Chapter 18
The Dental Ecology of Ring-Tailed Lemurs (*Lemur catta*)

Frank P. Cuozzo and Michelle L. Sauther

Abstract Ring-tailed lemurs (*Lemur catta*) are among the best-known primates. Long-term study of their behavior, ecology and dentition at a single locality, the Beza Mahafaly Special Reserve, Madagascar, has enabled a detailed understanding of their dental ecology. Patterns of dental pathology including tooth wear, tooth loss and abscessed canines correspond to use of specific resources and habitats and differ from patterns seen in sympatric primate species. Regular use of tamarind fruit (*Tamarindus indicus*) likely leads to a distinct pattern of severe tooth wear and tooth loss, suggesting a "mismatch" between dental morphology and the animals' primary fallback food.

Resume Le lémur catta (*Lemur catta*) est l'un des primates les mieux connus. Une étude à long-terme de son comportement, son écologie, et sa dentition dans un site unique, la Réserve Spéciale de Beza Mahafaly a permis une meilleure compréhension des détails de son écologie dentaire. Les pathologies dentaires observées chez cette espèce, mais pas chez d'autres espèces sympatriques, notamment l'usure et la perte de dents et les abcès observés au niveau des canines correspondent à l'utilisation d'habitats et de ressources spécifiques. La consommation régulière de fruits de tamariniers (*Tamarindus indicus*) conduit probablement à une usure sévère et à une perte de dents qui suggèrent une mal-adaptation de la morphologie dentaire et de cette importante ressource secondaire.

F.P. Cuozzo (✉)
Department of Anthropology, University of North Dakota, Box 8374,
Grand Forks, ND 58202-8374, USA
e-mail: frank.cuozzo@und.nodak.edu

M.L. Sauther
Department of Anthropology, University of Colorado, Campus Box 233,
Boulder, CO 80309-0233, USA
e-mail: michelle.sauther@colorado.edu

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Introduction

Ring-tailed lemurs (*Lemur catta*) are among the best-known and most studied prosimian primates (Sauther et al. 1999; Gould 2006; Jolly et al. 2006), and the breadth and temporal depth of ring-tailed lemur research rivals that of the best-known anthropoids, chimpanzees and baboons (Cuozzo and Sauther 2006a). In addition to extensive behavioral, ecological and demographic studies (Sauther et al. 1999; Gould 2006), the dentition of this species ranks among the most thoroughly studied of any extant primate (reviewed in Cuozzo and Yamashita 2006). Over the past decade, detailed information on dental variation, morphology and function (Yamashita 1998, 2003; Sauther et al. 2001), disease and pathology (Sauther et al. 2002, 2006; Cuozzo and Sauther 2006b), tooth size change over time (Cuozzo and Sauther 2006a) and tooth wear (Cuozzo and Sauther 2004, 2006b; Cuozzo et al. 2010) has been published, focusing on ring-tailed lemurs inhabiting the tamarind-dominated gallery forest in the Beza Mahafaly Special Reserve (BMSR), southern Madagascar (Sauther et al. 1999, 2006; Cuozzo and Sauther 2004, 2006b). Comparative data on ring-tailed lemur tooth wear and oral health have also been collected in the limestone spiny forest at Tsimanampetsotse National Park (TNP), Madagascar (Cuozzo et al. 2008; Sauther and Cuozzo 2008).

We review ring-tailed lemur dental ecology, defining this, in part, as the study of patterns of dental pathology (i.e. abscessed teeth, tooth loss and dental damage) and tooth wear, as a reflection of feeding ecology, behavior and habitat variation, including the exploitation of areas affected by anthropogenic disturbance (i.e. forest fragmentation and/or areas with introduced plants). This approach allows us to study ecological change over time, as (1) teeth provide a direct record of individual life histories; (2) overall tooth wear as well as pathologies such as maxillary canine abscesses reflect long-term exploitation of particular foods, thus recording habitat use and (3) dental data are accessible in living individuals and correlate with specific behaviors and ecological variables. Since teeth are often preserved in the fossil record, data on dental ecology in living animals can be extrapolated to primate fossils, providing a comparative context for interpreting primate paleobiology (Cuozzo and Sauther 2006b; Millette et al. 2009).

Ring-Tailed Lemur Dental Pathology

Among extant primates, BMSR gallery forest ring-tailed lemurs display an exceptionally high frequency of severe tooth wear and antemortem tooth loss (Cuozzo and Sauther 2004, 2006a, b) (Fig. 18.1; Table 18.1), largely as a result of exploiting tamarind fruit (*Tamarindus indicus*), a major fallback food relied upon during the dry season (Sauther 1992, 1998; Yamashita 1998, 2002; Cuozzo and Sauther 2004, 2006a, b; Gould 2006; Gemmill and Gould 2008; Sauther and Cuozzo 2009). The fruit is mechanically challenging (Yamashita 2008), large with a tough exocarp,

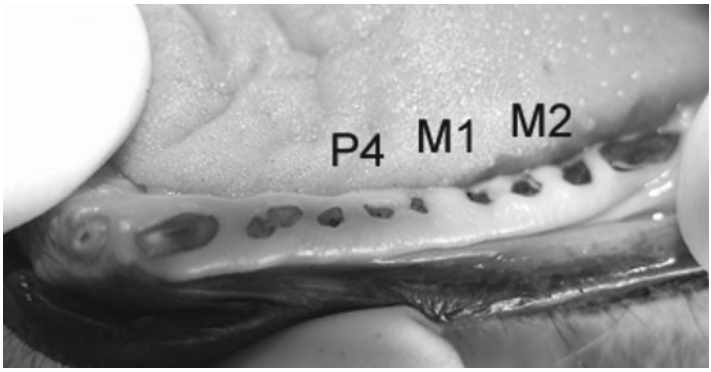

Fig. 18.1 Severe dental wear and antemortem tooth loss in a living ring-tailed lemur from the gallery forest at Beza Mahafaly (Blue 138). Note that the fourth premolar (P4) and the first and second molars (M1 and M2) retain only worn roots, worn to below the gumline, thus "functionally absent" as defined by Cuozzo and Sauther (2004, 2006b)

Table 18.1 Frequency of dental pathologies compared between two living, wild ring-tailed lemur populations in Madagascar

		Antemortem Tooth Loss		Maxillary Canine Abscesses	
Location[a]	*n*[b]	*n*	%	*n*	%
Beza Mahafaly	167	38	22.8	6	3.6
Tsimanampetsotse	24	1	4.2	0	0.0

[a]Beza Mahafaly is a gallery forest; Tsimanampetsotse is a limestone spiny forest (see text)
[b]Adults only (3 years and older)

and is the hardest food eaten by *L. catta* in the BMSR gallery forest (Yamashita 2000). Regular processing of the fruit leads to frequent and rapid wear of the thin-enameled crowns used to open it (posterior premolars and anterior molars; see Fig. 18.1). This dramatic pattern of tooth wear indicates a discordance between the dental morphology of *L. catta* (thin enamel, elongated shearing crests; Cuozzo and Sauther 2006b; Yamashita 2008) and their primary fallback food in the BMSR gallery forest (Cuozzo and Sauther 2006b; Sauther and Cuozzo 2009).

BMSR gallery forest *Lemur catta* also suffer from maxillary canine abscesses, which present as open wounds on the muzzle (Sauther et al. 2006) and are detectable in skeletal specimens (Fig. 18.2a, b; Table 18.1). Notably, all known cases occur in areas of severe anthropogenic impact, either where the forest understory has been removed through domestic livestock grazing or where ring-tailed lemurs exploit crops and/or other introduced plants that border on the reserve (Sauther et al. 2006). In contrast to sympatric Verreaux's sifaka (*Propithecus verreauxi*), in which a high frequency of canine abscesses (~30 % of the BMSR skeletal sample) appears related to processing tamarind fruit with their maxillary canines, canine abscesses in *L. catta* (3.6 %) are likely caused by tooth breakage as a result of processing other foods in disturbed areas in and around BMSR.

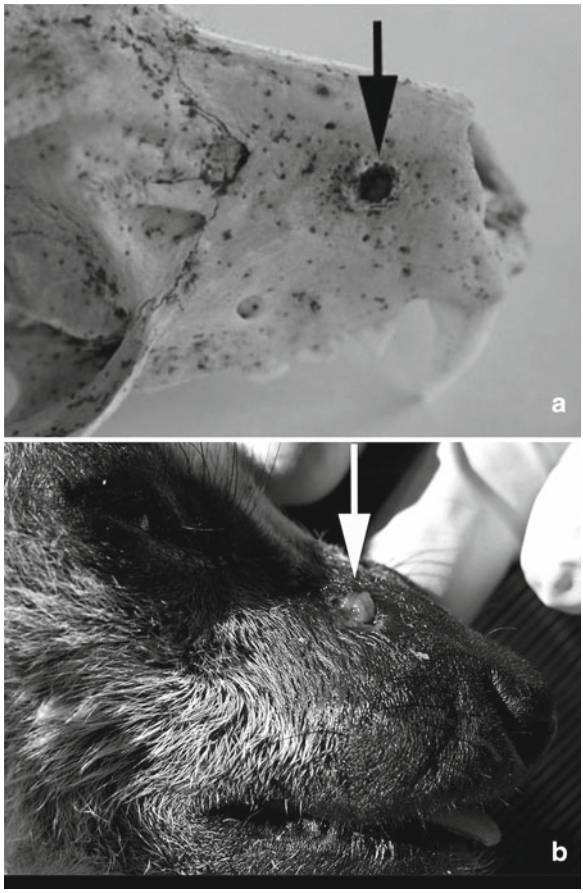

Fig. 18.2 Apical, maxillary canine abscesses in gallery forest Beza Mahafaly ring-tailed lemurs. (**a**) Bone damage at the apex of the right maxillary canine (*black arrow*) on the muzzle of a ring-tailed lemur skeletal specimen from Beza Mahafaly. (**b**) Open wound at the apex of the right maxillary canine (*white arrow*) on the muzzle of a living individual at Beza Mahafaly (Blue 127)

Comparative data on lemur salivary pH indicate long-term adjustments by ring-tailed lemurs to food resources with high acidity including *T. indicus* (Cuozzo et al. 2008). Comparing data from wild ring-tailed lemurs at BMSR and TNP, as well as a captive population, reveals that the extreme acidity of tamarind fruit is buffered by the oral chemistry of ring-tailed lemurs, which have high salivary pH. At BMSR, the folivorous Verreaux's sifaka (*Propithecus verreauxi*) consumes less acidic foods and has more acidic salivary pH.

Behavioral Responses to Dental Impairment

Combining long-term behavioral and ecological research with studies of dental pathology and tooth wear (e.g. Sauther et al. 1999; Gould 2006) is important for a comprehensive understanding of *L. catta* dental ecology. At BMSR ring-tailed

lemurs with severe dental wear and tooth loss compensate behaviorally for their impairment. Stable isotope values measured for $\delta^{13}C$ and $\delta^{15}N$ showed significant differences between dentally impaired individuals and other troop members, implying use of different resources (Loudon et al. 2007). In addition, individuals with marked tooth loss (>10 %) displayed different daily activity patterns, often feeding during periods when individuals without tooth loss were resting or engaging in social activities like grooming (Millette et al. 2009). These impaired individuals also engaged in interspecific coprophagy, i.e. the consumption of the feces of domestic animals and sometimes humans, which is a rare behavior among wild vertebrates (Fish et al. 2007). Our data are among the first to illustrate significant behavioral adjustments to dental pathologies among mammals and provide a comparative context for interpreting the dental ecology of living and fossil lemurs, as well as other primates including hominins (Cuozzo and Sauther 2004, 2006b; Millette et al. 2009).

Conclusions

Since the initial 1972 conference on prosimian primates (Martin et al. 1974), and subsequent congresses and their publications (Alterman et al. 1995; Harcourt et al. 1998), our understanding of prosimian teeth has advanced beyond the studies of dental morphology, metrics and development included in these earlier volumes. As a result of long-term prosimian field research (e.g. Jolly 1966; Sussman 1991; Richard et al. 1993; Sauther and Cuozzo, loc. cit.), we can now begin to synthesize a comprehensive picture of prosimian dental ecology. For example, King et al. (2005) used long-term behavioral and ecological data, combined with environmental data (rainfall patterns), to explore the relationship between tooth wear and reproductive success in *Propithecus edwardsi* at Ranomafana National Park, Madagascar. Building on such studies, including the synopsis of ring-tailed lemur dental studies described here, we can achieve the holistic understanding of the prosimian dentition envisaged by Seligsohn and Szalay (1974) in the first prosimian volume.

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