Dental and General Health in a Population of Wild Ring-Tailed Lemurs: A Life History Approach

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ABSTRACT Data are presented on dental and general health for seven groups of wild ring-tailed lemurs, *Lemur catta*, from the Beza Mahafaly Reserve, in southern Madagascar. As part of a study of population demography, adults were captured, collared, and tagged, and biometric measurements, dental casts, and analyses of dental and general health were made. Results indicate that patterns of dental health vary by individual, age, sex, and habitat. Prime adults show more dental attrition than young adults. Prime males living in more marginal habitats show greater mean attrition than those living in richer habitats. Dental damage, specifically to the toothcomb, indicates that mechanical stresses to this region may include the initial harvesting of foods, in addition to grooming. Males exhibit more evidence of past trauma, including scars and chipped teeth. These results indicate that environmental as well as social factors, such as female dominance, may lead to sex differences in health patterns among lemurs. Am J Phys Anthropol 117:122–132, 2002.

While the life history approach has traditionally focused on the population level, and recorded major life events such as age at weaning or first reproduction, the recent focus on individual life history patterns is especially useful for long-lived primate species (DeRousseau, 1990; Morbeck, et al., 1997). Variations in patterns of illness, injury, and dental health for natural populations of primates have important life history and evolutionary implications (Lovell, 1991). While such data are available for the haplorhine primates, especially the great apes (Lovell, 1991), comparable data for strepsirrhine primates are lacking. We present such information for seven wild groups of ring-tailed lemurs, *Lemur catta*, at the Beza Mahafaly Reserve, Madagascar.

MATERIALS AND METHODS

Age grades

In 1987 and again in 1995, a total of 95 members of a dry forest population of *L. catta* at Beza Mahafaly Special Reserve, Madagascar was captured, collared, and tagged as part of a long-term study of their demography and socioecology (Sussman, 1991; Sauther et al., 1999). For these individuals, biometric measurements and analyses of general and dental health were made. For the 1987 data set, dental casts were also made. The actual age was known for all subadults (1.5 years old) and most young individuals (2–2.5 years old) for the 1987 data set. For all older individuals, we could only assign relative ages. Greater attrition is associated with advanced age in various mammals (Brothwell, 1965; Morris, 1978; Phillips-Conroy et al., 2000); we thus included attrition as a measure of relative age. Our age "grades" (subadult, young, prime, and old) are based on the following criteria. For assignment into age grades, all criteria had to be true. Subadults were individuals who weighed less than 1,400 g, and had upper canines that were not fully erupted (upper canines are the last to erupt in *L. catta*; Schwartz, 1974; Eaglen, 1985), overall dental attrition scores that were ≤1.00 (see below), little or no wear on occlusal surfaces, no dentin exposure for any teeth, testicles that were undescended for males, and nipples that were <0.5 cm in length for females. Young adults had fully erupted canines, weights of more than 1,400 g but less than 2,000 g, overall dental attrition scores that were >1.00 but <1.50, some teeth that exhibited small wear facets but no dentin exposure, testicles that were small but descended for males, and nipples that were >0.5 cm in length for females. Prime individuals had weights that were more than

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2,000 g, overall dental attrition >1.5 but <2.5, with large wear facets on most teeth and small dentin exposure only at the cusps, male testicles that were large and fully descended, and female nipples that were >0.5 cm in length. Old individuals had weights of greater than 2,000 g, nipples that were >0.5 cm in length, overall dental attrition scores that were >2.5, no original cusps that remained, and at least one molar tooth that was worn to the point of actual pulp exposure. In actuality, all individuals placed in the old age grade had two or more molars exhibiting pulp exposure (mean frequency per mouth, 6.81; range, 2–21). Because this high level of attrition is the only marker we have for advanced age in this population, we do not include the old age data set in our analyses of dental attrition (see below), but we do retain this age grade for all other analyses. Frequencies of age grades by sex were as follows: old females, 11; old males, 16; prime females, 21; prime males, 21; young females, 7; young males, 13; subadult males, 4; and subadult females, 2.

General health

General health measurements are based on all 95 individuals, and include data taken from lemurs collared in 1995 (specific dental measurements were unavailable for this latter group). Presence/absence of wounds, healed scars, broken bones or other malformations, and ectoparasites (e.g., ticks or lice) were noted. Ring-tailed lemurs inhabit two general types of habitats within the Beza Mahafaly reserve. The habitat, near the Sakamena River, is lusher, with a higher water table and less severe food restriction during the dry season (Sauther, unpublished data). The other habitat is approximately 8 ha from the river, and is characterized by more xerophytic plant types which grade into a dry, thornscrub *Didierea* forest (a cactus-like habitat). We thus looked at habitat as a variable, dividing it into “marginal” and “riverine,” and for some analyses we compared individuals whose home ranges were found in one vs. the other habitat.

Dental attrition

Dental attrition was based on the 1987 data set and consists of measurements of 27 individual ringtailed lemurs, 12 adult females and 15 adult males, for which we have both field data (direct visual analysis of teeth) and usable dental casts. These individuals comprise the following age categories: prime male = 10, prime female = 7, young male = 5, young female = 5. We did not analyze subadults due to the small sample size (n = 6), nor did we include the old age category as explained above. To maintain independence, individual lemurs were the sampling unit. A total of 810 teeth or 30 teeth per individual were scored (the tiny I^{2-3} were not scored, nor were the upper canines as these were often broken off in the casts; see below). Individual teeth on each dental cast, along with field notes on each individual's actual dentition, were used to score these teeth. The general level of attrition was scored for each tooth based on the following categories: 0, unworn occlusal surfaces; 1, small wear facets and no dentin or pulp exposure; 2, large wear facets but no dentin or pulp exposure; 3, some dentin but no pulp exposure, few cusps still present, or for toothcomb or caniniform P_2, 1/2 remaining; and 4, pulp exposure, with cusps gone, dentin or pulp exposed across most of the surface, or for toothcomb or caniniform P_2, less than 1/4 left. To address whether specific groups of teeth showed greater or lesser attrition, we combined teeth in the following way: I_2, I_3, and C_1 (the lower canines are incisiform; Swindler, 1976) = “toothcomb”; P_2 = canines (P_2 is caniniform and also functions as a true canine in this species; Swindler, 1976); P^{2-4} and P_{3-4} = “premolars”; and M^{1-3} and M_{1-3} = “molars”.

Dental health

Dental health was assessed in the field for the sample of 42 individuals (including the old age category). For these data, all teeth were examined, including the upper canines and incisors. Caries were identified as a soft area on a tooth sometimes accompanied by a circular brown stain where the dental explorer could be inserted and offered slight resistance when removed. Gingivitis was scored when the dental probe could easily be inserted between the gingiva and tooth to at least a depth of 1 mm on the probe, and the surrounding gingiva was swollen. Abscesses were small, pimple-like swellings on the gums. Calculus was calcified plaque which was not a normal part of the tooth morphology and which could not easily be removed by scraping. The presence of chipped and/or cracked teeth was also noted, and this included all teeth except the tiny I^{2-3}. The presence of dark brown or black staining, which could not be easily removed by scraping, was also noted.

Statistical methods

All statistical tests employed the Statview statistical and data analysis software (Haycock et al., 1992). The Kolomogorov-Smirnov normality test was used and indicates a normal distribution ($P > 0.05$) for the general attrition data (Haycock et al., 1992). General attrition was compared across age grades, by sex, tooth group, and habitat, and were tested using the Student's *t*-test with significance set at $P = 0.05$. Tests are on either individuals or individual teeth, and are summarized in Tables 1–7. Dental and general health was analyzed using a χ^2 test for two independent samples, with significance set at $P = 0.05$. Because the same data set was used for multiple tests, a Bonferroni correction (Godfrey, 1986) was also used (48 tests/0.05 = 0.001). Because this correction is deliberately very conservative, it increases the possibility of a type II error. Therefore, we present the original P values and note which of

TABLE 1. Differences in general attrition scores by tooth group and age for lemur catta *at Beza Mahafaly*[1]

Tooth groups: group 1, group 2	t	P, Young (df = 18)	Mean dental attrition: Tooth group 1	Mean dental attrition: Tooth group 2
Toothcomb, premolars	0.23	0.82	1.30	1.35
Toothcomb, molars	0.45	0.66	1.30	1.40
Premolars, molars	0.22	0.83	1.36	1.40
Canine,[2] premolar	1.04	0.31	1.36	1.10
Canine, molar	1.24	0.23	1.10	1.40
Canine, toothcomb	0.85	0.41	1.10	1.30
		P, Prime (df = 32)		
Toothcomb, premolars	0.57	0.57	1.94	1.84
Toothcomb, molars	3.11	0.004[2]	1.94	2.49
Premolars, molars	4.02	0.0003[2,3]	1.84	2.49
Canine, premolar	1.13	0.27	1.65	1.84
Canine, molar	4.95	<0.0001[3,4]	1.65	2.49
Canine, toothcomb	1.59	0.12	1.65	1.94

[1] Comparisons by individual animal's tooth type.
[2] Caniniform P_2 (see text).
[3] Significant at $P \leq 0.05$.
[4] Still significant after Bonferroni correction.

TABLE 2. Mean dental attrition scores for young vs. prime lemur catta *adults at Beza Mahafaly*[1]

Tooth group	df	t	P	Mean dental attrition: Young	Mean dental attrition: Prime
Toothcomb	25	3.03	0.006[2]	1.30	1.94
Premolars	25	2.53	0.02[2]	1.35	1.84
Molars	25	5.64	<0.0001[3,4]	1.40	2.49
Canines[2]	25	2.54	0.02[2]	1.10	1.65

[1] Comparison by individual animal.
[2] Caniniform P_2 (see text).
[3] Significant as $P \leq 0.05$.
[4] Still significant after Bonferroni correction.

these remain significant with the Bonferroni correction.

RESULTS

General attrition scores

General attrition scores varied by tooth group, age, sex, and habitat. While there were no differences among young individuals relative to differential wear of tooth groups, in the prime age categories, the molars showed more mean attrition than any other tooth group (Table 1). Attrition was progressive, with marked increases from young to prime age categories for most teeth (Table 2). There were no marked sex differences for mean attrition scores among young or prime individuals, although there was a trend for prime females to show more attrition of the caniniform P_2 ($P = 0.06$) (Table 3). With regards to habitat type, we found that prime males in the lusher, riverine habitat showed markedly less dental attrition than prime males living within marginal habitats (Table 4). No other habitat effects were seen. There were no marked differences in wear patterns of molars or premolars between the left and right sides of the mouth.

Dental health

We found two cases of gingivitis: one was in a prime male involving C^1, and the other was in an old female involving M_2. We identified a total of three carious lesions, two for a prime female and one for a young male. Two of the caries were located on M_3 and one on M_1. A total of eight dental abscesses was seen, two of them periodontal and the rest periapical. Of these, five involved maxillary molar teeth, one involved the upper canine, and two occurred at the base of the toothcomb. Four individual females, two prime, one old, and one young age grade, each exhibited one abscessed tooth. One old and one prime male also exhibited this pathology, with the prime male individual having three abscesses (see below). There were no significant age-related patterns, although among older individuals we observed only one case of abscesses, one case of gingivitis, and no caries. Indeed, of the 42 lemurs in our sample, the individual with the worst dental health was a prime male from Yellow troop, number 18 (Fig. 1a). From our records of 1987, we noted that this male had:

TABLE 3. Sex differences in mean attrition scores by tooth type, age grade, and sex for lemur catta *at Beza Mahafaly*[1]

Age/sex	df	*t*	*P*	Mean dental attrition Females	Males
Toothcomb					
Young females, young males	8	0.63	0.55	1.40	1.20
Prime females, prime males	15	1.28	0.22	2.14	2.14
Premolars					
Young females, young males	8	0.93	0.39	1.50	1.20
Prime females, prime males	15	0.30	0.77	1.80	1.87
Molars					
Young females, young males	8	0.0		1.40	1.40
Prime females, prime males	15	0.84	0.42	2.60	2.41
Canines[2]					
Young females, young males	8	0.54	0.61	1.20	1.00
Prime females, prime males	15	2.03	0.06	1.93	1.45

[1] Comparison by individual animal.
[2] Caniniform P_2 (see text).

TABLE 4. Mean attrition scores by sex, age grade, and habitat for lemur catta *at Beza Mahafaly*[1]

Age/sex	df	*t*	*P*	Mean dental attrition by habitat Marginal	River
Young males	148	1.48	0.15	1.68	1.50
Young females[2]			0		
Prime males	298	4.59	<0.0001[3,4]	2.25	1.85
Prime females	208	1.40	0.16	2.00	2.17

[1] Comparison by individual teeth.
[2] Too few groups for analysis.
[3] Significant at $P \leq 0.05$.
[4] Still significant after Bonferroni correction.

"gingivitis, puffy, swollen gums around the upper canines, a lateral abscess involving M^1, another abscess at the base of the toothcomb, yet another abscess involving C^1, a chip on P_2, and calculus on C_1 and P_4."

This male remained with Yellow troop for several years, but had disappeared by the 1994 census. Female 57 from the Tan troop presents a striking contrast. In 1987 this old female was nearly completely edentulous (Fig. 1b), with most teeth worn to the gums, and only the toothcomb and upper canine still intact, albeit well worn. Yet she was in excellent health, lived through the 1990 census, and only disappeared by the 1991 census.

We also compared the total number of male and female teeth for the presence of dental calculus and staining. A higher number of male teeth exhibited calculus buildup than did female teeth (males = 31, females = 13; $\chi^2 = 4.187$, $P = 0.04$, df = 1). Dark deposits on the teeth were also common (n = 332), with over 42% of the population exhibiting this type of staining. These deposits were mainly seen on the molar and premolar teeth. With regards to total number of teeth involved, females showed more of such deposits than males (females = 171, males = 161, $\chi^2 = 7.99$, $P = 0.005$, df = 1).

The frequency of chipped or cracked dentition (n = 36) varied by teeth and tooth groups (Tables 5, 6). Relative to the functional groups of teeth, the toothcomb showed more of such damage than all other tooth groups except canine teeth, with toothcomb damage making up 61% of total damage observed. This is striking, given that the individual teeth that comprise the toothcomb are only 19% of the total dentition studied (molars = 37%; canines = 13%; premolars = 31%). The caniniform P_2 and C^1 also showed more damage than either premolars or molars, but they did not vary relative to each other. Sex differences were found with regards to the overall frequency of chipped/cracked dentition. Overall, males exhibited more damaged teeth than did females (female = 4, male = 32; $\chi^2 = 9.455$, $P = 0.002$, df = 1). Specifically, males exhibited more damage to both the caniniform P_2 and the toothcomb than did females (Fig. 2). Age was a factor for both males and females. Among males, 72% of such damage was limited to the old age grade, with only 18% seen among prime and young males. Among females, chipped/cracked teeth were limited to the old age grade.

General health

Overall, the population at Beza Mahafaly is in reasonably good health, with only 33% (n = 31) exhibiting ectoparasites or evidence of past trauma (Table 7). Ectoparasites included both ticks and lice, with ticks most commonly found around the eyes, and lice around the genitalia or inside the ears. Over 23% (n = 22) of the sample population had observable ectoparasites, but individuals varied with regard to actual number. For example, one young male (no. 78) from the Yellow troop had 18 ticks around his eyes and on his face (Fig. 3). We found no marked

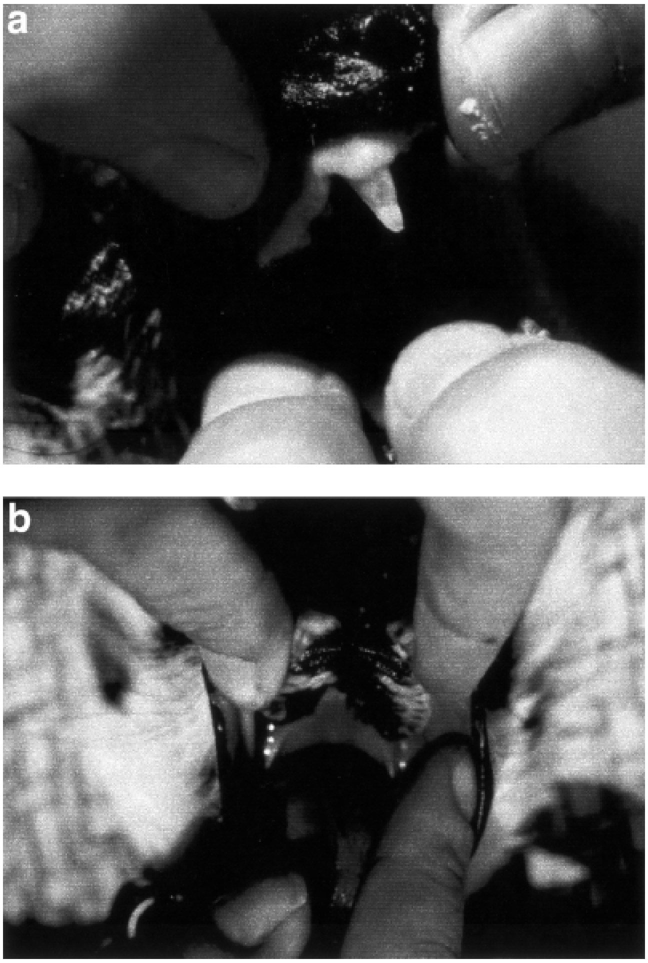

Fig. 1. **a:** Example of dental disease in ring-tailed lemurs. This prime male exhibits gingivitis, puffy and swollen gums, chipped teeth, and three abscessed teeth. Note also dark staining on the upper canine. **b:** Old female ring-tailed lemur whose teeth are worn to the gumline.

TABLE 5. Frequency of lemur catta *chipped and/or cracked teeth by individual tooth and tooth group*

Tooth/tooth group	Number chipped/cracked	Percentage total chipped/cracked (n = 36)
I_2/toothcomb	7	19.5
I_3/toothcomb	8	22.0
C_1 (incisiform canine)/ toothcomb	7	19.5
C^1/canine	3	8.3
P^2/premolar	0	0.0
P^3/premolar	1	2.8
P^4/premolar	0	0.0
M^1/molar	0	0.0
M^2/molar	0	0.0
M^3/molar	0	0.0
P_2 (caniniform premolar)/ canine	7	19.5
P_3/premolar	1	2.8
P_4/premolar	1	2.8
M_1/molar	0	0.0
M_2/molar	0	0.0
M_3/molar	1	2.8

TABLE 6. Comparison of presence of damaged teeth by tooth group for lemur catta *at Beza Mahafaly*

Tooth groups (df = 1)	Chi-square	*P*	Frequency
Toothcomb, premolars	35.73	<0.0001[1,2]	22.2
Toothcomb, molars	42.00	<0.0001[1,2]	22.1
Premolars, molars	0.55	0.46	1.2
Upper canines, premolars	6.97	<0.008[1]	2.3
Lower canines, premolars	24.78	<0.0001[1,2]	2.7
Upper canines, molars	12.34	<0.004[1]	1.3
Lower canines, molars	47.24	<0.0001[1,2]	1.7
Toothcomb, upper canines	2.28	0.13	22.3
Toothcomb, lower canines	0.0008	0.93	22.7
Upper canines, lower canines	1.63	0.20	2.7

[1] Significant at $P \leq 0.05$.
[2] Still significant after Bonferroni correction.

differences among age groups for frequency of individuals with ectoparasites. There were sex differences, with males having more ectoparasites than females (Fig. 4).

There were no significant age differences with regard to evidence of past trauma. There were sex differences, with more males exhibiting evidence of past trauma than females (Fig. 4). Female trauma involved one case of a recently healed wound on the index and middle finger. This female also had what appeared to be conjunctivitis of the eye. In addition, one female was missing the middle digit of her right hand, but it was difficult to determine if this was from past trauma or a congenital defect (Fig. 5). Male trauma included broken tails, numerous healed scars including some on the scrotum, and evidence of healed broken bones. One young male in particular, number 412 of Lavender troop (collared in 1995), showed numerous past trauma, including evidence of a broken left ankle, a broken femur, and a large healed scar on the nose. This male was still in the Lavender troop during the 1998 census. While ring-tailed lemurs normally have only two nipples, we also observed four females with two additional supernumerary nipples. These were smaller and were located just below the normal nipples.

DISCUSSION

Dental attrition

Effects of age. While long-term studies of known primate populations have added greatly to our understanding of individual variability in life-history patterns (Morbeck, 1997), such data are rare, especially for strepsirhine primates (e.g., Glander et al.,

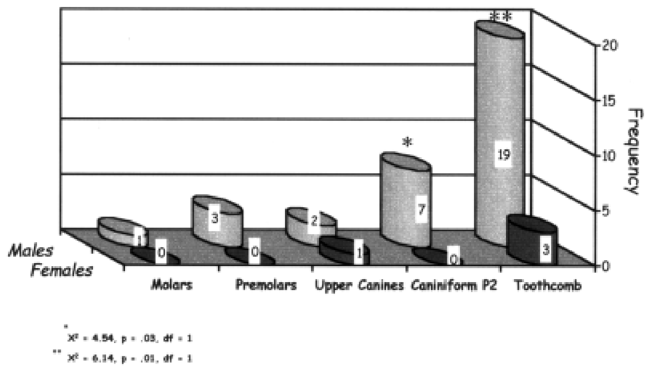

Fig. 2. Sex differences in frequency of chipped teeth for ring-tailed lemurs at Beza Mahafaly. * $\chi^2 = 4.54$, $P = 0.03$, df = 1. ** $\chi^2 = 6.14$, $P = 0.01$, df = 1.

1992; Richard et al., 2000). To our knowledge, these are the first published data on the general health and dental pathology for a natural population of lemurs. Although few studies have documented primate dental attrition relative to actual ages, those that do indicate that older individuals exhibit greater attrition (Kilgore, 1989; Phillips-Conroy et al., 2000). Ring-tailed lemurs appear to follow this pattern, with prime individuals showing greater attrition for most teeth, relative to young individuals. Thus, as might be expected, attrition appears to be a developmental trait that increases as wild ring-tailed lemurs age. This pattern is also seen among the Gombe chimpanzees, where severe attrition occurs primarily in individuals in their mid-thirties (Kilgore, 1989).

Tooth type and attrition. The heaviest attrition, with actual pulp exposure, most commonly involved the molar teeth. This is unremarkable, given that almost all actual processing of food is done at the back of the mouth. In fact, ring-tailed lemurs often raise their muzzles upward during fruit feeding, presumably to maintain food at the back of the mouth during mastication (Sauther, personal observations). This pattern of dental attrition may also relate to dental eruption patterns. For permanent dentition, the upper and lower M1–2 are the first to erupt in ring-tailed lemurs (upper and lower first molars erupt by 4 months of age, and the second molars erupt by 8 months of age; Eaglen, 1985). Data are not available to compare patterns of attrition among different wild populations of lemurs. However, a recent study indicates that *L. catta* at Beza Mahafaly do not feed on foods that are either excessively hard (based on puncture resistance) or strong (based on punch shear resistance) relative to lemurs living in rainforest habitats (Yamashita, 1996).

Among prime females, caniniform P_2 showed a trend for more attrition than in males. This was initially surprising, because ring-tailed lemurs are a female-dominant species that includes female feeding priority (Jolly, 1966; Sauther, 1992; Kappeler, 1993). It is thus unlikely that the observed sex difference is due to females feeding on more low-quality foods (e.g., grittier, more fibrous). One possible explanation for these differences may relate to food type. A keystone ring-tailed lemur food species is *Tamarindus indica* (Jolly, 1966; Sauther, 1998). This fruit is encased in a long pod that is normally inserted into the side of the mouth, with caniniform P_2 employed in breaking pieces off. The ripe fruit is covered in a fibrous, sticky matrix. Because females have priority of access to foods, it is possible that they focus more on this fruit over their lifetime, resulting in the differential patterns of wear seen. No clear sex differences in the use of this fruit were seen during a year-long study of two troops' feeding ecology (Sauther, 1992), but we lack any long-term data. In support of differential female use of *Tamarindus* fruit is the fact that this fruit stains the teeth a dark brown, and such staining was more common among females than males (see below).

Habitat quality. At Beza Mahafaly, the riverine habitat is associated with more mesic, closed-canopy forest, with a greater percentage of larger trees on wetter soils, while the marginal habitat has more xeric species and a higher number of small trees on drier soils (Sussman and Rakotozafy, 1994). Prime males in the more mesic, riverine habitat showed less dental attrition than prime males living within marginal habitats. Although Beza Mahafaly is a seasonal environment (Sauther, 1994), during the dry season fruits, herbs and young leaves are available for a longer period of time in the riverine habitat than in the marginal habitat (Sauther, unpublished data). Males living in more marginal habitats may thus be more directly affected by the quality of their ranges than females, who have feeding priority. For example, males feed more on low-quality mature leaves during periods of low food availability compared to females (Sauther, 1994). Prime natal ring-tailed lemur males normally migrate for the first time between 3–4 years of age. They then remain in these new groups for several years (Sussman, 1992), with some (Jones, 1983) but not all such transfers being made into adjacent groups (Sussman, 1992). It is thus possible that males born into troops occupying marginal habitats will spend their first 5–6 years within these habitats. Whether this is long enough to contribute to the attrition patterns seen requires more long-range data. Studies of baboons living within different habitats also posit ecological differences as important in explaining variability in occlusal wear (Phillips-Conroy et al., 2000).

Dental health

Analyses of dental pathologies among primates have focused primarily on the haplorhine primates (Hershkovitz, 1970), especially the great apes (Lovell, 1991). Carious lesions are more common in orangutans and chimpanzees than in other haplo-

TABLE 7. General health for lemur catta *at beza mahafaly*[1]

Individual no.	Sex	Age	Ectoparasites	Scars	Broken bones	Wounds	Other	Other/comments
78	M	Y	X					18 ticks on face, around eyes, and upper nose
42	F	O	X					Ticks on face, around genitals
5	M	O	X					Lice on genitals
30	M	O	X	X				Halitosis, thick fur with some bare spots, scars on left bicep, missing tip of tail
60	M	O	X					Ticks, two scars on bottom of left foot
20	M	P				X		Small wound on back
99	M	P	X					Three ticks on face
02	F	O	X					Four ticks on face
98	M	Y	X					Ticks on muzzle
38	M	Y	X	X				Lump on left nostril, long scar across muzzle
29	M	Y	X					Ticks on face
18	M	P	X					Lice
49	M	O		X				Healed scar on left scrotum
73	F	Y	X					Lice on stomach
33	F	P	X					One tick near lid of right eye
86	M	Y	X					One tick near lid of lower right eye
70	M	O	X		X			Right hand, middle digit is broken, malformed pad with nail coming off the side instead of the top, lice in ears and around genitals
61	M	P	X					Lice around genitals
49	M	O		X				Scar on right scrotum
404	M	Y	X					Ear lice
424	M	Y	X					Ear lice
464	M	Y			X			Broken tail
412	M	Y			X	X		Hard fibrous lump near head of left femur, broken left ankle, recently healed wound on nose
455	F	P				X		Wound on left foot, first and third fingers, conjunctivitis?
439	M	O			X			Middle finger of left hand is broken
90	M	P	X					Lice
81	M	SA	X					Lice around genitals
489	F	SA					X	Missing right middle finger (congenital?)
472	M	P					X	Diarrhea
10	M	P	X					Lice around genitals, ticks around eyes
53	F	P	X					Lice and ticks

[1] Y, young; SA, sub-adult; O, old; P, prime.

rhines (Lovell, 1991). Using skeletal populations, Lovell (1990a) found a mean of 0.59 carious teeth per mouth (total lesions divided by number of observable mouths) for common chimpanzees, 0.13 for gorillas, and 0.11 for orangutans, as compared to 0.07 for ring-tailed lemurs at Beza. However, if we compare this as a percentage of total individuals sampled which exhibit such pathologies (5% for *L. catta*), then ring-tailed lemurs are in the range of chimpanzees (5–15%), orangutans (2–12%), and both Old World (0–10%) and New World (1–26%) primates (Lovell, 1991). Using such a comparison also indicates that dental abscesses for ring-tailed lemurs also fall within the range of haplorhine primates (14% for *L. catta*; 0–50% for great apes; 3–15% for Old World monkeys; 8–34% for New World monkeys; Lovell, 1991). Calculus and its precursor, plaque, were rare in this population. Dental abscesses were mostly periapical and located on the molars. Although periapical abscesses are often related to prior breakage of the tooth crown (Hillson, 1986), obvious chipping or cracking of the involved teeth accompanied none of the abscesses. Such abscesses are also associated with higher levels of attrition and/or caries (Hillson, 1986). Greater attrition and caries found on the molars may relate to the pattern observed. Two clear cases of lateral periodontal abscesses were also seen and may be associated with diet, as we often observed green vegetation wedged between and around the molar teeth. Howler monkeys, which show higher numbers of abscessed teeth than other New World monkeys, also exhibit impacted hair or food around the teeth (Hall et al., 1967). In our sample, more females

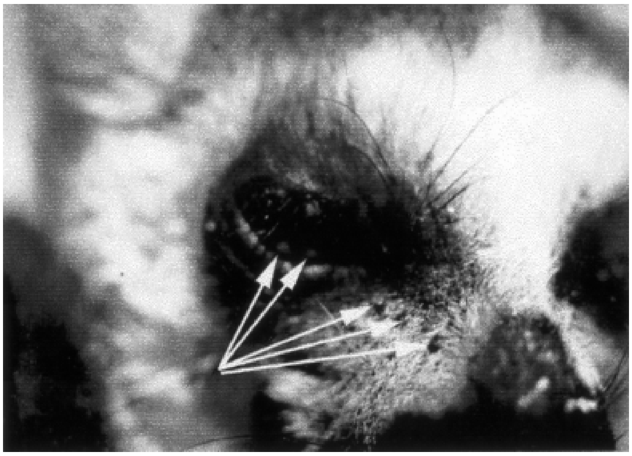

Fig. 3. Example of extreme ectoparasite infestation. This young male had 18 ticks around both eyes and his face (arrows).

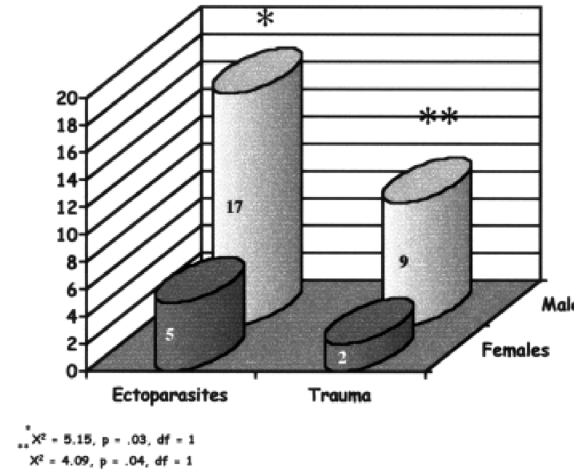

Fig. 4. Sex differences in general health for ring-tailed lemurs at Beza Mahafaly: frequency of individuals with ectoparasites and trauma. * $\chi^2 = 5.15$, $P = 0.03$, df = 1. ** $\chi^2 = 4.09$, $P = 0.04$, df = 1.

exhibited abscesses than males, although this was not significant. As female ring-tailed lemurs have feeding dominance and thus have greater access to fruits than males (Sauther, 1992), a diet higher in carbohydrates could differentially affect the dental health of the two sexes. Such a pattern has been suggested for wild Bornean orangutans, where a higher percentage of old females exhibited dental pathologies than males, and this may be associated with greater fruit feeding in females (Stoner, 1995). Stoner (1995) pointed out that a high percentage of sticky fruits such as figs could affect such patterns. In support of this, we also observed extensive staining of teeth that ranged from a dark brown to black for nearly 1/4 of the population. As already noted, more females than males exhibited this staining. Among wild gorillas, dark deposits are extensive along with calculus formation, and have been associated with periodontal disease (Lovell, 1990b). In the Beza population, staining is likely from one of their constant food items, the fruit of *T. indica*, which is not only very sticky when ripe, but also contains tartaric acid, a known staining agent (Haslam, 1966; Lewis and Elvin-Lewis, 1977).

Dental damage

Sex differences. Damage to teeth is clearly a developmental trait, occurring more often in old age grades. Sex differences seen are likely to be multicausal. Males showed more damage to the toothcomb and caniniform P_2 than did females. While intermale aggression can be quite severe just prior to and during the mating season (Jolly, 1966; Sauther, 1991), there is little evidence that the toothcomb is employed during aggression (Buettner-Janusch and Andrew, 1962). As noted above, studies of sex differences in foraging behavior for this population show that males focus more on leaves, and especially mature leaves during the dry season of limited food availability, than do females (Sauther, 1994). Although based only on field observations, leaves are often processed by pulling at vines or twigs with the toothcomb and caniniform P_2 (Sauther, personal observations). As leaves appear more difficult to pluck from a branch than fruits, they may thus engender more wear and/or other stresses to the teeth during harvesting. Such damage may also have a mechanical cause. In ring-tailed lemurs, caniniform P_2 acts as a honing mechanism for the upper canines (Swindler, 1976), and honing facets can be seen on our dental casts. While ring-tailed lemur dentition is primarily sexually monomorphic (Sauther et al., 1999), Kappeler (1996) did find sexual dimorphism in canine height in museum specimens of ring-tailed lemurs. Greater male P_2 damage may thus relate to more intense honing during the course of their lifetime. This may weaken the structure of these teeth, making them more prone to chipping and cracking. Male aggression during the mating season could also be a factor, since P_2 is functionally a canine. Frisch (1963), for example, found no sexual dimorphism for gibbon canine teeth,

Fig. 5. Possible congenital defect in a female ring-tailed lemur. This female's middle finger of her right hand is missing (arrow).

but did note that males suffered more canine fractures than females and related this to intermale aggression.

Role of toothcomb. In this population of ring-tailed lemurs, the toothcomb exhibited more cracks and chipping than most other tooth groups. Avis (1961) initially suggested that the toothcomb in prosimians could be viewed as a functional part of an adaptive complex designed to cut and crop vegetation, much like in ungulates and insectivores. Martin (1972) and Gingerich (1975) also argued that the toothcomb functions primarily as a feeding tool, specifically to scrape bark to allow gum feeding. Both the pale fork-marked lemur, *Phaner furcifer pallescens*, and the gray mouse lemur *Microcebus murinus* use the toothcomb to gouge bark in an effort to induce gum flow and sap in food trees (Martin, 1975). The sifaka, *Propithecus verreauxi*, uses the toothcomb for both grooming and to gouge and eat bark (Richard, 1978), and in captivity to scoop out the contents of fruits (Buettner-Janusch and Andrew, 1962). As reflected in its name, however, the toothcomb has been viewed by many as primarily a lemur-grooming tool (Buettner-Janusch and Andrew, 1962; Szalay and Seligsohn, 1977; Rosenberger and Strasser, 1981). Indeed, unlike monkeys and apes, lemurs do not groom with their hands at all. Using scanning electron microscopy, Rose et al. (1981) found hair grooves on the toothcomb of some Lorisinae which they attributed to grooming. In addition, they found similar microstriations for the most ancient lorisoid, *Nycticedoides simpsoni*, indicating a grooming function for the toothcomb by the late Miocene. Based on observations of captive animals, Buettner-Janusch and Andrew (1962) argued that lemurs rarely employ the toothcomb during feeding. Instead, they state that lemurs either break off food items using the canines and premolars, or they take food directly into the mouth and then quickly move it to the posterior teeth for processing. The relatively higher level of damage to the toothcomb among the Beza Mahafaly ring-tailed lemur population may have a developmental cause. In our study, there was a significant difference between young and prime lemurs for toothcomb wear (Table 2). In addition, most toothcomb damage was seen in the old age grade, indicating that a lifetime of oral grooming could weaken the toothcomb, making it more susceptible to breakage. This frequent damage may also be related to additional, nongrooming factors. A 13-month, in-depth study of feeding ecology at this site indicated that wild ring-tailed lemurs rarely pluck food items using their hands, but mainly do so by mouth (Sauther, 1992). The side of the mouth grasps large items, such as tamarind pods, and pieces are broken off using the caniniform P_2 and premolars, as noted by Buettner-Janusch and Andrew (1962). However, smaller fruits are often grasped between the toothcomb and the upper incisors and the interincisal median diastema, and pulled off the stem. In addition, leaves are commonly removed by pulling the vine or twig through the front of the mouth (Sauther, personal observations). The toothcomb was also observed being used to pull at the umbilical cord of newborn infants (Sauther, 1991), and it was employed during the daily ingestion of soil from termite nests and mounds (Sauther, 1992). It should be noted that based on examinations of our dental casts, as well as ring-tailed lemur skulls, the small upper incisors occlude with C_1 and I_3 of the toothcomb and could function to crop food items, as suggested by Avis (1961). The toothcomb may thus have a food-harvesting function in addition to grooming in *Lemur catta*. It would be useful to determine whether toothcomb microstructure damage from grooming vs. food harvesting could be differentiated, as this might provide additional information regarding the ecology and behavior of fossil lemurs.

General health

Overall, the population was in good health, but males suffered a higher number of ectoparasites and overall trauma than did females. Ring-tailed lemurs can remove ectoparasites from their own bodies, but not from their own faces, and they will engage in vigorous bouts of social allogrooming with others. Because males migrate into troops, they may be at a disadvantage regarding social grooming in that they will not have access to close relatives, as compared with females who normally remain in their natal groups (Sussman, 1991). This could have negative consequences, e.g., the prime male (no. 78) with 18 ticks on his face. Intense intermale aggression during the brief mating season may explain the higher incidence of male trauma. In addition, males may suffer higher predation pressure due to migrations. For example, a prime male (no. 7) was killed by a fossa or a large feral cat during his attempt to migrate out of his troop (Sauther, 1989). Evidence of sex differences for trauma among other nonhuman primates is equivocal (Lovell, 1991).

CONCLUSIONS

A life-history approach can elucidate the patterns and consequences of dental and general health in wild primate populations. As the ring-tailed lemurs of Beza Mahafaly live within a protected reserve that is part of the largest remaining tract of gallery forest in southern Madagascar (Sussman and Rakotozafy, 1994), health data from this population can provide a baseline to compare with other, more degraded habitats in Madagascar. Overall, the ring-tailed lemurs of Beza Mahafaly are relatively healthy, and they suffer similar levels of dental pathology relative to haplorhine primates. Many of the patterns are developmental, with older individuals exhibiting more tooth wear, but not greater dental pathologies. Indeed, some individuals were able to survive for many years with teeth that showed severe attrition (e.g., female no. 57). As female ring-tailed lemurs reproduce well into advanced ages (13+ years in the wild; Gould, personal communication), interindividual variability in general and dental health will be expected to have both immediate life-history implications as well as consequences for overall fitness. Future long-term analyses of this population should help elucidate such patterns. We can also see that males and females are living under different pressures that can result in different patterns of health. In ring-tailed lemurs, the mating season is short (2–3 weeks for any one troop; Sauther, 1991), and males engage in spectacular chases and jump-fights involving leaping into the air and slashing down with the canines (Jolly, 1966; Sauther, 1991). Many of the males bear the scars of these encounters. In addition, males must migrate from their natal groups to find mating partners (Jolly, 1966; Sussman, 1992). Without established social relationships within a group, a migrating male can suffer from a high load of ectoparasites that can be more than simply a nuisance. At another site, Berenty, such ticks have been associated with a degenerative eye disease in ring-tailed lemurs in which the eyes eventually atrophy (Porteous, 1998). In some cases this happens to both eyes, with obviously lethal results. Male ring-tailed lemurs also live in a female-dominant society (Jolly, 1966; Kappeler, 1993), and female feeding priority can affect female and male diet (Sauther, 1994) and thus long-term patterns of dental pathology for both males and females (this study). This study indicates that both environmental and social factors may play important roles in mediating individual variation in primate life histories.

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