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Received 1 April 1991

Revision received 10 November
1991 and accepted 10 November
1991

Keywords: aggression, polygyny,
monomorphism, prosimians,
Propithecus.

Aggressive competition between males, female-controlled polygyny and sexual monomorphism in a Malagasy primate, *Propithecus verreauxi*

The evolutionary determinants of sexual dimorphism among primates continue to be debated. This paper uses field observations of a Malagasy primate, *Propithecus verreauxi*, to argue that one problem underlying this debate is the unrecognized heterogeneity of mating system categories used in comparative analyses investigating the importance of sexual selection in determining sexual dimorphism. It is suggested that at least one new mating system category warrants recognition, that of female-controlled polygyny, with predictions for sexual dimorphism that are in contrast to those of male-controlled polygyny.

Journal of Human Evolution (1992) **22**, 395–406

Introduction

“... As a result of the contrasting selection pressures on males and females, sexual dimorphism in body size, growth, weaponry and aggressive behaviour is typically most pronounced in highly polygynous species and least in monogamous ones...” (Clutton-Brock, 1989). The longstanding and consensus causal model invoked in Clutton-Brock’s statement has been challenged by recent comparative studies exploring alternative explanations for sexual dimorphism, as well as by field observations that conflict with the model’s predictions. It has been argued that natural selection (Cheney & Wrangham, 1987; Demment, 1983; Milton, 1985*a*), phylogenetic inertia (Cheverud *et al.*, 1985, 1986), and non-selected allometric responses to evolutionary change in body size (Leutenegger & Cheverud, 1982, 1985) are as powerful as, or more powerful than, sexual selection in explaining patterns of sexual dimorphism among primates.

A fundamental and intractable difficulty with attempts to determine the causes of sexual dimorphism is that of inferring evolutionary causal links from neontological evidence (Ely & Kurland, 1989; Rodman & Mitani, 1987), an issue beyond the scope of this discussion. However, the divergence of conclusions reached about the significance of sexual dimorphism has been interpreted in several ways: (1) sexual selection is not the major determinant of sexual dimorphism in primates; the conditions favoring particular levels of dimorphism are complex and variable, and may involve a relative reduction in female size, for example, rather than an increase in male size (Kappeler, 1990); (2) the sexual selection model is broadly robust, but its underlying assumptions are not met in some species (Clutton-Brock, 1985; Gaulin & Sailor, 1984); (3) current comparative analyses cannot be used to reject the sexual selection model because of a range of methodological problems, including the measurement of sexual dimorphism, the assessment of the intensity of aggressive competition, the lumping of disparate taxa, and the analytic methods themselves (Ely & Kurland, 1989; Frayer & Wolpoff, 1985; Kay *et al.*, 1988; Smith, 1980); (4) the sexual selection model is too narrowly construed in comparative analyses, failing to recognize that competition between males may occur in several forms and that female choice may determine the particular form it takes (Fedigan, 1982; Small, 1989; Smuts, 1987*a*).

This paper is concerned with the third and last of these interpretations. Its point is conceptual and methodological: the categories of mating system used in investigations of the

determinants of sexual dimorphism contain unrecognized heterogeneity and do not allow meaningful inter-specific comparison, regardless of the merits of the particular analytic model employed. I will show the empirical difficulty of assessing the intensity of aggressive competition between males and linking it deterministically to available mating system categories, using as illustration observations of a Malagasy primate, *Propithecus verreauxi*, that I began studying as a student of John Napier's at the Unit of Primate Biology at Queen Elizabeth College, University of London. Usually classified as polygynous, male *P. verreauxi* are known to engage in fierce fights during the mating season (Jolly, 1966; Richard, 1974). On the face of it a good candidate to be sexually dimorphic, *P. verreauxi* is in fact monomorphic in body and canine tooth size, and has been recognized as an exception to the rule (e.g. Clutton-Brock, 1985). After reviewing the evidence on aggression and sexual behavior in this species, I shall argue that the apparent mismatch between behavioral and morphological traits in this species is not so much an anomaly as a symptom of broader problems with the assessment of aggressive competition and with the assignment of heterogeneous mating systems to the single category of polygyny, "where males mate with the same group of females in successive mating attempts" (Clutton-Brock, 1989).

A case study: *Propithecus verreauxi*

Subjects and methods

The sifaka, *Propithecus verreauxi*, lives in forests in south and west Madagascar. 124 sifakas have been marked, and a range of biometric data collected, in the Beza Mahafaly Special Reserve in southwest Madagascar, as part of a long-term study of sifaka biology and behavior that began in 1984 (Richard & Nicoll, 1987; Richard *et al.*, 1991, in press). There is no sexual dimorphism in body or canine tooth size in this population (Figure 1; unpublished data) or in skeletal samples examined by other researchers (Gingerich & Ryan, 1979; Jenkins & Albrecht, 1991; Kappeler, 1990).

All captured animals at Beza Mahafaly were assigned to one of five age classes (A–E), based on known birth date or degree of dental wear (Richard *et al.*, 1991). Recaptures now suggest that age classes represent 4–5 years apiece, and enable us to assign an estimated birth year to each animal. The data on inter-group transfer summarized below come from the longest monitored animals—44 marked males censused for 143 male-years, and 37 marked females censused for 106 female-years—as well as more recently captured animals, drawn from 32 social groups (Richard *et al.*, 1991). Within the marked population, four focal groups, comprising a total of 24 animals, were observed for 500 h between October 1984 and May 1985, and 250 h of quantitative behavioral data were collected on the 13 males in these groups. The description of mating behavior below comes from this study and from earlier research on two groups at Hazafotsy, in the extreme south of the island (Table 1) (Richard, 1974, 1978). Tightly synchronized within populations, mating occurs only once a year and is rarely seen, and resulting problems of small sample size are compounded by the wide range of behaviors associated with the few episodes of mating that have been observed.

Aggression between male sifakas

Aggression between male sifakas occurs in three contexts: inter-group transfer, daily life in the group, and the brief annual mating season. Its character and intensity differ within and between contexts, and this section presents an overview of this variation.

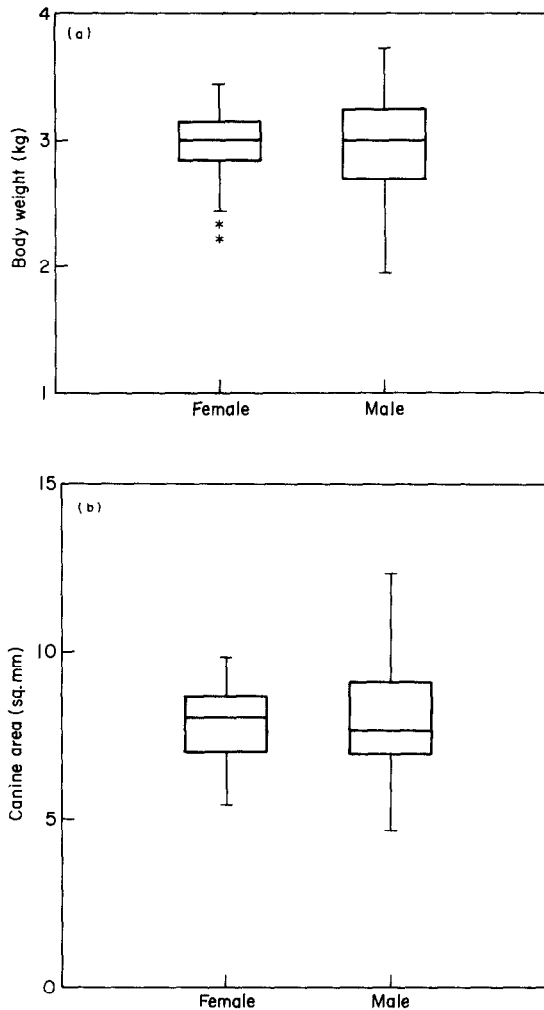


Figure 1. (a) Body weight of males ($n=41$; mean = 2.958 ± 0.399) and females ($n=34$; mean = 2.971 ± 0.337); (b) canine tooth area of males ($n=27$; mean = 8.091 ± 1.8839) and females ($n=12$; mean = 7.877 ± 1.281). Canine area was computed from maximum mesodistal length and buccolingual width, measured to the nearest 0.01 mm; animals in age class A were excluded. [Box plots follow conventions of Tukey (1977): the central bar indicates the median, the upper and lower edges of the central box the 25th and 75th percentiles; the distance between these is the H-spread; the whiskers (the vertical lines above and below) indicate the range of values that fall within 1.5 H-spreads of the median; * indicate values beyond 1.5 H-spread of the median.]

Inter-group transfer. Sifakas live in social groups of 2–13 individuals, that are quite variable in sexual composition (Table 1) (Richard *et al.*, in press). Females are typically philopatric, but all males disperse from their natal groups at the age of four to six years, and secondary dispersal is common (Richard *et al.*, in press). About half the males in the youngest age class (A) and 20–25% of males in each of the older age classes (B–E) transfer each year. Young males are more likely to transfer two or three times, and are more likely to transfer into groups with the same or a lower proportion of males—and a higher proportion of females—than in their group of origin. The tenure of males in groups increases through successive age classes to

Table 1 Composition by sex (F/M) and estimated age in July 1985 (in years for captured animals) of members of focal groups at Beza Mahafaly (A-D) and Hazafotsy (E, F) before, during and after the mating season

Sex/ID/Age (years) ¹	Before	During	After
(A) Sakamena Sud			
F No. 17 (adult)			
F No. 14 (1)			
M No. 4 (11)			
M No. 5 (7)	wanders	wanders	transfers
(B) Vavy Goa			
F No. 54 (adult)			
F No. 38 (adult)			
F No. 33 (2)			
M No. 11 (19)			
M No. 21 (juvenile)			
M No. 31 (6)			
M No. 26 (adult)			
(C) Vavy Masiaka			
F No. 35 (adult)			
F No. 36 (17)			
F No. 37 (adult)	disappears		
M No. 25 (17)			
M No. 29 (6)	wanders	wanders	transfers
M No. 30 (11)			
(D) Vaovao			
F No. 19 (adult)			
F No. 20 (14)			
F No. 73 (18)	dies		
M No. 8 (14)	evicted	wanders	disappears
M No. 7 (1)			
M No. 9 (juvenile)			
M No. 10 (9)	joins		
M No. 29 (6)		visits	joins
(E) Hazafotsy III			
F FD (adult)			
F FND (adult)			
M F (adult)			
M P (adult)		wanders & returns	
M Y (subadult)		wanders & returns	
M J (juvenile)			
(F) Hazafotsy IV			
F FI (adult)			
F FNI (adult)			
M R (adult)		evicted/disappears	
M Q (subadult)			
M INT (adult)		joins	

¹ Full identities and age classifications are given in the text.

an estimated mean of 3.7 years in the D class, and declines to 2.4 years in the E class. No adult male has spent more than 5 years in one group. This time span also corresponds to the age at which females in this population give birth for the first time.

The behavioral context and specifically the agonistic component of transfer, is quite variable and partially age-dependent (Richard *et al.*, in press). Young males, known or presumed to be in their natal groups, transfer gradually, dividing their time between their

natal group and other groups in which they appear as visitors on the periphery. These males are not expelled from their natal group. In contrast, both male and female group members evict older males from their group, by repeatedly chasing them. Entry to the group by adult males is sometimes, but not always, contested by males already resident in the group. Contests take the form of chasing, but not fights. In sum, sifaka males experience a lifetime continuum of transfer events; transfers are associated with differing intensities of aggression, and they are non-random with respect to the composition of the group into which males of different ages transfer.

Intra-group aggression outside the mating season. The rate of agonistic interactions between males in the six focal groups at Beza Mahafaly and Hazafotsy was very low outside the mating season [mean = 0.23 interactions/h, range = 0–0.45 (unpublished data from Beza Mahafaly)]. Most agonistic interactions occurred in the context of feeding, and took the form of displacement. Occasionally, one animal cuffed or snapped at another. The target of aggression in these cases always moved away, sometimes giving submissive signals in the form of chattering, baring teeth, cowering or tail-rolling. Males did not initiate agonistic interactions against adult females, and always gave way to them. Females did not give way to males or exhibit submissive signals to them. In each group there was one adult male who occasionally displaced or directed aggression at other males and was himself never the target of aggression by other males in the group. Rates of aggression were too low, however, to describe these males as “dominant”, and the broader connotations of this epithet seem inappropriate in a species in which the behavior of all males is more reminiscent of Woody Allen than of Sylvester Stallone. Nor were these males consistently spatially central. For want of a better term, we call them “established”.

In sum, like many cercopithecines (Rowell, 1988; Rowell & Olson, 1983), sifakas express or maintain social relationships more by spatial monitoring and adjustment than by explicit signals. As in cercopithecines, these relationships are asymmetric between males and females, but in sifakas the asymmetry favors females. A recent study of captive pairs of *P. verreauxi coquereli* at the Duke Primate Center suggests that females' control of their relationships with males goes beyond the context of aggression: males consistently followed females and were most active in maintaining spatial proximity (Kubzdela *et al.*, in press).

Aggression in the mating season. The onset of the mating season is signalled by a “pseudo-estrus” period of a few days in late January, when the vulva of some females becomes pink and slightly swollen, and the frequency of scent-marking by both sexes increases, along with agonistic interactions between males and visits to neighboring groups by males. A month later these indicators reappear, this time accompanied by mounting and copulation (Richard, 1974). Not all groups exhibit all these shifts. In fact, our limited sample suggests two distinct group profiles: *groups in transition* ($n = 3$), in which either resident and non-resident males engaged in extended battles (involving fights and chases) and the estrous female mated with the winner or, if no clear winner emerged, with a non-resident and non-combatant male; *stable groups* ($n = 3$), which were not visited by non-resident males during the mating season, where there was no increase in the frequency of aggression between resident males, and in which no mating was observed although one or more infants were born the following birth season.

The ferocity and bloodiness of battles between male sifaka during the mating season has long been noted (Jolly, 1966), but little studied. At Hazafotsy in 1971, a long bout of chasing

and fighting between the established male (R) and a non-group male (P) ended when male R left, moving slowly on all-fours and bleeding from several wounds. The winner, male P, mated. A similar episode then ensued between male P and another non-resident male (INT), during which the winner turned into a loser and returned to his original group, badly injured. The same female now mated with the new winner, male INT (Richard, 1974). At Beza Mahafaly, an equally extended contest took place between two established males (nos 4 and 10) from neighboring groups, but with a different outcome. Neither male suffered serious injury, and the contest ended when both males appeared exhausted. Neither was subsequently seen mating.

Observations of three other groups (one at Hazafotsy and two at Beza Mahafaly) during the mating season, revealed no increase in aggression, and no evidence of visiting males. Subsequent births showed that, while not observed, copulation did occur in all three groups. At Berenty, O'Connor (pers. comm.) witnessed a rapidly completed, "quiet copulation" between an established male and a female co-resident in the group. We assume that similarly unspectacular copulations occurred between females and established males in the stable groups reported here.

Females are not passive bystanders to male aggression during the mating season. Rather, their behavior appears to influence its occurrence and intensity; willingness to mate forestalls contests between males whereas refusal to mate seems to precipitate fights. In the "transitional" groups, each of the estrous females refused to mate with the established male, repelling him with cuffs or bites. These refusals were followed by chases and fights between resident and non-resident males. Two of the females (nos 17 and 20) seemed actively to provoke contests [see also Cords (1988) for similar observations in forest guenons]. These females belong to neighboring groups Sakamena Sud and Vaovao (Table 1). When the groups moved off at dawn, each female was closely followed by the established male in her group (nos 4 and 10, respectively). Female no. 20 gave a lost-call to which male no. 4 responded from a distance of about 150 m, and the two then moved toward one another, continuing to exchange lost-calls, followed by other members of their respective groups. When a *sifaka* loses contact with the group while foraging, it gives lost-calls to which other group members respond with "localizing" calls (Richard, 1978). In over 2000 h of observation outside the mating season, I have never heard group members respond to the lost-calls of animals from other groups.

Once the two groups were in visual contact, females nos 17 and 20 dashed at one another, as if to fight, but veered away at the last moment. The follower males were thereby left face-to-face a meter or so apart. This sequence was repeated for almost 3 h, and each time the males broke away and resumed their follower stations. A contest finally erupted between these males at noon, and they intermittently chased and fought until mid-afternoon. During this contest the females fed, rested, and observed the contest.

No clear winner emerged, the groups drifted apart, and female no. 20 again began lost-calling. Two non-group males responded with localizing calls and approached the group. One of these males (no. 29) immediately mounted female no. 20, who cuffed and bit male no. 10 when he attempted a few times to intervene. Male no. 29 did not participate in this aggression. Male no. 10 finished by lying spread-eagled on a tree-limb, chewing on a *Tamarindus indica* pod and watching while male no. 29 and female no. 20 continued to copulate. Male no. 29 was younger and smaller than either of the established males no. 4 and no. 10 (Figure 2). We do not know with whom female no. 17 mated, but she did give birth that year.

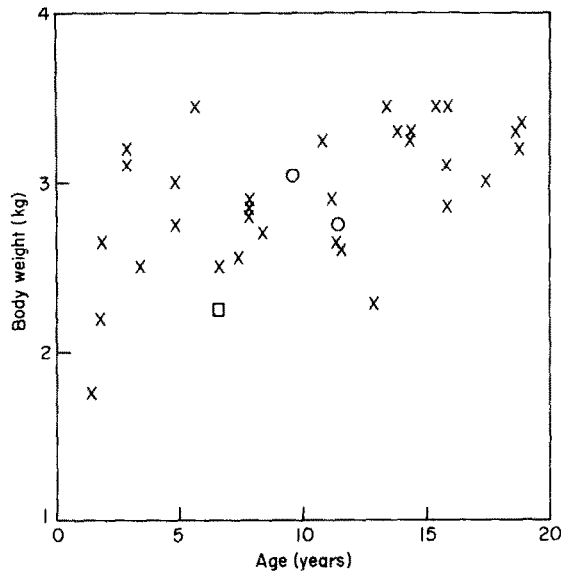


Figure 2. Body weight and estimated age of males in the Beza Mahafaly population in 1984–85. (○) Males nos 4 and 10; (□) male no. 29.

Discussion

Investigations of the importance of sexual selection in determining sexual dimorphism commonly divide primate mating systems into monogamous systems, in which the intensity of aggressive competition for mates between males is said to be low, and polygynous systems, in which the intensity of competition is said to be high. However, the empirical basis for this linkage has been challenged (Kay *et al.*, 1988), and a growing number of field studies have documented both the heterogeneity of mating patterns present in species commonly classified as polygynous and the importance of female choice in these systems (e.g., Andelman, 1987; Chish & Rowell, 1986; Cords, 1988; Dunbar, 1979; Goodall, 1986; Janson, 1984; Milton, 1985*a,b*).

The implications of these observations have yet to be integrated into quantitative models seeking to explain variation in sexual dimorphism among primates. In this discussion, I first consider appropriate measures of the intensity of aggressive competition between males and then argue that the longstanding dichotomy between monogamous and polygynous mating systems used by functional morphologists is conceptually and empirically inadequate. I propose that an abundance of evidence warrants recognition of at least one new category, that of female-controlled polygyny.

How intense is aggressive competition for mates between sifaka males, based on the case study presented here? Before trying to answer this question, we must decide whether all aggression between males should be viewed as a form of competition for mates (see also Klein, 1974; Nagel & Kummer, 1974). A contest over an estrous female is clearly a more direct form of competition than a contest over a food item, but arguably a male's ability to monopolize food enables him to build the necessary energy reserves to defend or contest access to estrous females successfully. In the absence of a clear way of differentiating the functions of aggression, all aggression will be considered here as a form of mate competition.

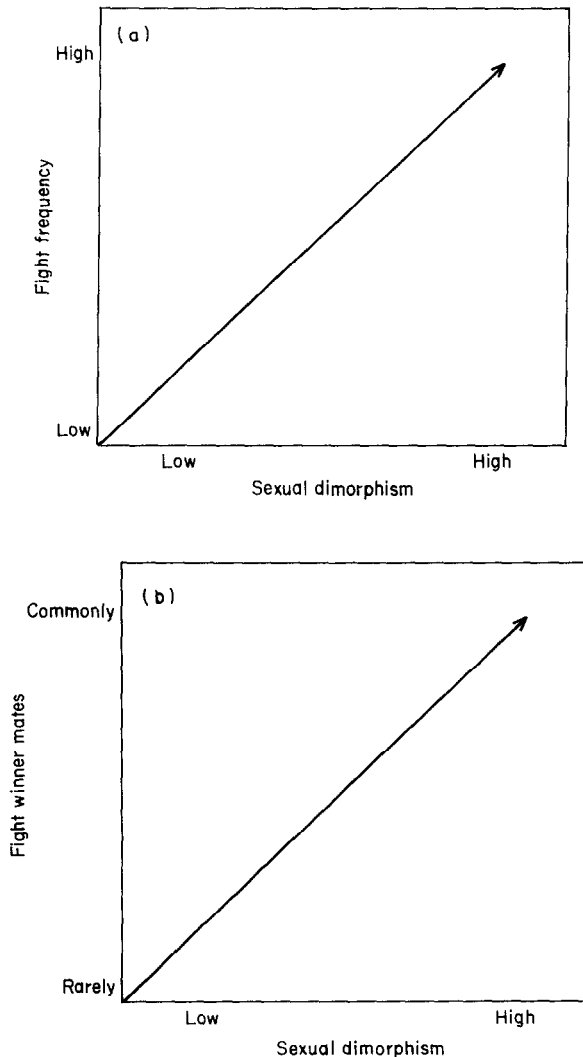


Figure 3. Predicted levels of sexual dimorphism under the (a) fight frequency and (b) fight winner hypotheses.

Contests between sifaka males take place in daily life but they are infrequent, and usually take the form of displacements, not fights. Contests take place in the context of transfer between groups, but they take the form of chasing. Finally, contests occur, sometimes, in the presence of estrous females; these contests sometimes involve fighting. In sum, males chase much more often than they fight, and so we might infer that agility rather than size is at a premium (Richard, 1974; Clutton-Brock & Harvey, 1976). Under this scenario, the absence of sexual dimorphism in sifakas is predicted by the low frequency and intensity of aggressive competition among males of this species [Figure 3(a)].

By focusing on the overall frequency and intensity of aggression rather than on its *reproductive outcome*, this explanation ignores a central assumption of the sexual selection/sexual dimorphism model, namely that sexual dimorphism will arise when the variance in

reproductive success is more strongly and positively influenced by size among males than it is among females (Clutton-Brock, 1985). In other words, the low *overall* frequency of fights among sifaka males is irrelevant: the only fight that counts is the one which gives a male sexual access to a female. If larger size is an advantage in fights and sexual access to females is decided by fights, then even if males rarely fight, large males should have an advantage over small ones, all things being equal. In the cases presented here, fight winners did mate with estrous females and, indeed, females sometimes appeared to precipitate fights between males. However, a female who had precipitated a contest was observed mating with a male who took no part in that contest, and mating occurred without evidence of any aggression in three of six groups observed during the mating season.

Does the search for a robust measure of the intensity of aggressive competition between males then reduce to ascertaining whether fight winners do most of the mating in a given year [Figure 3(b)]? The answer has to be no, because this approach ignores the life history component of variance in male reproductive success. We know that older sifaka males have longer tenure in a group, on average, than younger males do, but we cannot yet assess the variance in tenure length among age cohorts of males or establish the relationship between tenure length and a male's history as a fighter. As a working hypothesis, however, I propose that the sifaka mating system may be best characterized as one of female-controlled polygyny. This system shares some features of traditionally defined polygyny, which emphasizes the role of competition between males to monopolize access to females, but carries quite different predictions for sexual dimorphism. I further suggest that female-controlled polygyny may be an appropriate term by which to characterize the mating systems of other primates in which females, individually or in coalitions, direct significant levels of aggression toward males (see also Small, 1989; Smuts, 1987b).

The features shared by female- and male-controlled polygyny are: (1) a single male has sexual access to females in a group over several mating seasons; and (2) fierce fighting takes place between some males during the mating season. The key difference is that the long term reproductive success of males is determined in an arena of competitive submission to females, not competitive aggression between males: winning a fight may give a male sexual access to a female once, but does not ensure it in subsequent years and is not, indeed, the only way of achieving access in the first place. For example, sifaka females mate with males that win contests by outlasting their opponents in extended chasing matches. They also mate with males that win contests by fighting, and with males that do not enter the fray at all. A male's tenure in the group as an established male over several mating seasons may have more to do with his willingness to submit to females after the mating season is over than with how he first gained access to them. I infer that maximum tenure length is constrained by rising levels of consanguinity in the group, and that long-resident established males are usually expelled by females. This parallels recent findings on ringtailed lemurs (*Lemur catta*) (Pereira & Weiss, 1991), other differences in their social and mating system notwithstanding (Koyama, 1988; Pereira, 1991; Sauther, 1991; Sussman, 1991). As noted above, at Beza Mahafaly 5 years is both the maximum duration of any male's tenure and also the age at which females give birth for the first time (Richard *et al.*, in press).

In sum, the arena of competition between males shifts, and males who savage their opponents are not only exposed to higher risks of injury themselves, but their tenure as established male and preferred mate may also be curtailed through eviction from the group by females. The short-term advantages of fighting prowess may be offset by long-term advantages of submissiveness.

Conclusion

Broadly robust behavioral categories are a necessary prerequisite for inter-specific comparisons, but this paper attempts to show that the dichotomous division of primate mating systems and levels of aggressive competition is too broad to be robust or useful. *Propithecus verreauxi* is but one of a growing number of species now known to have mating systems and behavioral profiles that do not fit readily in either category. Given the practical constraints of funding and logistics, few studies of wild-living primates can be expected to track the long-term reproductive success of males by determining paternity, although such studies are needed to assess the reliability of behavioral measures of reproductive success. However, as the number of long-term field studies grows, it becomes increasingly possible to estimate the variance in male tenure length, and to monitor male histories of aggressive competition and their relationship to tenure length and mating success. A reassessment of primate mating systems by these criteria would provide a stronger starting point from which to examine the power of aggressive competition to predict the level of sexual dimorphism than the criteria used to date, and in the absence of such a reassessment the importance of size in aggressive competition will remain unclear.

Summary

1. The divergence of conclusions reached concerning the importance of sexual selection in determining sexual dimorphism can be interpreted in several ways.
2. This paper argues that the categories of mating system used in investigations of the determinants of sexual dimorphism contained unrecognized heterogeneity and do not allow meaningful interspecific comparison.
3. Data on aggression and sexual behavior in a Malagasy primate, *Propithecus verreauxi*, are used to illustrate the difficulty of assessing intensity of aggressive competition and the inadequacy of using polygyny as a single category of mating system.
4. It is proposed that measures of the intensity of aggressive competition must incorporate data on aggression throughout the lives of males, and that a discrete category of female-controlled polygyny should be recognized, which shares some features of male-controlled polygyny but has contrasting predictions for levels of sexual dimorphism.

Acknowledgements

This paper has benefitted from discussions with Xingbin Chen, Amos Deinard, Robert Dewar and Judith Kidd, and I am grateful for the assistance of Robert Dewar in preparing the figures. Leslie Aiello, Robin Dunbar, Michael Pereira and an anonymous reviewer provided helpful comments on an earlier draft of the paper. I thank Diane Brockman and Marion Schwartz for undertaking the painstaking task of measuring canine tooth area. The Beza Mahafaly Special Reserve was created under an international agreement between the University of Antananarivo, Washington University, Yale University, and the World Wildlife Fund, and I am grateful to those institutions for their role in making possible much of the research reviewed in this paper. My fieldwork at Beza Mahafaly was supported by a National Science Foundation grant (INT 8410362) and a Howard Foundation Fellowship.

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