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LION-PORCUPINE INTERACTIONS IN AFRICA, INCLUDING IMPACTS ON LION PREDATORY BEHAVIOR

Julian C. Kerbis Peterhans
College of Arts and Sciences, Roosevelt University
430 S Michigan Ave., Chicago, IL 60605, USA,
Science and Education, Field Museum of Natural History, Chicago, IL, USA
jkerbis@fieldmuseum.org

Gastone G. Celesia
Science and Education, Field Museum of Natural History, Chicago, IL, USA
Loyola University of Chicago, Stritch School of Medicine, Chicago, IL, USA
Chicago Council on Science and Technology, Chicago, IL, USA
3016 Heritage Oak Lane, Oak Brook, IL 60523
g.celesia@comcast.net

Thomas P. Gnoske
Gantz Family Collections Center, Field Museum of Natural History
1400 S Lake Shore Dr., Chicago, IL 60605
tgnoske@fieldmuseum.org

ABSTRACT

Although African crested porcupines *Hystrix* spp. represent 0.5–34% of lion *Panthera leo* kills, interactions between the two species are poorly documented. Here we review porcupine-lion interactions and their impact on lion behaviour, including: 1) lion predation on porcupines; 2) lions injured or killed by porcupine quills; and 3) a case of a lion severely injured by a porcupine quill. Porcupine quills can be effective weapons and sometimes seriously wound lions, resulting in death. Death from quills can be a slow process and under these circumstances, death may be the result of starvation or infection (septicaemia).

Keywords: predator-prey relations, quill, behaviour modification, Hayward-Kerley' threat index, septicaemia

INTRODUCTION

Aesop discussed interactions between Androcles, a lion, and a thorn, over 2600 years ago. In the 2nd century, Claudius Aelianus, for the first time, specifically discussed lion and porcupine interactions (Scholfield, 1959). In the 1600s, Jan van Riebeeck, Commander of the Cape for the Dutch East India Company from 1652 to 1662, discussed in his personal journal the first accounts of lion-porcupine interactions in sub-Saharan Africa (Thom, 1954). On 16

June 1656, he reported the presence of porcupine quills and legs in the stomach of a large adult male lion killed on the Cape. On 28–29 July 1656, an old famished lion that had killed a cow was shot; many quills were found embedded in its skin. On 19 August 1656, he reported that a third "*dead lion was found on the beach... A porcupine quill was found sticking in its chest, quite two hands deep. On being skinned, it was found to have been so badly wounded by porcupine quills that it had obviously been killed by that little animal*" (Thom, 1954, p.57). All three of these early accounts discuss lions' consumption of porcupines and injuries inflicted by them, illustrating that lions hunt porcupines, but hunting them is not without risk (Eloff, 1984, 2002; Hayward & Kerley, 2005). Here, we report a case of a lion *Panthera leo* (Linnaeus, 1758) maimed by a porcupine *Hystrix sp*. Linnaeus, 1758 and review the interactions between these two mammals.

MATERIAL AND METHODS

A search of the literature published between 1960 and May 2016 was conducted. Meta-analysis of the 23 independent studies found could not be carried out because of different methodologies and periods of observation. Some used only analyses of spoor, some used aerial views and/or observations by safari guides, some used direct observation and radio-tracking, and some were continuous while others were intermittent. Some classic studies on lion predatory behaviour (Mitchell, *et al*. 1965; Pienaar, 1969; Schaller, 1972) were disregarded because their counts of lion kills were based on *post-hoc* searches for carcasses, which are inherently biased against small prey (which can be completely consumed). Game Reserves (Hunter, 1998; Power, 2002; Radloff & Du Toit, 2004; Lehmann, 2007; Rapson & Bernard, 2007; Vorster, 2011) that are managed to support tourism were also excluded because such areas are no longer natural. We preferred real-time tracking of specific lions, studies with continuous observations and/or radio tracking and spoor analysis, or studies using fecal analysis, because these documented most predatory encounters, including small prey [see discussions by McBride (1984) and Eloff (2002)].

No systematic study of lions injured by porcupines was found, only anecdotes (*e.g*. Sutherland, 1846; Inverarity, 1891; Crawshay, 1899; Stevenson-Hamilton, 1912, 1947; Thom, 1954; Kingsley-Heath, 1965; Pienaar, 1969; Raven-Hart, 1971; Schaller, 1972; Skead, 1980; Kerbis Peterhans & Gnoske, 2001). We conducted a search in the lay press and on the internet of cases of lions injured by porcupines. We are aware of the limitations of such an endeavour. Videos and photographs from 1 May 2008 to 1 May 2016 were also evaluated. Only cases of lions with embedded quills were considered.

Our case study pertains to the 'Man-eater of Darajani', killed 6 January 1965, after having just killed a local hunter. Darajani, Kenya, is close to the north eastern boundary of Tsavo East National Park (NP). This lion's skull and skin were kept as trophies and currently reside in the personal collection of the senior author. We studied photographs and video taken of the event and the published account by the professional hunter involved (Kingsley-Heath, 1965). To prevent damage to the 'trophy', we CT scanned the skull through the skin at the Department of Radiology, School of Medicine, University of Chicago. A metal artefact reduction filter was used to eliminate impacts from metallic pieces inserted during taxidermy. Each CT scan slice had a thickness of 0.59 mm. Images of the Darajani lion skull were compared with the CT scans of the Field Museum of Natural History's (FMNH) two infamous 'Tsavo Man-eaters' (FMNH 23969, FMNH 23970; Kerbis Peterhans & Gnoske,

2001). The Darajani skull measurements were compared to our database of lion skull measurements.

Jacobs' Index (Jacobs, 1974) was used to evaluate predator 'preference'. This index is expressed by the formula: $D = (r - p)/ (r + p - 2rp)$ where r is the proportion of the total kills by a particular predator species at a site that are made up by a particular prey species and p is the proportional availability of that prey species. The index value ranges from +1 to -1. Jacobs suggests that +1 indicates maximum preference and -1 indicates maximum avoidance.

We follow Mills (2015) in defining an 'arid habitat' as one with less than 350 mm mean annual rainfall. The following abbreviations are used: TMVU (Tsavo Mobile Veterinary Unit), BEA (British East Africa), SA (South Africa).

RESULTS

Our case study of the 'Man-eater of Darajani' reveals an emaciated male with protruding backbone, scapula, ribs, limbs and pelvic carriage (figure 1). The lion's mane was sparse and partially developed; however, this is typical for lions of this age and in this region (Gnoske *et al.*, 2006). A porcupine quill with a total length of 239 mm was planted in the left nostril; 159 mm of it remained embedded (figure 2). There were a few other quills in the chest and shoulder (Kingsley-Heath, 1965). The quill in the nostril (figure 3) was complete but was creased where it emerged from the nostril, likely due to repeated impact. Both species of crested porcupine are present in Kenya and Tsavo is near the boundary of both species (Happold, 2013a,b). We could not determine the species based on the quill alone; therefore, we refer to this porcupine as '*Hystrix* sp.'

Figure 1. Darajani lion just after he was killed. Note the very thin body, scrawny mane and protruding shoulder, pelvic bones and ribs. Photo courtesy of John Perrott

Figure 2. Close-up of the Darajani lion head showing the portion of the quill over-hanging from the left nostril (modified from Kerbis Peterhans & Gnoske 2001).

Figure 3. Porcupine's quill from the Darajani lion. The quill is broken into two pieces. The longer piece, measuring 159 mm, was lodged into the lion's left nasal cavity.

Utilizing CT scan at high resolution, we determined that lion skull sutures (including the interparietal, interfrontal, basioccipital and squamous-parietal) were still open. The teeth were fully developed and unworn, thus establishing that the lion was a young adult approximately 4 years of age (Smuts *et al*., 1978). The CT scan (figure 4) showed that the turbinates were missing as a result of the taxidermy process, but the frontal sinuses, cribriform plate, mastoid bulla, *tentorium cerebellum, foramen magnum,* and all other cranial bones were of normal aspect. Skull measurements were within the normal range in comparison to a series of 29 Tsavo male lions in our database (unpublished data). Our measurements contradict Kingsley-Heath's statement that the Man-eater of Darajani had a

small emaciated body but a large skull. The discrepancy may be an illusion as a regular-sized head may appear bigger on the emaciated body of a poorly-maned lion.

Figure 4. Sagittal CT scan of the Darajani lion skull. The upper figure shows the left slice at the level of the canine teeth. Note the absence of turbinates, the good preservation of the cribriform plate and the normal foramen magnum. The lower illustration is a close up of the same CT slice. A model of the quill, measuring 159.09 mm is positioned in the nasal cavities. Note that the tip of the model is positioned 8.2 mm from the cribriform plate.

As shown in figure 4, the quill penetrated the nasal cavity and frontal sinus on the left. The tip of the quill reached to within 8.5–10 mm of the cribriform plate. A foreign object penetrating the ethmoturbinals (Pang *et al.*, 2016) and frontal sinus will produce an inflammatory response characterized by swelling, disturbance of function (*functio laesa*), heat (Serhan *et al.*, 2010) and seropurulent, and/or mucopurulent exudate (Beers & Berkow, 1999).

Jacob's Index is a measure of prey preference in relation to their abundance or availability. Hayward and Kerley (2005) report a Jacobs' Index of 0.58 for *H. africaeaustralis* Peters, 1852, suggesting that lions take porcupines in excess of their natural abundance. Hayward *et al.* (2011) show that lions encounter preferred prey species far more frequently than expected based on abundance. Indeed, animals with quills can be a popular choice of meat both for predators and humans (Kerbis Peterhans, pers. obs.). In their literature review of lion predatory behaviour, Hayward and Kerley (2005) analysed 32 studies from 48 locations and noted that of 22 684 lion kills, only 454 (2%) consisted of porcupines. Our review found 97 studies of lion's prey and/or kills. We found only 25 reports of lion prey that included 'small' prey (below 15 kg.) with 23 of them listing porcupines as prey. Ten reports were from studies that followed lions in 'real-time' and observed every lion-prey interaction (table 1). Porcupine frequency in the diet varied widely between 0% and 40.8% of lion kills.

There are no studies on the frequency of lions being injured by porcupine quills but there are at least 21 published reports of injuries, including at least 20 wounded and ten deaths (table 2). From 1 May 2008 to 1 May 2016 there are an additional 12 instances culled from the internet of lions' interaction with porcupines resulting in injury to at least 20 lions (table 3).

DISCUSSION

Our review of the literature reveals the complexity of lion-porcupine interactions. In prey-rich habitats lions are less likely to pursue porcupines while in prey-deficient habitats the reverse is true. Many variables impact this dynamic including rainfall, drought, man-made bore holes, drinking water, available fodder, and prey biomass. Figure 5 shows this complex relationship among porcupine kills, rainfall, and prey biomass.

Table 1 presents the contrast in frequency of lion predation upon porcupines between ecosystems varying in rainfall and prey biomass. In arid ecosystems (less than 350 mm mean annual rainfall) porcupine frequency in the diet averages 28.1% and can be as high as 40.8%. In higher rainfall ecosystems (over 350 mm mean annual rainfall) porcupine frequency in the diet averages 3.8%. Higher rainfall is correlated with higher prey biomass (Coe *et al.* 1976; Celesia *et al.* 2009). In most regions with higher prey biomass, porcupines usually represent less than 1% of kills (*e.g.* Etosha, Chobe and Serengeti, though Kruger is an outlier; figure 5, table 1). Where herbivore biomass is less than 300 kg/km^2 (*e.g.* Faro and Kalahari-Gemsbok/Kgalagadi), porcupines can become more important (7.5–40.8%). This dichotomy has been discussed by Eloff (2002) regarding the Kalahari duneveld lions [where common wildebeest *Connochaetes taurinus* (Burchell, 1824) are absent] in comparison with the adjacent Nossob River lion population studied by Mills (as cited in Eloff, 2002) (where wildebeest occur). At Eloff's site, porcupines accounted for 25.6–40.8% of the kills (table 1) with wildebeest contributing less than 4%, whereas at Mills' study site, porcupines accounted for less than 2.2% of the kills with wildebeest at 37% (Eloff, 2002).

Table 1. Panthera leo *kills of porcupine* (Hystrix africaeaustralis *or* Hystrix cristata*).*

	Place	Rainfall in mm	Prey Biomass kg/km^2	Date	Porcupine Number	Porcupine Percent	Total Kill Number	Reference
National Parks with Arid Ecosystem having Annual Rainfall < 350 mm								
	Kalahari Gemsbok National Park Northern part (Botswana/SAfr)	240	180	1970-1973	11	25.6	43	Eloff 1973
	Kalahari Gemsbok National Park (Botswana/South Africa)	250	180	1970-1983	20	40.8	49	Eloff 1984[A]
	Kgalagadi Transfrontier Park	150-250	200***	1972-1984	31	34.0	92	Mills 2015
	Tsavo East National Park (Kenya)	310 *	1141-1479*	1999	3	6.4	47	Andanje 2002
Total					65	28.1	231	
National Parks with Ecosystem having Annual Rainfall > 350 mm								
	Etosha National Park (Namibia)	351	6200	1894-1988	0	0	156	Stander 1992
	Kruger National Park South (South Africa)	600.8	3559	1986-1990	15	13.5	111	Mills & Shenk 1992,
	Chobe National Park (Botswana)	600	1424$^+$	1979-1981	0	0	120	McBride 1984
	Serengeti National Park (Tanzania)	800-1183^{++}	20200^{++}	1957-1965	1	0.8	125	Kruuk & Turner 1967
	Faro National Park (Cameroon)*	1200	16^{+++}	2000-2001	9	7.5	119	Breuer 2005
	Manovo-Gounda-St. Floris (Central African Republic)	1325	651	1984	3	2.7	111	Ruggiero 1991
Total					28	3.8	742	

*= Celesia *et al.* 2009 ** = Coe *et a.l* 1976 *** =Castley *et al*. 2002 $^+$= Viljoen 1993 $^{++}$=Hanby *et al*. 1995 $^{+++}$ = Angwafo 2006

A=data reported in 1973 were subtracted from this 1984 report

Table 2. Reports of lions injured or killed by porcupine's quills.

Description of porcupine/lion encounter	wounded	# killed	Sex	Location	Reference
One male lion killed by porcupine quill in chest, citing van Riebeek from 1656		1	m	Cape, SA	Thom (1954)
Two lions shot & found with embedded quills, citing van Riebeek from 1656	2		m?	Cape, SA	Thom (1954)
One lion 'strangled' in the jungle by a porcupine, citing Saar from 1662		1	m	Cape, SA	Skead (1980)
One lion killed by a porcupine, citing Fryke from 1681		1	m	Cape, SA	Skead (1980)
One lion killed by five porcupine quills, citing Valentyn from 1726		1	m	Cape, SA	Skead (1980)
One male lion killed by porcupine quill in chest, one male with many quills in skin	1	1	m,m	Rondeboshje nr Cape Town, SA	Sutherland (1846)
One male lion killed by porcupine, four quills in its body		1	m	Cape, SA	Tavernier (1889)
Old male lion with 3 quills left forepaw	1		m	Neugia Kitwi, BEA	Crawshay (1899)
Lions which sustained grievous injuries became cattle-killers***	2		?,?	Gir Forest	Mitra (2005)
One lioness blinded by quills	1		f	SA	Lydekker (1908)
Male lion a 'skeleton' from the effects of porcupine quills	1		m	Olifant River, SA	Stevenson-Hamilton (1912)
Several lions..had quills sticking in their paws and lips***	2		?,?	British East Africa, Somaliland	Pease (1914)
Lions hunt porcupine and many sustain nasty/fatal wounds***	2	1	?,?,?	Kruger NP	Pienaar (1969)
male Lion with >12 quills in the neck, shoulder, flanks, right leg (later died)		1	m	Kalahari	Owens & Owens (1984)
Two lions died as result of wounds caused by porcupines		2	?,?	Kalahari Gemsbok NP	Eloff (1984)
Old, solitary males often scarred from porcupine quills***	2		m,m	SA	Apps (2000)
Young male lion gets a porcupine quill stuck up its nostril	1		m	Kalahari	Daily Mail .Com, UK.2/9/2015
Masai Mara lioness licks its wounds after getting porcupine quills	1		f	Masai Mara	Daily Mail .Com, UK 5/4/2016
One lioness had a quill in her muzzle	1		f	Serengeti	Schaller (1972)
Male lion with quill embedded in left nostril, emaciated	1		m	Darajani, Kenya	Kingsley-Heath (1965)
One lioness injured by porcupine quills	1		f	Tsavo National Park, Kenya	TMVU Report (2010)
One lioness injured by porcupine quills	1		f	Tsavo National Park, Kenya	TMVU Report (2011)
Total Number of lions injured (including 9 that died)	20	10	15m, 5f, 10?		

***For reports not specifying exact numbers of lion (e.g. 'many', 'several') we assigned a number of 2

Table3. Credible Web reports of lions injured by porcupines

Description	Number of lions injured	Date uploaded	Location	Source: Videos or Photographs
Porcupines encounter lion pride.	7 injured	8/14/2010	Montage of misc videos with quills in 7 lions	Dee Barnes
Lion cubs eager for a meal find themselves in prickly situation	3 cubs	07/05/2008	Not stated	National Geographic www.youtube.com/watch
Lion battles with porcupine, Kruger NP, SA	1 lioness	23/10/2014	Kruger NP, SA	Henry Landman
Male lion full of porcupines' quills	1 lion	5/2/2016	Not stated. Images # 99480818; 99480821	www.shutterstock.com
Porcupine vs. Lion, lioness get quills during encounter	1 lioness	2/5/2010	Not stated	TheWizardWilly
Porcupine hunt	1 lion	1/28/2012	Kgalagadi TfP; SA & Botswana	Peet J van Eden
Lion picking porcupine quill out of his foot	1 lioness	1/26/2015	Kenya	quiltime
Lion-porcupine Interaction	1 lioness	12/25/2013	Kruger NP, nr Satara, SA	Latest Wildlife Sightings
Lioness with face full of porcupine quills	1 lioness	August 2012	Kruger NP, SA	wild4photographicsafari.blogspot.com
Lion looking up while drinking water with porcupine quills	1 lion	?	Kgalagadi TfP; SA & Botswana #135386543	gettyimages, Heinrich van den Berg
Dying lion with porcupine quills in his mouth	1 lion	?	Not stated. Image # 43745448	www.dreamstime.com
Lion with porcupine quill in right nostril	1 young lion	8/23/2011	Kgalagadi TfP; nr Mata Mata, SA	www.africabliss.com, Johannes van Niekerk
Total lions injured	20			

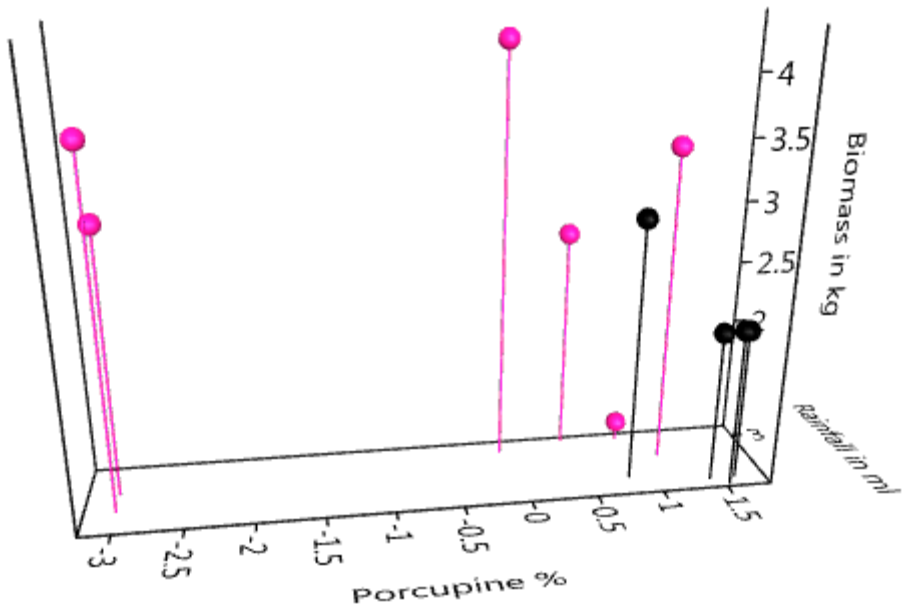

Figure 5. Three-dimensional graph of the relationships among prey biomass, rainfall and percent of porcupines killed by lions. All data are log transformed. The X axis represents percent of porcupines killed; Y axis represents prey biomass in kg; Z axis represents the mean rainfall in mm. Drawing in black indicates semiarid habitat, drawing in red represents non-arid habitat. Note that porcupine kills increase when preferred lion prey is scarce (low biomass) and when rainfall is low.

The wounding of lions by porcupines during severe drought suggests that lions turn to hunting porcupines when food-stressed. The Tsavo man-eating episode (1898) occurred during a severe drought (Hill, 1976; Kerbis Peterhans & Gnoske, 2001) and both had porcupine remains in their broken teeth (Gitahi *et al*. 2015).

Two adult female lions in Tsavo wounded by porcupines and treated by the TMVU (table 3; Tsavo Mobile Veterinary Unit Report 2010, 2011) were treated for porcupine wounds in 2010 and early February 2011. This occurred in the middle of one of the 13 most severe droughts in Kenya over 114 years (1900–2013: Masih *et al*. 2014; Mulama, 2016).

Two Kenyan man-eating lions in 1965 either were wounded by porcupines (the Darajani lion discussed above) or had eaten porcupines (FMNH 213656 that killed 10 people). This was also one of the 13 worst Kenyan drought years (Masih *et al*. 2014). The FMNH 213656 lion may have had its behaviour modified after it consumed a porcupine following severe trauma to its teeth. We found a large porcupine quill (29.6 mm in length by 7.4 mm diameter) tightly wedged into the entire pulp chamber of its broken lower left canine. Based on its CT scan (figure 6), it appears that the quill fractured and expanded as subsequent pressure was applied. This may have contributed to the presence of osteomyelitis found at the left anterior portion of the jaw at its junction with the abscessed broken lower left canine tooth.

The anti-predator defense of the porcupine can escalate to ‘active defense’ (Hayward & Kerley, 2005; Mori *et al*., 2013) by turning its back or side to the predator and backing into

the aggressor with its sharp quills (Hopkins, 2015). Stokes (1943) refers to a porcupine 'trick' of stopping suddenly when pursued by a predator, thereby impaling it. One of our colleagues was impaled by a porcupine that jumped backwards into him as he tried to rescue it from a garbage pit (see also Aydın *et al.*, 2017).

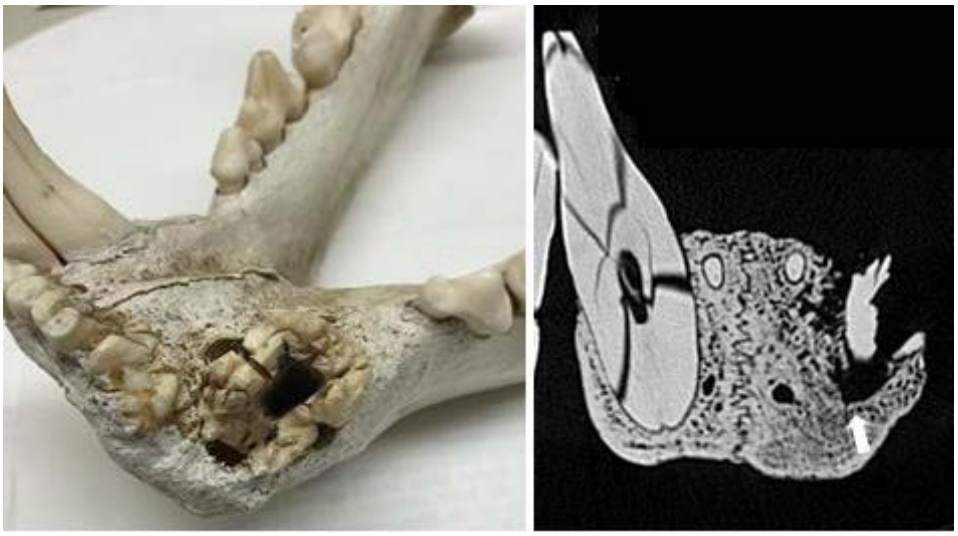

Figure 6. Left half of the figure represents the front of the mandible of Kenya male lion FMNH 213656. The right figure represents a coronal section by CT scan of the same specimen. Note that the left half of the mandible in front of P3 is larger than the right side. The white arrow indicates an abscess below the broken canine.

European and American carnivores have also been killed by porcupines (Mori *et al*, 2013; Elbroch *et al*. 2016). Not all injuries from porcupines are severe and at times the affected lion removes the quills from its nose or paws (Schaller, 1972). We speculate that female pride members and male cohorts assist one another in removing embedded quills as discussed in Hopkins (2015). If so, solitary males, including those dispersing from their natal prides, may be more vulnerable to impairment from quills.

Stevenson-Hamilton, who served as Game Warden of Sabi Game Reserve (now Kruger National Park) for 44 years, discussed several lions with porcupine injuries that attacked humans and/or their horses. He further discussed demographics of these lions; older males seldom showed signs of injury from porcupines while "*on the other hand, quite a percentage of young and those in the prime of life do, and are discovered to be thus practically incapacitated and often are mere skin and bone, showing that they have been unable to hunt, or at least catch animals on account of their injuries*". He adds "*it appears to be very exceptional however, for females to commit this imprudence, possible because they are accustomed to hunt in company and seldom go about alone as males often do*". He concluded that "*a great many males have a few porcupine quills sticking in their bodies*" (Stevenson-Hamilton, 1912, p. 176) and suggests that the pursuit of porcupines might be an activity more common among young male lions. Although we do not have data pertaining to age, 15 of the 20 wounded/killed lions in table 2 were males.

Debilitating limb injuries (including impalement by porcupine quills) prevent lions from capturing quick-footed prey and they may then select easier targets (*e.g*. livestock, people).

Mitra (2005), in a study of the lions in the Gir Forest, noted that lions injured by porcupines became cattle killers. Available data (Kingsley-Heath, 1965; Kerbis Peterhans *et al*. 1998; Kerbis Peterhans & Gnoske, 2001; Skuja, 2001; Mitra, 2005; Packer *et al*., 2005; Frank *et al*. 2006) establish that injured lions change their hunting behaviour. Death from quills is not immediate (Thom, 1954; Kingsley-Heath, 1965), but is probably more often slow due to festering infection (septicaemia) and starvation (Eloff, 1973, 1984).

Our work covers the varieties of lion-porcupine interactions and emphasizes three important issues: 1) porcupines can be a significant source of food, particularly during drought and in arid/semiarid and/or prey deficient landscapes where they represent up to 40.8 % of lion kills; 2) hunting porcupines can be risky and although most of the injuries may be mild, occasionally they result in prolonged damage and death; 3) severely injured lions may modify their behaviour and attack livestock and/or people. Finally, a commonality between Stevenson-Hamilton (1912, 1947) and our earlier data sets (Kerbis Peterhans & Gnoske, 2001) illustrates that young male lions sometimes engage in risky behaviour, especially when preferred prey are scarce. Indeed, the engagement of young males in risky behaviour is a common trait of many species, including our own.

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