

# Dental Topography Indicates Ecological Contraction of Lemur Communities

Laurie R. Godfrey,<sup>1\*</sup> Julia M. Winchester,<sup>2,3</sup> Stephen J. King,<sup>1</sup> Doug M. Boyer,<sup>2,4</sup> and Jukka Jernvall<sup>3</sup>

<sup>1</sup>Department of Anthropology, University of Massachusetts, Amherst, MA 01003

<sup>2</sup>Interdepartmental Doctoral Program in Anthropological Sciences, Stony Brook University, Stony Brook, NY 11794-8081

<sup>3</sup>Institute for Biotechnology, University of Helsinki, Helsinki, Finland

<sup>4</sup>Department of Anthropology and Archaeology, Brooklyn College, City University of New York, Brooklyn, NY 11210-2850

**KEY WORDS** dental ecology; complexity (OPCR); Dirichlet normal energy (DNE); subfossil lemurs

**ABSTRACT** Understanding the paleoecology of extinct subfossil lemurs requires reconstruction of dietary preferences. Tooth morphology is strongly correlated with diet in living primates and is appropriate for inferring dietary ecology. Recently, dental topographic analysis has shown great promise in reconstructing diet from molar tooth form. Compared with traditionally used shearing metrics, dental topography is better suited for the extraordinary diversity of tooth form among subfossil lemurs and has been shown to be less sensitive to phylogenetic sources of shape variation. Specifically, we computed orientation patch counts rotated (OPCR) and Dirichlet normal energy (DNE) of molar teeth belonging to 14 species of

subfossil lemurs and compared these values to those of an extant lemur sample. The two metrics succeeded in separating species in a manner that provides insights into both food processing and diet. We used them to examine the changes in lemur community ecology in Southern and Southwestern Madagascar that accompanied the extinction of giant lemurs. We show that the poverty of Madagascar's frugivore community is a long-standing phenomenon and that extinction of large-bodied lemurs in the South and Southwest resulted not merely in a loss of guild elements but also, most likely, in changes in the ecology of extant lemurs. *Am J Phys Anthropol* 148:215–227, 2012. ©2012 Wiley Periodicals, Inc.

If there is a place on earth where we can study the ecological consequences of major changes in faunal communities in the recent past, the place is Madagascar. Madagascar's megafauna disappeared over the past two millennia, after the arrival of humans. Among these were 17 species of giant lemur, several species of elephant bird, three hippopotami, a horned crocodile, and a large *Cryptoprocta* carnivore. Some components of the megafauna (including lemurs) were still extant only 500 years ago or more recently still (Simons, 1997; Burney et al., 2004).

A rich subfossil record (now including around 200 dated specimens, with dates for still-extant as well as extinct species) accords us an excellent opportunity to probe the sequence of changes in Madagascar's fauna in some detail (Crowley, 2010). This means that in examining today's faunal communities, we can ask questions regarding ecosystem functioning and change in a species-depleted world. Richard and Dewar (1991) raised the question of the ecological implications of megafaunal extinctions in their review of lemur ecology two decades ago, and others since have approached this question from various perspectives. For example, van Schaik and Kappeler (1996) argued that the still-extant lemur species reveal signs of "evolutionary disequilibrium," i.e., that they behave as they do only because they are transitioning into niches left "vacant" by animals that recently became extinct, and Cuzzo and Sauter (2006) interpreted dental wear and pathology patterns on *Lemur catta* at Beza Mahafaly as by-products of a recent shift in its diet (see also Martin, 1972). Whereas van Schaik and Kappeler's (1996) argument regarding

changes in activity rhythms of extant lemurs has received little support (e.g., Wright, 1999; Curtis and Rasmussen, 2002; Kirk, 2006; Tattersall, 2008), Cuzzo and Sauter's (2006) argument in favor of a recent dietary shift and thus, specifically, anatomical evidence of evolutionary disequilibrium for ring-tailed lemurs at Beza Mahafaly (see also Millette et al., 2009; Sauter and Cuzzo, 2009; Cuzzo FP and Sauter ML, in prep., "Dental evidence indicates evolutionary disequilibrium among sympatric diurnal lemurs in southern Madagascar") has garnered support from research at a nearby fossil site, documenting changes in ring-tailed lemur stable isotopes over time (Crowley, 2009; Crowley BE,

Additional Supporting Information may be found in the online version of this article.

Grant sponsor: NSF; Grant number: BCS-0721233. Grant sponsor: NSF; Grant number: BCS-0622544. Grant sponsor: John Simon Guggenheim Foundation. Grant sponsor: Evolving Earth Foundation Grant. Grant sponsor: American Society of Mammalogists Grant. Grant sponsor: NSF GRFP Grant.

\*Correspondence to: Laurie R. Godfrey, Department of Anthropology, 240 Hicks Way, University of Massachusetts, Amherst, MA 01003, United States. E-mail: lgodfrey@anthro.umass.edu

Received 1 March 2011; accepted 4 August 2011

DOI 10.1002/ajpa.21615  
Published online in Wiley Online Library  
(wileyonlinelibrary.com).

Godfrey LR, Guilderson TP, Zermeño P, Koch PL, and Dominy NJ, submitted, “Extinction and ecological retreat in a community of primates”). Furthermore, aspects of dental form suggested to Yamashita (1998) and Boyer (2008) that several lemurids may be relying on diets to which they are not primarily adapted. This is hardly surprising, as extinctions of the speed and magnitude manifested in Madagascar cannot occur without having ripple effects on surviving plants and animals.

Feeding ecology is of special interest because of the role primates play as seed dispersers, and thus potentially as “umbrella” taxa (Lyons et al., 2005; Lambert, 2011; Norconk et al., 2011), with widespread effects on numerous other species. Variation in frugivore diversity and behavior can strongly affect the dispersal of seeds, establishment of seedlings, and ultimately the distribution of trees (Bleher and Bohning-Gaese, 2001), but there is a certain amount of redundancy in seed disperser communities, which suggests that communities can suffer a fair amount of faunal loss without jeopardizing their ecological integrity (Bollen et al., 2004). The question is, just how much has guild structure of mammal communities in Madagascar been altered by extinction (Muldoon and Goodman, 2010)? Have key elements been lost? To what degree have extant lemurs moved into niches formerly occupied by their larger bodied counterparts? Or are the niches occupied by extinct lemurs “vacant” today?

In this article, we seek to characterize the dietary niche space occupied by primates in Madagascar in the recent past, and to understand how it has changed. While it is impossible to know precisely the ecological roles of extinct species, a number of tools offer clues (Walker, 1981). Dental morphology is one, which has been used to reconstruct the diets of extinct lemurs (Tattersall, 1973; Jungers et al., 2002; Godfrey et al., 2006). However, the extraordinary diversity of tooth form among these animals confounds the application of traditionally used metrics such as shearing quotients (SQs) (Kay et al., 1978; Kay, 1984; Covert, 1986) in certain groups. SQs and shearing ratios (SRs) cannot be measured in animals lacking shearing crests and cannot be compared in species with nonhomologous shearing crests. For this reason, for example, no archaeolemurids were included in Jungers et al.’s (2002) SQ comparisons, and *Daubentonia* was omitted from Bunn et al.’s (2011) correlation analysis.

Here, we use dental topography, which is not limited by extremes in morphological disparity in its ability to quantify teeth in a comparable manner. Dental topography has also been shown to be less sensitive to phylogenetic sources of shape variation than shearing metrics and uncorrelated with size (M’Kirera and Ungar, 2003; Evans et al., 2007; Boyer, 2008; Boyer et al., 2010; Bunn et al., 2011). Comparing distantly related animals (carnivores and rodents) differing greatly in gross tooth shape, Evans et al. (2007) demonstrated that the phenotypic “complexity” of dental occlusal surfaces captures variation in diet, independent of phylogeny. Applying phylogenetic methods to a large sample of euarchontans (including many primates), Boyer (2008) made a similar argument regarding dental topographic relief, i.e., the dietary signal is stronger than the phylogenetic signal.

We compute orientation patch count rotated (OPCR) or “dental complexity” and Dirichlet normal energy (DNE) metrics for 14 species of extinct lemurs, and we compare these values to those generated for a sample of 21

species of extant lemurs representing all surviving families and almost all surviving genera. Both OPCR and DNE have been reported to carry a dietary signal (Evans et al., 2007; Bunn et al., 2011). Orientation patch counts increase with increasing complexity of the occlusal surface of the tooth because of, for example, increased enamel folding, a higher number of cusps, or greater enamel crenulations. DNE is a measure of the degree to which a surface is curved and has been shown to be strongly correlated with measures of dental topographic “relief” (the latter being the relationship between a tooth’s 3D surface area and 2D footprint; M’Kirera and Ungar, 2003; King et al., 2005; Boyer, 2008; Bunn et al., 2011). DNE tends to increase with increasing curvature of the occlusal surface. Increasing curvature could result from taller or sharper cusps, or more or sharper shearing crests, for example. Bunn et al. (2011) record an  $r^2$  of 0.76 for the relationship between DNE and relief for a sample of living strepsirrhines, but suggest DNE may be preferable to relief because of its robustness to methodological assumptions and difference in data preparation. For these reasons, we use DNE instead of relief. Traditional measures of shearing capacity (SQ and SR) correlate more strongly with DNE than with OPCR, but far more weakly with DNE than does relief (Bunn et al., 2011). DNE is poorly correlated with OPCR ( $r^2 = 0.10$ ; Bunn et al., 2011) despite the fact that the two measures tend to increase with greater folivory (or more fiber in the diet); thus, the two are not redundant.

As we focus on teeth to assess the diets and ecology of living and fossil lemurs, this work fits directly the “dental ecology” theme described by Cuozzo and Sautner (this volume). Our tasks in this article are two fold. First, we apply new tools of dental topographic analysis to extinct lemurs in an effort to reconstruct aspects of their diets and food processing capabilities. Second, we examine the implications of the patterns we find for changes in dietary guilds of primates in Madagascar associated with the Holocene extinctions. For the latter exercise, we focus specifically on the arid and subarid ecoregions of Southern and Southwestern Madagascar. Understanding the status of primate communities in arid parts of Madagascar is particularly important, because mammalian species richness is significantly lower in dry forests than in humid forests, and therefore, of the remaining primate communities, those in the drier parts of Madagascar may be most vulnerable to extinction (Muldoon and Goodman, 2010). Furthermore, the South and Southwest are rich in sites containing thousands of bones of extinct and extant lemurs and thus least likely to be affected by extinct species sampling bias.

## MATERIALS AND METHODS

### Study sample and dietary categories

Our sample includes a total of 113 second mandibular molars of individuals belonging to 35 species in 22 lemur genera. All extinct and extant lemur genera except *Allocebus* are represented in this sample (see Supplementary data). Individuals exhibiting minimal amounts of wear were selected for these comparisons so that the results would not be confounded by wear. The comparative sample of living lemurs (84 individuals belonging to 21 species in 14 genera; Table 1) comprises the Malagasy-lemur subset of the sample of extant prosimians described in Bunn et al. (2011) and originally studied by Boyer (2008), who collected relief data. For those individ-

TABLE 1. Extant taxa comprising the study sample, number of individuals in each, assigned dietary category, and references used to assign that category

Taxon	N	Diet	Key references
<i>Indri indri</i>	9	Folivore	19
<i>Propithecus edwardsi</i>	1	Folivore	11
<i>P. diadema</i>	3	Folivore	13, 19–20
<i>P. verreauxi</i>	3	Folivore	24–25, 36
<i>Avahi laniger</i>	7	Folivore	2, 6, 10
<i>Lemur catta</i>	6	Frugivore/omnivore	27, 29, 31, 36
<i>Eulemur fulvus</i>	2	Frugivore/omnivore	4, 21
<i>E. rufus</i>	6	Frugivore/omnivore	8, 17, 31
<i>Varecia rubra</i>	2	Frugivore/omnivore	34
<i>V. variegata</i>	6	Frugivore/omnivore	1, 16, 23
<i>Hapalemur griseus</i>	5	Folivore	9
<i>Prolemur simus</i>	2	Folivore	32
<i>Daubentonia madagascariensis</i>	6	Frugivore/omnivore	15, 30
<i>Cheirogaleus major</i>	5	Frugivore/omnivore	14
<i>C. medius</i>	3	Frugivore/omnivore	3
<i>Mirza coquereli</i>	3	Frugivore/omnivore	12, 18
<i>Phaner furcifer</i>	3	Frugivore/omnivore	28
<i>Microcebus griseorufus</i>	7	Frugivore/omnivore	7, 22
<i>Lepilemur ruficaudatus</i>	1	Folivore	5
<i>L. edwardsi</i>	1	Folivore	4, 33, 35
<i>L. leucopus</i>	3	Folivore	26

References: <sup>1</sup>Balko, 1998; <sup>2</sup>Faulkner and Lehman, 2006; <sup>3</sup>Fietz and Ganzhorn, 1999; <sup>4</sup>Ganzhorn, 1988; <sup>5</sup>Ganzhorn, 2002; <sup>6</sup>Ganzhorn et al., 1985; <sup>7</sup>Génin, 2008; <sup>8</sup>Gerson, 2000; <sup>9</sup>Grassi, 2006; <sup>10</sup>Harcourt, 1991; <sup>11</sup>Hemingway, 1998; <sup>12</sup>Hladik et al., 1980; <sup>13</sup>Irwin, 2008; <sup>14</sup>Lahann, 2007; <sup>15</sup>Lhota et al., 2008; <sup>16</sup>Morland, 1992; <sup>17</sup>Overdorff, 1993; <sup>18</sup>Pages, 1980; <sup>19</sup>Powzyk, 1998; <sup>20</sup>Powzyk and Mowry, 2003; <sup>21</sup>Rasmussen, 1999; <sup>22</sup>Rasoazabary, 2011; <sup>23</sup>Ratsimbazafy, 2002; <sup>24</sup>Richard, 1974; <sup>25</sup>Richard, 1978; <sup>26</sup>Russell, 1980; <sup>27</sup>Sauter, 1991; <sup>28</sup>Schulke, 2003; <sup>29</sup>Simmen et al., 2003; <sup>30</sup>Sterling, 1994; <sup>31</sup>Sussman, 1974; <sup>32</sup>Tan, 1999; <sup>33</sup>Thalmann, 2001; <sup>34</sup>Vasey, 2000; <sup>35</sup>Warren and Crompton, 1997; <sup>36</sup>Yamashita, 2002.

uals ( $N = 71$ ) for which we also measured m1 area (i.e., m1 mesiodistal  $\times$  m1 buccolingual diameter) as a surrogate for body size, we confirmed that neither OPCR nor DNE is correlated with “size” ( $r = -0.03$  for OPCR and m1 area, NS;  $r = -0.01$  for DNE and m1 area, NS).

For extinct lemur taxa, we took impressions (President Plus Jet, regular body, Coltène) of the second mandibular molars of 29 individuals belonging to 14 species and to all eight extinct genera (Table 2). We made high-quality plaster casts (Fujirock, GC Europe, Leuven, Belgium) that were scanned using a three-dimensional (3D) piezo scanner (MDX-15, Roland) with 50- $\mu$ m resolution. An additional extinct lemur species, *Daubentonia robusta*, the giant aye-aye, belongs to an extant genus. Molars of *D. robusta* could not be included in our sample because none have been found; of all of the teeth of this species, only the incisors are known (MacPhee and Raholimavo, 1988). However, the feeding adaptations of *Daubentonia* (hypertrophied incisors, modifications of the hand) are highly derived among lemurs and known to be shared by both extinct and extant species (Lamberton, 1934; MacPhee and Raholimavo, 1988; Simons, 1994).

Bunn et al. (2011) characterized extant Malagasy lemurs as members of one of three diet preference groups (folivore, omnivore, and frugivore) on the basis of a review of the literature. (No Malagasy lemur can be classified as insectivorous.) Here, we followed Bunn et al.’s (2011) dietary classification system for extant

TABLE 2. Extinct taxa in the study sample, number of individuals in each taxon, and primary ecoregion or ecoregions

Taxon	N	Region
<i>Archaeoindris fontoynontii</i>	1	Central highlands
<i>Palaeopropithecus ingens</i>	2	South and Southwest
<i>P. maximus</i>	2	Central highlands
<i>P. kelyus</i>	1	Northwest
<i>Babakotia radofilai</i>	3	North and Northwest
<i>Mesopropithecus globiceps</i>	4	South and Southwest
<i>M. pithecooides</i>	2	Central highlands
<i>M. dolichobrachion</i>	2	North
<i>Archaeolemur majori</i>	1	South and Southwest
<i>A. sp. cf. edwardsi</i>	1	North and Northwest
<i>Hadropithecus stenognathus</i>	1	South and Southwest
<i>Pachylemur insignis</i>	6	South and Southwest
<i>P. jullyi</i>	2	Central highlands
<i>Megaladapis edwardsi</i>	1	South and Southwest

lemurs but combined their “frugivores” and “omnivores” into a single category, thus highlighting the distinction between lemurs that, while consuming varying amounts of fruit, depend primarily on leaves for protein (considered here “folivores”) and others for whom leaves are less important or sometimes never consumed. These species (considered here “frugivores/omnivores”) tend to supplement fruit with insects, insect larvae, other animal matter, or insect secretions.

The two groups differ in their roles as seed dispersers. Folivores tend to have guts that are destructive to seeds, while frugivores and omnivores tend to have simple guts that promote seed dispersal (endozoochory). This is a distinction of ecological importance and one that is critical to meaningful reconstructions of primate communities of the past.

For our analysis of changes in dental topographic eco-space, we selected only those lemurs that recently lived or still live in Madagascar’s Spiny Thicket or Succulent Woodland ecoregions (Burgess et al., 2004). This initially included 15 species (nine extant and six extinct). One species that could not be sampled directly was the giant extinct aye-aye, *Daubentonia robusta*. Because all fossil evidence points to *D. robusta* and the extant *D. madagascariensis* having similar diets, we used the latter as a proxy for the former when analyzing ecological changes in the South. Our total sample, then, for analyzing changes in dental topographic space from past to present in Southern Madagascar was 16 species (nine extant and seven “extinct”) representing every lemur genus present in this region of Madagascar today or in the recent past (Table 3). This included 21 individuals belonging to extinct species and 32 belonging to extant species.

### Variables measured

Two shape quantification metrics were calculated for each second lower molar in our database—OPCR and DNE (Fig. 1). OPCR measures the surface “complexity” of the tooth, and DNE uses changes in vectors normal to the surface to capture surface curvature. Scanned and digitized casts of second lower molars of extinct lemurs were converted to digital elevation models (DEMs) and scaled to the same length. The surface was then divided into “patches” of roughly equal orientation based on slope and topographic elevation, and the number of patches was counted to yield an “orientation patch count” or OPC, following Evans et al. (2007). To correct for variation in patch count due to slight differences in

TABLE 3. Primates of the South and Southwest (past and present). Taxa sampled are bolded

Genus and species	Past	Present
<b><i>Propithecus verreauxi</i></b>	x	x
<b><i>Lemur catta</i></b>	x	x
<b><i>Eulemur rufus</i></b>	x	x
<b><i>Cheirogaleus medius</i></b>	x	x
<b><i>Mirza coquereli</i></b>	x	x
<b><i>Phaner furcifer</i></b>	x	x
<b><i>Lepilemur ruficaudatus</i></b> , <i>L. leucopus</i> , <i>L. petteri</i>	x	x
<b><i>Microcebus griseorufus</i></b> , <i>M. murinus</i> , <i>M. berthae</i>	x	x
<b><i>Megaladapis edwardsi</i></b> , <i>M. madagascariensis</i>	x	–
<b><i>Archaeolemur majori</i></b>	x	–
<b><i>Hadropithecus stenognathus</i></b>	x	–
<b><i>Pachylemur insignis</i></b>	x	–
<b><i>Daubentonia robusta</i></b> <sup>a</sup>	x	–
<b><i>Mesopropithecus globiceps</i></b>	x	–
<b><i>Palaeopropithecus ingens</i></b>	x	–

<sup>a</sup> We used *D. madagascariensis* as a proxy for *D. robusta* in the past.

orientation of the tooth cast in the x–y plane, we averaged eight calculations, each made with the tooth cast fixed in a slightly different orientation. These averages are labeled OPCR, or “OPC rotated” values.

Data from subfossil specimens were initially prepared for DNE calculation by interpolating 3D polygonal surface meshes from the original DEMs using Surfer 8 (Golden Software) and SurferManipulator (Evans et al., 2007). The interpolation process created irregular jagged projections extending downward from mesh edges, representing the inferiormost aspects of tooth crowns detectable by the laser scanner. Because the irregularity of these projections could unpredictably influence DNE calculations, the Surface Editor module of Amira (Visage Imaging) was used to remove all elements of the mesh below the lowest point of the talonid basin for each molar. The SmoothSurface function of Amira was then used to smooth each surface mesh with 100 iterations and a lambda-value of 0.6. Finally, meshes were down-

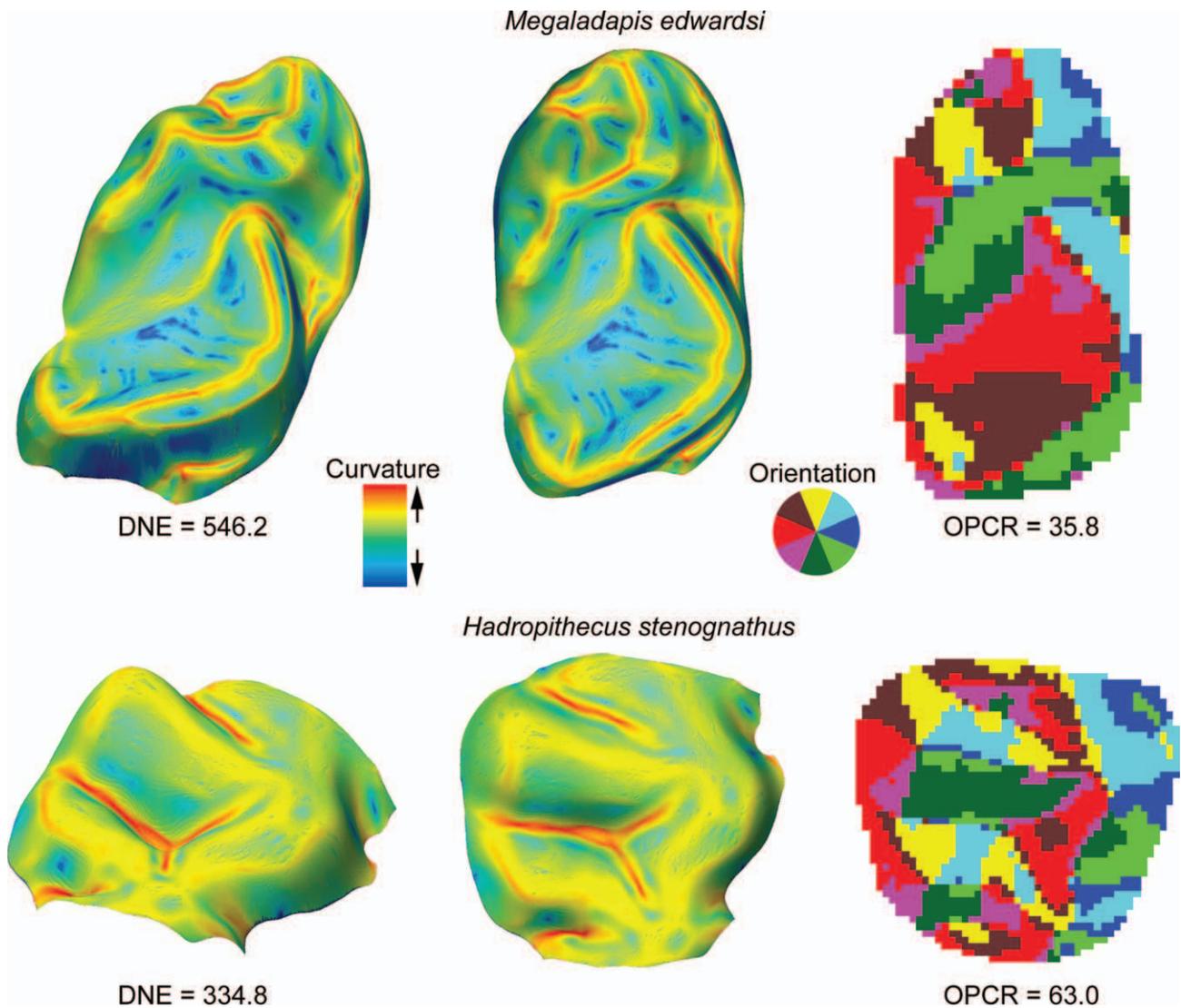


Fig. 1. Mapping of OPC and DNE across tooth surfaces is depicted for molars of *Megaladapis edwardsi* and *Hadropithecus stenognathus* in three-quarter and occlusal views. For DNE maps, warmer colors indicate higher curvature, while cooler colors indicate lower curvature. OPCR and total DNE values for each specimen are listed below the appropriate surface maps.

TABLE 4. Mean values (and standard errors in parentheses) of OPCR and DNE by species

Taxon	N	OPCR	DNE
<i>Archaeoindris fontoynontii</i> <sup>a</sup>	1	43.1	402.0
<i>Palaeopropithecus ingens</i> <sup>a,b</sup>	2	51.5 (1.4)	334.9 (6.5)
<i>P. maximus</i> <sup>a</sup>	2	48.0 (1.1)	220.4 (22.1)
<i>P. kelyus</i> <sup>a</sup>	1	47.5	276.6
<i>Babakotia radofilai</i> <sup>a</sup>	3	69.4 (3.8)	215.5 (18.7)
<i>Mesopropithecus globiceps</i> <sup>a,b</sup>	4	65.8 (1.1)	229.9 (37.8)
<i>M. pithecooides</i> <sup>a</sup>	2	63.1 (5.0)	244.3 (0.1)
<i>M. dolichobrachion</i> <sup>a</sup>	2	59.9 (0.8)	195.6 (13.6)
<i>Archaeolemur majori</i> <sup>a,b</sup>	1	46.0	151.3
<i>A. sp. cf. edwardsi</i> <sup>a</sup>	1	66.1	182.5
<i>Hadropithecus stenognathus</i> <sup>a,b</sup>	1	63.0	334.8
<i>Pachylemur insignis</i> <sup>a,b</sup>	6	37.9 (1.3)	148.5 (11.0)
<i>P. jullyi</i> <sup>a</sup>	2	44.9 (1.9)	198.6 (14.5)
<i>Megaladapis edwardsi</i> <sup>a,b</sup>	1	35.8	546.2
<i>Indri indri</i>	9	55.4 (1.9)	220.3 (5.6)
<i>Propithecus edwardsi</i>	1	51.0	297.4
<i>P. diadema</i>	3	50.9 (1.5)	240.2 (22.7)
<i>P. verreauxi</i> <sup>b</sup>	3	46.3 (1.8)	250.1 (15.6)
<i>Avahi laniger</i>	7	55.4 (1.0)	348.1 (15.7)
<i>Lemur catta</i> <sup>b</sup>	6	39.9 (1.0)	225.0 (9.2)
<i>Eulemur fulvus</i>	2	37.7 (3.4)	246.5 (26.8)
<i>E. rufus</i> <sup>b</sup>	6	40.9 (1.0)	248.1 (18.5)
<i>Varecia rubra</i>	2	35.0 (4.0)	180.8 (1.4)
<i>V. variegata</i>	6	36.0 (1.3)	209.8 (12.5)
<i>Hapalemur griseus</i>	5	51.3 (2.8)	268.0 (10.4)
<i>Prolemur simus</i>	2	74.0 (10.9)	336.6 (7.0)
<i>Daubentonia madagascariensis</i> <sup>c</sup>	6	46.8 (3.3)	105.1 (3.3)
<i>Cheirogaleus major</i>	5	40.9 (2.6)	183.0 (30.4)
<i>C. medius</i> <sup>b</sup>	3	41.8 (4.3)	163.3 (21.9)
<i>Mirza coquereli</i> <sup>b</sup>	3	43.3 (0.6)	246.8 (9.7)
<i>Phaner furcifer</i> <sup>b</sup>	3	46.0 (0.6)	188.8 (9.5)
<i>Microcebus griseorufus</i> <sup>b</sup>	7	45.9 (1.0)	274.7 (7.2)
<i>Lepilemur ruficaudatus</i> <sup>b</sup>	1	36.9	331.3
<i>L. edwardsi</i>	1	33.4	318.4
<i>L. leucopus</i> <sup>b</sup>	3	34.3 (1.1)	255.2 (9.1)

<sup>a</sup> Extinct.

<sup>b</sup> Species present in the South and/or Southwest.

<sup>c</sup> Used as a proxy for *D. robusta* in the South and Southwest.

sampled to 10,000 polygonal faces with the Simplifier module of Amira, and DNE was calculated from prepared surfaces using Teether 1.0, a MATLAB application (Bunn et al., 2011).

It should be noted that data from extant specimens were prepared in a slightly different fashion, most notably in that they were created in Amira from  $\mu$ CT scans of molar casts as opposed to laser scans. Further, for the purposes of preparing the data for DNE calculation, models were cropped to remove material inferior to the inferred root-crown junction. Bunn et al. (2011) showed that DNE is relatively robust to variable methods of cropping molar tooth models, and so this should not overly affect the comparability of these data sets. In all other regards, the data preparation was the same for both extinct and extant data sets.

### Data analysis

We used ANOVA to verify the significance of differences in OPCR and DNE for lemur species and discriminant function analysis (DFA, SPSS) of the correlation matrix with the jack-knife (leave out one) classification method to predict diets of “unknowns.” We used cross-validation to verify the efficacy of post hoc classification for cases with known diets. This means that dietary predictions were made for each individual belonging to

extant species (i.e., individuals with known diets) using functions derived from all cases except that one.

To document changes in ecological space in Southern and Southwestern Madagascar, we used the convex hull (or convex envelope) area function in Mathematica. This function measures the space occupied by selected groups on bivariate plots. A convex hull is the minimal geometric envelope containing all of the points that belong to the relevant “set” or group. We plotted species mean values for OPCR and DNE, and then compared sets, for example, lemur species in the past vs. in the present, to assess temporal changes in “dental ecological space” in Southern and Southwestern Madagascar.

## RESULTS

### Predicting diet

Table 4 gives mean values and standard errors of the mean for OPCR and DNE for all of the species in our sample. For our sample of 113 individuals, these two variables are uncorrelated ( $r = 0.169$ , NS) and thus provide largely nonredundant information (the correlation is significant at the 0.1 confidence level and thus might be viewed as weakly positive). Table 5 gives the diets predicted using DFA of OPCR alone, DNE alone and the two together; it also provides, for each species, the probability of membership in the group predicted on the basis of OPCR and DNE together.

An ANOVA calculated for differences in OPCR by species yielded an  $F$  of 13.8 ( $df = 34, 78, P < 0.001$ ). DFA of OPCR, taken alone, signaled significant differences between folivores and frugivore/omnivores. This analysis produced a highly significant function (Wilks' Lambda = 0.715, chi-square = 27.42 with 1  $df, P < 0.001$ ), with folivores tending to have high positive scores and frugivore/omnivores tending to have negative scores. A total of 79.8% of grouped individuals were correctly classified; the same success rate held for cross-validated cases.

Similarly, ANOVA revealed significant differences among species in DNE (or energy) ( $F = 13.4, df 34, 78, P < 0.001$ ). DNE was also successful in distinguishing folivores from frugivore/omnivores using DFA. The single function had a Wilks' Lambda of 0.753 and a chi-square of 23.08 ( $df = 1, P < 0.001$ ). Again, folivores had positive values on this function, and frugivore/omnivores had negative values. The success rate was lower than for OPCR, with 64.3% of grouped individuals correctly classified, both with and without cross-validation.

Of greater interest than the number of misclassified individuals is the number of misclassified species. Of the 21 extant lemur species in our analysis, five species were incorrectly classified using OPCR alone, and five species were incorrectly classified using DNE alone. Thus, at the species level, the success rate for both was identical—76.2%. In only one case (*Microcebus griseorufus*), however, did the two make the same error.

By combining OPCR and DNE into a single function, some resolution of these conflicting signals was possible. Taken together, OPCR and DNE do a better job of classifying individuals belonging to extant species in a manner consistent with their “known” diets. Unsurprisingly, DFA produced a highly significant function (Wilks' Lambda = 0.589, chi-square of 42.9,  $df = 2, P < 0.001$ ). Both complexity and energy were positively correlated with scores of individuals on Function 1, complexity more strongly than energy. Post hoc tests revealed 83.3% of grouped individuals to be correctly classified; this

TABLE 5. Predicted diets, with probability of membership in predicted group

Taxon	OPCR alone	DNE alone	OPCR and DNE	Probability of membership in predicted group (based on OPCR and DNE)
		Extinct species		
<i>Archaeoindris fontoynontii</i>	FR-OM	FOL	FOL	0.92
<i>Palaeopropithecus ingens</i>	FOL	FOL	FOL	0.93
<i>P. maximus</i>	—	—	—	—
<i>P. kelyus</i>	FOL	FOL	FOL	0.69
<i>Babakotia radofilai</i>	FOL	FR-OM	FOL	0.92
<i>Mesopropithecus globiceps</i>	FOL	—	FOL	0.91
<i>M. pithecoides</i>	FOL	FOL	FOL	0.92
<i>M. dolichobrachion</i>	FOL	FR-OM	FOL	0.76
<i>Archaeolemur majori</i>	FR-OM	FR-OM	FR-OM	0.86
<i>A. sp. cf. edwardsi</i>	FOL	FR-OM	FOL	0.87
<i>Hadropithecus stenognathus</i>	FOL	FOL	FOL	0.99
<i>Pachylemur insignis</i>	FR-OM	FR-OM	FR-OM	0.95
<i>P. jullyi</i>	FR-OM	FR-OM	FR-OM	0.74
<i>Megaladapis edwardsi</i>	FR-OM	FOL	FOL	0.98
		Extant species		
<i>Indri indri</i>	FOL	FR-OM	FOL	0.70
<i>Propithecus edwardsi</i>	FOL	FOL	FOL	0.85
<i>P. diadema</i>	FOL	FR-OM	FOL	0.65
<i>P. verreauxi</i>	FOL	FOL	FOL	0.53
<i>Avahi laniger</i>	FOL	FOL	FOL	0.95
<i>Lemur catta</i>	FR-OM	FR-OM	FR-OM	0.79
<i>Eulemur fulvus</i>	FR-OM	—	FR-OM	0.74
<i>E. rufus</i>	FR-OM	FR-OM	FR-OM	0.66
<i>Varecia rubra</i>	FR-OM	FR-OM	FR-OM	0.94
<i>V. variegata</i>	FR-OM	FR-OM	FR-OM	0.88
<i>Hapalemur griseus</i>	FOL	FOL	FOL	0.72
<i>Prolemur simus</i>	FOL	FOL	FOL	0.99
<i>Daubentonia madagascariensis</i>	—	FR-OM	FR-OM	0.89
<i>Cheirogaleus major</i>	FR-OM	FR-OM	FR-OM	0.82
<i>C. medius</i>	FR-OM	FR-OM	FR-OM	0.87
<i>Mirza coquereli</i>	FR-OM	FOL	FR-OM	0.60
<i>Phaner furcifer</i>	FR-OM	FR-OM	FR-OM	0.75
<i>Microcebus griseorufus</i>	FOL	FOL	FOL	0.62
<i>Lepilemur ruficaudatus</i>	FR-OM	FOL	FOL	0.54
<i>L. edwardsi</i>	FR-OM	FOL	FR-OM	0.65
<i>L. leucopus</i>	FR-OM	FOL	FR-OM	0.83

percentage was slightly lower (81.0%) when cross-validation was used. Only three of the 21 species were incorrectly classified, including the one that was “missed” by both OPCR and DNE (*Microcebus griseorufus*), and two species in the same genus (*Lepilemur edwardsi* and *L. leucopus*), although a third species of *Lepilemur* (*L. ruficaudatus*) was correctly classified (Table 5). At the species level, post hoc classification success was 85.7%—considerably higher than for OPCR or DNE taken alone. Some species gave clear signals, with probabilities of membership in their predicted group of over 90% and a signal consistent for both OPCR and DNE. This included the most specialized of lemurs (e.g., *Prolemur simus* with a probability of membership in the folivore category of 0.99; *Avahi laniger* with a probability of membership in the same category of 0.95; and *Varecia rubra* with a probability of membership in the frugivore/omnivore category of 0.94). All indriids and lemurids were correctly classified (albeit some without strong confidence in classification success)—i.e., the indriids as folivores, and lemurids, with the exceptions of *Hapalemur* and *Prolemur*, as frugivore/omnivores. *Daubentonia madagascariensis* was correctly classified as a frugivore/omnivore. Only the most insectivorous of cheirogaleids in our sample, *M. griseorufus*, was incorrectly classified;

all other cheirogaleids emerged correctly as frugivore/omnivores.

The predicted diets of the 14 extinct lemur species in our database, based on OPCR alone, DNE alone, and the two taken together, are also listed in Table 5. Table 6 compares results of this study to those of prior reconstructions of their diets; the match is obvious. Eight of the 14 species had very high probabilities of membership in their predicted groups (>0.90). These included *Hadropithecus stenognathus*, *Megaladapis edwardsi*, *Archaeoindris fontoynontii*, *Palaeopropithecus ingens*, *Babakotia radofilai*, *Mesopropithecus globiceps*, and *M. pithecoides* (all predicted to be folivores), and *Pachylemur insignis* (classified as a frugivore/omnivore). All palaeopropithecids, with the exception of *Palaeopropithecus maximus* (which scored, on average, equidistantly between the folivore and frugivore/omnivore centroids) were classified as folivores. Both species belonging to the genus *Pachylemur*, a lemurid, emerged as frugivore/omnivores. The archaeolemurids showed evidence of dietary diversity, with *Hadropithecus* scoring definitively as a folivore, and *Archaeolemur* as having more fruit in its diet. In this case, *A. majori* was classified as a frugivore/omnivore and *A. sp. cf. edwardsi* as a folivore.

TABLE 6. Extinct taxa, prior dietary assessments (with references), and dietary assessment, this study

Taxon	Prior dietary inferences	Sources	This study
<i>Archaeoindris</i>	Folivore	4–6	Folivore
<i>Palaeopropithecus</i>	Folivore, some fruit and seeds	4–9	Folivore (mixed)
<i>Babakotia</i>	Folivore, some fruit and seeds, hard objects	4–8	Folivore
<i>Mesopropithecus</i>	Folivore/frugivore, some seeds	4–8	Folivore
<i>Archaeolemur</i>	Frugivore, omnivore, hard object feeder, generalist	1, 4–10, 13, 15–17	Frugivore/omnivore (generalist, mixed)
<i>Hadropithecus</i>	Folivore, CAM or C <sub>4</sub> foods, underground storage organs?	2–7, 12–13, 15–16	Folivore
<i>Pachylemur</i>	Frugivore, foods tougher or more obdurate than those consumed by <i>Varecia</i>	3–8, 10–11, 14	Frugivore/omnivore
<i>Megaladapis</i>	Folivore	4–9, 13	Folivore

Sources: <sup>1</sup>Burney et al., 1997; <sup>2</sup>Burney et al., 2004; <sup>3</sup>Crowley et al., 2011; <sup>4</sup>Godfrey et al., 1997; <sup>5</sup>Godfrey et al., 2004; <sup>6</sup>Godfrey et al., 2005; <sup>7</sup>Jungers et al., 2002; <sup>8</sup>Muchlinski et al., 2011; <sup>9</sup>Rafferty et al., 2002; <sup>10</sup>Ravosa, 1991; <sup>11</sup>Ravosa, 1992; <sup>12</sup>Ryan et al., 2008; <sup>13</sup>Scott et al., 2009; <sup>14</sup>Seligsohn and Szalay, 1974; <sup>15</sup>Tattersall, 1973; <sup>16</sup>Tattersall, 1982; <sup>17</sup>Vasey et al., in press.

TABLE 7. Comparison of convex hulls in the South and Southwest

Sample	Area
All extinct and extant species in the South and Southwest	8,331.02
Subset comprising all extinct species	7,724.63
Subset comprising all extant species	1,224.45
All frugivores and omnivores in the past (including extant species)	937.14
All folivores in the past (including extant species)	5,735.0
Extinct frugivores/omnivores only	187.86
Extant frugivores/omnivores only	408.71
Extinct folivores only	1,817.61
Extant folivores only	463.47

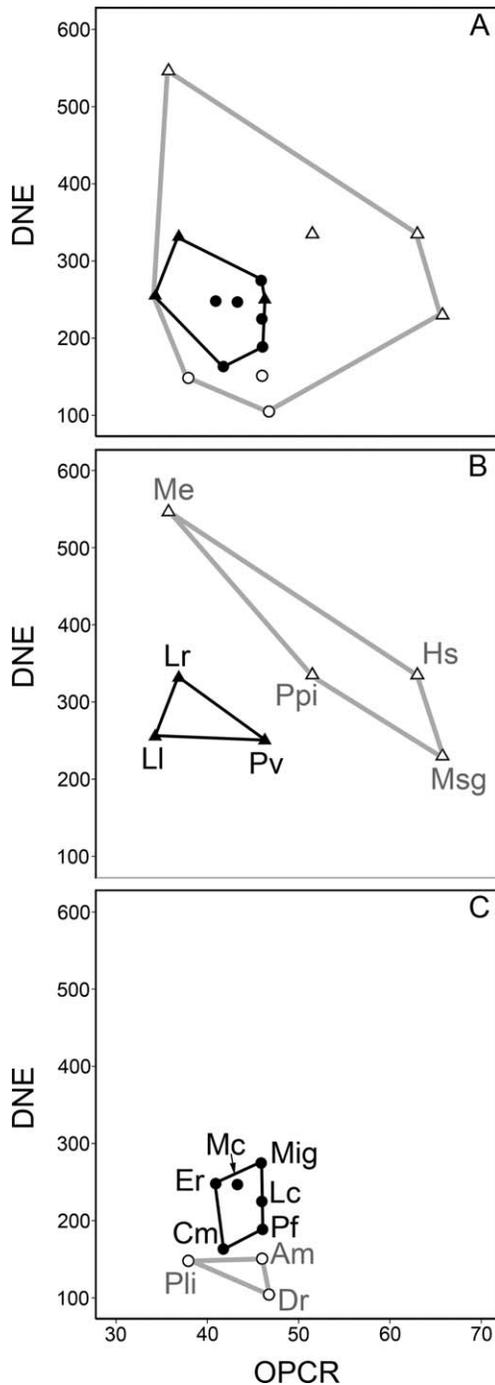
In all cases, when scores for OPCR and DNE are both high (e.g., *Prolemur simus*, *Hadropithecus stenognathus*), individuals are classified as having a diet dominated by structural carbohydrates (folivory). When scores for OPCR and DNE are both low (e.g., *Daubentonia madagascariensis*, *Varecia* spp., most cheirogaleids, *Pachylemur* spp., and *Archaeolemur majori*), individuals are classified unequivocally as frugivorous/omnivorous. Classification is less certain when DNE scores are higher than expected given the corresponding scores for OPCR, or when OPCR scores are higher than expected given DNE scores. Such deviations from a simple linear relationship account for the poor correlation between OPCR and DNE, but may provide useful information with regard to food processing or other aspects of the ecology of the species.

In our samples, the percentage of extant species that we classified (a priori) as folivorous was 47.6, which is slightly higher than the percentage of extant species classified by DFA as folivorous (42.9). In contrast, 10/14 (71.4%) of extinct species were classified by DFA as folivorous, one (7.1%) as equivocal, and only three (21.4%) as frugivorous/omnivorous. *Daubentonia robusta* (a likely frugivore/omnivore) is not included in this sample, but even with this species included, the percentage of frugivore/omnivores in our sample of extinct lemur species is low, and the percentage of folivores (66.7%) extraordinarily high. Finally, it is noteworthy that eight of the 14 sampled extinct lemurs have probabilities of membership in the predicted group higher than 0.90.

### Econiche contraction in the South and Southwest

The dental topographic ecospace occupied by lemurs in Southern and Southwestern Madagascar has contracted dramatically over the past 2000 years (Table 7, Fig. 2). This applies to both folivores and frugivore/omnivores. Figure 2A graphically shows the contraction of total dental topographic econiche space. Extant species fall well within the convex hull that comprises total dental topographic niche space. Panel B compares extinct to extant folivores, and Panel C compares extinct to extant frugivore/omnivores. The extinct species have the most extreme (highest and lowest) values for both OPCR and DNE. There is no overlap between the econiche spaces occupied by extinct vs. extant folivores or extinct vs. extant frugivore/omnivores. These differences are not simply a reflection of the loss of large-bodied species, as neither OPCR nor DNE is correlated with body size in our sample.

To interpret this contraction, we must consider the biological significance of variation in OPCR and DNE values. Folivores can have molars with high relief (high DNE), high complexity (high OPCR), or both. There are at least two explanations for this diversity that are not mutually exclusive: 1) different plants or parts of plants present unique combinations of physical properties requiring different combinations of topographic features for their processing. If we can demonstrate which resources are best masticated by simple teeth with high relief (DNE) and which are better masticated by teeth with greater occlusal complexity (OPCR), then this information can be used to identify food preferences of extinct taxa in a more refined way. Alternatively, 2) the features of teeth may be responses to nutritional properties of foods coupled with the metabolic requirements of the animals themselves. Regardless of their material properties, certain foods may require greater reduction prior to being swallowed to maximize their nutritional value. Furthermore, species that are less active, or that have low resting metabolism, may require less nutritional value to be extracted from a given quantity of food than do more active animals consuming the same foods. At issue here is the question of how (not whether) an animal processes foliage—i.e., its emphasis on shearing, mashing, or grinding. This may in turn have implications for the kinds of foliage it can consume efficiently, or for the mean food particle size produced.



**Fig. 2.** A. Contraction, from past to present, of total dental topographic eoniche space in Southern and Southwestern Madagascar, showing convex hulls fitted to species mean values for OPCR and DNE. Open triangles and circles are species means for extinct folivores and frugivore/omnivores, respectively; closed triangles and circles are species means for extant folivores and frugivore/omnivores, respectively. B. Comparison of extinct to extant folivores (Me = *Megaladapis edwardsi*, Hs = *Hadropithecus stenognathus*, Msg = *Mesopropithecus globiceps*, Ppi = *Palaeopropithecus ingens*, Lr = *Lepilemur ruficaudatus*, Pv = *Propithecus verreauxi*, and Lf = *Lepilemur leucopus*). C. Comparison of extinct to extant frugivore/omnivores (Pli = *Pachylemur insignis*, Am = *Archaeolemur majori*, Dr = *Daubentonia robusta*, Er = *Eulemur rufus*, Mc = *Mirza coquereli*, Mig = *Microcebus griseorufus*, Lc = *Lemur catta*, Pf = *Phaner furcifer*, and Cm = *Cheirogaleus medius*).

For example, *Lepilemur* spp., *Hapalemur griseus* and *Prolemur simus* are all folivorous, but they have teeth with very different occlusal surface form, particularly in terms of surface complexity (very low OPCR in *Lepilemur*, moderate in *Hapalemur*, and very high in *Prolemur*). *P. simus* feeds on bamboo culm, *H. griseus* feeds on the leaves of bamboo and other foods, and *Lepilemur* spp. consume tree foliage. The high DNE in all three genera reflects the presence of well-developed shearing crests that may allow the fragmentation of tough plant matter. The exceptionally high OPCR values in *P. simus* may be related to the differences in material properties of bamboo culm vs. bamboo leaves and tree foliage. Alternatively, these values may have less to do with the structural properties of bamboo culm and more to do with its low nutritional content/processing intensity ratio. In other words, perhaps *Prolemur* must triturate its food to a greater degree to derive from it a nutritional value comparable with that obtained by other species from other, richer foods. The very low OPCR of *Lepilemur* (cf. *Hapalemur*) may have nothing to do with the material properties of the leaves it consumes per se but instead may reflect this taxon's low metabolic rate and, thus, leaf nutritional quality that is high relative to the animal's need for energy (Nash, 1998).

With these considerations in mind, we offer the following interpretations of the observed changes in dental topographic ecospace in Southwestern Madagascar from the past to the present (Fig. 2A–C):

1. Some of the folivores that disappeared from the South and Southwest likely differed from extant folivores of this region in being able to process foods that were exceptionally tough or of exceptionally poor nutrient value (measured as nutritional content/processing intensity), or both. *Hadropithecus* (Fig. 2, Panel B, Hs) and *Mesopropithecus* (Fig. 2, Panel B, Msg), both of which had high OPCR values coupled with moderate to high DNE values, were likely capable of processing foods that required heavy comminution. In contrast, *Megaladapis* (Fig. 2, Panel B, Me), which displayed exceptionally high DNE values coupled with exceptionally low OPCR values, may have been efficient at slicing leaves, but likely spent relatively little time processing them. *Palaeopropithecus ingens* (Fig. 2, Panel B, Ppi) was closer to extant folivores of the South and Southwest in its OPCR and DNE values, and not particularly close to *Hadropithecus*, *Mesopropithecus*, or *Megaladapis*.
2. Prior to the recent extinctions, a dedicated frugivore, *Pachylemur* (Fig. 2, Panel C: Pli), lived in the arid South and Southwest. With mean scores for both DNE and OPCR very like those of *Varecia* (which lives today in much more humid environments), *Pachylemur* was likely more frugivorous than those lemurs (*Lemur catta* and *Eulemur rufus*) that survive today in the Southwest.

Also situated close to *Pachylemur* are *Archaeolemur majori* and *Daubentonia* (Fig. 2, Panel C, Am and "Dr") with similarly low or lower DNE scores and only slightly higher OPCR scores. The molars of *Archaeolemur* differed from those of *Pachylemur* and other lemurs in having thick, heavily decussated enamel. It likely resembled *Daubentonia robusta*, which in turn likely resembled living *Daubentonia madagascariensis*, in

exploiting structurally defended resources (Sterling, 1994). No extant lemur living today in the South or Southwest has similar dental adaptations.

## DISCUSSION AND CONCLUSIONS

### Primate communities past and present

Our data support the conclusion that the dearth of frugivores on Madagascar today is not an artifact of differential extinction. Indeed, the relative size of Madagascar's primate frugivore guild has increased from the past to the present because of differential extinction of large-bodied, folivorous species. Given the wealth of fossils (including bones of extant species) at subfossil sites particularly in the South and Southwest, we believe it is unlikely that this is an artifact of sampling bias. Only Eastern Madagascar lacks primate subfossil sites, and many of the extant species found in Eastern Madagascar are represented at subfossil sites in the North. This implies that the poverty of Madagascar's frugivore community is real and long-standing. Goodman and Ganzhorn (1997) related Madagascar's impoverished frugivore community to a reduced diversity and density of *Ficus* trees in Madagascar, Wright et al. (2005) to Madagascar's short season of peak fruit production, Bollen et al. (2004) to fruiting unpredictability and low productivity, and Ganzhorn et al. (2009) to concentrations of nitrogen in the fruits themselves that are marginally at or below what is needed to satisfy primate protein needs.

### Loss of guild elements

Our data show that the extinction of large-bodied lemurs in the South and Southwest resulted in a contraction of the total "econiche space" occupied by the lemurs of this region. The extant lemurs do not occupy dental topographic niche space "vacated" by their extinct relatives. This is not merely a reflection of a reduction in the body size range of Madagascar's lemurs; it reflects the loss of particular guild elements. The variables that comprise our "dental topographic econiche space" are uncorrelated with each other and are not scale dependent. Extinct species fall in virtually all corners of the niche space occupied by lemurs in Southern Madagascar.

The notion that at least some of the extinct lemurs were consuming foods distinct from those consumed by living lemurs of the South or Southwest has been corroborated by studies of their carbon and nitrogen isotope values (Burney et al., 2004; Crowley et al., 2011; Crowley BE, Godfrey LR, Guilderson TP, Zerbeño P, Koch PL, and Dominy NJ, submitted, "Extinction and ecological retreat in a community of primates"). *Hadropithecus* consumed CAM or C<sub>4</sub> resources; its carbon isotope values were unlike those of any other lemur, living or extinct, in the South or elsewhere. *Mesopropithecus* was more variable, but also aberrant in having a diet rich in CAM or C<sub>4</sub> resources.

The hypothesis that differences in OPCR and DNE values relate at least partly to differences in the energetic needs of species has garnered some support from data collected by Fred Spoor and colleagues on the semi-circular canals of extinct and extant lemurs (Spoor et al., 2007; Walker et al., 2008). These authors published "predicted agility" scores based on the dimensions of the semicircular canal. One measurement (the average canal radius or SCR) captures overall agility. We checked the

correlations between SCR scores, OPCR scores, and DNE scores for extinct and extant lemur species for which all three are available. For 21 lemur species (extinct and extant), OPCR and SCR are significantly positively correlated ( $r = 0.61$ ,  $P = 0.004$ ). The correlation between DNE and SCR is insignificant and negative. If one examines only the extinct lemurs, the sample with all three measurements currently available drops to 6, rendering the relationship insignificant for both variables at the  $\alpha = 0.05$  level, but significant at the  $\alpha = 0.1$  level (for OPCR and SCR,  $r = 0.76$ ; for DNE and SCR,  $r = -0.73$ ). This is exactly what one would predict if in fact a mismatch in OPCR and DNE scores reflects different degrees of trituration in animals needing more (or less) energy from the foods they are consuming. As dental complexity increases, activity levels increase. However, DNE scores can be very high in animals that are quite inactive (e.g., *Lepilemur*, presumably *Megaladapis*) and thus do not need to process foods heavily. A more detailed study of these relationships is clearly warranted, but this is outside the scope of the current manuscript.

### Evolutionary disequilibrium?

Finally, we turn to the question of evolutionary disequilibrium. There is evidence from stable isotope research that the niches of extant lemurs in Southern Madagascar have changed somewhat over the past several thousand years. Specifically, modern lemurs from riparian reserves in the South and Southwest have isotope values that differ from those of extant subfossils from the same general region (Crowley, 2009; Crowley BE, Godfrey LR, Guilderson TP, Zerbeño P, Koch PL, and Dominy NJ, submitted, "Extinction and ecological retreat in a community of primates"). Cuzzo and Sauter (2006) have marshaled evidence that ring-tailed lemurs living today in riparian reserves are eating considerable amounts of a food (the fruit of the tamarind trees) that their teeth are not prepared to handle (the enamel is too thin), and that therefore causes rapid, pathological wear and tooth loss (see also Sauter and Cuzzo, 2009; Cuzzo FP and Sauter ML, in prep, "Dental evidence indicates evolutionary disequilibrium among sympatric diurnal lemurs in southern Madagascar"; Yamashita et al., this volume). There is further evidence of ring-tailed lemurs consuming introduced plants that cannot be representative of past resources (Jolly, 2009; Kelley, 2011), some of which have other negative consequences (e.g., Jolly, 2009). In fact, the specific foods consumed by ring-tailed lemurs vary tremendously by location; the presence of *Tamarindus indica* is no guarantee that its fruit and leaves will be consumed (Kelley, 2009, 2011). Sussman et al. (2006) point out that ~90% of the area occupied by ring-tailed lemurs is low canopy density forest; yet almost all dietary data for this species have been compiled in high canopy density forest. Under such circumstances, we cannot be sure that the typical diet of ring-tailed lemurs has been accurately documented.

How can analysis of OPCR and DNE scores elucidate cases of potential evolutionary disequilibrium? Generally, researchers assume that if a misclassification occurs, it is because the constructed dietary categories are poor or because selection on dental form responds to pressures other than those normally assumed. Our hypothesis that dental topography reveals energetic requirements and

not just the type of foods consumed falls into this second category. There is yet another possibility, i.e., that dental topography reveals past diet. If there is in fact some evolutionary disequilibrium, the resources consumed by a species today (either as staples or as fallback foods) may not be those foods its teeth are adapted to process well. Thus, it is possible that classification “failure” is not a failure at all but rather a reflection of a recent dietary behavioral shift—so recent that evolution has not had sufficient time to have reshaped the teeth. Even if the shift is insufficient to result in classificatory failure, a critical ecological role may be occupied by species whose teeth appear to be less than ideal for that role. Such situations are of interest to scientists probing behavioral shifts that establish new selective regimes.

We suggest that such a scenario may apply to ring-tailed lemurs and at least some species of *Eulemur*. In the cases of *Lemur catta* and *Eulemur* spp., there is no apparent mismatch between diet predicted on the basis of OPCR and DNE metrics (i.e., frugivore/omnivore) and the observed diet (i.e., frugivore/omnivore), although the relatively low probability of membership in the frugivore/omnivore category (79% for *L. catta*, 74% for *E. fulvus*, and 66% for *E. rufus*) might signal a mixed diet with a fair amount of foliage or with a large amount of very fibrous fruit. In general, *Lemur* and *Eulemur* spp. prefer fruit to foliage and will consume fruit when they can (e.g., Jolly, 1966; Goodman et al., 2006; Kelley, 2011). They are also excellent seed dispersers with relatively short gastrointestinal transport time (Campbell et al., 2004a,b). We classified all *Eulemur* and *Lemur* as “frugivorous.”

However, despite their preference for fruit, both ring-tailed lemurs and *Eulemur* spp. consume considerable foliage under certain circumstances (Sussman, 1977; Sauther, 1992; Pinkus et al., 2006; Simmen et al., 2006). Depending on the behavioral criterion applied or the field study consulted, these lemurids can be classified as folivorous or frugivorous (cf., Boyer, 2008; Muchlinski et al., 2011; Bunn et al., 2011; this paper). What is intriguing also is anatomical evidence that they may be poorly adapted for processing those resources upon which they most heavily rely. Yamashita (1998) was the first to notice features of the teeth of ring-tailed lemurs that were unexpected for frugivorous species (see also Cuzzo and Sauther, 2006). Boyer (2008) made a parallel argument regarding *Eulemur rufus* from Ranomafana. Our data show that the DNE values for *Lemur catta* and *Eulemur rufus* fall squarely in the middle of the array of lemurids that ranges from *Pachylemur* and *Varecia* (with low DNE) to *Hapalemur* and *Prolemur* (with high and very high values). In addition, the gastrointestinal tract of *Lemur catta*, while not as elongated as that of indriids, is nevertheless long in comparison with that of the more frugivorous *Varecia*, and its cecum is relatively larger (Campbell et al., 2000). *Eulemur* spp. and *Lemur catta* also resemble *Hapalemur* (and not *Varecia* or *Pachylemur*) in having relatively small infraorbital foramina, a characteristic of folivorous species (Muchlinski et al., 2011).

Stable isotope values of subfossil and modern ring-tailed lemurs are also consistent with the hypothesis of greater past folivory. They suggest a relatively greater concentration on CAM plants in the past (Crowley, 2009; Crowley BE, Godfrey LR, Guilderson TP, Zermeño P, Koch PL, and Dominy NJ, submitted, “Extinction and ecological retreat in a community of primates”), which in

turn suggests a larger proportion of foliage, as the dominant endemic CAM plants of Madagascar have fruits that are primarily adapted for wind transport. In Madagascar, primate-dispersed endemic fruit are  $C_3$ . Ring-tailed lemurs do consume considerable amounts of CAM plants in some habitats today, including some that are introduced and have edible fruit (see Loudon et al., 2008, on Tsimanampesotse; Kelley, 2009, 2011, on Cap Sainte-Marie).

Perhaps, we are dealing with an example of evolutionary disequilibrium caused by the loss of the primary occupiers (*Pachylemur* and *Archaeolemur*) of frugivore niches. Taxa that are more capable of persisting on leaves may be allowed, if not obliged (in terms of natural selection) to consume more fruit when important components of the frugivore guild disappear (Boyer, 2008). A detailed study of the dental topographic features of ring-tailed lemur molars through time may be warranted; subfossil ring-tailed lemur jaws do exist, and the teeth have not been analyzed with such questions in mind.

Finally, we consider the example of *Microcebus griseorufus*. Stable isotopes suggest that the diet of this species, like ring-tailed lemurs, changed over the past several thousand years. This is also the only cheirogaleid in our database that was consistently misclassified. Of course, our dietary categories do not include insectivory and thus do not allow discrimination of folivorous and insectivorous species. It is likely that strong relief reflects a relatively high proportion of insects in the diet; nevertheless, it is certainly the case that *Microcebus* is omnivorous and not folivorous and that it does not have the very high relief typical of insectivorous species. It is also possible that its relatively high crests are relics of the past. Today, *M. griseorufus* depends primarily on exudates, particularly during the dry season (Génin, 2008; Rasoazanabary, 2011). Isotopic evidence is consistent with a shift in diet—this species may have consumed more insects in the recent past (Crowley BE, Godfrey LR, Guilderson TP, Zermeño P, Koch PL, and Dominy NJ, submitted, “Extinction and ecological retreat in a community of primates”).

Wholesale shifts in diet may be extremely rare, and evolutionary changes in dental occlusal morphology to accommodate any such behavioral shifts may require more than 1,000 or 2,000 years. Such disequilibrium is largely invisible to ecologists studying the behavior of animals in their present environments. Nevertheless, by using dental topographic analysis in conjunction with stable isotope research, researchers may be able to develop detailed hypotheses regarding recent dietary shifts. Working out the interplay between the mechanical “structural quality,” necessary “quantity” as dictated by nutritional quality and metabolism, and the correspondence to tooth form for a spectrum of food resources would be an adaptationist victory, indeed. Having accomplished such a goal, one could begin to identify animals that are consuming the “wrong” (or at least suboptimal) resources. Thus, for example, we might identify folivores that are, in certain habitats, consuming resources that would be better processed by teeth that are more complex or by teeth that have greater relief. Documenting disparities between dental topography and foods consumed can become an effective tool, helping us to understand why some lemurs (*Lemur catta*, *Eulemur* spp.) that consume consistently high proportions of fruit in populations observable today have teeth that seem to belie this proclivity (Cuzzo and Sauther, 2006; Boyer,

2008) and suggest greater past folivory. Used in such a manner, the study of dental occlusal topography can provide insights into recent subtle changes in feeding behavior that might improve our understanding of teeth in their ecological contexts.

### ACKNOWLEDGMENTS

We thank Frank Cuzzo, Michelle Sauter, and Peter Ungar for inviting us to participate in this symposium, for their encouragement, and for their editorial advice. This research was funded in part by NSF BCS-0721233 to P.C. Wright, LRG, and JJ; a fellowship from the John Simon Guggenheim Foundation (LRG); an NSF DDIG, Evolving Earth Foundation Grant and American Society of Mammalogists grant (DMB); and an NSF GRFP grant (JB). This manuscript benefited greatly from information provided by two anonymous reviewers and from Marina Blanco, Brooke Crowley, Alistair Evans, Elizabeth Kelley, Kathleen Muldoon, Mike Sutherland, and Stacey Tecot. Marina Blanco produced Figure 2.

### LITERATURE CITED

- Balko E. 1998. A behaviorally plastic response to forest composition and logging disturbance by *Varecia variegata variegata* in Ranomafana National Park, Madagascar. PhD dissertation, State University of New York, Syracuse.
- Bleher B, Bohning-Gaese K. 2001. Consequences of frugivore diversity for seed dispersal, seedling establishment and the spatial pattern of seedlings and trees. *Oecologia* 129:385–394.
- Bollen A, Van Elsacker L, Ganzhorn JU. 2004. Relations between fruits and disperser assemblages in a Malagasy littoral forest: a community-level approach. *J Trop Ecol* 20:599–612 Part 6.
- Boyer DM. 2008. Relief index of second mandibular molars is a correlate of diet among prosimian primates and other euarchontan mammals. *J Hum Evol* 55:1118–1137.
- Boyer DM, Evans AR, Jernvall J. 2010. Evidence of dietary differentiation among late Paleocene—early Eocene pliesiadapids (Mammalia, Primates). *Am J Phys Anthropol* 142:194–210.
- Bunn JM, Boyer DM, Lipman Y, St. Clair EM, Jernvall J, Daubechies I. 2011. Dirichlet normal surface energy of tooth crowns, a new technique of molar shape quantification for dietary inference, compared with previous methods in isolation and in combination. *Am J Phys Anthropol* 145:247–261.
- Burgess N, D'Amico Hales J, Underwood E, Dinerstein E, Olson D, Itoua I, Schipper J, Ricketts T, Newman K. 2004. Terrestrial ecoregions of Africa and Madagascar: a conservation assessment. Washington, DC: Island Press.
- Burney DA, Burney LP, Godfrey LR, Jungers WL, Goodman SM, Wright HT, Jull AJT. 2004. A chronology for late prehistoric Madagascar. *J Hum Evol* 47:25–63.
- Burney DA, James HF, Grady FV, Rafamantanantsoa JG, Rami-lisonina, Wright HT, Cowart JB. 1997. Environmental change, extinction and human activity: evidence from caves in NW Madagascar. *J Biogeogr* 24:755–767.
- Campbell JL, Eisemann JH, Williams CV, Glenn KM. 2000. Description of the gastrointestinal tract of five lemur species: *Propithecus tattersalli*, *Propithecus verreauxi coquereli*, *Varecia variegata*, *Haplemur griseus*, and *Lemur catta*. *Am J Primatol* 52:133–142.
- Campbell JL, Williams CV, Eisemann JH. 2004a. Characterizing gastrointestinal transit time in four lemur species using barium-impregnated polyethylene spheres (BIPS). *Am J Primatol* 64:309–321.
- Campbell JL, Williams CV, Eisemann JH. 2004b. Use of total dietary fiber across four lemur species (*Propithecus verreauxi coquereli*, *Haplemur griseus griseus*, *Varecia variegata*, and *Eulemur fulvus*): does fiber type affect digestive efficiency? *Am J Primatol* 64:323–335.
- Covert HH. 1986. Biology of early Cenozoic primates. In: Swindler DR, Erwin J, editors. *Comparative primate biology*, Vol. 1: systematics, evolution, and anatomy. New York: Alan R Liss. p 335–359.
- Crowley BE. 2009. The stable isotope ecology of Madagascar's lemurs. PhD dissertation, Department of Ecology and Evolutionary Biology, University of California, Santa Cruz.
- Crowley BE. 2010. A refined chronology of prehistoric Madagascar and the demise of the megafauna. *Quat Sci Rev* 29:2591–2603.
- Crowley BE, Godfrey LR, Irwin MT. 2011. A glance to the past: subfossils, stable isotopes, seed dispersal, and lemur species loss in southern Madagascar. *Am J Primatol* 73:25–37.
- Cuzzo FP, Sauter ML. 2006. Severe wear and tooth loss in wild ring-tailed lemurs (*Lemur catta*): a function of feeding ecology, dental structure, and individual life history. *J Hum Evol* 51:490–505.
- Curtis DJ, Rasmussen MA. 2002. Cathemerality in lemurs. *Evol Anthropol* 11:83–86.
- Cuzzo FP, Sauter ML. In press. What is dental ecology? *Am J Phys Anthropol*.
- Evans AL, Wilson GP, Fortelius M, Jernvall J. 2007. High-level similarity of dentitions in carnivorans and rodents. *Nature* 445:78–81.
- Faulkner AL, Lehman SM. 2006. Feeding patterns in a small-bodied nocturnal folivore (*Avahi laniger*) and the influence of leaf chemistry: a preliminary study. *Folia Primatol* 77:218–227.
- Fietz J, Ganzhorn J. 1999. Feeding ecology of the hibernating primate *Cheirogaleus medius*: how does it get so fat? *Oecologia* 121:157–164.
- Ganzhorn JU. 1988. Food partitioning among Malagasy primates. *Oecologia* 75:436–450.
- Ganzhorn JU. 2002. Distribution of a folivorous lemur in relation to seasonally varying food resources: integrating quantitative and qualitative aspects of food characteristics. *Oecologia* 131:427–435.
- Ganzhorn JU, Abraham J-P, Razanahoera-Rakotomalala M. 1985. Some aspects of the natural history and food selection of *Avahi laniger*. *Primates* 26:452–463.
- Ganzhorn JU, Arrigo-Nelson S, Boinski S, Bollen A, Carrai V, Derby A, Donati G, Koenig A, Kowalewski M, Lahann P, Norscia I, Polowinsky SY, Schwitzer C, Stevenson PR, Talebi MG, Tan C, Vogel ER, Wright PC. 2009. Possible fruit protein effects on primate communities in Madagascar and the Neotropics. *PLoS One* 4:Art No e8253.
- Génin F. 2008. Life in unpredictable environments: first investigation of the natural history of *Microcebus griseorufus*. *Int J Primatol* 29:303–321.
- Gerson J. 2000. Social relationships in wild red-fronted brown lemurs (*Eulemur fulvus rufus*). PhD dissertation, Duke University, Durham, NC.
- Godfrey LR, Jungers WL, Reed KE, Simons EL, Chatrath PS. 1997. Subfossil lemurs: inferences about past and present primate communities. In: Goodman SM, Patterson BD, editors. *Natural change and human impact in Madagascar*. Washington, DC: Smithsonian Institution. p 218–256.
- Godfrey LR, Jungers WL, Schwartz GT. 2006. Ecology and extinction of Madagascar's subfossil lemurs. In: Gould L, Sauter ML, editors. *Lemurs: ecology and adaptation*. New York: Springer. p 41–64.
- Godfrey LR, Semperebon GM, Jungers WL, Sutherland MR, Simons EL, Solounias N. 2004. Dental use wear in extinct lemurs: evidence of diet and niche differentiation. *J Hum Evol* 47:145–169.
- Godfrey LR, Semperebon GM, Schwartz GT, Burney DA, Jungers WL, Flanagan EK, Cuzzo FP, King SJ. 2005. New insights into old lemurs: the trophic adaptations of the Archaeolemuriidae. *Int J Primatol* 26:825–854.
- Goodman SM, Ganzhorn JU. 1997. Rarity of figs (*Ficus*) on Madagascar and its relationship to a depauperate frugivore community. *Rev Ecol—Terre Vie* 52:321–329.
- Goodman SM, Rakotoarisoa SV, Wilmé L. 2006. The distribution and biogeography of the ringtailed lemur (*Lemur catta*) in Madagascar. In: Jolly A, Sussman RW, Koyama N, Rasamima-

- nana H, editors. Ringtailed lemur biology. New York: Springer. p 3–15.
- Grassi C. 2006. Variability in habitat, diet, and social structure of *Hapalemur griseus* in Ranomafana National Park, Madagascar. *Am J Phys Anthropol* 131:50–63.
- Harcourt C. 1991. Diet and behaviour of a nocturnal lemur, *Avahi laniger*, in the wild. *J Zool* 223:667–674.
- Hemingway CA. 1998. Selectivity and variability in the diet of Milne-Edwards' Sifakas (*Propithecus diadema edwardsi*): implications for folivory and seed-eating. *Int J Primatol* 19:355–377.
- Hladik CM, Charles-Dominique P, Petter JJ. 1980. Feeding strategies of five nocturnal prosimians in the dry forest of the west coast of Madagascar. In: Charles-Dominique P, Cooper HM, Hladik A, Hladik CM, Pages E, Pariente GF, Petter-Rousseaux A, Shilling A, editors. Nocturnal Malagasy primates. New York: Academic Press. p 41–73.
- Irwin MT. 2008. Feeding ecology of *Propithecus diadema* in forest fragments and continuous forest. *Int J Primatol* 29:95–115.
- Jolly A. 1966. Lemur behavior. Chicago: University of Chicago Press.
- Jolly A. 2009. Coat condition of ringtailed lemurs, *Lemur catta*, at Berenty Reserve, Madagascar: II. Coat and tail alopecia associated with *Leucaena leucocephala*, 2001–2006. *Am J Primatol* 71:199–205.
- Jungers WL, Godfrey LR, Simons EL, Wunderlich RE, Richmond BG, Chatrath PS. 2002. Ecomorphology and behavior of giant extinct lemurs from Madagascar. In: Plavcan JM, Kay RF, Jungers WL, van Schaik CP, editors. Reconstructing behavior in the primate fossil record. New York: Kluwer Academic/Plenum. p 371–411.
- Kay RF. 1984. On the use of anatomical features to infer foraging behavior in extinct primates. In: Rodman PS, Cant JGH, editors. Adaptations for foraging in nonhuman primates. New York: Columbia University Press. p 21–53.
- Kay RF, Sussman RW, Tattersall I. 1978. Dietary and dental variations in the genus Lemur, with comments concerning dietary-dental correlations among Malagasy primates. *Am J Phys Anthropol* 49:119–128.
- Kelley EA. 2009. Ranging behavior and home range area of *Lemur catta* (ring-tailed lemurs) in the Cap Sainte-Marie region, Madagascar: does an absence in pattern reflect extreme flexibility of habitat and feeding site use? *Am J Primatol* 71(Suppl 1):103.
- Kelley EA. 2011. *Lemur catta* in the region of Cap Sainte-Marie, Madagascar: introduced cacti, xerophytic Didiereaceae-*Euphorbia* bush, and tombs. PhD dissertation, Washington University, St. Louis, MO.
- King SJ, Arrigo-Nelson SJ, Pochron ST, Semperebon GM, Godfrey LR, Wright PC, Jernvall J. 2005. Dental senescence in a long-lived primate links infant survival to rainfall. *Proc Natl Acad Sci U S A* 102:16579–16583.
- Kirk EC. 2006. Eye morphology in catheimeral lemurs and other mammals. *Folia Primatol* 77:27–49.
- Lahann P. 2007. Feeding ecology and seed dispersal of sympatric cheirogaleid lemurs (*Microcebus murinus*, *Cheirogaleus medius*, *Cheirogaleus major*) in the littoral rainforest of south-east Madagascar. *J Zool* 271:88–98.
- Lambert JE. 2011. Primate seed dispersers as umbrella species: a case study from Kibale National Park, Uganda, with implications for Afrotropical forest conservation. *Am J Primatol* 73:9–24.
- Lamberton C. 1934. Contribution à la connaissance de la faune subfossile de Madagascar: Lémuriens et Ratites. *Chiromys robustus* sp. nov. Lamb. Mémoires de l'Académie malgache 17:40–46 plus plates.
- Lhota S, Junek T, Bartos L, Kubena AA. 2008. Specialized use of two fingers in free-ranging aye-ayes. *Am J Primatol* 70:786–795.
- Loudon JE, Whitelaw DC, Sponheimer M, Sauther ML, Cuzzo FP, Youssouf IAJ. 2008. Lemurs eating isotopes: a stable isotope analysis of ring-tailed lemurs (*Lemur catta*) and their menu at the Beza Mahafaly Special Reserve. *Am J Phys Anthropol* 135 Suppl 46:142.
- Lyons KG, Brigham CA, Traut BH, Schwartz MW. 2005. Rare species and ecosystem functioning. *Cons Biol* 19:1019–1024.
- MacPhee RDE, Raholimavo EM. 1988. Modified subfossil aye-aye incisors from southwestern Madagascar—species allocation and paleoecological significance. *Folia Primatol* 51:126–142.
- Martin RD. 1972. Adaptive radiation and behaviour of the Malagasy lemurs. *Philos Trans R Soc Lond [Biol]* 264:295–352.
- Millette JB, Sauther ML, Cuzzo FP. 2009. Behavioral responses to tooth loss in wild ring-tailed lemurs (*Lemur catta*) at the Beza Mahafaly Special Reserve, Madagascar. *Am J Phys Anthropol* 140:120–134.
- M'Kirera F, Ungar PS. 2003. Occlusal relief changes with molar wear in *Pan troglodytes troglodytes* and *Gorilla gorilla gorilla*. *Am J Primatol* 60:31–41.
- Morland H. 1992. Social organization and ecology of black and white ruffed lemurs (*Varecia variegata variegata*) in Lowland Rain Forest, Nosy Mangabe, Madagascar. PhD dissertation, Yale University, New Haven.
- Muchlinski MN, Godfrey LR, Muldoon KM, Tongaso L. 2011. Evidence for dietary niche separation based on infraorbital foramen size variation among subfossil lemurs. *Folia Primatol* 81:330–345.
- Muldoon KM, Goodman SM. 2010. Ecological biogeography of Malagasy non-volant mammals: community structure is correlated with habitat. *J Biogeogr* 37:1144–1159.
- Nash LT. 1998. Vertical clingers and sleepers: seasonal influences on the activities and substrate use of *Lepilemur leucopus* at Beza Mahafaly Special Reserve, Madagascar. *Folia Primatol* 69(Suppl 1):204–217.
- Norconk MA, Boinski S, Forget P-M. 2011. Primates in 21st century ecosystems: does primate conservation promote ecosystem conservation? *Am J Primatol* 73:3–8.
- Overdorff DJ. 1993. Similarities, differences and seasonal patterns in the diets of *Eulemur rubriventer* and *Eulemur fulvus rufus* in the Ranomafana National Park, Madagascar. *Int J Primatol* 14:721–753.
- Pages E. 1980. Ethoecology of *Microcebus coquereli* during the dry season. In: Charles-Dominique P, Cooper HM, Hladik A, Hladik CM, Pages E, Pariente GF, Petter-Rousseaux A, Shilling A, editors. Nocturnal Malagasy primates. New York: Academic Press. p 97–116.
- Pinkus S, Smith JNM, Jolly A. 2006. Feeding competition between introduced *Eulemur fulvus* and native *Lemur catta* during the birth season at Berenty Reserve, southern Madagascar. In: Jolly A, Sussman RW, Koyama N, Rasamimanana H, editors. Ringtailed lemur biology. New York: Springer. p 119–140.
- Powzyk J. 1998. The socio-ecology of two sympatric indrids, *Propithecus diadema diadema* and *Indri indri*: a comparison of feeding strategies and their possible repercussions on species-specific behaviors. PhD dissertation, Duke University, Durham, NC.
- Powzyk JA, Mowry CB. 2003. Dietary and feeding differences between sympatric *Propithecus diadema diadema* and *Indri indri*. *Int J Primatol* 24:1143–1162.
- Rafferty KL, Teaford MF, Jungers WL. 2002. Molar microwear of subfossil lemurs: improving the resolution of dietary inferences. *J Hum Evol* 43:645–657.
- Rasmussen MA. 1999. Ecological influences on the activity cycle in two catheimeral primates: the mongoose lemur (*Eulemur mongoz*) and the common brown lemur (*Eulemur fulvus fulvus*). PhD dissertation, Duke University, Durham, NC.
- Rasoazanabary E. 2011. The human factor in mouse lemur (*Microcebus griseorufus*) conservation: local resource utilization and habitat disturbance at Beza Mahafaly, SW Madagascar. PhD dissertation, University of Massachusetts, Amherst, MA.
- Ratsimbazafy JH. 2002. On the brink of extinction and the process of recovery: responses of black and white ruffed lemurs (*Varecia variegata variegata*) to disturbance in Manombo Forest, Madagascar. PhD dissertation, SUNY Stony Brook, New York.
- Ravosa MJ. 1991. Structural allometry of the prosimian mandibular corpus and symphysis. *J Hum Evol* 20:3–20.

- Ravosa MJ. 1992. Allometry and heterochrony in extant and extinct Malagasy primates. *J Hum Evol* 23:197–217.
- Richard AF. 1974. Intra-specific variation in the social organization and ecology of *Propithecus verreauxi*. *Folia Primatol* 22:178–207.
- Richard AF. 1978. Variability in feeding behavior of a Malagasy prosimian, *Propithecus verreauxi*: Lemuriformes. In: Montgomery G, editor. The ecology of arboreal folivores. Washington, DC: Smithsonian Institution Press. p 519–533.
- Richard AF, Dewar RE. 1991. Lemur ecology. *Ann Rev Ecol Syst* 22:145–175.
- Russell RJ. 1980. The environmental physiology and ecology of *Lepilemur ruficaudatus* (= *L. leucopus*) in southern Madagascar. *Am J Phys Anthropol* 52:272–274.
- Ryan TM, Burney DA, Godfrey LR, Göhlich U, Jungers WL, Vasey N, Ramilisonina, Walker A, Weber GW. 2008. A reconstruction of the Vienna skull of *Hadropithecus stenognathus*. *Proc Natl Acad Sci U S A* 105:10698–10701.
- Sauter ML. 1991. Reproductive behavior of free-ranging *Lemur catta* at Beza Mahafaly Special Reserve, Madagascar. *Am J Phys Anthropol* 84:463–477.
- Sauter ML. 1992. The effect of reproductive state, social rank and group size on resource use among free-ranging ring-tailed lemurs (*Lemur catta*) of Madagascar. PhD dissertation, Washington University, St. Louis, MO.
- Sauter ML, Cuzzo FP. 2009. The impact of fallback foods on wild ring-tailed lemur biology: a comparison of intact and anthropogenically disturbed habitat. *Am J Phys Anthropol* 140:671–686.
- Schulke O. 2003. To breed or not to breed—food competition and other factors involved in female breeding decisions in the pair-living nocturnal fork-marked lemur (*Phaner furcifer*). *Behav Ecol Sociobiol* 55:11–21.
- Scott JR, Godfrey LR, Jungers WL, Scott RS, Simons EL, Teaford MF, Ungar PS, Walker A. 2009. Dental microwear texture analysis of subspecies of fossil lemurs from Madagascar. *J Hum Evol* 56:405–416.
- Seligsohn D, Szalay FS. 1974. Dental occlusion and the masticatory apparatus in *Lemur* and *Varecia*: their bearing on the systematics of living and fossil primates. In: Martin RD, Doyle GA, Walker AC, editors. Prosimian anatomy, biochemistry and evolution. London: Duckworth. p 543–561.
- Simmen B, Hladik A, Ramasiarisoa P. 2003. Food intake and dietary overlap in native *Lemur catta* and *Propithecus verreauxi* and introduced *Eulemur fulvus* at Berenty, Southern Madagascar. *Int J Primatol* 24:948–967.
- Simmen B, Sauter ML, Soma T, Rasamimanana H, Sussman RW, Jolly A, Tarnaud L, Hladik A. 2006. Plant species fed on by *Lemur catta* in gallery forests of the Southern Domain of Madagascar. In: Jolly A, Sussman RW, Koyama N, Rasamimanana H, editors. Ringtailed lemur biology. New York: Springer. p 55–68.
- Simons EL. 1994. The giant aye-aye *Daubentonia robusta*. *Folia Primatol* 62:14–21.
- Simons EL. 1997. Lemurs: old and new. In: Goodman SM, Patterson BD, editors. Natural change and human impacts in Madagascar. Washington, DC: Smithsonian Press. p 142–168.
- Spoor F, Garland T, Krovitz G, Ryan T, Silcox MT, Walker A. 2007. The primate semicircular canal system and locomotion. *Proc Natl Acad Sci U S A* 104:10808–10812.
- Sterling EJ. 1994. Aye-ayes—specialists on structurally defended resources. *Folia Primatol* 62:142–154.
- Sussman RW. 1974. Ecological distinctions in sympatric species of lemur. In: Martin RD, Doyle GA, Walker AC, editors. Prosimian biology. London: Duckworth. p 75–108.
- Sussman RW. 1977. Socialization, social structure, and ecology of two sympatric species of lemur. In: Chevalier-Skolnikoff S, Poirier FE, editors. Primate bio-social development: biological, social, and ecological determinants. New York and London: Garland Publishing. p 515–528.
- Sussman RW, Sweeney S, Green GM, Porton I, Andrianansolondraibe OL, Ratsirarson J. 2006. A preliminary estimate of *Lemur catta* population density using satellite imagery. In: Jolly A, Sussman RW, Koyama N, Rasamimanana H, editors. Ringtailed lemur biology. New York: Springer. p 16–31.
- Tan CL. 1999. Group composition, home range size, and diet of three sympatric bamboo lemur species (genus *Hapalemur*) in Ranomafana National Park, Madagascar. *Int J Primatol* 20:547–566.
- Tattersall I. 1973. Cranial anatomy of Archaeolemurinae (Lemuroidea, Primates). *Anthropological Papers of the American Museum of Natural History* 52:1–110.
- Tattersall I. 1982. The primates of Madagascar. New York: Columbia University Press.
- Tattersall I. 2008. Avoiding commitment: cathemerality among primates. *Biol Rhythm Res* 39:213–228.
- Thalmann U. 2001. Food resource characteristics in two nocturnal lemurs with different social behavior: *Avahi occidentalis* and *Lepilemur edwardsi*. *Int J Primatol* 22:287–324.
- van Schaik CP, Kappeler PM. 1996. The social systems of gregarious lemurs: lack of convergence with anthropoids due to evolutionary disequilibrium? *Ethology* 102:915–941.
- Vasey N. 2000. Niche separation in *Varecia variegata rubra* and *Eulemur fulvus albifrons*: I. Interspecific patterns. *Am J Phys Anthropol* 112:411–431.
- Vasey N, Burney DA, Godfrey LR. In press. *Archaeolemur* coprolites from Anjohikely Cave in northwestern Madagascar reveal dietary diversity and cave use in a subspecies of lemur. In: Masters J, Gamba M, Génin F, editors. Leaping ahead: advances in prosimian biology. New York: Springer.
- Walker A. 1981. Diet and teeth: dietary hypotheses and human evolution. *Phil Trans R Soc Lond B* 292:57–64.
- Walker A, Ryan TM, Silcox MT, Simons EL, Spoor F. 2008. The semicircular canal system and locomotion: the case of extinct lemuroids and lorisooids. *Evol Anthropol* 17:135–145.
- Warren RD, Crompton RH. 1997. A comparative study of the ranging behaviour, activity rhythms and sociality of *Lepilemur edwardsi* (Primates, Lepilemuridae) and *Avahi occidentalis* (Primates, Indriidae) at Ampijoroa, Madagascar. *J Zool* 243:397–415.
- Wright PC. 1999. Lemur traits and Madagascar ecology: coping with an island environment. *Yrbk Phys Anthropol* 42:31–72.
- Wright PC, Razafindratsita VR, Pochron ST, Jernvall J. 2005. The key to Madagascar frugivores. In: Dew JL, Boubli JP, editors. Tropical fruits and frugivores: the search for strong interactors. New York: Springer. p 121–138.
- Yamashita N. 1998. Functional dental correlates of food properties in five Malagasy lemur species. *Am J Phys Anthropol* 106:169–188.
- Yamashita N. 2002. Diets of two lemur species in different microhabitats in Beza Mahafaly Special Reserve, Madagascar. *Int J Primatol* 23:1025–1051.
- Yamashita N, Cuzzo FP, Sauter ML. Interpreting food processing through dietary mechanical properties: a *Lemur catta* case study. *Am J Phys Anthropol*.