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Mechanical food properties and dental topography differentiate three populations of *Lemur catta* in southwest Madagascar

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ABSTRACT

Determining the proximate causes of tooth wear remains a major focus of dental study. Here we compare the diets of three ring-tailed lemur (*Lemur catta*) populations and examine how different dietary components may contribute to patterns of wear-related tooth shape. Casts were made from dental impressions collected between 2003 and 2010 from lemurs in the gallery and spiny/mixed forests of the Bezá Mahafaly Special Reserve (BMSR; Parcels 1 and 2) and the spiny/mixed forests of Tsimanampesotse National Park (TNP), Madagascar. Tooth shape variables (occlusal relief and slope, angularity) were analyzed using dental topographic analysis. Focal observations and food mechanical properties (FMPs: toughness, hardness, elastic modulus) were conducted and tested, respectively, during wet and dry seasons from 2008 to 2012. We found that FMPs correlate with patterns of dental topography in these three populations. Specifically, food toughness and elastic modulus correlate with the dental variables, but hardness does not. Average food toughness and elastic modulus, but not hardness, are highest in BMSR Parcel 2, followed by BMSR Parcel 1 and TNP. Occlusal relief and slope, which serve as proxies for tooth wear, show the greatest wear in Parcel 2 and the least in TNP. Angularity is also more pronounced in TNP. Further, dental topographic patterns correspond to reliance on *Tamarindus indica* (tamarind) fruit. Both BMSR populations consume tamarind at high frequencies in the dry season, but the fruits are rare at TNP and only occasionally consumed. Thus, high seasonal tamarind consumption and its mechanical values help explain the low dental relief and slope among BMSR lemurs. By investigating the ecology of a single widespread species across a variety of habitats, we have been able to link specific components of diet to patterns of dental topography in this species. This provides a context for interpreting wear-related tooth shape changes more generally, illustrating that populations can develop different dental wear patterns resulting from a mix of intrinsic factors (thin enamel) and local conditions (food properties, frequency of consumption).

1. Introduction

Understanding the process of how mammalian teeth wear has garnered considerable attention (e.g., Baker et al., 1959; Kay and Covert, 1983; Teaford and Tylenda, 1991; Ungar et al., 1995; Ungar, 1998; Teaford, 2000; Dennis et al., 2004; Lucas, 2004; Nystrom et al., 2004; Cuozzo and Sauther, 2006; Sanson et al., 2007; Galbany et al., 2011; Rabenold and Pearson, 2011, 2014; Lucas et al., 2013; Pampush et al., 2013). These studies have identified numerous potential causal variables that include food mechanical properties, biogenic silica, exogenous grit, chemical properties of food, and food processing (e.g., Ungar et al., 1995; Sanson et al., 2007; Cuozzo et al., 2008; Rabenold and Pearson, 2011, 2014; Yamashita et al., 2012a; Lucas et al., 2013, 2014). However, to date, there remains a lack of consensus on which of these variables, or combination of variables, are the proximate

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causes of mammalian tooth wear (e.g., Lucas et al., 2013, 2014; Rabenold and Pearson, 2014).

Since 2006 we have been investigating the degree to which food mechanical properties (FMPs) contribute to differences in tooth shape in populations of ring-tailed lemurs (*Lemur catta*) from southwestern Madagascar. One of the benefits of studying dental topography in wild ring-tailed lemurs is the large body of ecological and behavioral information available for this species (e.g., Gould et al., 2003; Jolly et al., 2006; Sauther et al., 2015; and see below). Accordingly, ring-tailed lemurs are an ideal study species for dental ecology, which combines examination of dentition with detailed ecological information (Cuozzo and Sauther, 2012).

L. catta populations inhabit environments in southern Madagascar ranging from gallery forest to desert scrub (Goodman and Langrand, 1996; Sauther et al., 1999; Kelley, 2013; LaFleur et al., 2014). Until recently, they were primarily studied in gallery forest habitats (e.g., Jolly, 1966; Sauther et al., 1999), although current research outside these areas has expanded our knowledge of the ecological flexibility of these animals (e.g., Kelley, 2013; LaFleur et al., 2014; Sauther et al., 2015). The riverine gallery forests of Bezá Mahafaly Special Reserve (BMSR) and Berenty reserve, where ring-tailed lemurs have been studied for more than 25 years, are dominated by *Tamarindus indica* trees (e.g., Jolly, 1966; Sussman and Rakotozafy, 1994; Blumenfeld-Jones et al., 2006). The fruits of this tree are the dominant food in the diets of the ring-tailed lemurs in these forests (e.g., Sauther, 1998; Yamashita, 2002; Blumenfeld-Jones et al., 2006; Gould, 2006). Our earlier work has established that dependence on the fruit of *T. indica* is related to the degree of postcanine dental wear in the BMSR populations (Cuozzo and Sauther, 2006; Cuozzo and Sauther, 2008; Yamashita et al., 2012a). This fruit, particularly the outer shell of the ripe fruit, is the most mechanically challenging food (e.g., toughest, hardest, stiffest) in the ring-tailed lemur diet at this site (Yamashita et al., 2012a). The mechanical properties and the methods used by the lemurs to orally process the fruit contribute to the patterns of extreme wear and tooth loss observed in these populations (Yamashita et al., 2012a). The lemurs insert the long tamarind pod into the side of the mouth and bite repeatedly to crack the stiff outer shell. It is in precisely this location where we observe the heaviest wear. Furthermore, ring-tailed lemurs have thin dental enamel and the repeated stresses incurred from feeding on a relatively large fruit most likely contribute to producing microcracks in the enamel that radiate out from the enamel-dentine junction (Lucas et al., 2008; Constantino et al., 2009). Such cracks have been observed in ring-tailed lemur teeth (Campbell et al., 2012).

In this paper, we extend our analyses of diet and dental topography (i.e., dental ecology) to include a population of ring-tailed lemurs in the spiny and mixed forests of Tsimanampesotse National Park (TNP), which lies 135 km southwest of BMSR, and lemurs from the drier spiny and mixed forest in the western section of BMSR. Though tamarind is present in all three sites, it differs in abundance, thus allowing us to refine our hypothesis that consumption of the fruit is a primary cause of tooth wear in ring-tailed lemurs. Tamarind trees are common in the BMSR gallery forest, less common in the BMSR spiny and mixed forests 5 km to the west, and restricted to the base of a plateau and in limestone depressions at TNP (Sussman and Rakotozafy, 1994; Axel and Maurer, 2010; LaFleur, 2012). In our analyses, we compare three dental topographic variables with food mechanical properties, diet, and habitat across three populations of ring-tailed lemurs. Our primary goals in this paper are to determine if 1) dental topographic variables and 2) food mechanical properties differ by site and 3) if the dental and food properties variables are correlated among sites (definitions for dental terms are below).

2. Materials and methods

2.1. Study sites and species

Our study populations inhabit the riverine gallery forest (Parcel 1 [P1]) and degraded dry/spiny forest (Parcel 2 [P2]) of the Bezá Mahafaly Special Reserve (BMSR; 23°30′S, 44°40′E) and the mixed deciduous and spiny forest habitats of Tsimanampesotse National Park (TNP; 24° 07′S, 43°45′E). The two sites in BMSR are 5 km apart, with the gallery forest extending approximately 1 km west of the ephemeral Sakamena River. TNP is approximately 135 km southwest of BMSR and 7 km east of the Mozambique Channel (Fig. 1).

All three sites experience distinct wet and dry seasons, although the average durations vary by site. Generally, a warm, wet season occurs from November to March and a cool, dry season from April to October. Parcel 1 in BMSR comprises an 80 ha plot surrounded by a protective fence that serves to keep livestock out of the forest but does not prohibit lemur movement across the reserve boundary. A tamarind-dominated gallery forest forms the eastern boundary along the seasonal Sakamena River, and the forest becomes progressively drier to the west (Sussman and Rakotozafy, 1994; Sussman and Ratsirarson, 2006). Outside the fenced-in portion, the forest has been degraded by grazing livestock and other human actions (e.g., Cuozzo and Sauther, 2004; Sauther et al., 2006; Sauther and Cuozzo, 2009). Parcel 2 and the surrounding area are composed of a patchwork of dry, deciduous forest and spiny forest (Axel and Maurer, 2010). Our study groups are in Parcel 2 as well as to the north and west of this area. The ring-tailed lemur troops in this area primarily inhabit the dry forest, although groups also

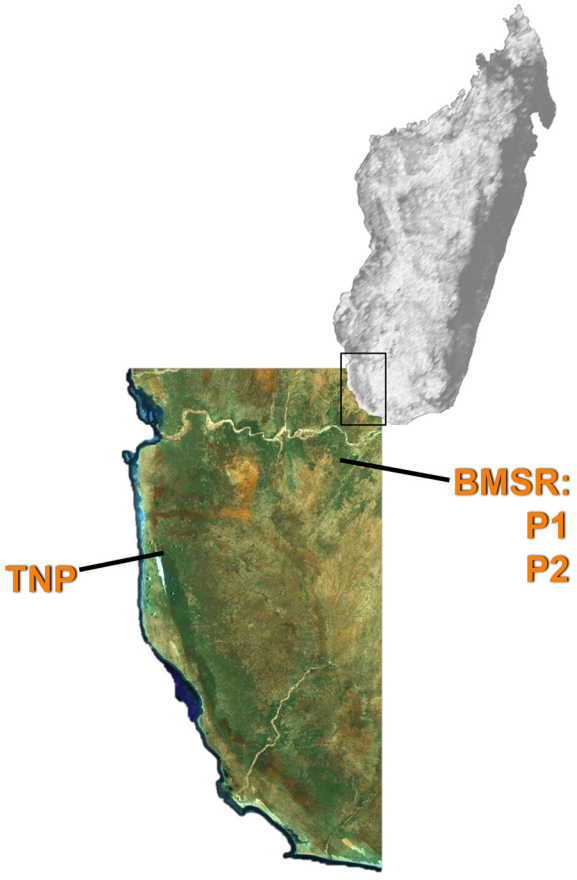

Figure 1. Location of the three study sites in southwest Madagascar (terrain map modified from Google maps, 2014).