

# Evolution in the hypervariable environment of Madagascar

Robert E. Dewar\*<sup>†</sup> and Alison F. Richard<sup>‡</sup>

\*McDonald Institute of Archaeological Research, University of Cambridge, Downing Street, Cambridge CB2 3ER, England; and <sup>‡</sup>Office of the Vice-Chancellor, University of Cambridge, Cambridge CB2 1TN, England

Communicated by Henry T. Wright, University of Michigan, Ann Arbor, MI, June 29, 2007 (received for review August 26, 2005)

**We show that the diverse ecoregions of Madagascar share one distinctive climatic feature: unpredictable intra- or interannual precipitation compared with other regions with comparable rainfall. Climatic unpredictability is associated with unpredictable patterns of fruiting and flowering. It is argued that these features have shaped the evolution of distinctive characteristics in the mammalian fauna of the island. Endemic Herpestidae and Tenrecidae and members of five endemic primate families differ from closely related species elsewhere, exhibiting extremes of "fastness" and "slowness" in their life histories. Climatic features may also account for the dearth of frugivorous birds and mammals in Madagascar, and for the evolutionary prevalence of species with large body mass.**

climate | life history | unpredictability | mammals

Recent field research on Madagascar has revealed related vertebrates with both the fastest and slowest life histories. How can such differences evolve under similar environmental conditions? The unique natural communities of Madagascar are famous, but efforts to explain their evolution are unsatisfactory. We show here that the climates of Madagascar are distinctive, with highly unpredictable rainfall, and argue that some of the natural communities of the island represent evolutionary responses to this unusually variable climatic regime.

The communities of Madagascar are characterized by high levels of endemism, great species diversity in some taxonomic groups, and a complete absence of others. These three features are dramatically evident in the native nonflying mammals. The four orders native to and widespread within Madagascar (Carnivora, Insectivora, Primata, and Rodentia) are all represented by endemic genera or families. The only other Recent mammals are the African bush pig (*Potamochoerus larvatus*), the extinct pygmy hippopotamus species (*Hippopotamus* spp.), and the poorly known and extinct *Plesiorcycteropus*. Groups widely distributed elsewhere, such as the canids, felids, cervids, bovids, and anthropoid primates, are absent. Successful colonization by mammals has been rare (1). The high level of endemism has been attributed to the long isolation of the island from other continents. This isolation predates the evolution of most recent families of mammals, and the limited suite of Malagasy mammals has been attributed to chance dispersals across the Mozambique Canal over the past 70 million years (1, 2).

The Malagasy fauna exhibit other distinctive features not readily explained by isolation. For example, the biological peculiarities of the primates of Madagascar have been widely noted (3). The extreme seasonality and unpredictability and frequent tropical cyclones of Madagascar have been invoked to explain these peculiarities and relate them to a special need to conserve energy (3, 4). However, Madagascar does not exhibit an unusual degree of seasonality (5), and, lacking comparative evidence until now, there has been no assessment of the unpredictability of the climate of Madagascar compared with other landmasses.

Several authors (6, 7) also have remarked on the low number of frugivorous species of birds and mammals in Madagascar. In other tropical communities, the dominant arboreal frugivores

are primates; however, in Madagascar, there are very few medium- to large-sized frugivorous lemurs, and the proportion of fruit in the diets of extant Malagasy lemurs is low compared with other primate communities (8). With decreasing body mass, primate species tend to include more fruit and less foliage in their diet, but medium-sized lemurs (down to 1 kg body mass) tend to be folivorous rather than frugivorous (5).

## Madagascar: Environmental Variation

**Year-to-Year Variability.** Dewar and Wallis (9) examined interannual variation in rainfall on tropical landmasses. Of a global sample of 1,492 stations, only two stations were in Madagascar. To explore patterns of interannual rainfall variability in Madagascar, we sought additional monthly rainfall data (Global Historical Climatological Network version 2; [www.ncdc.noaa.gov/oa/climate/research/ghcn/ghcngrid.html](http://www.ncdc.noaa.gov/oa/climate/research/ghcn/ghcngrid.html)) (Table 1). Fig. 1 shows the geographical distribution of interannual rainfall variability at 15 Malagasy stations. In the north and the southwest were regions with unusually high interannual variation. All of the other regions fell within the global midrange spread identified by Dewar and Wallis (9), but most western stations showed more interannual variation than the median, and eastern regions somewhat less. Thus, some regions of Madagascar differ markedly from global distributions, but unusual interannual variability in rainfall is not a general characteristic of the island.

**Predictability of Monthly Rainfall.** Colwell (10) proposed a method for examining the predictability ( $P$ ) of periodic phenomena and used monthly rainfall patterns as an illustration.  $P$  falls on a scale of 0 to 1, with higher values representing greater predictability.  $P$  is the sum of  $C$  and  $M$ , where  $C$  is a measure of constancy (in our case, the extent to which rainfall is constant and thereby predictable) from month to month, and  $M$  is a measure of contingency (the extent to which rains fall in similar amounts in each month from year to year).

$P$  was calculated for the 15 sites in Madagascar. We selected a matching sample of stations from the nearly 600 continental African stations used by Dewar and Wallis (9). For each Malagasy station, we selected the African station with the mean annual rainfall closest to it (Table 1).  $P$  did not covary positively with the length of the climate record in the total sample ( $r = 0.108$ ,  $P = 0.571$ ) nor in either the continental ( $r = 0.403$ ,  $P = 0.136$ ) or Malagasy ( $r = 0.198$ ,  $P = 0.479$ ) subsets.  $P$  was, however, significantly different for the African and Malagasy samples ( $F_{1,28} = 28.68$ ,  $P < 0.0001$ ): continental stations were, as a group, much more predictable than those in Madagascar. In Madagascar,  $P$  covaried positively with mean annual rainfall ( $r =$

Author contributions: R.E.D. designed research; R.E.D. performed research; R.E.D. and A.F.R. analyzed data; and R.E.D. and A.F.R. wrote the paper.

The authors declare no conflict of interest.

Freely available online through the PNAS open access option.

<sup>†</sup>To whom correspondence should be addressed. E-mail: [red30@cam.ac.uk](mailto:red30@cam.ac.uk).

© 2007 by The National Academy of Sciences of the USA

**Table 1. Rainfall stations of Madagascar and Africa**

Station	Location	Latitude	Longitude	Elevation, m	MAR, mm	<i>P</i>	<i>C</i>	<i>M</i>	<i>n</i>
Toliary	Madagascar	-23.34	43.67	5	386	0.281	0.074	0.206	53
Behara	Madagascar	-24.95	46.38	244	532	0.270	0.154	0.116	41
Betioky	Madagascar	-23.71	44.38	263	666	0.320	0.088	0.233	48
Ranohira	Madagascar	-22.55	45.41	765	966	0.340	0.083	0.257	49
Antsiranana	Madagascar	-12.27	49.28	33	1034	0.296	0.047	0.249	49
Maintirano	Madagascar	-18.07	44.03	13	1043	0.356	0.080	0.275	47
Fianarantsoa	Madagascar	-21.43	47.08	1162	1179	0.421	0.162	0.259	60
Iharana	Madagascar	-13.24	50.03	2	1301	0.405	0.294	0.111	31
Antananarivo	Madagascar	-18.92	47.52	1400	1368	0.352	0.073	0.279	108
Mahajanga	Madagascar	-15.72	46.32	36	1539	0.424	0.104	0.320	42
Taolagnaro	Madagascar	-25.03	47.00	14	1620	0.401	0.333	0.068	47
Anlalava	Madagascar	-14.63	47.75	23	1824	0.438	0.113	0.325	34
Antalaha	Madagascar	-14.88	50.28	4	2244	0.370	0.239	0.131	36
Mananjary	Madagascar	-21.22	48.33	13	2726	0.411	0.292	0.119	32
Toamasina	Madagascar	-18.14	49.38	7	3338	0.437	0.277	0.163	47
En Nahud	Sudan	12.70	28.43	610	388	0.613	0.302	0.310	77
Mourdiah	Mali	14.40	-7.40	314	532	0.581	0.240	0.341	56
Nkayi	Zimbabwe	-19.00	28.9	1130	666	0.441	0.149	0.292	49
Koutiala	Mali	12.38	-5.47	365	964	0.563	0.190	0.372	64
Ngara	Tanzania	-2.40	30.60	1463	1031	0.473	0.242	0.232	52
Kelo	Chad	9.30	15.80	378	1043	0.652	0.252	0.400	33
Dabakala	Ivory Coast	8.30	-4.40	244	1180	0.434	0.213	0.221	52
Minna	Nigeria	9.62	6.53	262	1303	0.579	0.238	0.341	64
Yei	Sudan	4.00	30.60	1036	1363	0.527	0.251	0.276	29
Sassandra	Ivory Coast	4.95	6.08	62	1539	0.371	0.167	0.204	60
Meiganga	Cameroon	6.53	14.37	1027	1618	0.592	0.243	0.350	36
Lagos	Nigeria	6.60	3.40	19	1813	0.387	0.152	0.235	82
Lauderdale	Malawi	-12.00	33.80	930	2166	0.399	0.189	0.210	65
Edea	Cameroon	3.80	10.10	31	2522	0.612	0.346	0.266	37
Harbel	Liberia	6.20	-10.20	53	3396	0.559	0.228	0.332	41

Elevation is given as meters above sea level. MAR, mean annual rainfall; *P*, *C*, and *M* are as defined in ref. 11; *n*, number of years of records used.

0.727,  $P = 0.002$ ), but *P* did not covary with annual precipitation in continental Africa ( $r = 0.092$ ,  $P = 0.743$ ).

Although some stations in Africa fall within the range of unpredictability exhibited by the Malagasy stations, all of the Malagasy stations are strikingly unpredictable (Fig. 2). Their low *P* values result from two patterns: either markedly low contingency with unexceptional constancy or low constancy with unexceptional, even high contingency in relation to the African data set (Fig. 3).

The five stations from the east coast of Madagascar (Iharana, Antalaha, Toamasina, Mananjary, and Taolagnaro) form a cluster on the lower right of Fig. 3. With some rain in every month, they have relatively high scores for constancy; however, with a poorly predictable seasonal pattern, they score low on contingency. Stations in the center, north, west, and south form another cluster in the upper left of Fig. 3, reflecting higher contingency and lower constancy: more predictable patterning of rainfall seasons but low constancy as the result of the long dry season.

The distinctive and unusually high variability in precipitation in Madagascar is likely to be the product of several determinants, all of them linked to the global configuration of continents and oceans. These determinants, and the resulting climatic patterns affecting Madagascar today, were probably established when the continents bordering the Indian Ocean achieved their current positions, and the Indian Ocean monsoon system developed. A recent review argues that climatic conditions were essentially modern throughout Madagascar by  $\approx 5$  million years ago (11).

### Patterns of Fruiting and Flowering

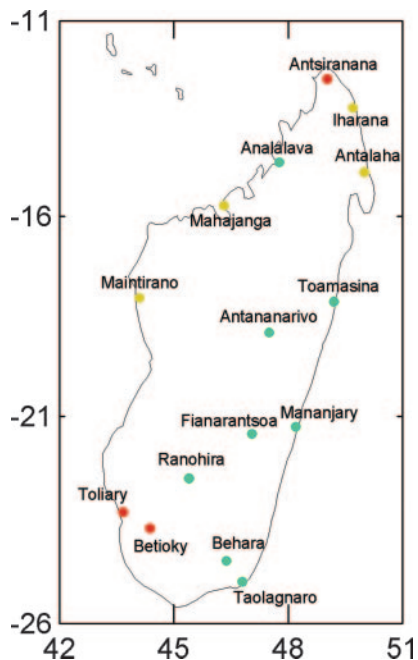
Terborgh and van Schaik (12) have proposed that the underrepresentation of frugivores in Madagascar is due to a distinctive

phenology of the forests. The authors predicted that fruiting in Madagascar would be confined to a very narrow season of the year, thus requiring consumers to rely heavily on resources other than fruit at other times of year. Subsequent phenological studies at three sites along the east coast (13–18) instead reveal considerable year-to-year variability in the timing and quantities of available fruit overall and, in many cases, of fruit available from individual species.

### Evolutionary Responses to Environmental Unpredictability

Harvey *et al.* (19) argue that the variation in life histories of placental mammals is best explained as a product of differences in fertility and mortality schedules, memorably as “living fast and dying young” (20). Moreover, models of stochastic demography show that high environmental variance in survivorship or fertility can reverse evolutionary patterns predicted under fixed vital rates and stable age structures (21, 22). Depending on initial life-history parameters and the level of environmental stochasticity, selection favors a shift toward either more iteroparity or more-concentrated breeding over a shorter life span. When adult survivorship is highly variable, reproduction should occur earlier in the life cycle; when the variance is most important in fertility and juvenile survivorship, selection will be for a longer reproductive span or “bet hedging.”

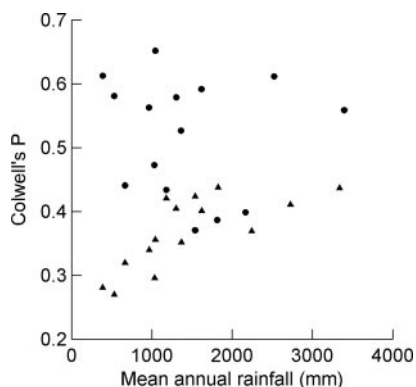
Madagascar’s variable climate appears to have been an important evolutionary determinant across the array of native mammals and probably the bird community as well. Malagasy mammalian life histories, and the array of recently extinct species have characteristics that are best understood as responses to environmental variability.



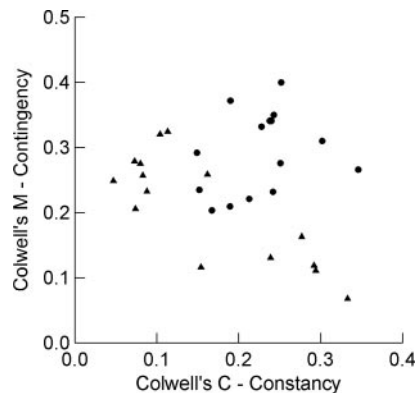
**Fig. 1.** Residuals from a global nonlinear regression of interannual rainfall variation against mean annual rainfall at 15 stations in Madagascar, as in ref. 9: stations with variation, adjusted for mean, that is >75% of global stations are shown in red, stations with variation that falls between the median and the 75th percentile are shown in yellow, and those with variation between the 25th percentile and the median are shown as green.

**Carnivora.** The native carnivorous mammals of Madagascar are assigned to seven endemic genera, members of a monophyletic radiation of herpestids (1). This radiation is ecologically diverse (23) but displays a shared distinctiveness in life-history traits that sets its members apart from other herpestids.

Without exception, Malagasy herpestids give birth only once a year in a species-specific birth season, and most give birth to a single offspring each year. Both of these traits are highly unusual in herpestids elsewhere and cannot be attributed to differences in female body mass (23, 24) (Fig. 4). The median mass of Malagasy species is 1.60 kg (range, 0.8 to 9.5 kg;  $n = 5$ ) compared with 1.24 kg (range, 0.27 to 3.5 kg;  $n = 16$ ) in species from Asia and Africa. Analysis of variance of log (interbirth interval) reveals a highly significant difference between Malagasy (median, 12 months) and non-Malagasy species (median, 6 months) ( $F_{1,10} = 19.04$ ;  $P < 0.001$ ). An ANOVA of litter size



**Fig. 2.** Colwell's  $P$  in relation to mean rainfall for 15 Madagascar stations (triangles) and 15 matching stations from continental Africa (circles).



**Fig. 3.** Colwell's  $C$  (constancy) vs. Colwell's  $M$  (contingency) for 15 Madagascar stations (triangles) and 15 matching stations from continental Africa (circles).

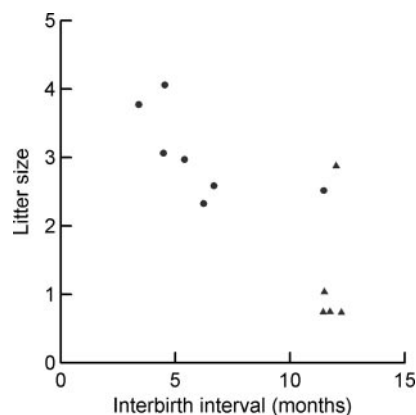
makes a similar distinction (median of Malagasy species, 1; median of other herpestids, 3;  $F_{1,19} = 26.97$ ;  $P < 0.0001$ ).

**Primates.** The extant lemurs, the primate radiation of Madagascar, are assigned to five endemic families (25). Many lemurs share features unusual compared with other primates, including low basal metabolic rate and life-history patterns exhibiting extremes of "slowness" and "fastness" (3, 26, 27).

For example, *Propithecus verreauxi* is a widely distributed, diurnal, folivorous member of the family Indriidae. An 18-year study of a population of *P. verreauxi* at Beza Mahafaly in southwest Madagascar has demonstrated high adult survivorship, highly irregular fertility, and irregular and low first-year survivorship. *P. verreauxi* is "slower" than other mammals for which comparable data are available: females delay reproduction later and continue reproduction much longer than expected for a 3-kg mammal and have life expectancies at birth that are much longer than expected (27). We interpret these results as a manifestation of bet-hedging, evolved in response to environmental unpredictability and its impact on infant and juvenile survival.

A population of *Lemur catta* (adult mass, 2.2 kg) at Beza Mahafaly exhibits similarly irregular and low first-year survivorship but, in combination with lower adult survivorship, much earlier age at first reproduction and higher fertility (28). This has been interpreted as an alternative "response...to unusual climate and environmental conditions" (28).

Tilden and Oftedal (29, 30) has shown that, compared with



**Fig. 4.** Interbirth interval and litter size for Malagasy herpestids (triangles) and continental African and Asian herpestids (circles). The slight random jitter has been added for clarity.

African bushbabies (*Otolemur* spp.), several species of Malagasy lemurs have low rates of maternal reproductive investment during gestation and lactation. In relation to maternal body mass, for example, energy transfer by lactating *Eulemur fulvus* is very low compared with other mammals. This is consistent with a risk-spreading strategy, where variance in survival is greatest at weaning and where survivorship is environmentally controlled.

In contrast, Martin (31) reported that one of the smallest lemurs, the 60-g *Microcebus murinus*, may give birth for the first time at the age of 12 months, producing litters of two to three infants twice during a single year when environmental conditions are good, thus establishing *Microcebus* as the “fastest” of primates, with the highest potential rate of reproduction in the order (32). High, adult-biased predation rates on *Microcebus* are reported in some areas (33). In this instance, high adult predation rates and environmental unpredictability may together drive this species toward a different “solution,” involving an unusually speeded-up life-history strategy.

**Other Mammals.** The Tenrecidae comprise 28 species, ranging in body mass from 3 g to  $\approx$ 2 kg. Little is known about patterns of mortality in the wild, but the metabolic and reproductive patterns of tenrecs are well known and unusual (34, 35). Unlike most mammalian radiations, there is no correlation between maternal body mass and gestation length among tenrecs (36); there is no positive correlation between body mass and reported longevity in zoos (37); and litter size covaries positively with body mass, with the largest tenrec (*Tenrec ecaudatus*) having the largest known litters of any mammal, up to 32 neonates. *Tenrec* approaches a semelparous pattern, with evidence that adult survivorship is very low, and that females that attempt a second year of breeding have much reduced success.

Of the 22 species of endemic rodents (38), the only well studied species, *Hypogeomys antimena*, is a 1.1-kg, hopping herbivore living in burrows and often described as the “rabbit” of Madagascar (39). However, the practice of *Hypogeomys antimena* to give birth to a single offspring once a year is decidedly not rabbit-like.

**Extinct Species.** The recent wave of size-biased extinctions obscures the evolutionary prevalence of species with large body mass among the native species of Madagascar. This is evident in at least three major radiations on the island. First, the preponderance of large-bodied, folivorous primates before the Holocene extinctions exceeds that of primate radiations elsewhere (5, 40). Second, Madagascar experienced the recent extinction of a diverse radiation of ratite birds of the family Aepyornithidae, including *Aepyornis maximus*, which, at  $\approx$ 450 kg, was the heaviest of all birds. Third, among the most common extinct species are two giant tortoises. Large body mass thus evolved repeatedly among the vertebrates of Madagascar, and by mid-Holocene times, the herbivore community strongly reflected this pattern. The causes of gigantism in the Malagasy fauna are unknown, but the ubiquity of gigantism suggests a general environmental feature, and increase in body mass is associated with delays in age of maturation (41).

## Discussion

**Evolutionary Consequences of Hypervariability.** The climate of Madagascar is characterized by very high unpredictability of rainfall. The eastern region experiences this as high intraannual

variability in the patterning of rainfall. In the north and the south, it takes the form of high interannual variability in total precipitation. We hypothesize that this unpredictability is primarily responsible for the unusual phenology of the forests of Madagascar and that the unpredictability of fruit has limited the evolution of flower- and fruit-eating species. Of equal importance is that the unpredictability of resources must contribute to variance in vital rates among many of its vertebrates. A high level of reproductive variance has been demonstrated for the best-studied species, and there are congruent reports for other, less well known species.

The life-history patterns of Malagasy mammals studied thus far contrast with those of closely related taxa in other regions. In some cases, like certain lemurs and the Carnivora, selection appears to have favored extension of the reproductive span or reduced litter size. In other cases, like *T. ecaudatus* or *M. murinus*, selection has favored concentrated reproduction unusually early in life. The result is an island whose native mammals differ strikingly from those in tropical regions with more predictable climates. The distinctive features of the climate of Madagascar may also be linked to the gigantism characteristic of the fauna of the island through the effect of these features on the evolution of life-history patterns.

On the few tropical landmasses where rainfall variability is as high as it is on Madagascar, unusual life histories have been reported, and it has been suggested that they evolved in response to unpredictability. For example, the odd life-history characteristics of the Galapagos cactus finch have been attributed to environmental variation (42). Very unusual life histories in Australia have likewise been ascribed to unpredictability (43). Further research in regions of comparable variability would provide additional tests of our ideas, as would studies of the life histories and demography of other mammal populations in Madagascar itself.

Biogeographers have long explained the rarity of mammalian groups on Madagascar as the result of infrequent “sweepstakes dispersal” across the canal of Mozambique. We suggest that two different filters may have winnowed the vertebrates of Madagascar: isolation by the surrounding sea and the emergence of a regime of environmental hypervariability during the late Cenozoic that posed strong challenges for both some residents and immigrants.

Discussions of the distinctiveness of the fauna of Madagascar have a tendency to trail off, in need of a yet-to-be-identified *deus ex machina*. The unpredictability of the climate documented in this paper may be a critical environmental feature for the vertebrates of Madagascar. We suggest some of the ways in which this unusual environmental context may have shaped the evolution of species and communities on the island, recognizing that these arguments are but a starting point for a broader reconsideration of the evolutionary biology of one of the world’s most intriguing landmasses. Future field studies of the natural communities of Madagascar may provide opportunities for confirmation and modification of the role of environmental variability in the shaping of those communities.

We thank the staff of the Direction de Météorologie et Hydrologie (Antananarivo, Madagascar) and John F. Griffiths (Texas A & M University, College Station, TX) for assistance in acquiring rainfall data and R. Colwell, J. Diamond, R. D. Martin, M. Nicoll, M. Schwartz, S. Stearns, J. Wallis, A. Yoder, and S. Zack for insights and helpful discussion.

1. Yoder AD, Burns MM, Zehr M, Delefosse T, Veron G, Goodman SM, Flynn JJ (2003) *Nature* 421:734–737.
2. Krause DW, Hartman JH, Wells NA (1997) in *Natural Change and Human Impact in Madagascar*, eds Goodman SM, Patterson BD (Smithsonian Institution Press, Washington, DC), pp 3–43.
3. Wright PC (1999) *Yrbk Phys Anthropol* 42:31–72.
4. Ganzhorn JU (1995) *Ambio* 24:124–125.
5. Richard AF, Dewar RE (1991) *Annu Rev Ecol Syst* 22:145–175.
6. Fleming TR, Breitwisch R, Whitesides GH (1987) *Annu Rev Ecol Syst* 18:91–109.
7. Goodman SM, Ganzhorn JU (1997) *Rev Ecol (Terre Vie)* 52:321–329.
8. Fleagle JG, Reed KE (1996) *J Hum Evol* 30:489–510.
9. Dewar RE, Wallis JR (1999) *J Climate* 12:3457–3466.
10. Colwell RK (1974) *Ecology* 55:1148–1153.
11. Wells NA (2003) in *The Natural History of Madagascar*, eds Goodman SM, Benstead JP (Univ Chicago Press, Chicago), pp 16–34.

12. Terborgh J, van Schaik CP (1987) in *Organization of Communities, Past and Present*, eds Gee HR, Giller PS (Blackwell, Oxford), pp 205–226.
13. Morland HS (1991) PhD thesis (Yale Univ, New Haven, CT).
14. Sterling EJ (1993) PhD thesis (Yale Univ, New Haven, CT).
15. Meyers DM, Wright PC (1993) in *Lemur Social Systems and Their Ecological Basis*, eds Kappeler PM, Ganzhorn JU (Plenum, New York), pp 179–192.
16. Overdorff DJ (1991) PhD thesis (Duke Univ, Durham, NC).
17. Hemingway CA (1995) PhD thesis (Duke Univ, Durham, NC).
18. Hemingway CA (1996) *Int J Primatol* 17:637–660.
19. Harvey PH, Read AF, Promislow DEL (1989) *Oxford Surv Evol Biol* 6:13–32.
20. Promislow DEL, Harvey PH (1990) *J Zool* 220:417–437.
21. Tuljapurkar S (1990) *Population Dynamics in Variable Environments* (Springer, New York).
22. Orzack SH, Tuljapurkar S (2001) *Ecology* 82:2659–2665.
23. Albignac R (1973) *Faune de Madagascar*, Mammifères carnivores (Office de la Recherche Scientifique et Technique Outre-Mer/Centre National Recherche Scientifique, Paris), Vol 36.
24. Gittleman JL (1986) *Am Nat* 127:744–771.
25. Yoder AD (1997) *Evol Anthropol* 6:11–22.
26. Martin RD (1990) *Primate Origins and Evolution* (Princeton Univ Press, Princeton).
27. Richard AF, Dewar RE, Schwartz M, Ratsirarson J (2002) *J Zool* 256:421–436.
28. Gould L, Sussman RW, Sauther ML (2003) *Am J Phys Anthropol* 120:182–194.
29. Tilden CR, Oftedal OT (1995) in *Creatures of the Dark: The Nocturnal Prosimians*, eds Alterman L, Doyle GA, Izard MK (Plenum, New York), pp 119–132.
30. Tilden CR, Oftedal OT (1997) *Am J Primatol* 41:195–211.
31. Martin RD (1972) *Z Tierpsychol* 9(Suppl):43–89.
32. Ross C (1988) *J Zool* 214:199–220.
33. Goodman SM, Langrand O, Raxworthy CJ (1993) *Ostrich* 64:160–171.
34. Stephenson PJ, Racey PA (1997) *Comp Biochem Physiol* 112A:215–223.
35. Eisenberg JF, Gould E (1970) *The Tenrecs: A Study in Mammalian Behavior and Evolution* (Smithsonian Contrib Zool, Washington, DC).
36. Eisenberg JF (1981) *The Mammalian Radiations: An Analysis of Trends in Evolution*, (Univ of Chicago Press, Chicago).
37. Eisenberg JF (1988) in *Evolution of Life Histories of Mammals*, ed Boyce MS (Yale Univ Press, New Haven, CT), pp 291–310.
38. Goodman SM, Ganzhorn JU, Rakotondravony D (2003) in *The Natural History of Madagascar*, eds Goodman SM, Benstead JP (Univ of Chicago Press, Chicago), pp 1159–1186.
39. Sommer ML (1997) *J Zool* 241:301–314.
40. Godfrey L, Jungers W, Reed KE, Simons EL, Chatrath PS (1997) in *Natural Change and Human Impact in Madagascar*, eds Goodman SM, Patterson BD, (Smithsonian Institution Press, Washington, DC), pp 218–256.
41. Charnov EL (1993) *Life History Invariants: Some Explorations of Symmetry in Evolutionary Ecology* (Oxford Univ Press, Oxford).
42. Grant BR, Grant PR (1989) *Evolutionary Dynamics of a Natural Population: The Large Cactus Finch of the Galapagos* (Univ of Chicago Press, Chicago).
43. Flannery T (1994) *The Future Eaters: An Ecological History of the Australasian Lands and People* (Grove, New York).