Age and Individual Foraging Behavior Predict Tooth Wear in Amboseli Baboons

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ABSTRACT   Teeth represent an essential component of the foraging apparatus for any mammal, and tooth wear can have significant implications for survival and reproduction. This study focuses on tooth wear in wild baboons in Amboseli, southern Kenya. We obtained mandibular and maxillary tooth impressions from 95 baboons and analyzed digital images of replicas made from these impressions. We measured tooth wear as the percent dentine exposure (PDE, the percent of the occlusal surface on which dentine was exposed), and we examined the relationship of PDE to age, behavior, and life history variables. We found that PDE increased significantly with age for both sexes in all three molar types. In females, we also tested the hypotheses that long-term patterns of feeding behavior, social dominance rank, and one measure of maternal investment (the cumulative number of months that a female had dependent infants during her lifetime) would predict tooth wear when we controlled for age. The hypothesis that feeding behavior predicted tooth wear was supported. The percent of feeding time spent consuming grass corms predicted PDE when controlling for age. However, PDE was not associated with social dominance rank or maternal investment. Am J Phys Anthropol 144:51–59, 2011. © 2010 Wiley-Liss, Inc.

Teeth represent an essential component of the foraging apparatus for any mammal and tooth wear can have significant implications for survival and reproduction (Lanyon and Sanson, 1986; Buss, 1990; Logan and Sanson, 2002; Hillson, 2005; King et al., 2005; Veiberg et al., 2007). Data from a number of mammal species provide evidence for the adaptive importance of teeth, the functional significance of tooth wear, and the relationship between tooth wear and age. For instance, rodents have ever growing incisors and their foraging behavior results in constant wearing and sharpening, which in turn results in the teeth being kept at a constant height in the jaw throughout life (Hillson, 2005). Further, Williams and Kay (2001) found that rodent species adapted to more abrasive diets, such as grass, had relatively higher molar crowns than other rodents. Among roe deer, those with larger teeth have a longer life expectancy, which links tooth endurance to expected lifespan (Veiberg et al., 2007). Elephants provide another example. After the sixth set of teeth is worn to a point about half its original height, the animal can no longer masticate food adequately; thus elephants rarely live beyond this stage of tooth wear (Buss, 1990). Tooth wear also has been related to individual fitness in one study of primates. King et al., (2005) found that in sifakas (Propithecus edwardsi), older females lost their infants at higher rates than younger females. They argued that tooth wear in older females was likely to be an important factor in this relationship. One attempt to replicate this study in another species (deer) failed to find an effect of tooth wear on infant survival (Nussey et al., 2007). Nonetheless, these examples highlight the importance of having functional teeth in mammals and even connect life history components (adult and potentially offspring survival) to the persistence of functional teeth.

A number of previous studies of tooth wear as a function of age have been done in wild mammal populations, including deer (Skogland, 1988; Kojola et al., 1998; Hewison et al., 1999; Nussey et al., 2007; Veiberg et al., 2007), gazelles (Munro et al., 2009), koalas (Lanyon and Sanson, 1986; Logan and Sanson, 2002), raccoons (Grau et al., 1970), wolves (Gipson et al., 2000), and several species of primates (Phillips-Conroy et al., 2000; Morbeck et al., 2002; Dennis et al., 2004; King et al., 2005; Cuozzo and Sauther, 2006), all of them indicating that tooth wear in molars increases with age.

Dental attrition has also been used to assign ages or determine age at death in human populations (Brothwell, 1981) for both anthropological research and forensic analyses (Helm and Prydsö, 1979; Molnar et al., 1983; Song and Jia, 1989; Kambe et al., 1991; Li and Ji, 1995; Kim et al., 2000; Mandojana et al., 2001; Valenzuela et al., 2002; Oliveira et al., 2006; Reppien et al., 2006). However, the weaknesses and limitations of age estimation by examination of dental attrition as the sole indicator of age have also been well documented (Ajmal et al., 2001; Ball, 2002). For one thing, the relationship between tooth wear and age has been reported for only a few wild primate species (baboons; Phillips-Conroy et al., 2000, howler monkeys; Dennis et al., 2004, and sifakas; King et al., 2005), and the sparseness of this set of samples makes it difficult to infer age from wear with confidence in fossil species. By adding another data set to the existing small collection, we add important information about how the precise relationship between age and tooth wear can vary within and across living systems. In addition, age alone is unlikely to explain all observed variation in tooth wear. For instance, Kojola et al. (1998) found that lichen biomass was correlated with tooth wear in different reindeer herds from Finland, and Nussey et al. (2007) found that among Scottish red deer, higher tooth wear rates were related to higher gritty food consumption. These studies and our own observations about variance in tooth wear for age motivated us to test hypotheses about other variables that affect tooth wear in addition to age.

Here, we examine age, individual foraging differences, and individual life history differences as potential sources of variance in tooth wear in a wild primate population, the baboon population of Amboseli (Kenya). Continuous, individual-based data have been collected on this population since 1971 by the Amboseli Baboon Research Project (ABRP). Detailed longitudinal data on demography, ecology, behavior, and physiology for a large number of individuals are available (Altmann and Alberts, 2003, 2005; Alberts et al., 2005).

We had two goals in this cross-sectional analysis. First, we sought to provide a finely-calibrated measure of tooth wear as a function of age for the Amboseli baboons, which represent an entirely wild-feeding population of known-aged individuals. Our data represent an addition to the limited literature on tooth wear in known-aged primates. To accomplish this, we performed bivariate analyses, separately for each molar, regressing tooth wear on age.

Our second goal was to test the hypotheses that long-term patterns of feeding behavior, social dominance rank, and one measure of maternal investment (the cumulative number of months that a female had dependent infants during her lifetime) would predict tooth wear when we controlled for age. Feeding behavior and food choice, in particular, have obvious potential to impact tooth wear and so we examined tooth wear as a function of individual food choice and dietary differences. Social dominance rank is known to influence many aspects of life history and behavior in this species and in a number of other cercopithecine primates (reviewed in Silk, 1987, 2009). Higher ranking individuals in general have priority of access to resources and so we predicted that higher ranking females would show less tooth wear for their age. Specifically, we predicted that higher ranking individuals would have access to better quality and less abrasive foods more often than lower ranking individuals, including

riper fruits or younger leaves and grass blades, which contain fewer phytoliths and hence present lower toughness properties than mature leaves and unripe fruits (Choong, 1996; Teaford et al., 2006; Wollstonecroft et al., 2008). Previous studies have not detected effects of dominance rank on time spent foraging for the wild-feeding baboons in this population (Altmann, 2001; Post et al., 1980), but Post et al. (1980) found that low ranking animals were aggressively interrupted during feeding bouts more often than high ranking animals. In addition, the pervasive impact of dominance rank on multiple aspects of behavior and life history in cercopithecine primates motivated us to assess its impact on tooth wear. Maternal investment has the potential to impact tooth wear through its relationship to energetic costs. We predicted that females that had spent relatively more time with dependent infants for their age would show more tooth wear for their age, reflecting more time spent foraging during periods of maternal investment.

MATERIALS AND METHODS
Study population

The Amboseli basin (2°40′ south and 1,100 m above sea level) is a semiarid savanna in southern Kenya, near the base of Mount Kilimanjaro in East Africa. The average annual rainfall is 348 mm, but with a marked seasonal pattern, and interannual variability between 150 and 500 mm (Altmann et al., 2002). The area is populated by yellow baboons, *Papio cynocephalus*, that exhibit some admixture with anubis baboons (*P. anubis*), which occasionally immigrate into the basin (Alberts and Altmann, 2001, Tung et al., 2008). The Amboseli baboons have been intensively studied for almost four decades (see www.princeton.edu/~baboon for a complete bibliography and Baboon Project Monitoring Guide).

Behavioral and life history data

Subjects were members of five social groups of wild-feeding baboons. All individuals in the study groups were recognized on sight and habituated to the presence of human observers. Demographic and reproductive records for this analysis were drawn from our long-term database, BABASE. Each female's reproductive state was recorded on a near-daily basis, so that all births in study groups were registered within a few days of their occurrence. All females had been known from birth as members of the long-term study population and their birthdates were known within a few days (hence, their ages were known exactly). Of the 41 males in this study (see below) only 25 had been known from birth and their ages were known exactly. The remaining 16 male subjects had immigrated into the study population as adults, and their birthdates were estimated based on patterns of growth, maturation, and change in physical features over time (see Alberts et al., 2006). In particular, our age estimates are based on patterns of aging in known-aged males whom we observed continuously for between 5 and 14 years of adulthood. They employ mul-

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tiple aging criteria (body carriage, body condition, skin condition, fur condition, canine condition), and multiyear longitudinal observations of aging in male baboons (i.e., we assess changes in these features over time). For 10 of these 16 individuals, the field team assigned error estimates of ±1 year, and for six individuals error estimates were ±2 years.

The proportion of time spent in various major activities was established using point (or scan) sampling at one-minute intervals within 10-minute focal samples (Altmann, 1974). Such samples have been collected on all adult females in the study population since 1984. Activities were categorized as feeding (including food processing), walking while not feeding, grooming, being groomed, other social activities, or resting (Alberts et al., 2005). When feeding was recorded, the identity of the food item was also recorded, allowing us to determine the importance of different food types for tooth wear. A total of 69,213 individual point (or scan) samples of feeding behavior on 54 females from the age of 25 months onwards, spanning the years 1991–2008, were analyzed here. Samples were collected throughout each year, during both dry and wet seasons. The number of samples per female per year and the number of years of sampling varied over females, depending upon their age and several other factors (range for mean number of samples per year: 57.3–293.3; range for number of years of samples: 3–17; Supporting Information Table).

Immobilization of study subjects and acquisition of tooth casts

Between 2006 and 2008, a subset of baboons was briefly immobilized by a dart propelled from a blowpipe that delivered a dose of an anaesthetic, Telazol®, a technique that has been used successfully in this and other primate populations (e.g., Glander et al., 1991; Altmann et al., 1996, 2010 (in press); Sapolsky et al., 1997; Tung et al., 2009). Various data were collected from each anesthetized animal, including tooth casts for morphological and dental microwear analysis.

Once animals were immobilized, enamel tooth surfaces were washed with pressurized water and brushed lightly to remove food remains and then dried with a foot-powered air pump. Tooth casts were obtained for the left hemimandible and hemimaxilla using Colténe® Speedex putty. When the replication material had cured, the mold was removed, labeled, and stored in a plastic bag. From these negative molds, replicas were made at University of Barcelona using polyurethane, which is stable, easy to use and clean, and provides high quality casts (Galbany et al., 2004, 2006). Dental replicas from 54 females and 41 males were obtained and analyzed for the present study.

Analysis of tooth casts

Each tooth cast was photographed and digital images were obtained. Tooth casts were oriented based on the enamel–gum junction surface, which was perpendicular to the camera objective. On each image, the perimeters of all dental crowns were traced with Imat software, developed by the Unit of Treatment of Images and Computer Support of the Serveis Cientificotècnics at the University of Barcelona. In all cases, we used a 21-inch monitor and 1,600 × 1,200 pixel resolution. Imat software automatically calculates several metric variables from the established dental crown perimeters, including total occlusal
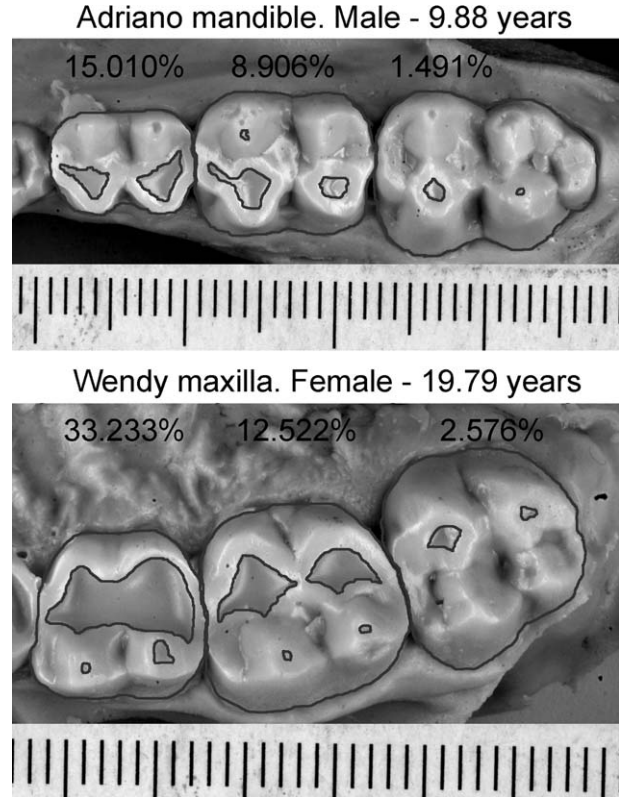

Fig. 1. Molar occlusal images with crown and dentine areas, as well as percent of dentine exposure (PDE) values.

area, which is the area of molar crown in occlusal view (Estebaranz et al., 2004). Areas of dentine exposure were measured and percent of dentine exposure (PDE) was calculated for each molar tooth by dividing dentine exposure areas by total area of molar crown (Fig. 1). PDE was obtained for each upper and lower molar (M1: first molar, M2: second molar, and M3: third molar). For each molar position (M1, M2, and M3) in each individual, the mean PDE was calculated by taking the mean value of PDE for the upper and the lower molar. In cases where an individual had missing or broken teeth or the replica was of insufficient quality, the PDE for that molar position was calculated based on only the one available molar (M1, $N = 9$; M2, $N = 8$; M3, $N = 16$). Data on PDE for all individuals, all molars, are provided in the appendix.

Statistical analyses

To determine the relationship between PDE and age in this cross-sectional data set, separately for males and females (our first goal), we performed separate analyses for each molar and each sex and modeled PDE as a quadratic function of age in six separate regressions (i.e., one each for UM1, UM2, UM3, LM1, LM2, LM3). Next we examined the effects of diet, parental care, and social dominance rank on tooth wear, for females only (comparable data on diet and parental care were not available for males). To do this, we obtained the residuals of the relationship between age and PDE for each molar and used these residuals as dependent variables in three subsequent bivariate analyses using individual foraging behavior, parental care, and social dominance

TABLE 1. *Quadratic regressions for all female and male molars, predicting molar wear (PDE) from age*

	Teeth	R^2	F	P value	Equation
Females	M1	0.906	241.213	<0.001	$PDE = 0.092 \times age^2 - 0.557 \times age + 2.861$
	M2	0.790	94.370	<0.001	$PDE = 0.070 \times age^2 - 0.455 \times age + 0.858$
	M3	0.507	16.989	<0.001	$PDE = 0.040 \times age^2 - 0.522 \times age + 1.868$
Males	M1	0.741	54.371	<0.001	$PDE = 0.214 \times age^2 - 4.184 \times age + 24.526$
	M2	0.694	43.149	<0.001	$PDE = 0.023 \times age^2 + 0.488 \times age - 3.535$
	M3	0.677	37.788	<0.001	$PDE = 0.024 \times age^2 - 0.068 \times age - 0.881$

rank, respectively, as the predictor variables. Each of the predictors is described below.

To examine individual foraging behavior as a predictor, we measured the percent of feeding time during which each female consumed particular foods, from the period beginning at 25 months of age and continuing to her darting date. These foods included the major constituents of the baboons' diet: grass corm, fruits, grass blades, grass blade bases, grass seeds, and acacia seeds (Alberts et al., 2005). We chose 25 months as the beginning of the feeding analysis period for each female because the first molar erupts at ~25 months of age (Phillips-Conroy and Jolly, 1988; Kahumbu and Eley, 1991). We included feeding data from the entire period of time during which the tooth enamel of at least one permanent molar could be abraded by food. For 31 of the 54 females, we had feeding data from every year of their lives, beginning at age 25 months and continuing until the date the tooth impressions were made. For the remaining 23 females, we lacked feeding data for some years (particularly those females born before 1989), but for each of these older females we had at least six, and up to 16, years of feeding data. We assumed that, even if some years of data were missing for older females, the 6–16 years of feeding data collected prior to darting were sufficiently representative of the female's entire lifetime feeding patterns to examine these data as predictors of tooth wear. We view this as a reasonable assumption, because tooth wear is an enduring and non-reversible process that occurs over a long period of time, and even our incomplete records include many years of data.

We chose the other two predictor variables in the bivariate analyses: number of months spending with a dependent infant and social dominance rank, because of their potential to impact feeding behavior, and hence tooth wear. To examine the importance of parental care, we measured the total number of months that females spent with dependent offspring (aged 12 months or less) during their lifetime up to the darting date, when tooth casts were obtained. We reasoned that having a dependent infant involves "eating for two" and that this might be reflected in tooth wear. To examine the importance of social dominance rank, we used the dominance rank position of each female at her darting date, when casts were obtained. We reasoned that, because dominance rank predicts priority of access to resources and impacts many life history traits, high ranking females would have access to the highest quality foods, which would result in less tooth wear for high ranking females compared with low ranking females of the same age. Because dominance ranks of adult females tend to be quite stable over the lifetime (Hausfater et al., 1982; Silk, 1987), dominance rank at the time of darting is a good measure of the female's lifetime experience of social rank.

In addition to these bivariate analyses of residuals, we performed a stepwise multiple linear regression, in which we regressed all these life history and behavioral variables together, on percent of dentine exposure for each molar separately. These multivariate analyses allowed us to control for multiple variables simultaneously, but we maintained
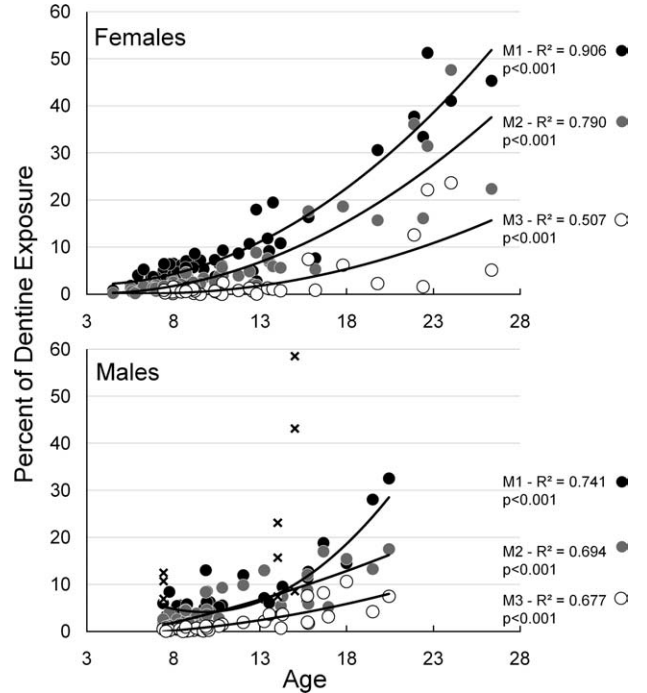

Fig. 2. Quadratic regressions for predicting PDE from age for all molars (M1: first molar, M2; second molar, and M3: third molar) and both sexes. X represent males that were not included in the analyses because they exhibited extremely high tooth wear, possibly caused by pathologies.

the bivariate analyses to allow us to see clearly the simple relationships between variables. We performed these analyses for each molar using two subsamples: a) all the females, for examining M1 and M2 ($n = 54$) and b) only females that had erupted M3, for examining M3 ($n = 37$).

RESULTS

Cross-sectional analyses of percent dentine exposure for each molar (M1, M2, and M3) and both sexes revealed significant quadratic relationships with age in simple linear regressions, in which age was the sole predictor variable ($P < 0.001$ in all cases). In females, $R^2 = 0.906$ for M1, 0.790 for M2, and 0.507 for M3. Males showed somewhat lower R^2 values: $R^2 = 0.741$ for M1, 0.694 for M2, and 0.677 for M3 (Table 1, Fig. 2). The female sample was both larger than the male sample ($n = 54$ versus 41) and exhibited a wider range of ages (4.51–26.35 years old for females, versus 7.40–20.45 years old for males).

We next examined, for all females, the residual variance from the simple linear models predicting PDE from age for each molar. Negative residuals indicate that a given individual had less worn molars for its age, whereas positive residuals indicate relatively more worn molars for its age.
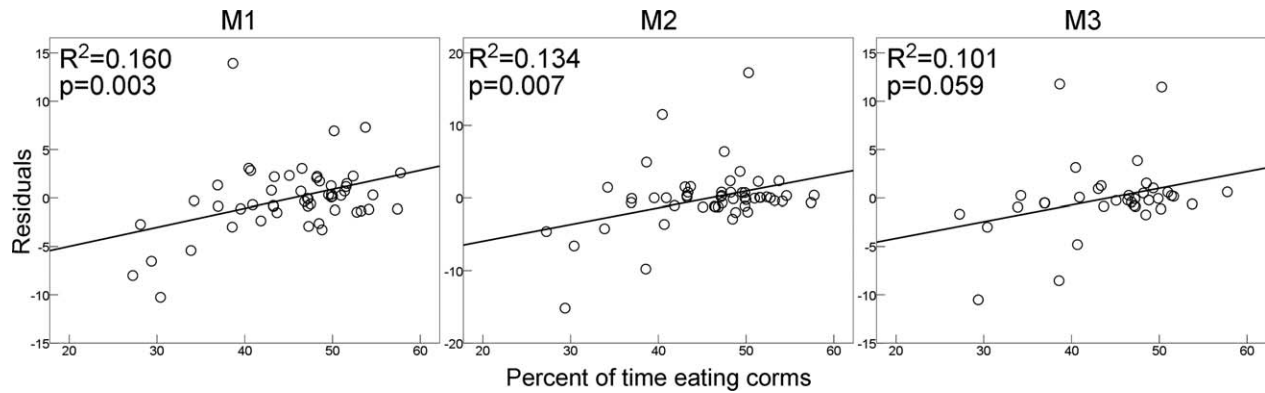
Fig. 3. Significant linear regressions for predicting residuals of tooth wear from percent time eating corms. Residuals were obtained in the quadratic regressions from percent of time consuming corms for first molar (M1), second molar (M2), and third molar (M3).

TABLE 2. *Stepwise multiple regression analyses for predicting molar wear (PDE) from behavioral and life history variables for all females* (n = 54)

Step no.	Variable	R^2	Coefficient	P value
M1				
1	Age	0.851	2.251	<0.001
2	Corms	0.869	0.231	0.015
	Constant		−25.019	<0.001
Regression equation: PDE(M1) = 2.251 × (age) + 0.231 × (corms) − 25.019				
M2				
1	Age	0.742	1.754	<0.001
2	Corms	0.777	0.284	0.009
	Constant		−26.196	<0.001
Regression equation: PDE(M2) = 1.754 × (age) + 0.284 × (corms) − 26.196				
M3				
1	Age	0.473	0.732	<0.001
	Constant		−6.679	0.001
Regression equation: PDE(M3) = 0.732 × (age) − 6.679				

TABLE 3. *Stepwise multiple regression analyses for predicting molar wear (PDE) from behavioral and life history variables for only females with erupted M3* (n = 37)

Step no.	Variable	R^2	Coefficient	P value
M1				
1	Age	0.854	2.626	<0.001
2	Corms	0.884	0.361	0.012
	Constant		−36.924	<0.001
Regression equation: PDE(M1) = 2.626 × (age) + 0.361 × (corms) − 36.924				
M2				
1	Age	0.734	2.090	<0.001
2	Corms	0.800	0.443	0.004
	Constant		−38.743	<0.001
Regression equation: PDE(M2) = 2.090 × (age) + 0.443 × (corms) − 38.743				
M3				
1	Age	0.477	0.913	<0.001
2	Corms	0.546	0.235	0.049
	Constant		−19.829	0.004
Regression equation: PDE(M3) = 0.477 × (age) + 0.546 × (corms) − 19.829				

We found a positive significant, though small, relationship between the residuals for M1 and the percent of feeding time during which each baboon consumed one particular food item, grass corms ($R^2 = 0.160$; $P = 0.003$). That is, females that spent more of their feeding time on grass corms had slightly greater tooth wear residuals (showed more wear for their age) than females that spent less feeding time on grass corms. The residuals for M2 revealed a significant relationship in the same direction ($R^2 = 0.134$; $P = 0.007$), and there was a similar trend in residuals for M3 ($R^2 = 0.101$; $P = 0.059$) (Fig. 3). Time spent consuming other types of foods, including fruits, grass blades, grass blade bases, grass seeds or acacia seeds, did not show any significant relationship with residuals for any molar. No relationship was found between molar wear residuals and the time females spent with dependent infants or female social dominance ranks.

Our stepwise multiple linear regressions, which included all of the predictor variables (age, time spent feeding on corms, time spent with dependent infants, and female dominance ranks) in one model per molar (where the M1 model combined the upper and lower M1, the M2 model combined the upper and lower M2, etc) produced similar results to our bivariate and residuals analyses. For M1, R^2 for the complete model was 0.869, with the majority of variance explained by age ($R^2 = 0.851$) and a smaller amount explained by time spent eating corms (Tables 2 and 3). For M2, age and corms together explained 77.7% of the var-

iance, with no other variables being included in the model. For M3, only age was included in the model and explained 47.3% of the variance (Tables 2 and 3).

Our second set of stepwise multiple linear regressions was restricted to those females that had totally erupted M3 and included the same predictor variables. This set of regressions revealed significant effects of corms eating on M3 wear. For M1, R^2 for the complete model was 0.884, also with a majority of variance explained by age ($R^2 = 0.854$). For M2, age and corms together explained 80.0% of the variance. Finally, for M3, age and corms were both included in the model, explaining 47.7% and 6.9% of the variance, respectively.

DISCUSSION
Tooth wear and age

Our results clearly show that tooth wear in Amboseli baboons reflects age. This result is in agreement with the handful of other studies on tooth wear in wild primates (sifakas: King et al., 2005; Wright et al., 2008; howler monkeys: Dennis et al., 2004; rhesus macaques: Kay and Cant, 1988). In Amboseli, there was a strong signal of age in wear on all the molars, and for both males and females. In all cases, the relationship was quadratic, indicating an accelerating process of dentine exposure with age. The models for female molars explained more of

the variance than the models for male molars. One likely explanation for this difference was our smaller sample size for males and the smaller age range represented by our male sample. In fact, when we reduced the age range of our female sample so that it was equivalent to the age range for our male sample, the R^2 values in the female models decreased and became close to those obtained in the male models.

Percent of dentine exposure for a given age was highest in M1 for both sexes, followed by M2 and M3, which reflects the order of eruption for these molars. M1 forms and erupts first, at ~25 months in wild male and female yellow baboons, followed by M2, which erupts at ~52 months in wild males and 50 in wild females, and then M3, which erupts at ~77 months in wild males and 92 in wild females (ages for lowers are given for all molars; Phillips-Conroy and Jolly, 1988; Kahumbu and Eley, 1991, for data on wild yellow baboons; see also Swindler and Meekins, 1991, for data on captive yellow baboons; Dirks et al., 2002, for data on wild hamadryas baboons). Moreover, variability in PDE, which is highest for M3 and lowest for M1, especially in females, can be also explained because of the variance in age at molar eruption in baboons, which is very low in M1, higher for M2, and highest for M3 (Phillips-Conroy and Jolly, 1988; Hlusko and Mahaney, 2009; Leigh et al., 2009). To enhance the utility of these data, we have provided data on age and PDE for each individual in the study and for each of the six molar teeth separately in the appendix.

Diet selection and tooth wear

The observation that individual feeding differences within a population contribute to differences in tooth wear beyond that of simple ageing indicates that macroscopic tooth wear is affected by individual behavioral differences. That is, individual Amboseli baboons, all living in the same habitat at the same time, made different diet choices throughout their life courses, for reasons that are not yet understood (for a detailed discussion of individual diet choice and differences, see Altmann, 1998). Importantly, these individual diet choices had consequences for the extent of tooth wear that these animals experienced for their age. Because tooth wear may impact foraging ability these individual diet choices may, in turn, have consequences for traits that are associated with health and survival, such as body condition and body mass index (Kojola et al., 1998; Logan and Sanson, 2002; Veiberg et al., 2007). This study sets the stage for a more detailed analysis of how individual behavior in this population may mitigate or amplify processes involved in senescence.

Grass corms are consumed extensively in this population, especially during the dry season when young leaves and fruits are scarce (Altmann, 1998; Alberts et al., 2005). To consume grass corms, baboons must dig them from the soil, as they are an underground part of *Graminiacea*. Although baboons have been observed removing the soil that covers the corms by rubbing them with their hands, this does not fully eliminate the dirt and grit. As a result, baboons regularly consume very abrasive particles and siliceous minerals, including quartz. This mineral is harder than tooth enamel on the Mohs scale of mineral hardness (Mohs, 1824; Tabor, 1954), and hence can easily scratch and abrade enamel (Ungar et al., 1995; Romero et al., 2009).

Phytoliths contained in grass itself are also potential abrasives that may contribute to tooth wear. These are found in many plants and have been related to dental abrasion in humans. Specifically, diets that contain a high proportion of phytoliths, such as the cereal-based diets that characterize some agricultural human populations, result in higher microwear densities than hunter-gatherer populations, which consume a more balanced, mixed diet (Lalueza Fox and Pérez-Pérez, 1993; Lalueza Fox et al., 1996). Enamel abrasion and tooth wear due to consumption of gritty food has also been documented in the Scottish red deer (Nussey et al., 2007), for which local population densities predicted tooth wear residuals (from an age-based model) in a manner that was consistent with an extremely limited availability of good-quality grazing (i.e., foods with low phytolith content) in some areas.

The observed association between corm consumption and tooth wear and the absence of an effect of other foods also containing phytoliths (for instance, grass blades, grass blade bases, and grass seeds) suggest that the effects of phytoliths in this population are at least partially swamped by the effects of extrinsic particles (specifically abrasive sediments that include siliceous minerals). Such particles are very abundant in foods obtained from underground storage organs such as grass corms, and much less abundant in above-ground foods. Nonetheless, phytoliths cannot be ruled out as a source of tooth wear in Amboseli. Phytoliths are known to affect enamel at a microscopic level, being responsible of the formation of both microwear features (Baker et al., 1959; Teaford, 1994; Ungar, 1994; Pérez-Pérez et al., 1999, 2003; Ungar et al., 2008) and macroscopic tooth wear (Nussey et al., 2007).

Life history and tooth wear

We predicted that other variables, specifically social dominance rank and the number of cumulative months that females had spent with dependent infants, could also accelerate dentine exposure because they might affect the quantity and/or quality of foods consumed. Dependent infants represent an intensive energy investment for female baboons (Altmann and Samuels, 1992; Altmann, 2001) and social dominance rank is known to affect priority of access to resources, with consequent effects on many life history and behavioral traits (reviewed in Silk, 1987; see also Altmann et al., 1988, and Altmann and Alberts, 2003 for specific data on Amboseli baboons). However, none of our analyses showed any relationship between these behavioral factors and tooth wear in any of the molar teeth studied. It may be that, though present, the effects of these variables are small relative to age and corm consumption, so that they would only be evident in a much larger sample size.

ACKNOWLEDGMENTS

APPENDIX

Age and PDE for each individual in the study for each of the six molars

Animal ID	Age	M_1	M^1	M_2	M^2	M_3	M^3
			Females				
OCT	4.51	1.091	0.430	0.239	(I)	(I)	(I)
LYM	5.53	2.162	1.347	2.176	0.398	(I)	(I)
NAR	5.60	1.223	1.752	0.507	0.515	(I)	(I)
RWA	5.79	0.949	1.783	0.401	0.000	(I)	(I)
EAG	5.95	4.135	3.799	0.999	0.439	(I)	(I)
LUR	6.29	8.243	2.188	2.244	0.850	(I)	(I)
LAO	6.71	4.445	2.703	2.375	1.029	(I)	(I)
RHO	6.82	3.622	3.636	0.316	2.357	(I)	(I)
WIF	6.96	3.851	1.288	2.057	0.349	(I)	(I)
EVA	7.00	3.233	1.318	0.864	0.497	(I)	(I)
LYE	7.00	5.293	1.780	3.108	0.589	(I)	(I)
WIP	7.16	(IV)	0.848	(IV)	(III)	(IV)	(I)
LAN	7.43	(III)	5.048	(III)	1.375	(III)	(I)
YOG	7.45	5.571	7.209	2.598	0.868	0.802	(I)
NOO	7.51	4.741	1.576	1.665	1.153	0.516	0.000
ABB	7.74	2.422	0.962	0.841	0.156	(I)	(I)
YAI	7.79	4.111	8.579	2.606	0.824	(I)	(I)
MBE	7.95	2.990	4.854	3.065	3.199	0.694	0.264
CAB	7.96	4.660	3.640	2.784	1.247	0.130	(III)
MON	7.99	6.017	6.886	3.339	1.634	1.495	(III)
WIR	8.12	3.581	2.913	1.059	1.243	(I)	(I)
PAI	8.22	5.620	3.648	1.818	1.426	(I)	(I)
OPH	8.45	6.135	6.226	2.553	1.595	0.732	0.190
WYN	8.72	4.465	6.893	4.573	4.425	0.809	0.347
OXY	8.73	9.454	4.673	4.585	4.593	0.382	1.283
LIW	8.80	6.513	5.173	4.233	3.397	1.303	(III)
VAI	9.14	6.438	4.936	3.014	2.021	1.012	(III)
HON	9.17	(III)	7.780	(III)	1.330	(III)	0.159
SCE	9.23	7.823	9.334	1.921	0.909	0.697	(III)
NIK	9.55	8.169	6.275	3.043	1.518	(III)	0.000
LIZ	9.74	5.542	5.175	3.525	3.268	(III)	(III)
VOG	10.38	6.306	8.336	3.160	2.004	0.829	0.511
DUN	10.43	3.636	3.855	2.531	1.008	0.511	(III)
LOL	10.64	5.735	7.189	4.457	3.316	0.506	0.094
NUT	10.80	3.832	8.228	2.293	9.109	0.000	(III)
HYM	10.85	7.617	11.074	3.720	4.386	2.613	2.216
KOL	11.75	10.010	7.246	5.767	2.160	1.087	0.504
SOR	12.38	14.181	7.250	5.802	3.857	1.840	0.714
NOB	12.57	6.015	3.854	3.466	0.537	1.142	0.131
LOC	12.77	17.025	18.971	9.532	8.146	1.054	(III)
WAD	12.80	1.534	3.967	1.170	2.671	0.000	0.059
VET	13.43	11.811	11.907	6.620	8.514	1.409	1.096
FAC	13.53	6.498	11.886	6.540	7.249	1.834	0.549
VOT	13.74	18.121	20.778	4.904	6.961	1.052	(III)
HOL	14.19	8.928	12.654	6.050	5.222	1.001	0.446
LAZ	15.80	16.702	15.983	16.036	19.105	7.078	7.679
WAS	16.18	7.493	7.684	8.228	2.323	0.811	0.808
DRO	17.79	(II)	(III)	18.615	(III)	6.166	(III)
WEN	19.79	27.914	33.233	18.891	12.522	1.976	2.576
LUN	21.90	34.763	40.635	(II)	36.056	13.730	11.487
KEL	22.40	38.012	28.781	19.907	12.270	1.550	(I)
LIM	22.66	53.384	49.096	35.624	27.383	28.975	15.418
CHE	24.01	41.048	41.136	46.071	49.241	26.875	20.486
KAT	26.35	37.377	53.257	29.026	15.781	6.796	3.498
			Males				
LOB	7.40	6.600	5.407	1.817	3.199	0.562	0.480
DAG	7.42	1.897	1.709	1.492	0.650	(I)	(I)
RAJ*	7.43	10.727	14.260	11.190	10.242	6.956	6.771
WRI	7.58	3.936	2.387	1.204	0.906	0.153	0.000
DAS	7.67	1.286	1.328	0.803	0.819	0.567	0.335
CAD	7.76	10.470	6.403	5.326	2.564	0.394	0.397
NOZ	7.76	2.264	1.414	2.182	0.349	0.000	0.378
LOG	8.21	5.808	5.125	2.251	2.909	0.261	0.742
THR	8.35	3.767	3.629	1.994	0.942	0.585	0.311

Appendix (Continued)

Animal ID	Age	M_1	M^1	M_2	M^2	M_3	M^3
LAX	8.37	6.337	4.637	3.114	1.779	0.677	0.270
ARA	8.56	5.579	2.741	0.287	0.257	0.000	(III)
KAG	8.70	4.565	4.683	3.516	5.397	1.104	0.825
NAW	8.79	4.732	6.715	3.196	2.033	0.000	0.169
VIB	8.89	2.696	2.859	1.838	1.870	0.000	0.303
DUB	9.18	2.387	1.068	1.067	0.511	0.211	0.341
VOY	9.32	6.245	1.434	5.101	2.558	0.795	0.599
LUI	9.55	2.853	(IV)	2.797	(IV)	(III)	(IV)
VAP	9.56	1.492	2.027	1.508	1.520	0.472	0.129
NJU	9.59	2.837	1.025	2.002	1.684	0.436	0.345
GAB	9.72	3.326	2.831	1.014	1.012	0.000	0.233
LOZ	9.78	5.949	3.899	3.221	2.391	0.788	0.719
ARS	9.84	2.329	4.540	2.313	2.402	0.486	0.000
ADR	9.88	15.010	11.030	8.906	7.794	1.491	0.664
QUA	9.93	7.551	9.524	3.345	3.669	0.716	0.638
WAB	9.93	5.106	7.245	3.404	5.667	0.898	1.019
OJU	10.03	4.254	4.118	1.061	1.815	0.000	0.535
LEB	10.10	5.602	6.876	4.491	3.832	1.138	0.942
WIV	10.62	5.223	(III)	2.784	(III)	1.124	(III)
VEI	10.81	(II)	5.565	11.143	7.514	1.645	1.305
AMO	12.04	11.868	12.114	7.582	12.141	0.524	3.340
HIB	13.25	6.402	7.892	9.406	16.516	1.878	2.383
GAN	13.53	6.035	6.165	4.306	2.134	1.288	6.037
EDU*	14.03	(II)	15.688	22.327	23.932	9.539	5.304
LOF	14.20	3.803	3.930	5.931	4.963	0.725	0.636
NYU	14.29	9.348	9.639	8.682	6.316	2.416	4.779
BAG*	15.00	58.574	(III)	64.741	21.633	7.936	9.186
LIB	15.73	6.725	6.079	8.349	9.368	7.369	7.806
TAL	15.75	(III)	11.450	(III)	12.023	1.562	2.427
KER	15.79	10.409	14.897	4.992	6.792	0.867	2.613
JAG	16.66	12.320	25.269	15.560	18.382	7.343	9.118
APO	16.94	(II)	5.310	3.974	6.452	3.080	3.139
PLA	17.99	17.823	11.226	16.293	14.605	8.724	12.446
MOR	19.51	28.096	(II)	15.415	11.174	5.119	3.331
ALE	20.45	38.846	26.159	16.942	18.153	7.018	7.964

Abbreviations: M_1, lower M1; M^1, upper M1; M_2, lower M2; M^2, upper M2; M_3, lower M3; and M^3, upper M3. (I) Molar was not yet erupted or only partially erupted, (II) molar was missing or broken, (III) molar cast was of insufficient quality; and (IV) non-existent cast. Three males marked with an asterisk (*) were not included in the analyses because they exhibited extremely high tooth wear, possibly caused by pathologies.

LITERATURE CITED

Ajmal M, Mody B, Kumar G. 2001. Age estimation using three established methods. A study on Indian population. Forensic Sci Int 122:150–154.

Alberts SC, Altmann J. 2001. Immigration and hybridization patterns of yellow and anubis baboons in Amboseli, Kenya. Am J Primatol 53:139–154.

Alberts SC, Buchan JC, Altmann J. 2006. Sexual selection in wild baboons: from mating opportunities to paternity success. Anim Behav 72:1177–1196.

Alberts SC, Hollister-Smith J, Mututua RS, Sayialel SN, Muruthi PM, Warutere JK, Altmann J. 2005. Seasonality and long-term change in a savannah environment. In: Brockman DK, Van Schaik CP, editors. Seasonality in primates: studies of living and extinct human and non-human primates. Cambridge: Cambridge University Press. p 157–196.

Altmann J. 1974. Observational study of behavior: sampling methods. Behaviour 49:227–267.

Altmann J. 2001. Baboon mother and infants, 2nd ed. Chicago: University of Chicago Press.

Altmann J, Alberts SC. 2003. Variability in reproductive success viewed from a life-history perspective in baboons. Am J Hum Biol 15:401–409.

Altmann J, Alberts SC. 2005. Growth rates in a wild primate population: ecological influences and maternal effects. Behav Ecol Sociobiol 57:490–501.

Altmann J, Alberts SC, Altmann SA, Roy SB. 2002. Dramatic change in local climate patterns in the Amboseli basin. Afr J Ecol 40:248–251.

Altmann J, Alberts SC, Haines SA, Dubach J, Muruthi P, Coote T, Geffen E, Cheesman DJ, Mututua RS, Saiyalel SN, Wayne RK, Lacy RC, Bruford MW. 1996. Behavior predicts genetic structure in a wild primate group. Proc Nat Acad Sci USA 93:5797–5801.

Altmann J, Gesquiere L, Galbany J, Onyango PO, Alberts SC. The life history context of reproductive aging in a wild primate model. Ann NY Acad Sci (in press).

Altmann J, Hausfater G, Altmann SA. 1988. Determinants of reproductive success in savannah baboons *Papio cynocephalus*. In: Clutton-Brock TH, editor. Reproductive success. Chicago: University of Chicago Press. p 403–418.

Altmann J, Samuels A. 1992. Costs of maternal care: infant-carrying in baboons. Behav Ecol Sociobiol 29:391–398.

Altmann SA. 1998. Foraging for survival: yearling baboons in Africa. Chicago: University of Chicago Press.

Baker G, Jones HP, Wardrop ID. 1959. Causes of wear in sheep's teeth. Nature 184:1583–1584.

Ball J. 2002. A critique of age estimation using attrition as the sole indicator. J Forensic Odontostomatol 3:132–135.

Brothwell DR. 1981. Digging up bones. London: Natural History Museum Publications.

Buss IO. 1990. Elephant life. Fifteen years of high population density. Ames, IA: Iowa State University Press.

Choong MF. 1996. What makes a leaf tough and how this affects the pattern of *Castanopsis fissa* leaf consumption by caterpillars. Funct Ecol 10:668–674.

Cuozzo FP, Sauther ML. 2006. Severe wear and tooth loss in wild ring-tailed lemurs (*Lemur catta*): a function of feeding ecology, dental structure, and individual life history. J Hum Evol 51:490–505.

Dennis JC, Ungar PS, Teaford MF, Glander KE. 2004. Dental topography and molar wear in *Alouatta palliata* from Costa Rica. Am J Phys Anthropol 125:152–161.

Dirks W, Reid DJ, Jolly CJ, Phillips-Conroy JE, Brett FL. 2002. Out of the mouths of baboons: stress, life history, and dental development in the Awash National Park hybrid zone, Ethiopia. Am J Phys Anthropol 118:239–252.

Estebaranz F, Martínez LM, Hiraldo O, Espurz V, Bonnin A, Farrés M, Pérez-Pérez A. 2004. Tooth crown size and dentine exposure in Australopithecus and early Homo: testing hypotheses of dietary related selective pressures. Anthropologie 42:59–63.

Galbany J, Estebaranz F, Martínez LM, Romero A, De Juan, Turbón D, Pérez-Pérez A. 2006. Comparative analysis of dental enamel polyvinylsiloxane impression and polyurethane casting methods for SEM research. Microsc Res Tech 69:246–252.

Galbany J, Martínez LM, Pérez-Pérez A. 2004. Tooth replication techniques. SEM imaging and microwear analysis in primates: methodological obstacles. Anthropologie 42:5–12.

Gipson PS, Ballard WB, Nowak RM, Mech LD. 2000. Accuracy and precision of estimating age of gray wolves by tooth wear. J Wildl Manage 64:752–758.

Glander KE, Fedigan LM, Fedigan L, Chapman C. 1991. Field methods for capture and measurement of three monkey species in Costa Rica. Folia Primatol 57:70–82.

Grau GA, Sanderson GC, Rogers JP. 1970. Age determination of raccoons. J Wildl Manage 34:364–372.

Hausfater G, Altmann J, Altmann S. 1982. Long-term consistency of dominance relations among female baboons (*Papio cynocephalus*). Science 217:752–755.

Helm S, Prydsö U. 1979. Assessment of age-at-death from mandibular molar attrition in medieval Danes. Scand J Dent Res 87:79–90.

Hewison AJM, Vincent JP, Angibault JM, Delorme D, Van Laere G, Gaillard JM. 1999. Tests of estimation of age from tooth wear on roe deer of known age: variation within and among populations. Can J Zool 77:58–67.

Hillson S. 2005. Teeth. Cambridge: Cambridge University Press.

Hlusko LJ, Mahaney MC. 2009. The baboon model for dental development. In: VandeBerg JL, Williams-Blangero S, Tardif SD, editors. The baboon in biomedical research. New York: Springer. p 207–223.

Kahumbu P, Eley RM. 1991. Teeth emergence in wild olive baboons in Kenya and formulation of a dental schedule for aging wild baboon populations. Am J Primatol 23:1–9.

Kambe T, Yonemitsu K, Kibayashi K, Tsunenari S. 1991. Application of a computer assisted image analyzer to the assessment of area and number of sites of dental attrition and its use for age estimation. Forensic Sci Int 50:97–109.

Kay RF, Cant JGH. 1988. Age assessment using cementum annulus counts and tooth wear in a free-ranging population of *Macaca mulatta*. Am J Primatol 15:1–15.

Kim YK, Kho HS, Lee KH. 2000. Age estimation by occlusal tooth wear. J Forensic Sci 45:303–309.

King SJ, Arrigo-Nelson SJ, Pochron ST, Semprebon GM, Godfrey LR, Wright PC, Jernvall J. 2005. Dental senescence in a long-lived primate links infant survival to rainfall. Proc Nat Acad Sci USA 102:16579–16583.

Kojola I, Helle T, Huhta E, Niva A. 1998. Foraging conditions, tooth wear and herbivore body reserves: a study of female reindeer. Oecologia 117:26–30.

Lalueza Fox C, Juan J, Albert RM. 1996. Phytolith analysis on dental calculus, enamel surface, and burial soil: information about diet and paleoenvironment. Am J Phys Anthropol 101:101–113.

Lalueza Fox C, Pérez-Pérez A. 1993. The diet of the Neanderthal child Gibraltar 2 (Devil's Tower) through the study of the vestibular striation pattern. J Hum Evol 24:29–41.

Lanyon JM, Sanson GD. 1986. Koala (*Phascolarctos cinereus*) dentition and nutrition. II. Implications of tooth wear in nutrition. J Zool 209:169–181.

Leigh SR, Berstein RM, Konigsberg LW. 2009. Dental eruption, age estimation, and life histories in papionin primates. Am J Phys Anthropol 138:174 (abstract).

Li C, Ji G. 1995. Age estimation from the permanent molar in northeast China by the method of average stage of attrition. Forensic Sci Int 75:189–196.

Logan M, Sanson GD. 2002. The effect of tooth wear on the feeding behaviour of free-ranging koalas (*Phascolarctos cinereus*. Goldfuss). J Zool Lon 256:63–69.

Mandojana JM, Martin-de las Heras S, Valenzuela A, Valenzuela M, Luna JD. 2001. Differences in morphological age-related dental changes depending on postmortem interval. J Forensic Sci 46:889–892.

Mohs F. 1824. Grund·riβ der mineralogie [Vol2]. Zweite Theil. Physiographie. Mit 10 Kupfertafeln. Dresden, in der Arnoldischen Buchhandlung.

Molnar S, McKee JK, Molnar I. 1983. Measurements of tooth wear among Australian aborigines. I. Serial loss of the enamel crown. Am J Phys Anthropol 61:51–65.

Morbeck ME, Galloway A, Sumner DR. 2002. Getting old at Gombe: skeletal aging in wild-ranging chimpanzees. In: Erwin JM, Hof PR, editors. Aging in nonhuman primates. Basel: Karger. p 48–62.

Munro ND, Bar-Oz G, Stutz AJ. 2009. Aging mountain gazelle (*Gazella gazella*): refining methods of tooth eruption and wear and bone fusion. J Archeol Sci 36:752–763.

Nussey DH, Metherell B, Moyes K, Donald A, Guinness FE, Clutton-Brock TH. 2007. The relationship between tooth wear, habitat quality and late-life reproduction in a wild deer population. J Anim Ecol 76:402–412.

Oliveira RN, Silva SFSM, Kawano A, Antunes JLF. 2006. Estimating age by tooth wear of prehistoric human remains of Brazilian archaeological sites. Int J Osteoachaeol 16:407–414.

Pérez-Pérez A, Bermúdez de Castro JM, Arsuaga JL. 1999. Non-occlusal dental microwear analysis of 300,000 year-old Homo heilderbergensis teeth from Sima de los Huesos (Sierra de Atapuerca, Spain): implications of intrapopulation variability for dietary analysis of hominid fossil remains. Am J Phys Anthropol 108:433–457.

Pérez-Pérez A, Espurz V, Bermúdez de Castro JM, de Lumley MA, Turbón D. 2003. Non-occlusal dental microwear variability in a sample of middle and upper Pleistocene human populations from Europe and the near east. J Hum Evol 44:497–513.

Phillips-Conroy JE, Bergman T, Jolly CJ. 2000. Quantitative assessment of occlusal wear and age estimation in Ethiopian and Tanzanian baboons. In: Whitehead PF, Jolly CJ, editors. Old world monkeys. Cambridge: Cambridge University Press. p 321–340.

Phillips-Conroy JE, Jolly CJ. 1988. Dental eruption schedules of wild and captive baboons. Am J Primatol 15:17–29.

Post DG, Hausfater G, McCuskey SA. 1980. Feeding behavior of yellow baboons (*Papio cynocephalus*): relationship to age, gender and dominance rank. Folia Primatol 34:170–195.

Reppien K, Sejrsen B, Lynnerup N. 2006. Evaluation of postmortem estimated dental age versus real age: a retrospective 21-year survey. Forensic Sci Int 159 (S1):84–88.

Romero A, Galbany J, Martínez-Ruiz N, De Juan J. 2009. *In vivo* turnover rates in human buccal dental-microwear. Am J Phys Anthropol 138:223–224 (abstract).

Sapolsky RM, Alberts SC, Altmann J. 1997. Hypercortisolism associated with social subordinance or social isolation among wild baboons. Arch Gen Psychiatry 54:1137–1143.

Silk JB. 1987. Social behavior in evolutionary perspective. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. Primate societies. Chicago: University of Chicago Press. p 318–329.

Silk JB. 2009. Nepotistic cooperation in non-human primate groups. Phil Trans R Soc B 364:3243–3254.

Skogland T. 1988. Tooth wear by food limitation and its history consequences in wild reindeer. Oikos 51:238–242.

Song HW, Jia JT. 1989. The estimation of tooth age from attrition of the occlusal surface. Med Sci Law 29:69–73.

Swindler DR, Meekins D. 1991. Dental development of the permanent mandibular teeth in the baboon, *Papio cynocephalus*. Am J Hum Biol 3:571–580.

Tabor D. 1954. Mohs's hardness scale—a physical interpretation. Proc Phys Soc B 67:249–257.

Teaford MF. 1994. Dental microwear and dental function. Evol Anthropol 3:17–30.

Teaford MF, Lucas PW, Ungar PS, Glander KE. 2006. Mechanical defenses in leaves eaten by Costa Rican howling monkeys (*Alouatta palliata*). Am J Phys Anthropol 129:99–104.

Tung J, Charpentier MJE, Garfield D, Altmann J, Alberts SC. 2008. Genetic evidence reveals temporal change in hybridization patterns in a wild baboon population. Mol Ecol 17:1998–2011.

Tung J, Primus A, Bouley AJ, Severson TF, Alberts SC, Wray GA. 2009. Evolution of a malaria resistance gene in wild primates. Nature 460:388–391.

Ungar PS. 1994. Patterns of ingestive behavior and anterior tooth use differences in sympatric anthropoid primates. Am J Phys Anthropol 95:197–219.

Ungar PS, Grine FE, Teaford MF. 2008. Dental microwear and diet of the Plio-Pleistocene Hominin *Paranthropus boisei*. PLoS ONE 3:e2044.

Ungar PS, Teaford MF, Glander KE, Pastor RF. 1995. Dust accumulation in the canopy: a potential cause of dental microwear in primates. Am J Phys Anthropol 97:93–99.

Valenzuela A, Martin-de las Heras S, Mandojana JM, De Dios Luna J, Valenzuela M, Villanueva E. 2002. Multiple regression models for age estimation by assessment of morphologic dental changes according to teeth source. Am J Forensic Med Pathol 23:386–389.

Veiberg V, Mysterud A, Gaillard JM, Delorme D, Van Laere G, Klein F. 2007. Bigger teeth for longer life? Longevity and molar height in two roe deer populations. Biol Lett 3:268–270.

Williams SH, Kay RF. 2001. Comparative test of adaptive explanations for hypsodonty in ungulates and rodents. J Mammal Evol 8:207–229.

Wollstonecroft MM, Ellis, PR, Hillman, GC, Fuller DQ. 2008. Advances in plant food processing in the Near Eastern Epipalaeolithic and implications for improved edibility and nutrient bioaccessibility: an experimental assessment of *Bolboschoenus maritimus* (L.) Palla (sea club-rush). Veg Hist Archaeobot 17 (S1):S19–S27.

Wright P, King SJ, Baden A, Jernvall J. 2008. Aging in wild female lemurs: sustained fertility with increased infant mortality. In: Atsalis S, Margulis SW, Hof PR, editors. Primate reproductive aging. Basel: Karger.