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Periodontal Health in Free-Ranging Baboons of Ethiopia and Kenya

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ABSTRACT Frontal and lateral intraoral photographs of 19 baboons from the Awash National Park, Ethiopia and 37 baboons from Amboseli National Park, Kenya, were used to assess periodontal health. The Awash baboons, and two groups (Alto's and Hook's) at Amboseli, fed entirely from natural sources, but baboons from the third Amboseli group (Lodge) fed largely on food refuse from one of the park's lodges. Juveniles and adults were evaluated separately. Intraoral photographs were seriated based on visual appraisals of periodontal health.

In both age groups, the best periodontal health was seen in Awash animals; Alto's and Hook's animals were intermediate, and the poorest health was seen in the Lodge sample. The periodontal health decreased with age in adult baboons, as reported in humans. Geochemistry, genetics, age, and diet (particularly variations in bacterial flora) were considered as factors contributing to the intergroup differences. Although it is not possible at present to exclude any of these as a contributing cause, we consider that diet in the broad sense (including food, water, and contamination by oral bacteria of human origin) probably plays a major role. © 1993 Wiley-Liss, Inc.

Suboptimal periodontal health is common in human populations (Carranza, 1979; Page and Schroeder, 1982; Waerhaug, 1966) and in a variety of other mammals, including primates. Of the factors impinging upon periodontal health, diet has been implicated as especially influential, yet, in humans, its effect is difficult to disentangle from variation in other culturally determined factors. In free-ranging mammals, the health and integrity of teeth and their supporting structures directly affect longevity, and hence survivorship and demographic structure. However, opportunities to investigate the environmental correlates of periodontal health in free-ranging populations rarely arise, and no comparative study of periodontal health in wild primate populations has been reported.

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In this paper we describe a case in which data collected (for other purposes) from two wild primate populations permit a relatively controlled comparison between the effects of a natural diet and one that is high in refined foods. We report data on the periodontal health of baboons *(Papio hamadryas* sensu lato) in the Awash National Park, Ethiopia and in Amboseli National Park, Kenya. Both populations have been the subject of long-term study. At Awash, the study population consists of at least 12 social groups. The sample reported here was drawn from two of these, consisting largely of anubis *(P.h. anubis)* and hybrid baboons. The hybrid members of these groups are the product of breeding between resident anubis females and immigrant male hamadryas *(P.h. hamadryas),* with subsequent interbreeding and backcrossing among the offspring (Phillips-Conroy and Jolly, 1986; Phillips-Conroy et al., 1991, 1992). Their habitat includes a belt of trees of *Acacia clavigera* and *Acacia tortilis, Celtis, Zizyphus,* and *Ficus* spp. bordering the Awash River. This strip grades into thornscrub dominated by *Acacia senegal, Acacia nubica,* and *Grewia* spp. Herb cover varies strongly by season, and is subject to seasonally intense grazing and browsing by domestic livestock. Baboons drink exclusively from the Awash River except during the rainy season when abundant puddles can be found.

The Amboseli population consists of yellow baboons *(P.h. cynocephalus)* although some interbreeding with anubis has been reported from this site (Samuels and Altmann, 1986). The baboons inhabit savanna and *A. tortilis* and *Acacia xanthophloea* woodland with associated shrubs. Seasonal grazing by domestic stock occurs in some parts of their home ranges. This population has been the subject of continuous long-term study, and members of three groups in adjacent ranges are fully habituated and individually recognizable by human observers. Two groups (Alto's and Hook's, henceforth lumped together as "Alto/Hook") range in relatively undisturbed portions of the park. Alto/Hook baboons fed entirely on wild foods that consist of plant material, invertebrates, and vertebrate flesh (Muruthi, 1989; Post, 1982). By contrast, the range of the third Amboseli group—Lodge—includes one of the park's tourist hotels as well as areas supplying more natural forage. The daily delivery of food refuse to the Lodge's garbage pit provided the main focus for the daily activity patterns and feeding behavior of the Lodge group (Altmann and Muruthi, 1988; Muruthi et al., 1991). On a typical day, they would move from their sleeping grove to a water trough near the dump, where they remained until mid-afternoon, when new refuse was added. After about 2 hours feeding they would return to their sleeping site, a distance of 1 km. Although they ate some natural foods, most of their intake consisted of discarded human foodstuffs (Muruthi, 1989). The most commonly eaten items in the Lodge group's diet were fruits, vegetables, milk products, ugali (maize porridge) bread, cooked meat, baked goods, and jam (Fig. 1). Only two frequently eaten foods—gum of *A. xanthophloea* and *Withania somnifera*—are naturally occurring. Although their caloric intake was not significantly greater than that of Alto/Hook baboons (Muruthi et al., 1991), Lodge group baboons spent much time resting and little time feeding and presumably expended little energy. The high frequency of obesity found among them has been attributed to this regime (Altmann et al., 1992).

The three samples permit tests for differences between populations (Alto/Hook and Awash) that are geographically separated and taxonomically distinct, but have very similar, natural diets, and tests between populations (Alto/Hook and Lodge) that belong to the same taxon and deme, live as neighbors, yet have very different dietary regimes. At the same time, the study permits an evaluation of baboons as models for human periodontal disease, an issue that is addressed at greater length elsewhere (Hildebolt et al., 1993).

Although assessment of periodontal health was not part of the original research plan at Amboseli, intraoral photographs taken to document dental eruption permitted such assessment, and as a result, three-way comparisons among Alto/Hook, Lodge, and Awash baboons. In the case of the Awash baboons, assessments based upon photographs could be compared with more

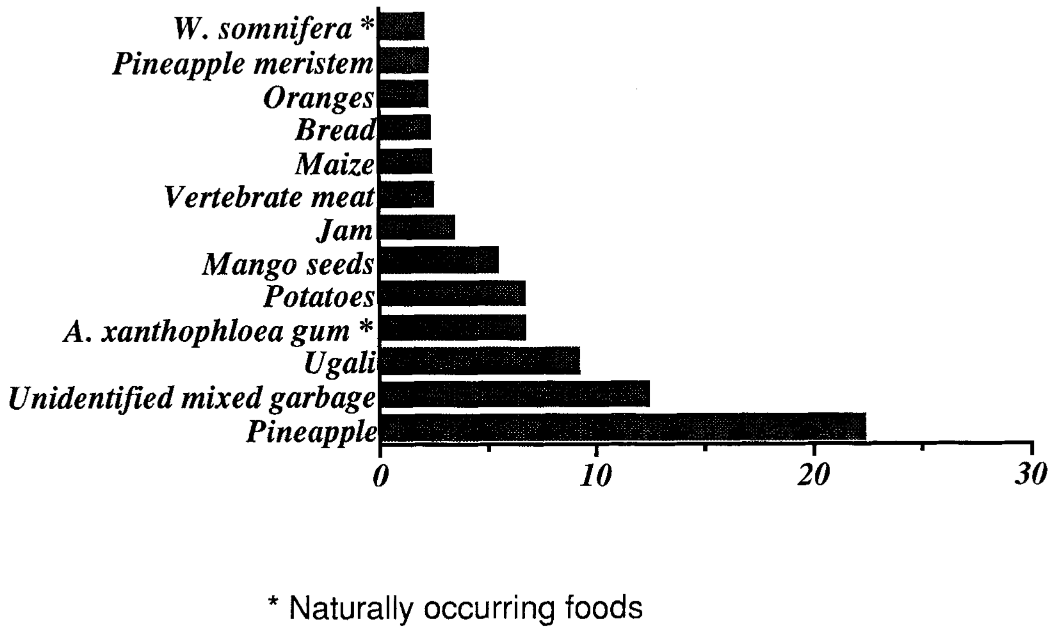

Fig. 1. Foods eaten by Lodge group females by mean percent contribution to daily energy intake.

detailed periodontal health data including scores for plaque, calculus, gingivitis, periodontal probing, and alveolar bone loss (as determined from dental radiographs).

METHODS

At Awash, animals were caught in cage traps, then tranquilized using ketamine (Vetalar, Parke Davis: 7.5 mg/kg body weight); at Amboseli they were darted and tranquilized using Telazol (tiletamine hydrochloride and rolazepam, 250 mg). At Awash, lip retractors were used to expose the teeth and gums for photography (Fig. 2). Fingers were used to retract the lips at Amboseli. Frontal and lateral intraoral photographs were taken of the anesthetized animal.

Animals were separated into two categories: juvenile or adult, the criterion being gingival eruption of one or both of the third upper molars. The adult sample consisted of 31 males; 12 were from Awash, 13 from Alto/Hook and 6 from Lodge group. Of the 25 juveniles, 7 (5 male and 2 female) were from Awash, 10 (7 male and 3 female) were from Alto/Hook and 8 (6 male and 2 female) from Lodge group.

Fig. 2. Young adult male Awash baboon, illustrating lip retractors and healthy periodontal tissues.

Assessment of periodontal health was carried out in two stages. In the first, photographs from the 1989 Amboseli sample and the 1990 Awash sample were used. The color prints made from the intraoral exposures were ranked for periodontal health, with juvenile and adult series treated separately. All rankings were made by a single, experienced observer. The prints for all groups

(Awash, Alto/Hook, and Lodge) were pooled, and arranged in order from best to worst periodontal health (animals with the lower numbers, e.g. 1, 2, 3 were those evaluated as in the best periodontal health, and thus ranked high in this spectrum of periodontal health). The analysis was done without reference to the origin of the animals. ID numbers on the photographs indicated whether the animal was from Awash or Amboseli, but not whether from Alto/Hook or Lodge groups. Data on age were not available to the observer who performed the rankings.

Gingival recession was the most heavily weighted diagnostic used in the ranking. Views of the anterior teeth, which were generally better than those of the posterior teeth, were used for the initial seriation. Posterior teeth were used to seriate cases that would otherwise have had equal ranks. In instances where cases still could not be differentiated on the basis of recession, evidence of gingivitis was also taken into account. Bleeding gingivae were considered to be a strong indication of inflammation. Exposed root surfaces on primary teeth that were being evulsed by juveniles were not considered to be indications of poor periodontal health.

In the second phase of assessment, animals darted in the 1990 field season from Alto, Hook, and Lodge groups were added to the original sample, and the procedure repeated without reference to previous rankings. The results from the second seriation agreed very well with the initial ranking: in no instance did an animal's position in the series change by more than two positions. Ages of most of the Amboseli animals were known, but those of the Awash animals were estimated on the basis of dental eruption and dental wear, using standards previously developed for this and other populations (Phillips-Conroy, 1978; Phillips-Conroy and Jolly, 1988).

At Awash, we were able to couple the method assessing periodontal health from ranking of intraoral photographs with more traditional methods used to evaluate periodontal health. Dental radiographs taken in the field allowed quantification of alveolar bone loss. These methods are fully described elsewhere (Hildebolt et al., 1993). The correlation between the method we describe below—periodontal ranks based on seriation of dental photographs—and alveolar bone loss measurements derived from dental radiographs was 0.72 ($P = 0.008$; Fig. 3). Thus, we conclude that, although comparisons based on commonly used clinical measurements (particularly radiographic measurements) would be ideal, we are justified in making comparative use of the photographic data serendipitously available to us.

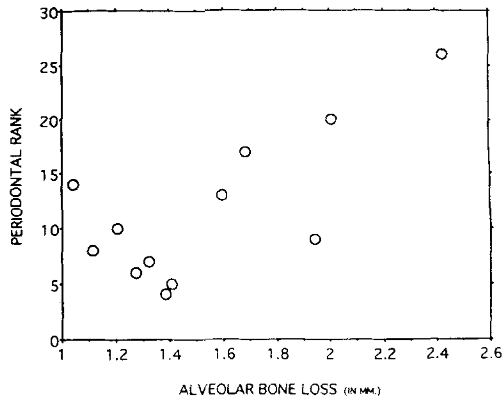

Fig. 3. Relationship between periodontal health ranks and quantitative measurements of alveolar bone loss (after Hildebolt et al., 1993). Several of the points represent more than one individual.

Because of the small sample sizes, and potential violation of assumptions of parametric statistics, we based our statistical analyses on tests that made the fewest assumptions about the nature of the data. We selected a bootstrap test based on randomization rather than more traditional nonparametric methods. Randomization preserves statistical power without sacrificing sensitivity, and improves upon traditional methods in relieving the user from assumptions about independence and randomness of the sample (Cheverud et al., 1989; Edgington, 1987).

Three sets of pair-wise comparisons were made: Awash-Alto/Hook; Awash-Lodge; and Alto/Hook-Lodge. Randomization via bootstrapping produced distribution-free tests in the following way. In comparing mean ranks for two groups of unequal sample sizes, repeated samples of the same size as the smaller sample were drawn, with replace-

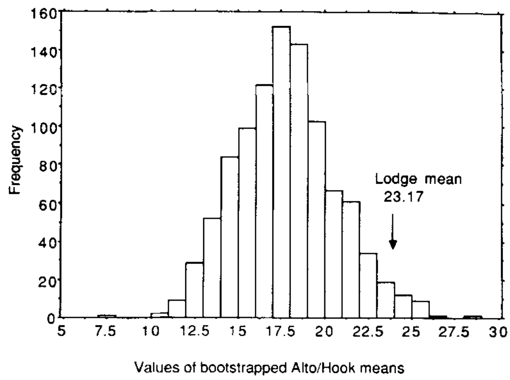

Fig. 4. Frequency distribution of values of bootstrapped means of periodontal ranks generated from Alto/Hook of sample size n = 6. Thirty-five of the 1,000 randomly generated means had values in excess of the Lodge group mean of 23.17. Thus Alto/Hook and Lodge group are significantly different from one another at the $P < .035$ level (one-tailed test).

TABLE 1. Mean ranks for periodontal scores of Awash and Amboseli baboons [1]

Sample	Juveniles	All adults
Awash	7.57 (7)	10.58 (12)
Alto/Hook	11.5 (10)	17.69 (13)
Lodge	19.63 (8)	23.17 (6)

[1] Sample size is given in parentheses

TABLE 2. Significance levels of mean differences based on 1,000 iterations of periodontal rank and age (all comparisons are one-tailed tests, except where indicated)

	Juveniles	Adults	
Sample	Periodontal rank	Periodontal rank	Age
Awash:Alto/Hook	.036 (two-tailed)	<.002* (two-tailed)	.815
Awash:Lodge	<.001*	<.001*	.066
Alto/Hook:Lodge	<.001*	.035*	.005*

* Significant at the .05 level or better

ment, from the larger sample. This procedure was repeated 1,000 times (although 500 iterations are generally considered sufficient), and sample means for the 1,000 iterations were plotted. The original small sample was determined to be significantly different from the large sample if its mean rank was higher than 95% of the randomized mean ranks (for a one-tailed test with $P = 0.05$).

With the null hypothesis that animals feeding on natural diets should not differ in any systematic way in mean periodontal ranks, the Awash-Alto/Hook comparison was made using a two-sided test. However, testing the hypothesis that garbage-eating animals would have reduced periodontal health relative to those feeding on natural diets required that the Awash-Lodge and Alto/Hook-Lodge comparisons be evaluated as one-sided tests. Figure 4 illustrates one such test comparing the mean of periodontal ranks of Alto/Hook with Lodge groups. The appropriateness of such methods in the biological sciences, and their improvement upon standard nonparametric techniques is underscored by Manly, who argues that "classical tests can be thought of as approximations for randomization tests" (Manly, 1991, p. 17).

RESULTS

Juveniles

Awash baboons had the highest ranks (i.e., best periodontal health), Lodge baboons had the lowest, and Alto/Hook animals were intermediate. Mean ranks for juveniles from Awash, Alto/Hook, and Lodge were 7.57, 11.5, and 19.63, respectively (Table 1). Lodge animals were significantly different from both other groups when the data were randomized as described above ($P < 0.001$), while the Awash-Alto/Hook comparison approached significance ($P = 0.072$, two-tailed test, Table 2). Figure 5 presents a boxplot of periodontal ranks for each of the three juvenile samples. Figure 6 illustrates the range of periodontal health seen in juveniles: Figure 6a shows the juvenile in the best periodontal health, a 30-month-old male from Awash, while Figure 6b shows the juvenile with the lowest periodontal rank, a 34-month-old male from Lodge group. Figure 7 is a plot of the individual ranks against age, indicating, in baboon juveniles, as in humans, no clear relationship between periodontal rank and age. Figure 7 appears to indicate a statistically significant inverse relationship between age and periodontal rank ($P = 0.02$, $R^2 = 0.65$) in the Lodge juveniles. Deleting the oldest Lodge juvenile changes this relationship to a nonsignificant one ($P = 0.16$). Thus we consider

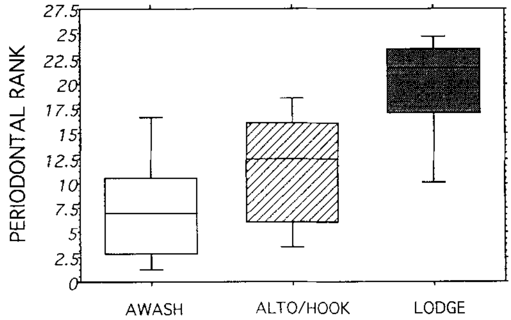

Fig. 5. Box and whiskers plots of periodontal health ranks in juvenile Awash, Alto/Hook, and Lodge baboons: the box encloses the 25th through 75th percentiles; the whiskers indicate the 10 and 90% percentiles.

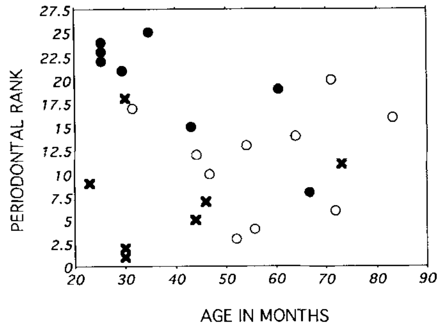

Fig. 7. Relationship between juvenile periodontal health and age.

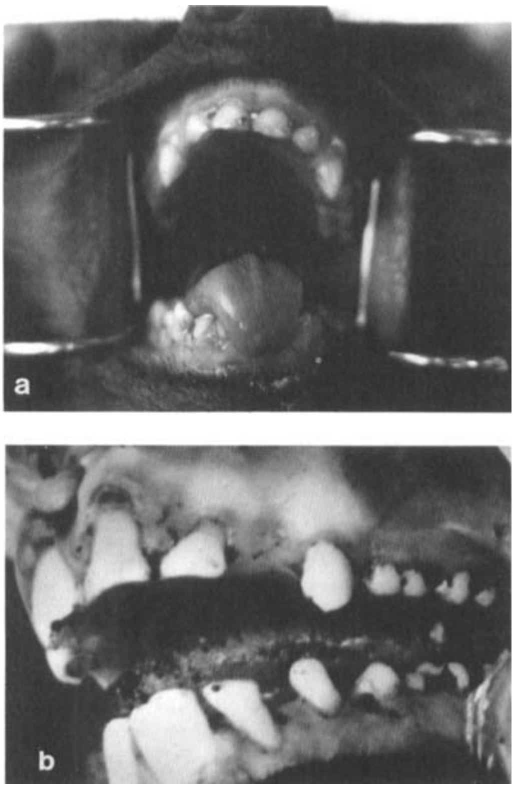

Fig. 6. a: Awash juvenile with the highest periodontal rank. b: Lodge juvenile with the lowest periodontal rank

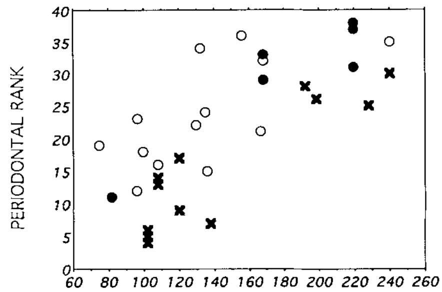

Fig. 8. Relationship between periodontal health ranks and age in adult baboons.

the apparent relationship between age and periodontal rank in Lodge juveniles in Figure 7 to be spurious, in contrast to the overall pattern shown by Lodge juveniles of the lowest periodontal ranks among individuals which were also the youngest juveniles in the study.

Adults

Both Awash and Alto/Hook were represented by young and old adults but Lodge group had four old animals and only one young adult. In humans, periodontal health decreases with age (Carranza, 1979; Waerhaug, 1966). In baboons, a plot of periodontal health against age for adult males (Fig. 8) showed a trend toward poorer periodontal health in older animals, corresponding to age-health interrelationships in humans. Given this trend, we examined the age distributions of each of the three groups to see whether or not they might significantly dif-

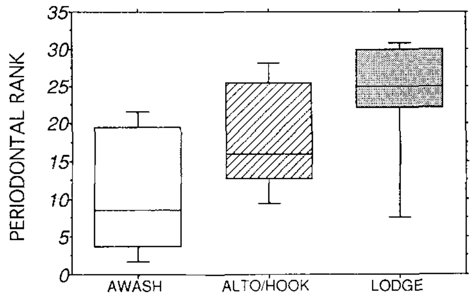

Fig. 9. Box and whiskers plots of periodontal health ranks in adult Awash, Alto/Hook, and Lodge baboons: The box encloses the 25th through 75th percentiles; the whiskers indicate the 10 and 90% percentiles.

fer from one another and hence account for differences in ranks between sites.

The mean age of Awash males was 146.5 months; the mean age of Alto/Hook males was 133.7 months, and the mean age of Lodge males was 179.2 months. Alto/Hook males on average were significantly younger than Lodge males ($P = 0.005$) but the Awash-Alto/Hook and Awash-Lodge comparisons showed no significant difference ($P = 0.815$ and $P = 0.066$, respectively, Table 2). As among the juveniles, Lodge group adult males have the lowest mean periodontal rank (23.17) and Awash the highest (10.58) with Alto/Hook animals intermediate (17.7) (Table 1). All three groups were significantly different from each other. (Awash vs. Lodge and Awash vs. Alto/Hook, $P < 0.001$; Alto/Hook vs. Lodge, $P = 0.035$, Table 2). Figure 9 shows boxplots of periodontal ranks for all adults. Animals with varying stages of periodontal disease are presented in Figures 2, 10, and 11. Figure 2 is of a young adult male (90-030; 102 months) from Awash with the highest rank and virtually no indication of alveolar bone resorption or of gingival inflammation. Figure 10 is of the animal with the lowest periodontal rank—a Lodge male (219 months); the extreme degree of gingival recession has exposed the incisor roots nearly to their apices. Figure 11 shows a comparably aged Awash male in the sample (228 months). This male had the lowest rank of the Awash sample, and although he is missing a number of teeth (presumably due to severe wear with resulting pulpal pathology and tooth

Fig. 10. Lodge adult with lowest periodontal rank of all adults. Note exposed root surfaces with concomitant resorption of alveolar bone below the cementoenamel junction.

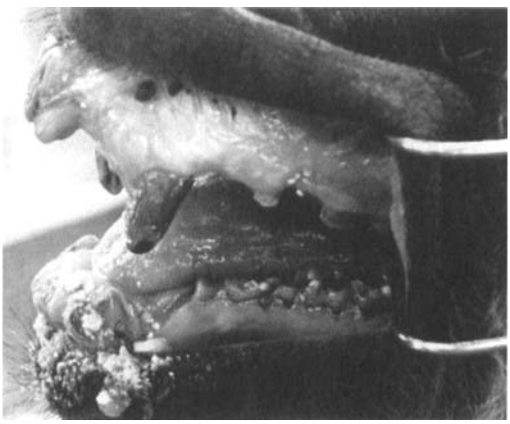

Fig. 11. Awash adult with highest periodontal rank. This animal shows tooth loss due to severe tooth wear and pulpal pathology leading to evulsion of the teeth. However the gingival tissue appears normal with no apparent alveolar resorption.

exfoliation) his periodontal tissues appear to be in good health.

DISCUSSION

The two most commonly used clinical measures of periodontal health are periodontal probing measurements and measurements derived from dental radiographs (Greenstein and Caton, 1990; Lang and Bragger, 1991). These data (and measures of plaque, calculus, and gingivitis) were available only for the Awash baboons and are fully presented elsewhere (Hildebolt et al., 1993). We acknowledge that the use of intraoral photographs for rating periodontal health is inferior to the commonly used clinical measures, particularly measurements derived from dental radiographs and periodontal probing measurements (Greenstein and Caton, 1990; Lang and Bragger, 1991); however, these clinical measurements were not available for the Amboseli baboons, which were the basis of this study. Furthermore, although full-mouth scoring would be preferable to partial-mouth scoring, the extensive literature on partial mouth scoring (the use of a few measurements to represent an individual) shows a high degree of interrelationship between abbreviated indices (as used in this study) and indices based on measurements for all teeth (Shrout et al., 1990).

Our Awash data did allow us to explore whether the periodontal health ranks were highly correlated with the more standard measures of clinical health, such as radiographic alveolar bone loss, periodontal pocket depth, and gingival attachment level. The radiographic analysis indicated an average bone loss for adult Awash baboons of only 1.5 mm and for juveniles of only 0.97 mm (Hildebolt et al., 1993). This slight amount of bone loss was interpreted as indicating that the Awash baboons had good periodontal health. This finding is supported by other clinical measures for the Awash baboons in that the most common plaque and calculus scores were 0 (less than 1% of measurements were above 0). There was mild bleeding on probing in 74% of the animals, but none of the baboons was judged to have severe gingivitis.

Although a periodontal pocket, as determined by periodontal probing, does not necessarily indicate current disease activity, it is considered to be pathognomonic of past adult periodontal disease activity and indicates cumulative damage to the junctional epithelium and sulcar epithelium, with the concomitant apical migration of the junctional epithelium and destruction of the periodontal ligament and alveolar bone (Barrington and Nevins, 1990; Caton, 1989; Greenstein and Caton, 1990). For the Awash baboons, no animal had an average pocket depth measurement as great as 2 mm.

A more time-consuming measurement is that of the attachment level (AL). The inherent problems associated with making such measurements with a standard manual probe are well known (Jeffcoat, 1991). AL measurements for the Awash baboons were made from the cementoenamel junction. Because the cementoenamel junction was typically subgingival and field lighting conditions were less than optimal, AL measurements for an animal could often only be estimated. In no animal was an average AL measurement as high as 2 mm observed over all teeth examined, although some large isolated defects were seen, presumably the result of pulpal pathology or trauma from fighting. Eight animals had defects with ALs greater than 2 mm: one of these was a juvenile, with AL measurements of 2–3 mm on the mandibular anterior teeth. Two young adults had isolated AL measurements of 2 and 4 mm while the remaining five older adults had isolated AL measurements ranging from 2–13 mm. The low AL measurements indicate good periodontal health for the Awash baboons.

Thus, the traditional periodontal assessment methods agree with the periodontal ranks for the Awash population, supporting a diagnosis of good periodontal health for the Awash baboons. The high correlation between periodontal rank and quantitative bone loss seen in the Awash study, coupled with the obvious visual differences between Amboseli and Awash animals, justified applying the seriation method to this particular study.

Among both juveniles and adults, there is a trend from highest periodontal ranks (best periodontal health) in the Awash sample, through intermediate values in Alto/Hook, to the lowest values in the Lodge sample. These results suggest two phenomena for discussion: 1) the contrast between Alto/Hook and Awash, two samples drawn from populations living in different habitats, but under closely similar natural conditions, and 2) the difference between Alto/Hook and Lodge, whose members live in the same habitat, are drawn from the same genetic population, but differ in their foraging patterns, diet, and interactions with humans. It should be noted that the latter discussion is somewhat complicated by the fact that, whereas juveniles had spent their whole lives in the group where they were captured, this would not be the case for the adult males. Most male baboons leave their natal group at 8–10 years and migrate into another, usually adjacent groups (Pusey and Packer, 1986). Thus, most adult males were born in a group other than the one in which they were trapped, and their periodontal scores are the result of a history of residence in different groups. This complicates the interpretation of the differences seen. For example, the young adult that ranked fifth lowest in the entire adult sample was trapped in Hook's group. Although he had lived there for 4 years when darted, he was thought to have been born in a garbage-feeding group.

A number of different factors, alone or in combination, might contribute to the observed differences. In human subjects, alveolar resorption is generally considered to be a measure of past or current periodontal disease, although it can also be caused by pulpal pathology and traumatic injuries (Hildebolt and Molnar, 1991). Factors possibly implicated in periodontal disease include age, oral hygiene (Lindhe and Rylander, 1975; Loe, 1967; Lovdal et al., 1961), genetic heritage, oral microbial flora (Carranza, 1979; Page and Schroeder, 1982; Schluger et al., 1978), and diet (Carranza, 1979; Goldman and Cohen, 1980; Page and Schroeder, 1982; Schluger et al., 1978). In general the baboons show a relationship between age and periodontal health similar to that seen in human groups. The older the animal, the more likely it is to have poor periodontal health. To some extent, this age effect may explain the difference between the two Amboseli samples, as Lodge group contains more aged animals (Fig. 8). However, it is not a complete explanation, since low periodontal ranks are seen in Lodge animals of all ages, including juveniles. Moreover, Awash adults are not significantly younger than those of Lodge group, so age does not explain the difference between them.

Since Awash and Amboseli baboons belong to different subspecies, a genetic difference might conceivably be invoked to account for their difference in periodontal health. However, there is no indication of such a subspecific difference in museum material (unpublished observations), and in any case this could not explain the difference between the two Amboseli groups, which belong not only to the same subspecies, but to the same deme.

Although baboons, as far as we know, do not consciously practice oral hygiene, it is of interest that at Awash and Amboseli baboons eat the leaves and berries of a shrub, *Salvadora persica,* whose twigs are used by the local people (Kerrayu and Maasai, respectively) as toothbrush sticks (personal observations). Since all groups ate this plant, this behavior does not distinguish the populations, but may nontheless contribute to their periodontal health. The active principle in *Salvadora* is isothiocyanate, a cyanogenic glycoside, which has proven antimicrobial qualities (Elvin-Lewis, 1982; personal communication).

Research on the impact of diet upon periodontal health has been summarized by several authors (Carranza, 1979; Goldman and Cohen, 1980; Page and Schroeder, 1982; Schluger et al., 1978), but although numerous vitamins, minerals, carbohydrates, and proteins have received attention, along with dietary composition and consistency, the relationships between diet and periodontal health in human beings remain largely an enigma. Diet, however, is a complex term, encompassing not only food itself, but the soil, water, and mineral substrates upon which the food grows. Geochemistry has been implicated in differences in periodontal health in prehistoric human populations (Hildebolt et al., 1988) and it may be that some such factor is involved in the Awash-Alto/Hook difference. However, at the level of comparison presently possible, their physical habitats and dietary regimens seem remarkably similar. Both inhabit dry savannas on volcanic soil, where the water supply is partly subterranean and partly pluvial in origin, and where food availability shows strong seasonality.

A causal role for diet seems much more plausible in the case of the Alto/Hook-Lodge difference. It is clear from many studies that the conditions of captivity are conducive to poor periodontal condition in nonhuman primates. Several investigators (Ammons et al., 1972; Colyer, 1947; Hall et al., 1967) found that wild-caught marmosets suffer little from periodontal disease, which was widespread and severe in captive marmosets. Others (Goldman, 1947; Hall et al., 1967; Page et al., 1972) indicate similar findings for howler monkeys. The refuse-based diet of Lodge animals has much in common with the diets commonly fed in captivity, especially in its soft consistency, low fiber, and (probably) its high proportion of simple carbohydrates. It is relevant to note that a role for a high-sucrose diet in inflammatory response and delayed healing has been demonstrated in experimentally induced periodontitis in rats (Abiko and Shimono, 1989).

Another contributing agent, also due to refuse feeding, may be anthropogenic oral flora. Studies of the enteric bacteria of Lodge and Alto/Hook animals have previously shown the former to have much higher levels of antibiotic-resistant enteric bacteria, presumably contracted from eating human-contaminated foods (Rolland et al., 1985). It is possible, though unproven, that the Lodge baboons suffered from pathogenic oral bacteria of human origin, contracted in the same way.

Clearly, the etiological factors we suggest do not explain all the variation in periodontal health in these populations. For example, a young adult male trapped in the Lodge group is known to have been born there, and so when captured had been feeding on refuse for its entire life (nearly 7 years). This animal's periodontal condition is much better than expected from group membership alone. A variety of other, individually-variable attributes of life history, of which dominance rank is one, may influence access to different food sources and hence the impact of the group's foraging habits on the health of its various members. For example, among the Lodge group members, lower ranking and young animals may be partially excluded from feeding on the most attractive but pathogenic foods in the pit.

Researchers working on human periodontal disease etiology have commented that ". . . The picture generally presented . . . is one of an exceedingly complex interaction of local and oral factors with systemic, emotional and environmental conditions" (Schluger et al., 1978). Our study suggests that the etiology of this condition may be no less complex in baboons. Comparative studies in which detailed clinical data are collected may aid in identifying potential etiologic agents.

Studies such as this may contribute to our understanding of periodontal pathology in human prehistory and history. For example, the transition from hunting and gathering to food production in both Old and New Worlds was attended by an increase in a variety of dental pathologies, including periodontal disease as well as caries and hypoplasia. In western Europe, the prevalence of coronal caries increased markedly from the Mesolithic to the Neolithic (Larsen et al., 1991; Molnar and Molnar, 1985), and has continued to increase steadily since the Bronze Age (Brabant, 1967). Root caries too are thought to be a recent phenomenon (Banting, 1984; Hildebolt, 1987; Miles, 1969; Molnar and Molnar, 1985). Although there are relatively few studies of periodontal disease in early human populations, it has been suggested that these too became more prevalent with the rise of food production, with a marked increase associated with urbanization and industrialization (Barker, 1975; Barmes, 1977; Costa, 1980; Heithersay, 1959; Homan, 1977; Lavelle, 1973; Mayhall, 1977; Sagne and Olsson, 1977; Wilkinson et al., 1929).

It is generally agreed that changes in the quality of the diet, especially those directly associated with the introduction of food production, are likely to have contributed heavily to such increases in the prevalence of dental pathology (Cohen and Armelagos, 1984). However, many aspects of culture besides diet are involved in these changes in subsistence and residence patterns, making it difficult to isolate the effects of the dietary changes themselves. By contrast, in our baboon comparisons, diet (with concomitant attritional environment) is the major variable that differentiates the groups, and its role is therefore less ambiguous. We suggest that detailed studies of the interrelationships between feeding habits and periodontal disease rates in wild baboon populations such as these may offer some clues to the direct effects of dietary change upon dental pathology during major events of human cultural evolution.

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