

Cooperation and individuality among man-eating lions

Justin D. Yeakey^{a,1}, Bruce D. Patterson^b, Kena Fox-Dobbs^c, Mercedes M. Okumura^d, Thure E. Cerling^e, Jonathan W. Moore^f, Paul L. Koch^g, and Nathaniel J. Dominy^{a,h,1}

^aDepartment of Ecology and Evolutionary Biology, University of California, Santa Cruz, 1156 High Street, Santa Cruz, CA 95064; ^bDepartment of Zoology, Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, IL 60605; ^cDepartment of Geology, University of Puget Sound, 1500 North Warner Street, CMB 1048, Tacoma, WA 98416-1048; ^dLeverhulme Centre for Human Evolutionary Studies, University of Cambridge, Fitzwilliam Street, Cambridge CB2 1QH, United Kingdom; ^eDepartment of Geology and Geophysics, University of Utah, 135 South 1460 E, Salt Lake City, UT 84112; ^fDepartment of Ecology and Evolutionary Biology, University of California, Santa Cruz, 100 Shaffer Road, Santa Cruz, CA 95060; and Departments of ^gEarth and Planetary Sciences and ^hAnthropology, University of California, Santa Cruz, 1156 High Street, Santa Cruz, CA 95064

Edited by Kristen Hawkes, University of Utah, Salt Lake City, UT, and approved September 25, 2009 (received for review May 13, 2009)

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

Author contributions: J.D.Y., B.D.P., P.L.K., and N.J.D. designed research; J.D.Y., B.D.P., and N.J.D. performed research; K.F.-D., M.M.O., and T.E.C. contributed new reagents/analytic tools; J.D.Y., B.D.P., K.F.-D., J.W.M., P.L.K., and N.J.D. analyzed data; and J.D.Y., B.D.P., P.L.K., and N.J.D. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

¹To whom correspondence may be addressed. E-mail: jyeakey@pmc.ucsc.edu or njdominy@ucsc.edu.

This article contains supporting information online at www.pnas.org/cgi/content/full/0905309106/DCSupplemental.

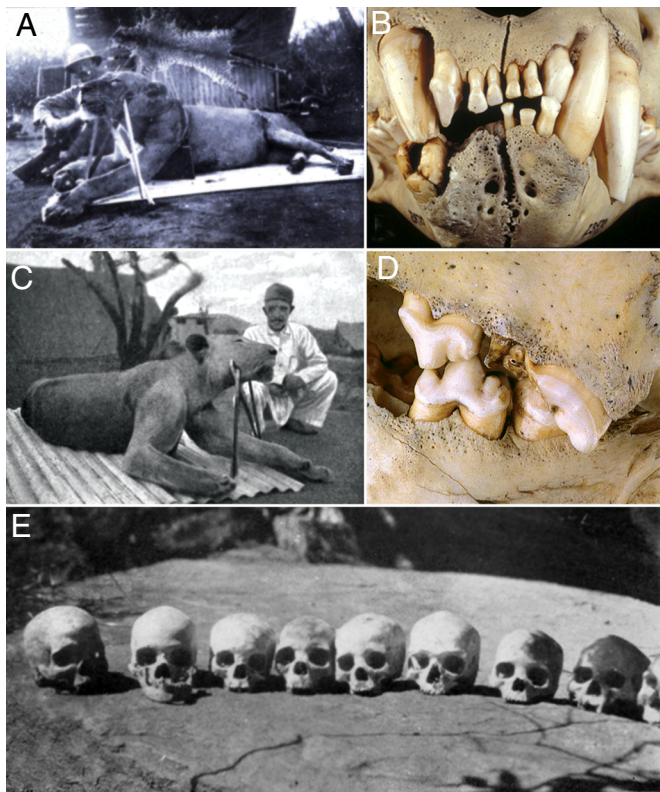


Fig. 1. The man-eaters of Tsavo and a Taita ancestral shrine. (A) Lieutenant Colonel J. H. Patterson and lion FMNH 23970 shot December 9, 1898 (16) (FMNH photo archives no. z93658, Field Museum of Natural History). (B) Articulated jaws of FMNH 23970 revealing a fractured lower right canine (and subsequent 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.

ACKNOWLEDGMENTS. We thank A. K. Behrensmeier, E. E. Butler, C. E. Chow, C. T. Darimont, J. A. Estes, L. Gahegan, P. Hluzova, J. B. Hopkins, S. D. Newsome, J. D. Phelps, J. W. Ridges, W. Stanley, R. H. Tuttle, E. R. Vogel, P. V. Wheatley, and C. C. Wilmers for helpful comments and discussions. We thank the Duckworth Laboratory, the Field Museum of Natural History, and the Smithsonian National Museum of Natural History for access to unpublished field reports. Modern samples were imported under CITES import no. US-012 (PRT 701716). This study was approved by the Chancellor's Animal Research Committee of University of California (UC)-Santa Cruz (no. Domin0806) and approved as exempt by the Institutional Review Board of UC-Santa Cruz (no. HS0801187). This study was funded by the Earthwatch Institute, the David and Lucile Packard Foundation, and a grant from the UC-Santa Cruz Committee on Research.

- Bolnick DI, et al. (2002) The ecology of individuals: Incidence and implications of individual specialization. *Am Nat* 161:1–28.
- Bolnick DI, Svanbäck R, Araujo MS, Persson L (2007) Comparative support for the niche variation hypothesis that more generalized populations also are more heterogeneous. *Proc Natl Acad Sci USA* 104:10075–10079.
- Darimont CT, Paquet PC, Reimchen TE (2009) Landscape heterogeneity and marine subsidy generate extensive intrapopulation niche diversity in a large terrestrial vertebrate. *J Anim Ecol* 78:126–133.
- Schaller GB (1972) *The Serengeti Lion: A Study of Predator-Prey Relations* (Univ of Chicago Press, Chicago).
- Packer C, Scheel D, Pusey AE (1990) Why lions form groups: Food is not enough. *Am Nat* 136:1–19.
- Packer C, et al. (2005) Ecological change, group territoriality, and population dynamics in Serengeti lions. *Science* 307:390–393.
- Stander PE (1992) Cooperative hunting in lions: The role of the individual. *Behav Ecol Sociobiol* 29:445–454.
- Heinsohn R, Packer C (1995) Complex cooperative strategies in group-territorial African lions. *Science* 269:1260–1262.
- Packer C, Rutman L (1988) The evolution of cooperative hunting. *Am Nat* 132:159–198.
- Estes JA, Riedman ML, Staedler MM, Tinker MT, Lyon BE (2003) Individual variation in prey selection by sea otters: Patterns, causes and implications. *J Anim Ecol* 72:144–155.
- Packer C, Ikanda D, Kissui B, Kushnir H (2005) Lion attacks on humans in Tanzania. *Nature* 436:927–928.
- Kerbis Peterhans JC, Gnoske TP (2001) The science of 'man-eating' among lions *Panthera leo* with a reconstruction of the natural history of the 'man-eaters of Tsavo.' *J East Afr Nat Hist* 90:1–40.
- Merritt EH (1975) A History of the Taita of Kenya to 1900. PhD dissertation (Department of History, Indiana University, Bloomington, IN).
- Patterson BD (2004) *The Lions of Tsavo: Exploring the Legacy of Africa's Notorious Man-Eaters* (McGraw-Hill, New York).
- Patterson JH (1925) *The Man-Eating Lions of Tsavo* (Field Museum of Natural History, Chicago).
- Patterson JH (1907) *The Man-Eaters of Tsavo and Other East African Adventures* (Macmillan, London).
- Neiburger EJ, Patterson BD (2002) A forensic dental determination of serial killings by three African lions. *Gen Dent* 50:40–42.
- Patterson BD, Neiburger EJ, Kasiki SM (2003) Tooth breakage and dental disease as causes of carnivore-human conflicts. *J Mammal* 84:190–196.
- Newsome SD, Martinez del Rio C, Bearhop S, Phillips DL (2007) A niche for isotopic ecology. *Front Ecol Environ* 5:429–436.
- Moore JW, Semmens BX (2008) Incorporating uncertainty and prior information into stable isotope mixing models. *Ecol Lett* 11:470–480.
- Tieszen LL, Boutton TW, Tesdahl KG, Slade NA (1983) Fractionation and turnover of stable carbon isotopes in animal tissues: Implications for $\delta^{13}\text{C}$ analysis of diet. *Oecologia* 57:32–37.
- Leakey LSB (1929) *The East African Archaeological Expedition: Season 1928–1929. Report for September, October and November*. Unpublished report (National Anthropological Archives, Smithsonian Institution, Washington, DC).
- Ambrose SH (1986) Stable carbon and nitrogen isotope analysis of human and animal diet in Africa. *J Hum Evol* 15:707–731.
- Ambrose SH, Deniro MJ (1986) Reconstruction of African human diet using bone-collagen carbon and nitrogen isotope ratios. *Nature* 319:321–324.
- Bostock PG (1950) *The Peoples of Kenya: The Taita* (Macmillan, London).
- Hobley CW (1895) Upon a visit to Tsavo and the Taita Highlands. *Geogr J* 5:545–561.
- Ambrose SH, Norr L (1993) in *Prehistoric Human Bone: Archaeology at the Molecular Level*, eds Lambert JB, Grupe G (Springer, Berlin), pp 1–37.
- Ambrose SH, Deniro MJ (1986) The isotopic ecology of East African mammals. *Oecologia* 69:395–406.
- Corbett J (1944) *Man-Eaters of Kumaon* (H. Milford, London).
- Livingstone D (1868) *Missionary Travels and Researches in South Africa* (Harper and Brothers, New York).
- Green B, Anderson J, Whately T (1984) Water and sodium turnover and estimated food consumption in free-living lions (*Panthera leo*) and spotted hyaenas (*Crocuta crocuta*). *J Mammal* 65:593–599.
- Kays RW, Patterson BD (2002) Mane variation in African lions and its social correlates. *Can J Zool* 80:471–478.
- Packer C, Pusey AE, Eberly LE (2001) Egalitarianism in female African lions. *Science* 293:690–693.
- Eppinger M, et al. (2006) Who ate whom? Adaptive *Helicobacter* genomic changes that accompanied a host jump from early humans to large felines. *PLoS Genet* 2:1097–1110.
- Kitson E (1931) A study of the negro skull with special reference to the crania from Kenya Colony. *Biometrika* 23:271–314.
- Nardoto GB, Godoy PB, Ferraz ESB, Ometto JPHB, Martinelli LA (2006) Stable carbon and nitrogen isotopic fractionation between diet and swine tissues. *Sci Agric* 63:579–582.
- Roth JD, Hobson KA (2000) Stable carbon and nitrogen isotopic fractionation between diet and tissue of captive red fox: Implications for dietary reconstruction. *Can J Zool* 78:848–852.
- Leuenberger M, Siegenthaler U, Langway C (1992) Carbon isotope composition of atmospheric CO_2 during the last ice age from an Antarctic ice core. *Nature* 357:488–490.
- Hollis C (1901) Notes on the history and customs of the people of Taveta, East Africa. *J Roy Afr Soc* 1:98–125.