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Cheetah cub survival revisited: a re-evaluation of the role of predation, especially by lions, and implications for conservation

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Abstract

Cheetah cub survival on the Serengeti Plains (SP) was found to be exceptionally low, because of high predation rates, thought to be especially by lions. These results have contributed to the perception that cheetah cubs are particularly vulnerable to predation, and that areas with large carnivores may not be suitable for cheetah conservation. Here we show that survival of cheetah cubs in the Kgalagadi Transfrontier Park was seven times higher than on the SP and, although predation was the most common form of mortality, lions were not found to be involved. Moreover, we suggest that scrutiny of the Serengeti data does not unequivocally prove the dominance of lions as predators of cheetah cubs there. We discuss these findings in the context of cheetah conservation, suggesting that further research on coexistence between cheetahs and other carnivores should receive attention and that the high mortality rates of cubs found on the SP may not be as widespread as is commonly believed. Furthermore, we recommend that maintaining the link between biodiversity and ecosystem functioning should receive more attention in carnivore conservation.

Introduction

Determining the rate of cheetah *Acinonyx jubatus* cub survival in the wild is difficult. This has been achieved on the Serengeti Plains (SP) where 4.8% of 125 cubs monitored from the den to adolescence survived. Predation, mainly by lions, is held to be the major mortality factor (Caro, 1994; Laurenson, 1994; Kelly & Durant, 2000; Durant, Kelly & Caro, 2004). This has contributed to a widespread perception that cheetah cubs are particularly vulnerable to predation by large carnivores, especially lions, and has had a widespread influence on conservation planning for cheetahs (Caro, 1994; Merola, 1994; Nowell & Jackson, 1996; Crooks, Sanjayan & Doak, 1998; Kelly & Durant, 2000; Durant *et al.*, 2007). It has led to a perception that protected areas may not be the most suitable areas in which to conserve cheetahs, and that efforts might, in some cases, be better directed at areas free of large carnivores (Laurenson, 1992; Nowell & Jackson, 1996; Marker, 1998; Kelly & Durant, 2000; Marker & Dickman, 2003; Purchase, Vhurumuku & Purchase, 2006; Wachter *et al.*, 2011). Here we compare survival rates and causes of mortality of cheetah cubs from the SP with those of a similarly monitored sample of cubs from the Kgalagadi (Kalahari) Transfrontier Park (KTP), South Africa/Botswana and discuss the question of predation on cheetah cubs, especially the role of lions. In light of these findings, we discuss strategies for cheetah conservation research within an ecosystem dynamics framework.

Methods

The Kgalagadi study area was a 6000-km^2 region in the south of the park (25°46′S 20°23′E), which is the most arid part of the KTP. The dominant landscape comprises undulating sand dunes covered with shrubby grassland and two dry river-beds of open tree savannah cutting through the dunes (Van Rooyen *et al.*, 2008). In contrast, the SP is a vast gently undulating plain of 5200 km^2 interspersed with groups of granite and gneiss outcrops (Sinclair, 1977). Both areas are nested in large protected areas with the full complement of mammalian carnivores, although the composition and densities are different (Table 1).

Carnivore density estimates

The lion population on the SP has fluctuated markedly in recent years (Packer *et al.*, 2005). We therefore calculated the density of lions and other large carnivores on the SP from the nearest numerical assessment we could find to the time of the aforementioned cheetah cub survival study and assumed that the area covered by the plains was 5200 km^2 (Caro, 1994). We did not include leopards as they were not shown to be present on the SP, although they are in the adjoining woodlands (Caro, 1994).

In comparison with the SP, lion numbers have remained quite stable in the KTP in recent years (Mills *et al.*, 1978;

Table 1 Large carnivore densities (per 100 km^2) on the Serengeti Plains and the Kgalagadi Transfrontier Park

	Serengeti Plains	Southern Kalahari
Lion	3.8	1
Spotted hyaena	100	0.9
Brown hyaena	Absent	1.2
Leopard	Absent	0.2
Cheetah	2.1	0.6
Wild dog	1.2	Absent

Castley *et al*., 2002; Funston, 2011). We used data from spoor surveys (Funston, 2001; Funston *et al*., 2010) conducted a few years before the cheetah cub predation study.

Cub survival monitoring

Six adult female cheetahs were fitted with conventional very high-frequency radio collars (Advanced Telemetry Sytems, Isanti, MN, USA) between 2006 and 2012, and monitored for periods ranging from 20 to 68 months (total 311 cheetah-months). Each one was located at least once a month while collared. Once a den had been found, we approached it at the first opportunity that the mother left it to count and age the cubs. Of 17 litters found in the den, 10 were judged to be under 2 weeks of age when first found (eyes not completely open, poor mobility) and seven were older. The mean (3.4) and range (2–5) litter size of cubs under 2 weeks of age did not differ significantly from the mean (3.3) and range (2–4) of cubs older than 2 weeks old when first found (*t*-test $P = 0.8899$; two-tailed), indicating no loss of cubs in the older litters before we found them. Three litters belonging to three different female cheetahs disappeared before we were able to count the cubs. We have assumed that they contained 3.4 cubs (the mean litter size of newborn cubs).

We visited the dens at least once every 5 days. If the den was deserted, we searched the area for clues as to the disappearance of the cubs, especially looking for tracks of potential predators in the sand. Such non-trivial handling and activities around cheetah dens has been found not to affect their reproductive success (Laurenson & Caro, 1994) and all collars used were removed at the termination of the study.

Once the cubs had left the den, we regularly located and followed the cheetahs for up to 14 days at a time. All female cheetahs with cubs were located at least once a month.

Results

Carnivore densities

Spotted hyaenas *Crocuta crocuta* occurred at an extraordinary high density on the SP, but at a low density in the KTP (Table 1). The lion density on the SP, although considerably lower than the spotted hyaena density, was nearly 3.8 times higher than in the KTP. Leopards *Panthera pardus* were absent from the SP, which is outside the distribution range of the brown hyaena (Smithers, 1982), which is the most common large carnivore in the KTP. A few wild dogs *Lycaon pictus* inhabited the SP, but were absent from the KTP. Cheetah densities were 3.5 times lower in the KTP than on the SP. There were 1.8 lions for every cheetah on the SP and 1.7 in the KTP. Apart from the vast difference in spotted hyaena densities between the two areas, the SP contained 3.8 lions per 100 km^2, compared with 2.4 lions/leopards/brown hyaenas per 100 km^2 in the KTP; 1.6 times as many.

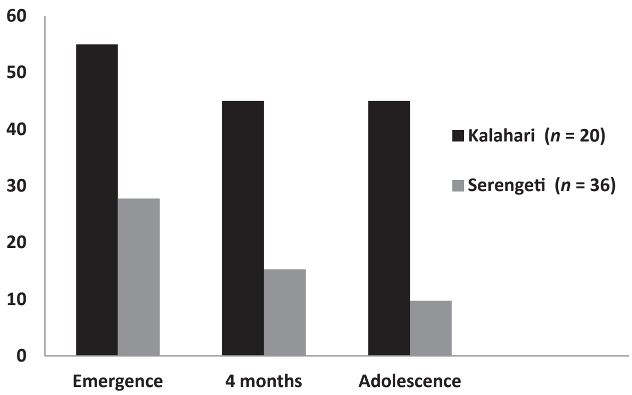

Figure 1 A comparison of the percentage of cheetah litters that survived from the time they were found in the den to: (1) emergence from the den; (2) 4 months of age; and (3) adolescence (14 months) in the Kgalagadi Transfrontier Park and Serengeti Plains.

Overall cheetah cub survival

Survival rates from the time the cubs were located in the den until they reached adolescence at 14 months (Laurenson, 1994), were very different in the two populations. For litters (Fig. 1), at least one cub survived to adolescence in 45.0% of KTP litters, compared with 9.7% of SP litters [number of litters that survived/died from birth to adolescence, KTP vs. SP, χ^2 (with Yates' correction) = 7.70; $P = 0.0055$; two-tailed]. Of cubs born, 35.7% survived to 14 months in the KTP compared with 4.8% in the SP (Fig. 2). We were unable to test for significance because cub deaths in the den were mainly of complete litters (see next section) and therefore not independent.

Survival in the den

In the KTP, 55% of litters and 53.6% of cubs survived to emergence, whereas on the SP, 27.8% of litters and 28.8% of cubs did [number of litters that survived/died from birth to emergence, KTP vs. SP, χ^2 (with Yates' correction) = 2.99; $P = 0.0838$; two-tailed].

Lion predation was claimed to be the main mortality cause in the den on the SP, although only 6.7% was known to be caused by lions, and 32.6% was ascribed to lions on circumstantial evidence (Laurenson, 1994). An additional 30.9% mortality was unknown, but was also considered to have been mainly due to predation as entire, seemingly healthy litters,

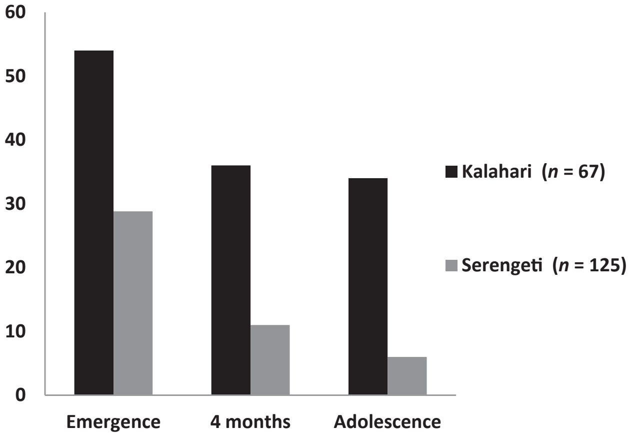

Figure 2 A comparison of the percentage of cheetah cubs that survived from the time they were found in the den to: (1) emergence from the den; (2) 4 months of age; and (3) adolescence (14 months) in the Kgalagadi Transfrontier Park and Serengeti Plains.

disappeared simultaneously (Laurenson, 1994), as would be expected from a predator attack on altricial cubs. In these instances, lions were also considered to be the main perpetrators. Opportunistic observations of lions killing cubs at dens other than those included in the intensive study were quoted from several sources as support for this contention (Laurenson, 1994). However, it is possible that other predators were responsible.

We were also often unsure of the cause of mortality in the den. Of 31 dead cubs, we were only certain of the cause in two of the litters involving four of the cubs. In the first, a litter of five, tracks in the sand revealed that three were taken by a leopard. In the other, a litter of two, one cub was thin and uncoordinated and disappeared at 4 weeks of age, too weak to survive.

All 27 remaining cubs disappeared simultaneously, when the mothers and cubs were doing well. We ascribed these disappearances to predation. However, we only obtained supporting evidence in two cases. Once we found bone splinters, hair and traces of blood in the sand, but no indication of what the predator might have been. In the other, a honey badger *Mellivora capensis* and black backed jackals *Canis mesomelas* were in the vicinity at the time. Although we searched the area within hours of the cubs disappearance, we found no tracks of large carnivores. Therefore, at most, only 22 of 67 (32.8%) cubs monitored could have been killed by lions or other large carnivores in the den. Equally, they could have been killed by smaller predators such as jackals or honey badgers, both of which have been reported to kill altricial young of other carnivores (Begg *et al*., 2003; Kamler *et al*., 2012).

Assuming that cub deaths from unknown causes occurred in the same proportions as definite or probable causes (Laurenson, 1994), predation accounted for a significantly greater proportion of cub deaths in the den in the KTP than in the SP [Table 2; predation vs. other causes of mortality in the den, KTP vs. SP χ^2 (with Yates' correction) = 6.32; $P = 0.0119$; two-tailed]. Although predation was important in the SP, other factors such as desertion and environmental factors played a non-trivial role (43.1%) in small cub mortality. In the KTP, predation was the overwhelming cause of mortality in the den, notwithstanding the fact that the survival rate in the SP at this age was far lower than in the KTP.

Table 2 Percent causes of mortality of cubs while in the den on the Serengeti Plains and in the Kalahari

Cause	Serengeti (*n* = 89)	Kalahari (*n* = 31)
Predation	56.9	88.9
Abandoned	22.8	0.0
Exposure	10.6	0.0
Fire	6.5	0.0
Poor condition	3.3	11.1

Post-emergence survival

From the time the cubs emerged from the den until they reached 4 months, the survival rates in the two studies continued to be different; 66.6% of the cubs in the KTP survived compared with only 37.5% from the SP [number of cubs that survived/died, from emergence – 4 months, KTP vs. SP χ^2 = (with Yates' correction) 8.01; $P = 0.0047$; two-tailed]. Again, few direct observations were made. In the SP, on two occasions, spotted hyaenas were seen carrying off a total of five dead cubs, and further opportunistic observations, not part of the intensive study, revealed lions, as well as other predators such as a leopards and Masai dogs *Canis familiaris* killing cubs (Laurenson, 1994).

Of 12 cubs that disappeared between emergence and 4 months in the KTP, seven disappeared suddenly, one at a time, and are strong candidates for predation. One survived for 2 weeks with an injured leg, but lost condition and disappeared. Three out of another litter of four disappeared one by one over a 34-day period when the mother was struggling to obtain food. During this period, she only caught one hare (*Lepus* spp) during 11 days observation. The ultimate cause was probably starvation. The 12th cub to disappear apparently became lost.

Survival from 4 to 14 months was again significantly different in the two areas (number of cubs that survived/died, 4–14 months, KTP vs. SP, Fisher's exact test $P = 0.0071$; two-tailed). In the SP, 54.5% survived, but there were no clues as to the reasons for the disappearance of any of them (Laurenson, 1994). In the KTP, 95.8% survived. The single cub that died sustained a serious injury to its leg and disappeared soon afterwards.

Summarizing the data from leaving the den to adolescence, seven KTP cubs were probably killed by predators, three died of starvation, two incurred injuries after which they were unable to keep up with their mother and one became lost. Most of the SP animals were assumed to have been killed by lions or spotted hyaenas, although only 5/30 (16.7%) were observed being killed by spotted hyaenas (Laurenson, 1994).

Discussion

Combining observations from both the intensive study and opportunistic observations, it was concluded that predation accounted for 73.2% of cheetah cub deaths on the SP with 78.2% of these being killed by lions (Laurenson, 1994). Clearly, predation is an important cause of cub mortality in both areas and the overall rate is higher in the SP, although relatively higher in the KTP, where other factors such as desertion and environmental factors were not recorded. This is almost certainly at least partly due to the greater large carnivore density in the SP, but the large number of unknown predation events may not have always been lions. Other predators such as leopards, domestic dogs and even secretary birds *Sagittarius serpentarius* have been observed killing small cheetah cubs on the SP (Laurenson, 1994), and other smaller carnivorous animals are capable of doing so as well.

There are difficulties with the anecdotal, opportunistic observations on which much of the interpretation of the SP data relies (Laurenson, 1994). They may be biased towards predation by large carnivores, especially lions, which are charismatic and likely to draw attention. Additionally, such observations are random and are spread over several years and areas, so it is difficult to quantify their true frequency. Cubs dying from starvation, disease or abandonment are possibly more likely to die unobtrusively. Those killed by less charismatic predators like jackals or hyaenas might also be less likely to be noted. Furthermore, the fact that 43.1% of the cubs in the den died from non-predation causes on the SP should not be overlooked.

Additional data of cheetah cub survival in the den from other areas are unavailable. Nevertheless, the high post-emergence mortality found in the SP has not been found in other areas. In Phinda Resource Reserve, South Africa, 75% of cheetah cubs seen after emergence survived to 1 year and 62% to independence at the same time that lions were introduced onto the reserve. This was at least partially ascribed to the fact that there were abundant refuges for female cheetahs and cubs (Hunter, 1998). On a small fenced South African reserve that also contained lions, the survival of cheetah cubs after emergence to 1 year was 60% (Bisset & Bernard, 2011), although they also found that mortality of cubs and young adult cheetahs is elevated in the presence of lions and other carnivores. Fears that the translocation of cheetahs into Matusadona National Park, Zimbabwe would be unsuccessful because at the time of their release, the park had one of the highest densities of lions in any protected area of Africa (approximately 6.1 lions per 100 km^2 for the first 5 years after reintroduction) turned out to be unfounded, and 10 years later, cheetahs were established in the area (Purchase *et al.*, 2006). In a lion- and spotted hyaena-free area in Namibia, 11/14 cubs monitored from emergence to independence survived (Wachter *et al.*, 2011), which is not statistically significantly different from the survival of cubs in our study (number of cubs that survived/died from emergence to independence, KTP vs. Namibia, Fisher's exact' test $P = 0.501$). In another lion- and spotted hyaena-free area in Namibia, it was reported that fewer than 50% of cubs reach independence (Marker *et al.*, 2003). So there does not necessarily seem to be greater cheetah cub survival in large predator-free areas than in areas with large predators.

The low survival of cheetah cubs reported by Laurenson (1994) on the SP may be exceptional. The extremely open landscape may make cheetah cubs vulnerable to predation as they can be detected from afar and there is a paucity of thicker bush refuges. Additionally, this study was carried out when the lion density was high and mortality may be lower during periods of low lion density (Durant *et al.*, 2010). Furthermore, the migratory patterns of the cheetah's principle prey, Thomson's gazelle *Gazella thomsoni* (Durant *et al.*, 1988; Caro, 1994) may sometimes compromise the ability of female cheetahs with small cubs to find food, if the gazelle move too far away from the den. This might lead to higher levels of mortality because of abandonment. In the KTP, this is less likely as the major prey species for female cheetahs, steenbok *Raphicerus campestris* (M.G.L. Mills, pers. obs.) is sedentary (Smithers, 1982).

Most areas in the cheetah's range are arid bush or savanna woodland (Smithers, 1982; Sunquist & Sunquist, 2002), where cover and decreased visibility may make cheetah cubs less vulnerable to predators and where prey dispersion patterns are variable. We have shown that in one area, cub survival is higher than is generally held, even though predation on cubs occurs. We have also suggested that lions may not be the devastating predators they have often been taken to be. Small, altricial cheetah cubs are just as prone to predation by jackals as lions when their mother is out hunting.

An ongoing debate in conservation is the relative merits of single-species versus ecosystem-oriented conservation (Lindenmayer *et al.*, 2007). Bowen (1999) saw this as a divergence between systematists, supporting the importance of phylogeny, ecologists arguing for the protection of populations or ecosystems, and evolutionary biologists promoting the factors that enhance adaptation and biodiversity, and proposed that it could be resolved if conservation efforts are directed towards preserving processes of life. Cheetah conservation plans and the results we have presented here illustrate this conundrum.

Coexistence between cheetahs and other carnivores is a fundamental aspect of African savanna community ecology. High levels of cub mortality and intra-guild predation are natural elements in a multispecies system and an aspect of cheetah, and probably over species' population dynamics (Mills, 2005). Indeed, the cub survival rate of 34.3% for Kalahari cheetahs is similar to what was found for leopard cubs (37%) in the Sabi Sand Game Reserve, South Africa (Balme *et al.*, 2012). The exceptionally high cheetah cub mortality found on the SP should not be taken as typical for the species. Yet, a prevailing attitude exists that the species is severely impacted by this process to the point where, as we have mentioned, it may be better to invest scarce funds for cheetah conservation in areas where other large carnivores are absent. This is illustrated in the regional conservation strategies for cheetahs in Southern and Eastern Africa (IUCN/SSC, 2007*a*,*b*) where the emphasis is on promoting coexistence between cheetahs, people and their domestic animals, and no mention is made of improving an understanding of their coexistence with carnivores. Such thinking is founded on a top–down focus, but African predator densities may be related more to the biomass of their preferred prey than to their competitors (Hayward, O'Brien & Kerley, 2007).

Lindenmayer *et al*. (2007) argue for an approach that targets limited resources for conservation research at projects that may close important knowledge gaps, while also promoting ongoing synergies between single-species and ecosystem-oriented research. We concur and agree with Caro & Laurenson (1994) that this process needs to be studied over a wider selection of landscapes in order to better understand diversity of intra- and interspecific community dynamics and ecosystem function, and to promote the conservation of all facets; compositional, structural and functional, of biodiversity (Noss, 1990). As examples, the Serengeti woodlands, the Central Kalahari Game Reserve, Botswana and Ruaha National Park, Tanzania are important areas for investigation.

The link between biodiversity and ecosystem functioning (Reiss *et al*., 2009) should be a crucial goal for conservation. Although conserving cheetahs outside conservation areas is not redundant, especially where this facilitates the maintenance of corridors (Bennet, 1999), quality not quantity should be the primary aim. For this, functional ecosystems are essential and lions are needed.

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