber & Kitron 1997; Kinzey 1997; Hager & Welker 2001; Waeber & Hemelrijk 2003; Barelli et al. 2008), mating system (Sillentullberg & Moller 1993; Plavcan 1999; Wright 1999; Hager & Welker 2001; Gordon 2006; Sterling & McCreless 2006) and paternal care (Wright 1990; Overdorff 1996; Kinzey 1997; Fuentes 2002) was recorded for monomorphic primate species for which relevant data were found. Species were considered monomorphic if ♂/♀ size ratios ranged from 0.9 to 1.1 based on the literature (Strier 1990; Mitani et al. 1996; Weckerly 1998; Smith & Cheverud 2002; Gordon 2006).

*More than one dominance pattern reported.

†Malagasy lemurs.

females are dominant over males except during rut, when males compete intensely for mates (Bunnell 1980). In giant river otters, *Pteronura brasiliensis*, the one breeding female is dominant over all other group members, including males (Duplaix 1980).

Support for the cost-asymmetry hypothesis also comes from the avian literature. In monogamous, actively breeding birds, female dominance is the rule rather than the exception, even in species with similar-sized sexes (see Smith 1980 for review). In bird species such as house sparrows, *Passer domesticus*, in which males invest little in territorial defence, females tend to be dominant year round (as in lemurs; Jawor 2000). However, for those that show strong territorial behaviour, dominance commonly alternates to favour the sex in greatest need of resources (Smith 1980), lending support to the cost-asymmetry hypothesis

described here. During egg production, when female investment greatly exceeds that of the males (Trivers 1972), female dominance is most common, but a reversal in dominance often occurs outside of the breeding season, when male investment is greater than that of females due to intense competition for breeding sites (Smith 1980). This seasonal change in payoff asymmetry over resources is likely to be a driving mechanism for observed seasonal dominance reversal in many species. In the bird literature, seasonal dominance switching is ascribed to seasonal differences in selective pressures for sex-biased dominance (Smith 1980; Jawor 2000). The cost-asymmetry hypothesis supports this but suggests that predicted contest outcomes between males and females could arise even before any selection on dominance traits operates. In monomorphic species, the sex with the higher costs of reproduction will have

the higher payoff for winning a fight, resulting in an asymmetric, intersexual contest. This should increase the selective pressure on traits involved in dominance and submission on both sides (Maynard Smith 1982).

Conclusion

The cost-asymmetry hypothesis predicts the general patterns of intersexual dominance across primates and is consistent with observations in nonprimate mammals and birds. Given the simplicity and parsimonious nature of this explanation for female dominance over males in lemurs, the conundrum then becomes, why do lemurs, and strepsirrhines in general, lack sexual dimorphism in size? The lack of dimorphism is particularly intriguing for polygynous species with high operational sex ratios (Kappeler 2000), which give them the potential for intense mating competition (Emlen & Oring 1977). In such systems, male mate guarding is expected to be advantageous and should enhance selective pressure on male size (Clutton-Brock et al. 1977). I suggest that research on female dominance in lemurs and other monomorphic taxa should be redirected towards understanding the evolution of monomorphic size in species with male-biased operational sex ratios. This question has recently been explored in terms of the advantages of cryptic male mate-guarding strategies across primates in a parallel study (Dunham & Rudolf, unpublished data).

Thanks to Drs Susanne Shultz and Volker Rudolf for valuable discussion and comments on the manuscript.

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