

Cooperation and individuality among man-eating lions

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Cooperation is the cornerstone of lion social behavior. In a notorious case, a coalition of two adult male lions from Tsavo, southern Kenya, cooperatively killed dozens of railway workers in 1898. The “man-eaters of Tsavo” have since become the subject of numerous popular accounts, including three Hollywood films. Yet the full extent of the lions’ man-eating behavior is unknown; estimates range widely from 28 to 135 victims. Here we use stable isotope ratios to quantify increasing dietary specialization on novel prey during a time of food limitation. For one lion, the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of bone collagen and hair keratin (which reflect dietary inputs over years and months, respectively) reveal isotopic changes that are consistent with a progressive dietary specialization on humans. These findings not only support the hypothesis that prey scarcity drives individual dietary specialization, but also demonstrate that sustained dietary individuality can exist within a cooperative framework. The intensity of human predation (up to 30% reliance during the final months of 1898) is also associated with severe craniodental infirmities, which may have further promoted the inclusion of unconventional prey under perturbed environmental conditions.

individual dietary specialization | *Panthera leo* | Taita | Tsavo

Individual dietary specialization can result from high intraspecific competition (1, 2). It has been reported in many animal populations (1, 3); however, its effects on the social behaviors of cooperative species are poorly understood. Among lions, cooperative behaviors are well known (4–7), yet the presence of laggards (8), cheaters (9), and specialized hunters (7) within social networks hints at highly complex, complementary individual behaviors. Recent work has shown that food limitation can drive individual dietary specialization within a population of carnivores (3, 10), including lions that prey on humans (11), but such idiosyncratic behaviors are rarely cooperative. Here we explore the environmental circumstances associated with a celebrated case of sustained man eating by a coalition of lions and use isotopic data to quantify individual dietary specialization through time.

The Tsavo region of Kenya witnessed profound environmental changes toward the end of the 19th century. Reduced elephant populations resulted in the expansion of woodlands and the reduction of grass-eating (grazing) herbivores (12). The severe Mwakisenge drought of 1897–1900 (13), and the rinderpest viral epidemics of 1889 and 1898 (affecting wild and domestic bovines), combined to further reduce herbivore populations in Tsavo (12, 14). With the construction of the Uganda Railway in 1898, this reduction in carnivore prey species was attended by an increased human presence along the railway, both resident Taita agropastoralists (13) and some Indian laborers (12).

From March to December 1898, a coalition of two male lions (as inferred by paired track marks and frequent sightings) (15) killed 28 laborers and “scores of unfortunate African natives” during the construction of the railway through Tsavo (16). The death toll was later revised to 135 humans (15), although the

accuracy of this value has been challenged (12). On December 9, Lieutenant Colonel J. H. Patterson D.S.O., a British officer and engineer, killed lion FMNH 23970 (Field Museum of Natural History) (Fig. 1A). The skull evinced craniodental pathologies, including malocclusion of the jaws and a fractured lower right canine (17) (Fig. 1B). On December 29, Patterson killed lion FMNH 23969 (Fig. 1C), the skull of which revealed a fractured upper left carnassial (17) (Fig. 1D), which is relatively common among lions (18). Given that the attacks on humans and livestock ceased after December 9 and December 29, respectively, and on the basis of the appearance of each lion (the skins were described as being uniquely scored by thorns) (15), it is almost certain that the lions Patterson killed were those responsible for the human depredations.

To investigate the relative importance of potential prey groups to each lion, we determined the stable carbon ($^{13}\text{C}/^{12}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$) isotope ratios (reported in δ notation) of bone or tooth collagen and hair keratin. $\delta^{13}\text{C}$ values (which distinguish plants that use C_3 and C_4 photosynthesis and are maintained in the tissues of consumers) and $\delta^{15}\text{N}$ values (which increase with trophic level) are used to characterize niche space (19) and estimate the percent contributions from multiple prey items (20). Analysis of dietary input across different time windows over an animal’s lifetime is possible because different biological tissues are renewed at different rates. Bone collagen is regenerated slowly, whereas hair incorporates dietary information over a period of months (21). For the 7- to 8-year-old FMNH 23969 and 23970, bone collagen is a good estimate of dietary input over their lifespan (multiyear average). Keratin from tail-tuft hairs (averaging 2.6 ± 0.5 cm from base to tip) offers a complementary dietary window over an estimated 3-month period before death (final-months average). Finally, for comparative purposes, we sampled a population of modern Tsavo lions from a region between Tsavo West and Tsavo East National Parks (hereafter TSWNP and TENP, respectively). We sampled skin and muscle tissue, which records a dietary input of several weeks.

Results

Characterization of Prey Sources. The isotopic ratios of potential prey were obtained from the tooth collagen of Tsavo herbivores (collected by T. E. Cerling between 1999 and 2000, which include samples from a 1970 die-off) and the bone collagen of Taita

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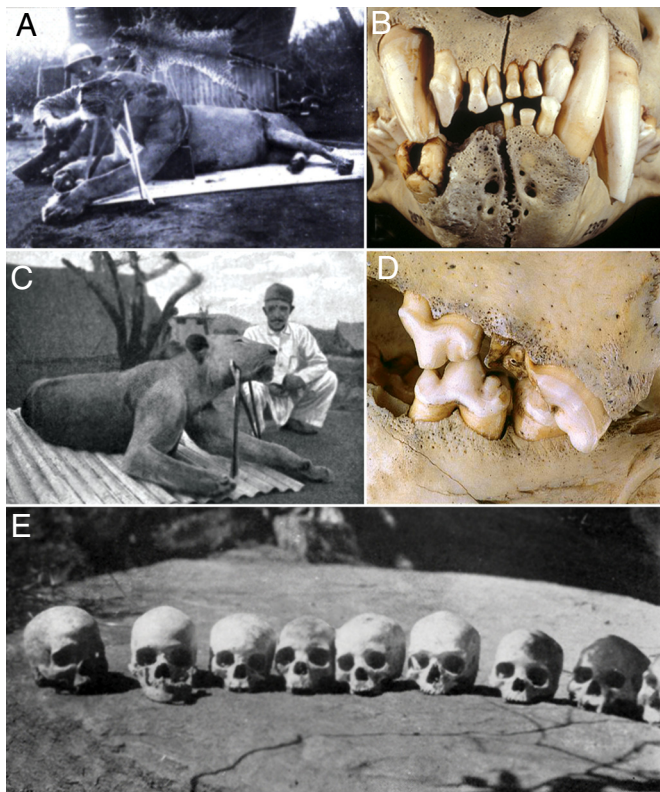


Fig. 1. The man-eaters of Tsavo and a Taita ancestral shrine. (A) Lieutenant Colonel J. H. Patterson and lion FMNH 23970 shot December 9, 1898 (16) (FMNH photo archives no. z93658, Field Museum of Natural History). (B) Articulated jaws of FMNH 23970 revealing a fractured lower right canine (and subsequent root-tip abscess), missing lower incisors, supererupted upper right incisors, and rotation and malocclusion of the upper right canine. Cranial asymmetry of 23970 occurred after injury and before death (14) (FMNH photo archives no. z94320.11c, Field Museum). (C) Lion FMNH 23969 shot December 29, 1898 (16). (D) Articulated jaws of FMNH 23969, revealing a fractured upper left carnassial with a double pulp exposure (17) (FMNH photo archives z94321.6c, Field Museum). (E) A Taita ancestral shrine photographed in 1929 by L. S. B. Leakey (22, 35). Such a shrine results from the unusual funerary practices of the Taita; after approximately 1 year of burial in a seated position, skulls are exhumed, severed, and enshrined in ancestral caves or rock shelters (25, 39).

agropastoralists (skulls collected by L. S. B. Leakey during the East African Archaeological Expedition of 1929; Fig. 1E) (22). Because the attacks occurred central to and at the boundary of TWNP and TENP, we analyzed browsers (*Giraffa camelopardalis*, *Taurotragus oryx*, *Tragelaphus imberbis*), browser/mixed-feeders (*Aepyceros melampus*), and grazers (*Equus burcellii*, *Kobus ellipsiprymnus*, *Oryx beisa*, *Syncerus caffer*) from both regions. After adjusting for (i) tissue-specific isotopic fractionations among lion populations and potential prey (corrected to bone collagen values), (ii) trophic differences between predator and prey tissues (corrected by adding +1‰ and +3.5‰ to prey $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, respectively), and (iii) the global decrease in the $\delta^{13}\text{C}$ value of atmospheric CO_2 [see Dataset S1], our results reveal low $\delta^{13}\text{C}$ values for browsers and high $\delta^{13}\text{C}$ values for grazers (reflecting isotopic differences between C_3 and C_4 photosynthetic pathways), and a significant difference between the $\delta^{15}\text{N}$ values of herbivores in TWNP and TENP (Fig. S1), suggesting that the $\delta^{15}\text{N}$ values of herbivores vary with declining rainfall from west to east (14).

To account for differences in herbivore diets and regional differences in rainfall, we binned the browsers and grazers of TWNP and TENP separately; herbivores from unknown local-

ities were added to the nearest bin (which had little impact on final group values) (see Dataset S1). Our final bins include: TENP browsers (mean \pm 1 standard deviation: $\delta^{13}\text{C} = -18.4 \pm 1.7\text{‰}$; $\delta^{15}\text{N} = 18.1 \pm 1.3\text{‰}$; $n = 7$), TWNP browsers ($\delta^{13}\text{C} = -21.4 \pm 0.7\text{‰}$; $\delta^{15}\text{N} = 11.4 \pm 0.5\text{‰}$; $n = 2$), TENP grazers ($\delta^{13}\text{C} = -8.6 \pm 1.3\text{‰}$; $\delta^{15}\text{N} = 16.1 \pm 1.5\text{‰}$; $n = 8$), and TWNP grazers ($\delta^{13}\text{C} = -7.8 \pm 0.9\text{‰}$; $\delta^{15}\text{N} = 14.0 \pm 1.8\text{‰}$; $n = 8$; Fig. 2A) (all values for fully corrected data). The Taita population ($n = 12$) has intermediate $\delta^{13}\text{C}$ values ($-13.0 \pm 1.3\text{‰}$) and low $\delta^{15}\text{N}$ values ($11.4 \pm 0.9\text{‰}$) (Fig. 2A) and is comparable to other agropastoral populations in Kenya (23, 24). Such isotope values are consistent with a mixed diet of corn and *mbaazi* (25, 26). Corn is a protein-poor, carbohydrate-rich, C_4 food, whereas *mbaazi* is a proteinaceous pea soup made from *Cajanus* spp. and *Vigna* spp. (N-fixing C_3 legumes with low $\delta^{15}\text{N}$ values). Accordingly, *mbaazi* was likely the dominant source of protein (and therefore nitrogen) in Taita diets. Although protein is normally the primary predictor of collagen $\delta^{13}\text{C}$ values, carbohydrate carbon can have an increasing influence on collagen when total dietary protein is low (see figure 3 in ref. 27); hence, our Taita $\delta^{13}\text{C}$ values reflect a mix of C_3 (*mbaazi*) and C_4 (corn) foods.

Calculation of Prey Contribution to Diet. To quantify the contribution of each potential prey source to the diets of each lion, we used a Bayesian isotope mixing model (mixSIR v. 1.0.4) (20). Because there are several estimations involved in correcting tissue-specific and trophic fractionations, mixSIR includes these potential sources of error into the final posterior distributions of each source in a mix. We used noninformative priors to limit treatment of the data to that of our isotopic results.

Modern Tsavo lions evinced isotope values consistent with a diet composed entirely of grazers from TWNP ($\delta^{13}\text{C} = -8.9\text{‰} \pm 0.7\text{‰}$; $\delta^{15}\text{N} = 13.0\text{‰} \pm 0.3\text{‰}$; $n = 5$), suggesting that they consumed prey from western Tsavo for a period of weeks before sample collection. Their reliance on grazers (84%; this and hereafter are median values of the posterior distribution from mixSIR, indicating the most probable contribution of prey) is similar to previous isotopic data for East African lions (28).

The putative man-eaters showed distinct isotope values. Throughout much of its life, FMNH 23969 had a diet similar to modern Tsavo lions and was heavily reliant on TWNP grazers (multiyear average: $\delta^{13}\text{C} = -10.1\text{‰}$; $\delta^{15}\text{N} = 13.6\text{‰}$; median contribution = 41%). Toward the end of its life, the lion continued to rely on grazing animals, although subsisted on herbivores from TWNP and TENP to similar extents (final-months average: $\delta^{13}\text{C} = -11.1\text{‰}$; $\delta^{15}\text{N} = 14.6\text{‰}$; median contributions = 30% TWNP grazers, 37% TENP grazers). By contrast, lion FMNH 23970 progressed from a diet focused on grazers (multiyear average: $\delta^{13}\text{C} = -12.1\text{‰}$; $\delta^{15}\text{N} = 14.3\text{‰}$; median contributions = 25% TWNP grazers, 30% TENP grazers) to one emphasizing browsers, browser/mixed-feeders, and humans toward the end of 1898 (final-months average: $\delta^{13}\text{C} = -13.4\text{‰}$; $\delta^{15}\text{N} = 13.0\text{‰}$; median contributions = 23% TWNP browsers, 30% Taita agropastoralists). This latter result (Fig. 2A and B and Table S1) verifies historical accounts that assigned the lion's share of human deaths to FMNH 23970 (14, 16). This finding also agrees well with the infirmity hypothesis (18, 29, 30), which holds that physically impaired pantherids are more likely to resort to human depredation.

Discussion

The results from our model also enable us to estimate the extent of the lions' man-eating behavior. Our estimate is based on the following assumptions: (i) lions require an average of approximately 6 kg of food \cdot day $^{-1}$ (31); (ii) 2.6 ± 0.5 cm of hair keratin reflects dietary input during the final 3 months of life (21); (iii) approximately 20 kg of consumable tissue per person (25% of an 80-kg human) was consumed after each attack, which is consis-

followed by a methanol rinse. We analyzed samples with a Finnegan Delta Plus Continuous Flow mass spectrometer in the Departments of Earth and Planetary Sciences and Ocean Sciences, University of California-Santa Cruz. Isotopic ratios are expressed as δ values: $\delta = 1,000((R_{\text{sample}}/R_{\text{standard}}) - 1)$ where R = either $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$; reference standards are Vienna PeeDee-belemnite for carbon and atmospheric N_2 for nitrogen. We used tissue-specific fractionations to adjust samples to collagen-comparable values. A +2.2‰ ^{13}C -enrichment was applied to skin/tissue and a +0.7‰ ^{13}C -enrichment was applied to hair (36, 37). Changes in nitrogen between tissue types were negligible. A +1‰ $\delta^{13}\text{C}$ and a +3.5‰ ^{15}N -enrichment was applied to prey sources to correct for trophic level differences (37). Finally, to account for the global decrease of ^{13}C in atmospheric CO_2 over the last 150 years, we applied a -1.1‰ adjustment to the FMNH lions and Taita remains, and a -0.6 and -0.1‰ $\delta^{13}\text{C}$ adjustment to the 1971 and 1999–2000 fauna, respectively (38) (see Dataset S1). To account for possible error in all adjustments, we incorpo-

rated fractionation uncertainty into mixSIR (v.1.0.4) (20) for calculating the contribution of each dietary source; $\delta^{13}\text{C}$: 0.5‰, $\delta^{15}\text{N}$: 0.7‰. We used uninformative priors and 1×10^6 iterations.

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