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Risk and opportunity for humans coexisting with large carnivores

Models of Plio-Pleistocene hominid behavioral ecology often emphasize competition with large carnivores. This paper describes competition between modern humans and large carnivores in rural Uganda, including active, confrontational scavenging of carnivore kills by humans and carnivore attacks on humans. Information gathered from Ugandan Game Department archives (1923–1994) reveals that twentieth-century agropastoralists regularly tried to scavenge from leopard (*Panthera pardus*) and lion (*Panthera leo*) kills, and that these large carnivores have preyed on hundreds of humans in Uganda over the past several decades. Men were most often targets of carnivore attack, particularly while engaged in hunting-related activities. However attacks on men were less often lethal than attacks on women and children. Analyses show that lion attacks were more dangerous than leopard attacks. These data support recent contentions that hominids armed with even simple weapons can succeed in active, confrontational scavenging by chasing carnivores from kills. Hominids sharing East African habitats with large carnivores may have been regularly subject to attack.

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Introduction

Hominids and large carnivores have coexisted in Africa for more than 4 million years (Brain, 1981; Marean, 1989; Turner, 1992; Marean & Ehrhardt, 1995). This co-existence produced risk and opportunity for human ancestors. The risk to hominids stems from predation and has long been acknowledged, even if its magnitude is uncertain. The opportunity to benefit from coexistence with carnivores arises if hominids can obtain meat from their kills. There is ample evidence that early hominids scavenged (Bunn & Ezzo, 1993, for review). But did hominids simply scavenge the remains of abandoned kills, or did they confront and chase large carnivores off their kills (Shipman, 1986; Blumenschine, 1987, 1988, 1989; Potts, 1987; Cavallo & Blumenschine, 1989; Speth, 1989; Bunn & Ezzo, 1993)? We propose that the evolutionary significance of hominid–carnivore competition can be illuminated by attention to the interactions between these two groups in modern times.

We describe competitive interactions between humans and large carnivores in twentieth-century rural Uganda, to infuse new data into long-standing debates about the importance of carnivore predation on hominids and scavenging by hominids of the Pleistocene in East Africa. Evolutionary inference cannot be drawn uncritically from modern contexts. For example, the effect of firearms and modern subsistence activities must be considered. Yet human–carnivore interactions in rural Uganda during this century deserve attention because substantial populations of large carnivores survived amidst scattered human settlements until very recently (Naughton-Treves, 1996). Historical information, when carefully collected, can provide insight for students of human evolution.

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Methods

During much of the 20th century, conflict between humans and wildlife in Uganda has been widespread (Graham, 1973; Naughton-Treves, 1996). Agricultural settlements were scattered within a matrix of bush and forest, particularly in western Uganda (Taylor, 1962; Edmunds, 1997; Naughton-Treves, 1997). Lions and leopards inhabited every district in Uganda, but were particularly common in the western and northeast regions of Uganda (Ugandan Game Department Archives—UGDA, 1923–1994). Human–wildlife conflict occurred in more densely settled areas as well, even at the margins of cities like Kampala (UGDA, 1940–1946: p. 14). Large carnivores still attack humans on occasion, although these events are primarily restricted to the borders of parks and reserves (Naughton-Treves, 1997; Anonymous, 1997).

Systematic data on rates of encounter between humans and carnivores are unavailable. However, government archives do provide valuable information, if used cautiously. The UGDA recorded human–wildlife conflict nearly continuously from 1923 to 1994. Until 1962, expatriate Game Wardens of the British Protectorate of Uganda, reported (a) human casualties (injuries and fatalities) caused by large, wild animals, and (b) wildlife killed as part of "problem animal control operations." After 1962, Game Wardens of the newly independent Uganda continued record-keeping, albeit in less detail.

For a study of competitive interactions between humans and large carnivores, the value of the archives lies in the dual mission of the Game Department. Not only were they protecting the local citizenry from wildlife, they were often protecting wildlife from local people. For example:

> "... The lion population continues to be fairly strong and well distributed but because of ... the necessity to shoot cattle-killers and man-eaters, lion must be carefully looked after or else they will become rare."
>
> (UGDA, 1962–1963: p. 9)

Because the Game Department was charged with controlling problem animal populations while protecting them from extinction, they documented human–wildlife conflict as precisely as possible. Budgetary concerns also demanded precision. Thus they tallied rounds of ammunition, personnel losses, ivory revenues, etc. The accuracy of the government archives is further demonstrated by numerous fatalities mentioned, but not assigned to wildlife because no evidence could be found. The cautious search for evidence rather than off-hand attribution to wildlife characterizes the archives generally.

The Game Department archives unfortunately contain gaps and inaccuracies. The archives span many decades and were collected by many different observers, some of whom reported second- or third-hand information. Gaps reflect periods of warfare and civil instability (e.g., 1981–1986). Moreover, periodic change in administrative protocol may have affected the completeness of reporting. None of these sources of error introduces systematic bias, however, and yet three potential sources of systematic bias exist. First, we do not have reliable estimates of human or carnivore population density by region. Thus we are unable to calculate per capita attack rates or mortality rates. Second, the Game Department detailed casualties among employees and expatriates, but often failed to identify whether civilian victims were men, women or children. In fact, for 10% of reports, the number of civilian casualties was simply recorded as "few" or "many." We score these vague enumerations conservatively (one and two casualties, respectively). Finally, the archives are limited to official reports by game wardens; as a result the data are likely

Table 1 **Large carnivore attacks on humans in Uganda (1923–1994)**

	Attacks on humans			Percentage of attacks leading to fatality, by age-sex class	
	n	Injuries	Fatalities	Men	Women and children
Lions	275	25·1%	74·9%	53·0%	87·5%
Leopards	114	67·5%	32·5%	8·0%	75·0%
Hyenas	4	0·0%	100·0%	—	100·0%
Overall *N*	393	146	247	114	24

to underestimate illicit hunting and successful scavenging from kills.

To explore the effect of firearms in self-defense against carnivores, we classify victims dichotomously. Victims identified as farmers, pastoralists, or simply ''natives'' were considered poorly armed. Game guards, government employees, chiefs, and expatriates were classified as well-armed. Some victims (porter, tracker, poacher) were excluded as ambiguous. This dichotomy was increasingly blurred in the 1970s when many rural people held firearms (Rothchild & Chazan, 1988), so we restrict this analysis to pre-civil war data. Although gross, this dichotomy should distinguish victims who differ in their capacity to defend against carnivore attacks.

Results

Human casualties and losses

Between 1923 and 1994, government authorities recorded 636 human casualties (injuries plus fatalities) caused by wildlife. Excluding years with poor record-keeping (1940–1945, 1969–1970, 1980–1985) the annual average for the remaining 58 years was ca. 11 casualties per year (s.d. 15, range 0–67). It should be noted that severe injuries and fatalities are more likely to be reported than mild injuries or close encounters.

Of the 636 reported casualties, lions caused 275, leopards 114 and spotted hyenas, *Crocuta crocuta*, four (Table 1). Large carnivores were therefore jointly responsible for 61·1% of all human casualties. For comparison, large herbivores (mainly elephants, *Loxodonta africana*, hippopotami, *Hippopotamus amphibius*, and buffalo, *Syncerus caffer*) caused 33·5% of casualties and primates (baboons, *Papio cynocephalus*, and chimpanzees, *Pan troglodytes*) caused 5·4%. Information on the context of attacks (habitat type or party size of humans or carnivores) was not provided in the Archives.

Of the 393 human casualties caused by large carnivores, 247 were fatalities (62·8%). Because of small sample size, we dispense with analysis of hyena attacks hereafter. Lions and leopards differed markedly in the proportion of fatal attacks on humans (75·0% by lions *vs.* 32·5% by leopards). Buffaloes, baboons, elephants and hippopotami killed more of their victims than did leopards, with fatality rates of 49·2% (n=130), 70·9% (n=31), 67·3% (n=46) and 86·7% (n=30) respectively. Only hippopotamus attacks produced a higher percentage of fatalities than lion attacks. This may reflect the danger of drowning when fishers were attacked by hippopotami. Likewise, the apparent deadliness of baboons may reflect reporting biased towards the most severe attacks, typically involving children guarding fields (Naughton-Treves, 1996).

Of the 393 casualties to carnivores, 29·0% were men, 2·1% women, 4·0% children and

64·9% unidentified by age–sex class (Table 1). The unidentified fatalities were mainly rural Ugandans, whose deaths garnered less official attention that those of government employees. All government employees mentioned were men, but this does not explain the strong sex bias among casualties. Restricting the analysis to rural victims, 73% of identified casualties were men, 11% women and 16% children. Thus, the disproportionate mortality rate of men is not entirely a result of better records on male government employees. Nor is there any evidence that deaths of local women and children were under-reported, although local administrators were predominantly men and men probably reported casualties more often than women and children.

Men, women and children were vulnerable to different carnivores. Women and children were attacked by lions less often than by leopards ($n=24$: 33% *vs.* 67%). Men showed the converse pattern ($n=114$: lions 66% *vs.* leopards 33%). Both lions and leopards were more likely to kill women and children, than they were to kill men (Table 1). In sum, men were more often attacked by large carnivores, but women and children were more likely to die when attacked.

Using data from pre-civil war Uganda only, we examined the safety provided by firearms (estimated from the identity of the victims). When men were attacked by leopards, government employees suffered 0% mortality ($n=10$ casualties), while the poorly-armed locals suffered 11% mortality ($n=27$ casualties). When men fell afoul of lions, government employees suffered 60% mortality ($n=5$), while locals suffered 49% mortality ($n=69$). However, activity and party size may also have differed between the two groups, not just weaponry; this possibility could not be evaluated with these data.

The severity of attacks, measured as the ratio of fatalities to total casualties, declined over time for leopards, but not for lions (Figure 1). The decline in leopard fatalities may reflect a change in the age–sex composition of the victims (i.e., men die less often from leopard attacks than women and children, so increasing numbers of attacks on men would lower mortality rates) or a change in the behavior of predators or their victims. From the 1920s to 1930s, the proportion of men among the casualties of lions and leopards increased from 64% to 68%. By the 1940s and 1950s this proportion had increased dramatically to 82% and 85% respectively. The last decade with fairly continuous annual reports was the 1970s, when 93% of casualties were men. Hence, it appears that the observed decline in leopard fatalities over time can be explained in part by an increasing proportion of adult male victims (with their concomitant higher survival chances).

Reports of casualties sometimes indicated whether the victims were engaged in hunting ($n=162$) or non-hunting activities ($n=114$), immediately prior to attack. When some form of hunting activity was indicated, men constituted 99·3% of casualties. When the records identified a non-hunting activity (gathering, travelling, farming), men constituted 60·5% of casualties.

Some human fatalities resulted from defense of livestock against large carnivores (UGDA, 1946: p. 15). Livestock losses to leopards and lions were rarely enumerated, but in a single year in Mengo district, 23 cattle, 690 goats and 104 sheep were reported killed by lions and leopards (UGDA, 1927: p. 26). In their turn, humans scavenged from carnivore kills.

Human scavenging

There are nine reports which describe human scavenging from lion or leopard kills. In three of these, reference is made to this general practice, rather than to a specific incident:

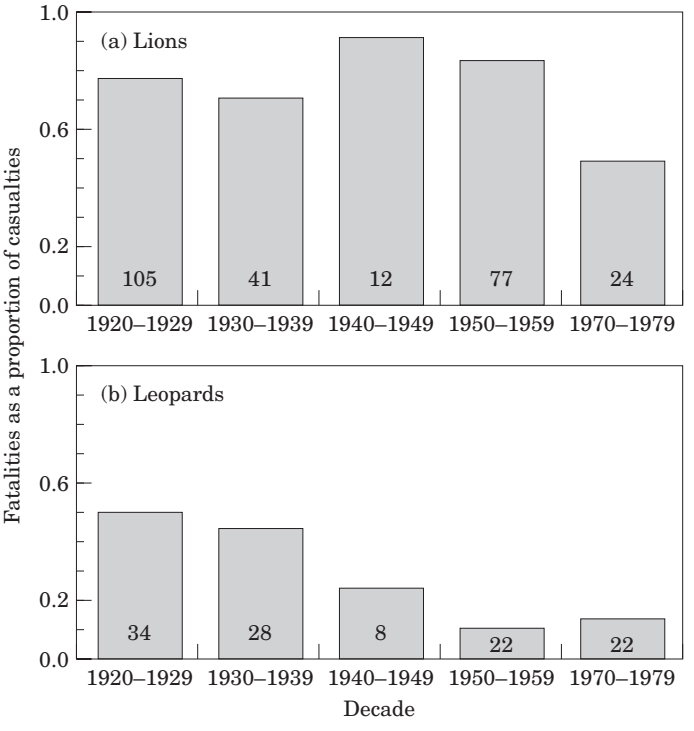

Figure 1. The proportion of carnivore attacks which resulted in death graphed over time (*y*-axis values were summed for each decade). Numbers within bars are sample sizes of casualties from lion attacks (a) and leopard attacks (b).

"... this lion ... was well-known to the [locals] ... It had regular beats, and, whenever it killed, the natives helped themselves to a portion of the 'kill'—naturally they were not anxious to lose their benefactor."

(UGDA, 1926: p. 26)

"... natives were out at dawn in all directions, looking for kills, and having located a duiker which had just been caught [by a leopard], instead of devouring it as so many would have done, posted a guard over the remains and hastened with the news to the Warden, who now turned poisoner, and by means of some judiciously introduced strychnine, terminated the mischievous careers of two leopards that evening ..."

(UGDA, 1932: p. 10)

"... One Game Guard was ... patrolling when he saw vultures and hoped to find meat left perhaps by lion or leopard, only to be confronted by an infuriated cow elephant which had just dropped a calf."

(UGDA, 1954: p. 67)

These three anecdotes suggest that scavenging was common, without specifying whether it was generally passive or involved active confrontation of carnivores. There were also six reports describing nine casualties resulting from active, confrontational scavenging (five injuries caused by lions defending their kills and four by leopards). Three examples:

"... a man ... collecting firewood ... came upon a lion eating a kob. Very foolishly he tried to drive the lion away to steal its meat, which the animal resented, showing its displeasure by springing on him and mauling him severely."

(UGDA, 1953: p. 36)

"... a Game Guard was slightly mauled by a leopard when he attempted to drive the animal off a kob that it had just killed. The leopard objected and attacked the Guard, who only managed to kill the animal after it had bitten

him in the thigh and arm. The Game Guard was punished for molesting the leopard.''

(UGDA, 1954: p. 36–37)

''. . . A leopard with two cubs spread alarm and despondency in . . . Toro in 1959. She was repeatedly driven off her kills by meat-greedy local people, and retaliated by attacking various innocent persons. A woman, a child, and a man were all victims, but luckily none was seriously injured.''

(UGDA, 1960: p. 39)

In sum, for several decades, humans have tried to scavenge from the kills of large carnivores. These attempts were often made by single individuals, even when unarmed. When these attempts failed or misfired in some way, the Game Department was notified. In all likelihood, most successes went unreported.

Humans killing large carnivores

Many carnivores were killed in retaliation both for livestock losses and human fatalities. We use two sources to estimate the number of carnivores killed by humans. Between 1923 and 1994, the Game Department killed 106 leopards and 376 lions during problem animal control operations. They also recorded the export of an additional 9162 leopard skins and 112 lion skins between 1924 and 1960.

During the first half of the century, the Game Department rewarded local citizens who killed problem carnivores:

''. . . Every endeavor is made to foster a spirit of aggression and retaliation, and rewards are paid to the lion slayers in all cases . . . brought to notice.''

(UGDA, 1929: p. 24)

''. . . Kigezi district continues to harbor some exceedingly large and dangerous leopards. One notorious man-eater, which had no less than eight human victims to its credit, was . . . killed by three local spearmen.''

(UGDA, 1929: p. 25)

By 1945, sport and commercial exploitation of leopards had caused a decline in their population, leading to their legal protection:

''. . . Revolutionary change in an animal's status resulted from Legal Notice No. 9 of 1945, which raised the hitherto persecuted and generally outlawed leopard, from the ranks of vermin, to that of the privileged which may be legally slain only by those licensed to do so.''

(UGDA, 1940–1946: p. 6)

In 1959, lions received similar protected status. Nonetheless, the Game Department subsequently killed 231 lions and leopards between 1970 and 1979. As recently as 1995, two lions were killed in Kabarole District under official control operations (Ugandan Wildlife Authority Report, 1995).

Discussion

The meticulous records of the Ugandan Game Department provide a rare glimpse into conflict between large carnivores and humans in East Africa. Carnivores repeatedly preyed on humans and their livestock in Uganda, and in turn, humans killed carnivores and occasionally drove them from their kills to scavenge meat. Despite the apparent symmetry of this relationship, large carnivores appear to have lost the competition, as witnessed by their endangered status and diminishing range in recent years. What may surprise the reader is how many humans suffered predation in Uganda this century, or even last year (Anonymous, 1997). Our data undermine a long-standing assumption:

''. . . if present-day evidence is valid large carnivores do not attack humans unless they are 'man-eaters' as a result of a disability or old age . . . As Louis Leakey used to say 'Man is not cat food'.''

(Clark, 1996: p. 343)

The Ugandan archives show that humans are occasionally ''cat food'', at least when the cats are provoked. Furthermore, only 14·0% of the lion attacks described in the archives were attributed to wounded animals, and 14·9% in the case of leopards. Even granting

that a proportion of carnivore injuries or disabilities were overlooked, the data still suggest that healthy animals were involved in attacks on humans. The evolutionary significance of this mortality requires scrutiny.

Conventional wisdom places a gulf between modern lifestyles and technologies and those of our hominid ancestors. For example, agropastoralists with firearms are thought to interact with carnivores in a manner wholly different from hominids of the Pleistocene. We argue that this gulf is large at the societal level, but far smaller when one considers individual humans hunted by lions or finding a leopard at a kill.

Carnivores killed rural Ugandans engaged in many different activities; some of these activities resemble those of Plio-Pleistocene hominids (e.g., hunting and gathering), while others do not (e.g., animal husbandry). While very few rural Ugandans today encounter large carnivores, some, like the Batoro and Banyoro, continue to hunt and collect food, fuelwood and medicinals in habitat occupied by the same carnivore species since the Pleistocene (Naughton-Treves, 1996; Edmunds, 1997). Even today, rural Ugandans face lethal conflict with large carnivores, but at a greatly reduced frequency due to the decline of carnivore populations in the last few decades. While the frequency of human–carnivore competition has declined, encounters remain life-threatening. Hence, we propose that twentieth-century predation on humans is likely to differ mainly in degree, not in kind, from that faced by Pleistocene hominids.

Some readers will argue that modern weapons have fundamentally altered the nature of human–carnivore conflict. After all, well-armed government authorities and professional hunters exterminated hundreds of leopards and lions without suffering commensurate losses. Yet, according to this dataset, well-armed hunters, once attacked, were as likely to be killed as the poorly armed victims. Nor were firearms required for active scavenging, as the anecdotes show. Humans armed with spears drove carnivores off kills even 70 years ago. The willingness of unarmed Ugandans, even women and children (see Results), to scavenge meat and risk attack by large carnivores testifies to much more than opportunism created by weaponry. Evidence from several other East African societies supports the argument that humans frequently chase carnivores from their kills. For example, the Bisa foraging people scavenge meat from lions (Marks, 1976: p. 78), as do the Hadza using no firearms (Woodburn, 1970; O'Connell *et al.*, 1988). In fact, the latter obtain 20% of their meat in this manner (O'Connell *et al.*, 1988; Bunn & Ezzo, 1993). Lightly armed or unarmed agriculturalists near a park in southern India are known to chase dholes (*Cuon alpinus*), leopards and tigers (*Panthera tigris*) from their kills (U. Karanth, pers. comm.). In sum, it is by no means inconceivable that hominids with little more than stone tools or long sticks might have driven carnivores from kills, particularly if they acted in a cooperative and coordinated fashion.

The Ugandan data support the view that early hominids could have chased large carnivores from their kills (Blumenschine, 1987, 1988, 1989; Bunn & Ezzo, 1993), but offer two refinements. First, encounters with lions were far more dangerous than with leopards. Therefore, we would predict that hominids scavenged more often from leopards than from lions and the habitat use of hominids might have been influenced by lion densities. Second, men were most often attacked by carnivores, although they were less likely to be killed than women and children. Men were attacked more often by lions than by leopards, while the converse held for women and children. This pattern may reflect a sexual division of labor or sex-differentiated ranging patterns among humans. We propose that this sex bias in

vulnerability to carnivores extends beyond the present data set.

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References

Anonymous (1997). Crocodiles kill 32 on Victoria shores. African Network News Bulletin, Uganda News, Kampala, Oct. 15, 1997.

Blumenschine, R. J. (1987). Characteristics of an early hominid scavenging niche. *Curr. Anth.* **28,** 383–407.

Blumenschine, R. J. (1988). Reinstating an early hominid scavenging niche: A reply to Potts. *Curr. Anth.* **29,** 483–487.

Blumenschine, R. J. (1989). A landscape taphonomic model of the scale of prehistoric scavenging opportunities. *J. hum. Evol.* **18,** 345–379.

Brain, C. (1981). *The Hunters or the Hunted? An Introduction to African Cave Taphonomy*. Chicago: University of Chicago Press.

Bunn, H. T. & Ezzo, J. A. (1993). Hunting and scavenging by Plio-Pleistocene hominids: Nutritional constraints, archaeological patterns, and behavioural implications. *J. Arch. Sci.* **20,** 365–398.

Cavallo, J. & Blumenschine, R. J. (1989). Tree-stored leopard kills: Expanding the hominid scavenging niche. *J. hum. Evol.* **18,** 393–399.

Clark, J. D. (1996). Commentary. *Curr. Anth.* **37,** 343.

Edmunds, D. (1997). Continuity and change in the resource management institutions of communities bordering the Kibale Forest park, Uganda. Ph.D. Dissertation, Clark University.

Graham, A. D. (1973). *The Gardeners of Eden*. London: George Allen & Unwin.

Marean, C. W. (1989). Sabertooth cats and their relevance to early hominid diet and evolution. *J. hum. Evol.* **18,** 559–582.

Marean, C. W. & Ehrhardt, C. L. (1995). Paleoanthropological and paleoecological implications of the taphonomy of a sabertooth den. *J. hum. Evol.* **29,** 515–547.

Marks, S. (1976). *Large Mammals and a Brave People: Subsistence Hunters in Zambia*. Seattle: University of Washington Press.

Naughton-Treves, L. (1996). Uneasy neighbors: Farmers and wildlife around Kibale National Park. Ph.D. Dissertation, University of Florida.

Naughton-Treves, L. (1997). Farming the forest edge: vulnerable places and people around Kibale National Park. *Geog. Rev.* **87,** 27–46.

O'Connell, J. F., Hawkes, K. & Blurton-Jones, N. G. (1988). Hadza scavenging: implications for Plio-Pleistocene hominid subsistence. *Curr. Anthropol.* **29,** 356–363.

Potts, R. (1987). Reconstructions of early hominid socioecology: A critique of primate models. In (W. G. Kinzey, Ed.) *The Evolution of Human Behavior: Primate Models*, pp. 28–47. Albany: SUNY Press.

Rothchild, D. & Chazan, N. (1988). *The Precarious Balance: State and Society in Africa*. Boulder: Westview Press.

Shipman, P. (1986). Scavenging or hunting in early hominids: theoretical framework and tests. *Am. Anth.* **88,** 27–43.

Speth, J. D. (1989). Early hominid hunting and scavenging: the role of meat as an energy source. *J. hum. Evol.* **18,** 329–343.

Taylor, B. K. (1962). *The Western Lacustrine Bantu*. London: Sydney Press.

Turner, A. (1992). Large carnivores and earliest European hominids: changing determinants of resource availability during the Lower and Middle Pleistocene. *J. hum. Evol.* **22,** 109–126.

Woodburn, J. (1970). *Hunters and Gatherers: The Material Culture of the Nomadic Hadza*. London: British Museum.