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Management-induced niche shift? The activity of cheetahs in the presence of lions

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Habitat loss, persecution and population declines have resulted in the restriction of many large carnivores, including cheetahs (*Acinonyx jubatus*), to fenced reserves. These reserves are often small and the likelihood of interference competition between dominant and subordinate predators is increased, while the possibility of spatial avoidance is reduced. Given artificial space limitations, subordinate predators may reduce competitive interactions along niche axes other than habitat type such as time, coined a 'management-induced niche shift'. We collected data on the activity patterns of male and female cheetahs using continuous follows and satellite GPS collars on two small, fenced reserves in the Eastern Cape Province of South Africa, one with lions (*Panthera leo*) and one without lions. There was a significant difference in the activity patterns of male and female cheetahs between the two reserves. In the presence of lions, nocturnal activity of cheetahs was greatly reduced, particularly for females. There was a corresponding increase in crepuscular activity for male cheetahs and diurnal activity for female cheetahs. In the context of other studies, our results suggest that space limitation affects cheetah response to lions and provides the first quazi-experimental evidence of a management-induced niche shift.

Key words: fenced reserves, *Acinonyx jubatus*, *Panthera leo*, GPS collars, direct observation.

INTRODUCTION

Within the large carnivore guilds of the African savanna, dominant predators such as lions (*Panthera leo*) may have a negative effect on the survival rates of subordinate predators such as cheetahs (*Acinonyx jubatus*) (Laurenson, 1994, 1995; Caro, 1994; Durant, 1998, 2000). In the Serengeti National Park, Tanzania, 73% of cheetah cub mortality is due to lions and spotted hyaenas (*Crocuta crocuta*), and 12.9% of cheetah kills are kleptoparasitized by the same predators (Laurenson, 1995; Hunter, Durant & Caro, 2007). Subordinate predators such as cheetahs and African wild dogs (*Lycaon pictus*) may use temporal and/or spatial avoidance strategies to reduce competitive interactions with dominant kleptoparastic and intra-guild predators (Creel & Creel, 1996; Durant, 1998; Hayward & Slotow, 2009). Evidence of temporal avoidance is seen in the typical activity patterns of lions which hunt mostly at night while cheetahs have little or no nocturnal activity (Schaller, 1972; Caro, 1994; Hayward & Slotow, 2009). However, more recent studies have shown that there is some degree of temporal overlap between the two species, and cheetahs do not necessarily avoid areas with high lion density (Cozzi *et al*., 2012; Vanak *et al*., 2013). Instead, cheetahs appear to use fine-scale avoidance strategies by, for example, staying further away from lions in open habitats compared to wooded areas to minimize the risk of lion encounters (Broekhuis, Cozzi, Valeix, McNutt & Macdonald, 2013; Swanson *et al*., 2014).

Human-induced habitat loss and fragmentation have resulted in population declines of many large carnivores, which have become amongst the most endangered of all mammals (Ripple *et al.,* 2014; Treves & Bruskotter, 2014). Furthermore, as human populations expand, conflict between people and free-ranging, large mammalian predators increases (Gittleman, Funk, Macdonald & Wayne, 2001; Treves & Karanth, 2003; Ripple *et al.,* 2014;

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Treves & Bruskotter, 2014), and often the predators are restricted to fenced conservation areas or reserves (Woodroffe & Ginsberg, 1998; Hayward *et al*., 2007; Finlayson *et al*., 2008; Safi & Pettorelli, 2010). 'Reserve' is defined as an area fenced with predator-proof electrified fencing that can be managed as a distinct ecological unit (Hayward *et al.,* 2007). In South Africa, the change in land use from agriculture to conservation and ecotourism (Smith & Wilson, 2002; Langholz & Kerley, 2006) has led to the reintroduction of large carnivores, including cheetahs and lions, into reserves within their historical ranges (Hofmeyr & van Dyk, 1998; Hunter *et al*., 2006; Hayward *et al*., 2007). These reserves are often too small to allow spatial avoidance between dominant and subordinate predators (Hayward & Slotow, 2009; Saleni *et al*., 2007) and Saleni *et al.* (2007) predicted that, under these conditions, temporal avoidance would become an important part of niche separation amongst members of a carnivore guild. The altered ecology of a species responding to constraints imposed by reserves has been termed a 'management-induced niche shift' (Saleni *et al.,* 2007). Since many small reserves hold both dominant and subordinate species, and were established to conserve endangered species, the ability of the subordinate species to make such a niche shift is central to their survival under these special conditions (Saleni *et al.,* 2007).

We have used observations from two small reserves, one with cheetahs and lions and the other with cheetahs only, to look for evidence of a management-induced niche shift in the behaviour of cheetahs. We assumed that in small enclosed areas, where the density of both prey and predators is high, the likelihood of interference competition will also be high. Furthermore, the constrained space will make avoidance by spatial separation unlikely, even at a fine scale. We therefore hypothesized that cheetahs on a reserve with lions would demonstrate a significantly different temporal activity pattern than cheetahs on a reserve without lions.

METHODS

This study occurred in two phases and used different methods for tracking the research animals, based on available resources.

Study sites

The initial phase (2004–2006) was at Kwandwe Private Game Reserve (Kwandwe; 200 km^2; *c.* 33°09′S; 26°37′E), north of Grahamstown, in the Eastern Cape Province, South Africa. Kwandwe has a warm temperate climate with an average annual rainfall of 410 mm, and is situated within the Albany Thicket Biome, characterized by a mosaic of open savanna-like areas and more thickly wooded areas (Mucina & Rutherford, 2006). A large carnivore guild, including lions, leopards (*Panthera pardus*), brown hyaenas (*Hyaena brunnea*), cheetahs and African wild dogs, was present at the time of data collection. Our study of cheetah activity was part of the routine monitoring by reserve management that followed the reintroduction of this species (Bissett, 2007; Bissett & Bernard, 2007).

The second phase (2011–2012) was conducted at Mountain Zebra National Park (MZNP). At the time of our study, MZNP had no other large mammalian carnivores and is situated 140 km North of Kwandwe. This created an opportunity to compare cheetah activity between the two reserves, one with and one without lions. MZNP (210 km^2; *c.* 32°14′S, 25°30′E), west of Cradock, has a cool and arid climate with a mean annual rainfall of 400 mm. The vegetation is mostly Nama Karoo (Mucina & Rutherford, 2006) with mountainous open grasslands and more thickly vegetated drainage lines in the valleys.

Data collection

At Kwandwe, study animals were fitted with either a VHF radio-collar or an implanted VHF transmitter (Africa Wildlife Tracking, Rietfontein, Gauteng, South Africa) which incorporated Telonics high power transmitters (Telonics, Mesa, AZ, U.S.A) (see Bissett, 2007; Bissett & Bernard, 2007 for details). Data were collected during 12, two week-long periods of continuous observations when focal animals were followed for 24 hours per day. The location of the focal animal was recorded using a handheld GPS unit (Garmin GPS 72) each time it stopped moving (Bissett, 2007; Bissett & Bernard, 2007). Data were collected for the same coalition of three male cheetahs during six of the periods of continuous observations and for a single adult female in the other six periods of observation, with three different adult females being followed (Table 1). Of the three adult female cheetahs being followed, two had cubs during four of the six continuous observation periods, whereas during the other two observation periods the females were solitary.

Table 1. Summary of available data showing the number of two week-long periods of continuous observations per season, individual cheetahs identified with a letter in the square brackets and the number of days of observations in parentheses for each study site.

	Kwandwe (2004–2006)		MZNP (2011–2012)	
	Male cheetah	Female cheetah	Male cheetah	Female cheetah
Autumn (Mar–Apr)	1/[A](14)	2/[B,C](29)	1/[E,F,G](23)	1/[H,I](18)
Winter (Jun–Aug)	2/[A](27)	1/[B](14)	1/[F,G](11)	1/[H,I](10)
Spring (Sept–Nov)	1/[A](15)	2/[B,C](26)	1/[F,G](12)	1/[H,I](11)
Summer (Dec–Feb)	2/[A](29)	1/[D](14)	1/[F,G](13)	1/[J,K](11)

At MZNP, study animals were fitted with GSM collars (Africa Wildlife Tracking, Rietfontein, Gauteng, South Africa) by South African National Parks veterinary and conservation staff for routine monitoring purposes. Collars were set to record a GPS fix every 30 minutes for a minimum of 4 days (range: 4–11 days) and data were collected for solitary male ($n = 3$ different animals) and solitary female ($n = 4$) cheetahs (Table 1). These methods provided records of 168 days of cheetah activity at Kwandwe and 109 days of cheetah activity at MZNP (Table 1).

Data analysis

Activity was defined as movement of a distance greater than 100 m an hour, based on observations (Kwandwe) or consecutive GPS fixes (MZNP) and records were converted to binary data (1 = movement or 0 = no movement) per hour. For each study period, the time of sunrise and sunset was obtained from the 'timeanddate' website for Grahamstown and Cradock (www.timeanddate.com/worldclock/astronomy.html). Activity patterns were classified as diurnal (activity between 1 hour after sunrise and 1 hour before sunset), nocturnal (activity between 1 hour after sunset and 1 hour before sunrise) or crepuscular (activity between 1 h before and 1 h after sunrise and 1 h before and 1 h after sunset). Data were pooled by reserve and sex for the analysis. There was no significant difference between the activity patterns of single females and females with cubs (one-way ANOVA; $F_{(1,142)} = 0.55$, $P > 0.05$) and the data for all females were pooled. For each sex and reserve, the proportion of activity that was nocturnal, diurnal and crepuscular was calculated. A Watson's two-sample test of homogeneity was used to determine whether or not male and female cheetah activity patterns differed significantly between reserves. For each of the two comparisons (male × reserve and female × reserve) we used a randomization approach with 9999 iterations to account for repeated measures (Pewsey, Neuhauser & Ruxton, 2013). Data analyses were conducted in R (R Development Core Team, 2011) using the package 'circular' (Agostinelli & Lund, 2013).

RESULTS

There were significant differences between the activity patterns of both male and female cheetahs on Kwandwe compared to MZNP ($U = 0.47$, $P < 0.05$; $U = 1.24$, $P < 0.05$).

Males and females displayed more nocturnal activity on MZNP than their counterparts on Kwandwe, the females dramatically so (48% *versus* 33% (Fig. 1A, B) and 30% *versus* 2% (Fig. 1C, D), respectively). Females on Kwandwe displayed much greater diurnal activity than females on MZNP (61% *vs* 27%) with similar levels of crepuscular activity (37% *vs* 33%; Fig. 1C, D). Males on Kwandwe displayed much greater crepuscular activity than males on MZNP (42% *vs* 26%); however, there was no difference in diurnal activity (26% *vs* 26%; Fig. 1A, B).

DISCUSSION

There were significant differences in the activity patterns of male and female cheetahs on a reserve with lions compared to the reserve without lions. In the absence of lions, cheetahs were active throughout the 24 hour day. In the presence of lions, male and female cheetahs were crepuscular with little (male) or no (female) activity at night, suggesting that a management-induced niche shift in cheetah behaviour occurred in response to the presence of lions. While the differences can be understood by the presence of lions and the likelihood of increased interference competition in a small reserve, the reserves differed in other ways and it is possible that various other factors that affect hunting success also influenced activity patterns.

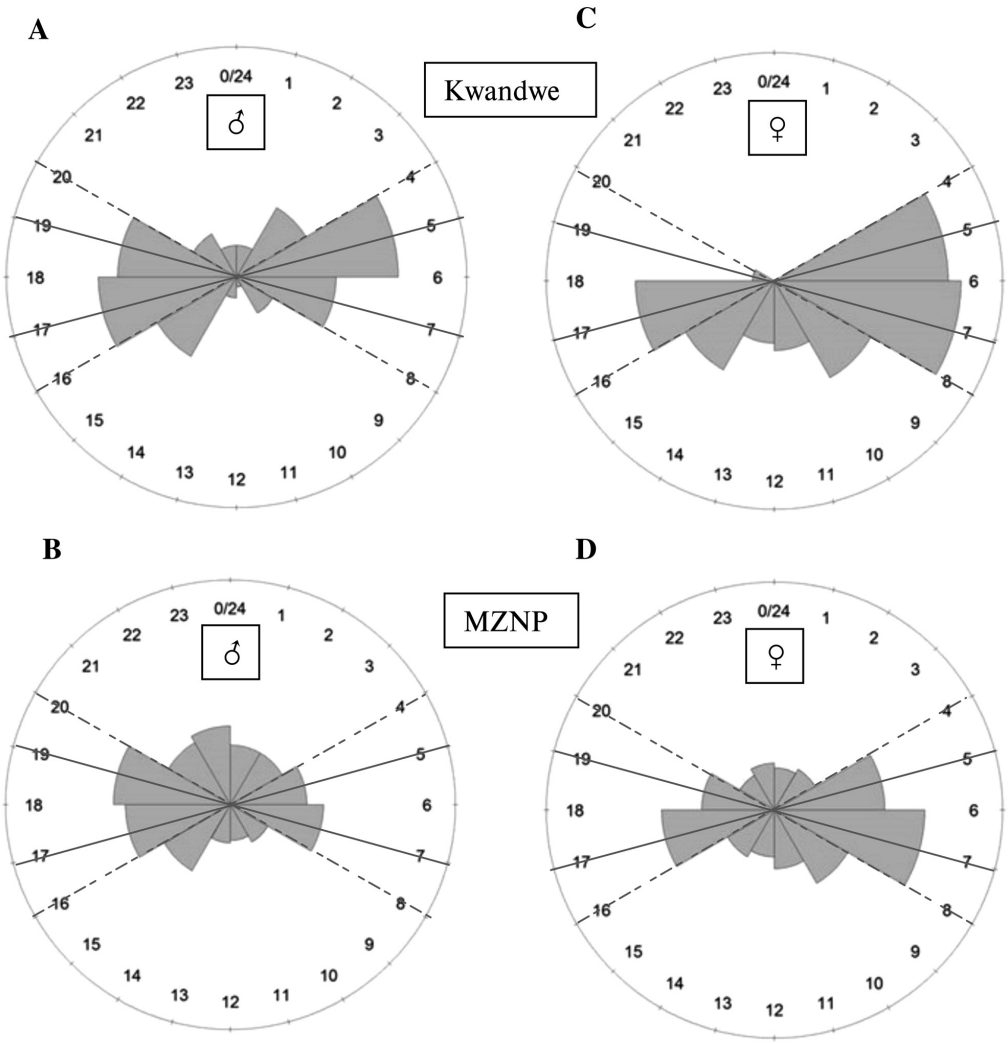

Fig. 1. Daily activity patterns of male and female cheetahs on Kwandwe and MZNP during the 24-h cycle. The length of the wedges is proportional to the amount of time the cheetahs were active. On average, night was between 19:00–5:00; day was between 7:00–17:00 and crepuscular was between 5:00–7:00 and 17:00–19:00. The dashed lines show the earliest start and latest end of crepuscular activity at the solstices.

MZNP is dominated by open grasslands and dwarf shrubs (Pond, Beesley, Brown & Bezuidenhout, 2002) where large herds of potential prey occur. On Kwandwe, 70% of the reserve comprises thicket vegetation (Bissett & Bernard, 2007), thus supporting large numbers of browsers such as greater kudu (*Tragelaphus strepsiceros),* which occur in smaller groups (Skinner & Chimimba, 2005). It is possible that the larger herds on MZNP are more vigilant compared to the kudu at Kwandwe (FitzGibbon, 1988, 1990; Burger, Safina & Gockfeld, 2000), making it more difficult for the cheetahs to approach (Caro, 1994; Hilborn, Pettorelli, David, Orme & Durant, 2012). This could reduce the likelihood of hunting success during the day and partially explain the increased nocturnal activity. However, prey abundance was high on both reserves, and prey composition was similar with kudu, springbok (*Antidorcas marsupialis*), mountain reedbuck (*Redunca fulvorufula*), black wildebeest (*Connochaetes gnou*), blesbok (*Damaliscus pygargus phillipsi),* common duiker (*Sylvicapra grimmia*) and steenbok (*Raphicerus campestris*; Bissett, 2007) being the dominant prey.

While dominant predators were not present at MZNP during our study, black-backed jackals

(*Canis mesomelas*) have been observed chasing cheetahs off their kills at this site (C. Bissett, pers. obs. 2013). However, black-backed jackals are mostly crepuscular and nocturnal (Ferguson, Galpin & de Wet, 1988), and their interference is unlikely to explain the increased nocturnal activity of cheetahs at MZNP. Nevertheless, it may partly explain why cheetahs were active throughout the 24 hour day at MZNP. If hunts are unsuccessful, or if prey is kleptoparasitized by jackals, then further hunting is necessary and the hours of activity may be extended.

Kwandwe and MZNP were both managed as ecotourism reserves and therefore there was very little human disturbance, which is unlikely to explain differences in activity patterns.

Cheetahs are generally reported to be diurnal with peaks of activity during sunrise and sunset (Caro, 1994; Houser, Somers & Boast, 2009) and this is supported by a review of previous studies conducted on South African reserves (Hayward & Slotow, 2009). Lions are typically less active during the day with most hunts occurring at night (Schaller, 1972; Eloff, 1984; Stander, 1992; Hayward & Slotow, 2009) and one explanation for the diurnal activity of cheetahs has been temporal avoidance of superior predators (Caro, 1994; Durant, 2000; Hayward & Slotow, 2009). However, there is increasing evidence that cheetahs are frequently active at night even in areas that have high lion densities (Houser *et al.*, 2009; Cozzi *et al.*, 2012), and that competitive interactions are avoided at a finer scale. For example, where cheetahs and lions coexist, cheetahs may use the same habitats as the lions, but will flee when hearing lion calls (Cozzi *et al.*, 2012; Vanak *et al.*, 2013). On Kwandwe, in the presence of lions, the female cheetahs were inactive at night and this probably represents a temporal avoidance of lions. By contrast, the coalition of three male cheetahs was more active at night and this may be due to the crepuscular/nocturnal activity of their preferred prey species, kudu (Skinner & Chimimba, 2005; Bissett & Bernard, 2007) and their social system, which provides some strength in numbers and increased vigilance (Caro, 1994). Differences in activity patterns of male and female cheetahs have been reported previously and in Botswana male cheetahs are more active in the late evening and early morning, whereas female cheetahs are more active in the late afternoon (Houser *et al.*, 2009).

The activity patterns of large mammalian predators are understood to have evolved to maximize hunting success, minimize the risk from intra-guild predators, and retain a degree of behavioural flexibility (Durant, 1998; Creel, 2001; Hayward & Hayward, 2007; Hayward & Slotow, 2009; Cozzi *et al.*, 2012). The flexibility in behaviour allows predators to respond to natural changes in bottom-up (such as activity patterns of prey species) and top-down pressure (such as interference competition and kleptoparasitism from superior predators) by adjusting the pattern of activity to continue to maximize hunting success and minimize the risk from intra-guild predators (Hayward & Slotow, 2009). The same flexibility would allow a predator to respond to a management-induced change as is suggested in the present study.

The differences in activity reported here might not be a result of the presence or absence of lions alone, but of other factors such as those discussed earlier, working together to shape behaviour. Whatever the case, the results suggest that cheetahs are able to adjust their activity in response to management interventions and that a small reserve with cheetahs and lions can play a role in the conservation of the subordinate species. Future research should therefore aim to disentangle these effects, and the most robust approach is likely to be an assessment before and after a lion reintroduction.

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