Lion predation on elephants in the Savuti, Chobe National Park, Botswana

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Lions rarely prey on elephants. Botswana's Savuti lions, however, switch to preying on elephants during the late dry season (August–November), and the frequency of this has increased in the last two decades (1985–2005). An opportunity to document this phenomenon was made possible with infrared viewing and filming equipment. A pride of 30 lions killed one elephant every three days. Seven of eight elephants killed were between four and 11 years old, as deduced from molar teeth ageing, and this age group represented over half the kills recorded by Joubert (2006). It is suggested that this weaned, maternally less dependent age class, may be more vulnerable to lion predation. Lions prey on elephants since the density of conventional ungulate prey is reduced as a result of an annual migration, and artificial water provisioning has prompted an increasingly sedentary population of elephants. Notes are presented on the lion's behaviour in hunting elephants and the evolutionary significance of this.

Key words: prey switching, elephant, lion, predator–prey relationships, Chobe National Park, Botswana.

INTRODUCTION

Elephants (*Loxondonta Africana*) are rarely preyed upon by lions (*Panthera leo*) (Skinner & Smithers 1990), and when this does occur it has been associated with yearling calves (Pienaar 1969; McBride 1984), or those weakened by poaching (Ruggiero 1991) or drought (Loveridge *et al.* 2006). However, in the Savuti area of the Chobe National Park (CNP), Botswana, the frequency of elephant predation by lions has increased from the 1990s onwards, and is not confined to weak or juvenile elephants (Joubert 2006). During the 1970s McBride (1984) recorded two instances of this, but a decade later Viljoen (1993) had not reported this at all. Subsequently, Joubert (1997) provided videographic evidence of a definite increase in this phenomenon (*Ultimate Enemies,* National Geographic, Washington D.C., 1997). He estimated that during 1990, 20% of the total food consumption of lions comprised elephants (Joubert 1997), and between 1993 and 1996 he observed 74 elephant kills, with a marked increase in the number of kills observed, as well as hunting success, by this pride over these years (Joubert 2006).

Adult lions weigh, on average, 190 and 126 kg in males and females, respectively (Smuts 1982; Skinner & Smithers 1990), and adult elephant males and females weigh six and four tonnes respectively (Skinner & Smithers 1990), while the subadults weigh less than half the weight of the females. This ratio of between 1:10–15, is certainly the largest predator to prey weight ratio known among terrestrial mammals (e.g. Packer 1986).

Lions typically prey on medium-sized ungulates in the size range 190–550 kg, with 350 kg being the preferred size (Hayward & Kerley 2005). With regard to large prey (>500 kg), buffalo (*Syncerus caffra*) are preferred in many savanna ecosystems (Mitchell *et al.* 1965; Makacha & Schaller 1969; Saba 1979; Prins & Iason 1989; Mills *et al.* 1995; Funston *et al.* 1998), particularly when male lions are present (Funston *et al.* 2001). Giraffes (*Giraffa camelopardalis*) too, are favoured (Pienaar 1969; McBride 1984; Hayward & Kerley 2005), and are at the upper end of the preferred weight range of lions (Hayward & Kerley 2005). There are isolated cases of lions killing other 'megaherbivores' such as hippopotamus (*Hippopotamus africanae*) (Bourlière 1963; Pienaar 1969) and both African rhinoceros species (Pienaar 1969; Brain *et al.* 1999; Matipano 2004). Predators generally select prey species according to body size, with larger predators preying on larger prey (Pyke *et al.* 1977; Scheel 1993; Radloff & Du Toit 2004). Furthermore, group-living lions exhibit a prey-size profile skewed toward large prey (Gittleman 1989; Hayward & Kerley 2005). The predatory habits of the Savuti lions are expected to have energetic implications and would be of academic interest.

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Elephant predation by the Savuti lions takes place predominantly during the months between August and November, and peaks during the month of October (Joubert 1997). An opportunity to observe elephant predation by lions was possible through a BBC Natural History Unit-commissioned film (*Planet Earth Series: Great Plains,* BBC, Bristol, 2007) of this phenomenon. The media of observation was unique in that it was infrared lighting, which is in contrast to the use of white light (e.g. *Ultimate Enemies*), which invariably has an impact on animal behaviour (Kremers & Van Norren 1989). Field guides from the local safari lodges are not permitted to drive at night, so the actual hunting and killing of elephants has rarely been witnessed. Apart from being documented in a film, elephant predation by lions has also been recorded anecdotally in a book (Joubert 1997), and later in a publication (Joubert 2006), but a dearth of detailed information prompted further investigation. Here we describe the patterns and nature of lion preying on elephants, in the context of the local elephant population.

STUDY AREA & METHODS

The Savuti area is situated within CNP in northern Botswana. The mean annual rainfall is 550 mm per annum. The mean maximum and minimum temperatures are 35°C and 18°C, and October is the hottest, driest month. The Savuti is characterized by a channel with a highly variable water flow, which eventually drains into the Mababe depression, after its passage across the Savuti marsh. The flow is thought to be determined by tectonic forces and it stopped flowing in 1982 (Walker 1991). Since 1995 water has been artificially provided at three waterholes (Barnes 1999), which additionally serve a game scout and tourist camps.

The tree layer is dominated by camelthorn trees (*Acacia erioloba*), with *Combretum mossambicense,* and *Lonchocarpus nelsii,* in the shrub layer.

The area is characterized by seasonal movements of herbivores, which influences lion prey use in the area, to the extent of limiting the lion population size (Viljoen 1993). The dry season (May–October) herbivore biomass is estimated to be 2000 kg/ km^2, which is 13–14 times lower than the wet season (November–April) biomass (Joos-Vandewalle 1988; Viljoen 1993). At the onset of the dry season, migratory lion prey such as zebra (*Equus burchelli*) and buffalo move to the Linyanti river system to the northwest (Viljoen 1993). During October 2005, elephants dominated (>90%) the herbivore community, both numerically and in biomass, which was similar to previously estimated elephant biomass fraction of all herbivores of 85% for the dry season (Joos-Vandewalle 1988). Small (<10-member) herds of tsessebe (*Damaliscus lunatus*), kudu (*Tragelaphus strepsiceros*), blue wildebeest (*Connochaetes taurinus*), and eland (*Tragelaphus oryx*) were present, with a larger number of impala (*Aepyceros melampus*) (20–30). There were an estimated 32 263 elephants in CNP during the dry season of 2004 (BDWNP 2004), and typically about *c.* 800 elephants reside at Savuti when all the waterpoints are pumped (Barnes 1999), which was the case in 2005. The water points were once ephemeral pans (Walker 1991) and are still officially referred to as pans although they are artificially pumped, and they are referred to as such in this paper.

The Savuti pride consisted of 30 lions during the study, including: 4–7 adult males, 8 adult females, 4 subadult males, 5 subadult females, and 6 cubs of both sexes (<1 year). The pride normally comprised 27 lions, ranging up to 30 when all the males were present. One male died of a suspected snake bite on 20 October 2005. Adult male lion membership was never consistent.

Between 4 and 28 October we followed the Savuti lion pride from sunset to sunrise with the objective of filming elephant predation. Two vehicles were used, one fitted with infrared lighting equipment. Observations of the lions were made with Cobra optic infrared binoculars at distances up to 100 m. In moonlit conditions or during crepuscular hours, Leica 10 × 40 binoculars were used. We used a Garmin GPS to record all locations for the determination of daily movement. Details on interactions and hunts were recorded, whether successful or not, and the outcomes were noted. We noted the environmental variable, moonlight. To be recorded as being moonlit, the moon had to be above half moon, and the moon had to be 30° above the horizon. A moonless period was when the moon was less than half, and if full, when it was below 30° of the horizon. Binary logistic regression was used to explore the relationship between moonlit hours and the occurrence of elephant kills.

At carcasses we noted the number of lions present to determine daily food consumption. This was based on the assumption of the following per capita daily consumption ratio of a) 1.5, b) 1, and c) 0.5, for a) adult males, b) females, subadults and c) cubs (<1 year), respectively (e.g. Viljoen 1993). We used the edible fraction from Viljoen (1993), and

masses from the literature for the eland (Skinner & Smithers 1990). The weights of the elephants were obtained from the ratio of known weight and height of adult females (Laws 1970), to that of age-specific heights of elephants (*eg.* Shrader *et al.* 2006) estimated for the kills we recorded. We made detailed descriptions of predatory behaviour and interactions with elephants. When observing family herds, we noted the herd sizes, arrival times, rates, and directions from which they came. For elephant carcasses, we photographed their skulls, molar teeth, feet and tusks. In the field we determined the sex of elephants attacked by lions. A post-event analysis of the still images was used to determine their age based on their shoulder heights (Shrader *et al.* 2006) relative to the total length of a lion (Smuts 1982; Skinner & Smithers 1990). We photographed all carcasses to accurately age the carcasses. We used the ageing criteria of molar eruption and wear (Laws 1967; Hanks 1972; Jachman 1988), tusk size (Pilgram & Western 1986), foot circumference (Western *et al.* 1983), and shoulder heights from field estimates (Shrader *et al.* 2006). Molar tooth ageing was done by sending the photographs to the University of Pretoria's Conservation Ecology Research Unit (CERU).

RESULTS

Lion predatory behaviour

Hunting success

Four of 18 hunting attempts on elephants were successful (Table 1). The reasons for failed hunts, where there was actual physical contact with the lions, were: a) effective protection of an infant elephant by its mother, b) marginally large (*c.* 15 years old) male knocking off lions, and c) 10-year-old male was able to shrug lions off by running into a thicket. Of failed hunts, one occurred during daylight and most others were in moonlit conditions, and when elephant herd size exceeded six. Successful hunts took place during dark evenings and when elephant herd size was less than five, and when the hunting group exceeded 27 lions (Table 1).

Predatory behaviour

The lions usually targeted groups of six or fewer elephants, and they attempted to split larger groups by running at them. Subadult lions frequently participated in hunts (Table 1). The hunting that was witnessed was initiated by the lionesses that would storm at, and single out an elephant of an appropriate size. In two of four successful hunts, a younger elephant was present that was not selected, possibly owing to maternal intervention. The first lioness reaching the elephant would attempt to jump onto the elephant's back, digging her claws into the elephant's hindquarters, and creating purchase for a lunge to the rump. A second lioness would follow suit and also 'ride' the elephants back, and while atop would persistently bite at the victim's spine. Two other lionesses were observed to hang onto either hindleg, and would also bite at the root of the tail if they could reach it. The other lions, including cubs, would run after the elephant. The elephants continued to run until they suddenly collapsed. Three of the kills observed took between one and two minutes from the time the first lioness was aboard until the victim was on its side on the ground. When the elephant was down, a male lion was observed tearing it open at the armpit region, and subadults were observed clamping the trunk. In the chases to kill the elephant, there were five to six adult males, seven adult females, four subadult males and five subadult females involved (Table 1). The cubs simply trailed behind in the chase, and were present when the elephant was down and dying.

Predation of elephants and other vertebrates

The lions killed a number of smaller vertebrates during the study period, including carnivores, which were not eaten (Table 2).

On average, elephant kills were made 272 ± 220 m (n = 8, range 10–600, Table 3) from the nearest water point, and the lions travelled a mean of 0.73 ± 0.7 km (range 0.1–2.5 km) per night over the study period.

There was no significant relationship between moonlit hours and the occurrence of elephant kills (P = 0.301, Minitab version 14). Elephant kills were, however, made during the first half and last quarter of the month, which appears to coincide with when the moon is less than full.

Ageing of kills

Subjectively, all of the elephant kill victims were aged at 10–12 years (Fig. 1), although the various ageing procedures employed showed that most victims were in fact between four and 11 years of age (Table 3).

Daily food intake

For the period 4–25 October, it was estimated

Table 1. Summary of all chases and hunting attempts observed of elephants and other ungulate species during October 2005.

Dates	Species	Hunting group size	Lion group composition	Prey group size	Physical contact	Hunting success	Night/Day	Moonlight
08 Oct 05	Elephant	28	6 ad. males, 7 ad. females, 4 subad. males, 5 subad. females, 6 cubs	5	Yes	Yes	Night	Dark
09 Oct 05	Elephant	27	5 ad. males, 7 ad. females, 4 subad. males, 5 subad. females, 6 cubs	3	Yes	Yes	Night	Dark
10 Oct 05	Elephant	3	2 ad. females, one subad. male	12	No	No	Night	Dark
13 Oct 05	Elephant	9	4 ad. females, 3 subad. males, 2 subad. females	20	No	No	Night	Dark
14 Oct 05	Elephant	27	5 ad. males, 7 ad.females, 4 subad. males, 5 subad. females, 6 cubs	3	Yes	Yes	Night	Dark
16 Oct 05	Elephant	15	2 ad. males, 4 ad. females, 4 subad. males, 5 subad. females	2	Yes	No	Night	Moonlit
16 Oct 05	Eland	28	6 ad. males, 6 ad. females, 4 subad. males, 5 subad. females, 6 cubs	1	Yes	Yes	Night	Dark
17 Oct 05	Elephant	24	2 ad. males, 7 ad. females, 4 subad. males, 5 subad. females, 6 cubs	11	No	No	Night	Moonlit
20 Oct 05	Elephant	4	4 ad. females	2	No	No	Night	Moonlit
21 Oct 05	Elephant	20	2 ad. males, 8 ad. females, 4 subad. males, 5 subad. females, 1 cub	1	Yes	No	Night	Moonlit
21 Oct 05	Elephant	12	8 ad. females, 4 subad. males	2	No	No	Night	Moonlit
21 Oct 05	Elephant	14	8 ad. females, 4 subad. males, 2 subad. females	3	No	No	Night	Moonlit
21 Oct 05	Elephant	21	4 ad. males, 8 ad. females, 4 subad. males, 5 subad. females	6	No	No	Night	Moonlit
22 Oct 05	Elephant	4	2 ad. females, 2 subad. males	3	No	No	Night	Moonlit
22 Oct 05	Elephant	6	3 ad. females, 2 subad. males 1 subad. female	1	No	No	Night	Moonlit
22 Oct 05	Elephant	6	3 ad. females, 2 subad. males, 1 subad. female	3	No	No	Night	Moonlit
23 Oct 05	Impala	6	2 ad. females, 4 subad. males	3	No	No	Day	—
23 Oct 05	Elephant	6	4 ad. females, 2 subad. males	1	Yes	No	Day	—
23 Oct 05	Elephant	29	6 ad. males, 8 ad. females, 4 subad. males, 5 subad. females, 6 cubs	4	Yes	Yes	Night	Dark
25 Oct 05	Elephant	15	6 ad. females, 4 subad. males, 5 subad. females	6	No	No	Night	Moonlit

that a lionesses ate an average of 10 ± 15 kg meat per day, 92% of which was elephant.

Elephant behaviour

Elephants would arrive at waterholes cautiously and would be bunched together, and temporal streaming was occasionally seen. Upon detecting lions they would trumpet, charge, or throw sand at them if they were aware where they were. Mean herd size did not differ (t_s = 0.6, 0.1 < P < 0.25, d.f. = 108) when moonless (10 ± 5, n = 68) compared to moonlit (9 ± 7, n = 42) periods.

Directions from which family herds came to the pans

Mean family herd size was 9.2 ± 6 (n = 110, range 2–24), and most elephant family herds

Table 2. List of animal species killed by the Savuti lion pride during the period 4–28 October 2005.

Animal species	Number of kills	Consumed or not
Elephant	8	Consumed
Eland, *Taurotragus oryx*	2	Consumed
Springhare, *Pedetes capensis*	1	Consumed*
Selous' mongoose, *Paracynictis selousi*	1	Not consumed
Leopard, *Panthera pardus*	1	Not consumed
Black-backed jackal, *Canis mesomelas*	1	Not consumed
Cape turtle dove *Streptopelia capicola*	1	Consumed*

*One individual within the pride fed upon these prey items – these were regarded as negligible to the pride's use of prey.

arrived from areas to the north and northwest of the Savuti pans (Fig. 2). The lions would normally lie in wait on the northern and eastern sides of DDS and Pump pan, respectively

Arrival rate of elephant breeding herds to the pans

There was great variation in the arrival of family herds at different times during the night. There did however appear to be a higher arrival rate of family herds to water points when they were floodlit (Fig. 3). There was no apparent trend for elephants to aggregate into larger herds during the more vulnerable darker moonless evenings (Fig. 3).

DISCUSSION

Predation on exceedingly large prey, like the elephant has the risk of injury associated with it, and high energy expenditure in handling and subduing prey. The rewards of energy gain have to be off-set by these risks (Elliott *et al.* 1977; Pyke *et al.* 1977; Karanth & Sunquist 1995; Sunquist & Sunquist 1997; Hayward & Kerley 2005). The Savuti lions appear to have capitalized upon this. Despite a high variance, the mean daily food intake was twice that which Viljoen (1993) recorded for the Savuti dry season (i.e. 4.6 kg/lioness/day), which does suggest that the handling costs of attacking elephants are offset by a high reward.

During the dry season in the Chobe, warthog (*Phacochoerus africana*) are normally preyed on (McBride 1984; Viljoen 1993), despite being suboptimal prey (Hayward *et al.* 2007), and since the herbivore biomass is completely dominated by elephant, the lions have no choice but to attempt to capture elephant. This was probably facilitated by the large pride of *c.* 30 individuals, although at any one time when the quarry is being dispatched, there are not more than five lions trying to subdue it. Joubert (2006) pointed out that the strategy to kill buffalo is similar to that employed with elephant. The strategy is to weigh down the hindquarters to ensure collapse of the elephant. We presume that their limbs are relatively weaker than most cursorial ungulates, which have high recoil energy, and flexion of their limbs enables escape from attacking lions (Scheel 1993). An elephant's muscular structure is designed for heavy weight bearing, and in the hindlimb they have a relatively thin gastrocnemius muscle (Weissengruber & Forstenpointner 2004).

Five of the eight elephant kills were aged between four and seven years, and with a much larger sample (Fig. 1), Joubert (2006) found that 42% of the elephants he observed killed by lions were a similar age range (e.g. 4–9 years). The second most important age group (e.g. 8–11 years), was also reported by Joubert (2006) as the second most

Table 3. A summary of the elephant and eland predation events from 4–28 October for the Savuti lion pride.

Species	Victim no.	Date	Time of kill	Time taken to die (min)	Time taken to consume (hours)	Sex and age of kills	Distance from water (m)	Moon status at time of kill
Elephant	1	04 Oct 05	–	–	22	Male, 8–11 yrs	140	–
Elephant	2	08 Oct 05	02:15	–	17	Male, 4–7 yrs	125	Moonless
Elephant	3	09 Oct 05	02:40	10	22	Male, 4–7 yrs	340	Moonless
Elephant	4	12 Oct 05	02:45	–	40	Male, 4–7 yrs	255	Moonless
Elephant	5	14 Oct 05	04:45	–	37	Male, 4–7 yrs	125	Moonless
Eland	a	16 Oct 05	00:10	–	2	Adult female	140	Moonless
Elephant	6	23 Oct 05	20:15	30	31	Male, 4–7 yrs	580	Moonless
Eland	b	25 Oct 05	–	–	1	Adult female	360	–
Elephant	7	27 Oct 05	–	–	–	Unk sex, 8–11 yrs	600	–
Elephant	8	28 Oct 05	23:00	–	–	Unk sex, 1–3 yrs	10	Moonless

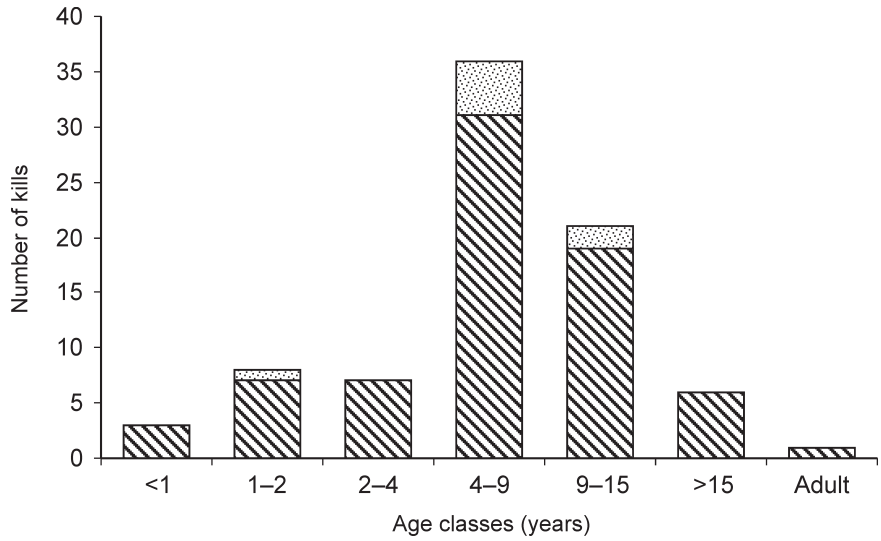

Fig. 1. Age class distribution of elephants observed being killed by lions from 1993 to 1996 (from Joubert 2006, hatched bars; and the present study (2005, stippled bars)).

vulnerable group to predation (Fig. 1). Furthermore, these appeared to be males, which is the more vulnerable sex of elephant kills (e.g. 61% of known-sex kills, Joubert 2006). Elephants between four and 15 years, and in particular males, appear to be the most vulnerable to lion predation. It is during these years that young elephants are weaned and gradually become more peripheral and less associated with the family herds (Moss 1988), in particularly the males (Lee & Moss 1985), and this might explain their vulnerability. Juvenile elephants are most often preyed on when they are orphaned through the action of poachers (Ruggiero 1991), and when they lag behind when a herd is on the move during drought periods (Loveridge *et al.* 2006), but in the Savuti success rates on infant elephants are very low (Joubert 2006) owing to the high degree of maternal care.

Elephants have moderate eyesight (Estes 1991), and it is probably poor at night, unlike lions, so this may explain why all successful kills were made on dark nights. Poor hunting success in moonlit con-

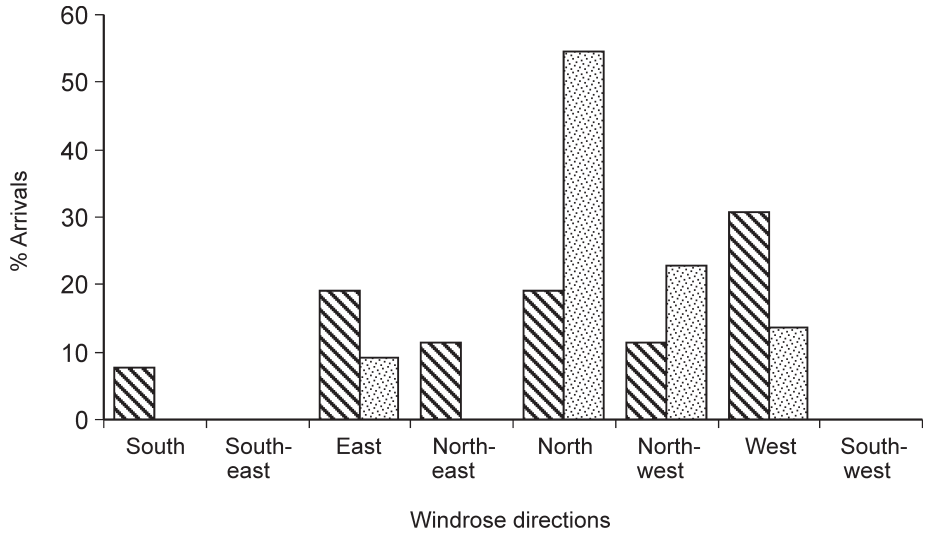

Fig. 2. Directions from which elephant family herds were seen arriving from when observations were made at Pump pan (n = 26, hatched bars) and the Desert & Delta Safaris (DDS) pan (n = 66, stippled bars).

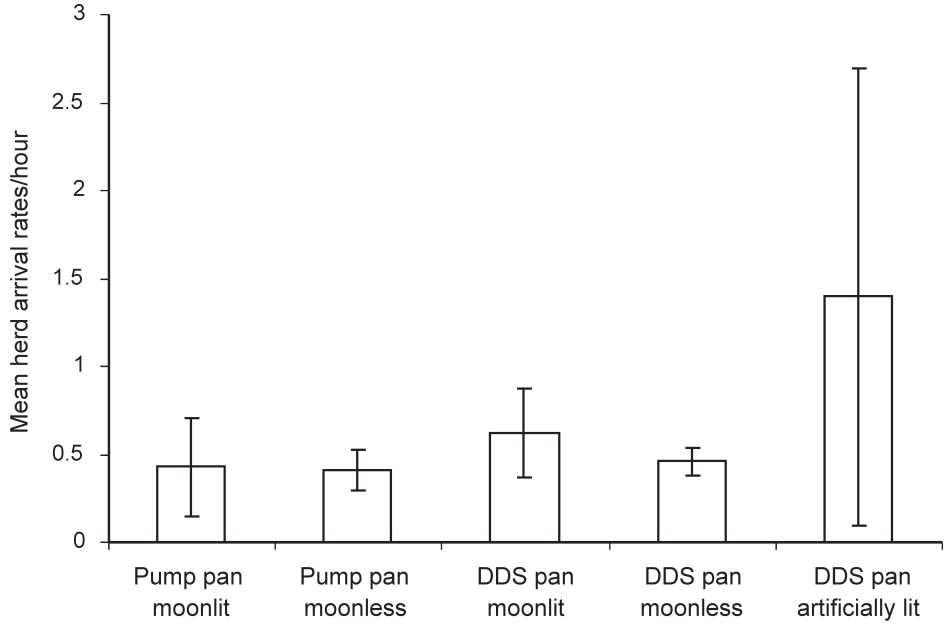

Fig. 3. The arrival rates of family herds to the Pump and Desert & Delta Safaris (DDS) pans during conditions of moonlight and darkness, and when artificially floodlit. The artificial light shone from the south of the pan from a camp. The error bars represent the standard deviation of the mean.

ditions is well known for lions (Funston *et al.* 2001; Van Orsdol 1984; Joubert 1996). Interestingly, there was a higher arrival rate of family herds to the artificially lit water point (Fig. 3), which may be due to the improved lion detectability in enhanced lighting conditions. The mean herd size of nine is the norm for elephant family herds (Moss 1988), and there was no difference in herd size under moonlit or moonless conditions, and no inclination to form into larger multi-tiered groups, as can be suspected when predation is an imminent threat (Hamilton 1971; Wittemyer *et al.* 2005). Generally, Savuti elephants arrived during the earlier part of an evening, with 65% drinking before midnight, which is similar to Etosha elephants (71%: Du Preez & Grobler 1977). Nighttime arrivals may be a means to avoid bull harassment. However, elephant bulls were present day and night, so this remains speculative. CNP elephants do have contracted dry season ranges (Chase 2002) and adult bulls normally roam more than 10 km from water sources, while family units are always within 3.5 km (Stokke & Du Toit 2002). Most elephant herds arrived from the north of both pans (Fig. 2), which suggests that they spend the day in a general area along a course of an expected migration route, should they be compelled to travel to the nearest perennial water source – the Linyanti river system. The high rate of water turn-over in juveniles and lactating cows, and the lack of infant mobility, means that family units are unable to range far from water during the dry season (Stokke & Du Toit 2002). However, since female elephants are more selective foragers than adult males (Stokke 1999), and since mature camelthorn trees and seedling regeneration have both declined within 5 km from Savuti water points (Barnes 1999), elephant family herds are compelled to forage further away. So an optimal foraging trade-off is evident for the elephants, while contending with predation risk.

From an evolutionary perspective, the lions might be reverting to a role they once had as predators of megaherbivores. Alongside other sympatric large felids, like the sabre-toothed cats (*Megantereon*), lions may once have exerted significant top-down control on the megaherbivore community on the African savannas (Ewer 1986; Whitney-Smith 2001; Turner & Anton 2004). Lion pride sizes have declined appreciably in some African ecosystems (Bauer *et al.* 2003), probably owing to human hunting with modern weaponry (Bauer *et al.* 2003; Whitman & Packer 2007), rendering megaherbivores less vulnerable to lion predation (Owen-Smith 1988). During the Pleistocene, lions were hunters of megaherbivores (Ewer 1986;

Guthrie 1990; Turner & Anton 2004), and historically, the larger lion prides that were thought to occur may have been more predisposed to attacking larger megaherbivores (Bauer *et al.* 2003; Whitney-Smith 2001).

Reports of this phenomenon are mostly confined to the Savuti, but there are accounts from elsewhere in Botswana, such as the Linyanti, Kwando and Chobe river systems (Joubert 2006). This phenomenon appears partly to be an artifact of intervention and the behavioural flexibility of an intelligent predator. On the one hand, the installation of artificial watering points has encouraged residency in the elephant population, and negated the traditional seasonal movement to a perennial water source. This high resident population of elephant has primed the lions to specialize on them as a dry-season staple prey. Mindful of the burgeoning elephant population in southern Africa (Blanc *et al.* 2005), this type of top-down control would be appreciated in the context of elephant management. The role of the Savuti area as a sink in the context of the greater northern Botswana elephant population (e.g. Van Aarde & Jackson 2007) is worth exploring.

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