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RESEARCH ARTICLE

Variation in Dental Wear and Tooth Loss Among Known-Aged, Older Ring-Tailed Lemurs (*Lemur catta*): A Comparison Between Wild and Captive Individuals

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Tooth wear is generally an age-related phenomenon, often assumed to occur at similar rates within populations of primates and other mammals, and has been suggested as a correlate of reduced offspring survival among wild lemurs. Few long-term wild studies have combined detailed study of primate behavior and ecology with dental analyses. Here, we present data on dental wear and tooth loss in older (>10 years old) wild and captive ring-tailed lemurs (*Lemur catta*). Among older ring-tailed lemurs at the Beza Mahafaly Special Reserve (BMSR), Madagascar ($n = 6$), the percentage of severe dental wear and tooth loss ranges from 6 to 50%. Among these six individuals, the oldest (19 years old) exhibits the second lowest frequency of tooth loss (14%). The majority of captive lemurs at the Indianapolis Zoo ($n = 7$) are older than the oldest BMSR lemur, yet display significantly less overall tooth wear for 19 of 36 tooth positions, with only two individuals exhibiting antemortem tooth loss. Among the captive lemurs, only one lemur (a nearly 29 year old male) has lost more than one tooth. This individual is only missing anterior teeth, in contrast to lemurs at BMSR, where the majority of lost teeth are postcanine teeth associated with processing specific fallback foods. Postcanine teeth also show significantly more overall wear at BMSR than in the captive sample. At BMSR, degree of severe wear and tooth loss varies in same aged, older individuals, likely reflecting differences in microhabitat, and thus the availability and use of different foods. This pattern becomes apparent before "old age," as seen in individuals as young as 7 years. Among the four "older" female lemurs at BMSR, severe wear and/or tooth loss do not predict offspring survival. Am. J. Primatol. 72:1026–1037, 2010. © 2010 Wiley-Liss, Inc.

Key words: tooth wear; aging; dental senescence; offspring survival; life history; mammal; captivity effects

INTRODUCTION

Tooth wear, a product of an individual's life experience, results from a complex interaction of variables including diet, food properties, behavior, tooth morphology, and enamel structure [e.g., Bermúdez de Castro et al., 2003; Hillson, 1986, 2005; Kaidonis, 2008; Lucas, 2004; Maas & Dumont, 1999; Phillips-Conroy et al., 2001]. As described by Hillson [1996; p 239], dental attrition "must in general be an age-affected phenomenon," and tooth wear is viewed as a natural aging phenomenon among mammals [e.g., Finch, 1990]. However, Hillson [1996] has also noted that there have been few studies of dental wear in known-aged humans. This is also true for wild nonhuman primates, as populations with available longitudinal dental data for known-aged individuals are rare [e.g., Cuozzo & Sauther, 2006b; Dennis et al., 2004; King et al., 2005; Richard et al., 2002; Wright et al., 2008].

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Tooth wear is often assumed to proceed at the same rate across individuals within single-species populations, frequently leading to the use of tooth wear stages (i.e., the sequence of abrasion [a result of tooth–food interaction] and/or attrition [produced by tooth–tooth interaction]) being used as an age surrogate in the study of both living and extinct primates and other mammals [e.g., Brockman et al., 2008; Jaeger et al., 2004; Jones, 2006; King et al., 2005; Renaud, 2005; Richard et al., 1991, 2002; Stander, 1997; Wright et al., 2008]. Despite the frequent use of tooth wear in age estimation of wild primates and other mammals, a number of workers have acknowledged the challenges of interpreting tooth wear as solely a product of age, noting the potential for error in mammalian age estimation on the basis of tooth wear, resulting from individual, sex, population, and habitat variation [e.g., Gipson et al., 2000; Stander, 1997]. For example, the rate and onset of tooth wear seems to vary between two baboon localities, with wear potentially being influenced by the amount of ground cover, seasonal food availability, and socioecology, such as individual rank [Phillips-Conroy et al., 2001]. Also, Teaford and Glander [1996] observed short-term differences in accumulated microscopic wear features among female howler monkeys (*Alouatta palliata*) from a single population, possibly reflecting differences in time spent feeding linked to reproductive status (i.e., pregnant or lactating), in addition to potential differences in foods consumed by their respective troops.

A number of researchers have addressed the phenomenon of how tooth wear varies among modern humans [e.g., Kaifu, 1999, 2000; Lovejoy, 1985; Molnar, 1971a,b, 1972; Smith, 1984; Tomenchuck & Mayhall, 1979]. For example, rate and pattern of tooth wear correspond to cultural attributes, such as subsistence mode (e.g., agricultural vs. hunting/gathering societies), and vary over time in the archaeological record [e.g., Kaifu, 1999, 2000; Molnar, 1971a, 1972; Smith, 1984]. Wear rates have also been shown to vary between males and females within single populations [e.g., Molnar, 1971b; Tomenchuck & Mayhall, 1979]. However, at least one earlier study has also concluded that patterns of wear in a modern human population are consistent across individuals and strongly correlate with age [Lovejoy, 1985]. In one of the few long-term studies of tooth wear in a single wild primate population, Dennis et al. [2004], utilizing dental topographic analysis, also concluded that overall tooth wear follows a population-specific pattern, being consistent across the different microhabitats used by a single population of mantled howler monkeys (*A. palliata*). Bermúdez de Castro et al. [2003] concluded that, despite substantial variation in tooth wear between human populations, variation in wear rates within a population can be quantified and can be used to asses age in unknown, fossil individuals. As seen in this brief review, there remains a lack of consensus concerning the relationship between tooth wear, its pattern of variation, and its efficacy as an indicator of age in living primate and human populations.

Research Questions

Ring-tailed lemurs at BMSR have been the focus of intense study for more than 20 years [Sauther et al., 1999; Sauther & Cuozzo, 2008, 2009; Sussman, 1991; Sussman & Ratsirarson, 2006]. Long-term study of this population has documented a series of dental health patterns [Cuozzo & Sauther, 2004, 2006a,b; Cuozzo et al., 2008; Sauther & Cuozzo, 2009; Sauther et al., 2002, 2006], including a high frequency of severe tooth wear and antemortem tooth loss. Beginning in 2003, F. P. C. and M. L. S. initiated a systematic study of the dentition of this lemur population, in part to identify the proximate causes of this phenomenon [e.g., Cuozzo & Sauther, 2004, 2006a,b; Cuozzo et al., 2008; Sauther & Cuozzo, 2009]. At BMSR, more than 20% of all individuals studied have lost at least one tooth. The vast majority have been lost owing to excessive wear rather than disease or other pathology [Cuozzo & Sauther, 2004, 2006b], with several individuals having lost more than 80% of their teeth [Cuozzo & Sauther, 2006b; Sauther et al., 2002]. In addition, the pattern of wear and subsequent tooth loss shows a strong relationship with the teeth used to process tamarind fruit (*Tamarindus indica*), a mechanically challenging food [e.g., Yamashita, 2008], and an important fallback resource of BMSR gallery forest ring-tailed lemurs [Cuozzo & Sauther, 2006b; Cuozzo et al., 2008; Sauther & Cuozzo, 2009]. Although the pattern of severe wear and loss is well-known for the BMSR population, with dramatic increases in tooth loss sometimes occurring within as little as 1 year [Cuozzo & Sauther, 2006b], we have yet to explore this issue in the context of longevity and advanced age. Given the comprehensive long-term study of BMSR *Lemur catta* and the documented, advancing ages of a number of individuals in the population, we can now begin to address questions relating tooth wear, behavior, ecology, and age.

Here, we assess the degree of dental macrowear and tooth loss in known-aged, older ($>$10 years old) ring-tailed lemurs at BMSR. Patterns of dental macrowear (i.e., gross surface wear) reflect the cumulative effects of food processing and, in contrast, to patterns of dental microwear, reflect interaction with the overall environment, and thus provide a summary of the cumulative effects of all foods eaten [Phillips-Conroy et al., 2001]. Primate dental macrowear has been examined far less frequently than dental microwear [e.g., Ungar, 1998, 2002], which has been studied intensely for more than three decades in humans, nonhuman primates, and other mammals [e.g., see Teaford, 2000; Walker et al., 1978].

Specifically, we evaluate the premise that same-aged wild primates within a single population experience similar degrees of overall tooth wear. Also, we explore the potential relationship between behavior, ecology, and tooth wear in these individuals, thereby providing rare data to assess the assumed connections between tooth wear and aging within a wild primate population. Given the rarity of wild lemur (and other primate) populations with known-aged older individuals, in 2005 we initiated the longitudinal study of a captive population of ring-tailed lemurs at the Indianapolis Zoo [e.g., Cuozzo et al., 2008; Sauther & Cuozzo, 2008] to provide a broader interpretive context for our work in Madagascar. Specifically, we integrated the study of these captive, known-aged lemurs, with controlled diets, annual medical evaluations, dental cleanings, and no predation, to provide a comparative template of patterns of dental wear one might expect in an ''optimal'' population. Although some captive mammals exhibit patterns of tooth wear that exceed those seen in wild populations [e.g., Clauss et al., 2007; Jurado et al., 2008; Kaiser et al., 2009], given their regular medical and dental care, we expected less overall tooth wear and fewer lost teeth in the captive *Lemur catta* sample when compared with the BMSR population. To our knowledge, ours are the first data comparing dental macrowear between wild and captive similar-aged individuals within a single primate species.

METHODS

All methods and materials received approval by and followed standard animal handling guidelines and protocols of the Institutional Animal Care and Use Committees of the University of North Dakota and the University of Colorado. Data collection in Madagascar was conducted with approval by the MNP (Madagascar National Parks, formerly known as ANGAP, Association Nationale pour la Gestion des Aires Protégées), the body governing research in Madagascar's protected areas. Additionally, all research was conducted in compliance with the American Society of Primatologists' Principles for the Ethical Treatment of non-Human Primates.

Samples and Localities

Across five field seasons (2003–2007) at the Beza Mahafaly Special Reserve, southern Madagascar (23°30′S, 44°40′E), detailed dental data were collected from 183 (167 adult) wild ring-tailed lemurs (304 total examinations, including repeat captures of specific individuals). Ages for wild individuals are known only to the year on the basis of their initial capture, as either a subadult (2nd year) or young adult (3rd year) determined using our established data on age and dental development, body mass, linear somatic and general health measures, and our long-term censusing of the population. Of the 183 individuals examined at BMSR through 2007, six individuals of known age are more than 10 years old. Data on tooth wear and dental health were also collected from 18 individual ring-tailed lemurs at the Indianapolis Zoo during three periods, December 29–30, 2005, December 18–19, 2006, and November 30/December 1, 2007, with 17 lemurs studied across at least 2 years. This includes two individuals, transferred from the Indianapolis Zoo to the Fort Wayne (Indiana) Children's Zoo, and examined in December 2007. Birth dates of all captive individuals are known, with 7 of the 17 lemurs in the sample more than 10 years old. At BMSR, the oldest documented ring-tailed lemur (early in her 21st year) disappeared from the population late in 2007, which we take to be near the maximum lifespan of ring-tailed lemurs at BMSR. Given the intense predation pressure at this site from introduced dogs (*Canis* sp.) and cats (*Felis* sp.) [e.g., Brockman et al., 2008; Gould & Sauther, 2007; Sauther & Cuozzo, unpublished data] and the persistence of endemic predators, such as raptors and the fossa (*Cyrptoprocta ferox* [Sauther & Cuozzo, unpublished data]), we find this to be quite extraordinary. In contrast, at the Indianapolis Zoo, five members of the population exceed 20 years of age, with the oldest approaching 29 years old as of 2007. All lemurs in the BMSR population are identified by a numbered collar, placed upon their initial capture (see animal handling methods described below). On occasion, numbers and/or collars are replaced owing to damage, which results in some individuals being assigned a new number, which we note throughout this article, when relevant.

Dental Analyses

Tooth wear and/or loss in both samples were scored using an ordinal scale (Table I). A score of zero indicates no occlusal wear (i.e., primarily seen in newly erupted teeth at BMSR). A score of five

TABLE I. Gross Tooth Wear Ordinal Scale

0—Unworn occlusal surface (i.e., a newly erupted tooth)
1—Small wear facets and no dentine or pulp exposure
2—Large wear facets and no dentine or pulp exposure
3—Some dentine and pulp exposure, few cusps still present; for canine and tooth comb, 1/2 remaining
4—Pulp exposure, with cusps gone, dentine or pulp exposed across most of the surface, or partial crown remaining; for canine and toothcomb, less than 1/4 remaining
5—Tooth worn to or below gum line with only roots/partial roots remaining (i.e., functional loss); OR no presence of the tooth remains (i.e., healed gingiva only, or in skeletal specimens, remodeled alveoli)

indicates a ''functionally absent'' tooth, i.e., either worn to or below the gumline with only worn roots remaining [e.g., Cuozzo & Sauther, 2004, 2006b] or complete absence of the tooth (i.e., no roots remaining). All dental data in both samples were collected by F.P.C., thereby eliminating the potential for interobserver error. We compared mean wear scores for each tooth position between the wild and captive samples using student's *t*-tests, with a significance level of $P = 0.05$.

Lemur Anesthesia

BMSR ring-tailed lemurs were captured using either a Tel-inject (Telinject USA Inc., Agua Dulce, CA) or Dan-Inject blow dart system (Dan-Inject, North America, Fort Collins, CO) and ketamine hydrochloride (Ketaset, Fort Dodge Laboratories, Fort Dodge, IA), ketamine and diazepam (Valium, Roche Inc., France) or Telazol® (Fort Dodge Laboratories). Doses were determined based on protocols developed over the past 20 years and more than 400 safe captures of ring-tailed lemurs at BMSR [see Miller et al., 2007]. Captures primarily occurred early in the morning to provide adequate recovery time. A trained veterinarian and/or veterinary students were onsite to monitor the health of each individual lemur. In addition to dental data, information on physical health, including weight, body temperature, heart and respiratory rate were recorded. After data were collected, lemurs were placed in covered dog kennels and kept in a quiet place for recovery. Upon recovery, individuals were released in the area where they were originally captured, normally within 6 hr. However, several individuals were released after a full night's recovery. All individuals returned to their troops and maintained their earlier social status. Following standards outlined by the U.S. CITES Management Authority (a unit of the U.S. Fish and Wildlife Service), all research team members since 2003 wore protective surgical masks and gloves in order to preclude disease transfer while handling lemurs. Captive ring-tailed lemurs were anesthetized under manual restraint by facemask with isoflurane for their annual physical examinations. Once fully anesthetized, lemurs were intubated and maintained under anesthesia with isoflurane. Lemurs were given a complete physical examination, including weight, body temperature, heart and respiratory rate. Following collection of biological data, each captive lemur received a dental examination and tooth cleaning, a practice that dates to the mid 1980s. Anesthesia protocols followed industry standards and were approved by the senior veterinarian at the Indianapolis Zoo. A licensed veterinarian or technicians under veterinary supervision administered anesthesia.

RESULTS

In Table II we compare the degree of tooth loss most often resulting from severe wear in individuals more than 10 years old in the BMSR and Indianapolis Zoo samples. At BMSR, all six exhibit at least some tooth loss, with Green 422 (new 16) having the greatest degree of loss (50%). In the Indianapolis Zoo sample, only two of the seven exhibit tooth loss, with ''Junior'' (SSP 768), the oldest lemur studied at close to 29 years old, missing 25% of his teeth. The two zoo individuals with missing teeth do not include the ''absent'' missing left maxillary canine in ''Kate'' (SSP 1120), which was partially removed by surgery in 1999. In 2006, the remaining partial root of this tooth was barely visible at the gumline. The ''absent'' left maxillary first incisor in ''Kate'' is also not included, as this represents a case of incisor agenesis, a polymorphism seen in several wild ring-tailed lemurs at BMSR (including Green 459, also not scored as absent) and Tsimanampesotse National Park, Madagascar [Sauther & Cuozzo, 2008].

In Table III we compare the percentage of tooth loss in *Lemur catta* at BMSR with the Indianapolis Zoo sample. Of the 167 adult ring-tailed lemurs at BMSR examined between 2003 and 2007, 22.8% exhibit at least one missing tooth compared with only 11.7% of the Indianapolis Zoo sample ($n = 17$). In the Indianapolis Zoo population, no individual displays $>30\%$ tooth loss. In contrast, 7.2% of the BMSR sample has more than 30% tooth loss, with 3.6% having more than 50% loss. Of note, Orange 156

TABLE II. Tooth Loss in Known Aged Ring-Tailed Lemurs Greater Than 10 Years Old at the Indianapolis Zoo and Beza Mahafaly Special Reserve (BMSR)

Location	Individual[a]	Sex	Age[b]	% tooth loss
BMSR	Orange 156 (new #266)	Female	19	14
BMSR	Green 459	Female	16	19
BMSR	Green 422 (new #16)	Male	15	50
BMSR	Black 432	Female	13	36
BMSR	Tan East 488	Male	14	22
BMSR	Yellow 489	Female	11	6
Indy	Junior (768)	Male	28.7	25
Indy	Kate (1120)	Female	24.8	0
Indy	Roy (1227)	Male	23.8	0
Indy	Kim (1683)	Female	20.8	0
Indy	Mick (1733)	Male	20.6	3
Indy	Andy (1816)	Male	19.8	0
Indy	Leadan (2519)	Female	14.3	0

[a]Numerical identification for Indianapolis Zoo individuals is the SSP studbook number.
[b]Age at time of most recent examination (see text). (A) At BMSR, age is determined on the basis of age at first capture, either at 2 or 3 years of age, based on dental development, body mass, and other developmental markers. (B) Exact birth dates are known for captive individuals.

TABLE III. Number and Percentage of Antemortem Tooth Loss in Individual Adult (≥3 Years Old) Ring-Tailed Lemurs From Beza Mahafaly Special Reserve Compared with the Indianapolis Zoo

% antemortem tooth loss[a]	Beza Mahafaly	Indianapolis Zoo
0	129 (77.2%)	15 (88.3%)
1–10	13 (7.8%)	1 (5.9%)
11–20	10 (6.0%)	0
21–30	3 (1.8%)	1 (5.9%)
31–40	5 (3.0%)	0
41–50	1 (0.6%)	0
51–60	4 (2.4%)	0
61–70	1 (0.6%)	0
71–80	0	0
81–90	1 (0.6%)	0
91–100	0	0
	$n = 167$	$n = 17$

[a]% tooth loss represents the number of teeth missing in an individual ÷ by the total number of tooth positions (36) × 100.

(new 266), the oldest known living individual at BMSR (nearly 20 years old when last examined in 2007), exhibits only 14% loss. Among the older adults at BMSR, 24% of their teeth are missing (52 teeth scored as missing, out of 216 total teeth scored [*Lemur catta* has 36 teeth; see review in Cuozzo & Yamashita, 2006]). The majority of these missing teeth are postcanine teeth, with first molars the most frequently lost. The pattern for older BMSR ring-tailed lemurs is similar to that for the overall population, in which first molars, followed by third and fourth premolars, are most frequently lost [Cuozzo & Sauther, 2006b]. In contrast, the teeth scored as missing among the captive sample are all anterior teeth (incisors, canines, or second premolars).

In Table IV we present the ordinal wear scores (see wear definitions in Table I) for each maxillary and mandibular tooth position, respectively, for each individual in both samples. Table V compares the mean ordinal wear scores between the BMSR and Indianapolis Zoo samples, for each maxillary and mandibular tooth position. As we expected, the BMSR sample exhibits significantly greater wear scores for a number of tooth positions (19 of 36 positions). Among the maxillary teeth, left and right P3 through M1 show significantly greater wear at BMSR. These three tooth positions are frequently lost owing to excessive wear at BMSR, a pattern associated with processing mechanically and physically challenging foods, specifically fruit of the tamarind tree (*T. indica*), an important fallback food among ring-tailed lemurs inhabiting several riverine gallery forests of southern Madagascar [e.g., Cuozzo & Sauther, 2004, 2006a,b; Cuozzo et al., 2008; Gemmill & Gould, 2008; Mertl-Millhollen et al., 2006; Sauther & Cuozzo, 2009]. Among the mandibular teeth, all tooth comb positions at BMSR show significantly more wear than in the captive sample.

TABLE IV. (a) Maxillary and (b) Mandibular Tooth Gross Wear Scores for Individual Ring-Tailed Lemurs Greater Than 10 Years Old at the Indianapolis Zoo and Beza Mahafaly Special Reserve[a,b]

Individual[c]	L/R	I^1	I^2	C	P^2	P^3	P^4	M^1	M^2	M^3
(a)										
Orange 156 (new ♯266)	L	4	4	4	4	4	4	5	4	3
BMSR	R	4	4	3	3	4	4	5	4	3
Green 459	L	*	4	3	3	4	4	5	4	3
BMSR	R	3	3	3	3	4	4	5	4	3
Green 422 (new ♯16)	L	4	4	4	5	5	5	5	4	4
BMSR	R	4	4	4	5	5	5	5	4	4
Tan East 488	L	4	4	3	4	5	5	5	4	4
BMSR	R	4	4	4	5	5	5	5	4	4
Yellow 489	L	2	2	2	2	3	3	4	3	3
BMSR	R	2	2	2	2	3	3	4	3	3
Junior (768)	L	*	*	*	*	3	4	4	4	3
Indy	R	*	*	*	4	4	4	4	4	3
Kate (1120)	L	*	3	*	3	3	3	4	4	3
Indy	R	3	3	2	2	2	3	4	4	3
Roy (1227)	L	1	1	2	2	3	3	3	3	3
Indy	R	1	1	1	2	3	3	3	3	3
Kim (1683)	L	3	4	2	3	3	3	3	3	3
Indy	R	4	4	2	3	3	3	3	3	3
Mick (1733)	L	3	3	2	*	3	4	4	4	3
Indy	R	3	3	3	3	3	3	4	4	3
Andy (1816)	L	2	2	1	1	2	2	3	2	2
Indy	R	2	2	3	3	2	3	3	2	2
Leadan (2519)	L	2	2	2	2	2	3	3	3	3
Indy	R	2	2	2	2	2	3	3	3	3
(b)										
Orange 156 (new ♯266)	L	*	3	3	4	4	4	4	4	4
BMSR	R	*	3	3	3	4	4	4	4	3
Green 459	L	4	4	4	3	4	5	*	4	5
BMSR	R	4	4	4	3	4	4	5	4	5
Green 422 (new ♯16)	L	4	4	4	4	5	5	5	5	5
BMSR	R	4	4	4	4	5	5	5	5	5
Tan East 488	L	4	4	4	3	4	4	4	4	4
BMSR	R	4	4	4	3	4	4	5	4	4
Yellow 489	L	4	4	4	2	3	3	4	4	3
BMSR	R	*	*	3	2	2	3	4	4	3
Junior (768)	L	3	3	3	*	3	4	4	4	4
Indy	R	3	*	*	3	4	4	4	4	4
Kate (1120)	L	*	*	*	2	3	3	4	4	3
Indy	R	*	*	*	2	3	3	4	4	3
Roy (1227)	L	2	2	*	1	3	3	4	4	3
Indy	R	2	2	2	2	3	3	4	4	4
Kim (1683)	L	2	2	2	2	3	3	3	3	2
Indy	R	*	2	2	2	3	3	3	3	2
Mick (1733)	L	3	3	3	2	3	4	4	4	4
Indy	R	3	3	3	2	3	4	4	4	4
Andy (1816)	L	*	*	1	1	2	2	3	2	2
Indy	R	*	1	1	2	2	2	3	3	2
Leadan (2519)	L	2	2	2	2	2	3	3	3	3
Indy	R	2	2	2	2	2	3	3	3	3

[a]See Table I for wear score definitions.
[b]An asterisk indicates a damaged, lost, or medically removed tooth, not possible to score for wear; or, a case of dental agenesis.
[c]Ordinal wear scores are not available for Black 432 as wear scores described here were not collected until 2005, after this individual was last observed in the study population.

TABLE V. Comparison of (a) Maxillary and (b) Mandibular Tooth Gross Wear Scores for Individual Ring-Tailed Lemurs Greater Than 10 Years Old Compared Between the Indianapolis Zoo and Beza Mahafaly Special Reserve

Tooth position	L/R	BMSR mean	*n*	SD	Indy mean	*n*	SD	*P*-value[a]	*t*-value	DF
(a)										
I1	L	3.50	4	1.000	2.20	5	0.837	0.0708	2.129	7
	R	3.40	5	0.894	2.50	6	1.049	0.1649	1.512	9
I2	L	3.60	5	0.894	2.50	6	1.049	0.0977	1.848	9
	R	3.40	5	0.894	2.50	6	1.049	0.1649	1.512	9
C	L	3.20	5	0.837	1.80	5	0.447	**0.0109**	3.300	8
	R	3.20	5	0.837	2.17	6	0.753	0.0594	2.157	9
P2	L	3.60	5	1.140	2.20	5	0.837	0.0578	2.214	8
	R	3.60	5	1.342	2.71	7	0.756	0.1730	1.467	10
P3	L	4.20	5	0.837	2.71	7	0.488	**0.0030**	3.902	10
	R	4.20	5	0.837	2.71	7	0.756	**0.0093**	1.486	10
P4	L	4.20	5	0.837	3.14	7	0.690	**0.0373**	2.400	10
	R	4.20	5	0.837	3.14	7	0.378	**0.0137**	2.985	10
M1	L	4.80	5	0.447	3.43	7	0.535	**0.0009**	4.671	10
	R	4.80	5	0.447	3.43	7	0.535	**0.0009**	4.671	10
M2	L	3.80	5	0.447	3.29	7	0.756	0.2066	1.351	10
	R	3.80	5	0.447	3.29	7	0.756	0.2066	1.351	10
M3	L	3.40	5	0.548	2.86	7	0.378	0.0682	2.044	10
	R	3.40	5	0.548	2.86	7	0.378	0.0682	2.044	10
(b)										
i1	L	4.00	4	0.000	2.40	5	0.548	**0.0007**	5.761	7
	R	4.00	3	0.000	2.50	4	0.577	**0.0071**	4.392	5
i2	L	3.80	5	0.447	2.40	5	0.548	**0.0022**	4.427	8
	R	3.75	4	0.500	2.00	5	0.707	**0.0042**	4.162	7
c	L	3.80	5	0.447	2.20	5	0.837	**0.0055**	3.771	8
	R	3.60	5	0.548	2.00	5	0.707	**0.0039**	4.000	8
p2	L	3.20	5	0.837	1.67	6	0.516	**0.0047**	3.337	9
	R	3.00	5	0.707	2.14	7	0.378	**0.0209**	2.739	10
p3	L	4.00	5	0.707	2.71	7	0.488	**0.0038**	3.750	10
	R	3.80	5	1.095	2.86	7	0.690	0.0956	1.840	10
p4	L	4.20	5	0.837	3.14	7	0.690	**0.0373**	2.400	10
	R	4.00	5	0.707	3.14	7	0.690	0.0620	2.100	10
m1	L	4.25	4	0.500	3.57	7	0.535	0.0685	2.069	9
	R	4.60	5	0.548	3.57	7	0.535	**0.0087**	3.254	10
m2	L	4.20	5	0.447	3.43	7	0.787	0.0783	1.961	10
	R	4.60	5	0.447	3.57	7	0.535	0.0579	2.141	10
m3	L	4.20	5	0.837	3.00	7	0.816	**0.0323**	2.485	10
	R	4.00	5	1.000	3.14	7	0.900	0.1509	1.555	10

[a]Significant *P*-values in bold ($P<0.05$).

At BMSR, *Lemur catta* use their toothcombs for various functions, including food procurement (e.g., stripping of leaves), during social grooming and to remove ectoparasites, which are ubiquitous in the population [Cuozzo & Sauther, 2006b; Millette et al., 2009; Sauther et al., 2002; Yamashita, 2003]. Food provisioning and an absence of ectoparasites in the captive sample likely contribute to reduced toothcomb wear in the zoo population.

Comparing the individual wild lemurs, the degree of tooth wear and tooth loss between Orange 156/266 and Green 459 at BMSR is especially notable (Fig. 1A, B). Although exhibiting some wear, all left mandibular teeth are present and retain tooth crowns in Orange 156/266 (Fig. 1A). Green 459, despite her being younger than Orange 156/266 (16 years vs. 19 years, respectively), exhibits markedly greater tooth wear and more lost teeth (Fig. 1B). This contrast is seen in the individual mandibular tooth wear scores of these two lemurs (Table IV), in which none of the postcanine mandibular teeth in Orange 156/266 displays a wear score above "4" on our ordinal scale, which contrasts with five of the 12 premolar and molar teeth in Green 459 having wear scores of "5." This illustrates the potential for tooth wear to vary notably among lemurs of the same sex, living in a single population.

DISCUSSION

Captive vs. Wild Ring-Tailed Lemur Tooth Wear

Studies of captive primates and other mammals have proven productive for understanding how teeth

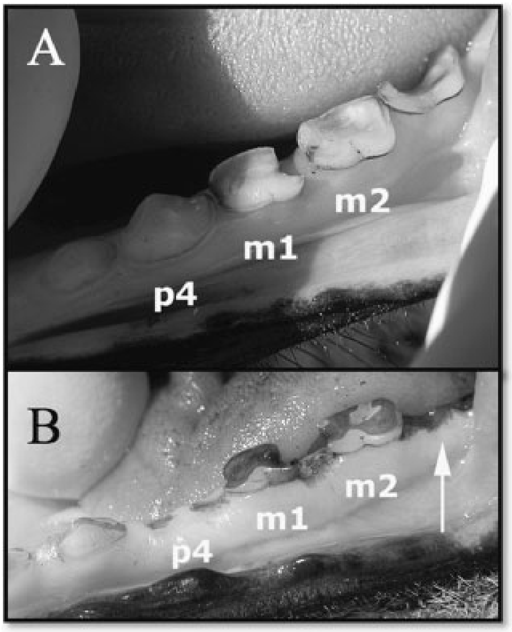

Fig. 1. Severe tooth wear and subsequent tooth loss variation in two older ring-tailed lemurs at Beza Mahafaly—left mandibular teeth: (**A**) Orange 156 (new 266), 19 years of age when examined in 2007; (**B**) Green 459, 16 years of age when examined in 2007. White arrow indicates absent third mandibular molar.

wear, and more broadly, the effects that captivity can have on the dental and overall health of nondomestic mammals. For example, Teaford and Oyen [1989] studied the effect of diet on tooth wear within a single species of captive vervet monkeys fed different diets. In this study, the authors illustrated that differences in food properties (e.g., specifically food hardness) resulted in different rates and degrees of wear in a single primate species. A high frequency of dental malocclusion in primates and other captive mammals is also seen, often viewed as a result of dietary influences [e.g., Corruccini & Beecher, 1982; Fitch & Fagan, 1982; see review in Young, 1997]. Also, among a number of mammal species, particularly but not only large ungulates, patterns of tooth wear and frequency of other dental pathologies far exceed those recorded in wild conspecifics [e.g., Clauss et al., 2007; Fitch & Fagan, 1982; Kaiser et al., 2009]. For example, captive populations of some browsing species (e.g., giraffes, *Giraffa camelopardalis*) exhibit significantly more tooth wear than their wild counterparts, which is viewed as a product of consuming grass hay and processed foods with high amounts of silica [Clauss et al., 2007, but see Sanson et al., 2007 for a counterargument on silica and tooth wear]. Also, Jurado et al. [2008] suggest that severe tooth wear in captive blackbucks (*Antilope cervicapra*) resulted from husbandry practices, specifically, regularly being fed on sandy soils. In contrast to these herbivorous mammals, Gipson et al. [2000] observed a similar pattern of tooth wear between captive and wild wolves (*Canis lupus*).

Reduced dental health in some captive mammals has been suggested as one factor limiting lifespan among these taxa in captivity [e.g., Clauss et al., 2007; Jurado et al., 2008; Kaiser et al., 2009]. However, given annual veterinary and dental examinations, tooth cleanings, and a controlled diet, we expected less overall tooth wear and few cases of tooth loss in the Indianapolis Zoo ring-tailed lemur population, when compared with the BMSR sample. For most of their lives, the older Indianapolis Zoo lemurs fed primarily on Purina Monkey Chow (1980s through 2002). Since then, these lemurs have been fed several, more nutritionally specialized processed diets, including Marion Zoological (Plymouth, MN) leaf-eater diet, Mazuri (PMI Nutrition International, Richmond, IN) leaf-eater and callitrichid gel, and most recently Mazuri high-fiber sticks and biscuits made from Konjac Foods flour (Sunnyvale, CA). Thus, since at least 2002, this population has fed on foods that do not present the same physical challenges as tamarind fruit, which dominates the diet of the BMSR lemurs.

At the Indianapolis Zoo, only two individuals exhibit tooth loss, one of which is missing only a single tooth (See Table II). The second individual exhibiting tooth loss is the oldest in the population (almost 29 years of age) and exceeds the oldest known lemurs at BMSR by nearly a decade. Yet, the degree of loss in this individual (25%) is far less than several lemurs in the BMSR population, including two who are only half the age of ''Junior'' at the Indianapolis Zoo. Jurado et al. [2008] noted that few studies have directly assessed the potential link between increased dental wear, reduced dental health, and longevity in captive mammals, when compared with data from wild mammals of the same species. In contrast to the studies noted earlier [Clauss et al., 2007; Kaiser et al., 2009], in which the authors suggest that among some captive mammals, longevity may be reduced, in part owing to reduced dental health; we illustrate that among our captive sample of ring-tailed lemurs, lifespan is at least a decade longer or more than their wild counterparts and corresponds to significantly less tooth wear and/or antemortem tooth loss. Extended ring-tailed lemur lifespan is also seen at other zoological parks; for example, ''Mamu,'' a female ring-tailed lemur from the Pueblo Zoo (Colorado) who died at age 37 in 2007 [Villers, 2007], was nearly twice the age of the oldest lemur at BMSR.

Can we thus assume that with dental and veterinary care, a controlled diet, and an absence of predation, captivity for ring-tailed lemurs is an ''optimal'' environment? Given the extreme seasonality in rainfall and resource availability among ring-tailed lemurs in southern Madagascar [e.g., Gould et al., 1999, 2003; Sauther, 1998; Sauther & Cuozzo, 2009; Sauther et al., 1999], the opportunity for captive lemurs to obtain constant food without the need to exploit foods with challenging physical, mechanical, and/or chemical properties, such as at BMSR, is a clear benefit in terms of longevity, limited tooth loss, and low frequency of severe wear. Jurado et al. [2008], citing Wenker et al. [1998], suggest that good dental health in captive animals is an indicator of adequate health care within a specific zoological context. This may be the case at the Indianapolis Zoo, given the long-term care and support of this zoo's lemur population, but also likely reflects the differences that ring-tailed lemurs encounter in captivity vs. the wild. For example, the limited amount of toothcomb wear in our captive sample (Table V) likely reflects differences in feeding ecology as well as socioecology, given the extensive use of the toothcomb at BMSR to probe potential foods, to remove ecoparasites (which are not seen in the captive population), and in the complex context of social grooming [e.g., Cuozzo et al., 2006b; Millette et al., 2009; Sauther et al., 2001, 2002].

Variation in Overall Tooth Wear at BMSR

At BMSR, the high frequency of tooth loss occurs primarily in the postcanine teeth, which are most often used when processing physically challenging tamarind fruit, the major fallback food used by this population [Cuozzo & Sauther, 2004, 2006b; Sauther & Cuozzo, 2009]. In contrast, all tooth loss in the captive sample involves the anterior teeth. This pattern of anterior teeth being lost, often a product of damage (i.e., the maxillary canine), is seen among a number of wild nonhuman primates, including hominoids, several New World monkey species, and *Galago* (= *Otolemur*) *garnetii*, in which canines are the most commonly lost tooth [e.g., Crofoot et al., 2009; Lovell, 1990; Masters et al., 1988; Smith et al., 1977]. This also corresponds to the sequence of wear in large wild felids (e.g., leopards, lions [Stander, 1997]), in which anterior teeth are the first to exhibit notable tooth wear followed by the premolars and molars. A pattern of greater anterior vs. posterior dental wear has also been described among wild and captive gorillas [Kilgore, cited in Nichols & Zihlman, 2002]. Thus, the pattern seen for BMSR lemurs, in which postcanine teeth are the most worn and most frequently lost, is distinct from that seen in other primates and wild felids.

In this study, we illustrate that, even in a small sample of older lemurs ($n = 6$), the degree of dental macrowear and the frequency of severe wear resulting in the loss of functional tooth crowns [see definition in Cuozzo & Sauther, 2006b] varies markedly. Importantly, the degree of overall occlusal wear and tooth loss do not directly correspond to age. Of the lemurs in our sample who are more than 10 years old, the two exhibiting the fewest functionally lost teeth (Table II) are both the youngest (age 11, 6% tooth loss) and the oldest (age 19, 14% tooth loss) in the study group. In addition, in the case of 156/266 (age 19) and 459 (age 16), the younger individual exhibits more tooth loss than the older. On the contrary, other individuals more than 10 years display up to 50% severe wear and tooth loss. Thus, among this wild population of nonhuman primates, the degree of tooth wear is not an accurate indicator of age.

This conclusion is further illustrated in a comparison of two younger, 7 year old ring-tailed lemurs examined at BMSR in 2008. Here, the first left maxillary molar in Orange 168/368 (Fig. 2A) exhibits far less wear (ordinal wear score of "3") than Yellow 187/319 (Fig. 2B; ordinal wear score of "5"). The groups to which these two lemurs belong (Orange and Yellow troops) have overlapping home ranges and frequently compete for resources. However, Yellow troop, in contrast to Orange troop, uses a wider range of habitats, including areas containing introduced plants and domesticated crops [Sauther & Cuozzo, pers. obs.]. Thus, differences in the degree of tooth wear in these two lemurs may reflect the feeding ecology of groups to which they belong, similar to one of the potential causes cited by Teaford

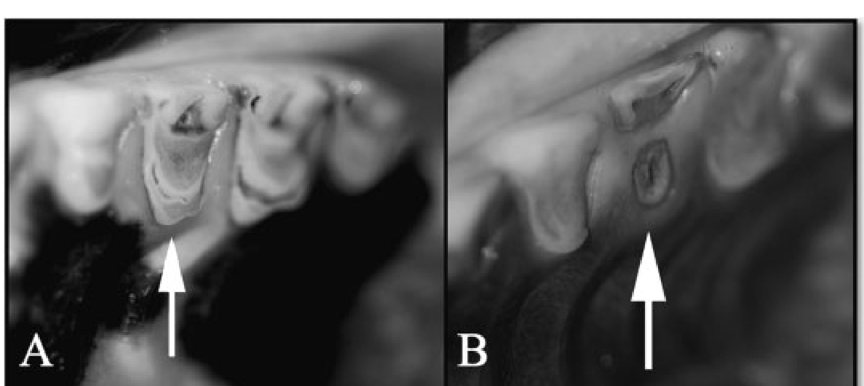

Fig. 2. Variation in left maxillary first molar wear (white arrows) in two 7 year old ring-tailed lemurs from the Beza Mahafaly Special Reserve. (**A**) Orange 168 (new ♯368); (**B**) Yellow 187 (new ♯319).

and Glander [1996; Teaford, 2000] to explain differences in the frequency of microwear features among female howler monkeys. The impact of microhabitat and resource use on tooth wear is also seen in Table II, in which individuals with the highest frequencies of tooth loss are found in groups that reside in and frequently utilize habitats that border the Sakamena River, which forms the eastern border of the Beza Mahafaly reserve [e.g., Sauther et al., 1999]. These troops (Black, Green, and Tan East) not only often consume endemic, but also introduced foods, including human cultivated crops [Gemmill & Gould, 2008; LaFleur & Gould, 2009; Sauther & Cuozzo, 2009]. Among the introduced foods consumed by these troops is *Argemone mexicana*, a physically challenging food which grows along the boundaries of the Sakamena River. This plant, with its tough, fibrous leaves, likely contributes to the pattern of tooth wear seen in those troops that consume this plant [Sauther & Cuozzo, 2009]. Regardless of the nature of dominant foods consumed, whether introduced or endemic, the variation in dental macrowear, we report among a sample of wild ring-tailed lemurs, varies between individual groups utilizing varied habitats in a limited spatial area (~100 ha) and refutes the premise that overall tooth wear is reliably consistent in a single-species primate population.

Dental Senescence and Offspring Survival at BMSR

What happens when teeth reach the end of their functional efficiency (i.e., dental senescence)? King et al. [2005] have argued that dental senescence has reproductive consequences. Among *Propithecus edwardsi* at Ranomafana National Park, Madagascar, severe tooth wear has been suggested as a factor impacting infant survival during periods of reduced rainfall, as the worn teeth of older females limits their ability to process foods to properly lactate during episodes of environmental stress [King et al., 2005; Wright et al., 2008]. However, the pattern of tooth wear described for Ranomafana sifaka, in which tooth crowns are retained even in the oldest individuals, albeit with reduced shearing capacity [King et al., 2005; Wright et al., 2008], does not approach the severity seen among BMSR ring-tailed lemurs, in which the entire tooth is frequently absent (see Fig. 2B). This leads to the possibility that severe wear in BMSR *Lemur catta* may also impact infant survival.

For each of the four older BMSR female lemurs we describe herein, long-term, ecological, behavioral, and demographic study allows us to evaluate the potential impact of tooth wear and/or loss on the survival of their offspring. Despite varying degrees of tooth loss, ranging from 3 to 25% in the year of giving birth, each of these four individuals successfully reproduced. As severe wear and/or tooth loss likely has limited impact on an individual's ability to conceive, the degree of tooth loss when each weaned their infants is of greater importance. Orange 156/266, at age 15, produced a set of male twins in 2002 (Orange 261 and 274) and successfully weaned each of them in 2003, when she displayed 3% tooth loss and moderate-to-heavy maxillary molar wear [Cuozzo & Sauther, 2006b]. These male twins were first captured in 2004 as subadults (2nd year) and migrated from their natal troop in late 2005 (early in their 4th year). In December 2009, Orange 261 was observed in an uncollared troop, more than 5 km from the BMSR gallery forest, where he has resided since his initial 2005 migration. After his migration, Orange 274 has not been observed in or near BMSR. In 2006, at age 18 and with 11% tooth loss, Orange 156/266 again demonstrated infant survival through weaning. At age 11, Yellow 489 with 6% loss was observed in October 2005 with an infant, but this female disappeared with her offspring during the rains of 2005/2006, when she and other members of her troop were trapped across the ephemeral Sakamena River when it began to flow and she never returned to the reserve (Whitelaw, personal communication).

More interesting are the cases concerning Black 432 and Green 459. Black 432 successfully weaned a male infant in 2004 at age 13 while exhibiting 36% tooth loss. As of December 2009, her son was present in the population (Black 222/223), still residing in Black troop early in his 7th year. Green 459 gave birth to a male in the fall of 2004 at age 14 (Green 275/284) and successfully weaned him with 8% tooth loss. This is all the more exceptional, given that she did so during the aftermath of a cyclone in 2005, which markedly reduced the availability of food resources in the area [LaFleur & Gould, 2009]. As of December 2009, he was a healthy adult early in his 6th year, now residing in Red troop. These examples suggest that severe tooth wear is not predictive of infant survival among BMSR ring-tailed lemurs and that there may be species differences regarding the impact of dental wear on offspring survival.

Many factors may influence a female's ability to produce surviving offspring at advanced ages, despite severe dental wear and tooth loss. These include female feeding priority and food access [e.g., Sauther, 1992; Sauther et al., 1999] and modifications in feeding behaviors observed among dentally impaired ring-tailed lemurs at BMSR [Cuozzo & Sauther, 2006b; Fish et al., 2007; Millette et al., 2009]. An additional factor is social rank. Higher ranking females at BMSR have feeding priority [e.g., Sauther, 1992; Sauther et al., 1999], and this likely provides greater access to foods especially in times of resource stress. Black 432, who weaned her infant in 2004 while exhibiting 36% tooth loss, was the second ranking female in Black troop at that time. This troop lives primarily in degraded habitat, south of the protected BMSR gallery forest [Sauther & Cuozzo, 2009]. Thus, Black 432's high rank likely allowed access to the limited resources available in this area, contributing to the survival of her offspring despite dental impairment.

Most interesting is the case of Green 459. As noted above, she successfully weaned her son during the period following a major cyclone in January 2005. This environmental catastrophe included the flooding of the BMSR gallery forest and caused a dramatic reduction in the availability of tamarind fruit during the period of weaning, heading into the dry season. Given the rarity of the primary BMSR ring-tailed lemur fallback food during the dry season of 2005, Green 459's position as the alpha female in this troop, whose matriline has been dominant since 1987 [Sauther & Gould, unpublished data], likely allowed her access to the few foods available during this stressful period. Thus, in addition to dental impairment [King et al., 2005], socioecology likely influences infant survival during periods of environmental stress.

We recognize the need for continued work on the questions we address herein, specifically information from larger samples. However, given the rarity of known-aged "older" wild primates, our new data provide an important point of reference for assessing the causes of variation in primate tooth wear and, more importantly, the relationship between tooth wear, age, behavior, and ecology. Since 2003, we have captured and collared 43 individual ring-tailed lemurs during their 2nd year at BMSR, and approximately 60% of these individuals remain in the population and under study. As several of these individuals are now approaching 10 years of age, in just a few years, we will soon have detailed knowledge on tooth wear variation in the context of individual life histories, behavior, and ecology for a much larger sample. This will allow us to further test the ideas we present here and will contribute to our growing knowledge of primate aging, as well as provide a better understanding of the factors that lead to variation in tooth wear within a single species.

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