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TOOTH BREAKAGE AND DENTAL DISEASE AS CAUSES OF CARNIVORE–HUMAN CONFLICTS

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Large carnivores that become marauders and man-eaters are frequently thought to be old or infirm, apparently incapable of normal predatory behavior. To evaluate whether this "infirmity theory" offers a general explanation for animal–human conflicts, we examined teeth and jaws of lions (*Panthera leo*) in museum collections. Although tooth wear and breakage are normal in lions, they are rarely accompanied by severe pathologies. Although the infirmity theory may explain specific instances of carnivore–human conflict, including the infamous case of Tsavo's man-eating lions, most other conflicts can be linked to alternative explanations, especially prey depletion in human-dominated areas, which trigger the opportunity and necessity of exploiting people or livestock (or both) as prey.

Key words: animal–human conflict, conservation, East Africa, infirmity theory, Kenya, *Panthera leo*

Carnivores worldwide are threatened by shrinking populations and geographic ranges. Even in areas where they are not targets of direct persecution, carnivores typically have large area and energy requirements that limit population size. In addition, the dietary dependence of carnivores on other animals often brings them into conflict with humans, especially in areas where native wildlife has been extirpated and replaced by domesticated stock. Attacks on humans and livestock invariably motivate campaigns of eradication. Understanding the circumstances that lead large carnivores to alter their food habits and attack humans and domestic livestock is a crucial issue for conservation of apex predators (Frank 1998).

Few carnivores have suffered more dramatic reductions of range and population sizes than the lion (*Panthera leo*). During the late Pleistocene, the lion was perhaps the most widely distributed terrestrial mammal, with a range from southern Africa to northern Europe, across the whole of Asia and North America south as far as the Talara seeps of Peru (Kurtén and Anderson 1980; Turner and Antón 1997). Lions remained widespread into historic times, occurring in North Africa, easternmost Europe and Asia Minor, and southwest Asia. Only 2 centuries ago, their range stretched into central India (Pocock 1931). But loss of habitat and shrinking populations of prey have triggered dramatic contraction of lion populations and range. The species now occupies a small fraction of its range of just 100 years ago (Kingdon 1997), although lions can recover and reestablish themselves when accorded adequate space and protection (Hunter 1998; Stuart-Hill and Grossman 1993). The continual threat that lions pose to rural people and their herds of cattle, sheep, and goats is a primary reason for the persecution and extirpation of lions (Frank 1998).

Conventional wisdom and numerous anecdotes suggest that chronically injured or

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infirm carnivores are especially dangerous to people and their livestock. Deprived of the ability to hunt and kill natural prey, such individuals may be predisposed to attack humans and stock. The famous tiger hunter Jim Corbett repeatedly found that notorious man-eating tigers had broken teeth or claws, crippling arthritis, necrotic appendages, or prior gunshot wounds (Corbett 1946, 1955, 1957). In 2 studies of marauding jaguars (*Panthera onca*) killed while attacking or preying on livestock, most individuals had prior human-inflicted wounds that diminished their ability to hunt (Hoogesteijn et al. 1993). The "infirmity theory" also has been invoked repeatedly to explain attacks by African lions. In many parts of Africa, rural people customarily explain the disappearance of goats and other livestock by saying "Ah, there is an old toothless lion about. We must turn out and kill him, or he will soon begin eating us" (Fitzsimons 1919). Although purely anecdotal and post hoc, numerous authors have invoked the infirmity theory to explain instances of man-eating and marauding by *Panthera leo* (Dyer 1973; Kruuk 1980; Taylor 1959; Yamazaki and Bwalya 1999).

In related work, the 2 senior authors examined 3 notorious man-eating lions from Africa and found that each exhibited tooth and jaw breakage; 2 had sustained traumas consistent with the infirmity theory (Neiburger and Patterson 2000a, 2000b, 2002). One of the infamous "man-eating lions of Tsavo" (Patterson 1925) had a broken lower canine that had developed a severe root-tip abscess. The Mfuwe man-eater (Prothero 1996; W. Hosek, in litt.) had a fistulous lesion and occluded mandibular foramen associated with repair of a severe mandibular fracture. Both injuries would have prevented the lions from delivering a killing bite (Leyhausen 1979) to either the nape or throat of typical bovid or equid prey. Either might cause lions to alter hunting and predatory behavior in ways that elevate the likelihood of their including humans and livestock as prey.

However, broken teeth and bones are common among large carnivores, casting doubt on a causal relationship between tooth breakage and man-eating or marauding behaviors. Van Valkenburgh (1988) tallied the incidence and frequency of tooth breakage in various carnivore taxa as represented in major museum collections, finding that >25% of individuals in modern free-ranging populations have ≥1 broken teeth (Van Valkenburgh 1988; Van Valkenburgh and Hertel 1993). On average, 53.1% of the broken teeth in her lion sample were canines, followed by carnassials (26.5%), and incisors and premolars (each 10.2%). Because most animals with broken teeth behave normally, instances of man-eating seemingly require additional causes. Dental diseases associated with these breaks, such as severe caries, bone erosion along the jaw margins, pulp exposures and abscesses, may be more directly responsible for the altered behavior of man-eaters. Herein, we survey both tooth breakage and apparent dental disease to ascertain whether dental diseases of the sort that we associated with the man-eaters also typified "normal" lions.

MATERIALS AND METHODS

We examined the holdings of skulls of *P. leo* with permanent dentitions in 3 international study collections. These coincided with those studied by Van Valkenburgh (1988) in her dental survey: the Field Museum of Natural History, Chicago (FMNH; $n = 22$), the National Museum of Natural History, Washington, D.C. (USNM; $n = 72$), and the National Museums of Kenya, Nairobi (NMK; $n = 66$). The majority of specimens in all 3 collections were taken by sport hunters during the 1st half of the 20th century, and most represented free-living lions without recorded misdemeanors against humans. Frequencies of damaged dentitions in these collections should approximate those obtained in free-living lions. We also examined a collection of lion skulls in Tsavo East National Park, Kenya (TENP; $n = 23$), representing lions that were killed outside the park by rangers of the Kenya Wildlife Service. Most were obtained during animal control operations against man-eaters, marauders, or threatening lions, although 2 resulted from euthanasia of mortally injured lions. If tooth breakage or dental disease is routinely responsible for bringing lions into conflict with humans, this sample should exhibit higher frequencies of such traumas than the museum collections.

Like Van Valkenburgh, we distinguished teeth broken before and after death by assessing tooth wear. Only tooth fractures that became subsequently worn were tallied in our study. Breakage and wear on each of the 30 teeth (i 3/3, c 1/1, p 3/3, m 1/0, total 30) were recorded on data sheets by the 2 senior authors. Superficial dental disease was evaluated (by EJN), either by direct examination (FMNH collection) or by studying digital images recorded on a digital camcorder (Sony DCR 900). Unlike Van Valkenburgh, we considered unbroken teeth that were sufficiently worn to expose pulp cavities ≥1 mm in diameter to be "damaged" because such exposure opens the tooth and jaw to infection and abscesses that could affect behavior. Consequently, the incidence of damaged teeth in our samples exceeds that reported by Van Valkenburgh, whose definition reflected her principal interest in dental strength. Lack of access to radiographic facilities restricted our assessments to superficial dental disease: pulp exposures, alveolar erosion, pitting of the jaws, and the like. To estimate age, we used tooth-wear and suture-closure criteria established for a large sample of known-age, free-living lions from South Africa (Smuts et al. 1978). Our analysis was based on 153 specimens for which both age and dental damage could be accurately determined.

To examine frequencies of damaged dentitions and variation among discrete age classes, we used nonparametric methods (Siegel 1956) to assess correlation (Spearman rank) and differences (Mann–Whitney *U*-test for 2 samples; Kruskal–Wallis median test for 2 samples and multiple groups). An alpha value of $P = 0.05$ was used to evaluate statistical significance, although we considered alpha values below 0.1 as marginal.

Results

Over all samples, 63 of 153 lions had damaged dentitions. This damage often takes the form of worn and broken teeth, which exposes the pulp cavity of the tooth to infection and decay (Fig. 1). Less frequently, erosion of the alveolus and pitting of jaw margins accompanied tooth wear and breakage. In a few cases, major traumas to the head and face had produced aberrant occlusion patterns, often reflected in asymmetrical wear on the teeth. The prevalence of such damage in 41.1% of the lions we examined underscores the hazards of killing and feeding on large powerful prey and the intense selection pressures that must operate on anatomy and behavior of predators.

The frequency of damaged dentitions varied over 10 adult year-classes ($\chi^2 = 38.35$, $d.f. = 9$, $P < 0.0001$) but not by sex ($\chi^2 = 3.53$, $d.f. = 1$, $P = 0.06$). Older lions were more likely to have damaged dentitions than younger lions, and frequency of damaged dentitions was positively correlated across age classes 3–12 years ($r_s = 0.82$, $n = 10$, $P = 0.004$). A quarter (24%) of lions less than 6 years had damaged dentitions, whereas 82% of older lions exhibited damage of some sort ($U = 1{,}658$; $P < 0.0001$). Age profiles of each sample (Fig. 2) also reflect this tendency for older age classes to contain higher proportions of damaged individuals, tending to be "top-heavy" on the left side.

Contrary to predictions, the Tsavo East sample containing "problem lions" did not exhibit a higher incidence of damaged dentitions. We observed no significant differences among samples from different museums in the incidence of dental damages ($\chi^2 = 5.15$, $d.f. = 3$, $P = 0.16$). Only 23% of the TENP sample was damaged, whereas damaged dentitions comprised 33%, 43%, and 50% of the FMNH, USNM, and NMK samples, respectively. These differences may simply reflect age differences among the samples (Fig. 3). Lions in the TENP sample averaged 4.9 years, whereas FMNH, USNM, and NMK lions averaged 6.0, 6.2, and 5.5 years, respectively; age differences between samples are significant ($\chi^2 = 10.99$, $d.f. = 3$, $P = 0.01$).

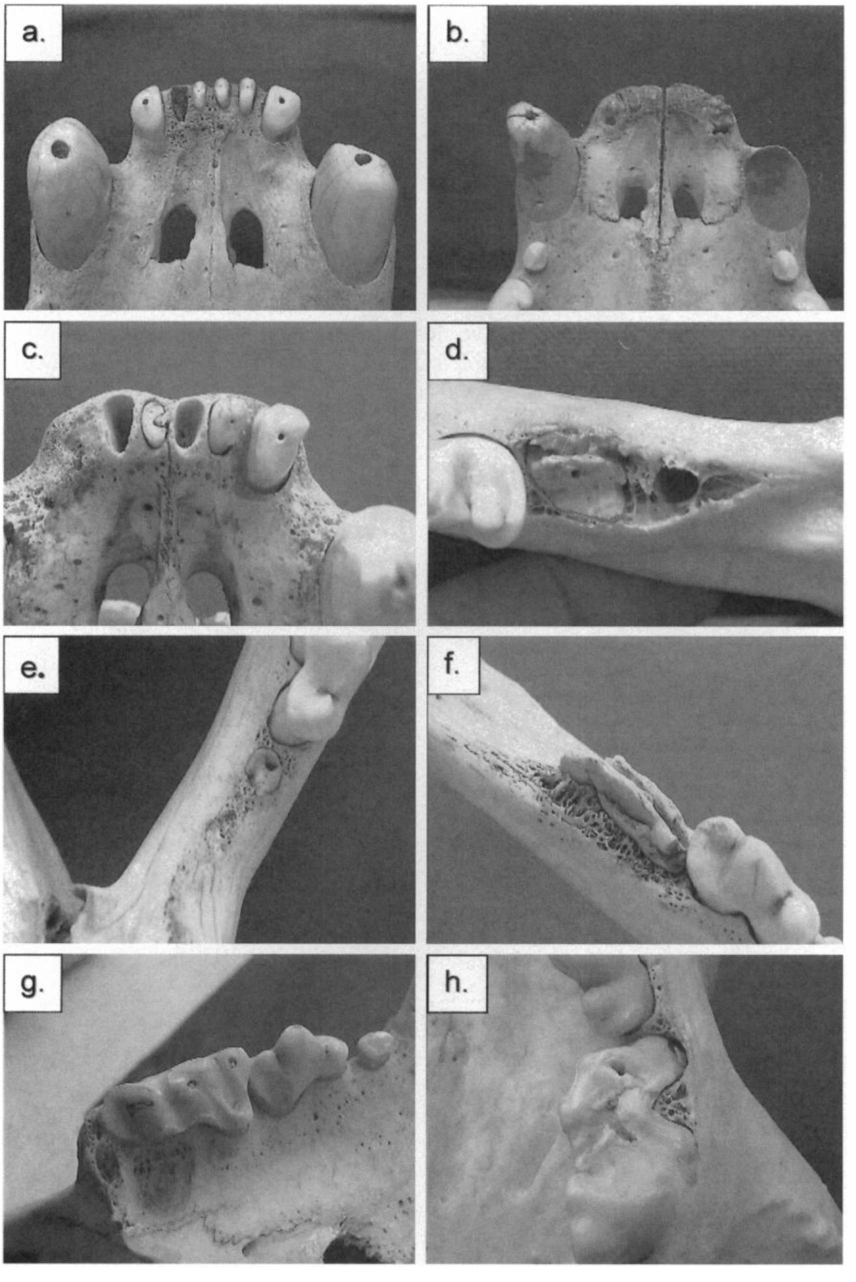

FIG. 1.—Examples of dental damage in lions, *Panthera leo*: a) maxilla—incisors and canines with pulp exposures (NMK OM 3388 [National Museums of Kenya; Osteology, Mammals]), b) maxilla—broken incisors and right canine with pulp exposures (NMK OM 2517), c) maxilla—broken incisor, incisors and canine with pulp exposures (NMK OM 2536), d) mandible—broken left p4 with alveolar erosion (NMK OM 7713), e) mandible—broken left p2 with alveolar erosion (NMK OM 2506), f) mandible—broken left p4 with alveolar erosion (NMK OM 2524), g) maxilla—right P4 with pulp exposures from wear (NMK OM 2517), h) maxilla—left P4 with pulp exposures and alveolar erosion (NMK OM 7932).

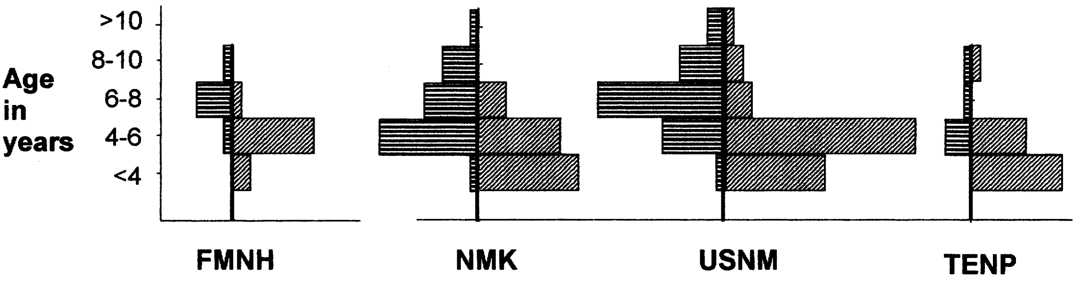

FIG. 2.—Age tables for 4 samples of lions (*Panthera leo*) showing the relative frequency of individuals with dental damage. Bars to left of vertical line denote individuals with damaged dentitions, and those to the right denote intact ones. Sample sizes are Field Museum of Natural History (FMNH), 18; National Museums of Kenya (NMK), 46; National Museum of Natural History (USNM), 67; Tsavo East National Park (TENP), 22.

DISCUSSION

Our results establish that approximately 40% of the lions we examined had damaged dentitions. Few would argue that broken teeth or heavily pitted jaws constitute damage, but exposed pulp cavities constitute a more equivocal class of conditions. Pulp exposures are normal for older lions, particularly on the canine and incisor teeth (Smuts et al. 1978). Accordingly, virtually any old lion will show some signs of dental damage, whether or not the pulp exposure has given rise to associated infections or abscesses. The high incidence of pulp exposures undoubtedly contributes to the higher incidence of dental damages among older lions. It also explains the discrepancies between the dental damages we report and those noted on 3 of the same collections by Van Valkenburgh (1988).

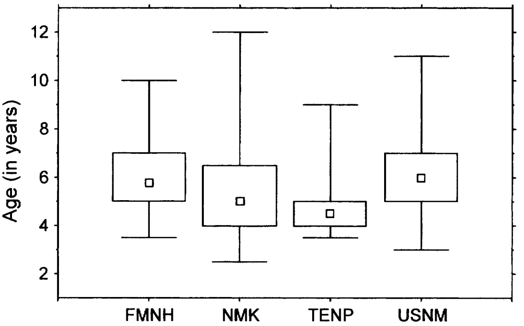

FIG. 3.—Age distribution for 4 samples of lions. Box indicates middle 2 quartiles, small square indicates median, and vertical line represents range. Museum abbreviations as for Fig. 2.

We defined dental damages on the basis of superficial evidence. Our survey did not use radiographic or magnetic-resonance imaging that would help to identify and delimit internal decay. However, our inspections resemble those used to detect human caries. To qualify as "damaged" in our study, a pulp exposure had to exceed 1 mm in diameter—few caries of this magnitude remain undetected or untreated in humans. Rather, the large number of substantial pulp exposures we detected in lions, coupled with a much lower incidence of associated pathologies, implicate some undetermined mechanisms for retarding the onset of infection, be they components of the saliva, elements of the immune system, or structural components of the teeth.

Contrary to the infirmity theory, we found that the lowest incidence of dental damage among the sample we predicted would show the highest incidence, the "problem-lion" sample from TENP, Kenya. A striking feature of this sample was its age profile. With the exception of 1 old female that had attacked, killed, and partially consumed a child (S. Andanje, in litt.) and 2 others euthanized for injuries sustained from buffaloes, the TENP sample consisted mainly of younger lions, apparently in excellent health, taken on the farms and ranches that border the park near Voi.

Lions typically leave their natal prides at 2–3 years of age (Bertram 1978; Schaller 1972). Although males almost invariably disperse, females also must leave productive prides in highly favorable habitats because continual recruitment of females would otherwise swell prides to unsustainable size. Most problem lions from Tsavo are ≤5 years of age (Fig. 3). Studies elsewhere suggest that these lions would be too young to contest established territories in the park; instead, they disperse outside the park onto neighboring farms and ranches where they come into conflict with humans. If the lions shot by animal control rangers of the Kenya Wildlife Service typify the greater population of lions living outside the park, then ranchlands constitute a dispersal "sink" for lions; most individuals are born elsewhere (in this case, within the parks), and mortality exceeds reproduction. Under such conditions, conflicts between lions and humans may arise from low availability of natural prey without accompanying infirmity or disease in the predators. Demographic and ecological studies of lions in Tsavo's ranchlands are needed to confirm these inferences. However, they accord with findings that a minority of lion attacks on humans in Uganda involve incapacitated animals (Treves and Naughton-Treves 1999).

Any phenomenon as complex as man-eating and marauding seldom has a single cause. Despite its widespread use to explain man-eating post facto, the infirmity theory clearly lacks predictive power. Numerous factors may lead carnivores to man-eating, either singly or in interaction (e.g., Kerbis Peterhans et al. 1998); opportunity and necessity are apt to be 2 of the most prevalent (B. D. Patterson, in litt.). The diverse causation behind these phenomena in turn requires diverse solutions; for example, Stander (1990) advocated translocation for the occasional stock raider but elimination for more habitual offenders. Finally, animal–human conflicts and their resolution are equally complex from a human standpoint: local culture, government policy, and international trade all influence the attitudes of local people toward predators (Woodroffe 2000). The fates of many carnivore species depend on an understanding of the interactions among these variables.

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