

Environmental and phylogenetic correlates of *Eulemur* behavior and ecology (Primates: Lemuridae)

Kerry Ossi · Jason M. Kamilar

Received: 9 August 2005 / Revised: 27 May 2006 / Accepted: 31 May 2006 / Published online: 9 August 2006
© Springer-Verlag 2006

Abstract The extent of diversity within closely related taxa may be a function of their shared evolutionary history or of selective forces causing adaptive changes. Examining variation among taxa within a single genus may help to identify flexibility in trait variation because recently diverged populations are more likely living in the environment of adaptation. This study examines correlates of diversity in *Eulemur*, a genus that has a wide distribution in a variety of habitat types throughout Madagascar. Previously published data were gathered from 11 long-term studies of *Eulemur* populations. Variables were categorized into multiple datasets: (1) environmental characteristics, (2) social organization, and (3) ecology, which included subsets for ranging behavior, diet, and activity budget. Molecular phylogenies from the literature were used to create the fourth and final dataset, a dissimilarity matrix of evolutionary distance among the 12 species and subspecies. Principal components and cluster analyses were implemented to examine the overall ecological similarity among *Eulemur* populations and to determine which variables contribute most to the variation among taxa. Partial Mantel tests were conducted to test for correlations among the

dataset matrices. The results suggest ecological flexibility for the genus, in particular, populations in similar environments displayed similar activity patterns. In contrast, social organization showed no relationship with environment but was correlated with phylogenetic distance among populations. While *Eulemur* seems to demonstrate some flexibility for ecological adaptations, characteristics related to group size and sex ratio more closely track phylogeny and thus may be less flexible.

Keywords Geographic variation · Intraspecific variation · Biogeography

Introduction

Together, shared evolutionary history and selective forces have contributed to the patterns of extensive behavioral and ecological diversity among animal taxa. A great portion of past research on this variation has typically examined behavior and ecology in relation to habitat or resource distribution (Horn 1968; Clutton-Brock and Harvey 1978; Barton et al. 1996; Koenig et al. 1998), as socioecological theory generally interprets such variation as adaptive, often in response to environmental pressures (Rubenstein and Wrangham 1986; van Schaik 1989; Lott 1991; Sterck et al. 1997; Kappeler 1999). The numerous instances of intraspecific variation across populations as well as individual variation over time demonstrate the significance of considering behavior as inherently flexible (Gould and Johnston 1972; Foster and Endler 1999).

Yet some researchers have lamented the relative neglect of phylogeny and its significance for behavioral variation. Prum (1994) described past efforts to model

Electronic supplementary material Supplementary material is available in the online version of this article at <http://dx.doi.org/10.1007/s00265-006-0236-7> and is accessible to authorized users.

Communicated by C. Nunn

K. Ossi · J. M. Kamilar (✉)
Interdepartmental Doctoral Program in Anthropological Sciences,
Stony Brook University,
Stony Brook, NY 11794-4364, USA
e-mail: Jason.Kamilar@sunysb.edu

K. Ossi
e-mail: kossi@ic.sunysb.edu

social behavioral evolution among vertebrates as “ahistorical”. Behavioral traits typically had been regarded as more plastic and less likely to display a phylogenetic signal (e.g., Blomberg et al. 2003; Wilson 1975; Atz 1970); however, de Queiroz and Wimberger (1993) found that a dataset of behavioral traits exhibited no real difference from a morphological dataset in degree of homoplasy. Blomberg and Garland (2002) define “phylogenetic signal” as occurring when closely related species tend to display similar traits more than by chance. Possible mechanisms that may lead to a phylogenetic signal include biological constraint limiting trait variation or stabilizing selection maintaining a trait over time.

In studies of primate behavior and ecology, there has been less effort to investigate patterns of phylogeny (Lockwood and Fleagle 1999). Traditionally, researchers attempted to answer questions regarding the possible adaptation of traits by using “natural experiments” (Brooks and McLennan 1991). This would generally entail one of two scenarios: either studying closely related taxa under different environmental conditions or examining distantly related species in similar habitats. In the first situation, any observed differences among taxa were thought to be the result of selective forces, while in the second, any similarities among taxa were believed to be convergent adaptations due to natural selection and not evolutionary relatedness.

The past decade or so has seen a growing number of studies attempting to integrate the evolutionary history of taxa by using techniques from phylogenetic systematics to investigate primate behavioral variation (e.g., Di Fiore and Rendall 1994; methods reviewed in Nunn and Barton 2001). These studies have often employed broad, cross-species or cross-genera comparisons, but more recent research has incorporated phylogenetic approaches when examining narrow evolutionary units (Thierry et al. 2000; Doran et al. 2002; Korstjens et al. 2002). An approach that focuses on taxa within a genus or species to examine the factors contributing to ecological and behavioral diversity should provide a clearer picture because subjects would have relatively recent divergence times with possible opportunities for continuing gene flow (i.e., subspecies). Therefore, variation among populations is not likely attributable to evolutionary history but rather to selection pressures of the near-present-day environment. With the increasing availability of genetic data for many primate populations, it is becoming more feasible to tease apart these factors and their relative contributions toward the behavior and ecology of primates.

The genus *Eulemur*, a member of the lemurid family from Madagascar, provides a particularly appropriate study group for investigating the relationship of behavior with both environmental selective forces and evolutionary

relatedness. Over the past decade, *Eulemur* species have been the focus of a number of long-term field studies providing reliable data across seasons for multiple populations (Colquhoun 1993, 1997; Overdorff 1993; Freed 1996; Curtis 1997; Donati, unpublished data; Vasey 1997; Rasmussen 1999; Gerson 2000; Ostner 2002). These studies have revealed a relatively high degree of variability in certain traits. Generally, *Eulemur* diets tend to be more frugivorous, yet high levels of folivory have been noted in some western populations including *Eulemur fulvus rufus* (Sussman 1977; Gerson 2000).

In addition to the documented dietary diversity within the genus, there is variation in social organization as well. Two general patterns of social organization exist: small pair-bonded groups (*Eulemur mongoz* and *Eulemur rubriventer*) and larger multimale, multifemale social groups (*E. fulvus*, *Eulemur macaco*, and *Eulemur coronatus*). These two forms of social organization display associated differences in their group cohesion as well as other characteristics, although a number of these social organization traits have not been systematically quantified for many populations. Perhaps the most interesting aspect of *Eulemur* behavioral variation concerns their activity patterns. All *Eulemur* populations exhibit cathemeral activity patterns (i.e., active day and night), yet the degree of cathemerality is variable among taxa (Curtis and Rasmussen 2002). The amount of nocturnal activity varies to some extent with habitat type and possibly diet (Engqvist and Richard 1991), while other researchers have tested for potential correlations with ambient light temperatures, day length, and seasonal changes (food availability and diet: Andrews and Birkinshaw 1998; Colquhoun 1998; Curtis et al. 1999; Donati et al. 2001; Kappeler and Erkert 2003). Measures of cathemerality, however, have not been standardized quantitatively across studies, leaving interpopulation comparisons somewhat problematic.

All wild *Eulemur* populations are found on the island of Madagascar, a setting characterized by extensive environmental and climatic variability. Both an east–west divide and a north–south gradient in the island’s environment have been described (Tattersall and Sussman 1975; Ganzhorn et al. 1999). In general, the east has more high-elevation humid forests with an eastern coastal belt that is rainy year-round (Jury 2003), while the west has lower elevation dry forests (Du Puy and Moat 2003; Yoder and Heckman 2006). From north to south, Madagascar’s forests become drier, particularly on the western coast. Yet, despite this high degree of habitat diversity, *Eulemur* species can be found in almost every forested area in the country (Tattersall and Sussman 1998). Two radiations are likely to have taken place, one at the species level and the second in the form of multiple *E. fulvus* subspecies (Tattersall and Sussman 1998). One species in particular, *E. fulvus*, has the

widest distribution of any diurnal or cathemeral lemur. Thus, because members of the genus seem to demonstrate ability for populating diverse or variable habitats, they make ideal subjects for the aims of this study.

In addition to behavioral ecology studies, molecular data are available from many of these taxa and have been used to construct phylogenies (Pastorini et al. 2002; Wyner et al. 2000; Yoder and Irwin 1999). As a whole, the monophyletic group (Tattersall and Schwartz 1991) consists of five species: *E. macaco*, *E. mongoz*, *E. coronatus*, *E. rubriventer*, and *E. fulvus*. The first four species roughly ring the island's perimeter and are allopatric, but each one is often sympatric with one or more subspecies of *E. fulvus* (Overdorff and Johnson 2003). Several researchers explicitly examined intrasite ecological variation and evidence of niche separation among sympatric species (Overdorff 1991; Freed 1996; Vasey 1997). Overall, differences between *Eulemur* species at the same site often appear only at a fine-grained level, for example, vertical space use, seasonal shifts in diet or activity cycle, or feeding on different parts of the same plant species (Sussman 2002; Overdorff and Johnson 2003).

This study aims to examine the relative importance of environmental characteristics and evolutionary relatedness in 12 populations of *Eulemur* from eight sites across Madagascar. If environmental characteristics play a greater role in shaping aspects of *Eulemur* socioecology, then there should be a positive correlation between the environmental similarity of sites and the behavioral and ecological traits displayed by populations at those sites while controlling for their evolutionary relatedness. Alternatively, if phylogenetic history is an important predictor of *Eulemur* variation, then there should be a positive correlation between the phylogenetic distance among populations and their socioecological traits while controlling for the environmental similarity of sites.

Materials and methods

Data collection

Data were gathered from the published literature for 12 different *Eulemur* populations covering sites across the range of Madagascar (Table 1, Fig. 1). Studies were included in the analyses if data were collected for at least 8 months in duration to account for possible seasonal effects. Two of the 12 studies were 8 to 10 months in duration, and all others were a year or more. Of the yearlong studies, two were missing subsets of data for the full year. For *E. fulvus rufus* at Kirindy, data on dietary percentages were available for only 4 months and were included for analysis after a long-term researcher at the site confirmed that the general proportions were consistent year

round (Ostner, personal communication). For the second, activity budget data for *Eulemur fulvus collaris* at St. Luce were available for only 2 months and were not included in any of our analyses. For both of these populations, all other variables and data subsets were available for a complete annual cycle. Other study sites and/or data were considered for inclusion but were not used if the total dataset was too short in duration (e.g., *Eulemur fulvus albocollaris*: Johnson 2002, Vevembe data range from 2 to 6 months in duration). Overall, the study included at least one population from each of the five species of *Eulemur*. Multiple populations were included for two species: two populations of *E. mongoz* and seven populations of *E. fulvus*. Four *E. fulvus* populations are found at sites where they are sympatric with other *Eulemur* species.

Data organization

Twenty variables were categorized into one of three datasets: ENVIRONMENT, SOCIAL ORGANIZATION, and ECOLOGY, the last of which includes three data subsets (see S1). In addition, the evolutionary relationships among populations were included in a PHYLOGENY dataset. The ENVIRONMENT variables included (a) mean annual rainfall (millimeters), (b) number of dry months (<50 mm), (c) altitude (meters), (d) mean minimum annual temperature, (e) mean maximum annual temperature, (f) mean temperature range, and (g) number of sympatric primate species. Together, these variables serve to characterize the environmental context that *Eulemur* may experience at a particular locale. The first six variables affect the diversity, abundance, and availability of food and water resources (Rosenzweig 1968; Bronikowski and Altmann

Table 1 *Eulemur* populations and study sites included in the analyses

Site	Taxon	Reference
Ampijoroa	<i>E. mongoz</i> , <i>E. fulvus fulvus</i>	1
Ambato Massif	<i>E. macaco</i>	2
Andranobe	<i>E. fulvus albifrons</i>	3, 4
Anjamena	<i>E. mongoz</i> , <i>E. fulvus rufus</i>	5, 6
Kirindy	<i>E. fulvus rufus</i>	7, 8
Mt. d'Ambre	<i>E. coronatus</i> , <i>E. fulvus sanfordi</i>	9
Ranomafana	<i>E. fulvus rufus</i> , <i>E. rubriventer</i>	10, 11, 12
St. Luce	<i>E. fulvus collaris</i>	13

1 Rasmussen 1999, 2 Colquhoun 1997, 3 Vasey 1997, 4 Vasey 2000, 5 Curtis 1997, 6 Gerson 2000, 7 Ostner 2002, 8 Donati et al. 1999, 9 Freed 1996, 10 Overdorff 1991, 11 Overdorff 1996, 12 Overdorff and Ehart (unpublished data), 13 Donati (unpublished data). Donati's diet data were collected over a 4-month period, which were the most comprehensive data available. An independent researcher (Julia Ostner) studying *Eulemur fulvus rufus* at Kirindy for more than a year corroborated the high degree of frugivory throughout that time in the population. Additionally, data support the year-round availability of fruit at Kirindy (Ganzhorn et al. 1999).

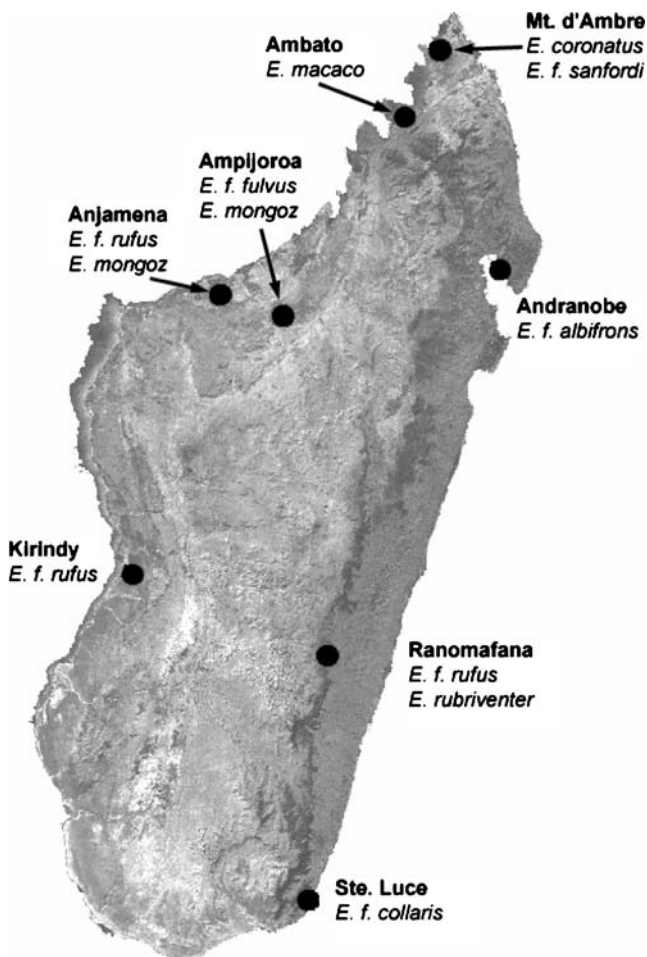


Fig. 1 Map of Madagascar showing the sites and *Eulemur* populations included in the study

1996; Chapman and Chapman 1999). The number of sympatric primates serves to estimate overall habitat quality (Cowlshaw and Hacker 1997) and/or interspecific competition (Struhsaker 1978). In Madagascar, lemur species richness has been shown to positively correlate with characteristics such as increasing rainfall, tree-size diversity, and tree species richness (Ganzhorn et al. 1997). Although the number of sympatric species is sometimes considered an ecological factor, our ECOLOGY dataset, discussed below, is comprised of ecological behaviors specific to each population. We include the number of sympatric species here with the assumption that it is another characteristic of the environment that may influence *Eulemur* behavior.

For behavioral traits, there are two datasets: SOCIAL ORGANIZATION (from here on referred to as SOC ORG) and ECOLOGY. SOC ORG consists of (a) mean group size, (b) mean number of females per group, (c) mean number of males per group, and (d) the mean adult sex ratio. Additional social variables such as group cohesion, mating system, and territoriality were considered for

analysis yet omitted from the study because comparable cross-study data were lacking. For ECOLOGY, the variables were further divided into three subsets: (1) RANGING consists of (a) home-range size (hectares), (b) daily path length (meters), and (c) defensibility index as a measure of territoriality (Mitani and Rodman 1979); (2) DIET includes (a) fruit (%), (b) leaves (%), and (c) flowers (%); and (3) ACTIVITY BUDGET is composed of (a) feed (%), (b) travel (%), and (c) rest (%). Percentages of time spent in social activities were considered but again not included for analysis because these data were not available for all populations. Variables such as vertical space use and those related to seasonal fluctuations including variation in patterns of cathemerality also had to be excluded because of difficulty determining comparable measures across studies.

The final dataset, PHYLOGENY, was constructed as a relative phylogenetic distance matrix based on the molecular phylogenies of Pastorini et al. (2002 from their Fig. 3b) and Pastorini et al. (2000) (Fig. 2 and S2). These phylogenetic hypotheses were chosen since they sampled individuals from the sites used in our study or nearby areas.

To examine the sensitivity of our results in the context of this phylogenetic hypothesis, we also used phylogenies from Yoder and Irwin (1999 from their Fig. 3b) and Wyner et al. (2000 from their Fig. 2). However, both of these studies lacked data for several populations included in our analyses. In these cases, Pastorini's data were used for the missing populations. Consequently, the combined Pastorini + Wyner et al. cladogram was the same as Pastorini except that the *E. mongoz* clade was swapped with the clade containing *E. coronatus* + *E. macaco* (see S3a). Similarly, the combined Pastorini + Yoder and Irwin tree was identical to Pastorini's tree except that the *E. mongoz* clade was swapped with *E. rubriventer* (see S3b).

The relative phylogenetic distance between taxa was defined by the node depth (i.e., relative node age) between taxa (Barraclough and Vogler 2000). This technique was employed since the phylogenies were constructed from more than one study, which did not report comparable phylogenetic data.

Data analysis

Several multivariate methods were used to examine the variation in the datasets and test the relationships among them. First, we examined the overall similarity among the populations by performing hierarchical cluster analyses using the unweighted pair group method with arithmetic mean for the ENVIRONMENT, ECOLOGY, and SOC ORG datasets (McGarigal et al. 2000). All variables were standardized using z-scores (Sokal and Rohlf 1995). The cluster analyses were based on squared Euclidian distance matrices.

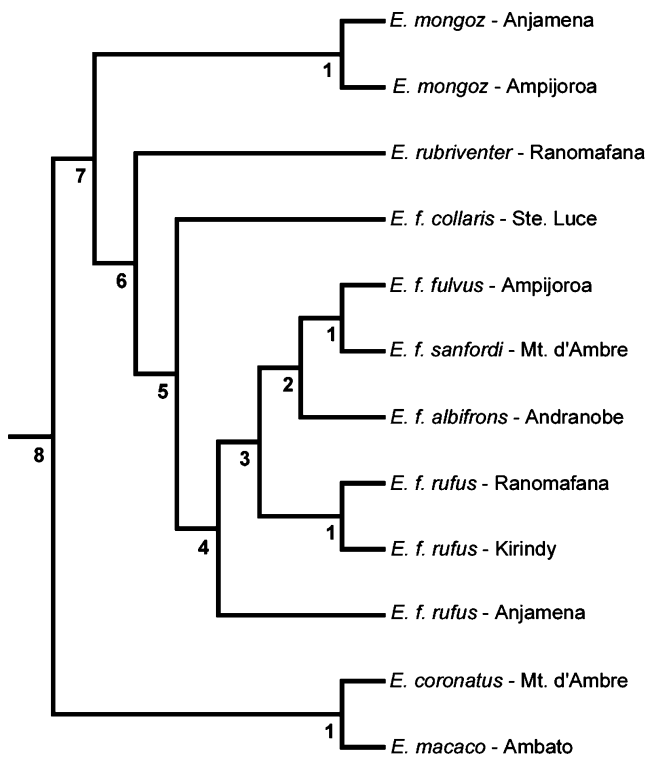


Fig. 2 A combined phylogenetic tree based on cladograms from Pastorini et al. (2000, 2002). The node depth (i.e., relative node age) is indicated next to each node of the tree. Node depth was used as a relative measure of the phylogenetic relatedness between taxa. For example, the relative phylogenetic distance between *E. fulvus rufus* at Kirindy and *E. fulvus rufus* at Ranomafana is 1. The relative phylogenetic distance between *E. fulvus rufus* at Kirindy and *E. rubriventer* at Ranomafana is 6

The potential relationships between the ENVIRONMENT and PHYLOGENY matrices to the ECOLOGY and SOC ORG matrices were tested using partial Mantel tests (Mantel 1967; Smouse et al. 1986). This method uses a randomization approach to conduct pairwise comparisons between the elements of two distance matrices while holding a third distance matrix constant. In this case, the independent matrix was ENVIRONMENT (and each individual variable) and the dependent matrix was either SOC ORG or ECOLOGY (or one of its subsets) while controlling for PHYLOGENY. For each non-PHYLOGENY dataset, all variables were transformed into z-scores (Sokal and Rohlf 1995). Subsequently, a squared Euclidian distance matrix was created for each variable, and a multivariate squared Euclidian distance matrix was created for each dataset. To examine the relative effects of evolutionary relatedness, partial Mantel tests were also conducted with PHYLOGENY as the predictor matrix while controlling for ENVIRONMENT. Ten thousand randomizations were performed for each test to determine statistical significance. Following previous authors (Ortolani and Caro 1996; Nakagawa 2004), we set alpha to 0.05 for the Mantel tests. All tests were one-tailed.

A principal components analysis (PCA) was also performed, combining all 20 variables from the ENVIRONMENT, SOC ORG, and ECOLOGY datasets to examine which variables explain the majority of the variation in the datasets and how the variables relate to each other (Tabachnick and Fidell 1989). Twenty components were extracted to account for all of the variation in the original data (Rohlf, personal communication). Principal components that exhibited eigenvalues greater than 1 were deemed important (Tabachnick and Fidell 1989). The cluster analyses and principal components analyses were conducted with SPSS version 12.0 for Windows. The partial Mantel tests were conducted with the PASSAGE (Rosenberg 2001) and Permute! (methods described in Legendre et al. 1994) software packages.

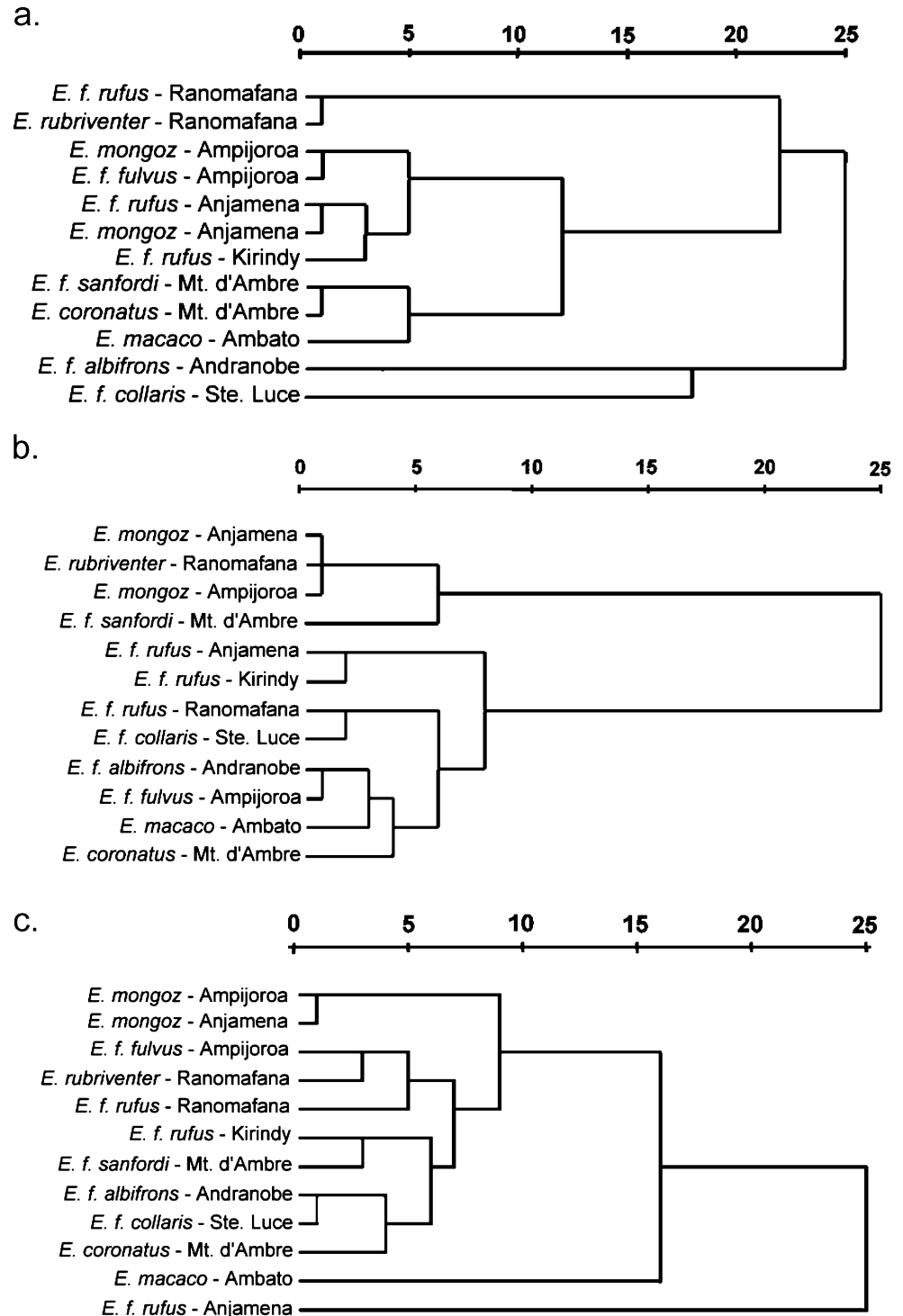
Results

The analyses using the three different phylogenetic hypotheses produced similar findings; consequently, only the results from the Pastorini phylogeny will be reported. The results showed that both phylogenetic relatedness and environmental characteristics are correlated with the social and ecological variation of *Eulemur* taxa but for different sets of traits. The cluster analysis using the ENVIRONMENT dataset yielded expected results, with taxa from the same sites grouping together as shown in Fig. 3a. The dendrogram for the SOC ORG cluster analysis gives little fine-scale resolution, but all except one *E. fulvus* subspecies cluster broadly together separate from *E. mongoz* and *E. rubriventer* (Fig. 3b). The ECOLOGY cluster analysis resulted in a dendrogram with no clear pattern in support of a correlation with either phylogeny or environment (Fig. 3c).

Based on Mantel tests, neither ENVIRONMENT nor PHYLOGENY significantly correlated with the combined ECOLOGY dataset (Table 2). Yet when the ECOLOGY subsets were analyzed individually, the partial Mantel tests yielded a significant relationship between ENVIRONMENT and ACTIVITY BUDGET similarity while holding PHYLOGENY constant (Mantel $r=0.32$, $p=0.03$). Partial Mantel tests between the individual variables of the ENVIRONMENT dataset and ACTIVITY BUDGET revealed that populations living in sites with a similar number of dry months (Mantel $r=0.37$, $p<0.01$), similar altitude (Mantel $r=0.25$, $p=0.04$), and maximum temperature (Mantel $r=0.32$, $p=0.03$) displayed a similar activity budget. Finally, there was no significant relationship between ENVIRONMENT and DIET (Mantel $r=-0.17$, $p=0.84$) or RANGING (Mantel $r=-0.11$, $p=0.78$).

There was no relationship between PHYLOGENY and ACTIVITY BUDGET when controlling for ENVIRONMENT (Table 2). In contrast, the SOC ORG dataset

Fig. 3 Dendrograms of the cluster analyses using the **a** ENVIRONMENT, **b** SOC ORG, and **c** ECOLOGY datasets. The units indicate rescaled squared Euclidian distances



demonstrated no significant association with the ENVIRONMENT matrix. However, the partial Mantel test yielded a significant correlation between PHYLOGENY and SOC ORG (Mantel $r=0.28$, $p=0.04$) when controlling for ENVIRONMENT. Therefore, populations that were more closely related exhibited greater similarity in social organization characteristics.

The results of the PCA combining ENVIRONMENT, ECOLOGY, and SOC ORG better pinpoint which key variables explain the most variation among *Eulemur* taxa and suggest a relationship between some of the individual variables (Table 3). The first two components account for slightly more than 50% of the overall variation in the datasets (Table 3). The variables correlated with the first

Table 2 Partial Mantel test correlation coefficients^a examining the relationship between environmental and phylogenetic effects and *Eulemur* behavior and ecology

	ECOLOGY ^b	Activity budget	Diet	Ranging	SOCIAL ORGANIZATION
ENVIRONMENT	-0.06	0.32	-0.17	-0.11	-0.11
Rain	-0.06	-0.04	-0.14	-0.08	-0.07
Dry months	0.03	0.37	-0.10	-0.11	-0.06
Altitude	-0.07	0.25	-0.07	-0.14	0.01
Sym primates	-0.08	0.10	-0.15	-0.08	-0.02
Min temp	-0.06	0.10	-0.20	-0.02	-0.10
Max temp	0.08	0.32	0.07	-0.03	0.07
Temp range	0.00	0.06	0.03	0.06	-0.18
PHYLOGENY	0.08	0.05	-0.16	0.14	0.32

Bold text indicates $p \leq 0.05$; all tests are one-tailed

Rain Mean annual rainfall per year, *Dry months* mean number of months per year that have <50 mm of rain, *Altitude* mean altitude of study site, *Sym primates* the number of sympatric primates at the study site, *Min temp* mean minimum monthly temperature, *Max temp* mean maximum monthly temperature, *Temp range* difference between the mean minimum and maximum monthly temperatures

^aThe Mantel test correlation coefficient is comparable to a Pearson's correlation coefficient, yet it usually produces lower values for the equivalent p value (Legendre 2000).

^bThe ECOLOGY dataset is comprised of all variables found in Activity budget, Diet, and Ranging.

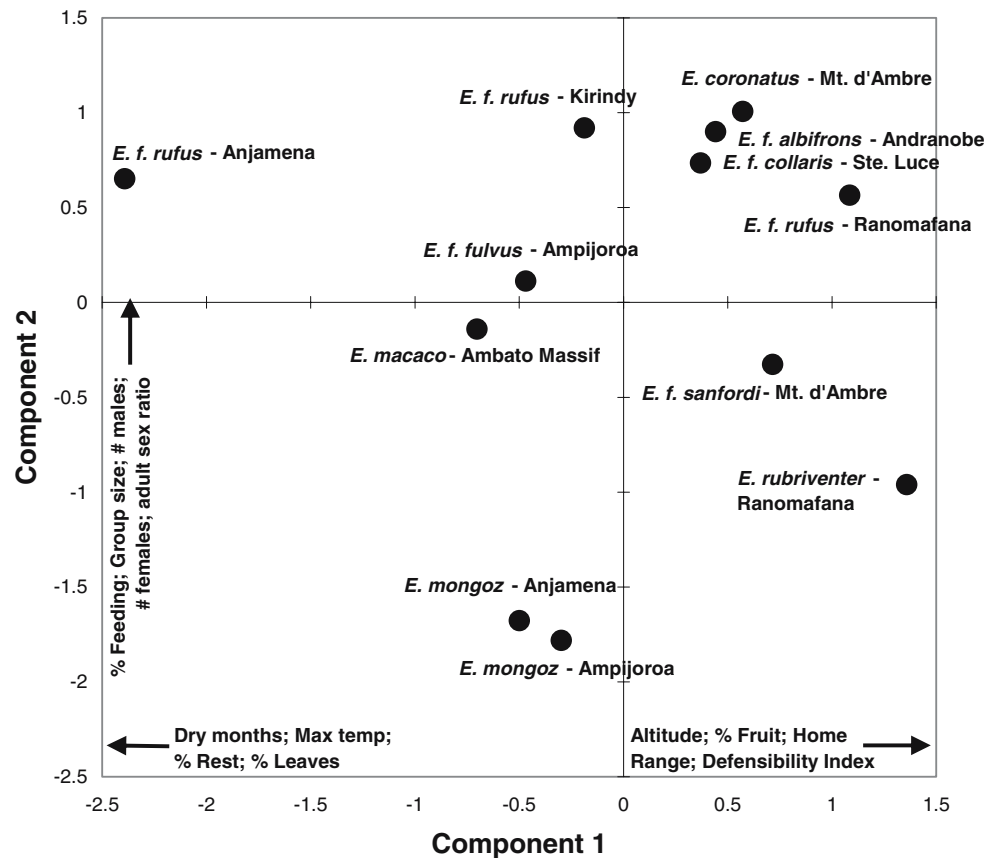
component indicate that populations found in habitats with few dry months and low maximum temperatures spend less time resting and eat a low proportion of leaves. These variables were negatively correlated with greater frugivory, larger home ranges, and a higher defensibility index for sites with a higher altitude. The second component was correlated most strongly with several variables from the SOC ORG dataset, including mean group size and number of males per

group. In addition, these variables were positively correlated with time spent feeding (Fig. 4). It is interesting to note that the distribution of populations along the y -axis of the PCA reflects the relationship between evolutionary relatedness and social organization characteristics. All but one of the *E. fulvus* populations group in the upper quadrants of the PCA plot, whereas all remaining populations except for *E. coronatus* are found in the lower quadrants.

Table 3 Factor loadings for the first five principal components

Component	1	2	3	4	5
Eigenvalue	5.90	4.18	2.88	2.65	2.12
Variance (%)	29.48	20.90	14.41	13.26	10.59
Cumulative variance	29.48	50.38	64.79	78.05	88.64
Variable					
Annual rainfall (mm)	0.389	0.252	0.275	-0.381	0.623
Altitude (m)	0.720	0.003	-0.458	-0.271	-0.224
# Sympatric primates	0.475	-0.131	-0.772	0.086	-0.136
Dry months	-0.634	-0.326	0.008	0.228	-0.636
Min temp	-0.597	-0.101	0.544	-0.354	-0.287
Max temp	-0.709	0.039	0.341	0.508	0.295
Temp range	-0.312	0.110	-0.029	0.767	0.501
Feed (%)	0.510	0.704	0.197	0.263	0.018
Move (%)	0.594	0.174	-0.382	-0.182	0.587
Rest (%)	-0.683	-0.568	-0.140	0.156	0.164
Fruit (%)	0.682	0.200	0.275	0.279	-0.447
Leaves (%)	-0.682	-0.143	-0.587	-0.251	0.201
Floral (%)	0.131	-0.223	0.751	-0.075	0.375
Mean group size	-0.446	0.834	0.033	-0.250	-0.091
Males/group	-0.243	0.929	-0.139	-0.077	-0.087
Females/group	-0.220	0.889	0.253	-0.188	-0.192
Adult sex ratio	-0.384	0.770	-0.331	0.359	-0.005
Home range (ha)	0.756	-0.201	0.407	-0.055	-0.097
Daily path length (m)	0.263	0.111	-0.100	0.803	-0.024
Defensibility index	0.722	-0.120	0.173	0.500	-0.145

Fig. 4 Biplot of the first two components of the principal components analysis for *Eulemur* sites using all datasets. Variables that loaded on the axis at an absolute value of 0.6 or higher were emphasized



Discussion

This study examined whether environmental or evolutionary factors best predicted the behavioral and ecological variation among closely related taxa. Our findings suggest evidence for both depending on the set of traits in question. First, the data show that *Eulemur* activity budgets are more alike in similar environments but not in more closely related taxa. It is interesting to note that behaviors characterizing *Eulemur* social organization demonstrated no such environmental relationship. Instead, *Eulemur* taxa that were more closely related demonstrated similar social organization characteristics while controlling for environmental conditions.

Environmental influences

For *Eulemur* taxa, activity budget was the only ecological component to significantly correlate with environmental variation. This suggests that some degree of behavioral flexibility allows for a response to different environmental conditions. In particular, results highlight a positive relationship between the number of dry months and the proportion of time spent resting. If more dry months are an indication of stronger seasonal differences at a site, this finding suggests that *Eulemur* taxa may have managed to

inhabit drier, more seasonal habitats by adopting an energy conservation strategy. That is, in less productive environments, these species adjust by becoming less active.

Unexpectedly, measures of diet and environmental factors did not have a significant relationship, at least while controlling for evolutionary relatedness. However, the PCA results indicate dietary differences between populations in drier vs wetter habitats (Fig. 4). The proportion of leaves eaten correlated with the number of dry months and maximum temperature. Relying more heavily on leaves as a fallback may be a response to living in more seasonal forests, which may help explain why these populations also tend to be energy conservers.

Similar adaptive strategies have been observed for other taxa, in which the proportion of resting time increased in response to lower quality habitat or seasonal shortages of food resources (*Colobus polykomos*: Dasilva 1992; *Macaca sylvanus*: Menon and Poirier 1996; but see *Trachypithecus leucocephalus*: Li and Rogers 2004). A recent study by Curtis (2004) showed that seasonal changes in feeding behavior for *E. mongoz* at Anjamena might support an energy conservation strategy during the dry season. However, nutritional analyses instead demonstrated that actual nutrient intake did not change across seasons, and, via their dietary shift, *E. mongoz* appeared to compensate fully for nutrient requirements (Curtis 2004).

In our findings, altitude also showed an association with activity budget. Givnish (1999) reported that there tends to be a relationship between primate diversity and altitude, which is probably tied to the correlation of plant diversity and abundance with altitude. This broad-scale relationship suggests that habitat quality should change along an altitudinal gradient, and seemingly *Eulemur* activity budget may have varied likewise. Further support comes from the PCA results, which indicate that higher altitude sites are correlated with a greater proportion of fruit eating and negatively correlated with time spent resting. Thus, higher altitude in this study may simply be representing greater fruit abundance or even better quality habitat. Lower elevations in Madagascar tend to lack large tracts of humid forests (Goodman and Ganzhorn 2004); therefore, lower altitude sites may have lower fruit availability simply because there is less forested area.

The final environmental variable to correlate with activity budget was maximum temperature. This relationship may indicate that high temperatures have selected for thermoregulatory strategies (Curtis et al. 1999), such that animals shift activity periods to avoid heat stress. In this case, populations coping with higher maximum temperatures also spent more time resting. In turn, it is possible that these same populations might compensate for resting during peak temperatures by increasing their nocturnal activity.

As the previous description suggests, the environmental association with activity budget is likely capturing aspects of the timing of *Eulemur* activity. *Eulemur* taxa have been traditionally classified as cathemeral. Recent reviews, however, have demonstrated that a single cathemeral label does not represent the full range of diversity of *Eulemur* activity patterns. Overdorff and Johnson (2003) and Curtis and Rasmussen (2002) suggest that activity patterns show systematic variation according to environmental differences among sites. These patterns range from year-round 24-h activity to complete seasonal shifts between diurnal and nocturnal activities (e.g., *E. macaco macaco*, Colquhoun 1997; *E. mongoz*, Curtis et al. 1999; reviewed in Curtis and Rasmussen 2002).

Most studies included in this work collected the majority of data during daytime observations. As a result, variation in activity budgets may be reflecting differences in activity patterns. If populations that tend to rest more during the day are simply being more active at night, then this would point to explanations other than strict energy conservation. Yet differences in activity rhythms across populations will have other direct repercussions for the overall activity budget. For example, a population may spend more or less overall time feeding depending on the proportion of time spent feeding at night, which affects foraging efficiency via changes in search time, predation risk, or level of

competitive interference. In addition to potential thermoregulatory benefits, Curtis et al. (1999) suggest that the ability to shift to nocturnal activity during dry months may be a behavioral adaptation for reducing interspecific competition at a time of resource shortfall.

The connection between environmental conditions and the type of cathemeral pattern exhibited by *Eulemur* populations may provide evidence supporting Wright's energy frugality hypothesis, in which these taxa are maximizing the use of scarce resources by adapting cathemeral activity patterns (Wright 1999). Alternatively, the evolutionary disequilibrium hypothesis (van Schaik and Kappeler 1996) proposed that this and other lemur characteristics are not necessarily stable adaptations but are instead a consequence of relatively recent, large ecological changes in Madagascar, such as extinction events that opened up this new diurnal niche space to a formerly nocturnal ancestor. Even so, the fact that patterns of cathemerality across *Eulemur* taxa at present tend to vary according to environment seems to offer less support for assumptions of evolutionary disequilibrium.

Phylogenetic signal in social organization

As opposed to activity budget, environmental characteristics had no relationship with the social organization of *Eulemur* populations. Instead, populations that were more closely related displayed more similar social organization traits, independently of environmental characteristics. This connection between phylogeny and social organization also has been seen on a broader scale in cercopithecoid primates. A taxonomically focused study on savanna baboons found little group size and composition differences among subspecies even though they are found in diverse habitats (Kamilar 2006). Di Fiore and Rendall (1994) showed that cercopithecoid monkeys exhibited relatively similar social organizations and behaviors despite living in a wide variety of habitats. In addition, Thierry et al. (2000) conducted a cladistic analysis of several macaque species, demonstrating that many of their social organization characteristics are phylogenetically conserved.

The connection between evolutionary relatedness and social organization similarity is not limited to primates. In a review of equid socioecology, Linklater (2000) showed that wild-horse species displayed a remarkably uniform social and spatial organization despite living under diverse environmental and demographic contexts. Similarly, a phylogenetic analysis of several Neotropical passerine birds found a strong phylogenetic signal in lekking behavior and stated that adaptive plasticity models were insufficient in explaining the existing behavioral variation (Prum 1994). Finally, broad-scale cladistic analyses examining the rela-

tive degree of homoplasy in behavioral traits for several mammalian clades have shown that many behaviors related to mating display a relatively strong phylogenetic signal (de Queiroz and Wimberger 1993) compared to other aspects of behavior and ecology (Proctor 1996). Although Blomberg and Garland (2002) caution against using phylogenetic signal as evidence against adaptation by selection, our analyses controlled for environmental traits, which strengthens the conclusion that the environmental characteristics investigated in this study have not been a strong selective force on *Eulemur* social organization.

However, conserved behavior could be explained via nonenvironmental pressures. Such pressures may be shaping *Eulemur* social organization if, for example, risks such as infanticide change with group composition. Ostner and Kappeler (1999) suggested that the relatively high number of males in groups of red-fronted lemurs (*E. fulvus rufus*) provides reproductive benefits for both sexes by lowering the probability of takeover by extratroup males and, in turn, the risk of infanticide. Thus, because male and female interests overlap in this case, selective forces may have helped to stabilize features of group composition, such as even sex ratios, over evolutionary time (see PCA axis 2, Fig. 4).

It is interesting to note that Vasey (2000) suggested that populations of *Varecia variegata* display the reverse pattern. She found that ecological traits remained highly consistent across *Varecia* populations while social organization showed great variability. The contrast between the patterns of variability in *Eulemur* and *Varecia* ecology and social organization suggests that the behavior of even closely related lemurid taxa may be differentially dependent on environmental and phylogenetic factors. Furthermore, this difference may have implications for evolutionary dispersal patterns in light of *Varecia*'s restricted distribution relative to the extensive geographic range of *Eulemur*. Future analyses using only *E. fulvus* populations could verify whether this contrast with *Varecia* holds up or whether it results from conducting analyses at different taxonomic levels.

In conclusion, our study lends support to past claims that *Eulemur*'s ecological diversity may be responsible for its widespread presence throughout Madagascar. The potential for flexibility in activity patterns may have allowed for behavioral adaptations, facilitating dispersal into regions with different environmental conditions. The contrasting results for *Eulemur* social organization emphasize the importance of considering the possible role of evolutionary history in behavioral variation.

Acknowledgements We would like to sincerely thank Julia Ostner, Andreas Koenig, Carola Borries, John Fleagle, Charlie Janson, Pat Wright, Steig Johnson, William Jungers, and Wendy Erb for their

insightful discussion and advice. We are grateful to Deborah Curtis, Giuseppe Donati, Ben Freed, Jayne Gerson, Julia Ostner, Deborah Overdorff, Michelle Rasmussen, and Natalie Vasey for their generous help, providing additional data from their study populations, and to Jennifer Pastorini for her assistance with the molecular data. Julia Ostner, Andreas Koenig, John Fleagle, and Carola Borries provided constructive comments on an earlier version of this manuscript. Also, we would like to thank Charles Nunn and two anonymous reviewers for their very helpful comments that strengthened this manuscript. JMK was supported by an NSF Dissertation Improvement grant (BCS-0452814) while conducting this research.

References

- Andrews J, Birkinshaw C (1998) A comparison between the daytime and night-time diet, activity and feeding height of the black lemur, *Eulemur macaco* (Primates: Lemnidae), in Lokobe Forest, Madagascar. *Folia Primatol* 69:175–182
- Atz JW (1970) The application of the idea of homology to behavior. In: Aronson LR, Tolbach E, Lehrman DS, Rosenblatt JS (eds) Development and evolution of behavior. Freeman, San Francisco, pp 53–74
- Barracough T, Vogler A (2000) Detecting the geographical pattern of speciation from species-level phylogenies. *Am Nat* 155:419–434
- Barton RA, Byrne RW, Whiten A (1996) Ecology, feeding competition and social structure in baboons. *Behav Ecol Sociobiol* 38:321–329
- Blomberg SP, Garland T (2002) Tempo and mode in evolution: phylogenetic inertia, adaptation and comparative methods. *J Evol Biol* 15:899–910
- Blomberg SP, Garland T, Ives A (2003) Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* 57:717–745
- Bronikowski AM, Altmann J (1996) Foraging in a variable environment: weather patterns and the behavioral ecology of baboons. *Behav Ecol Sociobiol* 39:11–25
- Brooks DR, McLennan DA (1991) Phylogeny, ecology, and behavior. University of Chicago Press, Chicago
- Chapman CA, Chapman LJ (1999) Implications of small scale variation in ecological conditions for the diet and density of red colobus monkeys. *Primates* 40:215–231
- Clutton-Brock TH, Harvey PH (1978) Mammals, resources and reproductive strategies. *Nature* 273:191–195
- Colquhoun I (1993) The socioecology of *Eulemur macaco*: a preliminary report. In: Kappeler P, Ganzhorn J (eds) Lemur social systems and their ecological basis. Plenum, New York, pp 11–23
- Colquhoun I (1997) A predictive socioecological study of the black lemur (*Eulemur macaco macaco*) in northwestern Madagascar. Ph.D. Thesis, Washington University, St. Louis
- Colquhoun I (1998) Cathemeral behavior of *Eulemur macaco macaco* at Ambato Massif, Madagascar. *Folia Primatol* 69:22–34
- Cowlishaw G, Hacker J (1997) Distribution, diversity, and latitude in African primates. *Am Nat* 150:505–512
- Curtis DJ (1997) The mongoose lemur (*Eulemur mongoz*): a study in behaviour and ecology. Ph.D. Thesis, University of Zurich, Zurich
- Curtis DJ (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. *Am J Phys Anthropol* 124:234–247
- Curtis DJ, Rasmussen M (2002) Cathemerality in lemurs. *Evol Anthropol* 11:83–86

- Curtis DJ, Zaramody A, Martin RD (1999) Cathemerality in the mongoose lemur, *Eulemur mongoz*. *Am J Primatol* 47:279–298
- Dasilva GL (1992) The western black-and-white colobus as a low-energy strategist: activity budgets, energy expenditure and energy intake. *J Anim Ecol* 61:79–91
- de Queiroz A, Wimberger PH (1993) The usefulness of behavior for phylogeny estimation: levels of homoplasy in behavioral and morphological characters. *Evolution* 47:46–60
- Di Fiore A, Rendall D (1994) Evolution of social organization: a reappraisal for primates by using phylogenetic methods. *Proc Natl Acad Sci U S A* 91:9941–9945
- Donati G, Lunardini A, Kappeler PM (1999) Cathemeral activity of red-fronted brown lemurs (*Eulemur fulvus rufus*) in the Kirindy Forest/CFPP. In: Rakotosamimanana B, Rasamimanana H, Ganzhorn JU, Goodman SM (eds) *New directions in lemur studies*. Kluwer/Plenum, New York, pp 119–137
- Donati G, Lunardini A, Kappeler P, Borgognini Tarli S (2001) Nocturnal activity in the cathemeral red-fronted lemur (*Eulemur fulvus rufus*), with observations during a lunar eclipse. *Am J Primatol* 53:69–78
- Doran D, Jungers W, Sugiyama Y, Fleagle J, Heesy C (2002) Multivariate and phylogenetic approaches to understanding chimpanzee and bonobo behavioral diversity. In: Boesch C, Hohmann G, Marchant L (eds) *Behavioural diversity in chimpanzees and bonobos*. Cambridge University Press, New York, pp 14–34
- Du Puy D, Moat J (2003) Using geological substrate to identify and map primary vegetation types in Madagascar and the implications for planning biodiversity conservation. In: Goodman S, Benstead J (eds) *The natural history of Madagascar*. The University of Chicago Press, Chicago, pp 51–66
- Engqvist A, Richard A (1991) Diet as a possible determinant of cathemeral activity patterns in primates. *Folia Primatol* 57:169–172
- Foster SA, Endler JA (1999) Geographic variation in behavior: perspectives on evolutionary mechanisms. Oxford University Press, Oxford
- Freed B (1996) Co-occurrence among crowned lemurs (*Lemur coronatus*) and Sanford's lemurs (*Lemur fulvus sanfordi*) of Madagascar. Ph.D. Dissertation, Washington University, St. Louis
- Ganzhorn JU, Malcomber S, Andrianantoanina O, Goodman SM (1997) Habitat characteristics and lemur species richness in Madagascar. *Biotropica* 29(3):331–343
- Ganzhorn JU, Wright PC, Ratsimbazafy J (1999) Primate communities: Madagascar. In: Fleagle JG, Janson CH, Reed K (eds) *Primate communities*. Cambridge University Press, Cambridge, pp 75–89
- Gerson JS (2000) Social relationships in wild red-fronted brown lemurs (*Eulemur fulvus rufus*). Ph.D. Dissertation, Duke University, Durham, p 251
- Givnish T (1999) On the causes of gradients in tropical tree diversity. *J Ecol* 87:193–210
- Goodman S, Ganzhorn J (2004) Biogeography of lemurs in the humid forests of Madagascar: the role of elevational distribution and rivers. *J Biogeogr* 31:47–55
- Gould SJ, Johnston RF (1972) Geographic variation. *Ann Rev Ecol Syst* 3:457–498
- Horn HS (1968) The adaptive significance of colonial nesting in the Brewer's blackbird (*Euphagus cyanocephalus*). *Ecology* 49:682–694
- Johnson SE (2002) Ecology and speciation in brown lemurs: white-collared lemurs (*Eulemur albocollaris*) and hybrids (*Eulemur albocollaris* × *Eulemur fulvus rufus*) in southeastern Madagascar. Ph.D. Thesis, University of Texas, Austin
- Jury M (2003) The climate of Madagascar. In: Goodman S, Benstead J (eds) *The natural history of Madagascar*. The University of Chicago Press, Chicago, pp 75–85
- Kamilar JM (2006) Geographic variation in savanna baboon (*Papio*) ecology and its taxonomic and evolutionary implications. In: Lehman SM, Fleagle JG (eds) *Primate Biogeography*. Springer, Berlin Heidelberg New York, pp 169–200
- Kappeler P (1999) Convergence and divergence in primate social systems. In: Fleagle J, Janson C, Reed K (eds) *Primate communities*. Cambridge University Press, Cambridge, pp 158–170
- Kappeler P, Erkert H (2003) On the move around the clock: correlates and determinants of cathemeral activity in wild redfronted lemurs (*Eulemur fulvus rufus*). *Behav Ecol Sociobiol* 54:359–369
- Koenig A, Beise J, Chalise MK, Ganzhorn JU (1998) When females should contest for food—testing hypotheses about resource density, distribution, size, and quality with Hanuman langurs (*Presbytis entellus*). *Behav Ecol Sociobiol* 42:225–237
- Korstjens AH, Sterck EHM, Noe R (2002) How adaptive or phylogenetically inert is primate social behaviour? A test with two sympatric colobines. *Behaviour* 139:203–225
- Legendre P (2000) Comparison of permutation methods for the partial correlation and partial Mantel tests. *J Stat Comput Simul* 67:37–73
- Legendre P, Lapointe FJ, Casgrain P (1994) Modeling brain evolution from behavior: a permutational regression approach. *Evolution* 48:1487–1499
- Li Z, Rogers E (2004) Habitat quality and activity budgets of white-headed langurs in Fusui, China. *Int J Primatol* 25:41–54
- Linklater WL (2000) Adaptive explanation in socio-ecology: Lessons from the Equidae. *Biol Rev* 75:1–20
- Lockwood CA, Fleagle JG (1999) The recognition and evaluation of homoplasy in primate and human evolution. *Yearb Phys Anthropol* 42:189–232
- Lott DF (1991) Intra-specific variation in the social systems of wild vertebrates. Cambridge University Press, Cambridge
- Mantel N (1967) The detection of disease clustering and a generalized regression approach. *Cancer Res* 27:209–220
- McGarigal K, Cushman S, Stafford S (2000) *Multivariate statistics for wildlife and ecology research*. Springer, Berlin Heidelberg New York
- Menon S, Poirier FE (1996) Lion-tailed macaques (*Macaca silenus*) in a disturbed forest fragment: activity patterns and time budget. *Int J Primatol* 17:969–985
- Mitani JC, Rodman PS (1979) Territoriality: the relation of ranging pattern and home range size to defendability, with an analysis of territoriality among primate species. *Behav Ecol Sociobiol* 5:241–251
- Nakagawa S (2004) A farewell to Bonferroni: the problems of low statistical power and publication bias. *Behav Ecol* 15:1044–1045
- Nunn CL, Barton RA (2001) Comparative methods for studying primate adaptation and allometry. *Evol Anthropol* 10:81–98
- Ortolani A, Caro TM (1996) The adaptive significance of color patterns in carnivores: phylogenetic tests of classic hypotheses. In: Gittleman JL (ed) *Carnivore behavior, ecology, and evolution*. Comstock, Ithaca, pp 132–188
- Ostner J (2002) Sex-specific reproductive strategies of red-fronted lemurs (*Eulemur fulvus rufus*, Primates, Lemuridae). Ph.D. Dissertation, Universität Würzburg, Würzburg
- Ostner J, Kappeler P (1999) Central males instead of multiple pairs in redfronted lemurs, *Eulemur fulvus rufus* (Primates, Lemuridae). *Anim Behav* 58:1069–1078
- Overdorff D (1991) Ecological correlates to social structure in two prosimian primates: *Eulemur fulvus rufous* and *Eulemur rubriventer* in Madagascar. Ph.D. Dissertation, Duke University, Durham, p 313
- Overdorff D (1993) Similarities, differences, and seasonal differences in the diets of *Eulemur rubriventer* and *Eulemur fulvus rufus* in the Ranomafana National Park, Madagascar. *Int J Primatol* 14:721–753

- Overdorff D (1996) Ecological correlates to activity and habitat use of two prosimian primates: *Eulemur rubriventer* and *Eulemur fulvus rufus* in Madagascar. *Am J Primatol* 40:327–342
- Overdorff D, Johnson S (2003) *Eulemur*, true lemurs. In: Goodman S, Benstead J (eds) The natural history of Madagascar. The University of Chicago Press, Chicago, pp 1320–1324
- Pastorini J, Forstner M, Martin R (2000) Relationships among brown lemurs (*Eulemur fulvus*) based on mitochondrial DNA sequences. *Mol Phylogenet Evol* 16:418–429
- Pastorini J, Forstner M, Martin R (2002) Phylogenetic relationships among Lemuridae (Primates): evidence from mtDNA. *J Hum Evol* 43:463–478
- Proctor H (1996) Behavioral characters and homoplasy: perception versus practice. In: Sanderson MJ, Hufford L (eds) Homoplasy: the recurrence of similarity in evolution. Academic, New York, pp 131–149
- Prum RO (1994) Phylogenetic analysis of the evolution of alternative social behavior in the manakins (Aves: Pipridae). *Evolution* 48:1657–1675
- Rasmussen M (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
- Rosenberg M (2001) PASSAGE. Pattern Analysis, Spatial Statistics, and Geographic Exegesis Version 1.0. Department of Biology, Arizona State University, Tempe, AZ
- Rosenzweig M (1968) Net primary productivity of terrestrial communities: prediction from climatological data. *Am Nat* 102:67–74
- Rubenstein DI, Wrangham RW (1986) Ecological aspects of social evolution. Princeton University Press, Princeton
- Smouse P, Long J, Sokal RR (1986) Multiple regression and correlation extensions of the Mantel test of matrix correspondence. *Syst Zool* 35:627–632
- Sokal RR, Rohlf FJ (1995) Biometry: the principles and practice of statistics in biological research, 3rd edn. Freeman, New York
- Sterck EHM, Watts DP, van Schaik CP (1997) The evolution of female social relationships in nonhuman primates. *Behav Ecol Sociobiol* 41:291–309
- Struhsaker T (1978) Food habits of five monkey species in the Kibale Forest, Uganda. In: Chivers D, Herbert J (eds) Recent advances in primatology, vol 1. Behaviour. Academic, New York, pp 225–248
- Sussman RW (1977) Feeding behaviour of *Lemur catta* and *Lemur fulvus*. In: Clutton-Brock TH (ed) Primate ecology: studies of feeding and ranging behaviour in lemurs, monkeys, and apes. Academic, New York, pp 1–36
- Sussman R (2002) Adaptive array of lemurs of Madagascar revisited. *Evol Anthropol* 11:75–78
- Tabachnick BG, Fidell LS (1989) Using multivariate statistics, 2nd edn. Harper and Row, New York
- Tattersall I, Schwartz JH (1991) Phylogeny and nomenclature in the “Lemur-group” of Malagasy strepsirrhine primates. *Anthropol Pap Am Mus Nat Hist* 69:1–18
- Tattersall I, Sussman RW (1975) Notes on topography, climate, and vegetation of Madagascar. In: Tattersall I, Sussman RW (eds) Lemur biology. Plenum, New York, pp 13–21
- Tattersall I, Sussman R (1998) ‘Little brown lemurs’ of northern Madagascar. *Folia Primatol* 69:379–388
- Thierry B, Iwaniuk A, Pellis S (2000) The influence of phylogeny on the social behaviour of macaques (Primates: Cercopithecidae, genus *Macaca*). *Ethology* 106:713–728
- van Schaik CP (1989) The ecology of social relationships amongst female primates. In: Standen V, Foley RA (eds) Comparative socioecology. Blackwell, Oxford, pp 195–218
- van Schaik CP, Kappeler PM (1996) The social system of gregarious lemurs: lack of convergence with anthropoids due to evolutionary disequilibrium? *Ethology* 102:915–941
- Vasey N (1997) Community ecology and behavior of *Varecia variegata rubra* and *Lemur fulvus albifrons* on the Masoala Peninsula, Madagascar. Ph.D. dissertation, Washington University, St. Louis
- Vasey N (2000) Niche separation in *Varecia variegata rubra* and *Eulemur fulvus albifrons*: I. Interspecific patterns. *Am J Phys Anthropol* 112:411–431
- Wilson EO (1975) Sociobiology: the new synthesis. Harvard University Press, Cambridge
- Wright PC (1999) Lemur traits and Madagascar ecology: coping with an island environment. *Yearb Phys Anthropol* 42:31–72
- Wyner Y, DeSalle R, Absher R (2000) Phylogeny and character behavior in the family Lemuridae. *Mol Phylogenet Evol* 15:124–134
- Yoder AD, Heckman KL (2006) Mouse lemur phylogeography revises a model of ecogeographic constraint in Madagascar. In: Lehman SM, Fleagle JG (eds) Primate biogeography. Springer, Berlin Heidelberg New York, pp 255–268
- Yoder AD, Irwin JA (1999) Phylogeny of the Lemuridae: effects of character and taxon sampling on resolution of species relationships within *Eulemur*. *Cladistics* 15:351–361