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## **Extinction and ecological retreat in a community of primates**

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### **ONE SENTENCE SUMMARY**

Stable isotope data reveal evidence of recent disruption and niche contraction in a community of primates.

## **ABSTRACT**

Lemurs are an important part of Madagascar's faunal diversity. At least eight species have disappeared from Southwest Madagascar during the past two millennia, and the effects of these losses on surviving formerly sympatric species are unknown. Using radiocarbon and stable isotope data to examine temporal shifts in ecological niches of extant species, we tested the hypothesis that competitive release has allowed survivors to expand into the vacated niches of extinct species. We found, instead, that extant species occupy a contracted niche space, surviving in habitats that are moister than those typically occupied in the past. The ecological importance of more xeric habitats may be underestimated by current conservation strategies.

Lemurs represent a prodigious radiation of primates in Madagascar (1, 2). Yet many are at risk of extinction (2), and at least 17 species have vanished during the past 2000 years (3). The causes of these extinctions are debated but human impacts were probably a contributing factor (3-5). The effects of these extinctions on the ecology and behavior of living lemurs are unknown (6, 7). The principle of competitive release predicts that surviving lemurs would have expanded or shifted their diets, invading niches vacated by former competitors (8, 9). When the disappearance of competitor species results from factors that also affect available resources, however, release might not be expected. Alternatively, surviving lemurs may have experienced a contraction of the niche space they occupy. We call this alternative scenario ecological retreat.

The analysis of stable carbon and nitrogen isotope values ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , respectively) in extant and recently extinct sympatric lemur species affords us an opportunity to test the predictions of competitive release and ecological retreat (10). The isotopic niche of a population reflects aspects of habitat and diet, but in potentially condensed form (e.g., herbivorous species can have overlapping isotopic niches but exploit different plants). Isotopic niche axes are most useful when isotopic gradients across habitats or dietary resources are strong. Such is the case in Madagascar, where 1) different plant types (e.g.,  $\text{C}_3$ ,  $\text{C}_4$ , CAM) have dramatically different  $\delta^{13}\text{C}$  values, 2)  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values distinguish plants and lemurs from moist and dry habitats, and 3) plant and lemur  $\delta^{15}\text{N}$  values are strongly correlated (11). Accordingly, we can use the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  distributions of each species to distinguish populations feeding predominantly  $\text{C}_3$  versus CAM or  $\text{C}_4$  plants (or consumers of these plants) and living in drier versus moister habitats.

We analyzed bone collagen from four living (*Lemur catta*, *Lepilemur leucopus*, *Microcebus griseorufus*, and *Propithecus verreauxi*) and eight extinct species (*Archaeolemur majori*, *Daubentonia robusta*, *Hadropithecus stenognathus*, *Megaladapis edwardsi*, *M. madagascariensis*, *Mesopropithecus globiceps*, *Pachylemur insignis*, and *Palaeopropithecus ingens*) from a variety of localities in Southern Madagascar (Spiny Thicket Ecoregion, or STE Fig. 1). We included 117 Late Holocene subfossil bones and 207 modern bone and fur samples (3, 11-13), (14),(15). All modern specimens are from Beza Mahafaly Special Reserve (BMSR) (Fig. 1).

The STE was largely devoid of large-bodied lemurs by 900 calendar years before present (Cal BP) (5). To test for competitive release, we compared the pair-wise Euclidean distances and density overlap scores ( $\omega$ ) between isotopic centroids for each extinct species and each extant species represented in subfossil deposits first before and then after 900 Cal BP (16, 17). These two metrics respectively quantify isotopic similarities and the degree of isotopic overlap between each extant and each extinct species before and after the decline in extinct lemurs in the STE. Due to limited samples (table S2), we compared subfossil coastal *L. catta* to coastal extinct species, and subfossil inland *P. verreauxi* and *L. leucopus* to inland extinct species (15). Small sample sizes prevented overlap calculations for *L. leucopus*, and neither Euclidean distances nor overlap scores could be tested for *M. griseorufus* because the oldest dated specimen is 485 Cal BP.

Under competitive release, isotopic niches of extant lemurs are expected to converge on those of extinct taxa with similar dietary adaptations (9), resulting in decreased pair-wise Euclidean distances and increased density overlap values after 900 Cal BP (16, 17). For example, the isotopic niche of *Lepilemur leucopus*, an extant folivore (12), should converge on formerly sympatric but now extinct folivores, *Megaladapis edwardsi* or *M. madagascariensis* (18, 19). Similarly, *Lemur catta* (20) should shift toward extinct frugivores such as *Pachylemur insignis* or *Archaeolemur majori* (19, 21). Finally, the isotopic niche of *Propithecus verreauxi*, a folivore/frugivore (20), might converge on the isotopic niche of closely-related *Palaeopropithecus ingens* (18).

We found no evidence of competitive release for subfossil *Lemur catta* at coastal sites. The mean Euclidean distance between isotopic centroids for *L. catta* and coastal extinct lemurs was similar before and after 900 Cal BP (paired  $t=-0.72$ ,  $df=6$ ,  $p=0.50$ ), and species-specific pair-wise Euclidean distances shifted in a direction contrary to our expectations (tables 1, S2). Density overlap decreased after 900 Cal BP between *L. catta* and those extinct taxa with whom it overlapped significantly prior to 900 Cal BP (e.g., *Archaeolemur*, *Megaladapis*, *Pachylemur*, *Palaeopropithecus*) (table 1). Similarly, we found no evidence of competitive release for inland subfossil *Lepilemur leucopus*. The mean Euclidean distance between centroids for *L. leucopus* and extinct inland lemurs increased after 900 Cal BP (paired  $t=-14.61$ ,  $df=3$ ,  $p=0.001$ ; table 1). The isotopic centroid for *L. leucopus* shifted away from the centroids for all inland extinct species, including *Megaladapis* spp. In contrast, the mean pair-wise Euclidean distance between the centroids for *P. verreauxi* and extinct inland lemurs decreased after 900 Cal BP (paired  $t=13.91$ ,  $df=3$ ,  $p=0.001$ ; table 1). The isotopic centroid for *P. verreauxi* shifted towards those of all extinct species, although not disproportionately in the direction of *Palaeopropithecus ingens*. For *P. verreauxi*, density overlap after 900 Cal BP also increased with *Megaladapis*, *Pachylemur*, and *Palaeopropithecus*. Nevertheless, this result does not lend great support to competitive release, as average overlap values were small between *P. verreauxi* and the extinct taxa, and the overlap between *P. verreauxi* and *P. ingens* was minimal both pre- and post-900 Cal BP (table 1).

In contrast to the expectations of competitive release, we found evidence for a sharp contraction in the isotopic niche breadth of the entire STE lemur community after 900 Cal BP. Mean pair-wise Euclidean distances were significantly greater before 900 Cal BP ( $4.8 \pm 1.9$ , range 0.6 to 13.4) than after 900 Cal BP ( $1.9 \pm 0.7$ , range 1.3 to 3.1; unpooled  $t=4.54$ ,  $df=41.88$ ,  $p<0.001$ ; Fig. 2; tables S3, S4). The absence of competitive release could be explained if the extinct species exploited niches unavailable to extant taxa due to their smaller body size or physiological adaptations. For example, extinct lemurs may have been able to swallow seeds too large to be swallowed by their extant relatives (22); some may have had anatomical or physiological adaptations enabling them to process foods that are too mechanically resistant or toxic for processing by smaller-bodied living species. Alternatively, vacated niches may no longer exist because of human habitat alteration (23) or human presence in more open habitats may have discouraged remaining lemurs from inhabiting them. The combination of high  $\delta^{13}\text{C}$  values, dental microwear, and dental morphology indicate that *Hadropithecus* consumed CAM or  $\text{C}_4$  plants (24), and the loss of this mode of life certainly contributes to overall niche collapse in the STE.

Comparing isotopic data for extant taxa from past to present, we found stability of community niche breadths (tables S5, S6). There are no detectable differences in either the variance ( $F_{1,11}=0.018$ ,  $p=0.90$ ) or mean pair-wise Euclidean distance (pooled  $t=0.48$ ,  $df=10$ ,  $p=0.64$ ) between modern and subfossil extant lemur communities. Nevertheless, the isotopic niches of lemurs at BMSR do differ from those of the subfossil taxa. Modern species evince lower  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values than do their subfossil counterparts (Fig. 2;

table S2; carbon: unpooled  $t=5.98$ ,  $df=37.08$ ,  $p<0.0001$ ; nitrogen:  $t=4.70$ ,  $df=35.20$ ,  $p<0.0001$ ).

On the surface, such isotopic contraction agrees with the concept of niche collapse (25), although with a crucial difference. The shift in niche space for extant species is toward a novel isotopic space that was largely unoccupied by STE lemurs in the past (Fig. 2). Instead, this pattern supports the expectations of ecological retreat. The overall decrease in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values between ancient and modern individuals indicates an increasing reliance on mesic environments in the arid South. It is conceivable that our results reflect a taphonomic bias; mesic habitats may be under-represented in the subfossil record. This possibility, however, is unlikely. Some of the best-preserved subfossil localities had water-logged soils, including Taolambiby, which even today is adjacent to a perennial spring (3) (table S1). Yet isotope values for lemurs from these localities suggest that animals did not heavily exploit mesic forests in the past.

Protected riparian forests may be functioning as lemur refugia. Although humans have hunted lemurs in the STE for at least 2000 years (4), large-scale habitat modification, fragmentation, and degradation are likely recent phenomena in the STE (26, 27). In response to increasing indirect and direct anthropogenic pressures, STE lemurs may be actively avoiding humans. As a result, they may be overrepresented in protected, mesic riparian forests, raising the possibility of a mismatch between their anatomical adaptations and observed behaviors. The observation that *L. catta* in riparian reserves

relies heavily and to its detriment on *Tamarindus indica* is compelling evidence for this possibility (28), (29).

Such ecological retreat is not unique to lemurs. Retreat may be widespread and under-appreciated. Historical shifts in the isotope values of African proboscideans, Australian ratites, and north Pacific pinnipeds have also been attributed to dietary, habitat, or reproductive shifts in response to indirect or direct human pressures (23, 30, 31). The ecological consequences of retreat may be considerable and irreversible. Retreat affects the ecological roles that animals play. Interactions may shift (25) and seed dispersal may be affected (32). In addition, the genetic diversity of retreating species will likely decrease, reducing their resilience and increasing their risk of extinction (33).

The STE was recently listed as one of the 200 most important ecological regions in the world (34). Isotopic data suggest that prior to extensive human disturbance, many STE lemurs foraged in more open habitats, such as wooded savanna and spiny thicket (22). *Microcebus griseorufus*, *Lemur catta*, *Lepilemur leucopus*, and *Propithecus verreauxi* still occur in dry spiny forest and scrub (2), but these habitats are under-protected and rapidly shrinking (35). There is an urgent need for more work on both modern and subfossil lemurs from a broad range of habitats.

## References and Notes

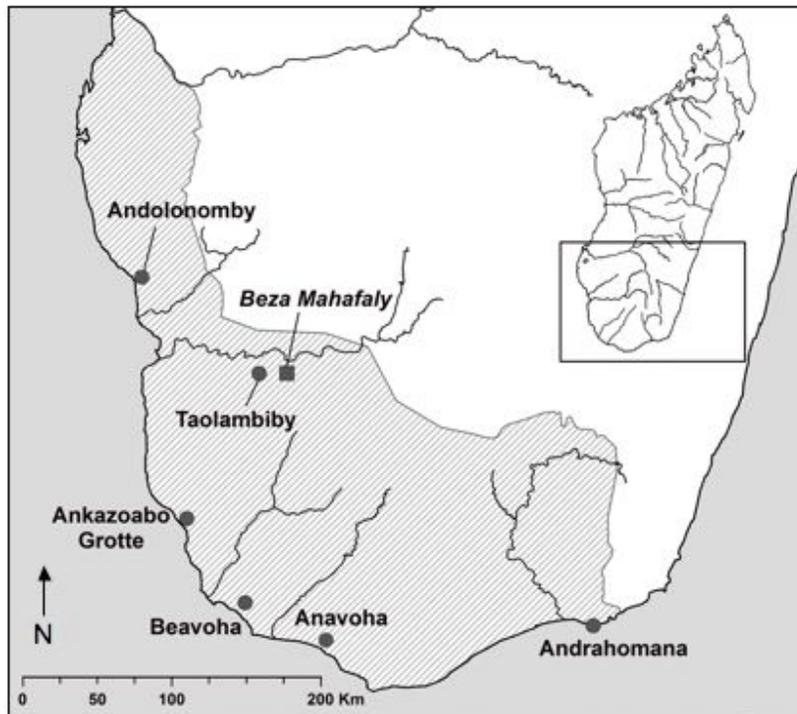
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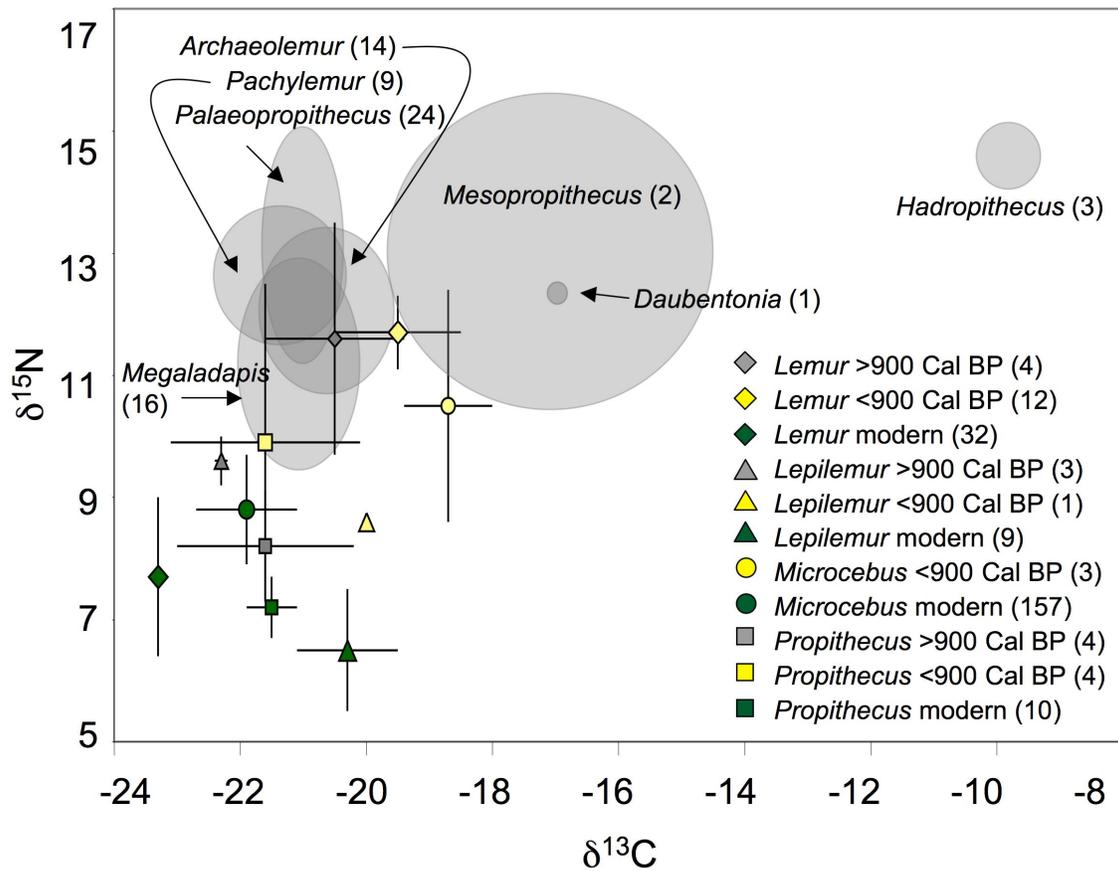
**Table 1** Euclidean distances and niche density overlap ( $\omega$ ) between each of the extant and extinct taxa before and after the decline in extinct species (ca. 900 Cal BP). Blank cells indicate insufficient data for comparisons (15). Small sample sizes prohibited niche overlap calculations for *Lepilemur leucopus*. Numbers in bold identify comparisons between taxa with similar dietary adaptations (18, 19, 21).

Extinct Genus	<i>Lemur catta</i> (Coastal)		<i>Lepilemur leucopus</i> (Inland)		<i>Propithecus verreauxi</i> (Inland)					
	Pre-900 Cal BP	Post-900 Cal BP	Pre-900 Cal BP	Post-900 Cal BP	Pre-900 Cal BP	Post-900 Cal BP				
	Distance	$\omega$	Distance	$\omega$	Distance	$\omega$				
<i>Archaeolemur</i>	<b>0.71</b>	<b>0.75</b>	<b>1.68</b>	<b>0.46</b>	2.45	3.85	3.81	0.00	2.83	
<i>Daubentonia</i>	2.93		2.15							
<i>Hadropithecus</i>	10.60	0.00	9.91	0.00						
<i>Megaladapis</i>	1.50	0.36	2.42	0.18	<b>1.27</b>	<b>2.36</b>	2.31	0.17	1.62	0.22
<i>Mesopropithecus</i>	3.01	0.00	2.42							
<i>Pachylemur</i>	<b>2.19</b>	<b>0.43</b>	<b>3.14</b>	<b>0.05</b>	2.62	4.12	4.02	0.00	3.11	0.11
<i>Palaeopropithecus</i>	2.03	0.53	2.90	0.13	2.53	3.98	<b>3.91</b>	<b>0.002</b>	<b>2.97</b>	<b>0.02</b>
Average	3.28	0.55	3.52	0.42	2.22	3.58	3.51	0.06	2.63	0.15

**Fig. 1** Map of localities included in this study. The Spiny Thicket Ecoregion is highlighted in gray.



**Fig. 2** Mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  ( $\pm 1\sigma$ ) values for all STE subfossil lemur taxa (including both coastal and inland sites) before and after 900 Cal BP, and modern lemurs from BMSR. Isotope values for extinct species are presented as shaded bubbles. N values for each genus are indicated in parentheses. Raw data are reported in [table S1](#).



### Supporting Online Material

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 Methods  
 Tables S1 to S6  
 References