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Rates of Agonism by Diurnal Lemuroids: Implications for Female Social Relationships

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Abstract Sterck and colleagues (Behaviour 134:749–774, 1997) focused attention on the evolutionary ecology of female social relationships within and between groups and proposed a model that distinguishes 4 categories of female relationships, which correspond to particular types of intra- and intergroup competition. They emphasized literature on haplorhines in their model because of numerous, detailed studies conducted on a range of species in the wild; in contrast, strepsirrhines such as the lemuroids are poorly represented. We evaluate more closely their classification of lemuroids as Dispersal-Egalitarian using a greater number of species of *Lemur*, *Eulemur*, *Varecia*, *Hapalemur*, *Indri*, and *Propithecus*. For the focal species we found that female philopatry occurs rarely, agonistic rates are relatively low, female dominance hierarchies are not stable and do not exist year-round, and intra- and intergroup female-female competition is infrequent. Therefore, our results support the suggestion that a majority of lemuroid taxa we surveyed correspond to the Dispersal-Egalitarian category with 2 probable exceptions: *Lemur catta* and *Propithecus edwardsi*. Because female *Lemur catta* are philopatric, have year-round dominance hierarchies with female matrilines, exhibit the highest rates of agonism in studied lemuroids, and have frequent intra- and intergroup female-female competition, it would seem that they more closely correspond to the category Resident-Nepotistic. However, maternal *Lemur catta* rarely support their offspring in agonistic contests and matrilineal rank is not inherited, which leads us to state that the species does not fit into any existing category that explains the nature of female social relationships. The relationships of female *Propithecus edwardsi* are also a challenge to categorize under the current model because some of their characteristics — typical female dispersal and low agonistic rates— fall into the Dispersal-Egalitarian category, yet other behaviors —intense targeted aggression and stable and year-round female dominance hierarchies— do not.

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Introduction

Social conflict is presumed to be a basic feature of primate social systems and plays a central role in many of the current models researchers use to explain patterns of primate grouping (Overdorff and Parga 2007; *cf.* Silk 2002a; Sussman and Garber 2004; Sussman *et al.* 2005). The frequency of intragroup conflict depends on group size, cohesiveness of groups, and how individuals resolve their own self-interests regarding access to food and mates (Caporael *et al.* 2005; Hemelrijk 2002; Nunn and van Schaik 2002; Silk 2007; Wrangham 1980, 1987), along with the avoidance of predators (Miller 2002; van Schaik 1983, 1989). Adult females in particular must maintain a delicate energetic balance between obtaining adequate nutritional resources and minimizing the energetic costs associated with finding food and caring for and protecting their offspring and themselves (King *et al.* 2005; Wright *et al.* 2005). The continuous processes involved in the formation and maintenance of relationships within groups often puts females at odds with each other and other individuals within their group (Mason and Mendoza 1993).

Researchers predict that conflict over access to food plays a significant role in shaping female behavioral strategies in many models concerning the evolution of primate social systems (Isbell 1991; Kappeler 1999; Sterck *et al.* 1997; van Schaik 1989; Wrangham 1980, 1987). Gaulin and Sailer (1985) think that food distribution determines the distribution of females and types of relationships they will have, which in turn will affect the distribution of and relationships among males. In his classic model of female-bonded relationships, Wrangham (1980, 1987) proposed that intergroup competition is the most important factor in primate sociality, and that there is a strong link among the defendability of food sources, the degree of female bonding, and female dispersal patterns. Integral to his model are kin selection and inclusive fitness because female-bonded groups occur when females are philopatric and kin establish close ties to enhance their access to clumped resources that they can defend against competitors. As a result, nepotistic dominance hierarchies may develop. However, groups tend to be non-female-bonded when food is evenly distributed so that each group member's food intake is affected equally, or when food is found in small, high-quality clumps that an individual can monopolize. With little intergroup feeding competition, there is little incentive for females to establish close bonds or to be philopatric.

Wrangham's (1980, 1987) model provided a clear direction for future research on primate sociality and stimulated others to develop ecological models for primates that have testable predictions. Reevaluations of his model have concentrated on 2 areas: assessment of the strength of intra- and intergroup contest and scramble competition and description of female relationships beyond that of female-bonded and non-female-bonded. For example, Van Schaik (1989) categorized relationships between female primates according to the types of competition they face and the intensity of that competition. He developed a complex model of competitive regimens with predictions about female relationships based on food density, population density, and levels of intra- and intergroup contest and scramble competition. Simply stated, food patches that are clumped, monopolizable, and of intermediate size compared to group size will evoke contest competition, while scramble competition will result over other types of patches. Isbell (1991) also considered intra- and intergroup contest and scramble competition, made predictions in her model about which ecological factors would influence competition among females over food sources, and introduced ranging behavior as another variable in female relationships. By examining the covariance of female aggression within and between groups and ranging behavior, she found that food abundance shapes intergroup female relationships, while food distribution shapes intragroup female relationships.

Sterck *et al.* (1997) built on the earlier models of predation and food distribution by including social variables such as infanticide, habitat saturation, and female dispersal costs, in an effort to explain more of the observed variation in social organization. They extended the classification of female relationships beyond the dichotomy of female-bonded and non-female-bonded into 4 categories of female relationships that correspond to 4 combinations of intra- and intergroup contest competition. They refer to the traditional category of female-bonded, characterized by strict matrilineal hierarchies but low intergroup competition, as Resident-Nepotistic, e.g., *Cebus* spp., *Saimiri sciureus*, *Cercopithecus aethiops*, most *Macaca* spp., *Theropithecus gelada*, most *Papio* spp., and to non-female-bonded as Dispersal-Egalitarian, e.g., *Lemur catta*, *Eulemur fulvus*, *Alouatta seniculus*, *Ateles* spp., *Brachyteles*, *Saimiri oerstedi*, *Papio ursinus*, *P. hamadryas*, *Colobus badius*. Further, they distinguish groups in which females are philopatric but experience greater levels of inter- than intragroup competition as Resident-Egalitarian, e.g., most *Cercopithecus* spp., *Erythrocebus patas*, *Cercocebus* spp. Under these conditions, there is no advantage for females to form hierarchical relationships and female kin maintain weaker, less differentiated relationships compared to those in Resident-Nepotistic groups. Finally, in Resident-Nepotistic-Tolerant groups, e.g., *Macaca nigra*, females are philopatric, maintain hierarchical dominance relationships, but are more tolerant of each other vs. females in Resident-Nepotistic groups. In this case, both intra- and intergroup competition are high enough for dominant females to maintain tolerant, cooperative relationships with other females to ensure greater cohesion when defending resources from other groups.

However, the attempt at a synthetic model of primate social organization is based on dominance asymmetry, nepotism, coalition formation, and dispersal that researchers now recognize as the most conservative behaviors in the evolutionary history of the Old World monkeys (Di Fiore and Rendall 1994; Thierry 2008), and it is supported primarily by studies conducted on New World and Old World monkeys, while only a few strepsirhine species are represented owing to a scarcity of data. The strepsirhine species included in their sample (*Lemur catta, Eulemur fulvus,* and *Propithecus verreauxi*) are classified as Dispersal-Egalitarian based on the following: 1) females disperse from their natal groups, 2) female dominance hierarchies are unstable or nonexistent, and 3) intra- and intergroup female competition is low (Sterck *et al.* 1997; *cf.* Kappeler 1999).

Due to a tremendous increase in the number of studies conducted on populations of lemurs in a variety of habitats in Madagascar, one can now evaluate closely the classification of lemuroids as Dispersal-Egalitarian using a greater number of species of *Lemur*, *Eulemur*, *Varecia*, *Hapalemur*, and *Propithecus*. Because strepsirhines are highly nonconvergent with haplorhines based on features such as small group size, female dominance over males, and nocturnal and cathemeral activity cycles (Curtis 2004; Curtis and Zaramody 1999; Kappeler 1999; Overdorff and Erhart 2001; Pereira *et al.* 1990; Richard 1987), and because lemuroid sociality evolved independently from the other primates (Kappeler 1999; Kappeler and Heymann 1996; Kappeler and van Schaik 2002), it is difficult to predict whether lemuroid taxa will fit the category of Dispersal-Egalitarian or any other category Sterck *et al.* (1997) proposed.

Methods

To evaluate the categorization of lemurs as Dispersal-Egalitarian (Sterck *et al.* 1997), we noted or derived the following information from available literature for wild lemur species: 1) dispersal patterns, 2) female-female agonistic rates (acts/number of females/total observation time), 3) presence or absence of stable dominance hierarchies, and 4) extent of intra- and intergroup group competition. We then compared the information with published reports on patterns for wild haplorhine species. For agonistic rates, we selected papers containing female rates of agonism or that provided the raw data —total number of agonistic acts for all adult females, the number of adult females, and total observation time for the study period— for computation. Agonism includes vocal and visual aggressive and submissive behaviors such as spats, fighting, threats, extended chasing, displacement, and avoidance. To increase the comparability of study results, we included only studies using focal individual sampling in the data set because recording *ad libitum* and all occurrence sampling may overestimate the frequency of a behavior (Altmann 1974). Agonistic data include information from 18 genera and 26 species (Table I). We compared agonistic rates for lemuroids, apes, Old World monkeys, and New World monkeys via a Mann-Whitney *U* test and set significance at $p \leq 0.05$. However, because agonism includes behaviors ranging from mild, e.g., avoidance, displacement, threats, spats, etc., to more serious, e.g., biting, fighting, extended chasing, and because some

Table I Philopatry for some lemuroids

Species	Philopatric
Eulemur coronatus[1]	Neither sex
E. rubiventer[2]	Neither sex
E. fulvus spp.[2]	Neither sex
E. macaco[3]	Neither sex
Indri indri[4]	Neither sex
Hapalemur griseus[5]	Neither sex
Propithecus tattersalli[6]	Neither sex
P. verreauxi[7]	Neither sex
P. edwardsi[8]	Neither sex
P. diadema[9]	Neither sex
Varecia variegata[10]	Neither sex
Lemur catta[11]	Females

[1] Wilson *et al.* 1989; [2] Overdorff 1993a; [3] Colquhoun 1997; [4] Powzyk 1997; [5] Grassi 2001; [6] Meyers 1993; [7] Richard *et al.* 1993; [8] Hemingway 1995; Pochron *et al.* 2004; King *et al.* 2005; [9] Powzyk 1997; [10] Balko 1998; [11] Sussman 1991, 1992.

researchers recorded most agonistic behaviors while others only focused on 1 or 2 behaviors, we refrained from using sophisticated statistics and view the results of agonistic comparisons as general values that are likely to have some variance.

Results

Dispersal

The only group-living, diurnal lemuroid species in which female philopatry appears to be the norm is *Lemur catta* (Budnitz and Dainis 1975; Jones 1983; Sussman 1991, 1992). In other species, researchers note that while females sometimes stay in their natal groups, they may also voluntarily leave or be forced to leave via targeted aggression (Balko 1998; Colquhoun 1997; Grassi 2001; Hemingway 1995; King *et al.* 2005; Meyers 1993; Overdorff 1993a; Pochron *et al.* 2004; Powzyk 1997; Richard *et al.* 1993; Wilson *et al.* 1989). In the majority of lemuroid taxa sampled (11/12 species or 92%), females (and males) regularly disperse from their natal groups (Table I). We suggest that, *contra* Kappeler (1999), female philopatry occurs rarely in group-living, diurnal lemuroids. However, it is important to note, that most long-term studies of lemuroids focus on only a handful of taxa. Thus, with additional data we could more strongly conclude that the number of female transfers from natal groups is both statistically and theoretically significant (Moore 1984).

Agonistic Rates

When agonistic rates (acts per hour) are compared (Table II; Fig. 1), there is a significant difference between female lemuroids and female Old World monkeys (lemuroids: $n=8$; Old World monkeys: $n=11$; Mann-Whitney U test, Z value = −3.22; $p=0.001$). However, we found no difference between female lemuroids and female apes (lemuroids: $n=8$; apes $n=2$; Mann- Whitney U test, Z value = 0.000; $p=0.99$), or between female lemuroids and female New World monkeys (lemuroids: $n=8$; New World monkeys: $n=5$; Mann-Whitney U test, Z value = −0.220; $p=0.82$).

Rates of agonism are only slightly higher (0.01/h) for female dominant lemur species than for nonfemale dominant species (0.007/h), and the difference is not significant (sample size: female dominant: $n=6$, nonfemale dominant: $n=5$; Mann-Whitney U test, Z value = −0.639, $p=0.52$; Table III, Fig. 2). With the exception of *Lemur catta*, all female dominant species we surveyed have as low or lower agonistic rates than those of the nonfemale dominant species (Table III).

Dominance Hierarchies

Very few workers who study lemurs have been able to construct year-round, linear dominance hierarchies for males and females, and we found information about possible female dominance hierarchies in only 36% of the lemur taxa we evaluated (Tables II and III). The primary reason seems to be the extremely low levels of agonism and the fact that most individuals fail to respond agonistically to aggression received, or individuals simply do not interact consistently with others in their social

Table II Female-female agonistic rates (acts per hour) for lemuroids, apes, New World monkeys, and Old World monkeys

Taxa	Female-female rate[a]
Old World monkeys	
Cercocebus torquatus[1]	0.11
Cercopithecus mitis[2]	0.03
C. aethiops[3]	0.02
Macaca fuscata[4]	0.05
M. fascicularius[5]	0.08
M. cyclopis[6]	0.004
Papio cynocephalus[7]	0.10
P. anubis[8]	0.03
Erythrocebus patas[9]	0.03
Semnopithecus entellus[10]	0.10
Presbytis thomasi[11]	0.06
New World monkeys	
Saimiri sciureus[12]	0.004
Cebus capucinus[13]	0.004
C. apella[14]	0.002
Brachyteles arachnoides[15]	0.001
Alouatta palliata[16]	0.04
Apes	
Pan troglodytes[17]	0.005
Gorilla gorilla[18]	0.003
Lemuroids	
Eulemur coronatus[19]	0.001
E. fulvus[20]	0.007
Hapalemur griseus[21]	0.003
Propithecus verreaux[22]	0.004
P. tattersalli[23]	0.003
P. edwardsi[24]	0.002
Varecia variegata[25]	0.009
Lemur catta[26]	0.04

[a] Acts/number of females/total observation time.

[1] Range and Noë 2002; [2] Cords 2000; [3] Isbell and Pruetz 1998; [4] Furuichi 1983; [5] Sterck and Steenbeek 1997; [6] Su and Birky 2007; [7] Hausfater 1975; [8] Barton and Whiten 1993; [9] Isbell and Pruetz 1998; [10] Koenig 2000; [11] Sterck and Steenbeek 1997; [12] Mitchell 1990; [13] Perry 1996; [14] Janson 1985; [15] Strier 1992; [16] Jones 1980; [17] Müller 2002; [18] Goodall 1986; [19] Watts 1985; [20] Freed 1996; [21] Overdorff *et al.* 2003; [22] Grassi 2001; [23] Richard 1978; [24] Meyers 1993; [25] Pochron *et al.* 2003; [26] Overdorff *et al.* 2005; [27] Jolly 1966.

group (Tattersall 1982; Wright 1999). When there is no clear agonistic response (especially submission) to aggression, winners and losers of agonistic contests cannot be identified (Pereira and Kappeler 1997). We report the exceptions below.

Lemur catta

Several researchers report dominance hierarchies for both males and females and the presence of female matrilines in *Lemur catta* (Budnitz and Dainis 1975; Gould 1992; Jolly 1966; Sauther 1992), though maternal rank does not seem to be inherited (Bauer *et al.* 2005; Taylor and Sussman 1985). Female hierarchies are more stable than those of males, and female agonistic rates are usually higher in both feeding and resting contexts. Sauther and Sussman (1993) report that the top-ranking female is a focal

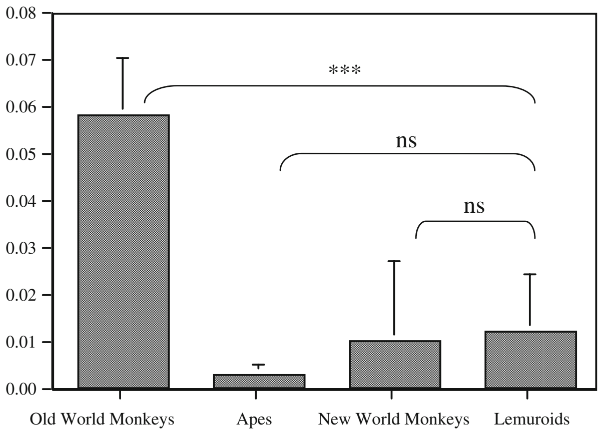

Fig. 1 Comparisons of mean female-female agonistic rates for lemuroid, New World monkey, Old World monkey, and ape genera. See Table II for references. ***Significant difference.

point for the group and has the highest rate of agonism, typically winning all aggressive encounters. Aggressive behaviors include chasing, cuffing, and scent-marking, while acts of submission are typically approach-retreat interactions between high- and low-ranking individuals (Jolly 1966; Sauther 1992). *Lemur catta* has the highest rates of agonism for lemuroids in the wild (Table II; Overdorff and Erhart 2001).

Varecia

Morland (1991) states that for *Varecia variegata* there is a loose dominance hierarchy among females, but none for males. However, she questions the validity of the female hierarchy because some group members did not interact, and aggression between females was highest during the mating season but almost nonexistent at other times (Morland 1993). Neither Balko (1998) nor Vasey (1998) were able to construct dominance hierarchies for males or females in their studies of *Varecia variegata* and *V. rubra*. Though Overdorff and colleagues (2005) were able to

Table III Mean agonistic rates (acts per hour) for female dominant and nonfemale dominant lemuroids

Taxa	Female dominance	Rate
Eulemur coronatus[1]	N	0.001
E. fulvus sanfordi[1]	N	0.003
E. f. rufus[2]	N	0.007
E. f. fulvus[3]	N	0.002
E. f. albocollaris[4]	N	0.02
Hapalemur griseus griseus[5]	Y	0.003
Propithecus verreuxi[6]	Y	0.004
P. tattersalli[7]	Y	0.003
P. edwardsi[8]	Y	0.002
Varecia variegata[9]	Y	0.009
Lemur catta[10]	Y	0.04

[1] Freed 1996; [2] Overdorff 1998; [3] Rasmussen 1999; [4] Johnson 2002; [5] Grassi 2001; [6] Richard 1978; [7] Meyers 1993; [8] Pochron *et al.* 2003; [9] Overdorff *et al.* 2005; [10] Jolly 1966.

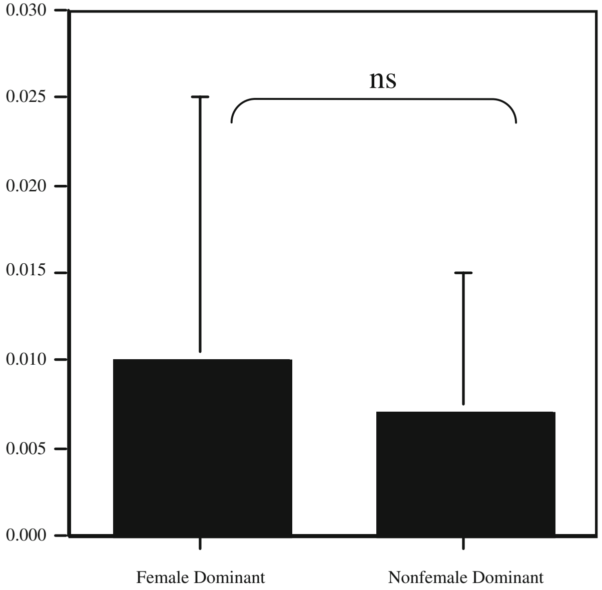

Fig. 2 Mean agonistic rates for female dominant and nonfemale dominant lemuroids. See Table III for a list of female dominant and nonfemale dominant species.

construct dominance hierarchies in a 3-yr study of *Varecia variegata*, hierarchies were unstable and nonlinear.

Propithecus

Richard (1978) was able to construct hierarchies during the breeding season for female *Propithecus verreauxi* based on priority of access to feeding resources as a criterion of dominance, though the same rank order was not always supported by other measures of dominance. Powzyk (1997) also reported seasonal female dominance hierarchies for *Propithecus diadema* and Pochron *et al.* (2003) documented year-round hierarchies for *P. edwardsi*. Pochron *et al.* (2003) found that, though agonistic and displacement interactions between female *Propithecus edwardsi* were infrequent (281/1,410 or 20% of all adult agonistic interactions; 53/542 or 10% of all displacements for adults), they were clearly decided interactions because one individual from the dyad gave submissive signals. Thus, they were able to divide females into ranks of dominant, equal, and subordinate (Pochron *et al.* 2003, 2005).

Intra- and Intergroup Competition

Intragroup female-female competition is rare in lemuroids, though it increases in a few species during reproductive periods (Wright 1999). A combination of extreme seasonal differences in food abundance and synchronized schedules of reproduction may increase competition among females to the point that some female group members are attacked and occasionally evicted (Jolly *et al.* 2002; Overdorff 1993b;

Pereira 1991; Wright 1999; Wright *et al.* 2005). Targeted aggression (Vick and Pereira 1989) among female lemurs is particularly severe during mating and birth seasons for *Lemur catta* (Jolly 1998), and can result in relentless aggression toward an adversary (Hood and Jolly 1995). In *Eulemur fulvus rufus, Varecia variegata,* and *Propithecus edwardsi*, aggression between females during the birth season can also escalate to the point that a targeted female is evicted from the group (Balko, *pers. comm.*, 2000; King *et al.* 2005; Overdorff 1998; Pochron *et al.* 2003; Wright 1995). For example, in 281 bouts of aggression recorded for *Propithecus edwardsi*, 191 instances (68%) were directed from one female to another, forcing the targeted female from the group (Pochron *et al.* 2003). Female *Propithecus edwardsi* migrate as a consequence of targeted aggression, which has also resulted in several infanticides and infant disappearances (Pochron *et al.* 2004).

Researchers reported intergroup encounters with female-female aggression only in ringtailed lemurs (Jolly *et al.* 1993; Nakamichi and Koyama 1997). Such encounters increase substantially during the birth season and vary in intensity from staring to serious wounding of females and loss of infants. Researchers have occasionally observed intergroup encounters in a few other species: *Propithecus edwardsi* (Wright 1995), *Eulemur fulvus rufus* (Overdorff and Erhart *unpub. data*), *Varecia variegata* (Balko, *pers. comm.*, 2000), and *Eulemur mongoz* (Colquhoun 1997; Curtis and Zaramody 1999), though they are typically uneventful and characterized by mutual retreat.

Discussion

Among the 4 possible categorizations for female relationships created by Sterck *et al.* (1997), we suggest that females from a majority of the lemuroid taxa we surveyed are most similar to Dispersal-Egalitarian because female dispersal is regular, low intra- and intergroup competition are the norm, and rates of agonism are typically low. When intragroup competition is weak, lemur females would theoretically have little to gain from maintaining dominance relationships or coalitions to compete for food and rank and they could disperse because they would not lose coalition partners. However, it is important to acknowledge that though rates of agonism are low for female lemuroids, targeted aggression can be intense and severe in some species (Hood and Jolly 1995; Jolly *et al.* 2002; King *et al.* 2005; Overdorff 1993b, 1998; Pereira 1991; Pochron *et al.* 2003; Wright 1995, 1999; Wright *et al.* 2005). Because targeted aggression occurs during reproductive periods it can have a seriously negative impact on a female's reproductive success that may last for multiple years (Nunn and Pereira 2000; Pochron *et al.* 2004). Further, it is possible that in some cases dominance hierarchies may exist for females, but are so well established that agonism is rare among females throughout most of the year. For example, in a 14-yr study of *Propithecus edwardsi*, Pochron *et al.* (2003, 2005) reported only 281 agonistic interactions (including targeted aggression) between females, yet in 96% of them the aggressor was clearly the winner, and it was possible to divide females into ranks of dominant, equal, and subordinate. The paucity of female coalitions in lemuroids may also reflect a lack of opportunity instead of a lack of interest in coalitions because of factors such as small group size

(Kappeler and Heymann 1996), a male-biased sex ratio (Kappeler 2000), a low birth rate, and an extremely high infant mortality rate (Gould *et al.* 2003; Jolly *et al.* 2002; Overdorff *et al.* 1999; Pochron *et al.* 2004; Richard *et al.* 1991, 2002; Sussman 1991; Wright 1995) that is about twice as great as that in anthropoids (Wright 1999). Thus, female lemuroids have fewer potential female coalition partners vs. most anthropoids, including daughters that they could retain in their groups as coalition partners (Pochron *et al.* 2004). This is an essential consideration because in many matrilineal societies, such as *Papio* spp. and *Macaca* spp., female primates interact more often with close kin and selectively support them in agonistic contexts (Silk 2002b, 2006).

Of the lemuroid species we evaluated, *Lemur catta* is one of the most difficult to categorize. They live in large groups of ≤10–27 individuals (Jolly 1966; Mertl-Millhollen *et al.* 1979; Sussman 1991), in which females are philopatric (Budnitz and Dainis 1975; Jones 1983; Sussman 1991, 1992), and agonistic rates are high vs. those of other lemur taxa (this study; Overdorff and Erhart 2001). Intra- and intergroup agonism between females increases during reproductive periods (Jolly *et al.* 1993; Nakamichi and Koyama 1997; Sauther 1993) and targeted aggression occurs in large groups (Koyoma *et al.* 2002; Sauther 1993; Taylor and Sussman 1985). In addition, female *Lemur catta* have year-round dominance hierarchies with female matrilines (Budnitz and Dainis 1975; Gould 1992; Jolly 1966; Sauther 1992), though females of high rank do not seem to have greater reproductive success (Takahata *et al.* 2005; *cf.* free-ranging, captive studies by Taylor 1986 and Parga 2006). It would seem, then, that *Lemur catta* would more closely correspond to the category Resident-Nepotistic of Sterck *et al.* (1997). However, matrilineal rank is not inherited in *Lemur catta* and mothers rarely support their offspring in agonistic contests (Nakamichi and Koyama 1997). Nakamichi and Koyama (1997) also report that alliances between wild adult females are unusual; instead females seem to rely on their own abilities when attaining their individual agonistic ranks (Bauer *et al.* 2005). As to why female *Lemur catta* so rarely form alliances, Pereira (1995, p. 164) hypothesizes “that peripheral neuroanatomy resulting in a relatively low visual acuity precludes frequent spontaneous intervention by ringtailed lemurs on behalf of kin and current dominants.” Therefore, we conclude that *Lemur catta* does not fit any of the categories Sterck *et al.* (1997) proposed to explain the evolutionary ecology of female social relationships.

Like Sterck *et al.* (1997), we also had difficulty categorizing *Propithecus*. Unlike *Lemur catta*, *Propithecus* spp. live in small groups of 2–12 individuals (Meyers 1993; Powzyk 1997; Richard *et al.* 1993; Wright 1995) and females typically disperse from their natal groups (Hemingway 1995; King *et al.* 2005; Meyers 1993; Pochron *et al.* 2004; Powzyk 1997). Researchers described female dominance hierarchies as seasonal —*Propithecus verreauxi* (Richard 1978) and *P. diadema* (Powzyk 1997)— and as year-round: *P. edwardsi* (Pochron *et al.* 2003). The difficulty that researchers have had in detecting female dominance hierarchies in *Propithecus* most likely reflects the fact that females are not always in permanent association with other females (Kappeler 2000; Pochron and Wright 2003). Instead, groups are pairs, polygynous, polyandrous, and polygynandrous (Pochron and Wright 2003). Even when there is >1 female in a group of *Propithecus*, rates of agonism are typically low (this study; Erhart and Overdorff 1999; Hemingway 1995;

Overdorff and Erhart 2001; Pochron *et al.* 2003), possibly because females are related, i.e., mother-daughter, sister, and grandmother-granddaughter dyads (Overdorff and Erhart, *unpub. data*; Pochron *et al.* 2003). Because *Propithecus* is a relatively long-lived, slow-reproducing species (Pochron *et al.* 2004; Richard *et al.* 2002), studies lasting more than a decade may be necessary to detect female dominance hierarchies in them (Pochron *et al.* 2003; Wright 1995). However, female *Propithecus* can experience increases in intra- and intergroup agonism during reproductive periods in groups with multiple females (Wright 1999), and Pochron *et al.* (2004) documented dispersal and infanticide as the result of targeted aggression. It seems that, like *Lemur catta*, *Propithecus* defies categorization.

The nature of female lemuroid relationships may be related to several ecological variables characteristic of Madagascar such as poor soils, low plant productivity, and an erratic and severe climate (Ganzhorn *et al.* 1999). Ganzhorn (1995), Gould *et al.* (1999), and Wright (1999) think that the variables result in unpredictable and highly seasonal changes in food availability and low dietary diversity. Compared to rain forests elsewhere (Nunes 1998; Struhsaker 1997; Terborgh 1983; van Schaik 1986), crown diameter is reduced by at least half in Madagascan rain forests (Balko 1998; Overdorff 1996), peak fruit production is 3 mo shorter on average (Wright 1997), and fruiting is not predictable from year to year nor is fruit available year-round (Hemingway 1996; Overdorff 1996). Therefore, the distribution of food in time and space may affect the size of groups in gregarious lemuroids. The small group size typical of lemurs (Kappeler and Heymann 1996) may reduce intragroup feeding competition and traveling costs and allow female lemuroids to keep competition below the level of reduced net food intake (Pochron *et al.* 2003), and it would result in little communal food defense during intergroup encounters (Wright 1999). Further, small food patches may favor reduced group cohesion. As a result of fewer individuals within subgroups, there may be less need for female-female agonistic conflict in feeding contexts. All of the nonfemale dominant lemuroid taxa fission into temporary subgroups on a regular basis (Overdorff and Erhart 2001). Researchers have long reported such flexibility in social organization for *Pan* (Goodall 1986) and the Atelinae: *Ateles* (van Roosmalen and Klein 1988), *Brachyteles* (Nishimura *et al.* 1988), *Lagothrix* (Emmons and Feer 1990), and may be more common across the Haplorhini than previously thought. Fissioning occurs in *Cacajao* (Ayres, 1989), *Macaca* (van Schaik and van Noordwijk 1986), and *Trachypithecus* (Newton and Dunbar 1994). In contrast, with the exception of *Varecia*, female dominant lemuroid species live in cohesive groups (Overdorff and Erhart 2001).

Female lemuroids may also use nonagonistic ways to increase their foraging efficiency. For example, by leading group movements and arriving into food patches first, female lemurs are able to influence their daily foraging efficiency and nutritional intake, which could improve a female's feeding ecology and long-term reproductive success (Erhart and Overdorff 1999; Trillmich *et al.* 2004). Determining group movement patterns is a form of social influence that is not based on agonistic ability. Leaders of group movements do not force others to follow them. Instead, the followers in essence create the leaders (Fedigan 1992). Therefore, characteristics of high dominance rank are not typically the qualities found in leaders of group movements. In addition, females may form bonds with males that can greatly influence dominance relations within a group (Overdorff 1998; Pereira and

McGlynn 1997). Male-female pairs of *Eulemur fulvus rufus* exchange agonistic support, and males even assist female friends to evict other females from groups (Vick and Pereira 1989). Most importantly, these male-female relationships can affect a female's ability to forage; Overdorff (1998) found that female *Eulemur fulvus rufus* have increased fruit feeding rates in the presence of male companions.

We began by stating that social conflict is thought to be an important organizing principle of primate social systems and that female primate social relationships are shaped by the competition they experience over food sources (Isbell 1991; Isbell and Young 2002; Kappeler 1999; Koenig 2002; Miller 2002; Nunn and van Schaik 2002; Sterck *et al.* 1997; van Schaik 1989; Wrangham 1980, 1987). Yet agonistic rates for females are extraordinarily low across the primate order, even for females in species that Sterck and colleagues (1997) referred to as having frequent coalitions, nepotistic relationships with formal submissive behaviors, and linear hierarchies: *Cebus* spp., *Saimiri sciureus*, *Cercopithecus aetheiops*, most *Macaca* spp., *Theropithecus gelada*, and most *Papio* spp. It seems that overall aggression and displacement rates within female relationships do not always match the competitive regimens of intra- and intergroup competition, and that predicted relationships between female relationships and feeding competition are only partially supported by available data (Koenig 2002; Snaith and Chapman 2007). The low agonistic rates of many female primates may reflect situations in which female reproductive success is limited by factors other than food abundance, such as disease, predation, infanticide, density-independent events, the effect of males, paternal relatedness, interspecific variation in cognitive abilities, and even time (Cooper *et al.* 2004; Fashing 2001; Isbell and Young 2002; Nunn and Altizer 2006; Overdorff 1998; Schülke and Ostner 2008; Thierry 2008). Therefore, though models that emphasize the effects of aggression and competition seem to have given primatologists a more unified perspective on the evolution of social behavior, several major issues need to be addressed.

One issue pertains to the lack of clear, operational definitions of common terms such as social organization, social structure, mating system, clumped foods, dispersed foods, strong social dominance, and weak social dominance (Isbell and Young 2002; Kappeler and van Schaik 2002; Pruetz 2009; Snaith and Chapman 2007). Because researchers have used the terms inconsistently and in a nonquantitative way, their application has been limited. Moreover, variability in behavior has undermined ideas about the nature of social systems such as the supposition that social organization determines social structure, while social structure influences mating systems (van Schaik and van Hooff 1983). Solitary strepsirrhines exhibit sociality and monogamous mating systems (Bearder 1999; Fietz 1999; Gursky 2000; Müller 1999), and in other species group composition and mating patterns can vary seasonally or between groups within populations (Cords 2002; Cords *et al.* 1986; Pochron and Wright 2003). Researchers rarely focused on difficult to measure variables, e.g., food depletion time, energy exchange rates, reproductive success, in comparison to variables that are easier to measure, e.g., patch size (Janson and van Schaik 1988; Isbell and Young 2002; Kappeler and van Schaik 2002; Koenig 2002; Koenig and Borries 2006). This is a problem because variables that are difficult to measure have the potential tell us more about the ultimate mechanisms that influence primate sociality than others that are easier to measure. In addition, several researchers have proposed that available methods and models could be more effectively used (Isbell and Young 2002; Koenig 2002; Koenig and Borries 2006), and new directions, methodologies, and paradigms need to be considered (Janson 2000). For example, Isbell (2004) proposed the dispersal/foraging model to explain variation in female dispersal patterns not explained by earlier models. She focused on how the locational and social costs of dispersal influence kin groups, rather than the inclusive benefits of kin defending food sources. Finally, it may not be possible to elucidate a socioecological model inclusive of all primate societies (Pruetz 2009; Snaith and Chapman 2007; Thierry 2008). As our knowledge of the behavioral variability of primates expands, it is tempting to add more factors to a synthetic model; however, it could result in a combinational explosion and render the model untestable (Thierry 2008). Instead it may be more fruitful to move away from broad-based models to more hypothesis-driven field studies on how the abundance, distribution, quality, and relative importance of food in a female's diet influences competition over food and how the competition may impact social organization in different taxa (Pruetz 2009; Snaith and Chapman 2007), and we may wish to consider a separate model to explain female relationships in the lemuroids owing to their nonconvergence with haplorhines in many features and their independent evolution of sociality (Kappeler 1999; Kappeler and Heymann 1996; Kappeler and van Schaik 2002). In short, we must "recognize that our focus on feeding competition captures only part of the puzzle" needed to explain social organization (Snaith and Chapman 2007, p. 104).

Our understanding of female relationships in lemuroids —and other primate species— would be greatly improved with additional long-term studies of multiple groups of various species and with the following specific information: 1) Better quantification of scramble and contest competition within and between groups, along with their intensity and energetic costs(Chapais 2004; Chapman and Chapman 2000; Koenig 2002; Pruetz 2009; Snaith and Chapman 2007). 2) Comparisons of the size and distribution of available food patches in relation to group size across multiple species (Isbell and Young 2002; Pruetz 2009), which would allow us to test finely the idea that small group size of lemuroids does indeed reduce intragroup feeding competition for females and would allow us to compare possible differences between female and nonfemale dominant groups. 3) Improved behavioral details concerning the context of group fissioning into temporary subgroups (Chapman *et al.* 1995; Kinzey and Cunnigham 1994). In conjunction with information regarding food availability, the data would help us to understand whether fissioning is a feeding strategy of females or occurs for other reasons. 4) More information regarding how females improve their foraging efficiency in nonfemale dominant species, particularly during reproductive periods. Because female reproductive success is thought to be tightly linked to foraging success, females should perform more innovative foraging behaviors than those of males. 5) Investigation into a variety of confounding factors Koenig (2002) noted, including how male reproductive strategies can affect female feeding competition, how the size of groups may enforce female dispersal, and how demography may alter female alliances. 6) Documenting the presence or absence of dominance relationships with more careful recording of agonism (Overdorff *et al.* 2005). In particular, researchers interested in lemuroid agonism need to pay particular attention to subtle aggressive and submissive behaviors. Human observers of arboreal subjects may simply miss hard-to-see behaviors, e.g. avoid, or may dismiss such behaviors as unimportant. Certainly, the easiest way to minimize aggressive interactions is to avoid them. In addition, nonovertly agonistic behaviors such as scent-marking (Gould and Overdorff 2002; Kappeler 1998; Kraus *et al.* 1999; Lewis 2005; Pochron *et al.* 2005) may be especially useful as indicators of dominance and competitive relationships for species that have low rates of aggression and displacement. 7) Reports of the severity of aggressive encounters. The effects of targeted aggression during reproductive periods range from the loss of reproductive opportunity to female-caused infanticide (Nunn and Pereira 2000; Pochron *et al.* 2004). Thus, low rates of agonism may be deceptive when episodic aggression is severe enough to impact female reproductive success. 8) Acknowledgment of the effect of phylogeny on social behavior because there is increasing evidence that phylogeny is a better predictor of the social behavior of a taxon than ecology is (Di Fiore and Rendall 1994; Fleagle and Reed 1996; Ossi and Kamilar 2006; Thierry 2007).

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References

Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, *49*, 227–265. doi:10.1163/156853974X00534.

Ayres, J. M. (1989). Comparative feeding ecology of the uakari and bearded saki, *Cacajao* and *Chiropotes*. *Journal of Human Evolution*, *18*, 697–716. doi:10.1016/0047-2484(89)90101-2.

Balko, E.A. (1998). *The Behavioral Plasticity of* Varecia variegata *in Ranomafana National Park, Madagascar*. Ph.D. dissertation, SUNY-College of Environmental Science and Foresty, Syracuse, NY.

Barton, R. A., & Whiten, A. (1993). Feeding competition among female olive baboons, *Papio anubis*. *Animal Behaviour*, *46*, 777–789. doi:10.1006/anbe.1993.1255.

Bauer, R. N., Gould, L., & Sauther, M. L. (2005). Correlates of dominance rank in female ring-tailed lemurs (*Lemur catta*) at the Beza Mahafaly Special Reserve, Madagascar. *American Journal of Physical Anthropology*, *40*, 70–71.

Bearder, S. K. (1999). Physical and social diversity among nocturnal primates: A new view based on long-term research. *Primates*, *40*, 267–282. doi:10.1007/BF02557715.

Budnitz, N., & Dainis, K. (1975). *Lemur catta*: Ecology and behavior. In I. Tattersall, & R. W. Sussman (Eds.), *Lemur biology* (pp. 219–235). New York: Plenum Press.

Caporael, L., Sloan Wilson, D., Hemelrijk, C., & Sheldon, K. M. (2005). Small groups from an evolutionary perspective. In M. S. Poole, & A. B. Hollingshead (Eds.), *Theories of small groups: Interdisciplinary perspectives* (pp. 369–398). Thousand Oaks, CA: Sage Publications.

Chapais, B. (2004). How kinship generates dominance structures: A comparative perspective. In B. Thierry, M. Singh, & W. Kaumanns (Eds.), *Macaque societies: A model for the study of social organization* (pp. 186–208). Cambridge, UK: Cambridge University Press.

Chapman, C. A., & Chapman, L. J. (2000). Determinants of group size in primates: The importance of travel costs. In S. Boinski, & P. A. Garber (Eds.), *On the move: How and why animals travel in groups* (pp. 470–490). Chicago: University of Chicago Press.

Chapman, C. A., Wrangham, R. W., & Chapman, L. J. (1995). Ecological constraints on group size: An analysis of spider monkey and chimpanzee subgroups. *Behavioral Ecology and Sociobiology*, *36*, 59–70. doi:10.1007/BF00175729.

Colquhoun, I. C. (1997). *A predictive sociological study of the black Lemur* (Eulemur macaco macaco) *in Northeastern Madagascar*. Ph.D. Dissertation, Washington University, St. Louis, MO.

Cooper, M. A., Aureli, F., & Singh, M. (2004). Between-group encounters among bonnet macaques (*Macaca radiata*). *Behavioral Ecology and Sociobiology*, *56*, 217–227. doi:10.1007/s00265-004-0779-4.

Cords, M. (2000). Agonistic and affiliative relationships in a blue monkey group. In P. F. Whitehead, & C. J. Jolly (Eds.), *Old world monkeys* (pp. 453–479). Cambridge, UK: Cambridge University Press.

Cords, M. (2002). When are there influxes in blue monkey groups? In M. E. Glenn, & M. Cords (Eds.), *The Guenons: Diversity and adaptation in African monkeys* (pp. 189–201). New York: Kluwer Academic/Plenum Press.

Cords, M., Mitchell, B. J., Tsingalia, H. M., & Rowell, T. E. (1986). Promiscuous mating among blue monkeys in the Kakamega Forest, Kenya. *Ethology*, *72*, 214–226.

Curtis, D. J. (2004). Diet and nutrition in wild mongoose lemurs (*Eulemur mongoz*) and their implications for the evolution of female dominance and small group size in lemurs. *American Journal of Physical Anthropology*, *124*, 234–247. doi:10.1002/ajpa.10268.

Curtis, D. J., & Zaramody, A. (1999). Social structure and seasonal variation in the behaviour of *Eulemur mongoz*. *Folia Primatologica*, *70*, 79–96. doi:10.1159/000021679.

Di Fiore, A., & Rendall, D. (1994). Evolution of social organization: A reappraisal for primates by using phylogenetic methods. *Proceedings of the National Academy of Sciences of the United States of America*, *91*, 9941–9945. doi:10.1073/pnas.91.21.9941.

Emmons, L. H., & Feer, E. (1990). *Monkeys (Primates). In Neotropical rainforest mammals: A field guide* pp. 134–153. Chicago: University of Chicago Press.

Erhart, E. M., & Overdorff, D. J. (1999). Female coordination of group travel in wild *Propithecus* and *Eulemur*. *International Journal of Primatology*, *20*, 927–940. doi:10.1023/A:1020830703012.

Fashing, P. J. (2001). Male and female strategies during intergroup encounters in guerezas (*Colobus guereza*): Evidence for resource defense mediated through males and a comparison with other primates. *Behavioral Ecology and Sociobiology*, *50*, 219–230. doi:10.1007/s002650100358.

Fedigan, L. M. (1992). *Primate paradigms: Sex roles and social bonds*. Chicago: University of Chicago Press.

Fietz, J. (1999). Monogamy as a rule rather than exception in nocturnal lemurs: The case of the fat-tailed dwarf lemur, *Cheirogaleus medius*. *Ethology*, *105*, 259–272. doi:10.1046/j.1439-0310.1999.00380.x.

Fleagle, J. G., & Reed, K. E. (1996). Comparing primate communities: A multivariate approach. *Journal of Human Evolution*, *30*, 489–510. doi:10.1006/jhev.1996.0039.

Freed, B. Z. (1996). *Co-occurrence among crowned Lemurs* (Lemur coronatus) *and Sanford's Lemur* (Lemur fulvus sanfordi) *of Madagascar*. Ph.D. dissertation, Washington University, St. Louis, MO.

Furuichi, T. (1983). Interindividual distance and influence of dominance on feeding in a natural Japanese macaque troop. *Primates*, *24*, 445–455. doi:10.1007/BF02381678.

Ganzhorn, J. U. (1995). Cyclones over Madagascar: Fate or fortune? *Ambio*, *24*, 124–125.

Ganzhorn, J. U., Wright, P. C., & Ratsimbazafy, H. J. (1999). Primate communities: Madagascar. In J. G. Fleagle, C. H. Janson, & K. Reed (Eds.), *Primate communities* (pp. 75–89). Cambridge, UK: Cambridge University Press.

Gaulin, S. J., & Sailer, L. D. (1985). Are females the ecological sex? *American Anthropologist*, *87*, 111–119. doi:10.1525/aa.1985.87.1.02a00100.

Goodall, J. (1986). *The Chimpanzees of Gombe: Patterns of behavior*. Cambridge, MA: Belknap Press of Harvard University Press.

Gould, L. (1992). Alloparental care in free-ranging *Lemur catta* at Berenty Reserve, Madagascar. *Folia Primatologica*, *58*, 72–83.

Gould, L., & Overdorff, D. J. (2002). Adult male scent-marking in *Lemur catta* and *Eulemur fulvus rufus*. *International Journal of Primatology*, *23*, 575–586. doi:10.1023/A:1014921701106.

Gould, L., Sussman, R. W., & Sauther, M. L. (1999). Natural disasters and primate populations: The effects of a 2-year drought on a naturally occurring population of ring-tailed lemurs (*Lemur catta*) in southwestern Madagascar. *International Journal of Primatology*, *20*, 69–84. doi:10.1023/A:1020584200807.

Gould, L., Sussman, R. W., & Sauther, M. L. (2003). Demographic and life-history patterns in a population of ring-tailed lemurs (*Lemur catta*) at Beza Mahafaly Reserve, Madagascar: A 15-year perspective. *American Journal of Physical Anthropology*, *120*, 182–194. doi:10.1002/ajpa.10151.

Grassi, C. (2001). *The Behavioral Ecology of* Hapalemur griseus griseus*: The Influences of Microhabitat and Population Density on this Small-Bodied Prosimian Folivore*. Ph.D. dissertation, University of Texas, Austin, TX.

Gursky, S. (2000). Sociality in the spectral tarsier, *Tarsius spectrum*. *American Journal of Primatology*, *51*, 89–101. doi:10.1002/(SICI)1098-2345(200005)51:1<89::AID-AJP7>3.0.CO;2-7.

Hausfater, G. (1975). *Dominance and reproduction in baboons (Papio cynocephalus): A quantitative analysis. In Contributions to primatology, Vol. 7* pp. 1–150. New York: Karger Press.

Hemelrijk, C. K. (2002). Understanding social behavior with the help of complexity science. *Ethology*, *108*, 655–671. doi:10.1046/j.1439-0310.2002.00812.x.

Hemingway, C. A. (1995). *Feeding and reproductive strategies of the Milne-Edwards' Sifaka,* Propithecus diadema edwardsi. Ph.D. dissertation, Duke University, Durham, North Carolina.

Hemingway, C. A. (1996). Morphology and phenology of seeds and whole fruit eaten by Milne-Edward's sifaka *Propithecus diadema edwardsi* in Ranomafana National Park, Madagascar. *International Journal of Primatology*, *17*, 637–659. doi:10.1007/BF02735259.

Hood, L. C., & Jolly, A. (1995). Troop fission in female *Lemur catta* at Berenty Reserve, Madagascar. *International Journal of Primatology*, *16*, 997–1015. doi:10.1007/BF02696113.

Isbell, L. A. (1991). Contest and scramble competition: Patterns of female aggression and ranging behavior among primates. *Behavioral Ecology*, *2*, 143–155. doi:10.1093/beheco/2.2.143.

Isbell, L. A. (2004). Is there no place like home? Ecological bases of female dispersal and philopatry and their consequences for the formation of kin groups. In C. Chapais, & C. Berman (Eds.), *Kinship and behavior in primates* (pp. 71–108). New York: Oxford University Press.

Isbell, L. A., & Pruetz, J. D. (1998). Differences between vervets (*Cercopithecus aethiops*) and patas (*Erythrocebus patas*) in agonistic interactions between adult females. *International Journal of Primatology*, *19*, 837–855. doi:10.1023/A:1020393329574.

Isbell, L. A., & Young, T. P. (2002). Ecological models of female social relationships in primates: Similarities, disparities, and some directions for future clarity. *Behaviour*, *139*, 177–202. doi:10.1163/156853902760102645.

Janson, C. H. (1985). Aggressive competition and individual food consumption in wild brown capuchin monkeys (*Cebus apella*). *Behavioral Ecology and Sociobiology*, *18*, 125–138. doi:10.1007/BF00299041.

Janson, C. H. (2000). Primate socio-ecology: The end of a golden era. *Evolutionary Anthropology*, *9*, 73–86. doi:10.1002/(SICI)1520-6505(2000)9:2<73::AID-EVAN2>3.0.CO;2-X.

Janson, C. H., & van Schaik, C. P. (1988). Recognizing the many faces of primate food competition: Methods. *Behaviour*, *105*, 165–186. doi:10.1163/156853988X00502.

Johnson, S. E. (2002). *Ecology and Speciation In Brown Lemurs: White-Collared Lemurs* (Eulemur albocollaris) *and Hybrids* (Eulemur albocollaris × Eulemur fulvus rufus) *in Southeastern Madagascar.* Ph.D. dissertation, University of Texas, Austin, TX.

Jolly, A. (1966). *Lemur behavior: A Madagascar field study.* Chicago: University of Chicago Press.

Jolly, A. (1998). Pair-bonding, female aggression, and the evolution of lemur societies. *Folia Primatologica*, *69*, 1–13. doi:10.1159/000052693.

Jolly, A., Dobson, A., Rasamimanana, H. M., Walker, J., O'Connor, S., Solberg, M., et al. (2002). Demography of Lemur catta at Berenty Reserve, Madagascar: Effects of troop size, habitat and rainfall. *International Journal of Primatology*, *23*, 327–353. doi:10.1023/A:1013835612314.

Jolly, A., Rasamimanana, H. R., Kinnaird, M. F., O'Brien, T. G., Crowley, H. M., Harcourt, C. S., et al. (1993). Territoriality in *Lemur catta* groups during the birth season at Berenty, Madagascar. In P. M. Kappeler, & J. U. Ganzhorn (Eds.), *Lemur social systems and their ecological basis* (pp. 85–109). New York: Plenum Press.

Jones, C. B. (1980). The functions of status in the mantled howler monkey, *Alouatta palliata* Gray: Interspecific competition for group membership in a folivorous neotropical primate. *Primates*, *21*, 389–405. doi:10.1007/BF02390468.

Jones, K. C. (1983). Inter-troop transfer of *Lemur catta* at Berenty, Madagascar. *Folia Primatologica*, *40*, 145–160.

Kappeler, P. M. (1998). To whom it may concern: The transmission and function of chemical signals in *Lemur catta*. *Behavioral Ecology and Sociobiology*, *42*, 411–421. doi:10.1007/s002650050455.

Kappeler, P. M. (1999). Lemur social structure and convergence in primate socioecology. In P. C. Lee (Ed.), *Comparative primate socioecology* (pp. 273–299). Cambridge, UK: Cambridge University Press.

Kappeler, P. M. (2000). Causes and consequences of unusual sex ratios in lemurs. In P. M. Kappeler (Ed.), *Primate males: Causes and consequences of variation in group composition* (pp. 55–63). Cambridge, UK: Cambridge University Press.

Kappeler, P. M., & Heymann, E. W. (1996). Nonconvergence in the evolution of primate life history and socio-ecology. *Biological Journal of the Linnean Society. Linnean Society of London*, *59*, 297–326.

Kappeler, P. M., & van Schaik, C. P. (2002). Evolution of primate social systems. *International Journal of Primatology*, *23*, 707–740. doi:10.1023/A:1015520830318.

King, S. J., Arrigo-Nelson, S. J., Pochron, S. T., Semprebon, G. M., Godfrey, L. R., Wright, P. C., et al. (2005). Dental senescence in a long-lived primate links infant survival to rainfall. *Proceedings of the National Academy of Sciences of the United States of America*, *102*, 16579–16583. doi:10.1073/pnas.0508377102.

Kinzey, W. G., & Cunningham, E. P. (1994). Variability in platyrrhine social organization. *American Journal of Primatology*, *34*, 185–198. doi:10.1002/ajp.1350340209.

Koenig, A. (2000). Competitive regimes in forest-dwelling Hanuman langur females (*Semnopithecus entellus*). *Behavioral Ecology and Sociobiology*, *48*, 93–109. doi:10.1007/s002650000198.

Koenig, A. (2002). Competition for resources and its behavioral consequences among female primates. *International Journal of Primatology*, *23*, 759–783. doi:10.1023/A:1015524931226.

Koenig, A., & Borries, C. (2006). The predictive power of socioecological models: A reconsideration of resource characteristics, agonism, and dominance hierarchies. In G. Hohmann, M. M. Robbins, & C. Boesch (Eds.), *Feeding ecology in apes and other primates: Ecological, physical and behavioral aspects* (pp. 263–284). New York: Cambridge University Press.

Koyoma, N., Nakamichi, M., Ichino, S., & Takahata, Y. (2002). Population and social dynamics changes in ring-tailed lemur troops at Berenty, Madagascar between 1989–1999. *Primates*, *43*, 291–314. doi:10.1007/BF02629604.

Kraus, C., Heistermann, M., & Kappeler, P. M. (1999). Physiological suppression of sexual function of subordinate males: A subtle form of intrasexual competition among male sifakas (*Propithecus verreauxi*)? *Physiology & Behavior*, *66*, 855–861. doi:10.1016/S0031-9384(99)00024-4.

Lewis, R. J. (2005). Sex differences in scent-marking in sifaka: Mating conflict or male services? *American Journal of Physical Anthropology*, *128*, 389–398. doi:10.1002/ajpa.20206.

Mason, W. A., & Mendoza, S. P. (1993). Primate social conflict: An overview of sources, forms, and consequences. In W. A. Mason, & S. P. Mendoza (Eds.), *Primate social conflict* (pp. 1–12). Albany: State University of New York.

Mertl-Millhollen, A. S., Gustafson, H. L., Budnitz, N., Dainis, K., & Jolly, A. (1979). Population and territory stability of the *Lemur catta* at Berenty, Madagascar. *Folia Primatologica*, *31*, 106–122.

Meyers, D. M. (1993). *The Effects of Resource Seasonality on Behavior and Reproduction in the Golden-crowned Sifaka* (Propithecus tattersalli, *Simons, 1988*) *in Three Malagasy Forests*. Ph.D. Dissertation, Duke University, Durham, North Carolina.

Miller, L. E. (2002). *Eat or be eaten: Predator sensitive foraging among primates*. New York: Cambridge University Press.

Mitchell, C. L. (1990). *The Ecological Basis for Female Social Dominance: A Behavioral Study of the Squirrel Monkey* (Saimiri sciureus). Ph.D. dissertation, Princeton University, Princeton, New Jersey.

Moore, J. (1984). Female transfer in primates. *International Journal of Primatology*, *5*, 537–590. doi:10.1007/BF02692285.

Morland, H. S. (1991). Preliminary report on the social organization of ruffed lemurs (*Varecia variegata variegata*) in a northeast Madagascar rainforest. *Folia Primatologica*, *56*, 157–161. doi:10.1159/000133075.

Morland, H. S. (1993). Reproductive activity of ruffed lemurs (*Varecia variegata variegata*) in a Madagascar rainforest. *American Journal of Physical Anthropology*, *97*, 71–82. doi:10.1002/ajpa.1330910105.

Müller, A. E. (1999). Social organization of the fat-tailed dwarf lemur (*Cheirogaleus medius*) in northwestern Madagascar. In B. Rakotosamimanana, H. Rasiminmanana, & J. U. Ganzhorn (Eds.), *New directions in Lemur studies* (pp. 139–157). New York: Plenum Press.

Müller, M. N. (2002). Agonistic relations among Kanyawara chimpanzees. In C. Boesch, G. Hohmann, & L. F. Marchant (Eds.), *Behavioural diversity in chimpanzees and bonobos* (pp. 112–124). Cambridge: Cambridge University Press.

Nakamichi, M., & Koyama, N. (1997). Social relationships among ring-tailed lemurs (*Lemur catta*) in two free-ranging troops at Berenty Reserve, Madagascar. *International Journal of Primatology*, *18*, 73–93. doi:10.1023/A:1026393223883.

Newton, P., & Dunbar, R. (1994). Colobine monkey societies. In A. Davies, & J. Oates (Eds.), *Colobine monkeys: Their ecology, behaviour and evolution* (pp. 311–346). Cambridge, UK: Cambridge University Press.

Nishimura, A., de Fonseca, G. A. B., Mittermeier, R. A., Young, A. L., Strier, K. B., & Valle, C. M. C. (1988). The muriqui, genus *Brachyteles*. In R. A. Mittermeier, A. B. Rylands, A. F. Coimbra-Filho, &

G. A. B. de Fonseca (Eds.), *Ecology and behavior of neotropical primates, Vol. 2* (pp. 577–610). Washington, DC: World Wildlife Fund.

Nunes, A. (1998). Diet and feeding ecology of *Ateles belzebuth belzebuth* at Maraca Ecology Station, Roraima, Brazil. *Folia Primatologica*, *69*, 61–76. doi:10.1159/000021573.

Nunn, C., & Altizer, S. (2006). *Infectious diseases in primates: Behavior, ecology and evolution*. New York: Oxford University Press.

Nunn, C. L., & Pereira, M. E. (2000). Group histories and offspring sex ratios in ringtailed lemur (*Lemur catta*). *Behavioral Ecology and Sociobiology*, *48*, 18–28. doi:10.1007/s002650000206.

Nunn, C. L., & van Schaik, C. (2002). A comparative approach to reconstructing the socioecology of extinct primates. In J. M. Plavcan, R. F. Kay, W. L. Jungers, & C. P. van Schaik (Eds.), *Reconstructing behavior in the primate fossil record* (pp. 159–215). New York: Kluwer Academic/ Plenum Publishers.

Ossi, K., & Kamilar, J. M. (2006). Environmental and phylogenetic correlates of *Eulemur* behavior and ecology (Primates: Lemuridae). *Behavioral Ecology and Sociobiology*, *61*, 53–64. doi:10.1007/s00265-006-0236-7.

Overdorff, D. J. (1993a). Ecological and reproductive correlates with ranging patterns in two prosimian primates in Madagascar. In P. M. Kappeler, & J. U. Ganzhorn (Eds.), *Lemur social systems and their ecological basis* (pp. 167–192). New York: Plenum Press.

Overdorff, D. J. (1993b). Similarities, differences, and seasonal patterns in the diets of *Eulemur rubriventer* and *Eulemur fulvus rufus* in the Ranomafana National Park, Madagascar. *International Journal of Primatology*, *14*, 721–753. doi:10.1007/BF02192188.

Overdorff, D. J. (1996). Ecological correlates to social structure in two prosimian primates in Madagascar. *American Journal of Physical Anthropology*, *100*, 487–506. doi:10.1002/(SICI)1096-8644(199608)100:4<487::AID-AJPA4>3.0.CO;2-O.

Overdorff, D. J. (1998). Are *Eulemur* species pairbonded? Social organization and mating strategies of *Eulemur fulvus rufus* in Madagascar. *American Journal of Physical Anthropology*, *105*, 153–166. doi:10.1002/(SICI)1096-8644(199802)105:2<153::AID-AJPA4>3.0.CO;2-W.

Overdorff, D. J., & Erhart, E. M. (2001). Social and ecological influences on female dominance in day-active prosimian primates. *American Journal of Physical Anthropology*, *32*, 116.

Overdorff, D. J., Erhart, E. M., & Mutschler, T. (2003). The influence of patch entry order on feeding priority in three prosimian species in southeastern Madagascar. *American Journal of Physical Anthropology*, *36*, 163.

Overdorff, D. J., Erhart, E. M., & Mutschler, T. (2005). Does female dominance facilitate feeding priority in black-and-white ruffed lemurs (*Varecia variegata*) in southeastern Madagascar? *American Journal of Primatology*, *66*, 7–22. doi:10.1002/ajp.20125.

Overdorff, D. J., Merenlender, A. M., Talata, P., Telo, A., & Forward, Z. (1999). Life history of *Eulemur fulvus rufus* from 1988–1998 in southeastern Madagascar. *American Journal of Physical Anthropology*, *108*, 295–310. doi:10.1002/(SICI)1096-8644(199903)108:3<295::AID-AJPA5>3.0.CO;2-Q.

Overdorff, D. J., & Parga, J. (2007). The new era of primate socioecology: Ecology and intersexual conflict. In C. J. Campbell, A. Fuentes, K. C. MacKinnon, M. Panger, & S. K. Bearder (Eds.), *Primates in perspective* (pp. 466–482). New York: Oxford University Press.

Parga, J. A. (2006). Male mate choice in *Lemur catta*. *International Journal of Primatology*, *27*, 107–131. doi:10.1007/s10764-005-9006-z.

Pereira, M. E. (1991). Asynchrony within estrous synchrony among ringtailed lemurs. *Physiology & Behavior*, *49*, 47–52. doi:10.1016/0031-9384(91)90228-G.

Pereira, M. E. (1995). Development and social dominance among group-living lemurs. *American Journal of Primatology*, *37*, 143–175. doi:10.1002/ajp.1350370207.

Pereira, M. E., & Kappeler, P. M. (1997). Divergent systems of agonistic behaviour in lemurid primates. *Behaviour*, *134*, 225–274. doi:10.1163/156853997X00467.

Pereira, M. E., Kaufman, R., Kappeler, P. M., & Overdorff, D. J. (1990). Female dominance does not characterize all of the Lemuridae. *Folia Primatologica*, *55*, 96–103.

Pereira, M. E., & McGlynn, C. A. (1997). Special relationships instead of female dominance for redfronted lemurs, *Eulemur fulvus rufus*. *American Journal of Primatology*, *43*, 239–258. doi:10.1002/(SICI)1098-2345(1997)43:3<239::AID-AJP4>3.0.CO;2-Y.

Perry, S. (1996). Female-female social relationships in wild white-faced capuchin monkeys, *Cebus capucinus*. *American Journal of Primatology*, *40*, 167–182. doi:10.1002/(SICI)1098-2345(1996)40:2<167::AID-AJP4>3.0.CO;2-W.

Pochron, S. T., Fitzgerald, J., Gilbert, C. C., Lawrence, D., Grgas, M., Rakotonirina, G., et al. (2003). Patterns of female dominance in *Propithecus diadema edwardsi* of Ranomafana National Park, Madagascar. *American Journal of Primatology*, *61*, 173–185. doi:10.1002/ajp.10119.

Pochron, S. T., Morelli, T. L., Terranova, P., Scirbons, J., & Wright, P. C. (2005). Sex differences in scent marking in Propithecus edwardsi of Ranomafana National Part, Madagascar. *American Journal of Primatology*, *66*, 97–110. doi:10.1002/ajp.20130.

Pochron, S. T., Tucker, W. T., & Wright, P. C. (2004). Demography, life history, and social structure in *Propithecus diadema edwardsi* from 1986–2000 in Ranomafana National Park, Madagascar. *American Journal of Physical Anthropology*, *125*, 61–72. doi:10.1002/ajpa.10266.

Pochron, S. T., & Wright, P. C. (2003). Variability in adult group compositions of a prosimian primate. *Behavioral Ecology and Sociobiology*, *54*, 285–293. doi:10.1007/s00265-003-0634-z.

Powzyk, J. A. (1997). *The Socioecology of Two Sympatric Indriids,* Propithecus diadema diadema *and* Indri indri: *A Comparison of Feeding Strategies and Their Possible Repercussions on Species-Specific Behavior*. Ph.D. dissertation, Duke University, Durham, NC.

Pruetz, J. D. E. (2009). *The socioecology of adult female Patas monkeys and Vervets in Kenya*. Upper Saddle River, NJ: Pearson/Prentice Hall.

Range, F., & Noë, R. (2002). Familiarity and dominance relations among female sooty mangabeys in the Tai National Park. *American Journal of Primatology*, *56*, 137–153. doi:10.1002/ajp.1070.

Rasmussen, M. A. (1999). *Ecological Influences on Activity Cycle in Two Cathemeral Primates, the Mongoose Lemur (*Eulemur mongoz*) and the Common Brown Lemur* (Eulemur fulvus fulvus). Ph.D. Dissertation, Duke University, Durham, North Carolina.

Richard, A. F. (1978). *Behavioral variation: Case study of a Malagasy Lemur*. Lewisburg: Bucknell University Press.

Richard, A. F. (1987). Malagasy prosimians: Female dominance. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker (Eds.), *Primate societies* (pp. 25–33). Chicago: University of Chicago Press.

Richard, A. F., Dewar, R. E., Schwartz, M., & Ratsirarson, J. (2002). Life in the slow lane? Demography and life histories of male and female sifaka (*Propithecus verreauxi verreauxi*). *Journal of Zoology*, *256*, 421–436.

Richard, A. F., Rakotomanga, P., & Schwartz, M. (1991). Demography of *Propithecus verreauxi* at Beza Mahafaly, Madagascar: Sex ratio, survival, and fertility, 1984–1988. *American Journal of Physical Anthropology*, *84*, 307–322. doi:10.1002/ajpa.1330840307.

Richard, A. F., Rakotomanga, P., & Schwartz, M. (1993). Dispersal by *Propithecus verreauxi* at Beza Mahafaly, Madagascar: 1984–1991. *American Journal of Primatology*, *30*, 1–20. doi:10.1002/ajp.1350300102.

Sauther, M. L. (1992). *The Effect of Reproductive State, Social Rank and Group Size on Resource Use Among Free-Ranging Ringtailed Lemurs* (Lemur catta). Ph.D. dissertation, Washington University, St. Louis, MO.

Sauther, M. L. (1993). Resource competition in wild populations of ringtailed lemurs (*Lemur catta*): Implications for female dominance. In P. M. Kappeler, & J. U. Ganzhorn (Eds.), *Lemur social systems and their ecological basis* (pp. 135–152). New York: Plenum Press.

Sauther, M. L., & Sussman, R. W. (1993). A new interpretation of the social organization and mating system of the ringtailed lemur (*Lemur catta*). In P. M. Kappeler, & J. U. Ganzhorn (Eds.), *Lemur social systems and their ecological basis* (pp. 111–121). New York: Plenum Press.

Schülke, O., & Ostner, J. (2008). Male reproductive skew, paternal relatedness, and female social relationships. *American Journal of Primatology*, *70*, 1–4. doi:10.1002/ajp.20546.

Silk, J. B. (2002a). Using the F-word in primatology. *Behaviour*, *139*, 421–446. doi:10.1163/156853902760102735.

Silk, J. B. (2002b). Kin selection in primate groups. *International Journal of Primatology*, *23*, 849–875. doi:10.1023/A:1015581016205.

Silk, J. B. (2006). Practicing Hamilton's rule: Kin selection in primate groups. In P. M. Kappeler, & C. P. van Schaik (Eds.), *Cooperation in primates and humans: Mechanisms and evolution* (pp. 25–46). Berlin: Springer Press.

Silk, J. B. (2007). The adaptive value of sociality in mammalian groups. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *362*, 539–559. doi:10.1098/rstb.2006.1994.

Snaith, T. V., & Chapman, C. A. (2007). Primate group size and interpreting socioecological models: Do folivores really play by different rules? *Evolutionary Anthropology*, *16*, 94–106. doi:10.1002/evan.20132.

Sterck, E. H. M., & Steenbeek, R. (1997). Female dominance relationships and food competition in the sympatric Thomas langur and long-tailed macaque. *Behaviour*, *134*, 749–774. doi:10.1163/156853997X00052.

Sterck, E. H. M., Watts, D. P., & van Schaik, C. P. (1997). The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology*, *41*, 291–309. doi:10.1007/s002650050390.

Strier, K. B. (1992). Causes and consequences of nonaggression in the woolly spider monkey, or muriqui (*Brachyteles arachnoides*). In J. Silverberg, & J. P. Gray (Eds.), *Aggression and peacefulness in humans and other primates* (pp. 100–116). New York: Oxford University Press.

Struhsaker, T. T. (1997). *Ecology of an African rain forest logging in Kibale and the conflict between conservation and exploitation*. Gainesville: University of Press of South Florida.

Su, H. H., & Birky, W. A. (2007). Within-group female-female agonistic interactions in Taiwanese Macaques (*Macaca cyclopis*). *American Journal of Primatology*, *69*, 199–211. doi:10.1002/ajp.20336.

Sussman, R. W. (1991). Demography and social organization of free-ranging *Lemur catta* in the Beza Mahafaly Reserve, Madagascar. *American Journal of Physical Anthropology*, *84*, 43–58. doi:10.1002/ajpa.1330840105.

Sussman, R. W. (1992). Male life history and intergroup mobility among ringtailed lemurs (*Lemur catta*). *International Journal of Primatology*, *13*, 395–413. doi:10.1007/BF02547825.

Sussman, R. W., & Garber, P. A. (2004). Rethinking sociality: Cooperation and aggression among primates. In R. W. Sussman, & A. R. Chapman (Eds.), *The origins and nature of sociality* (pp. 161–190). New York: Aldine de Gruyter.

Sussman, R. W., Garber, P. A., & Cheverud, J. M. (2005). Importance of cooperation and affiliation in the evolution of primate sociality. *American Journal of Physical Anthropology*, *128*, 84–97. doi:10.1002/ajpa.20196.

Takahata, Y., Koyama, N., Ichino, S., & Miyamoto, N. (2005). Inter- and within-troop competition of female ring-tailed lemurs: A preliminary report. *African Study Monographs*, *26*, 1–14.

Tattersall, I. (1982). *Behavior and ecology. The Primates of Madagascar* pp. 264–325. New York: Columbia University Press.

Taylor, L. L. (1986). *Kinship, Dominance, and Social Organization in a Semi-Free Ranging Group of Ringtailed Lemurs* (Lemur catta). Ph.D. dissertation, Washington University, St. Louis, Missouri.

Taylor, L. L., & Sussman, R. W. (1985). A preliminary study of kinship and social organization in a semi-free ranging group of *Lemur catta*. *International Journal of Primatology*, *6*, 601–614. doi:10.1007/BF02692291.

Terborgh, J. (1983). *Five new world primates: A study in comparative ecology*. Princeton, NJ: Princeton University Press.

Thierry, B. (2007). Unity in diversity: Lessons from macaque societies. *Evolutionary Anthropology*, *16*, 224–238. doi:10.1002/evan.20147.

Thierry, B. (2008). Primate socioecology, the lost dream of ecological determinism. *Evolutionary Anthropology*, *17*, 93–96. doi:10.1002/evan.20168.

Trillmich, J., Fichtel, C., & Kappeler, P. M. (2004). Coordination of group movements in wild Verreaux' sifakas (*Propithecus verreauxi*). *Behaviour*, *141*, 1103–1120 University of Chicago Press, Chicago. doi:10.1163/1568539042664579.

van Roosmalen, M. G. M., & Klein, L. L. (1988). The spider monkey, genus *Ateles*. In R. A. Mittermeier, A. B. Rylands, A. F. Coimbra-Filho, & G. A. B. de Fonseca (Eds.), *Ecology and behavior of neotropical primates*, *Vol. 2* (pp. 455–538). Washington, DC: World Wildlife Fund.

van Schaik, C. P. (1983). Why are diurnal primates living in groups? *Behaviour*, *87*, 120–144. doi:10.1163/156853983X00147.

van Schaik, C. P. (1986). Phenological changes in a Sumatran rain forest. *Journal of Tropical Ecology*, *2*, 237–247.

van Schaik, C. P. (1989). The ecology of social relationships amongst female primates. In V. Standen, & R. A. Foley (Eds.), *Comparative socioecology: The behavioural ecology of humans and other mammals* (pp. 195–218). Oxford: Blackwell.

van Schaik, C. P., & van Hooff, J. A. R. A. M. (1983). On the ultimate causes of primate social systems. *Behaviour*, *85*, 91–117. doi:10.1163/156853983X00057.

van Schaik, C. P., & van Noordwijk, M. A. (1986). The hidden costs of sociality: Intra-group variation in feeding strategies in Sumatran long-tailed macaques (*Macaca fascicularis*). *Behaviour*, *99*, 296–315. doi:10.1163/156853986X00595.

Vasey, N. (1998). *The Social Behavior of Red-Ruffed Lemurs* (Varecia variegata rubra) *in Masoala Peninsula*. Ph.D. dissertation, Washington University, St. Louis, MO.

Vick, L. G., & Pereira, M. E. (1989). Episodic targeting aggression and the histories of *Lemur* social groups. *Behavioral Ecology and Sociobiology*, *25*, 3–12. doi:10.1007/BF00299705.

Watts, D. P. (1985). Relations between group size and composition and feeding competition in mountain gorilla groups. *Animal Behaviour*, *33*, 72–85. doi:10.1016/S0003-3472(85)80121-4.

Wilson, J. M., Stewart, P. D., Famangason, G. S., Denning, A. M., & Hutchings, M. S. (1989). Ecology and conservation of the crowned lemur, *Lemur coronatus*, at Ankarana, Madagascar. *Folia Primatologica*, *52*, 1–26.

Wrangham, R. W. (1980). An ecological model of female-bonded primate groups. *Behaviour*, *75*, 262–300. doi:10.1163/156853980X00447.

Wrangham, R. W. (1987). Evolution of social structure. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker (Eds.), *Primate societies* (pp. 282–296). Chicago: University of Chicago Press.

Wright, P. C. (1995). Demography and life history of free-ranging *Propithecus diadema edwardsi* in Ranomafana National Park, Madagascar. *International Journal of Primatology*, *16*, 835–854. doi:10.1007/BF02735722.

Wright, P. C. (1997). Behavioral and ecological comparisons of neotropical and Malagasy primates. In W. G. Kinzey (Ed.), *New world primates: Ecology, evolution and behavior* (pp. 127–143). New York: Aldine de Gruyter.

Wright, P. C. (1999). Lemur traits and Madagascar ecology: Coping with an island environment. *American Journal of Physical Anthropology*, *42*, 31–72. doi:10.1002/(SICI)1096-8644(1999)110:29+<31::AID-AJPA3>3.0.CO;2-0.

Wright, P. C., Razafindratsita, V. R., Pochron, S. T., & Jernvall, J. (2005). The key to Madagascar frugivores. In J. L. Dew, & J. P. Boubli (Eds.),*Tropical fruits and frugivores: The search for strong interactors* (pp. 121–138). Dordrecht: Springer.