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# Influence of drought on predation of elephant (*Loxodonta africana*) calves by lions (*Panthera leo*) in an African wooded savannah

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## Abstract

Data were collected on species killed by lions *Panthera leo* in Hwange National Park, Zimbabwe between 1998 and 2004. Lions killed predominantly large to medium-sized herbivores, concentrating on buffalo *Syncerus caffer*, elephant *Loxodonta africana*, giraffe *Giraffa camelopardalis*, wildebeest *Connochaetes taurinus* and zebra *Equus burchelli*. These species made up 83% of all lion kills found and 94% of the biomass of kills actually observed. Elephant calves made up an unusually large proportion of lion prey during the study period (23% of kills recorded). All elephants killed were dependent juveniles. Elephant calves appear more vulnerable during the dry months of the year, particularly in years of below average rainfall. Elephant calves are usually well protected. However, high-density aggregations of elephants around limited water sources during the dry season may deplete local food resources, forcing elephant herds to travel large distances between water and forage. Under these circumstances, elephant calves may become lost or separated from family groups, accounting for their high incidence in lion diet.

## Introduction

Lions *Panthera leo* are the largest carnivores in Africa and an important member of the carnivore guild in most intact savannah ecosystems. Although predators may have only a small impact on migratory prey (Bertram, 1979), predation by lions on sedentary ungulate populations can have considerable impact and may account for up to 50% of ungulate biomass removed by predators in some ecosystems (Mills & Shenk, 1992; Mills & Biggs, 1993). Lions exhibit flexible and opportunistic dietary patterns, taking a wide range of prey species and scavenging as readily as they will hunt (Schaller, 1972). When available, medium-sized ungulate prey dominates the diet of lions, a strategy that may optimize food intake against energy expended in hunting (Schaller, 1972). However, in areas where prey is scarce, lions may utilize smaller prey items; for instance, in the Kalahari lion diet is dominated by 32% porcupines *Hystrix africaaustralis*, followed by 25% gemsbok *Oryx gazelle* (Eloff, 1984). Occasionally, lions kill very large prey items (e.g. rhinoceros *Diceros bicornis*; Brain, Forge & Erb, 1999; Matipano, 2004), but usually this behaviour is opportunistic (Schaller, 1972).

Elephant *Loxodonta africana* populations in southern Africa have burgeoned over the last few decades (Blanc *et al*., 2005) and may have a significant and perhaps damaging impact in some protected areas (e.g. Barnes, 1983; Melton, 1985; Mapaure & Campbell, 2002). The elephant population in north-western Zimbabwe is estimated at 49 310 ($1.97\,km^{-2}$), and carcass ratios (i.e. number of carcasses seen compared with carcasses and live animals; Douglas-Hamilton, Michelmore & Inamdar, 1992) suggest that the population is still expanding (Dunham, 2002; Dunham & Mackie, 2002). In some protected areas, elephants may make up the bulk of herbivore biomass. Because of their large size (adults: 3000–6000 kg), tight-knit social system and aggressive defence of family members within the social unit, elephants are relatively immune to predation by large carnivores. However, juvenile elephants may occasionally become susceptible to predation if they are separated from the family group (Schaller, 1972; Dunham, 1992; Joubert & Joubert, 1994). Drought may also weaken adult elephants; however, Dudley *et al*. (2001) found no evidence that large predators killed weakened elephants during the 1996–1997 drought in Hwange National Park (HNP), Zimbabwe, although they scavenged from carcasses. Similarly, there were few reports of predation on drought-weakened elephants in Mana Pools National Park, Zimbabwe during the 1983–1984 drought (Dunham, 1988, 1992, 1994). Here we report on the incidence of lion predation on elephant calves during years of below average rainfall in HNP. We hypothesized that in years when the elephant population was subjected to conditions of below average rainfall, the incidence of elephant calf predation would increase because the stress of nutritional and water deprivation would create circumstances under which calves are more likely to become lost or lag behind family units and therefore become vulnerable to predators.

# Methods

## Study area

HNP (between latitudes 18°30′ and 19°50′ and longitudes 25°45′ and 27°30′) is 14 900 $km^2$ in area and situated in north-western Zimbabwe. Two thirds of the park is composed of Aeolian Kalahari sands; the remaining one third is on Batoka basalt and Karoo sediments, which forms part of the Zambesi drainage basin. Vegetation on Kalahari sands is dominated by teak woodland *Baikiaea plurijuga*, mangwe *Terminalia sericea*, and *Combretum* spp. scrubland and wooded grassland. Batoka basalt and Karoo sediments are dominated by mopane *Coleospermum mopane* woodland and scrubland. Less than 10% of the park consists of open and bushed grassland (Rogers, 1993). The densities of common herbivore species in the study area were as follows: elephant 3.8 $km^{-2}$; buffalo *Syncerus caffer* 0.61 $km^{-2}$; impala *Aepyceros melampus* 0.22 $km^{-2}$; zebra *Equus burchelli* 0.19 $km^{-2}$; giraffe *Giraffa camelopardalis* 0.18 $km^{-2}$; sable *Hippotragus niger* 0.09 $km^{-2}$; kudu *Tragelaphus strepsiceros* 0.07 $km^{-2}$; eland *Taurotragus oryx* 0.03 $km^{-2}$; warthog *Phacochoerus aethiopicus* 0.02 $km^{-2}$; and wildebeest *Connochaetes taurinus* 0.02 $km^{-2}$ (calculated from Dunham, 2002 for central and northern management units).

The mean monthly temperatures range from 17.2 to 30.4 °C (range 12.6–35.1 °C) in the austral summer and from 8.0 to 26.5 °C (range –2.1 to 31.8 °C) in the austral winter, with a mean of 28 days of ground frost from May to August. The region receives a mean annual rainfall of 650 mm, falling from November to April. Little natural water exists on the Kalahari sands during the dry season (May–October); however, numerous small water holes (or 'pans'), situated in inter-dune troughs, drainage lines and on calcrete deposits, fill with rainwater during the wet season. The northern part of the park has two perennial rivers, with pools remaining in places during the dry season and a number of springs and seep lines. A system of groundwater seep basins (Nehimba, Shakwanki and Shabi-Shabi seeps) occurs through the centre of the park running in a westerly direction towards the Botswana border (Williamson, 1975; Dudley *et al*., 2001). In these places the water table is close to the surface and water can be obtained by digging. At seeps in dry years, elephants regularly excavate wells to obtain water (Skinner & Smithers, 1990). The Parks and Wildlife Management Authority (PWMA) supplies water for wildlife during the dry season at artificial water points throughout the northern and western parts of HNP (but not in the Shakwanki or Dzivanini wilderness areas). The supply of artificial water is an important management intervention, first introduced during the 1930s, which allows water-dependent species to occupy an area that is otherwise seasonally very dry (Davison, 1967). These water points are heavily used by wildlife during the dry season, and in dry years there is considerable aggregation of elephant groups (mean group size $6.5 \pm 10.8$; with some aggregations $>100$ individuals; M. Valeix, pers. comm.) in the vicinity of artificial water points (Bourgarel & Valeix, 2000).

## Data collection

Between 1998 and 2004 we opportunistically collected data on kills made by lions in HNP. Although we did not systematically search for lion kills, we investigated all signs of lion activity and predator kills (aggregations of vultures, presence of lions, hyaenas or other scavengers, visible carcasses or carcasses located by scent) during routine collection of home range and demographic data for 18 prides and 14 coalitions of lions in a *c.* 7000 $km^2$ area in the northern and central parts of HNP. We included records from kills known to have been made by lions, either from personal observations of hunts or from reliable observers (National Parks personnel, Safari guides or other researchers) or because we could determine, using signs on the carcass and in the vicinity (e.g. spoor, kill signs, faeces), that lions had killed the animal. For completeness, incidences of domestic livestock killed by lions are included, even though this was only sporadically reported in the more remote areas surrounding the park. As no livestock occurred within the study area, they are not included in analyses. It was possible to establish with some confidence elephants that had been killed by lions and those that had merely been scavenged. Lion kills usually had bite marks on the throat, trunk, ears and back, and usually had severe claw marks on the back, flanks and ears. These could easily be distinguished from marks made by feeding lions, which were focused on the soft parts of the carcass (groin, belly, face, tip of trunk and around the anus). In addition, there were usually substantial signs of struggle (flattened vegetation, drag marks) in the vicinity of the carcass if the elephant had been killed as opposed to those that had died of dehydration or starvation.

We recorded date, location and, where possible, pride compositions at each kill. In addition, we collected the lower mandible of all elephant carcasses that we determined to have been killed by lions. Elephant mandibles were aged using the *foramen mentale* method (FM) (Sikes, 1967; Jachmann, 1985, 1988; Dudley *et al*., 2001). In this method the progression of lamellar plates on the molar-in-use is assessed in relation to the *foramen mentale* on the lateral side of the lower mandible. The lamina and the molar on which it is found can be related to the age class of the elephant with reasonable accuracy up until the age of 30 years (Jachmann, 1988). We followed Dudley *et al.* (2001) to derive age classes from FM number and combined FM classes to give age categories $\leq 1$, $\leq 2$, etc.

## Data analysis

Statistical tests were undertaken using the software package SPSS for Windows (version 10.0.5, SPSS Inc.). To assess the importance of elephants to lions as a dietary item, we compared the incidence of elephants with other species in the lion diet. Because opportunistic collection of kill data can bias samples towards large prey items (because large carcasses are easier to locate and take longer to consume) and miss small prey items (as these may be consumed rapidly and entirely), we compared the kills we had observed with kills we found later when lions either were feeding or had fed and left the kill. To detect possible bias, we compared proportions of each species in our sample of 'observed kills' and 'found kills' using a Wilcoxon matched pairs test.

To gain an indication of the energetic importance of a species to lions in terms of the amount of food it was likely to yield, we calculated the total biomass of each species in our sample of observed kills. To calculate biomass of kills, we used mean adult male and female weights for each species from Estes (1991). To calculate biomass of juveniles of all species except elephants, we arbitrarily assigned 25% of the average male and female weight for the species as the weight of a juvenile. For the weight of juvenile elephants of different ages, we followed the growth curve given in Laws (1966).

Rainfall data for each year during the study period were obtained from metrological records kept by Hwange Main Camp Research Unit. We compared the incidence of elephant killed in each year with the rainfall in the previous wet season using Spearman's correlation.

## Results

In total we recorded 203 lion kills during the study period, 50 of which were directly observed hunts (Table 1). Of these kills 44 were elephants, eight of which were observed directly. In addition, we also observed 83 unsuccessful hunts. The proportional composition of lion diet did not differ between the sample where we observed the hunt and that where we found the kills later (Wilcoxon matched pairs test; $Z=-0.45$, $P=0.96$). Although the proportion of species in the two samples was not statistically different, the proportion of large (>400 kg) prey items (buffalo, giraffe, eland and elephant) in the 'found' sample exceeded those in the 'observed' sample where the hunt had also been seen and may, therefore, be overrepresented in the sample of kills where the hunt was not observed. Additionally, wildebeest, warthog and impala appear to be underrepresented in the 'found' sample compared with the 'observed' sample, suggesting that there may be some bias between the methods. However, these are also species that favour particularly open or lightly wooded habitats (Skinner & Smithers, 1990), increasing the probability that hunts will be observed, which could potentially inflate their proportion in the 'observed' over the 'found' samples. Similarly, we cannot completely discount the likelihood that species found predominantly in woodland habitats may be underrepresented in both 'found' and 'observed' samples. Notwithstanding these potential biases, zebra, a species utilizing open areas, and kudu, a species preferring wooded habitats, occurred in similar proportions in both samples.

Buffalo were the most frequently taken prey species, making up 32% of all kills recorded. Elephants made up 22%, wildebeest 11%, giraffe 9% and zebra 7% of lion diet. These five species together made up 83% of lion kills found and in addition made up 77% of all successful and unsuccessful observed hunts ($n=133$ hunts, 74% of observed kills; 78% of unsuccessful hunts). Other species killed included leopard tortoise *Geochelone pardalis*, bush pig *Potamochoerus porcus*, hyaena cub *Crocuta crocuta*, springhare *Pedetes capensis* and baboon *Papio ursinus*. Sable, roan *Hippotragus equinus* and tsessebe *Damaliscus lunatus* appear to be hunted only rarely, the latter two species probably due to low densities in the study area.

Buffalo made up the majority of biomass of prey killed in observed hunts (49%, 6450 kg) followed by elephant (16%, 2150 kg) and wildebeest (15%, 1920 kg). Giraffe and zebra made up 9% (1150 kg) and 5% (715 kg), respectively

**Table 1** Numbers and proportions of species killed or hunted by lions *Panthera leo* in Hwange National Park

| | Kills observed | | Carcasses found | | Total lion kills | | Unsuccessful hunts | |
|---|---|---|---|---|---|---|---|---|
| Species | Number | % | Number | % | Number | % | Number | % |
| Buffalo | 12 | 24.5 | 51 | 34.5 | 63 | 32.0 | 32 | 38.6 |
| Zebra | 4 | 8.2 | 10 | 6.8 | 14 | 7.1 | 16 | 19.3 |
| Wildebeest | 10 | 20.4 | 12 | 8.1 | 22 | 11.2 | 8 | 9.6 |
| Giraffe | 3 | 6.1 | 15 | 10.1 | 18 | 9.1 | 5 | 6.0 |
| Elephant | 8 | 16.3 | 36 | 24.3 | 44 | 22.3 | 4 | 4.8 |
| Warthog | 4 | 8.2 | 6 | 4.1 | 10 | 5.1 | 2 | 2.4 |
| Impala | 3 | 6.1 | 2 | 1.4 | 5 | 2.5 | 2 | 2.4 |
| Kudu | 1 | 2.0 | 4 | 2.7 | 5 | 2.5 | 3 | 3.6 |
| Sable | 0 | 0.0 | 1 | 0.7 | 1 | 0.5 | 2 | 0 |
| Waterbuck | 1 | 2.0 | 1 | 0.7 | 2 | 1.0 | 1 | 0 |
| Eland | 0 | 0.0 | 7 | 4.7 | 7 | 3.6 | 3 | 3.6 |
| Other | 3 | 6.1 | 3 | 2.0 | 6 | 3.0 | 5 | 3.6 |
| (Livestock) | 1 | – | 5 | – | 6 | – | 0 | – |
| Total | 50 | | 153 | | 203 | | 83 | |

Records of livestock killed are included for completeness, but not used in analysis as all livestock kills took place outside the national park.

(Fig. 1). These five species made up 94% of the biomass of kills directly observed. All other prey species made up a total of 6% (784 kg) of the biomass of observed lion hunts. The mean biomass of an individual prey item was $258 \pm 241.3$ kg.

We collected data on elephant kills in all years during the study period apart from 2001 and 2004, where we found no evidence that lions killed elephants. Elephant kills were found throughout the study area, although certain areas within the park appeared to be a focus for this behaviour, especially Nehimba Seeps (15 kills) and Shumba Pans (eight kills), both situated in the north-central part of HNP, and Somavundla Pans (six kills) in the east of the park (Fig. 2). These were all areas where very high numbers of elephants aggregated during the dry season in search of water, especially in years when water availability in the rest of the park was limited.

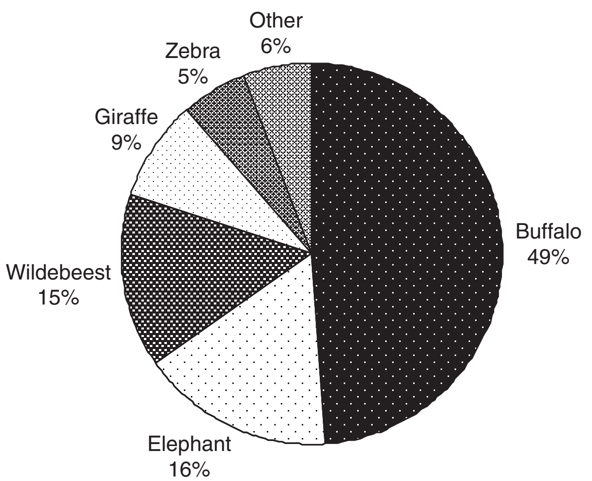


**Figure 1** Proportional contribution of each species to the biomass of observed kills made by lions *Panthera leo*, Hwange National Park 1998–2004.

We collected information on adult lion group sizes involved in elephant kills on 23 occasions. Single animals (in all cases males) killed elephants on three occasions, the oldest elephant calf taken by a single lion being 3 years old. More usually, groups of lions appear to have been involved in the kill. When only males were present, the mean group size was $1.8 \pm 1.3$ ($n = 5$; range 1–4); when only females were present, the mean group size was $7 \pm 2.9$ ($n = 15$; range 4–10); when a mixed group of males and females was present, there was a mean of $3.6 \pm 1.7$ females ($n = 3$; range 3–4) and $2 \pm 0.6$ males (range 1–4).

The mean age of elephants killed by lions was $2.4 \pm 1.5$ years (range: new born to 7.5 years; $n = 42$). The modal age class of elephants killed was from newborn to 1 year (FM classes molar I lamina 0 to molar I lamina 2; Fig. 3). All elephants were dependent juveniles [i.e. animals unable to survive without the maternal family unit (Moss, 1988), and 88% were less than 4 years old (FM classes molar I lamina 0 to molar II lamina 6)]. Seven of the eight observed kills of elephants were lone calves that had lost contact with their family units; only one was killed when adults from the family group were in the vicinity.

In years when elephants were killed, kills were not evenly dispersed throughout the year. Most kills occurred during the drier months of the year, with the majority being in October (the end of the dry season; Fig. 4). No elephant kills were recorded between December and March (the months when 80% of wet season rainfall occurs; Hwange Main

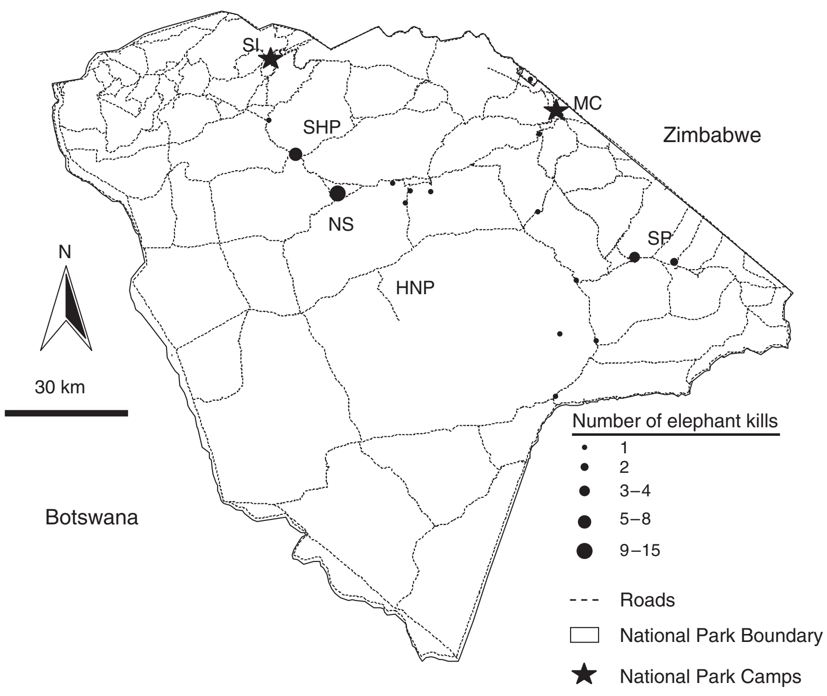


**Figure 2** Distribution of elephants *Loxodonta africana* killed by lions *Panthera leo* in Hwange National Park (HNP). MC, Hwange Main Camp; SI, Sinamatella Camp; SHP, Shumba Pans; NS, Nehimba Seeps; SP, Somavundla Pans.

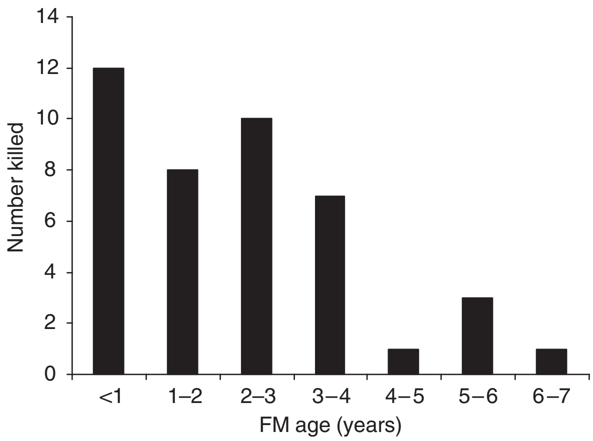


**Figure 3** Ages of elephant *Loxodonta africana* calves killed by lions *Panthera leo* during the study. FM, *foramen mentale* method.

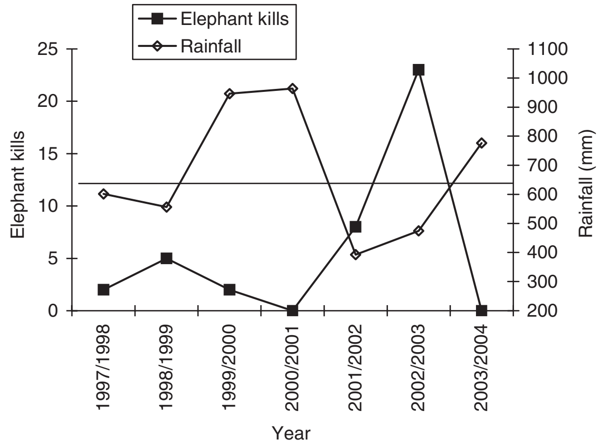


**Figure 5** Number of elephant *Loxodonta africana* kills found per year compared with rainfall in the previous wet season. Horizontal line represents mean yearly rainfall for Hwange National Park.

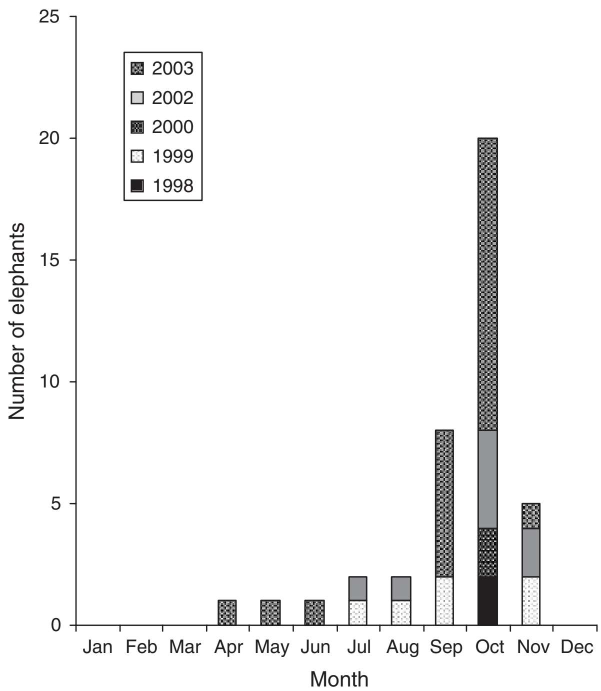


**Figure 4** Distribution of elephant *Loxodonta africana* calves killed by lions *Panthera leo* in each month, 1998–2004.

Camp Research Unit, unpubl. data). Over the study period the number of elephant carcasses found corresponded to the amount of rainfall in the previous wet season (Spearman's correlation –0.928; $P = 0.004$; Fig. 5). We found more elephant kills in dry seasons following wet seasons of below average rainfall (650 mm or less) and few or no kills in seasons following above average rainfall. In addition, two consecutive seasons of poor rainfall (2001/2002 and 2002/2003) appeared to have exacerbated the vulnerability of elephant calves to predation by lions, because during the 2003 dry season we found 23 elephant kills, over 50% of the entire sample.

## Discussion

As in many other studies of lion diet, large to medium-sized prey make up the bulk of the diet (Makacha & Schaller, 1969; Schaller, 1972; Mills & Shenk, 1992; Stander, 1992; Mills & Biggs, 1993; Mills, 1995). Although not without potential bias (overrepresentation of large prey items, underrepresentation of small items, underrepresentation of species favouring dense woodland), the data collected from all lion kills found indicated that buffalo, elephant, wildebeest, giraffe and zebra were the five most important prey species in the diet of lions in HNP during the study period. This is confirmed by observations of actual lion kills and the contribution of each prey species to the biomass of prey killed in observed hunts. With the exception of wildebeest, these are also the most common large to medium-sized herbivores in HNP (Dunham, 2002). Wildebeest are locally abundant and tend to be sedentary, which makes them vulnerable to predation (Mills & Shenk, 1992) especially solitary, territorial wildebeest bulls. Small species make up a comparatively negligible contribution to the energetic requirements of a large carnivore such as a lion in areas where medium to large-sized prey are readily available. So while small prey items may be underrepresented in our sample, they are also comparatively unimportant.

Unusually, elephants make up a considerable proportion (16% biomass) of lion diet in HNP and a significant proportion of the herbivore biomass that lions were observed killing. Although lions have occasionally been recorded killing young elephants (e.g. Schaller, 1972; McBride, 1982; Ruggiero, 1991; Dunham, 1992), it is, however, rare for this species to feature regularly in lion diet. Exceptions to this have been recorded in Chobe National Park, Botswana under drought conditions

(Joubert & Joubert, 1994) and in Gounda-St Floris National Park, Central African Republic, where lions killed young elephants orphaned by ivory poachers (Ruggiero, 1991). However, in most cases elephants are unavailable to lions as prey items; the adults are too large and aggressive (A. J. Loveridge *et al*., pers. obs.; Douglas-Hamilton *et al*., 2001) to be tackled even by a large pride and the juveniles are usually well defended.

Data analysed here suggest that in HNP elephant vulnerability to lion predation is correlated with rainfall, with more elephant calves killed in years following below average rainfall. The elephant population of HNP has grown dramatically over the last two decades because population control operations ceased in the mid-1980s (Valeix, 2002). The population of the park is estimated to be 44 492 (38 654–50 329) individuals (Dunham, 2002; Dunham & Mackie, 2002). Elephants are water dependent (Western, 1975), requiring between 80 and 160 L of water a day (Douglas-Hamilton *et al*., 2001), and may experience high mortality during drought periods (Williamson, 1975; Dunham, 1988; Dudley *et al*., 2001). Although the HNP elephant population disperses during the wet season (Williamson, 1975; A. J. Loveridge *et al*., pers. obs.), in the dry season elephants aggregate near water points and densities in habitats close to permanent water may reach 5.3 $km^{-2}$ (Bourgarel & Valeix, 2000). As elephants are predominantly browsers and require considerable intake of forage (75–150 kg $day^{-1}$; Skinner & Smithers, 1990; Douglas-Hamilton *et al*., 2001), high elephant population densities can cause substantial habitat damage. There have been clear changes in floral species composition in areas subject to heavy elephant browsing pressure and substantial resource depletion around artificial water points (Weir, 1972; Conybeare, 1991). The shortage of forage and water, as well as enormous social pressure, as unrelated family groups mingle in the vicinity of water points, causes considerable stress. The distance that elephant groups must travel regularly between areas of adequate forage to water in years of water shortage may be substantial. The stress of this situation may cause family groups to leave calves that are unable to follow the group. However, in the absence of behavioural observations of elephant herds, we were unable to conclude whether lone calves were abandoned or had simply become lost. Nevertheless, lone calves are extremely vulnerable to predation by large carnivores. We recorded 44 juvenile elephant kills between 1998 and 2004, with seven of eight observed kills being of lone calves. Although we did not undertake a systematic survey, it is likely that predation on elephant calves was widespread in HNP during the dry years of 1999, 2002 and 2003. In years that predation of elephant calves did occur, it was confined to the dry season when little water was available in the park, except at artificially supplied water points and limited natural seeps. Similar patterns of hyaena predation on elephant calves occurred in HNP during the dry season in years of poor rainfall (Teichmann *et al*., 2001; Salnicki, 2004).

Although the majority of elephants killed were assumed to be lone calves, lions did occasionally attempt to take elephant calves from family groups. We recorded two incidences where lions attacked a herd to capture juveniles, on one occasion successfully. On one occasion we were able to reconstruct the sequence of events from tracks we found in soft and wet substrate the morning after a hunt, while radio tracking the group of lions. Four male and three female lions ambushed a small family unit of elephants. One sub-adult elephant was caught but escaped after dragging a male lion for *c*. 10 m. At the same time a recently born calf (< 1 month old) was also caught and killed. In our interpretation the herd had panicked when ambushed and run away – and had not been able to defend the calf. However, in another observed hunt the lions were unsuccessful. On this occasion a small family group was attacked by a pride of lions (one adult female, two 3.5-year-old males and one 3.5-year-old female) in scrub surrounding a water point. One lioness jumped on the back of a 5–6-year-old juvenile elephant that had lagged behind the group. The two cow elephants returned and defended the juvenile elephant, which was able to escape.

The mean pride size in HNP is 2.5 adult females (A. J. Loveridge, unpubl. data). Lion pride sizes at elephant kills appear to be of above average size for HNP at seven adult females. It is possible that availability of elephant calves as prey items predisposes members of prides to remain in the same area. There is evidence that some very large prides (e.g. Shumba Pans pride – 10 adult females) split up in years of above average rainfall when prey remains relatively dispersed even during the dry season (A. J. Loveridge *et al*., pers. obs.). Alternatively, large pride sizes might also be due to the difficulty lions have in subduing elephant calves. Lions usually kill larger prey by suffocation (either clamping the nose or throat; Estes, 1991); clearly this is not possible for elephants. Consequently, elephant calves may take some time for lions to kill (Joubert & Joubert, 1994) and may require a cooperative effort.

Thirty-six per cent of our records of elephant calves killed by lions occurred at Nehimba seeps. This is an area where large die-offs of elephant have been recorded in the past (Williamson, 1975; Conybeare & Haynes, 1984; Dudley *et al*., 2001). On a single visit to the seeps in October 2003, we (A. J. L., J. E. H.) found 30 fresh elephant carcasses in a 500 m radius of the seeps; some had been killed and eaten by lions, but many appeared to have simply died of dehydration and malnutrition. In wet years, with above average rainfall, water remains in the seep depression throughout the year (A. J. Loveridge *et al*., pers. obs.); however, in years of below average rainfall the water dries up and elephants mine around 15–20 wells, sometimes several metres deep, into the edge of the depression. When large numbers of elephants congregate at the seeps, a great deal of social stress occurs, with the large bulls dominating the wells and excluding less dominant individuals (A. J. Loveridge *et al*., pers. obs.). Aggressive interactions are common among elephants competing for access to wells and we observed many elephants at the seeps with tusk wounds on their backs and flanks (A. J. Loveridge *et al*., pers. obs.). Because of the aggressive behaviour of larger animals, young to intermediate-size calves and sub-adults do not gain access to the wells and either are not able to drink before the family unit moves off or become separated from their family groups while waiting for access to water.

Very high population levels and water dependence cause high-density aggregations of elephants in areas close to water in Hwange (Weir & Davison, 1966; Weir, 1972) and other African parks (e.g. Tsavo National Park, Kenya: Bax & Sheldrick, 1963; Glover, 1963; Kruger National Park, South Africa: Brits, van Rooyen & van Rooyen, 2002). As a consequence of resource depletion in these areas and limited or reduced access to water because of social stress and competition, elephant mortality occurs in dry years. In HNP, in years of poor rainfall, an unusually large number of young calves become vulnerable to predation by large carnivores when they become separated from or are no longer able to follow their family groups. High levels of predation of juvenile elephants during dry years may be an indication that the elephant population in HNP, at least in dry years, is close to density dependence.

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