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THE SCIENCE OF 'MAN-EATING*' AMONG LIONS *PANTHERA LEO* WITH A RECONSTRUCTION OF THE NATURAL HISTORY OF THE 'MAN-EATERS OF TSAVO'

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ABSTRACT

The story of the 'Man-eaters of Tsavo' has been retold through script, cinema, and oral tradition in the 100+ years since their infamous 'reign of terror'. Despite their predictably broad popular appeal, the details pertaining to the natural history of these lions *Panthera leo* have never been reviewed. The skulls and skins of these lions have resided at the Field Museum of Natural History (Chicago) for over 75 years. An analysis of the skull of the primary culprit displays a traumatic injury that may have limited his predatory ability in subduing 'normal' prey. A sample of hairs, reflecting the diet of both man-eaters, is preserved in the broken and exposed cavities of their canines. Various additional circumstances likely contributed to their man-eating habit. The Tsavo incident closely followed the debut of rinderpest on the continent, which devastated cattle and buffalo, the primary prey of the Tsavo lion. The Tsavo 'nyika' consists of a dense thorn scrub thicket limiting visibility and passage, representing an ideal habitat for an 'ambush predator'. Finally, historical review of the literature reveals that 'man-eating' was not an isolated incident at Tsavo. This behaviour was well established in the vicinity of the railway bridge well before these infamous lions appeared, and continued well after their demise, suggesting a recurring opportunity, which may have evolved into a local behavioural tradition. In sum, virtually all of the recognised preconditions for man-eating outbreaks to occur were in effect at Tsavo in the 1890's.

INTRODUCTION

The 'Man-eaters of Tsavo' first gained infamy in the British press in 1900 (The Spectator, March 3) when they were reported to have caused a temporary halt to the construction of the

* We use the term 'man-eating' by convention, as attacks are not limited to 'men' and do not always conclude with consumption.

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'Uganda' Railway. This railway was to run from the Indian Ocean port of Mombasa, Kenya, to the shores of Lake Victoria, which was then located in Uganda. British engineer J.H. Patterson documented his attempts to dispatch the two adult male lions with detailed journal entries (Patterson, 1898–1899). These entries became the basis for his first-hand account, *In the Field* (London), first published at the turn of the century, and later as the basis for his book, *The Man-eaters of Tsavo and other East African Adventures* (Patterson, 1907). Every Kenyan schoolboy knows the story of the Tsavo lions, first through oral tradition and later through this popular reference. Two Hollywood films have further popularised the story: *Bwana Devil* (1953) and *The Ghost and the Darkness* (1997). Despite the popular appeal of this incident, no details concerning the lions themselves, or the circumstances surrounding this notorious man-eating outbreak, were published between Patterson's 1907 account and the brief review by Kerbis Peterhans *et al.* (1998). After reviewing historical accounts, recent literature, the original journals of J.H. Patterson, Game Department records, and the skulls and skins of the 'Man-eaters' themselves, we have identified these circumstances. This paper addresses some of the conditions that lead to man-eating in general and how these relate to the incidents at Tsavo over 100 years ago.

Several circumstances have often been associated with pantherid (big cat) attacks on humans. Sickly, injured, aged or emaciated pantherids, which are unable to secure their normal prey, can often become man-eaters (Corbett, 1944, 1948, 1954). Predators may also focus on abnormally behaving prey, with certain human behaviours probably qualifying. Among social carnivores (*e.g.* lions), the favouring of particular prey species (*e.g.* livestock or humans) can be passed from one generation of predators to the next, with the potential to become a local social tradition (Swayne, 1895; Taylor, 1959; Rushby, 1965). Historical records from Tsavo suggest that predation upon humans was a long-standing phenomenon. Humans were attacked and killed by lions in the Tsavo area well before construction of the railway began (1886, documented in Jackson, 1894) and continue at present, over 100 years after the infamous pair was dispatched (Kenya Wildlife Service, 1994–1998). Another factor, anecdotally mentioned in the literature, is the absence, depletion, or removal of typical prey, causing the predators to seek alternative food sources such as livestock. This brings lions into contact with humans, sometimes resulting in the inclusion of humans in lions' diets. Lions also develop a taste for humans after being 'provisioned' with dead ones. Environmental variables can be important since heavy cover is essential for 'ambush predators' to successfully stalk their prey (Schaller, 1972; Funston *et al*, 2001). Seasonal factors are also thought to be important as game disperses during the rains, making them more difficult to locate and secure (Jackson, 1894). In late 19th century Tsavo, all of these factors were in play concurrently and all may have played a role in the development of the world's most renowned man-eating outbreak. What follows therefore, is a critical review of these different scenarios and the likely role each of them may have played in the events at Tsavo over 100 years ago.

NOTES ON THE NATURAL HISTORY OF THE 'MAN-EATERS OF TSAVO'

Unlike the Tsavo of today with large tracts of open expanse, the Tsavo of the 1890's was composed of a nearly impenetrable, thorn thicket known as 'nyika'. The quest for ivory during the 19th century had eliminated elephants (*Loxodonta africana*) from much of eastern Kenya, including most of Tsavo (Thorbahn, 1979). This is why many of the porters transporting ivory through Tsavo at the time, originated far up-country, sometimes even from

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Uganda (Patterson, 1907, Preston, n.d.). Elephants are a keystone species and have a major impact on the vegetation and the large mammal community. The elimination of elephants from Tsavo caused a proliferation of dense woody and thorny undergrowth and eliminated herds of grazing ungulates from the vicinity. Preston (n.d.) describes this thick habitat in detail. Browsers, including dik-dik *Madoqua* sp. and black rhino *Diceros bicornis* increased. A review of Patterson's field journals (1898–1899) quantifies the animal species he encountered (table 1). There were no wildebeest *Connochaetes taurinus*. Hartebeest (hartebeest/hirola, *Alcelaphus buselaphus/hunteri*) and zebra *Equus burchelli/grevyi* were around but not common. Patterson never once refers to buffalo *Syncerus caffer* or cattle *Bos taurus* ssp. in his journal. This can be traced to the arrival of rinderpest on the continent in 1891, which had a devastating impact on the bovine populations (Lugard, 1893; Mettam, 1937). By the 1960's, the Tsavo elephant population had recovered and Tsavo became known as one of the largest elephant sanctuaries in East Africa (Leuthold & Leuthold, 1976). Therefore, the two large mammal species (elephant and buffalo) comprising most of the mammalian biomass in Tsavo today (*ibid.*), were virtually absent in the 1890's. In sum, by 1898, Tsavo had already been severely impacted by humans, resulting in vast anthropogenic differences between the Tsavo environment of the 1890's and that of today.

The 'Man-eaters of Tsavo' themselves consist of two adult male lions that are virtually devoid of manes in the conventional sense. They display a slight sagittal crest of hair that can be typical of some maneless lions. The second lion killed (FMNH 23969, figure 1) had slight cheek tufts as well as darkened chest patches while the first lion was without these adornments. They were photographed by Colonel J.H. Patterson (1907) after they were dispatched in 1898. Except for the severely broken canine and remodeled mandible and cranium of the primary culprit (FMNH 23970; figure 2), the man-eaters of Tsavo were adult male lions in their prime (6.5–8.5 years of age). Their squamoso-parietal sutures are obliterated making them at least 6.5 years old (Smuts *et al.*, 1978), but their maxillo-premaxillary sutures are not even partially closed, making them under 9 years old. Their teeth also betray this age range as they are yellowing and there is visible wear on the canine, incisor, P^3 and P_4 (>5–6 years of age, *ibid.*). Although these individuals may have been siblings due to their association and similar size and morphology, FMNH 23969 displays more apical wear than FMNH 23970. We doubt that their difference in age extends beyond one or two years.

Both animals were huge individuals as Patterson's published photos (1907) demonstrate. Patterson uses the following in describing the first lion: "enormous brute", "powerful beast in every way", (Patterson, 1898–1899). FMNH 23970 was 2.95 m long (nose to tail) and 1.12 m in height at the shoulder while FMNH 23969 was 2.90 m long and 1.22 m in height at the shoulder (*ibid.*). East African male lions average 0.96 m height at shoulder and 2.67 m in length according to Meinertzhagen (1938) who collected in the Athi-Kapiti Plains and in the Serengeti. Guggisberg (1975) provides an additional measurement: 0.91 m in height at the shoulder and 2.74 m long.

Patterson (1907) claimed that the man-eaters were prime-aged, healthy males and was so cited by subsequent authors (*e.g.* Selous, 1908; Akeley, 1923; Bradley, 1926; Guggisberg, 1961; Cloudsley-Thompson, 1967). We can only assume that this referred to the condition of their limbs and torso and that he did not inspect their dentition. Residing in the collections of the Field Museum of Natural History (FMNH) for 75 years, the two Tsavo lion skulls had not been differentiated from one another in any way. One of us (TPG) rediscovered these skulls in the collections of the Field Museum in the 1980's and subsequently deduced which was the first man-eater shot by referring to Patterson's discussion of the deaths of each

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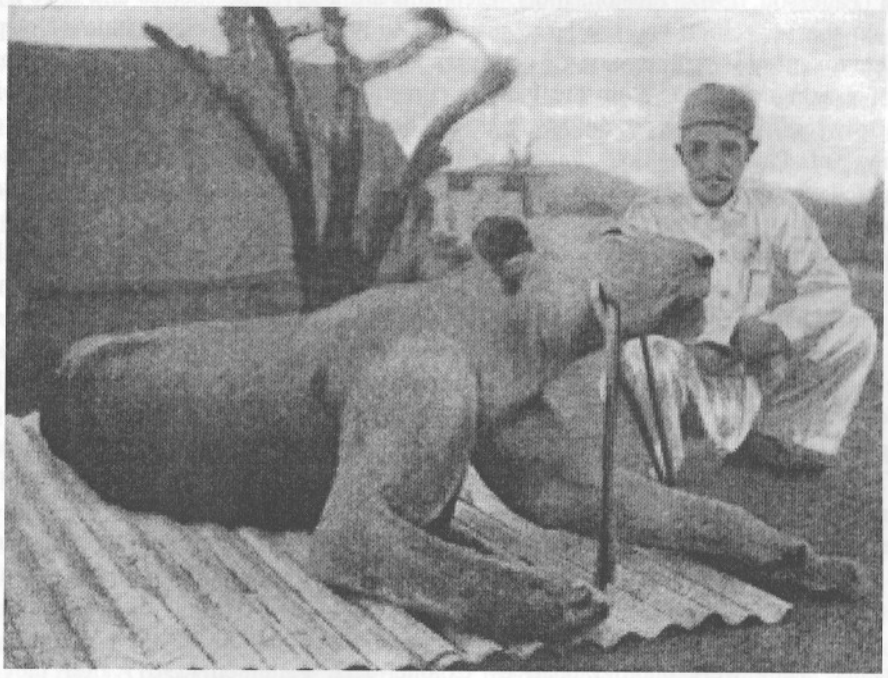


Figure 1. The second Tsavo man-eater slain (FMNH 23969).

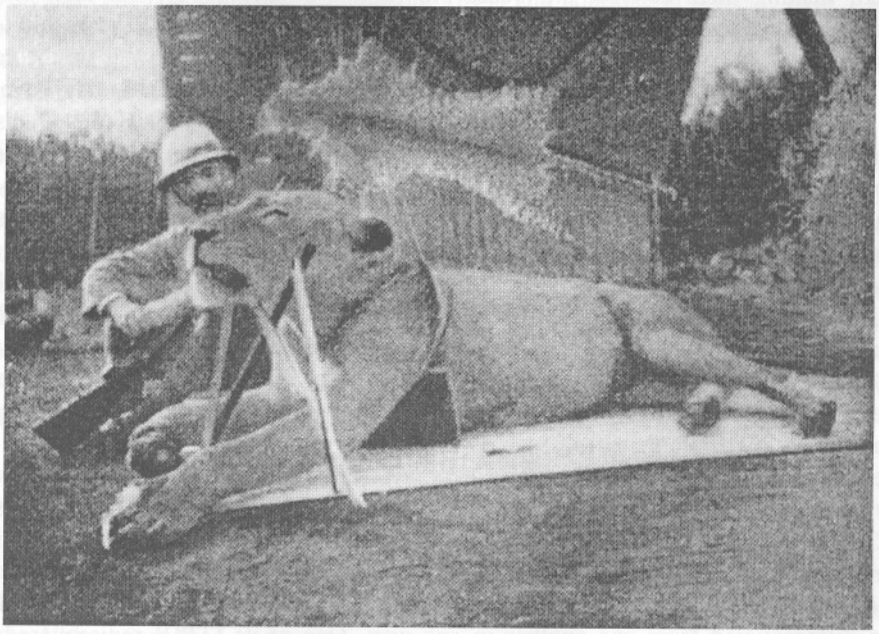


Figure 2. The first Tsavo man-eater slain (FMNH 23970).

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(Patterson, 1907). The first lion (FMNH 23970) was killed by shots to the body, while the second lion was shot with several bullets, including one to the head that shattered its zygomatic arch (FMNH 23969). Although Patterson states that he may have shot off the tip of the canine of the first man-eater slain (Patterson 1907, 1925), both lions are missing the apical end of their lower left canines due to pre-existing traumas.

Table 1. Fauna of Tsavo as represented in the field journal of J.H. Patterson, 1898–1899

Group	Common name	No. of times mentioned
Invertebrates	tsetse fly	1
	mosquito	1
	total	2
Reptiles	crocodile	1
	total	1
Birds	long-billed	1
	water fowl	1
	owl	1
	spur fowl	2
	sand grouse	3
	ostrich	4
	birds	5
	partridge	6
	guinea fowl	12
	total	35
Mammals	black panther	1
	baboon	1
	rabbit	1
	rat	1
	giraffe	1
	donkey	2
	monkey	2
	hippo	2
	waterbuck	2
	bushbuck	3
	leopard	3
	zebra	4
	wild cat	4
	hartebeest	4
	small deer	5
	goat	11
	rhino	14
	paa (dik dik)	16
	lion	70
	total	147

One of us (TPG) first noticed that the skull and mandible of FMNH 23970 were malformed due to a severely broken canine with exposed pulp vacuity. This observation was first noted in Kerbis Peterhans *et al.* (1998) with further details provided by Neiburger and Patterson (2000). This injury probably occurred fairly early in life as it led to obvious remodelling of the jaws (figures 3, 4). In particular, the root of the broken lower canine had been re-orientated

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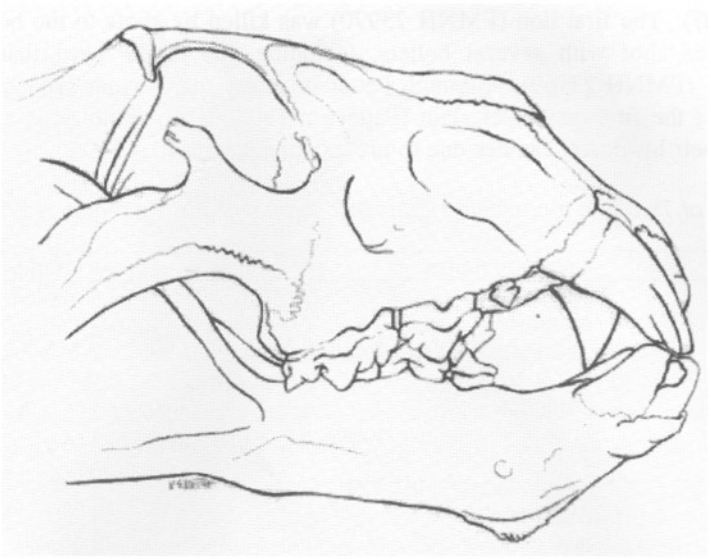


Figure 3. Lateral view of FMNH 23970 depicting forward projection of right upper canine. Compare with vertical left upper canine visible in rear (courtesy of K. Keith).

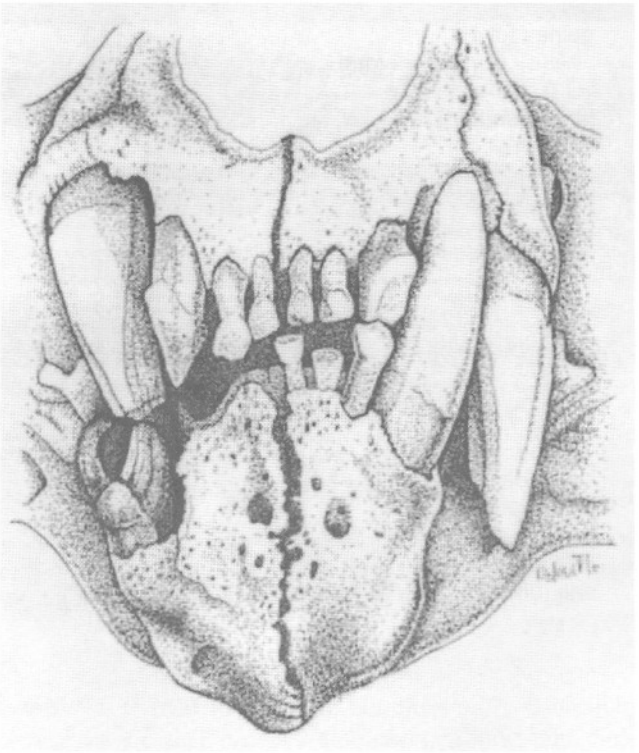


Figure 4. Anterior view of FMNH 23970 depicting broken cavity of lower right canine. Note asymmetry of upper incisors and canines due to broken and missing mandibular teeth (courtesy of K. Keith).

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towards the horizontal plane, and the mandible and associated dentition were completely asymmetric due to mal-occlusion. This injury (perhaps caused by a kick or a blow from the head/horn of a buffalo or zebra) could have prevented the lion from efficiently killing its normal prey.

The second man-eater (FMNH 23969) had slightly damaged teeth, specifically a broken upper left carnassial and broken lower right canine (photo in Patterson, 1907). The break to the upper left carnassial (P^4) is fairly fresh (several months in age) as reflected in its still sharp edges. The broken canine tip had been worn smooth from months, perhaps years, of wear. Despite these breaks, we do not believe these injuries were serious enough to affect this animal's predatory behaviour.

Their tenure as man-eaters may have been first mentioned by Ansorge (1899) who discussed lion attacks on a caravan in 1896 at the very crossing point of the Tsavo River over which the railway bridge was subsequently constructed. At this time, the Tsavo man-eaters would have been approximately 4.5 to 6.5 years old, full-grown 'sub-adults'. R.O. Preston followed Ansorge at the river crossing but preceded Patterson. Preston arrived in Tsavo in January of 1898 (Miller, 1971) and promptly recorded the deaths of two railhead workers due to lions (Preston, n.d.). J. H. Patterson arrived in March of 1898, and in late April 1898, attacks were again reported. By the time the 'reign of terror' was over, Patterson (1907, p.107) stated that the lions "had devoured between them no less than twenty-eight Indian coolies". The figure of 28 was cited by subsequent authors (Selous, 1908; Guggisberg, 1961; Miller, 1971). The first man-eater was killed on 9 December 1898 and the second on 29 December 1898 (Patterson, 1898–1899). Despite a gap of 20 days between the deaths of the two lions, there were no humans from the railway crew taken by the remaining man-eater. This leads us to believe that the first individual slain (FMNH 23970), with the long-term dental trauma, was the primary culprit. If we add the two deaths recorded by Preston prior to Patterson's arrival and the death discussed by Ansorge, the documented total could increase to 31.

Between March and December of 1898, a minimum of 28 humans was taken by these notorious lions. Over the years however, these figures have changed and the legend has grown. In his journal entries (1898–1899) Patterson only discusses the deaths of 14 individuals. In his 1907 book, he mentions 28 deaths of the imported and well-paid Indian labourers. We assume this figure is accurate since the British maintained precise accounting details (many of which are summarised in Hill, 1976). His only reference to victimised African labourers is summarised as "scores of unfortunate African natives of whom no official record was kept" (Patterson, 1907, p.107). In 1925 however, Patterson published a follow-up account where he states that 107 Africans were among the victims, thereby increasing the total killed on his watch to "135 Indian and African artisans and labourers" (p.1). Neiburger and Patterson (2000) expand the description to "135 armed men". Caputo (2000) expands the carnage to 140 people. The fact is, that there is no published record indicating that any more than 28 were officially recognised as being victims, although our review of the historical literature can possibly add three more.

If we are to assume however, that the figure of 135 is accurate, and further assume that 135 people would provide ca. 23 kg of edible meat per individual, the lions would have been left with 3060 kg of meat over the 10-month period. Schaller (1972) has estimated an adult male lion's daily intake to be ca. 7 kg of meat per day, resulting in 2540 kg per year, per lion, or 5080 kg for both adult male Tsavo lions for the 10-month period. Although these figures are well within an order of magnitude, there is no convincing evidence in Patterson's

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journals that this many people were killed by lions during his tenure in Tsavo. Furthermore, it appears that 'normal' prey were also consumed over this time period.

Although depicted as dedicated man-eaters, both lions came to bait and attacked livestock. The first lion slain approached a dead donkey used as bait, while the second carried off six tethered goats over a two-day period (17–18 December, 1898; Patterson 1898–1899). The severe injury to FMNH 23970 did not prevent it from feeding on 'normal' prey afterwards. Studies of their dietary preferences are currently being conducted through the analysis of several thousand animal hairs, removed from the broken canines of the man-eaters. Preliminary results provided by Ogeto Mwebi (personal communication) indicate that these hairs are mostly from the lions themselves, lodged in the canine vacuities during bouts of grooming. Mwebi (personal communication) has tentatively identified the following prey species: zebra, porcupine (*Hystrix cristata*), warthog (*Phacochoerus aethiopicus*), impala (*Aepycerus melampus*), eland (*Taurotragus oryx*), and oryx (*Oryx gazella*). To date, there is no evidence of human hair, which suggests that immediately following the break to the canine of the first man-eater, humans did not suddenly appear on the menu. If we do find evidence of humans, we will be able to distinguish African from Indian victims. However, since lions prefer human viscera and large fleshy parts, including the buttocks, thighs and arms (see figures of human victims in Kingsley-Heath, 1965; Beard, 1988), hair-bearing areas such as the cranium and perhaps the pubis may not be consumed. This may explain the absence of human hair in our samples. What is clear is that these lions were not obligatory man-eaters and that they continued to pursue prey other than humans.

FOSSIL RECORD AND MODERN HISTORY OF MAN-EATING

For as long as they have co-existed, primates, along with ungulates, have been the primary base of prey for African pantherids (Brain, 1981). For most of their history, extinct and living hominids have represented little more than a vulnerable, slow moving, bipedal source of protein for the big cats. In the Plio/Pleistocene of South Africa, *Australopithecus robustus* was the single most common prey item for leopards *Panthera pardus* with a minimum of 88 individuals represented at the site of Swartkrans (Brain, 1981). The newly discovered South African site of Drimolen promises similar results (Keyser *et al.*, 2000). The earliest reputed hominid fossil was also said to have been killed and dismembered by a carnivore (Fox, 2000). While *Homo* sp. seems to have been more effective in avoiding predation than *Australopithecus*, based on fewer remains in fossil lair sites (Brain, 1981), early *Homo*, nevertheless, remained on the menu. In fact, paleoanthropological material from South Africa, which has provided most of the fossil evidence for the early stages of human evolution, appears to have been primarily accumulated by large predators, particularly pantherids and hyaenids (Brain, 1981; Kerbis Peterhans, 1990).

European Paleolithic rock art depicts cave lions embedded with arrows or spears (figure 1 in Frobenius, 1933; Begouen and Breuil, 1958; Ruspoli, 1987). One of the earliest historical depictions of man-eating that we have found is the nearly 5,000 year old 'Battlefield Pallette' depicting a lion eating, and/or killing, dead or wounded Libyans during a clash with the Egyptians (Aldred, 1980). Bushmen rock artists illustrate numerous scenes of lions dismembering humans as well as human retaliation (Tongue, 1909). Stow (1905) writes that lion fed upon the flesh of Bushmen even more than their sheep. With the advent of the colonial era in Africa and Asia, documentation of man-eating became more regular. This coincided with the exploration of continental interiors in the 19th century, the debut of 'big

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game trophy hunting', and the construction of inland railways in the late 19th and early 20th centuries (Sowerby, 1923; Hill, 1976).

Man-eating is not unusual, nor necessarily 'aberrant'. From the late 19th century up until the present, man-eating incidents by pantherids in Africa and Asia have continued. During a five year period in the 1920's, 7,000 human deaths due to tigers *Panthera tigris* were reported in India (McDougal, 1987). The Sanga man-eaters killed over 161 people in SW Uganda in the mid to late 1920's (Temple-Perkins, 1955). In the 1930's, lions killed around 1500 people in a 150 square mile area of southern Tanzania (Rushby, 1965). Between 1978 and 1984, tigers killed a minimum of 128 people in Kheri, a small Indian District in Uttar Pradesh. Three hundred eighteen people were killed by tigers in the mangrove swamp forests of the Sundarbans Tiger Reserve between 1975 and 1981 (Sanyal, 1987). A minimum of 193 lion attacks resulting in 28 human deaths, were recorded from areas adjacent to the Gir Forest (India) between 1977 and 1991 (Saberwal *et al.,* 1994). In sum, human and pantherid conflicts have existed throughout their coexistence, with evidence for sustained and localised outbreaks of attacks on humans.

ACCESS TO INJURED, SICK OR DEAD HUMANS

Slave and Trade Caravan Routes

Most carnivores, especially lions and hyaenas *Crocuta crocuta*, are facultative predators and scavengers, actively hunting or scavenging depending on the circumstances (Schaller, 1972; Kruuk, 1972). The slave trade in East Africa promoted the consumption of humans, as dead or dying slaves were abandoned along caravan routes. A slave trader told A.J. Swann (cited in New, 1874) that any slave too weak to carry his load was abandoned or killed at once in order to discourage others from refusing to carry their burdens. During Livingstone's travels along caravan routes in central Africa, he often encountered human remains. He estimated that only one in five slaves reached the coast alive (cited in Miller, 1971). With 20,000 slaves imported each year to Zanzibar alone, there was probably a minimum of 80,000 humans lost annually along the northern caravan routes. This huge number of abandoned, sickly, dying, and dead, represented a regular bonanza to any carnivore prepared to take advantage of them.

The 'Uganda railway' was built along a Swahili caravan route that had been used for decades. The caravan route maps of Wakefield (1870) are quite similar to those of Johnston (1899) and the railway line is shown to closely parallel the route used by 'explorers and caravans' (Hill, 1976). At the Tsavo River, Patterson (1907) describes his tent as being pitched close to the former caravan route to 'Uganda'. He provides a photograph of the crossing point of the caravan trail over the Tsavo River (figure 5). Preston (n.d.) discusses this same caravan trail, stretching along the right (south) bank of the Sabaki River.

Trade routes also generate extensive 'debris fields' and condition the local carnivores to a highly predictable food source. People and goods moving along the caravan route included human slaves, porters, ivory, luggage, and foodstuffs. Coast-bound Wakamba traders transported livestock including sheep (*Ovis aries*), goats (*Capra hircus*) and cattle. In the late 19th century, European expeditions joined the mix, travelling along the same routes as those plied by Arab and African traders. First hand accounts of these caravans include those by French-Sheldon (1892), Lugard (1893), Neumann (1898), Ansorge (1899), Patterson (1907), and Preston (n.d.).

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Figure 5. Caravan crossing the Tsavo River (Patterson, 1907).

Despite proclamations banning the international trade in slaves (1873, 1876), and the similar edict in 1890, an illicit slave trade continued through the Tsavo region during the late 19th century; slave ownership was not banned until 1907 (Miller, 1971). One of the reasons the British claimed to have constructed the railway was that its development would help to put an end to the illicit slave trade, which still flourished in the late 19th century: "After a railway has existed for some time there cannot be....any other kind of locomotion to compete with it....If a railway could exist from this lake to the coast, caravans could no more be employed as they are employed now to carry ivory" (Lord Salisbury, 1891 quoted in Hill, 1976, p. 54). It was reasoned that an efficient and rapid alternative in the transport of goods would eliminate the profitability of all caravans.

However, even the end of the formalised slave trade did not end the regular loss of human life along this route. Selous (1908) depicts lions posted around campfires waiting for opportunities. Porters hired to carry ivory and trade goods were abandoned in the bush after dying from exposure (Portal, 1894) or suffering injuries or disease (French-Sheldon, 1892; Lugard, 1893). French-Sheldon's caravan came across an abandoned 'ill wretch' at Buru in 1891, "dying from hunger and neglect who was unable to proceed with a caravan....and turned adrift, without adequate means, to reach the coast as best he could or drop dead in the bush" (p. 203). At the end of a long days march, porters often limped into their camps with broken bones and severe injuries (French-Sheldon, 1892). Lugard (1893) describes liberating slaves in a caravan he encountered inTsavo in 1890, and speaks of a paralysed 'porter' being abandoned to hyenas at the Voi River. He concludes, "I have never seen anything approaching the carelessness of human life and the callousness to human suffering which seem to characterise some methods of African travel" (Vol II, p. 544).

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French-Sheldon (1892), Ansorge (1899) and Patterson (1907), passed westward along the Tsavo caravan route and criss-crossed with caravans moving east. In Patterson's chapter, entitled 'The Stricken Caravan' (1907), he describes a caravan of 4,000 porters (Basoga and Baganda) moving from Uganda to Mombasa in 1898. On their return to Uganda, the entourage again passed Patterson's camp on the Athi-Kapiti Plains. An epidemic of dysentery had swept through the contingent, perhaps linked to their drastic change in diet along the way. After each day's march, dozens were left along the route; the group could not stop as food and water were always at a premium. Thirteen dropped out in the vicinity of Patterson's tent and despite his best efforts, only seven were saved. Along the track, Patterson estimated finding a swollen corpse every 100 m. When passing one of their abandoned camps, Patterson encountered about 12 fresh graves that had already been disinterred by scavenging hyenas.

Burial practises, epidemics, warfare

Local burial practises can also encourage the development of man-eating behaviour by providing easy access to human corpses. The Masai simply abandoned their dead, and sometimes the 'near dead', in the bush to hyenas and lions as did the Kikuyu (Percival, 1925; Saitoti, 1980; Read, 1984). French-Sheldon (1892) describes coming across the corpse of a deceased Masai, weighted in armlets and leglets. Selous (1908) describes an incident near Bulawayo, Zimbabwe where an elderly woman was dragged alive and tied to a tree for the hyaenas. In the same volume, Selous depicts hyenas hovering around an abandoned corpse. Melliss (1895) describes picking up an elderly woman who could not keep up with her clan, and who was left to fend for herself along a Somali caravan route. Gouldsbury (1916) writes of the Somali:

> "Women generally, and more especially when old and decrepit, are of very little account among the Somali. If unable to keep up with the kafila (=caravan) on the march, they are often abandoned and left exhausted on the side of the road, either to follow as best they can or to be devoured by a hungry lion, should one happen to pass that way" (p. 167).

In the Taita Hills, above the Tsavo caravan route, the Wataita dig up their dead and then place skulls in rock shelters, while the people of Taveta disperse the bones of the dead in the bush and place the skulls in sacred tree hollows, rock shelters, or earthen pots (French-Sheldon, 1892; Adamson, 1967). The Wakamba peoples inhabiting the Tsavo region were said to leave the bodies of 'peasants and women' and even the mortally infirm in the bush 'for the hyaenas to devour' (Hobley, 1910; Lindblom, 1920).

In India, Corbett documents several instances of man-eating outbreaks by leopards and tigers. These include the Rudrapryag Leopard, which killed 150 humans (1918–1926) following an influenza outbreak that killed over one million people (Corbett, 1948), and the Panar Leopard which killed 400 humans (1905–1907) following a severe cholera outbreak (Corbett, 1954). Many Hindu families cannot afford the expensive funeral pyre necessary for a proper cremation. Instead, the dead are abandoned with a red-hot coal in their mouth. It is possible, but doubtful, that Hindu railway workers dying in Tsavo were disposed of in this fashion. There was no shortage of firewood; lions were kept at bay during the night with non-stop fires. In any case, not all of the imports were Hindi, as Patterson himself (1907) speaks of the rivalries between Muslim and Hindi labourers.

Between 1898 and 1899, an outbreak of small pox and famine in Kenya killed thousands of Wakikuyu. The dead and near dead were abandoned in the bush to be devoured by

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carnivores (Percvial, 1925). Once the diseases abated and the supplies of corpses ran out, the large numbers of hyenas turned their attentions towards living humans. Hyenas started taking children at dusk and grabbing adults as they slept (Percival, 1925). Miller (1971) estimates that 25,000 Africans were felled by disease and starvation during this time (1898–1900). Such inadvertent provisioning of carnivores has often been correlated with attacks on humans. Even today, provisioning of hyenas by tourist outfitters can lead to human fatalities (Singer, 2000).

Patterson (1907) and Hill (1976) again provide analogies for the situation in Tsavo in 1897–1898. A severe famine, caused in part by a severe drought caused thousands of local Wakamba to die of starvation during the time the railway was being built through Tsavo (Miller, 1971). In their desperation, Wakamba would attack and slaughter isolated railway maintenance gangs in order to steal their food (Patterson, 1907). Death among the Wakamba due to a smallpox outbreak was also devastating at this time. Despite massive relief efforts, there was not enough treatment (lymph) to go around (Miller, 1971). The human toll among the Indian coolies imported to work on the railroad was also substantial: 340 of 7,131 died between 1897 and March of 1898. Death was mostly due to malaria, diarrhoea, and dysentery; an additional 705 were debilitated (Hill, 1976), with many being returned to India.

During civil unrest and conflict, large pantherids have been known to kill humans after having regular access to human corpses. As discussed earlier, the 5,000-year-old 'Battlefield Palette' depicts lions consuming humans following a battle in Egypt (Aldred, 1980). In the Arakan district of Burma, tigers had not previously claimed many human victims but during World War II, they suddenly turned their attentions to live and dead soldiers (McDougal, 1987). Caputo (personal communication) describes at least three instances of tiger attacks on humans during his time in Vietnam (1966–1969), an observation confirmed by Jackson (1985).

A similar scenario was documented in Tsavo during World War I (von Lettow-Vorbeck, 1920). The Germans, colonial powers in Tanganyika, and the British, who colonised Kenya, had military conflicts in the vicinity of Tsavo National Park with lions also taking their share. General Phillips, based in Voi for three months in 1915, lost three Indian soldiers to lion in the vicinity of the Tsavo River (Trzebinski, 1986). When the war began, noted game ranger A. B. Percival was charged with defending the railway against sabotage from the Germans. Sentries were posted and according to Percival (1928):

> "Lions were a veritable curse; man after man on sentry duty was taken, till it seemed sheer cruelty to put a man on such duty at all. Sentries were doubled and still men were taken. It needs little imagination to realise the case: two men at their post, bush all round and close up—it was inviting attack by lions." (p. 286).

During WW I, the wounded and deceased not recovered by nightfall, were assumed to be taken by this carnivorous entourage (Percival, 1928).

PREDATION ON LIVESTOCK: HUMAN-CARNIVORE CONFLICT

Historical sources

The initial attraction of large carnivores to humans can also center on a supply of livestock and pack animals. Herodotus may have been the first to discuss lions killing domestic stock (baggage camels, *Camelus dromedarius*), when they were described attacking Xerxes' caravans during his trip through Paeonia (Rawlinson, 1992). In Africa, the first long-horned,

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Nile valley cattle (*Bos primigenius*) were domesticated by 4,000 BC (Rouse, 1972). The first long-horned, humped cattle (*Bos taurus indicus*) arrived in Africa about 2,000 B.C., when they crossed from southern Arabia into the horn of Africa. The presence of domestic stock, particularly cattle, contributed to future associations of livestock, humans and lions.

After coming into contact and conflict with humans while killing domestic stock (Swayne, 1895; Neumann, 1898; Borradaile, 1928), predators educate themselves on the sights, sounds, and activity patterns of humans; they may switch to herdsman and humans in general (Layard, 1887; Caldwell, 1925; Percival, 1925, 1928; Pitman, 1931; Hunter, 1952; Guggisberg, 1975; McDougal, 1987). Four of the eight man-eating tigers discussed by Corbett (1944, 1948, 1954) were also notorious cattle killers, confrontations that led to direct conflict with humans. For example, the Chuka man-eater (Corbett, 1954) attacked and killed cattle. On one occasion, it was disturbed by, and subsequently killed, a young herdsman looking for his cattle, thereby beginning his man-eating career. The Chowgarh man-eater alternated between preying upon cattle and humans and ultimately became more focused on humans after its large cub was killed. This cub had assisted her in bringing down cattle.

Swayne (1895) discussed a parasitic relationship between humans and lions in Somalia. This revolved around a detailed calendar of caravan movements which was influenced by shipping schedules and seasonal availability of caravan-transported goods:

> "The movements of the native encampments seem chiefly to influence the changes in the quarters of the lions, the latter following the karias (=herds) as they move to fresh pasture. When a family with its flocks and herds and its karias (*sic*), moves, its attendant lions, if there should be any, accompany it, being sometimes man-eaters and more often cattle-eaters. Last June my own caravan, while returning to the coast from Ogaden, was followed by a pair of hungry lions. We discovered this by chance, when some scouts of mine, happened to go back along the road" (p. 293–294).

Pitman (1931) describes an incident in SW Uganda in 1928 when four lions claimed 15 cattle in a few weeks. Little attention was paid to this incident and due to a communication gap, nothing more was heard for several months. Within nine months, humans were included among the victims. Before they were destroyed, they had claimed more than 250 head of cattle and no less than 22 humans.

In historic Tsavo, at least three circumstances brought about massive movements of people and their accompanying livestock: caravans, the building of the railway, and troop deployments during World War I. When mass movements occur, infirm and injured livestock and food debris are left to the carnivores. The situation for Tsavo was particularly acute, as the region is known as the 'nyika', a dry, thorny shrubland with particularly low prey density (Leuthold & Leuthold, 1976).

French-Sheldon (1892), Lugard (1893), Ansorge (1899), and Patterson (1907) all state that caravans, including those passing through Tsavo, were routinely stalked by hyenas and/or lions, attracted by the food refuse as well as the livestock (sheep, goats, cattle, and donkeys *Equus asinus*) that often accompanied these expeditions. French-Sheldon (1892) writes:

> "When we camped for the night we were obliged to form a hedge of thorn-bushes and circle the encampment with huge bonfires to keep the wild beasts from attacking us. It was terrifying to hear the continuous roar of lions resounding on all sides.....and to see the glare of hyena eyes in the darkness of the umbrageous surroundings. A sense of abject helplessness momentarily possessed me...."(p. 162).

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Bringing large numbers of domestic ungulates into a naturally prey-depauperate region as Tsavo, is an obvious attraction to the local carnivore community.

During the mid-1890's, advance railway crews in the Tsavo area were charged with clearing bush and the construction of embankments ahead of the Uganda Railway. Hill (1976) writes that in 1897–1898 over 90% of the 1502 camels, donkeys and cattle used for transport had died. These animals were victims of tsetse flies, lack of water in the Taru desert (Patterson, 1907; Hill, 1976), and other ailments. During World War I, there was substantial mortality among the thousands of transport animals fuelling the war effort against the Germans in the Tsavo region. The British were actually grateful that carcasses of dead and dying transport animals (up to 20 per day) could simply be abandoned in the bush, 100 m from camp. Lions and hyenas followed in the wake of troop movements and "were assured of a feast every night" (Percival 1928, p. 295). Percival states that, with such inadvertent provisioning, the boldness of the lions and hyenas around army camps grew. He continues:

> "When on safari in the reserve in 1919–1920, I was struck by the boldness of the hyenas; they hung round the camp at night, coming to such close quarters that they kept the dogs barking incessantly. I felt quite sure that this unusual temerity, greater than I have known the brutes to display anywhere else, may be explained by their experience during the war" (p. 295).

Percival portrayed lions of the coastal region as particularly large and aggressive. Soldiers mounted on horseback came across lions that:

> "....learned that food in the shape of horses abandoned on account of injuries or sickness were to be had without exertion on their part, and they dogged the mounted men day and night. As this was near the German lines, firing was strictly forbidden; hence the lions grew bold and exceedingly troublesome. They would come fearlessly up to the very outskirts of a camp" (p. 287).

Human-carnivore conflict in Tsavo: species profiles, sex, age, and seasonal data

In Kenya today, pastoral peoples can be compensated for the loss of domestic stock. Kenya Wildlife Service has established 'incident report' log-books that document the circumstances surrounding conflicts between carnivores and humans. Between 1994 and 1998, a total of 121 incidents between large carnivores and humans and their livestock were registered by KWS officials based in Voi (Tsavo East National Park, table 2). Lions were responsible for 93% of these incidents. Collectively, cheetah, leopard and hyenas accounted for only 7% of the incidents; they exclusively attacked sheep and goats. In areas where they co-occur with lions, leopards typically select for smaller prey (Kerbis Peterhans, 1990; Fay *et al.*, 1995; Treves and Naughton-Treves, 1999). Conversely, lion predominately attacked cattle (63%), with sheep and goats secondary (27%).

Specific data for lions is detailed in table 3. Male lions attacked cattle more often (41/71=58%) than female lions (30/71=42%), while females preferentially attacked sheep and goats (18/30=60% vs. 12/30=40%). Multiple killings were relatively common. Females with cubs killed more individuals per attack than either male lions or females without cubs, averaging 4.8 sheep/goats and 2.5 cows per attack. Male lions averaged 3.25 goats and 1.6 cows per attack, while solitary females killed an average of 1.4 sheep/goats and 1.3 cows per attack. Female lions with young were more prone to multiple kills, taking at least four goats on six occasions (on one occasion 20 were killed); 3–6 cows were killed on eight occasions. One male lion killed 18 goats, while individual leopards killed eight and 10 goats on separate occasions, obvious examples of 'surplus killing' (*sensu* Kruuk, 1972). According to Kenya

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Wildlife Service archives, the most recent incidents of 'man-eating' at Tsavo East N.P. were recorded in October 1994 and July 1998.

Table 2. Kenya Wildlife Service, Incident Log Books 1994-1998 representing 121 Incidents Voi, Tsavo East National Park

Species	Total no. of attacks (%)	No. of attacks on cattle (no. killed)	No. of attacks on sheep & goats (no. killed)	Attacks on people D/I/T*	Other attacks
Lion	112 (93%)	71 (127)	30 (108)	2/4/2	3
Leopard	4 (3%)				
Males	3		3 (21)		
Females	1		1 (5)		
Hyaena	2 (2%)				
Male	1		1 (1)		
Female	1			0/0/1	
Cheetah	3 (2%)				
Male	2		1 (4)	0/0/1	
Female	1		1 (1)		

*Death/Injury/Threat

Assuming an equal sex ratio, male lions were more likely to attack domestic stock than females (61 vs. 51 attacks). Data from most African localities indicate that adult female lions typically outnumber adult males by ratios ranging from 1.4:1 to 4:1: Lake Manyara 3:1 (Makacha and Schaller, 1969), Kafue 1.7:1 (Mitchel *et al.*, 1965), Nairobi National Park 3:1 (Rudnai, 1973), Serengeti plains 3:1 (Adamson, 1964) and 2:1 (Schaller, 1972), and Kruger National Park 1.4:1 (Anonymous, 1960). Schaller (1972) describes more equal, but male-heavy sex ratios in the Serengeti woodlands while Rogers (1974) describes the same for lions in Selous National Park, Tanzania. Preliminary data from Tsavo (Russell, personal communication) indicate a predominance of females. Among 64 lions distributed between five prides, Russell only documented 10 adult males. This suggests that the impact of male lions in Tsavo is especially disproportionate to their numbers. However, according to KWS archives, female lions with dependent cubs can be especially destructive; they accounted for the highest number of kills per attack. Between 1994 and 1998, adult male lions were mostly responsible for attacks on humans in Tsavo East National Park, accounting for five of six attacks (83%) and both deaths.

Several authors have speculated on possible seasonal correlations of human-lion conflict. For eastern Africa, Jackson (1894) claims that attacks should occur after the rains, between March and the end of July, when prey are dispersed. Guggisberg (1961) restates this hypothesis, but provides no data. He asserts that during the wet season in Tsavo, lions become more troublesome for pastoralists. He attributes this to the dispersal of game making them harder to secure. He further adds that the rustling of the taller grass during this time of year alerts potential prey to the approach of predators. However, modern data from the Tsavo East incident report logs do not support Guggisberg's assertion. The wettest months in Voi, Kenya (Tsavo East NP) are typically March, April, November, and December (Kenya Government, 1970). During the five-year period for which we have data, there were a total of 29 incidents with lions reported during these 20 months (4 months x 5 years), an average of 1.45 per month (figure 6). There were a total of 83 incidents with lions over this same

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Table 3. Condensed Lion Data, Incident Log Books 1994–1998 Voi, Tsavo East National Park.

	No. of attacks	No. of attacks on cattle	No of cattle killed	No. of attacks on sheep/goats	No. of sheep/goats killed	Attacks on people D/I/T*	Attacks on others‡
	112	71 (63%)	127	30 (27%)	108	8 (7%)	3 (3%)
Males	61	41 (67%)	66	12 (20%)	39	2/3/0 (8%)	3 (5%)
Females	51	30 (59%)	61	18 (35%)	69	0/1/2 (6%)	
Females w/young	33	19	47	13	62	0/0/1	
Females w/o young	18	11	14	5	7	0/1/1	

Percentages calculated by Row rather than Column
* D/I/T: Deaths/Injuries/Threats
‡ others: donkey, camel, ostrich (*Struthio camelus*)

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five-year period during the remaining eight months, actually a higher average of 2.1 per month. However, given the anomalous nature of the rains in recent years, and the impact of El Nino, a more thorough investigation would look at the specific rainfall pattern for each month under consideration, an angle we are currently pursuing.

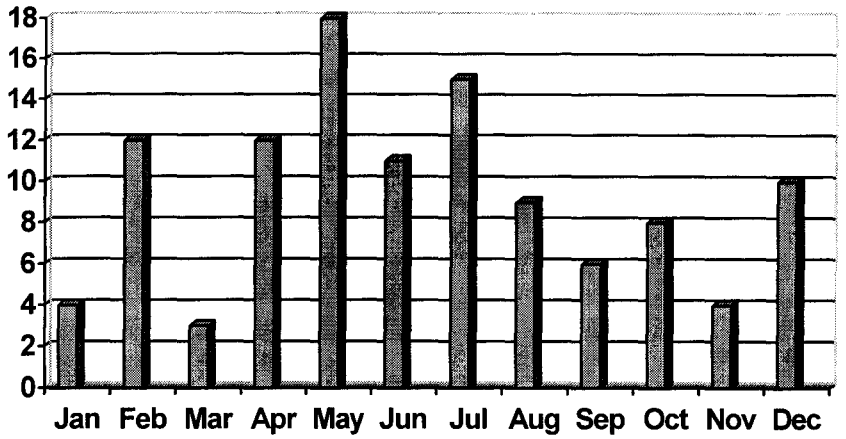


Figure 6. Monthly 'incidents' between lions, people and livestock, Tsavo East National Park 1994-1998.

However, if the season of vulnerability is expanded to the continuous five-month period suggested by Jackson (March–July), his seasonal hypothesis is confirmed. The March–July data yield 59 lion incidents over the 25-month 'wet' period (2.4/month) compared with 53 incidents over the 35-month 'dry' period (1.5/month). In fact, four of the five busiest months for 'incidents' occurred during these five months. This approach to seasonal data is appropriate because the rains provide temporary pools of water and new growth: these conditions extend beyond the period of actual rainfall and encourage ungulates to remain dispersed.

We were hopeful that the field journal of Patterson (1898–1899) would enable us to test the seasonal hypothesis, but he only documents 14 deaths at Tsavo in 1898. Remarkably however, all 14 are limited to the supposedly wettest months: March (n=4), April (n=4), November (n=3) and December (n=2), with the slight exception of a single person taken on 1 May. Patterson (1907) writes that some months then transpired (apparently May–October) before lions resumed their attacks. During this time however, he records five deaths from adjacent areas, including two from the railhead (now advanced), one from Ngomeni (10 miles away), and two others, but none from his camp on the Tsavo River. Nine deaths were not recorded in his journal and subsequent book. Although this might appear to confirm the seasonal hypothesis, 1898 was an anomaly in rainfall patterns. A severe drought began with the failure of the long rainy season in April/May (Hill, 1976) greatly contributing to the aforementioned starvation of the Wakamba.

MAN-EATING: A SOCIAL TRADITION

Prolonged, localised outbreaks

Although lions have diverse feeding preferences, specific lion populations are known to

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specialise on specific prey species. This indicates a behavioural tradition, which, in a social species, is passed down from one generation to the next (*e.g.* a cultural tradition). For the Busanga Flats, Mloszewski (1983) discusses 'buffalo-selective predation' reflected in lion proficiency in tracking buffalo herds, pulling down individuals, 'buffalo-killing proficiency', and even in their ignoring of other potential prey while seeking out remote buffalo. Other lion populations also have distinct prey species preferences (*e.g.* pigs, zebra/wildebeest, reviewed in Guggisberg, 1975).

In a few instances, lion specialisation on humans has been recorded. Rushby (1965) documented the most prolonged and devastating outbreak of man-eating by lions in Africa in the Njombe District of southern Tanzania (1932–1947). This incident may have started with the establishment of a game free corridor (to prevent the spread of rinderpest, discussed below) but its longevity is believed to be due to the development of a social tradition. This was good cattle country, which is often favoured lion prey. However, these lions became so fixed on humans that they ignored cattle, even when carrying off herd boys from the kraals.

Between 1932 and 1940 there were no accurate records of human victims, but detailed records were subsequently maintained. In the sub-chiefdom of Wangingombe alone, 249 were killed between 1941 and 1946. These figures account for victims from only one of three sub-chiefdoms where the killings occurred. In the other two sub-chiefdoms, the killings were at least as numerous. Additionally, there were killings outside these immediate boundaries. Rushby concludes that for the entire 15-year period, the death total was between 1000 and 1500. This is a remarkable figure since the area in question was only 80 km by 350 km in size. These killings only concluded with the death of the last of the man-eaters in 1947; in total, 15 suspected man-eating lions were killed.

These predators conducted their activities with a strategy that shows similarities with other incidents (Rushby, 1965). At sundown, lion(s) stalked people in a village, and taking advantage of available cover, approached as close as possible before a final rush. If two lions attacked, two victims might be taken. Then, using relays, the lions would carry their victims up to 2 km away. They did not attack the same village on consecutive occasions and their next attack could be up to 25 km away. Since their attacks persisted for 15 years, it is believed that at least three generations of man-eating lions were involved. The transmission of a behavioural specialisation (in this case a predatory one focusing on people) from one generation to the next illustrates a social tradition. According to Rushby: "There is no doubt that most of these lions were born and brought up to man-eating" (1965, p. 204). Repeated man-eating outbreaks occurred in the Ankole District of Uganda between 1924 and 1930. The episode did not conclude until the last of the 17 man-eaters was killed in 1930 (Temple-Perkins, 1955). The head Game Warden claimed that heredity must play a role (Pitman, 1931). Identical 'kill and flee' strategies were used by lions in Ram Hormuz (Persia) where, according to Layard (1887), the culprit never appeared in the same place for two consecutive days. Patterson (1907) repeats this discussion in reference to the Tsavo pair. Often, man-eating outbreaks only stop with the extermination of the responsible lions.

The Tsavo situation

As discussed earlier, man-eating in and around Tsavo was not limited to the claim of 135 human deaths during Patterson's nine-month stay while building the railway bridge over the Tsavo River. Instances of man-eating occurred before Patterson arrived on the scene and continued after he departed. To the best of our knowledge, the first recorded case of man-eating in the Tsavo vicinity was that recorded by Jackson (1894). Jackson's camp was attacked by a lion that grabbed the head of a sleeping porter. The lion succeeded in running

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of with the cloth head wrap that served to protect the man's head when carrying a load. The location of the attack was adjacent to today's Tsavo East and West National Parks and was described as the "gameless wilderness between Mount Kisigao and Mitati in the Teita country" (p. 238). Based on the records of birds collected by Jackson (Shelley, 1888), we estimate this date to be between October and December of 1886. In the vicinity of Tsavo, in 1891, a group of porters returned to camp missing the trailing member of their party (French-Sheldon, 1892). While a search party was being organised, they heard the final shrieks of their comrade.

Five years later (October, 1896), a party led by Ansorge was travelling through Tsavo (Ansorge, 1899). The group was warned by missionaries at Kibwezi not to stay in the vicinity of Ngomeni due to the presence of 'man-eaters'. In order to avoid Ngomeni, the group crossed the Tsavo River and camped on the opposite side (right bank). Nevertheless, lions attacked the group at night and one of the porters was carried off. After a short chase, the man was retrieved 200 m from the camp. The lion did not return to Ansorge's camp that night but evidently visited a Wakamba caravan camp 30 minutes away. A Wakamba native was carried off and killed at this camp and the entire party fled abandoning their provisions and some trade goods.

This could have been the same lion culprit(s) responsible for the human deaths during the construction of the railway bridge two years later. Two months before Patterson's arrival in Tsavo, railway engineer R.O. Preston recorded that lions killed two railhead workers. When a search was conducted, they found only their heads, hands and feet and bits of other skeletons (Preston, n.d.). Preston later writes that a total of 17 Punjabi workers were killed during his tenure in the vicinity. Less than one year later, after both man-eaters were slain, J. H. Patterson remarked that a total of 28 Indian workers were killed during the Tsavo phase of construction (Patterson, 1907). It is not clear if these totals overlap or if they are completely independent. There were no further human victims after the death of the first man-eater in December of 1898. If we add the 17 Punjabi victims mentioned by Preston and the single Akamba taken from Ansorge's caravan in 1896, the total number of documented victims could rise to 46. However, given his propensity to highlight the nature of the carnage, we would find it difficult to believe that Patterson did not include the 17 victims discussed by Preston in his totals.

Despite the deaths of the two primary culprits near the bridge over the Tsavo River, killings along the railway continued. In March of 1899, about three months after the second man-eater was shot, Engineer O'Hara, the head of a road-building crew working between Voi and Taveta, was dragged out of his tent and killed by a lion about 12 miles from Voi (Patterson, 1907; Preston, n.d.). In June of 1900, the 'Kima Killer' pulled Superintendent C.H. Ryall out of a railway carriage at Kima Station, 120 miles up the railway from Tsavo station (Patterson, 1907; Anonymous, 1961). Man-eating lions had already taken a number of victims in the vicinity of Kima, including one Asian and a number of Africans, as well as from stations at Makindu and Simba (respectively, 100 km and 130 km from Tsavo station).

Man-eating instances were again recorded in Tsavo during World War I. General Phillips, based in Voi for three months in 1915, lost three Indian soldiers to lions in the vicinity of the Tsavo River (Trzebinski, 1986). Percival (1928) lost great numbers of sentries guarding the railway lines from German saboteurs. Subsequently, man-eating subsided in Kenya, and indeed was eliminated for a time, after the near extermination of lions in the late 1910's and 1920's. Instances of man-eating eventually returned on a sporadic basis beginning with a killing along the Tana River in 1928 (Kenya Game Department, 1928): "For the first

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time in years an authentic case of man-eating was reported on the Tana. A Somali was taken near Sankuri and eaten."

During the 1950's, in the vicinity of Ngulia Camp in Tsavo West NP, a man-eating lion remained for several years, and tried to carry off a worker from a road crew during a camping safari led by lion expert Guggisberg (1961). In 1965, J. Perrott (Kingsley-Heath, 1965) killed a man-eater on the Darajani Track in Tsavo East. This lion had a porcupine quill embedded in its nostril. J. Stanley (pers. comm.) describes an incident in 1972 when a herdsman was killed by lions in Tsavo East N. P. Two recent deaths due to lions are recorded in Kenya Wildlife Service archives (1994–1998). In sum, man-eating lions have been active in Tsavo for over 100 years.

In Tsavo, other predators attacked people as well. Both Lugard (1893) and Ansorge (1899) mention that hyaenas carried off sleeping porters at night. The victims were often the infirm, emaciated and abandoned (*ibid*). In the Ngulia Hills of Tsavo, a leopard that had been provisioned as a tourist attraction became a man-eater in the 1980's (Isiche, personal communication).

SELECTION OF ABNORMALLY BEHAVING PREY

Lions often select ill or abnormally behaving prey (Schaller, 1972). Several examples suggest that lions also select 'abnormally' behaving humans. For a lion, abnormal human behaviour might include the deranged or inebriated. Capstick (1981) describes a man-eating outbreak in Zambia that began with the killing of the 'village idiot' from the town of Kalundi. Late night drunkenness coincided with a man-eating outbreak in and around Queen Elizabeth National Park (Uganda) in 1993. Thirteen adult male humans were taken by this adult female, with excellent teeth, known as the Kazinga Man-eater along the Kazinga channel in western Uganda (Kurtis Productions, 1999). Taylor (1959) also discusses the killing of a drunk by a leopard in Mozambique. In a similar vein, George Rushby, quoted in the Tanganyika Game Department, Annual Report, (1951–1952) describes the following:

> "In Ubena, a kind of bamboo is cultivated for the wine it produces during the rainy season. This wine becomes very potent when kept for a few days and during the tapping season, which has just commenced, there is much drunkenness in this district. When I was hunting the Ubena man eater, I frequently travelled along the main and side roads in my truck at night hoping to meet the lions. During the wine season, I came upon men late at night staggering or lying alongside the road in various stages of intoxication and these were aware that man-eaters were operating in that particular area at that time. It is possible that man-eating started in that area through some hungry lion coming across a dead drunk man at night time and could not resist an easy meal".

Perhaps lions interpret the laboured movements of cargo-laden bicyclists as 'abnormal behaviour'. In a number of recent man-eating incidents in the vicinity of Queen Elizabeth National Park (1991–1992), several victims were taken from bicycles by an aged male lion with worn teeth and blunt claws (L. Sieffert, personal communication). The recent video, *Maneaters* (Kurtis Productions, 1999), depicts these incidents and shows lions lurking in tall grass on opposite sides of a road frequented by bicyclists in the area. Taylor (1959) describes an identical situation in Mozambique in which a pair of lions on opposite sides of the path killed a bicyclist.

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Regarding the Tsavo situation however, there is no evidence of 'abnormal' behaviour on the part of the workers at Tsavo and no documented selection of Tsavo victims according to their activities. Aberrant behaviour cannot be documented as a contributing factor to the events at Tsavo in 1898–1899.

VEGETATION AND HABITAT FACTORS

Dense cover facilitates attacks by ambush predators (Mitchel *et al.,* 1965; Schaller, 1972; Prinns, 1996; Funston *et al.,* 2001). Even in the open Serengeti ecosystem, Schaller documents that 75% of lion kills occur near cover. Favoured areas include thickets, tall grasslands, and woodlands. Despite relatively small areas encompassing these habitats, 40–41% of all kills occurred near rivers where dense vegetation and broken terrain facilitate ambush. Lion predation on buffalo was especially focused on river edges.

Tigers are also ambush predators and show parallels with lions. Attacks on people by tigers in the Dudwa National Park, India, were facilitated by an invasion of villagers into the reserve in order to cut grass, collect firewood, and especially, by the tall sugar cane around the periphery (Singh, 1984). The sugar cane fields, analogous to normal tiger habitat, provide ideal cover for females, and an ideal setting to ambush people. Such attacks might also reflect vigorous female defense of their young, which may be nurtured and hidden in the grass thickets. In recent years, more than 100 people were killed by tigers in Dudwa (Wolfe and Sleeper, 1995).

Cover can also be an important factor when lions stalk people. Taylor (1959) asserts that a lion will never attack a person across a wide opening. In the Lindi District of Tanzania, large game is not plentiful and bush pig *Potamochoerus porcus* and warthog are the favoured prey of lions for much of the year. However, during the wet season, 'matette' grasses grow high and the rustling of these grasses alert warthog to the approach of lions. With increasing matette grass height, the ability of lion to capture pigs declines. During this time of year, man-eating incidents multiply (Harvey, 1932; Ionides, 1938; Taylor, 1959). Taylor (1959) discusses the tendency of man-eaters (both lions and leopards) to seek cover in this 'matette' grass. Tanzanian Game ranger Mahenge reports:

> "It is thought that the arrival of the man-eater around Ifakara during the rains may be due to the fact that the lion cannot move about in the long grass without their natural prey seeing the tips of the grass moving and consequently have to resort to feeding on humans who use the same paths day after day. It may also be that some of the lions get cut off by the floods which surround the Ifakara area and do not have game to feed on" (Mahenge, 1951–52).

Hunting guide and safari operator Richard Bonham independently reports (personal communication) that these same phenomena are operational today in south easterrn Tanzania. Alternatively, the withering away and/or burning of grasses in areas with a different prey base, may lead to an increase in the frequency of lion attacks on livestock and people. Neumann (1898) writes that in South Africa, after the grass has been burned during the dry winter season, lions are unable to approach their normal open country prey. Instead, they turn to livestock, particularly native cattle. For Kafue National Park (Zambia), Mitchel *et al.* (1965) claim that warthog are more easily killed in the wet season when the grass is tall. Lion preference shifts to buffalo during the dry season when they are concentrated along rivers. At this time, the tall grass has been burned by brush fires and grazing species have

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been forced onto the plains. It would be interesting to explore these contrasting seasonal predatory activities and trace the grass and pig species involved.

A belt of dry thorn bush thicket persists along the east African coast from Lamu to the Zambezi. This habitat never contains a high density of prey and is prone to man-eating outbreaks (Taylor, 1959). Lions in this thorn bush belt typically occur in small groups of two and three (not including cubs) and the mature males are often maneless. In the late 1890's, due to the demise of elephants from the ivory trade, the predominant vegetation in the region of Tsavo East National Park was this so-called 'nyika'. This thicket facilitated the ambush by Tsavo lions. Patterson and his crew were often able to hear the screams of lion victims and even able to hear the crunching of human bones, but could not see the victims. Patterson describes these thickets as too dense to pursue the man-eaters. His photograph of the railway line in 1898 (figure 7) illustrates the dense nature of the thickets. Such an environment encourages man-eating behaviour. Twenty years later, Percival (1928) still referred to this thick cover and encroaching bush as facilitating fatal attacks by lions on railroad sentries during World War I. The modern Tsavo environment has since changed remarkably. Increases in elephant numbers through the 1960's resulted in the removal of much of the brushy vegetation, opening up large tracts of open plains and changing the components of the mammalian biomass. Tsavo has became one of the largest elephant and buffalo sanctuaries in East Africa (Leuthold & Leuthold, 1976).

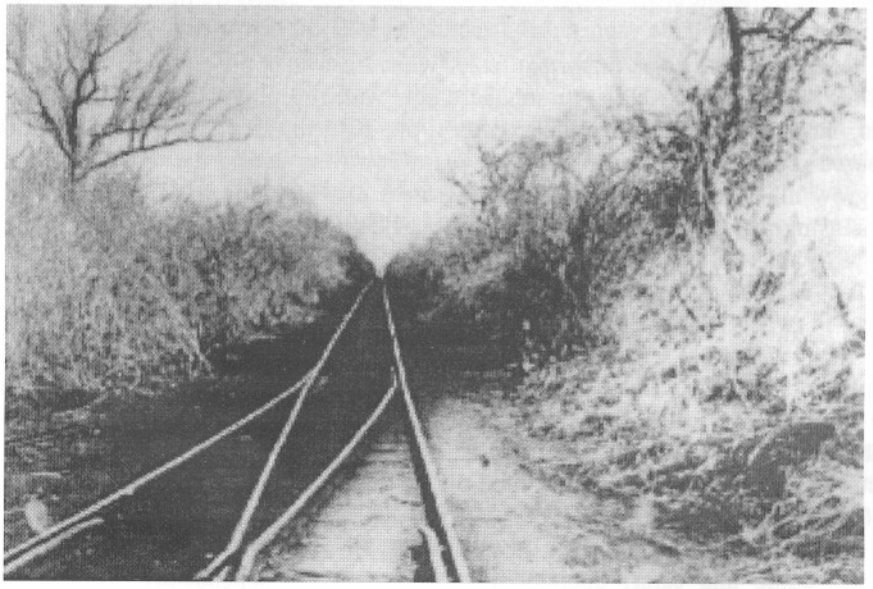


Figure 7. The dense Tsavo bush (nyika) along the railway (Patterson, 1907).

DEPLETION OF 'TYPICAL' PREY AND PREY DEPAUPERATE REGIONS

A frequently cited cause of man-eating behaviour has been thought to be the absence of, or the depletion of, 'typical' prey. In particular, disease (*e.g.* rinderpest), game control efforts, habitat dynamics, and destruction of natural habitats by humans, can have major negative impacts on game populations and their dependent predators. The prime cattle district of

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Uganda is named Ankole, a name now applied to the breed of long-horned cattle that are raised there. Beginning in 1924, the most severe outbreak of man-eating ever recorded in the country occurred in the vicinity of Sanga. Comprehensive records were not kept but the administrator in charge states that in less than four months, no less than 161 people were killed in 1924 (Temple-Perkins, 1955). Pitman (1931) claims that this incident of man-eating was due to an outbreak of rinderpest a few years earlier. In an effort to wipe out this disease, it was decided to destroy the wild ungulates in the region. Between the removal of their natural prey and the effects of the disease, lions were left without any prey base. The effects were disastrous. Despite bearing no apparent injuries, the Ankole District lions turned their attention to cattle, and thence to man. These circumstances were compounded by the fact that a major thoroughfare from Rwanda to Uganda ran through the district. Rwandese immigrants and labourers, traversing this route on foot, and camping in the open at night without fires, were taken without a formal record of their disappearance (Temple-Perkins, 1955). Attacks were so bold that entire villages were abandoned. One of the more famous Sanga man-eaters killed 84 people while another took over 40 (Temple-Perkins, 1955).

Rushby (1965) attributes the origins of the Njombe incident (discussed earlier) to the establishment of a game-free area in southern Tanzania designed to prevent the spread of rinderpest to the south. A 250-km long pole fence was erected along the southern border with Zambia. Three teams of European game observers and African scouts had orders to shoot out all game within 8 km on both sides of the game fence. Concerns for protecting livestock from the spread of this disease outweighed those for the protection of local peoples. The numbers of wild, hoofed animals killed, steadily increased from 245 in 1943 to 1059 in 1946. The area near Njombe is on a plateau of 1200 to 2000 m in elevation and was already known to be poor in game; most of the potential prey consisted of small antelope and pigs. Results were devastating; an estimated 1500 people may have been killed by lions over a 15-year period. Similar records come from Ndola, Zambia, where man-eaters would appear following great epidemics of rinderpest (Radcliffe-Holmes, 1929). Perfectly healthy and prime aged lions were among the culprits, suggesting that injuries, infirmity, or old age were not to blame.

In various localities throughout Africa, buffalo are the favoured prey of lions: Chobe National Park, Botswana (McBride, 1984), Central African Republic (Stockenstroom, 1987), Lake Manyara, Tanzania (Makacha & Schaller, 1969; Prins & Iason, 1989; Prins, 1996), Kafue National Park, Zambia (Mitchel *et al.*, 1965), Kruger National Park, South Africa (Funston *et al.*, 1998, 2001), Busanga Flats, Zambia (Mloszewski, 1983). Where they are buffalo specialists, lions associate themselves with particular buffalo herds (Mloszewski, 1983). In Tsavo East National Park, buffalo are the favoured prey of male lions (Lansing & Kerbis Peterhans, 2000). According to Russell (personal communication) and Packer (personal communication) Tsavo lions associate with specific buffalo herds. Buffalo are especially sensitive to rinderpest. Though it was not diagnosed at the time, rinderpest first arrived on the continent (Somalia) in 1889. Captain J. A. Haslem, Veterinary Chief of the Transport Department, was studying the disease in the coastal region of Kenya (Patterson, 1907). The disease ran through Kenya by mid-1890 (Lugard, 1893; Mettam, 1937) with devastating results:

> "The enormous extent of the devastation it has caused in Africa can hardly be exaggerated. Most of the tribes possessed vast herds of thousands on thousands of cattle, and of these, in some localities, hardly one is left; in others, the deaths have been limited to perhaps 90%' ....Never before....have the cattle died in such vast numbers; never before has the wild game suffered. Nearly all the buffalo and eland

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> are gone. The giraffe have suffered, and many of the small antelope...The pig (wart-hog) seem to have nearly all died....It is noticeable that the animals nearest akin to the cattle have died, *viz.* the buffalo and the most bovine of the antelopes, the eland' (Lugard 1893, p. 525, 527–528).

According to Hill (1976), a second outbreak occurred in 1897:

> "Rinderpest had broken out in the Ulu District and in Kikuyu land towards the end of 1897, and thousands of cattle died. Many wildebeeste, buffalo, hartebeeste, and eland also died, apparently from the disease, but the loss of game was not so severe as during the rinderpest epidemic of 1890–1" (p. 176).

Portal (1894) states that buffalo declined from hundreds of thousands throughout German and British East Africa to virtual extinction between 1890 and 1891. While reflecting on his travelling and hunting in the Tsavo region between 1893 and 1897, Neumann (1898) stated that game of any type was exceedingly scarce and that buffalo and cattle, in particular, were almost extinct from the great cattle plague of some years earlier. By 1903, cattle had still not recovered to the point where export could begin (Anonymous, 1947). There can be little doubt that favoured lion prey, particularly the bovines (cattle, buffalo) were still at low densities in Tsavo in the late 1890's (see also Wilson, 1913). As a first time visitor to East Africa in 1897, Patterson had no baseline for comparison. In his journal of 1898–1899, Patterson does not once refer to cattle or buffalo, while he refers to other domestic and game animals (not including lions) on 115 occasions (table 1). Even if water-dependent buffalo were to have been available to lions in Tsavo in 1897–98, they would have been found at Kanderi Swamp, as well as other riverine and lacustrine settings. However, Patterson (1907) also describes the draining of the swamps around Voi in order to control the spread of malaria. When Patterson returned to Tsavo in 1907 he was surprised that the cattle population had almost completely recovered (Patterson, 1909). This confirms that cattle must have been almost locally exterminated by disease during his earlier work in Tsavo.

During World War I, Percival (1928) describes the dependence of his troops on wild game, estimating that over 40,000 wild ungulates were necessary to feed the troops based in Tsavo during the 2 years of warfare. This dependency on wild game must have further stressed the Tsavo carnivores. Shortly after the troops departed from Tsavo, they moved into Masailand where they continued their depredation of wild game. The Masai promptly complained of the highest level ever of cattle-killing by lions (*ibid.*).

MAIMED PANTHERIDS

The classically recognised circumstances for man-eating revolve around malnourished, aged, or wounded animals. The earliest discussant of aged lions attacking people appears to be Polybius, cited by Pliny (Bostock & Riley, 1855), who states that in their old age, lions become man-eaters, attacking people in their towns because they no longer have the strength to pursue wild prey. Pliny further adds that such animals are aged as their teeth can be completely worn down.

Corbett (1944, 1948, 1954) provided detailed observations of such ailments during his years as the primary dispatcher of man-eating tigers and leopards on the Indian sub-continent during the first half of the 20th century. Such animals are unable to pursue, or hold and suffocate, their normal prey. Damaged limbs, teeth, and embedded porcupine quills appear to be the most common afflictions of some of the tigers, lions and leopards that become man-

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eaters. Of eight man-eating tigers and two leopards extensively discussed by Corbett (1944, 1948, 1954), severe physical anomalies were common to all: five of the individuals had at least one broken canine, three displayed severe porcupine quill damage, and one had an infected shotgun wound. One of the individuals with a broken canine was extremely old with worn-out and frayed claws. Three of the five female tigers had accompanying cubs.

In Africa, Stevenson-Hamilton (1954) states that embedded porcupine quills may be the biggest threat to lions after humans. He describes one feeble attack on a pack horse by an emaciated lion in his prime years that had its foot pads infested with porcupine quills. Kingsley-Heath (1965) and Piggott (Kingsley-Heath, 1965) shot a large, mature, emaciated lion in Darajani (adjacent to Tsavo) that had just killed a human. It was photographed (figure 8) with a porcupine quill embedded in its nostril. Its perfect canines however, suggested that he was of prime age. No less than three of the eight man-eating tigers discussed in detail by Corbet (1944, 1948, 1954) were victims of porcupine quills.

Taylor (1959) describes an incident when a local commissioner in Mozambique decided to trap a lion for close-up photographs. The lion, trapped by its front paw, ultimately tore off its own foot in order to escape. Now debilitated, it became a notorious man-eater, even climbing stairways in attempts to get at its victims. One of the recent man-eaters in the vicinity of Queen Elizabeth National Park (Uganda) had been caught in a poacher's snare during the mid-1990s. The damaged condition of its forelimb is recorded in its skeleton that is still preserved near the Mweya Lodge (Gnoske, personal observation). In July 1991, one of us (JCKP) was a first hand observer of an analogous situation in the Ituri Forest (Democratic Republic of Congo). There was panic in the town of Epulu as a prime-age leopard suddenly began killing domestic dogs in town. It was imperative to capture this leopard before people became victims. The leopard was captured and destroyed. The classic symbol of this doomed predator was the loss of its left-front paw to a human snare. The animal had little recourse but to then turn to the town that had unsuspectingly maimed him in the first place.

However, man-eating is not a guaranteed outcome of the serious trauma affecting the predatory behaviour of large pantherids. The Pipal Pani Tiger (Corbett, 1944) was gored and seriously wounded by a buffalo. It was later shot in the shoulder by a local hunter leaving him mildly lame. At this time it became a regular cattle killer. When it was finally killed, it was never known to have attacked humans. The Hardwar Tiger, whose body was said to be in 'perfect' condition and measured 3.0 m between the pegs, was a notorious cattle killer but never attacked humans. After being killed, the skull was prepared and the right maxillary canine was found growing in an oblique direction through the palate into the middle of the mouth (Colyer, 1951). The author concludes that the tiger must have suffered a serious injury to the deciduous canine in its youth.

The FMNH, The National Museums of Kenya (NMK), The Milwaukee Public Museum (MPM) and the United States National Museum (USNM) have lion specimens with dental problems exceeding those of the primary Tsavo culprit. Some have severe skeletal ailments as well. None were documented as having been man-eaters. Fifty percent of the length of the right upper canine of FMNH 75608 (figure 9) has been broken away, while the left upper canine has been broken to the gum line. Two additional lion specimens from areas adjacent to Tsavo are housed at the USNM (USNM 236920 from Moshi, Tanzania; USNM 174742, nr. Taveta, Kenya) suffered traumatic dental injuries leaving the pulp cavities exposed, but were not documented as having been man-eaters. Finally, the 12 injured lions we have observed in Tsavo over the past few years were not known to have attacked people or their livestock.

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a.



b.

Figure 8 a & b. The Darajani Man-eater with embedded porcupine quill in nostril (courtesy of J. Perrot).

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The inverse situation is also true. Healthy prime age and sub-adult lions often engage in attacks on domestic stock and humans. The Field Museum recently acquired (1998) the skull of the 'Man-eater of Mfuwe' (FMNH 163109), one of the largest man-eaters on record and with near-perfect teeth in the prime of his life (*ca.* 5–6 years old per criteria in Smuts *et al.*, 1978). Upon the arrival of this specimen at Field Museum, we immediately noted a bony swelling with abscess on its mandible. Although one might be tempted to attribute its man-eating behaviour to this injury, the occlusion of the teeth was not effected and the canines are in perfect condition. It is doubtful that this trauma contributed to its man-eating habits. A number of prime-condition Kenyan lions had serious reputations as cattle-killers but never became man-eaters. These include seven individuals with near-perfect teeth and skeletons housed at NMK (Department of Osteology): two individuals from Laikipia, two from the Tana watershed near Kangudo, and three from the vicinity of the Aberdares and Mt. Kenya. Two individuals were large sub-adults (NMK OM 7896, NMK OM 7150), four were of prime age (NMK OM 7936, NMK OM 7009, NMK OM 7895, NMK OM <uncatalogued>) and one was post-prime (NMK OM 7935). Interestingly, the post-prime lion is the heaviest free ranging lion ever recorded at 272 kilograms. Despite their apparent healthy skulls and skeletons, these individuals did become stock raiders, perhaps due to ever-impinging development impacting their prey base.

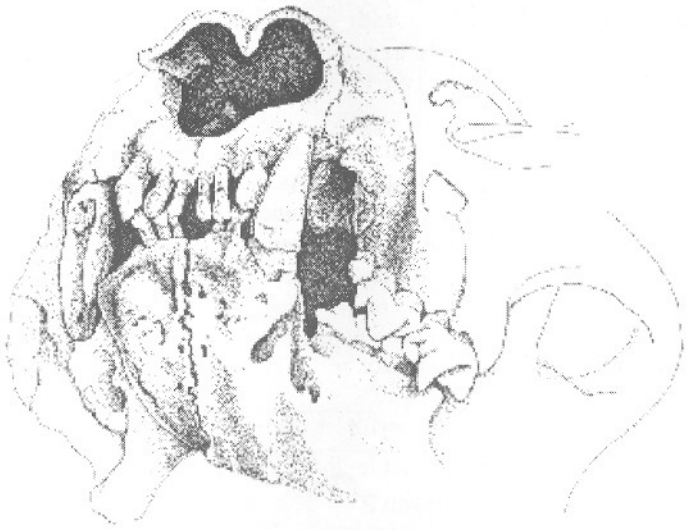


Figure 9. Pearson lion, FMNH 75608 (courtesy of K. Keith).

Lion preference for buffalo, an often dangerous prey species, can lead to debilitating injuries, even death (Roosevelt & Heller, 1914; Mangani, 1962; Schaller, 1972; Sinclair, 1977; Mloszewski, 1983). Today, in Tsavo East National Park, buffalo are the primary prey for lions (Lansing & Kerbis Peterhans, 2000; Gnoske, personal observation), especially along the Voi River drainage and other permanent waterways where buffalo congregate. In April of 1997, one maneless male lion was dispatched by KWS after suffering a broken foreleg during an encounter with a buffalo (Muhanga, personal communication). Our own observations in Tsavo document possible scenarios of impairment. Between 1998 and 2001, both of us observed mature lions with potentially debilitating injuries. These animals were

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located in fully protected areas adjacent to Voi, just within the southern boundary of Tsavo East N.P. In 1998, after killing a female buffalo, one lion was limping to the extent that KWS rangers considered its removal. A second lion suffered an injury to its right eye as well as to its forelimb. A third individual was filmed with blood coming from both ears. Two photographs by H. Schuetz taken in 2001 depict adult male lions, suffering from severe dental trauma (figures 10 & 11), on fresh kills of elephant and buffalo respectively. In total, we documented 12 injured lions, 10 of which were males. Four males and one female had moderately to severely broken canine teeth. Six males exhibited head trauma, one male suffered from back trauma, and three males and one female exhibited injured forelimbs. Several of these individuals displayed a combination of injuries. Despite these injuries, there is no evidence that these animals left the park to become man-eaters or cattle rustlers; they continued to pursue wild prey.

In order to investigate possible correlations between injuries, sex, and age with the appearance of problem lions in Tsavo today, we reviewed 29 'problem lion' skulls from the 'trophy room' of Tsavo East National Park Headquarters at Voi. We follow Smuts *et al.* (1978) in recognizing 3–4 year olds *e.g.* 'sub-adult'(Schaller, 1972) as those lions with a completely erupted and virtually unworn dentition, whereas 5–7 year olds (prime-age) display dental yellowing and visible canine wear as well as wear on the tips of the highest cusps of P^3 and P_4. Our analysis (table 4) shows that 10 of the 29 were from healthy prime-age individuals and 14 from sub-adults with only two of these 24 individuals exhibiting slightly damaged carnassial teeth. Of the remaining five aged or past-prime individuals, one displayed an upper left carnassial broken in life, two had moderately worn and broken canines, one was past prime with good canines, and one could be considered senile with severely worn canines. In sum, these skulls were derived from generally healthy, sub-adult and prime aged individuals with intact dentitions. As detailed earlier, one of the Tsavo man-eaters had a severely broken and mal-occluding canine that may have contributed to its man-eating habits, while the other individual had a broken carnassial and a slightly broken lower right canine tip, which would not have affected its predatory habits.

Table 4. Analysis of 29 skulls of problem lions housed at Problem Animal Control Offices, Kenya Wildlife Service, Tsavo East National Park, Voi.

Sub-adult (n=14)	Prime Adult (n=10)	Post-Prime (n=5)
11: Male, perfect teeth	5: Male, perfect teeth	2: Male, 2 worn/damaged canines ea.
2: Female, perfect teeth	1: Male, broken P^4	2: Female (prob), mod. worn teeth
1: Female, damaged P^4's	4: Female, perfect teeth	1: Female, blunt canines, broken P^4

We also sexed these animals by measuring their canine teeth. Smuts *et al.* (1978) documented no overlap in unworn canine heights of adult male and female lions from Kruger National Park, South Africa (n=122). Unless labels dictated otherwise, we assumed a minimum unworn canine height of 4.7 mm would represent male lions (females ranging from 3.7 mm to 4.6 mm). Sex determination from canine height corresponds with our independent sex determinations of lion skulls: males usually have an upper P^4 over 3.6 mm (TPG observations). Nineteen of 29 sexable lion skulls (66%) from Tsavo East culling operations are from males. Of the 19 Tsavo males, 11 had unworn canines (3–4 year olds) while only six displayed apical canine wear, defined by Smuts *et al.* (1967) as a characteristic of lions in the 5–6 year age class. In sum, problem lions adjacent to Tsavo East NP, Kenya, are typically

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Figure 10. Tsavo lion with dental trauma, seen on elephant carcass (courtesy of H. Schuetz, 2001).

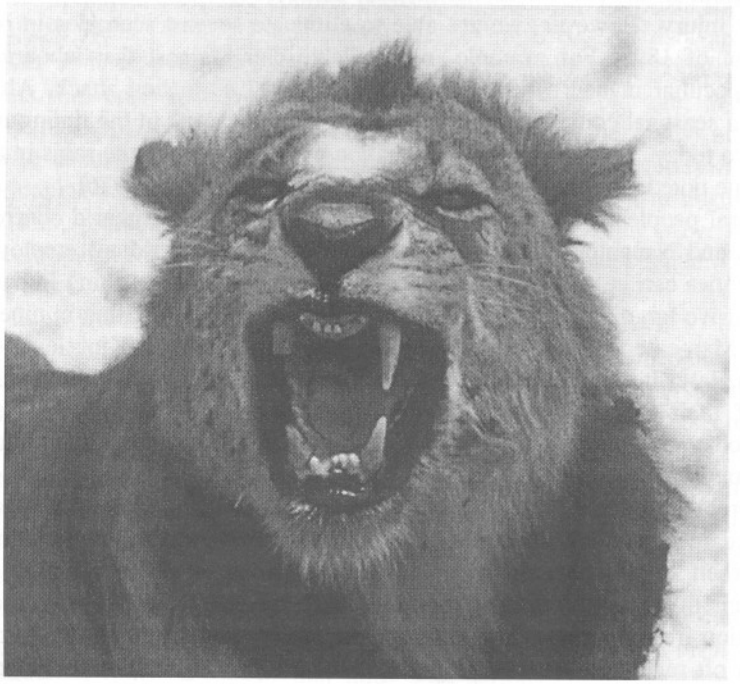


Figure 11. Tsavo lion with dental trauma, seen on buffalo carcass (courtesy of H. Schuetz, 2001).

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male (66%) in the 3–4 year old age category (58% of the males). Although the data is minimal, it appears that as lions age, females become potentially as problematic as older males: 7/14 (50%) of our Tsavo sample in the prime and aged categories are female. However, this may simply be due to their greater frequency in the population. Based on tooth wear (Van Valkenburgh, 1988), female lions are longer-lived, which may account for their greater frequency in the 'older' category.

It is likely that debilitating injuries to the limbs are more likely to lead to man-eating among lions than a severely broken canine. However, we are unable to confirm this due to the lack of post-cranial skeletons from animal control offices. D. King (personal communication) observed a female radio-collared lion in Tsavo, with canines worn to nubs, killing an adult female eland. Lions do not necessarily kill large bovines with their canines, but more often by breaking the necks or suffocating their victims (Selous, 1907, 1908; Gnoske, personal observation). Similar observations have been made on tigers for several locations in India (reviewed in Fletcher, 1911). These activities require a vice-like grip rather than an impaling stab wound. The forelimbs however, must function together. One forelimb is used to secure the victim's head and to control the horns while the other assists in pushing the animal off its feet, often breaking its neck.

DISCUSSION

This review of select man-eating incidents confirms that certain circumstances can lead to the development of man-eating behaviour among large pantherids, possibly including the Man-eaters of Tsavo. These circumstances include: inadvertent or purposeful provisioning, abandoned human corpses, livestock availability, lion demographics and social traditions, peculiar behaviour of the prey, seasonal factors, dense cover, prey-depleted landscapes, and impairment or injury. However, we are able to eliminate several scenarios in regard to the Tsavo situation of 1898. For example, no available data suggest that labourers in Tsavo behaved in a peculiar manner, thereby subjecting themselves to lion attack. Although there appears to be a seasonal component (rainy season vs. dry season) in the timing of attacks on bomas in Tsavo today, we discount any association with the onset of the rains in the Tsavo of 1898, due to the noted delay in the onset of the rains that year (Hill, 1976).

Both pastoral peoples and hunter-gatherers are vulnerable to pantherid confrontation and attack. Treves and Naughton-Treves (1999) have shown that individuals employed in meat-gathering activities can be victims of large carnivore attack while poaching in parks or while attempting to drive large pantherids off of their kills (six reports resulting in nine casualties). The Darajani Man-eater killed a poacher on the outskirts of Tsavo (Kingsley-Heath, 1965). Marks (1976) describes conflicts endured by the Bisa, of Zambia, who secure a major component of their meat by scavenging buffalo directly from lions. Similar cases are documented today in Queen Elizabeth National Park (Sieffert, personal communication). Pastoral communities, adjacent to protected areas, are also especially vulnerable. The only documented precise location of an attack on people in Tsavo in recent times states that the attack occurred in a 'cattle boma' or corral, to someone defending or providing for their livestock. Corbett (1944) also discusses several instances of tigers attacking pastoralists looking for their livestock. As discussed earlier, numerous authors have anecdotally claimed that the transition from domestic stock depredations, to conflict with humans, to predation on humans, is an oft-repeated scenario. In parts of India where tigers are protected, programs

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are underway which provide a source of wild, hoofed stock in order to satisfy predatory demand.

Our review of problem lion skulls derived from animals culled by the Kenya Wildlife Service shows an overall predominance (83%) of subadult (3–4 year olds) and prime-aged (5–7 year olds) individuals rather than aged individuals (over seven years old). Among the subadult and prime-aged lions, 70% are males. Sex ratios, determined from the skulls of 'problem' animals, are complemented by documented attacks of male lions on livestock and humans in Tsavo East National Park (54% and 83% respectively, table 2). This disproportionate impact by male lions may in fact be much higher if one were to assume heavily female-skewed sex ratios among adult lions as have been described for most lion populations. This male cohort, despite absolutely smaller numbers, appears to be the predominant 'problem' demographic component of the Tsavo lion population. The bias in male 'trouble-makers' among the pantherids is most pronounced among leopards where 143 of 152 (94%) known man-eaters are males (Turnbull-Kemp, 1967).

This demographic cohort mirrors the age at which 'subadult' males leave or are forced out of their natal groups (prides), described by Schaller (1972) as being between 2.5 and 3.5 years of age. Saberwal (1994) comes to similar conclusions for Indian lions: " subadult lions were represented disproportionately in conflicts with humans" (p. 504) and "subadult lions involved in attacks are likely those displaced from or dispersing from their natal territories" (p. 506). The second largest sex and age cohort, is represented by prime-aged male lions (table 3). This is the category into which the Tsavo man-eaters belong.

Corbett's observations (1944, 1948, 1954) document the frequently damaged condition of man-eating tigers and leopards in India. Under certain circumstances, these observations have been applied to African lions, perhaps including the man-eaters of Tsavo. However, the theory championed by Corbett (1944, 1948, 1954) that aged or impaired pantherids are the primary culprits in human-carnivore conflict needs to be modified. Our data suggest that only 15% of disruptive lions (including maneaters) are so impaired. No data are available to indicate whether 15% is a high incidence of impairment among lion populations. Schaller (1972) suggests that only 10% of lions in the Serengeti reach old age. We believe that impairments to the appendages (broken or snared limbs, porcupine quills) are much more likely to lead to attacks on livestock or people than broken teeth. Severely broken canines and extensive canine wear may have an effect on a lion's ability to grip ungulate prey, but trauma to incisors, premolars and molars have little effect in subduing prey. It is clear that severe canine impairment needs to be distinguished from other dental traumas when discussing impacts on predatory behaviour.

Even so, lions with severely broken canines have not been shown to be particularly troublesome. The cohort of sub-adult and prime aged males dispatched near Tsavo East N.P., are generally healthy individuals, at least from the cranio-dental perspective (table 3). These individuals, collected by Problem Animal Control (PAC), were responsible for having attacked livestock and threatening people. They are not aged or infirm. In fact, the frequency of broken canines (4/29=14%, table 3) and broken carnassials (3/29=10%, table 3) in the PAC skulls are equal to or less than their frequency in lion skulls housed in museum collections. For example, Van Valkenburgh (1988) documented 26 broken canines (21.5%) and 13 broken carnassials (10.7%) in a review of 121 lion skulls in museums.

Lions dispatched by the PAC unit contrast the group of living lions, documented by us within Tsavo East and outside of the areas patrolled by PAC, which do display significant cranio-dental trauma. It would appear that lions with serious cranio-dental trauma are not typically becoming cattle-killers and threatening people. Although there are a number of

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authentic and well-documented cases of impaired lions becoming man-eaters (Pliny, cited in Rawlinson, 1992; Selous, 1908; Taylor, 1959; Kingsley-Heath, 1965), they account for a low proportion of the cattle-killing and man-eating incidents recorded. Further, many of these examples illustrate problems unrelated to cranio-dental trauma (*e.g.* porcupine quills, starvation, old age, impaired limbs, etc.).

The most comprehensive review of the physical condition of man-eating pantherids (lions, tigers, and leopards) has been produced by Turnbull-Kemp (1967, table 2), who states that "a high percentage of the man-eaters among the three species considered here are mature individuals bearing no obvious injury and certainly unhampered by any wound or the like" (p. 133). We have partially reproduced his table here (table 5). Only 22% of the lions and 11% of the leopards displayed an injury in Turnbull-Kemp's data set (*ibid.*). Unfortunately, there is no breakdown on the nature of the injuries. If aged individuals are added, the figures rise only to 24% and 12% respectively. The data from Treves and Naughton-Treves (1999) provides further support for these low numbers: only 14% of the lion attacks (n=275) and 15% of the leopard attacks (n=114) were attributed to injured animals. Approximately 13% (3/29) of the skulls from the KWS animal control office at Voi, showed evidence of serious dental trauma or advanced age. Finally, Thessiger (personal communication) states that the 30 problem lions he shot in Northern Darfur (Sudan, 1935–1937) were generally healthy and of prime-age. Although certain injuries are overlooked (*e.g.* the Tsavo maneaters), the vast majority of attacks appear to be conducted by healthy animals. These unique data sets (tables 4–5) (Turnbull-Kemp, 1967; Naughton-Treves, 1999) stand in contrast to the often-quoted statement that man-eating lions are generally impaired animals. In fact, the greatest proponent of this belief was Corbet who popularised this notion based on a spectacular group (but limited number) of man-eating tigers that may be more prone to develop this habit due to their solitary habits. Post-cranial injury may play an occasional role and animals with impaired limbs need to be rehabilitated or eliminated, a policy currently practiced by the Kenya Wildlife Service. The great majority of man-eating and cattle killing lions, are sub-adult or prime-aged animals in good health.

Table 5. Age and condition data on 241 known man-eaters at death. (from Turnbull-Kemp, 1967)

	Lion	Tiger	Leopard
No. in sample	89	74	78
Aged (post-prime)	(18%)	(35%)*	(12%)
uninjured	12 (14%)	9 (12%)	7 (9%)
injured	2 (2%)	15 (20%)	1 (1+%)
aged dentition	2 (2%)	2 (3%)	1 (1+%)
Mature (prime)	(33%)	(47%)	(85%)
uninjured	24 (27%)	28 (38%)	62 (79.5%)
injured	5 (6%)	7 (9.5%)	4 (5+%)
Immature	(subadult) (50%)	(18%)	(4%)
uinjured	32 (36%)	12 (16+%)	0
injured	12 (14%)	1 (1+%)	3 (4%)

*figure corrected from Turnbull-Kemp's figure of 55.1%
figures rounded to nearest %

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It is also important to point out that this cohort of sub-adult and prime aged males (table 4) are healthy individuals, at least from the cranio-dental perspective. These individuals were responsible for having attacked livestock and threatening people. They are not aged or infirmed. They contrast the group of male lions, documented by us within Tsavo East and adjacent to the areas patrolled by KWS Problem Animal Control Units, that do display significant cranio-dental trauma. It would appear that lions with serious cranio-dental trauma are not often becoming cattle-killers and threatening people. It is also possible however, that this population has learned to remain within the park boundaries in order to avoid persecution. Although there have been a number of authentic and well-documented published cases of impaired lions becoming man-eaters, they appear to account for a low proportion of the cattle-killing and man-eating incidents recorded.

With regard to age, most (82%) of the man-eating lions discussed by Turnbull-Kemp were either 'mature' (33%) or 'immature' (50%), whereas only 18% were classified as 'aged'. Tigers and leopards on the other hand, display unique and distinct patterns. The great majority of the man-eating leopards (85%) were 'mature' animals. Compared with lions, twice as many of the man-eating tigers were listed as 'aged' (35% vs. 18%). As suggested by Turnbull-Kemp (1967), the solitary tiger might be more prone to man-eating when its physical condition (old age or injury) prevents it from subduing ungulate prey. When its condition deteriorates, the more social lion might be more likely to take advantage of prey brought down by affiliates, allies or 'pride-mates'. Conversely, lions are 2.5 to 3 times more likely to become man-eaters when 'immature' (50% in lions vs. 18% in tigers), an age category he defines as being approximately three years of age (equivalent to Schaller's (1972) 'subadult' category). This age group is the same problem cohort reflected in our data set from Tsavo East National Park. Leopards differ from both lions and tigers as they are basically mature and uninjured when they take to man-eating (85% mature, 80% mature and uninjured). Leopards are the smallest of these three large cat species and might find adult male humans a more formidable adversary. This may be why leopards are twice as likely to attack human women and children than lions (67% vs. 33%, n=138; Treves & Naughton-Treves, 1999) and also why larger male leopards are more likely to become man-eaters than the smaller females.

The Tsavo man-eaters can be classified in Turnbull-Kemp's (1967) 'mature' category. Although this is not consistent with Turnbull-Kemp's highest risk group ('immature' at 50%), fully one third of the man-eaters Turnbull-Kemp documents do fall into this age cohort. It is also possible however, that the Tsavo lions began their man-eating career two years earlier as documented by Ansorge (1899). The fact that they were male, further places them into the 'trouble-maker' category. However, given that the two acted together, there was no reason why the severely damaged canine and remodeled skull of one of them, turned both of them into man-eaters. Their social bonds, immense size, apparently healthy limbs, and mature age would allow them to tackle 'normal' prey. Indeed, this has been confirmed with the profile of wild species, represented by hairs extracted from their broken canines.

Adult male lions in Tsavo (Lansing & Kerbis Peterhans, 2000) and elsewhere preferentially target buffalo. When buffalo populations crash, buffalo-dependent lions can switch to alternative food supplies, including humans. Africa's most notorious episodes of man-eating were associated with the depletion of buffalo, or other prey animals. These include the Tsavo incident, the Ankole outbreak in Uganda (rinderpest outbreak killing buffalo and resultant game eradication) and the Njombe incident in southern Tanzania (associated with the development of a game free corridor). Domestic cattle on the outskirts of protected areas can act as buffalo surrogates for these lions; lions apparently see little

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difference between the two. Post-cranial injuries from encounters with buffalo can also impair lion ability to secure normal wild prey and push them into attacks on domestic stock and perhaps humans.

'Provisioning' of carnivores can lead to instances of man-eating. Provisioning of lions in the Gir Forest (India) was abolished following a correlation between lion provisioning and man-eating outbreaks (Saberwal *et al.*, 1994). Recent attacks on tourists adjacent to, and within national parks, by leopards and hyenas have led to a policy of non-provisioning for these large carnivores in parts of Africa, including parts of Kenya. Similarly, traditional practices of abandoning the dead in the bush can potentially stimulate predators to seize live individuals. It is especially ironic that cattle-loving Masai might attract lions to their bomas by abandoning their dead in the bush. Deceased humans were available in Tsavo (1898-1899) in the form of local 'burial' practices, hundreds of Wakamba dead from starvation, hundreds of railway workers dead from disease, and a recurring opportunity of abandoned or injured porters and slaves. Non-indigenous porters from outside localities often died from dysentery and a suite of pathogens to which they were not accustomed.

In regards to 'provisioning', it is important to note that many of the man-eaters we discuss here came to animal baits. These were not 'dedicated' or 'obligatory' man-eaters. For instance, the Mfuwe man-eater was attracted with hippopotamus parts (*Hippopotamus amphibious*), Corbet's man-eaters were regularly taken with cattle and goats. The Tsavo man-eaters continued to pursue wild prey immediately following the severe trauma experienced by FMNH 23970. They were lured to their deaths with a donkey and three tethered goats respectively.

Civil strife also plays a role in providing pantherids with human corpses as we have documented for the World Wars and Vietnam. In order to avoid detection, modern rebels will travel off-road, through uninhabited, predator-infested landscapes. Areas prone to man-eating today include Queen Elizabeth National Park (Uganda) and Kruger National Park (South Africa). Queen Elizabeth borders the Democratic Republic of Congo while Kruger borders Mozambique; both of these protected areas have functioned as highways for 'rebel' infiltrators who come into contact with large predators, sometimes with fatal results. Four rebels were recently killed by lions in western Uganda (New Vision, 13 May 1997) while infiltrating from the Democratic Republic of Congo. In order to keep a low profile, rebels also avoid using fires at night, further encouraging predators.

We have documented over 30 years of nearly continuous predation of humans along the caravan and railway route in the Tsavo region, suggesting that man-eating was a regular part of lion life in this area. An entourage of predators was attracted to caravan routes through which people, porters, livestock, and their transport animals passed. Caravan thoroughfares were oases in the thorny desert and were likely adopted as human hunting grounds by Tsavo lions for generations. The camps of the railway crew were extensive as they supported 2000–3000 individuals (Patterson, 1907) and provided a plentiful source of food debris and dead transport animals.

Several circumstances contributed to highlight the area of the Tsavo bridge as an attractive feeding ground. This is the point where the Tsavo River intercepts the traditional caravan route. Patterson notes that this was the unofficial point to ford the river for generations of caravans. This point is less than four kilometres from the confluence of the Tsavo and Athi Rivers. The Tsavo and Athi Rivers are the only year-round source of water in the vicinity. The Tsavo drains the glaciers of nearby Mt. Kilimanjaro. To anyone who has ambled through the equatorial heat of Tsavo, the Tsavo River is a welcome oasis in the heart of a sub-desert, thorn-scrub thicket. Even today, green-topped trees are restricted to the

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river's edge. Patterson (1907) himself joyfully described a walking excursion from his camp near the bridge: "walking stealthily along in the delightful shade of the overhanging palms" (p. 157). The area of the bridge was a rest and refuelling point for land caravans, all too eager to set up camp in the shade, adjacent to fresh water.....just in time for marauding nocturnal carnivores. This is why we believe this area was prone to man-eating throughout the days of the caravan.

For a long-lived species with a long period of infant-juvenile dependency, any regularly practised predatory behaviour can become a cultural tradition, passed down from one generation to the next (Taylor, 1959; Rushby, 1965). To call such behaviour 'aberrant' may be acceptable from an anthropogenic perspective but is 'normal' behaviour for the relevant predator. Over thirty years of documented man-eating at the turn of the 20th century in Tsavo may represent six generations of lions, all of whom may have been part of the same social tradition. The 15-year reign of the infamous 'man-eaters of Njombe', the Sanga man-eaters, and the modern behaviour of the swamp tigers of the Sundarbarns also fall into this category. At the turn of the 20th century, the well-travelled caravan route was replaced with a parallel rail line and ultimately an automobile route. These actions denied area carnivores access to vulnerable campers. In their frustration with the 'iron horse' in the first years of the railway, the big cats were even documented removing humans from railway carriages (Patterson, 1907; Anonymous, 1961). Their human depredations focused on the railway stations of Makindu, Kima, Voi and Simba (Miller, 1971).

The mega-fauna of Tsavo has been historically dynamic. In three major ways, the faunal composition during Patterson's time contributed to the propensity of Tsavo lions to select people as prey. The Tsavo nyika was quite limited in its capacity to maintain a high prey biomass and was dominated by large rhino and small antelope (*e.g.* dik-dik) well above and below the size preferred by lions. Taylor (1959) notes the propensity of lions to become man-eaters in such habitats. According to Patterson's journal entries (1898–1899) medium-sized, gregarious ungulates were either absent (wildebeest) or sparse (zebra). Humans became even more vulnerable to Tsavo lions with the dramatic reduction of buffalo, their favored prey under normal conditions. The biomass of buffalo in Tsavo is normally the highest among potential lion prey species (Leuthold & Leuthold, 1976). However, two waves of rinderpest had decimated the buffalo herds and the draining of the Kanderi Swamp prevented a prompt comeback. Ivory hunters had already eliminated the elephant population. In his journal (1898–1899), despite 185 references to the fauna of Tsavo, Patterson never once mentions buffalo, cattle or elephants. The absence of elephants had yet another effect on Tsavo lions: the thorny shrub vegetation became overgrown providing easy ambush and exit for predatory lions.

We cannot claim that any single cause will guarantee that a lion will turn into a 'man-eater', but it is clear that a variety of causes will increase the likelihood. In regard to the Tsavo situation, we have discounted several factors often proposed to account for man-eating outbreaks. These include peculiar behaviour of the prey, seasonal factors and broken teeth. However, several important pre-conditions for the development of man-eating were in place in Tsavo during the 1890's. These include a prey-depleted landscape, long standing behavioural traditions, inadvertent provisioning of humans and their livestock, and habitat factors. Although the human toll at Tsavo was claimed to exceed 100 individuals, it seems the total could have been higher. Given the circumstances at Tsavo in the 1890's, instead of asking how so many humans could have been dispatched, we wonder why there weren't more.

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