

Lemur Habitat and Dental Senescence in Ranomafana National Park, Madagascar

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ABSTRACT Not only can teeth provide clues about diet, but they also can be indicators of habitat quality. Conspecific groups living in different habitats with different kinds of foods may exhibit different rates of dental attrition because their teeth are less well adapted to some foods than to others. Ecological disequilibrium describes the situation in which animals live in habitats to which they are relatively poorly adapted. We test whether dental senescence, the wear-related decrease in dental functionality that is associated with decreased survival of infants born to older *Propithecus edwardsi* females, can be explained by ecological disequilibrium. Specifically, we compare the rates of dental wear in sifaka groups living in nearby habitats that differ in the degree of anthropogenically induced disturbance. We

hypothesize that sifakas living in disturbed areas have an unusual rate of tooth wear compared to those living in a more pristine area, and that dental senescence is a consequence of an atypically high wear rate in a degraded habitat. To test whether habitat quality affects tooth wear more generally, we compare rates of use-wear in two subsets of *Microcebus rufus* living in either relatively undisturbed or disturbed habitats. Contrary to our predictions, we did not detect different rates of tooth wear in disturbed versus undisturbed habitats for either species and consider that reproductively detrimental dental senescence in *P. edwardsi* females is unlikely to be a pathological consequence of ecological disequilibrium. *Am J Phys Anthropol* 148:228–237, 2012. © 2012 Wiley Periodicals, Inc.

The ability to obtain adequate nutrition is a primary determinant of evolutionary fitness in any given ecological niche. Teeth are one of the first organs to contact food and the only to substantially mechanically process food for nutrients in almost all mammalian species, and are thus responsible for transforming food items from their natural state into something that can be swallowed and further digested. As a result, tooth characteristics often reflect habitat characteristics including available food items (e.g., Fortelius, 1985; Janis and Fortelius, 1988; Mendoza and Palmqvist, 2008). A corollary to this observation is that dental adaptations can be food- and habitat-specific such that teeth may function poorly in habitats to which they are not well adapted. There has recently been increased interest in this topic among anthropologists and primatologists as exemplified by the symposium on primate dental ecology at the annual meetings of the American Association of Physical Anthropologists in Albuquerque, New Mexico in April, 2010 (Cuozzo and Sauter, 2010). In this article, we contribute to the field of dental ecology by examining the relationship between habitat disturbance and tooth use-wear in two species of rainforest lemur, *Propithecus edwardsi* and *Microcebus rufus*.

There are well-known relationships between primate dental morphology and diet (Kay, 1975; Lucas, 1979, 2004). Insectivores tend to have tall pointed cusps; folivores tend to have cusps that are connected by long shearing crests; and both frugivores and hard-object

feeders tend to have more bunodont teeth with low, rounded cusps. But teeth of all kinds wear down with use and age such that their morphology can change as individuals get older. Although it is clear that many taxa have morphological adaptations that compensate for use-wear and may even show increasing dental functionality with wear (Rensberger, 1973; Luke and Lucas, 1983; Fortelius, 1985; Lanyon and Sanson, 1986; King et al., 2005), it is also clear that, apart from ever-growing hypselodont teeth, eventually wear is detrimental. Diminished functional efficiency of heavily worn teeth may have negative consequences for the individual. For example, Logan and Sanson (2002) found that male koalas (*Phascolarctos cinereus*) with very worn molar teeth compensate for diminished chewing efficiency by increasing both the rate of chewing and the time spent eating,

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but they do so at the cost of time spent socializing, moving, and engaging in reproductive activity. Other researchers have found unusual dental pathologies (severe tooth wear, antemortem tooth loss) in populations of *Lemur catta* living in anthropogenically disturbed habitats but not in more pristine habitats (Cuozzo and Sauther, 2006, 2008; Millette et al., 2009; Sauther and Cuozzo, 2009). Some populations of the Svalbard reindeer (*Rangifer tarandus platyrhynchus*) are reported to experience unusual tooth wear because they are "...foraging in environments more extreme than where they evolved" (Veiberg et al., 2007:1146). The relationship between advanced tooth wear and habitat quality has been explored in other ungulates as well (e.g., Kojola et al., 1998; Nussey et al., 2007).

Senescence is the progressive diminution of function accompanied by decreased survival or reproductive success as animals age (Mysterud et al., 2001; Carranza et al., 2004). The loss of dental functionality in male red deer may signal the onset of their senescence (Loe et al., 2003; Carranza et al., 2004), and tooth wear has been suggested to have implications for senescence of other animals including reindeer (Skogland, 1988) and moose (Ericsson et al., 2001). Such dental senescence is also found in primates, but because primates have relatively long lifespans and low-crowned teeth, it can occur relatively earlier in the lifespan and before the functioning of other body systems has declined. In *Propithecus edwardsi*, extensive dental wear results in early dental senescence in females living beyond 18 years of age (King et al., 2005; Wright et al., 2008). These authors found that dental senescence in this species has negative reproductive implications because survival to adulthood of offspring born to old, dentally senescent females is compromised, especially in years when the annual lactation season is unusually dry. Given the high level of interannual variation in the monthly distribution of rain (King et al., 2011), resource-poor lactation seasons are not uncommon for these sifakas. Ungar and M'Kirera (2003) suggested that natural selection should favor teeth that wear in a manner that keeps them mechanically efficient and able to process preferred foods. Thus, the pattern of tooth wear in Milne-Edwards' sifakas may be maladaptive because it is associated with unsuccessful reproductive events and therefore decreases or limits the lifetime reproductive success of some individuals. This is particularly true in light of the fact that old, dentally senescent females remain fertile and produce new offspring at the same rate as younger females (Pochron et al., 2004; King et al., 2005). The persistence of fertility in dentally senescent female sifakas suggests that there should be a selective pressure to maintain dental health longer, even as teeth become worn. Dental senescence has not been documented in male sifakas, perhaps because no *P. edwardsi* male older than 19 years has ever been observed in nature.

Dentitions that lose functional efficiency prematurely may indicate that a recent environmental shift has occurred such that natural selection has not yet modulated the use-wear rate to reflect conditions in the changed habitat. Indeed, tooth wear may be a useful indicator to assess the impact of environmental change in living populations. Habitat-related differences in tooth wear rates can result from several factors including, but not limited to, dietary differences, differences in the mechanical properties and phytolith content of foods, or differences in rainfall and dust levels. The extreme dental pathology observed in *Lemur catta* in western Madagas-

car very likely reflects a recent environmental shift with a concomitant change in diet (Cuozzo and Sauther, 2006, 2008; Millette et al., 2009, Sauther and Cuozzo, 2009). These authors proposed that "ecological disequilibrium" can explain this dentally pathological condition. They demonstrated that gallery forest ring-tailed lemurs rely on a food for which they are not well adapted. Furthermore, they noted that dental pathology in ring-tailed lemurs is "...exacerbated in areas affected by anthropogenic change" (Sauther and Cuozzo, 2009:684).

We test whether the dental senescence observed in Milne-Edwards' sifakas is also a pathology due to ecological disequilibrium. Ecological disequilibrium is a plausible explanation in this case because recent anthropogenic environmental degradation is known to have occurred in a portion of this species' range, and previous research in nearby areas indicates that sifaka time budgets can differ in disturbed versus undisturbed habitats (Arrigo-Nelson, 2006). Additionally, even in the absence of dental senescence, difference of dental use-wear rates in different habitats may indicate that animals are better adapted to some habitats than to others. We compare tooth wear rates in two sifaka habitats that differ in the degree of anthropogenic disturbance. The level of disturbance is known to be associated with differences in resource availability and quality (Hemingway, 1995; Wright, 1997; Balko, 1998; Wright and Andriamihaja, 2002; Balko and Underwood, 2005; Tecot, 2008).

To test whether anthropogenic disturbance alters wear rates more generally, we also compare dental attrition rates at two localities in a second lemur species, *Microcebus rufus*, the brown mouse lemur. Neither dental senescence nor unusual dental pathology has been identified in *M. rufus*, but the lack of dental senescence is not surprising because mouse lemurs differ markedly from sifakas in their diets and life histories. Milne-Edwards' sifakas are largely folivorous (with some fruit and seeds; Hemingway, 1996, 1998; Wright, 1999; Arrigo-Nelson, 2006), whereas brown mouse lemurs consume fruit, insects, flowers, and nectar (Atsalis, 1999). Mouse lemurs reproduce at a faster rate than sifakas and live much shorter lives on average (Pochron et al., 2004; Atsalis, 2008; Blanco, 2008; King et al., 2011). It is possible that mouse lemurs simply do not live long enough to become dentally senescent. Nevertheless, we believe that mouse lemurs provide a valid comparison because the rate of tooth wear may vary according to habitat characteristics in any species.

Habitat destruction or fragmentation need not necessarily lead to a faster rate of tooth wear. Research on fragmented *Colobus vellerosus* habitat suggests that disturbed habitats can contain more pioneer plant species with higher quality leaves that may be easier, rather than more difficult, to process dentally (Wong et al., 2006; Wong and Sicotte, 2007). Nonetheless, because the teeth of Milne-Edwards' sifakas wear to the detriment of individuals, we hypothesize that sifaka dental senescence is a consequence of unusually high use-wear in populations in ecological disequilibrium. If this is true, then we predict that there is a higher rate of tooth wear and potentially greater prevalence of dental senescence in the more disturbed habitat.

MATERIALS AND METHODS

Study subjects

Treatment of live animals complied with the laws of the Republic of Madagascar, adhered to the American

Society of Primatologists' Principles for the Ethical Treatment of Nonhuman Primates, and was approved by IACUC, Stony Brook University and the University of Massachusetts, Amherst.

Sifaka data are from a long-term field study of the Milne-Edwards' sifaka that began in 1986 and continues today (Wright, 1995; Hemingway, 1998; Pochron et al., 2004; Arrigo-Nelson, 2006; Morelli, 2008; Morelli et al., 2009; King et al., 2011). Study animals are habituated to human observers. The sifakas we studied belonged to six social groups that ranged in size from two to nine individuals, and each group included one or two breeding females (Wright, 1995; Pochron and Wright, 2003; Morelli et al., 2009). *P. edwardsi* are female-dominant, diurnal, large-bodied (~6 kg) and sexually monomorphic rainforest lemurs (King et al., 2011). They reproduce seasonally, with 52 of 53 known births occurring during May, June, or July (Wright, 1995; Morelli, 2008; Morelli et al., 2009), and females give birth to singleton offspring approximately every 2 years (average = 1.7 years; Morelli et al., 2009). Lactation occurs during the drier season when sifakas survive largely on leaves (Wright, 1995, 1999). Females first give birth at 4 years of age or older (Morelli et al., 2009; King et al., 2011). *P. edwardsi* are primarily folivorous with seasonal peaks of fruit and seed consumption during the rainy austral summer (Hemingway, 1996, 1998; Wright, 1999; Arrigo-Nelson, 2006).

With veterinary supervision, team members captured, examined, and released study animals on an almost annual basis since 1987 (King et al., 2011) using a well-established and successful protocol (Glander et al., 1992; Wright, 1995). Our highly experienced capture team used lightweight darts to deliver Telazol[®] intramuscularly at 10 mg/kg of body mass. Team members transported captured animals to the nearby field station for examination. We attached color-coded tags and collars to each fully grown sifaka to facilitate individual identification in the field and during subsequent captures. Molds were made of the right mandibular teeth of sedated sifakas (Coltène President Jet Plus, light body polyvinylsiloxane).

The ages of individuals in the study population had previously been determined (King et al., 2005). Female Milne-Edwards' sifakas have a maximum lifespan of more than 30 years, and males are known to live to 19 years of age (King et al., 2011; Tecot et al., 2011). The difference in female and male lifespans appears to be related to sex differences in intergroup transfer behavior, with the rate of female transfer decreasing with age and the rate of male transfer remaining constant across adulthood (Tecot et al., 2011).

Microcebus rufus, the brown mouse lemur, is a small (30–60 g), seasonally breeding, nocturnal lemur (Atsalis, 2008; Blanco, 2008; Blanco and Meyer, 2009). Some individuals display seasonal changes in body mass and tail circumference and also exhibit torpor behavior (Atsalis, 2008; Blanco, 2008). The brown mouse lemur reproduces quickly, with some females reproducing for the first time at 1 year of age (Atsalis, 2008; Blanco, 2008). Mouse lemurs typically give birth to multiple offspring (Atsalis, 2008). Mouse lemurs live longer than many other similarly sized mammals, and at our research site are known to have a maximum lifespan of at least 8 years (Zohdy et al., 2009).

We (MBB and SZ) used a capture/recapture technique described in Blanco (2008) and Blanco and Meyer (2009)

to repeatedly sample the mouse lemur populations from 2003 to 2009. Individuals were identified by previously implanted electronic microchips. Dental impressions (Express, fast set, 3M Dental Products) were taken of the right mandibular tooth row of sedated animals.

Site

We observed both study species in the southeastern montane rainforest in, or adjacent to, Ranomafana National Park (RNP), Madagascar (21°02'–21°25' S and 47°18'–47°37' E) (Wright, 1992, 1995). Altitudes in the park range from 600 to 1,487 m. The yearly average rainfall at RNP is ~3,000 mm (RNP records; Tecot, 2008; King et al., 2011). Climatic conditions vary seasonally with highest rainfall and temperatures occurring from December through March. Within this general pattern there is considerable interannual variation, particularly in the amount and temporal distribution of rainfall (RNP records). There is a network of trails (>30 km in length) throughout the park that facilitates the observation of lemurs and other sympatric animals. We studied the two lemur species in three different habitats—Vatoharanana (Vato), Talatakely (Tala), and Campsite—which differ in the degree of anthropogenically induced disturbance. Campsite is relatively more disturbed than Tala, which in turn is relatively more disturbed than Vato, which is only minimally disturbed.

We compared tooth wear rates in sifakas living in Tala and Vato. Researchers have characterized the Tala area as having undergone significant anthropogenically induced habitat disturbance (Wright, 1997; Balko, 1998; Wright and Andriamihaja, 2002; Arrigo-Nelson, 2006; Tecot, 2008). There was a small settlement and market in the area during the 1930s and 1940s, and intensive logging took place in 1986–1987 (Wright, 1992, 1997; Wright and Andriamihaja, 2002). In particular, loggers removed many large fruit trees from the forest (Balko, 1998; Arrigo-Nelson, 2006). In contrast, Vato has suffered only minimal localized anthropogenic disturbance because it was lightly and selectively logged in 1986 (Overdorff, 1988; White et al., 1995; Balko, 1998; Grassi, 2001; Tecot, 2008). As a result of their different histories, these sites differ in the density and abundance of plant species (Turk, 1995; Wright, 1995; Balko, 1998; Tecot, 2008). Vato is characterized as continuous primary forest with steep mountain slopes, lower tree diversity and density, a continuous canopy, and trees larger in diameter at breast height, height, and crown volume compared with those in Tala (Overdorff, 1988; White et al., 1995; Balko, 1998; Dagosto and Yamashita, 1998; Grassi, 2001; Tecot, 2008). Trees are also more productive and food availability is more predictable at Vato than at Tala (Tecot, 2008). As a result, it has been stated that “(t)hese sites should be considered functionally different when studying groups of a species occupying both sites” (Tecot, 2008:156). In our analysis of sifaka tooth wear, the Tala habitat is “disturbed” relative to Vato which is “undisturbed.”

We compared mouse lemur tooth wear rates in Tala and Campsite. In this case, our “undisturbed” area is Tala (which is the relatively disturbed area for sifakas) and the relatively more “disturbed” area is Campsite. The nature of the Tala habitat was described above. Campsite is located just outside RNP and across the Namorona River, 0.48 km from Tala. The Campsite locality underwent extensive human-induced disturbance quite recently. In particular, humans practiced rice

TABLE 1. Tooth wear rates in *Propithecus edwardsi*

Locality ^a	Individual ID	Sex	Approx. age (years)	Mold interval (years)	Wear rate (mm/year)	Individual mean rate (mm/year)
Tala 1	2	M	14	1.4	0.303	0.303
Tala 1	3	F	14	1.5	0.330	0.190
Tala 1	3	F	15	1.4	0.049	
Tala 1	11	M	11	1.4	0.121	0.121
Tala 1	14	F	6	1.5	0.278	0.254
Tala 1	14	F	8	1.4	0.229	
Tala 1	18	M	4	1.5	0.521	0.381
Tala 1	18	M	6	1.5	0.242	
Tala 1	21	M	2	1.5	0.277	0.169
Tala 1	21	M	4	1.5	0.061	
Tala 1	22	F	2	1.5	0.261	0.261
Tala 1	24	M	2	1.5	0.158	0.165
Tala 1	24	M	4	1.4	0.171	
Tala 1	26	M	9	1.4	0.216	0.216
Tala 1	27	M	12	1.5	0.261	0.261
Tala 1	29	M	2	1.4	0.205	0.205
Vato	202	M	—	1.0	0.236	0.240
Vato	202	M	—	1.0	0.244	
Vato	204	M	4	1.0	0.024	0.088
Vato	204	M	5	1.0	0.153	
Vato	206	F	5	1.0	0.344	0.212
Vato	206	F	6	1.0	0.080	
Vato	207	F	—	1.0	0.207	0.207
Vato	209	M	—	1.0	0.093	0.093
Tala 2	3	F	20	6.1	0.297	0.206
Tala 2	3	F	25	2.0	0.115	
Tala 2	24	M	8	6.1	0.241	0.241
Tala 2	29	M	7	6.1	0.207	0.207
Tala 2	36	F	7	6.1	0.224	0.208
Tala 2	36	F	11	2.0	0.193	
Tala 2	59	M	2	2.0	0.172	0.172
Tala 2	62	M	5	2.0	0.230	0.230

^a Tala 1 = 1993–1995, disturbed. Tala 2 = 1995–2004, disturbed; Vato = 1993–1995, undisturbed.

paddy agriculture there in the 1990s until the early 2000s. Since that time there has been rapid regrowth of small trees and bushes. Humans continue to live in and pass through the Campsite locality today. Forest characteristics are visibly distinct at the two sites, but have not yet been systematically quantified. Large fruiting trees are lacking at Campsite and there is reduced availability of mistletoe, an important mouse lemur food (Atsalis, 2008), making Campsite more resource-deprived. Additionally, mouse lemurs have lived at Tala a long time, certainly prior to the selective logging in 1986–1987, whereas Campsite is a relatively new mouse lemur habitat that became available only with the recent regrowth of bushes and small trees.

Dental sample

***Propithecus edwardsi*.** We used 51 dental molds representing a total of 19 individuals from the 2 sites between 1993–2004 to calculate the rate of use-wear in *P. edwardsi*. Calculations of wear rates depend on having at least two observations of tooth wear in single individuals. Each rate calculation therefore employed two measurements, one from an older mold (younger instance of an individual) and one from a younger mold (older instance of an individual). Because we know the molding dates in all cases, the temporal duration between subsequent molds of the same individual is also known. In many cases, we used temporally adjacent data points for a single individual more than once. For example, if dental molds of an individual were available in 1993, 1994, and 1995, two nonoverlapping rate estimates could be calcu-

lated (1993–1994 and 1994–1995). Although a third rate might be calculated by comparing molds from 1993 to those from 1995, this value is dependent on the other two.

We calculated 24 use-wear rates for 16 different individuals between 1993 and 1995 at Tala and Vato. Molds from 11 individuals provided 16 wear rates for Tala during those years and we refer to that sample as “Tala 1” (Table 1). Molds from five individuals provided eight wear rates from Vato during the same years. We calculated an additional eight wear rates in six Tala individuals between 1995 and 2005 and refer to that sample as “Tala 2.” We calculated the mean wear rate for each individual, because different wear rates for the same individual are considered to violate the assumption of independence of data points. However, because three individuals (female ID 3; males IDs 24 and 29) lived in Tala during both time periods (Tala 1 and Tala 2), we calculated separate wear rates for each of those individuals in each habitat. Because of the nonindependence of the wear rates of these particular individuals in Tala across time, we conducted our analysis of habitat-specific wear rates in three ways. First, we excluded these three individuals from Tala 1. Second, we excluded these three individuals from Tala 2. Finally, we included these three individuals in both groups as if they represented independent observations.

***Microcebus rufus*.** To calculate dental use-wear rates in *M. rufus*, we used 79 tooth row molds representing 25 different individuals from the 2 mouse lemur sites between 2003 and 2009. Because we recorded the dates on which we molded the teeth, we were able to determine the elapsed time between moldings. Using the

TABLE 2. Tooth wear rates in *Microcebus rufus*

Locality ^a	Individual ID	Sex	Mold interval (months)	Wear rate (μ /months)	Individual mean rate (μ /months)
Tala	Ingrid	F	11	0.00073	
Tala	Ingrid	F	13	0.00098	0.00155
Tala	Ingrid	F	11	0.00294	
Tala	Anja	F	12	0.00095	0.00147
Tala	Anja	F	12	0.00198	
Tala	Stacey	F	11	0.00273	0.00161
Tala	Stacey	F	12	0.00093	
Tala	Stacey	F	12	0.00131	
Tala	Stacey	F	12	0.00148	
Tala	Marcela	F	11	0.00128	0.00141
Tala	Marcela	F	11	0.00155	
Tala	Carla	F	12	0.00122	0.00203
Tala	Carla	F	10	0.00283	
Tala	Claudia	F	11	0.00124	0.00153
Tala	Claudia	F	13	0.00182	
Tala	Jaqueline	F	12	0.00131	0.00135
Tala	Jaqueline	F	9	0.00032	
Tala	Jaqueline	F	12	0.00259	
Tala	Jaqueline	F	11	0.00117	
Tala	Preciosa	F	12	0.00103	0.00082
Tala	Preciosa	F	11	0.00061	
Tala	Aristide	M	11	0.00018	0.00214
Tala	Aristide	M	12	0.00409	
Tala	Ishmael	M	12	0.00216	0.00267
Tala	Ishmael	M	11	0.00318	
Tala	Kerry	M	13	0.00098	0.00081
Tala	Kerry	M	12	0.00063	
Tala	Mamy	M	13	0.00108	0.00161
Tala	Mamy	M	11	0.00214	
Tala	Mark	M	11	0.00141	0.00247
Tala	Mark	M	12	0.00353	
Tala	Napolean	M	12	0.00042	0.00075
Tala	Napolean	M	11	0.00139	
Tala	Napolean	M	12	0.00045	
Tala	Pascal	M	13	0.00111	0.00174
Tala	Pascal	M	10	0.00154	
Tala	Pascal	M	11	0.00257	
Tala	Ralala	M	23	0.00124	0.00102
Tala	Ralala	M	13	0.00080	
Tala	Mickey	M	14	0.00180	0.00134
Tala	Mickey	M	9	0.00088	
Tala	Ziggy	M	12	0.00128	0.00098
Tala	Ziggy	M	10	0.00082	
Tala	Ziggy	M	12	0.00085	
Tala	Loco	M	10	0.00115	0.00170
Tala	Loco	M	12	0.00224	
Campsite	Govinda	F	12	0.00165	0.00118
Campsite	Govinda	F	11	0.00071	
Campsite	Scott	M	9	0.00098	0.00120
Campsite	Scott	M	12	0.00142	
Campsite	Ryan	M	11	0.00121	0.00121
Campsite	Sam	M	11	0.00118	0.00118
Campsite	Ian	M	10	0.00143	0.00143
Campsite	Ferngully	F	22	0.00153	0.00153

^a Tala = undisturbed.
Campsite = disturbed.

same method of calculating rates between temporally adjacent pairs of samples for each individual, we calculated 46 tooth wear rates from 19 individuals in the Tala site, and 8 wear rates from 6 individuals from the Campsite locality (Table 2). Again, we calculated the mean wear rate for each individual.

Measurements

The dental measurements used to reflect progressive use-wear differed between *P. edwardsi* and *M. rufus* primarily due to logistical issues resulting from absolute

size differences. Although the measurement protocols are different for the two species, the calculated wear rates are equivalent in the sense that both represent ratios of linearized measurements of wear-exposed dentine. First we explain the measurement procedure for *P. edwardsi*. Dental molds of the second mandibular molars were cast in epoxy or plaster. This tooth was chosen to be consistent with previous studies of tooth morphology (e.g., Ungar and Williamson, 2000; Ungar and M'Kirera, 2003; Dennis et al., 2004; Ungar, 2004; King et al., 2005; Scott et al., 2005; Boyer, 2008). After orienting the casts to maximize the crown-base projec-

tion, yielding a roughly horizontal occlusal plane, we digitized them using a three-dimensional piezo scanner (MDX-15, Roland) with data points collected every 50 μm . We digitally isolated and measured the 2D area of dentine exposure using MFWorks 3.0 GIS software (2002, Keigan Systems, London, Ontario, Canada) in units of square millimeters, and defined wear rates as the increase in area of dentine exposure from one instance of an individual to the next divided by the time elapsed between sampling instances. More specifically, to make rates independent of the total area of dentine exposure, we calculated rates as the change in square roots of dentine exposure per unit time. Wear prior to the exposure of dentine was not measured. Details of the procedures used to measure the area of exposed dentine were described in King et al. (2005). We checked for a correlation between wear rate and age (Reduced major axis regression: Probability of no correlation = 0.82). We also checked for a correlation between wear rate and total dentine area exposed (Reduced major axis regression: Probability of no correlation = 0.822). In both cases there was no correlation, meaning that rate estimates should not be biased or confounded by different demographic structures at the sample sites.

The teeth of *M. rufus* are very small relative to the resolution of the 3D scanning modalities available to us at the time this study was conducted. Therefore, we used a different method developed by Zohdy et al. (2009) to measure increases in dentine exposure in *M. rufus*. These authors found that the amount of wear-exposed dentine can be approximated by a combination of two linear distances: the maximum diameters across the exposed dentine on the metaconid and the hypoconid. Measurements were digitally taken from stereomicroscope photographs (at 15 \times magnification) of field-collected dental molds. All distance measurements were taken in microns and standardized to the mesiodistal length of the tooth.

Statistics

We tested for sex differences in mean wear rates for each lemur species using the nonparametric Mann-Whitney U test with $\alpha = 0.05$. For *P. edwardsi* we compared wear rate subsets from the two sites and at two different time intervals for the Tala site, using the nonparametric Kruskal-Wallis test. We compared the mean wear rates in a total of three different subsets for *P. edwardsi* (rates from Tala 1, rates from Vato, and rates from Tala 2). We acknowledge that including data from Tala at two different times may confound habitat differences with time differences.

We treated the data from *M. rufus* similarly, but made only one comparison between the two sites across the same time frame. Therefore we used a nonparametric Mann-Whitney U test to compare mean wear rates in the two habitats.

RESULTS

Tables 1 and 2 present the sample and individual tooth wear rates for *P. edwardsi* and *M. rufus*, respectively. We first compared males and females and found no statistically significant sex difference in mean wear rates for *P. edwardsi* in any of the three subsets (Tala 1, Mann-Whitney $U = 10.5$, $P = 0.759$; Vato, Mann-Whitney $U = 2$, $P = 0.564$; Tala 2, Mann-Whitney $U = 5$, P

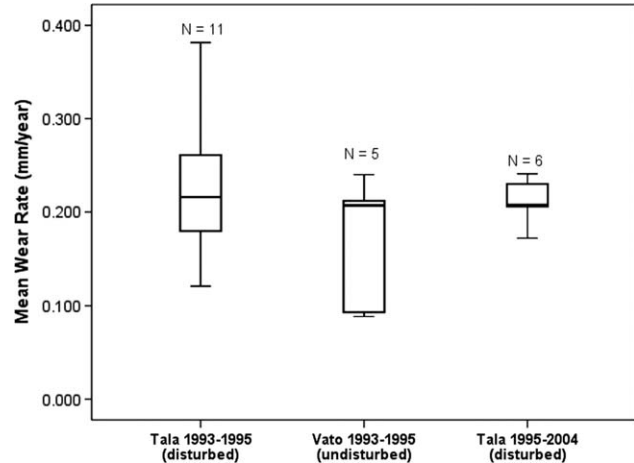


Fig. 1. Milne-Edwards' sifaka mean tooth wear rates in undisturbed (Vato) and disturbed (Tala, at two times) habitats.

= 0.643) or when individuals from all groups were combined (Mann-Whitney $U = 44$, $P = 0.549$). Neither did we find a sex difference in the mean rate of tooth wear in *M. rufus* at either locality (Tala, Mann-Whitney $U = 41$, $P = 0.804$; Campsite, Mann-Whitney $U = 4$, $P = 1.0$) nor when individuals from both localities were combined (Mann-Whitney $U = 80$, $P = 0.782$).

We compared wear rates across habitats in two ways. First, we compared rates in a sex-restricted subset of the sample (females only) because dental senescence has been observed only in females (however, we remind the reader that the typical onset age of dental senescence in females is similar to, or greater than, the age of the oldest male documented at our study sites: see above). Second, in order to enlarge our sample sizes and because there is no sex difference in the rate of wear in either species we included both males and females when comparing use-wear in different habitats.

Contrary to our expectations, we found no significant habitat-related wear rate differences in either *P. edwardsi* or *M. rufus*. Female sifakas do not differ in mean wear rate across Tala 1, Vato, and Tala 2. This is the case when female individual 3 (who was present in both Tala 1 and Tala 2) is excluded from Tala 1 (Kruskal-Wallis, Chi square: 3.714, $P = 0.156$), when she is excluded from Tala 2 (Kruskal-Wallis, Chi square: -0.429 , $P = 0.807$), or when she is included as a member of both Tala 1 and Tala 2 (Kruskal-Wallis, Chi square: 0.714, $P = 0.700$). The addition of male sifakas does not change these results. There is no observed difference in mean wear rates when individuals 3, 24, and 29 (Table 1) were excluded from Tala 1 (Kruskal-Wallis, Chi square: 4.037, $P = 0.133$), when the same individuals were excluded from Tala 2 (Kruskal-Wallis, Chi square: 1.642, $P = 0.440$) or when those individuals were included in both Tala 1 and Tala 2 (Kruskal-Wallis, Chi square: 1.523, $P = 0.467$).

We also found no habitat-related wear rate differences in *M. rufus* (Mann-Whitney $U = 98$, $P = 0.203$, sexes combined).

Dental wear rates are variable in both relatively pristine and disturbed habitats, but teeth do not wear predictably faster in disturbed habitats (Figs. 1 and 2). However, dentally senescent sifakas are more prevalent at the disturbed Tala locality as none has ever been

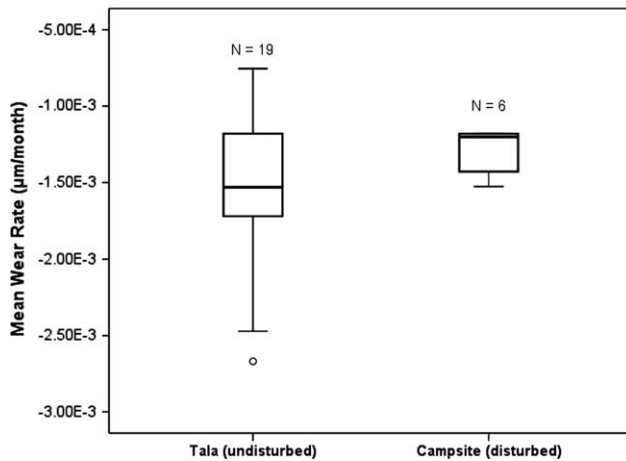


Fig. 2. Brown mouse lemur mean tooth wear rates in undisturbed (Tala) and disturbed (Campsite) habitats.

observed at the undisturbed Vato locality. Then again, none of the animals at the Vato site appears to have reached the age at which dental senescence begins in Tala individuals.

DISCUSSION

We tentatively follow the implications of our wear rate results and reject the hypothesis that dental senescence in Milne-Edwards' sifakas resulted from human habitat disturbance having placed sifakas in a state ecological disequilibrium whereby they must exploit and process food resources to which their teeth are not well adapted. However, future research with additional data (if possible) should reassess nonsignificant trends in median values of wear rates that suggest higher wear rates at disturbed localities (Figs. 1 and 2).

We documented considerable variance in wear rates within individuals and populations compared to rates among populations. Factors other than age including social rank, individual differences in maternal investment, and idiosyncratic foraging behaviors may contribute to such individual variation (Galbany et al., 2011). Social rank seems an unlikely factor in the case of Milne-Edwards' sifakas because females are socially dominant to males (Pochron et al., 2003), yet it is females that have shown dental senescence. Additionally, females of this species do not invest heavily in offspring (Pochron et al., 2004) yet have heavy tooth wear; however, the precise level of maternal investment versus tooth wear remains to be analyzed in depth. Future research will explore the relationship, if any, between individual dietary variation and tooth wear differences. What is clear is that there are no time-dependent environmental factors at work (at least on the scale of molding intervals), because there is no correlation between wear rate and year (Spearman's $\rho = -0.28$, $P = 0.12$).

The pathological tooth wear and antemortem tooth loss seen in some populations of *L. catta* appear to result from ecological disequilibrium, wherein animals in disturbed habitats are forced to dentally process a mechanically challenging and potentially introduced plant, tamarind, to which their teeth are not well adapted (Cuozzo and Sauter, 2008; Millette et al., 2009; Sauter and Cuozzo, 2009). The dental senescence previously documented in *P. edwardsi* living at Tala might also be seen

as a pathology limiting reproductive success (King et al., 2005; Wright et al., 2008) and requiring explanation. We have been unable to explain dental senescence as an outcome of unusual tooth wear due to ecological disequilibrium in an anthropogenically disturbed habitat. Regardless of whether anthropogenic habitat disturbance has altered sifaka diet, changed the mechanical properties or phytolith content of chosen foods, or increased the amount of ambient dust and other grit, sifaka teeth in disturbed habitats wear no faster than those in undisturbed habitats. Milne-Edwards' sifakas appear to be dentally adapted to both localities equally.

Why might our results differ from those found in *L. catta*? One possibility is that differences in the forest characteristics at Tala versus Vato are not as large as those experienced by populations of ring-tailed lemurs in the west. Whereas the sifaka habitats at RNP have been demonstrated to differ in the density, abundance, and size of plant species (Turk, 1995; Wright, 1995; Balko, 1998; Tecot, 2008), and in tree productivity and the predictability of lemur foods (Tecot, 2008), we have not demonstrated that sifakas at the two sites have different diets or diets differing in the average toughness of foods. It is possible that preferred sifaka foods are sufficiently abundant at both sites despite the known habitat differences, and the described ecological differences between Tala and Vato may be "invisible" to the sifakas. Such a situation has been suggested for *Colobus vellerosus* that find sufficient resources even in fragmented habitats (Wong et al., 2006; Wong and Sicotte, 2007). These authors noted that many primates "...live in what appear to be suboptimal habitats, yet seem to be able to survive" (Wong and Sicotte, 2007:245). Future research will benefit from quantifying the diets and the mechanical properties of foods in the two habitats rather than using forest characteristics as proxies for diet. Habitat-related dietary differences have been found at other nearby *P. edwardsi* localities (Arrigo-Nelson, 2006).

We consider it noteworthy that there are also no significant differences in the rates of tooth wear in the two mouse lemur localities that appear to differ more from each other than do the two sifaka localities. Although the absence of dental senescence in mouse lemurs might be related to their absolutely short lifespans, we did expect that the rates of tooth wear would differ in their two localities. Again, it is possible that even the dramatic habitat differences in Tala versus Campsite are invisible to brown mouse lemurs and that they eat the same foods in both localities. It may be more likely that ecological disequilibrium is found when a keystone resource is lost or when a novel food with damaging properties is introduced as found in *L. catta* (Cuozzo and Sauter, 2008; Millette et al., 2009; Sauter and Cuozzo, 2009) rather than when the availability of preferred foods is simply diminished.

The patterns of rainfall are nearly the same at Tala and Vato (RNP records) and this similarity may be a factor contributing to the similarity of sifaka tooth wear rates at the two localities. Furthermore, sifaka dental senescence is associated with diminished infant survival only during years when the lactation season is unusually dry (King et al., 2005; Wright et al., 2008). When rainfall is sufficient, there is no decrease in the survival of offspring of dentally senescent females. This observation suggests that dental senescence may relate more to the amount of rainfall than to diet per se. Rainfall variability has increased in Madagascar over the last century

(Ganzhorn, 1995) and predictive models project a long-term trend toward drier austral winters (the *P. edwardsi* lactation season) in southeastern Madagascar (Tadross et al., 2008; Dunham et al., 2011), perhaps as a consequence of recent global climate change. If such a trend toward drier lactation seasons has already begun, then dental senescence in this species may be a relatively new phenomenon suggesting that these sifakas are in ecological disequilibrium—that they are adapted to a level of rainfall that is now changing due to global forces. In particular, recent anthropogenically induced global climate change might be taking its toll on old sifakas with very worn teeth. If this is the case, then sifakas everywhere may be at risk and locally “good” habitats may not buffer them from global forces. As possible, future research evaluating habitats should give adequate consideration to long-term rainfall levels in addition to standard measures of forest quality and resource availability.

Another consideration of the diminished dental function in old female Milne-Edwards’ sifakas concerns the notion that dental senescence is pathological and reduces fitness. It is possible that longer tooth life, beyond the age at which dental senescence now occurs, would not increase lifetime reproductive success. Whereas King et al. (2005) documented that dental senescence is associated with decreased infant survival, it may not be the cause. Diminished dental function found in old female sifakas may reduce their nutritional intake such that they are unable to produce adequate milk for their infants; however, it is also possible that some other characteristic(s) of old individuals may be responsible for decreased infant survival. For example, old females may lack the locomotor agility and stamina, or the sensory acuity needed to adequately protect their infants from predation by *Cryptoprocta ferox*, a common agent of infant death (Irwin et al., 2009). Provisional analysis suggests that elderly sifaka females differ from younger adults in the allocation of time, with elderly animals spending less time traveling and more time feeding (Wright PC, unpublished data). These time budget differences are particularly emphasized when sifakas are in steep terrain, suggesting that vertical travel may be more arduous for elderly females.

Dental wear has frequently been proposed as a factor limiting the lifespans of wild animals, especially ruminants (Lucas, 2004). A meta-analysis of zoo records of captive wild ruminants suggests that this may not be entirely true, because unusual tooth wear across species was found only in animals that were older than those that died from other causes (Jurado et al., 2008). Living longer than average is a “prerequisite” for extreme dental attrition in ruminants in the same way that living longer is a prerequisite for some human geriatric diseases (Jurado et al., 2008). This observation may apply to *P. edwardsi* as well. Though females have been known to live longer than 30 years, the average age at death of eight females that survived to adulthood is ~19 years and dental senescence has never been observed in a sifaka younger than 18 years. No males in our population have lived beyond 19 years and none has exhibited dental senescence. Thus, most sifakas die of predation or other causes before reaching “old age” and dental senescence. In this light, we interpret the absence of dental senescence at the undisturbed Vato locality not as a consequence of habitat richness, but as a consequence of a more typical demography. Our sample from Vato simply

does not include any individuals that have lived long enough to exhibit dental senescence. If this interpretation is correct, then additional study of Vato should begin to discover aged, dentally senescent “outliers” there.

Female sifakas appear to adopt a bet-hedging strategy to maximize their fitness via increased longevity in Madagascar’s unpredictable environment (Richard et al., 2002; Pochron et al., 2004). Pochron et al. (2004:69–70) described it this way: “it pays to reduce reproductive effort in order to live longer and reproduce more times, sampling a larger number of reproductive conditions and increasing the number of offspring born into good conditions.” If selection has recently favored long female lifespans, then selection for increasing the “dental lifespan” may always be lagging. On the other hand, the mouse lemur life history strategy of reproducing quickly while young may not promote a lifespan long enough to uncover dental senescence.

Long lifespans may be adaptive in both human and sifaka females. If older human females contribute to the success of their already born offspring or to the success of their grandchildren, then their own reproductive success is enhanced via kin selection (Williams, 1957; Alexander, 1974; Hawkes et al., 1998; Hawkes, 2003; Sievert, 2006). If old sifakas, even those with severely worn teeth, can reproduce successfully in years when the lactation season is not unusually dry, then their own lifetime reproductive success may be enhanced.

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