

BRIEF REPORT

Female Social Dominance and Basal Metabolism in a Malagasy Primate, *Propithecus verreauxi*

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Tight energetic constraints on reproductively active females are hypothesized to be an important determinant of the phenomenon of female dominance in *Propithecus verreauxi*, a primate endemic to Madagascar. Five wild sifakas were captured in the Beza Mahafaly Special Reserve in southern Madagascar, and resting metabolic rates (RMR) were measured. Levels were low, as predicted, with the exception of a possibly pregnant female. Although the data were not conclusive, they were consistent with the hypothesis.

Key words: Madagascar, lemur, dominance, metabolic rate, *Propithecus verreauxi*, sifaka

INTRODUCTION

Social dominance of females over males is rare among mammals [Ralls, 1976; Hrdy, 1981], yet females are dominant in many, and perhaps all, of the primates of Madagascar [Pollock, 1979a; Jolly, 1984; Richard, in press]. Most dominance interactions among lemurs occur in the context of feeding, where females consistently supplant males [Jolly, 1966; Pollock, 1979b; Richard, 1978]. Hrdy [1981] tentatively attributes the social dominance of female lemurs to a male strategy of deferring to females in order to conserve energy for the brief, but energetically costly, annual mating season. Conversely, Jolly [1984] suggests that it arises from seasonal stresses experienced by the females themselves. She argues that lemur young are altricial and, like other altricial mammals, have a high growth rate that imposes a heavy energy demand on the mother. However, there are currently few physiological measurements of mammalian energy expenditure during reproduction to test these ideas.

In this paper preliminary data are presented on the metabolic rates of sifakas, *Propithecus verreauxi* (Indriidae), and we propose a modified version of Jolly's idea that high energy requirements imposed on reproductively active females are an important determinant of the phenomenon of female social dominance in the sifaka.

Our model contains three predictions. These are, first, that basal metabolic rates (BMR) are characteristically low in sifakas; second, that sifaka females elevate

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their BMR in order to reproduce successfully; and third, that the social dominance of females assures them priority of access to limited food resources and thereby helps them meet the high energy costs of reproduction. Our model is currently limited to the sifaka, and there is evidence suggesting that it is not applicable to all primates, or even all prosimians, with low BMR. For example, there is no evidence of female social dominance in several loriforms for which low rates are reported, and in *Colobus*, which has a low BMR [Muller et al, 1983] and a highly folivorous diet [Oates, 1977], females are not dominant over males [Oates, 1977; Struhsaker, 1975].

METHODS

Between May 8 and May 15, 1985, measures of the resting metabolic rate (RMR) of two males and three females were taken from a marked population of *P. v. verreauxi* living in gallery forest in the Beza Mahafaly Special Reserve in southern Madagascar. Animals were darted using a Telinject® blowgun (Telinject USA, Inc., Newhall, CA) and the anesthetic agent ketamine, caught in a sheet when the anesthetic took effect, and then carried back to camp. A full description of capture methods used in this study is included in Richard and Rakotomanga (unpublished manuscript) available on request from the first author.

In this paper, RMR refers to the metabolic rate of postabsorptive resting individuals. In nongestating, nonlactating individuals in thermoneutrality, RMR is the same as BMR. The metabolic rates of our subjects increased only at temperatures significantly above and below those at which we calculated RMR (ie, between 23° and 28°C, which is within the thermoneutral zone of *Lemur fulvus* with similar body mass [Daniels, 1984]). This suggests that the subjects in this study were in thermoneutrality.

RMR was measured during the normal resting phase of the activity cycle, when subjects were fully recovered from anesthesia and when ambient temperature stabilized in the probable thermoneutral zone, ie, during the early evening or morning. In practice, animals were captured in the morning, RMR was measured in the evening, and animals were released at the capture site the next morning. Ketamine remaining in the subjects' body tissues 8 or 9 hours after they were immobilized was unlikely to have had a significant effect on metabolic rate [White et al, 1982].

Oxygen consumption was measured in an open-circuit system. Air at a rate of 1 liter/minute was drawn through the 0.15 m³ holding cage, which was enclosed in a plastic sac and held in a quiet, dark room. CO₂ and water were extracted before analysis in an Applied Electrochemistry S3A oxygen analyzer. Data were analyzed only for periods when temperatures within the holding cage and oxygen consumption were steady for at least 20 min. All measurements were corrected to standard temperature and pressure conditions using the method of McNab [1978].

RESULTS

Table I shows the measurements made on four of the five subjects, including two separate runs for female #58. Results for the fifth subject, an adult female, were excluded because rapidly falling ambient temperatures during measurement made it impossible to establish a stable baseline.

DISCUSSION

The basal metabolic rate (BMR) of prosimians has been consistently found to be lower than that of anthropoid primates and lower than the BMR predicted by Kleiber's [1961] mass-dependent values for eutherians [Muller, 1985]. The BMR of mammalian folivores is also typically lower than predicted [McNab, 1978, 1980,

TABLE I. Resting Metabolic Rate of *Propithecus verreauxi* Captured at Beza Mahafaly in 1985

Date	Animal (Sex, No.)	Body mass (kg)	T _A ^a (°C)	VO ₂ /M ^b	% Kleiber ^c
May 8	M, 27	3.3	16.5	0.2037	45.3
May 10	M, 28	2.2	28.4	0.2904	62.3
May 10	F, 57	3.1	21.6	0.3289	71.7
May 11	F, 58	3.4	26.9	0.1886	42.1
May 11	F, 58	3.4	23.6	0.2046	45.7

^aAmbient temperature.

^bRate of oxygen consumption per unit body mass (ml O₂ · g⁻¹ · h⁻¹).

^c100 VO₂/(3.42 M^{0.75}).

1986]. Thus, it is reasonable to predict that the sifaka, a seasonally folivorous prosimian, is characterized by a low BMR. The preliminary data presented here are consonant with this prediction. The second prediction is more problematic. While there is strong evidence that mammals with BMR equalling or exceeding Kleiber's predicted rates show no increase during reproduction [Kaczmarski, 1966; Trojan & Wojciechowska, 1967; Migula, 1969; Myrcha et al, 1969; Dryden et al, 1974; Randolph et al, 1977], the situation in mammals with low BMR is more complex. In several species of therian mammals with characteristically low BMR, gestating and lactating females have been found to exhibit up to a threefold increase in RMR [Nicoll & Thompson, in press; Thompson & Nicoll, 1986]. Yet in the three-toed sloth (*Bradypus variegatus*), a specialist folivore with a low BMR [McNab, 1978], there is little or no evidence of an increase [Nagy & Montgomery, 1980].

While it is not clear whether gestating and lactating sifaka females increase their RMR, that is certainly one explanation for the pattern of variation in our preliminary measures (although other explanations, especially small sample size, are possible). By far the highest RMR (71.7% of Kleiber) was that of female #57, whereas the RMR values for female #58 (42.1–45.7% of Kleiber) were similar to the value obtained for the adult male subject. Weak circumstantial evidence suggests that #57 was gestating and #58 was not. In southwest Madagascar, sifakas mate in February and March and give birth in July and August. Interbirth interval is commonly two years [Jolly, 1966; Richard, 1978]. There were no yearlings present in #57's group in May 1985. We inferred that she did not give birth, or lose her infant shortly after giving birth, in 1984. One possible explanation for her high RMR value was that she was gestating. Conversely, there was a yearling present in #58's group, of which she was the only adult female member. We inferred that she had given birth in 1984 and was unlikely to have conceived in 1985. Unfortunately, a clearer determination of reproductive state at the time of measurement is unavailable because local events disrupted the census of females during the July/August 1985 birth season at the study site, and pregnancy detection by palpation was not yet reliable. Weight differences between females could not be used to determine reproductive state because of the wide range of morphological variation in this trait (2.7–3.5 kg, N = 23, Richard, previously unpublished data). The intermediate value obtained for #28 may have been due to his immaturity; an elevated RMR relative to that of adults is characteristic of immature individuals [Brody, 1943; Hill, 1976; Poczopko, 1979]. Biometric data collected on 43 males in the population suggest that, at least in southwestern Madagascar, male sifakas do not reach full size until their fourth year (Richard & Rakotomanga, unpublished manuscript). Based on

mass, morphometric measures, and dentition, we estimate that #28 was no more than 20 months old at the time of measurement.

The total energy expenditure during reproduction is similar in species with the same body mass but widely varying BMR [Nicoll & Thompson, in press; Thompson & Nicoll, 1986]. However, it is likely that the relative increase in energy expenditure during reproduction is greater in species that must increase a low RMR in order to reproduce successfully. This is because a substantial proportion of the total expenditure during reproduction is maternal metabolism. The increase in maternal metabolism to Kleiber's predicted rates in species with low BMR is an incremental cost absent in species with higher BMR or in species that maintain a low BMR during reproduction.

We hypothesize that female sifakas increase their energy intake during reproduction by selecting energy-rich food items and by increasing time spent feeding and the rate at which they harvest food. Although dietary differences between reproductive females and other animals have yet to be studied in the sifaka, seasonal shifts from a highly folivorous diet (75% of feeding time spent eating leaves) to a strongly frugivorous one (80% of feeding time spent eating fruit) have already been documented [Richard, 1978].

The third prediction of our model links the first two physiological ones to the well-documented phenomenon of female social dominance in sifakas: under conditions of limiting food availability, priority of access to food may confer an important, perhaps crucial, reproductive advantage on females. One possible alternative strategy would be to use fat stored during nonbreeding periods of superabundant food. This is not done by sifakas, judging from the very low muscle mass-to-size ratio, little or no subcutaneous fat deposition, and the lack of seasonal variation in mass (Richard & Rakotomanga, unpublished manuscript).

In sum, we suggest that the maternal elevation in metabolic rates constitutes a relatively high energy demand for female sifakas compared to species which show no increase in RMR during reproduction. If so, females are likely to have a strong interest in maintaining a position of social dominance that assures them priority of access to food. Males may acquiesce to female dominance because they thereby further their own reproductive interests by promoting the survival of their unborn young. Alternatively, they may acquiesce simply because they have less to lose than do females [Rapoport, 1966]. Given the mounting evidence that females do not always or, perhaps, usually mate with males in their own social group, the second alternative appears the more likely [Richard, 1974, 1985, & unpublished manuscript; O'Connor, personal communication; Ramer, personal communication].

The main goal of the study reported here was to establish the feasibility of measuring the resting metabolic rates of primates in the wild. Preliminary findings are consonant with our model, but we recognize that they cannot be construed as support for it. However, even if subsequent research fails to confirm the increase in RMR predicted for gestating and lactating females, in our opinion, the possibility that female social dominance is determined at least in part by high reproductive costs coupled with limited food availability deserves further scrutiny in this and other species.

CONCLUSIONS

1. We propose a model, suggesting that the need to elevate metabolic rate imposes a high energy demand on female sifakas compared to species which show no increase in RMR during reproduction and that, as a result, female sifakas are likely to have a strong interest in assuring themselves priority of access to limited food resources.

2. Physiological data are presented on four sifakas (*Propithecus verreauxi*). These animals were captured and held briefly in captivity in southern Madagascar, and during this time estimates of their resting metabolic rate were obtained. One adult male and one adult female had much lower RMR values than predicted from their body mass; one adult female approached predicted values; and a juvenile male showed an intermediate value. While this variation may be an artifact of methodological or sampling problems, the pattern of variation is at least consonant with our model.

3. Further research is needed to explore the influence of energetic constraints on social behavior in the sifaka and other species.

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