Activity patterns of reintroduced lion *Panthera leo* and spotted hyaena *Crocuta crocuta* in the Addo Elephant National Park, South Africa

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Abstract

Africa's large predator guild competes for a limited food resource base. To minimize the degree of competition, we hypothesized that the two largest members of this guild and its fiercest competitors, the lion and the spotted hyaena, would partition their activity patterns to avoid interacting. We used 96-h continuous follows of focal animal(s) to determine when the six radio-collared lions and eight radio-collared spotted hyaenas, reintroduced into Addo Elephant National Park in 2003/2004, were active using a binomial measure of activity which was defined as movements >100 m during each hourly period. Contrary to our predictions, lions and hyaenas did not partition their activity times, probably because of their current low population densities. Both species exhibited a crepuscular activity pattern although hyaenas were far less active during daylight. A sub-adult lioness minimized competitive interactions by becoming diurnal. This is likely to be a common strategy for lions that have been expelled from their natal pride to become nomadic, as it allows them to minimize kleptoparasitic and agonistic interactions from competitively dominant conspecifics and competitors. The increase in testosterone that occurs in males upon reaching sexual maturity, darkens their pelage and causes them to be more directly impacted by the heat, and thereby affords females an opportunity to escape from males during hot temperatures. Similarly, the longer pelage of young hyaenas restricts their activity to the cooler night-time.

Key words: behaviour, Carnivora, competition avoidance, crepuscular, interspecific competition, intraspecific competition, nocturnal, nomadism, temperature inhibition

Résumé

Les guildes de grands prédateurs africains sont en compétition pour des ressources alimentaires en quantité limitée. Pour minimiser le niveau de compétition, nous avions émis l'hypothèse que les deux plus grands membres de ce groupe, et ses compétiteurs les plus féroces, le lion et l'hyène tachetée, se répartissaient leurs schémas d'activités pour éviter les interactions. Nous avons passé 96 heures à suivre un ou des animaux focaux pour déterminer quand les six lions et les huit hyènes équipés de colliers radio, qui ont été réintroduits en 2003–2004 dans le *Addo Elephant National Park*, étaient actifs, en utilisant une mesure binomiale de l'activité qui était définie par des déplacements de plus de 100 mètres par période d'une heure. Contrairement à nos prédictions, les lions et les hyènes ne se répartissaient pas le temps d'activité, peut-être en raison de leur densité de population qui est actuellement faible. Les deux espèces présentaient un schéma d'activité crépusculaire, mais les hyènes étaient beaucoup moins actives en plein jour. Une lionne sub-adulte a minimisé les interactions en devenant diurne. Il est probable que ceci est une stratégie commune chez des lions qui ont été expulsés de leur famille d'origine et sont devenus nomades, parce que cela leur permet de minimiser les interactions kleptoparasitiques et agressives avec des congénères dominants ou des compétiteurs. L'augmentation du taux de testostérone qui touche les mâles qui atteignent la maturité sexuelle rend leur pelage plus sombre, ce qui les rend plus sensibles à la chaleur; ceci donne aux femelles une opportunité d'échapper aux mâles lorsque la température est élevée. De même, le pelage plus long des jeunes hyènes restreint leurs activités aux heures plus fraîches de la nuit.

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Introduction

Africa's large predator guild competes for a limited food resource base. Lions *Panthera leo* and spotted hyaenas *Crocuta crocuta* are the largest members of this guild and their high degree of preferred and actual dietary overlap (Hayward, 2006) has led their competition to be termed 'the battle of the giants' (Mills & Harvey, 2001). One way to minimize this competition is to partition their activity patterns. At low density, this may not be necessary as the chance of encountering a competitor is low; however, at high density this likelihood increases.

These two species are amongst the most common of Africa's large predators and they are also amongst the most studied. For example, at least 42 studies have been published on the diet of the lion and 17 on that of the spotted hyaena (Hayward & Kerley, 2005; Hayward, 2006). Yet despite being considered nocturnal predators (Stuart & Stuart, 2000; Mills & Harvey, 2001, p. 44), there have only been two published (Schaller, 1972; Mills & Biggs, 1993) and one unpublished study (Kruger, 1988) documenting the activity patterns of lions. Similarly, spotted hyaenas are considered nocturnal and crepuscular (Stuart & Stuart, 2000; Mills & Harvey, 2001, p. 44), but this has only been documented in three published (Kruuk, 1972; Mills, 1990; Gasaway, Mossestad & Stander, 1991) and one unpublished study (Kruger, 1988).

No study has investigated the temporal partitioning of activity periods between these two species. We aimed to document the activity patterns of reintroduced lion and spotted hyaena and to test whether their periods of activity overlapped or were partitioned. We also aimed to investigate the seasonal variation in the activity of lions and the effect of a shift in dominance on the activity of two male coalitions.

Materials and methods

We studied the activity patterns of lion and spotted hyaena in the Addo Elephant National Park (Addo; 33°30′S, 25°45′E), approximately 70 km north of Port Elizabeth in South Africa's Eastern Cape Province. Addo forms part of the densely vegetated Thicket Biome where the dominant plant species is spekboom *Portulacaria afra* (Johnson, Cowling & Phillipson, 1999; Vlok, Euston-Brown & Cowling, 2003).

Six unrelated lions (four males and two females) from the Kgalagadi Transfrontier Park were translocated in two groups (two males, one female) into the 13,400-ha Main Camp section of the park in November 2003 and were housed separately in bomas in the north (animals identified as AM1D, AM2D and AF1) and south (AM3S, AM4S and SAF) of the park. Eight unrelated spotted hyaenas were subsequently reintroduced in two separate releases, the first clan coming from Madikwe Game Reserve in December 2003 and the second were sourced from the Shingwedzi region of Kruger National Park, being released in October 2004.

All lions and up to six of the hyaenas were collared for the majority of this study. Sedation and collaring were performed as routine management activities by South African National Parks' veterinary and conservation staff.

Each season, from summer 2003/2004 (December) to spring 2005, a minimum of two lions were followed continuously for 96 h (Packer & Ruttan, 1988; Packer, Scheel & Pusey, 1990; Mills, 1992). Spotted hyaenas were also followed in this manner, although not as frequently. This provided records of 64 days of lion activity and 12 days of hyaena activity throughout the eight consecutive seasons. Incidental observations during >600 days over the 2-year study period supported our findings.

Activity patterns were measured as a binomial by recording whether or not the followed individual moved more than 100 m during each hour of the day. If an individual moved more than 100 m, it was recorded as being active during that hour. If the focal animal moved into thick vegetation then the activity was not measured until the animal was re-sighted. Binomial mean activity for each hour of the day (± 1 binomial SE) was then calculated (Zar, 1996). One sub-adult lioness behaved atypically compared with the rest of the lions upon release. Its activity pattern was analysed separately.

Upon release, the four males and adult female all joined together, despite being held in different bomas, and stayed together for 8 months. High levels of aggression were observed in this period, particularly when the adult female came into oestrus. During winter 2004, the pair of lions held in the northern boma (AM1D and AM2D) fought the southern coalition (AM3S and AM4S) for dominance and won, leading to the subordinate coalition entering into a nomadic existence whereby they walked the fence line and actively avoided interactions with the dominant coalition. We investigated how such a change in dominance hierarchy affected their activity patterns.

We used the t-test and Mann–Whitney tests to investigate whether there were pair-wise differences in the amount of activity throughout the day, and the Friedman ANOVA with the Tukey *post hoc* test was used to test differences in the mean amount of daily activity of all the lions (Zar, 1996). We used the log-rank (G) test (Zar, 1996) to detect pair-wise differences in the timing of activity throughout the day (e.g. Hayward *et al.*, 2005). The Kruskal–Wallis non-parametric one-way ANOVA on ranks with the Tukey *post hoc* test (Zar, 1996) was used to test whether there were differences in the timing of daily activity between males and females, and in seasonal activity patterns.

Results

Lions in Addo were active throughout the 24-h daily cycle (41 ± 4% of the day active) with crepuscular peaks around sunrise and sunset and reduced activity during the hottest parts of the day (Fig. 1). The adult lioness (active 54% of the day) was significantly more active than the rest of the lions individually (AM1D = 41%, AM2D = 41%, AM3S = 39%, SAF = 35% and AM4S = 32%). However, when the males were grouped together there was no significant difference (Table 1).

The sub-adult female lioness exhibited an extremely atypical activity pattern than has been reported elsewhere.

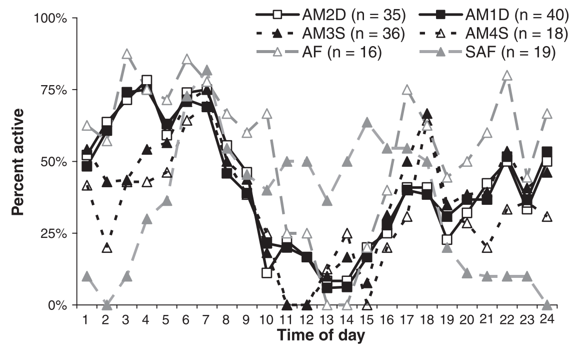

Fig 1 Mean activity times (± 1 SE) of six radio-collared lions in Addo Elephant National Park. The number of lion days each individual was observed (n) is also presented. *A* refers to adult, *M* to male, *F* to female, *SA* to sub-adult, *D* to dominant and *G* to subordinate.

It was almost completely diurnal with slight crepuscular peaks in activity around sunrise and throughout the afternoon (Figs 2 and 3). This activity pattern was significantly different from that of the males and the adult lioness (Table 1).

The shift in dominance hierarchy did not significantly alter the timing of activity, but it did reduce the amount of

Table 1 Statistics comparing the activity patterns of reintroduced lions and spotted hyaenas in Addo Elephant National Park

	Timing of activity			Amount of daily activity		
Comparison	G	d.f.	Probability	Statistic	d.f.	Probability
All lions				H = 29.15	5	<0.001[a]
Male lions versus females	0.935	1	0.50 < P < 0.25	t = −1.589	23	0.114
Male lions versus sub-adult lioness	4.382	1	0.05 < P < 0.03	U = 415.0	1	<0.001
Adult lioness versus sub-adult lioness	5.605	1	P < 0.025	t = 2.672	46	0.010
Male lions versus adult lioness	0.731	1	0.50 < P < 0.25	U = 415.0	120	<0.001
Dominant males before versus after dominance shift	2.44	1	0.25 < P < 0.10	t = 2.494	46	0.016
Subordinate males before versus after dominance shift	1.63	1	0.25 < P < 0.10	t = 3.083	46	0.003
Dominant versus subordinate coalition after the dominance shift	1.927	1	0.25 < P < 0.10	U = 596.5	48	0.869
Seasonal differences				H = 10.484	3	0.015[b]
All lions (excl. sub-adult lioness) versus hyaenas	2.63	1	0.25 < P < 0.10	U = 594.0	1	0.950
Males lions versus hyaenas	2.54	1	0.25 < P < 0.10	U = 407.5	1	<0.001
Adult lioness versus hyaenas	3.33	1	0.10 < P < 0.05	t = 1.400	46	0.168
Sub-adult lioness versus hyaenas	9.53	1	P < 0.005	t = 0.831	46	0.410

The log-rank test (G) was used to compare the timing of activity throughout the day and t-tests, Mann–Whitney U-tests and Kruskal–Wallis one-way ANOVA on ranks (H) were used to test the mean amount of activity throughout the day.

[a]Tukey's *post hoc* test revealed that the adult lioness was significantly more active than all other lions (4.20 < *q* < 7.31; P < 0.05 for each pair-wise comparison).

[b]Tukey's *post hoc* test revealed that lions were significantly less active in summer than winter (*q* = 3.928) or autumn (*q* = 3.704; P < 0.05 for both).

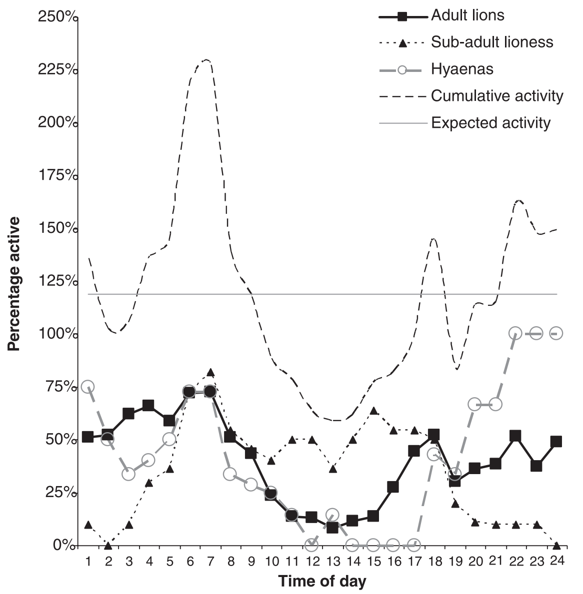

Fig 2 Mean activity times of adult and sub-adult collared lion and six adult spotted hyaena (observed over n = 19 days) that were reintroduced into Addo Elephant National Park in 2003/2004. Cumulative mean daily activity of reintroduced predators to Addo Elephant National Park is also shown (dashed line) and the grey line illustrates the shape of this curve if these predators were perfectly partitioning their temporal activity patterns.

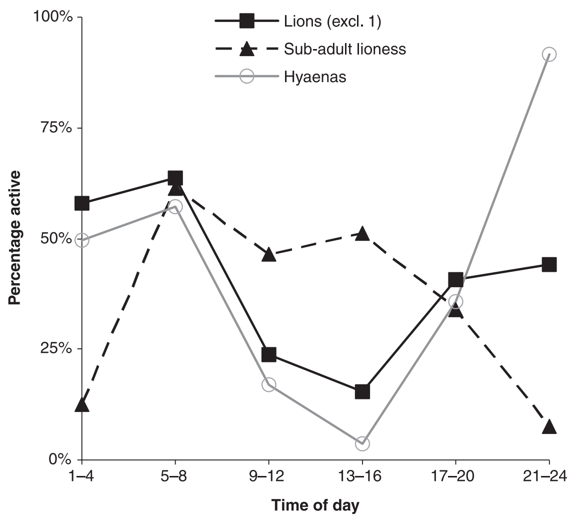

Fig 3 Comparative plot of the mean activity times of lion, hyaena and the sub-adult female lion in Addo Elephant National Park grouped into 4-hourly periods.

daily activity each male coalition performed (Table 1). Prior to the dominance shift, the males were active 50 ± 6% of each day, but this declined to 32 ± 4% for the dominant and 29 ± 3% for the subordinate coalition after the dominance shift. Slight differences were apparent in the activity patterns of the two male coalitions, with the dominant coalition reaching peak activity between midnight and dawn and the subordinate coalition becoming most active just after sunset (Fig. 4).

Lions were active later in the morning and earlier in the evening in the cooler months [autumn mean (± 1 SE) activity = 48 ± 6% for n = 32 lion days of observation and winter 50 ± 7%, n = 48] than in summer (26 ± 3%, n = 35; Fig. 5). Spring activity was intermediate (34 ± 3%, n = 29; Fig. 5). This was reflected in the overall daily activity where lions were significantly less active in the hot summer months, than they were in autumn and winter (Table 1).

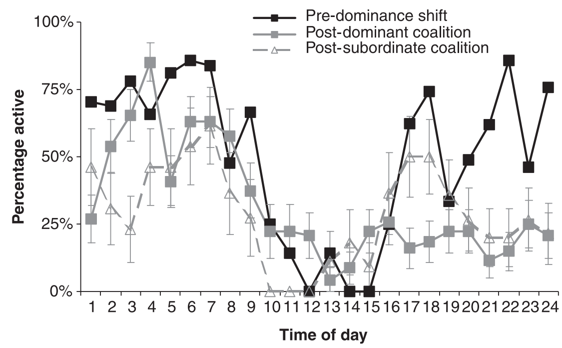

Fig 4 Plot of the mean activity patterns of the two male lion coalitions before (n = 59) and after the shift in dominance hierarchy in Addo Elephant National Park. The dominant coalition were followed for 34 lion days and the subordinate coalition for 18 lion days.

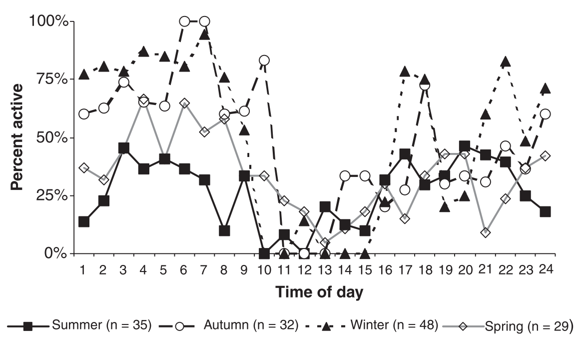

Fig 5 Seasonal activity patterns of reintroduced lions in Addo Elephant National Park. The number of lions days per season is also presented

The hyaenas in Addo exhibited an activity pattern similar to the adult lions, being predominantly nocturnal (42 ± 14% of the day active; Table 1) with similar levels of activity from 22.00 hours until midnight before a decline in activity at 03.00 hours and finally a dawn increase (Fig. 2). The hyaenas were completely inactive during the middle of the day. They exhibited an activity pattern similar to the male lions, but were significantly less active overall (Table 1). There was no significant difference in the activity of the hyaenas and the adult lioness; however the sub-adult lioness was significantly more active during the day (Table 1; Figs 2 and 3).

The percentage activity niche overlap for lions and spotted hyaenas was 75.1%, for lions and the sub-adult lioness was 58.9%, and for the sub-adult female lioness and hyaenas was 41.7%. If the predators were partitioning their activity through the day, we would expect a cumulative plot of their activity patterns to be relatively constant throughout the day (Fig. 2). Rather, the cumulative large predator activity reflects crepuscular activity, with a substantial peak around dawn, a decline during the warmer hours of the day despite the diurnal activity of the sub-adult lioness, and then another crepuscular peak at dusk followed by fairly constant activity throughout the night (Fig. 2).

Discussion

Lions and spotted hyaenas are fierce competitors (Mills & Harvey, 2001). As the dominant predators in Africa and with similar diets (Hayward, 2006) we expected them to partition their activity times to minimize interactions; however, this is not the case in Addo where their activity patterns overlap 75.1% of the time. This is probably because of the low density of each (0.04 lions and 0.07 hyaenas km^{-2}), reducing the likelihood of competitive or agonistic interactions (Fig. 2). At these low densities, competitors can readily minimize interactions through spatial partitioning of habitat, such that whenever Addo's lions move to the north of the park, the hyaenas moved dens to the south of the park (M.W. Hayward unpubl. data).

The activity pattern exhibited by the sub-adult lioness was interesting. It minimized the chances of interacting with inter- and intra-specific competitors to 41.7% and 58.9% of the time, respectively. Its competitors in Addo were four potentially kleptoparasitic and infanticidal male lions (Packer & Pusey, 1983, 1984, 1987; Packer *et al.*, 1990) and the two clans of spotted hyaenas (Cooper, 1991). It was also competing against an adult lioness, and in two interactions observed between the two prior to the birth of the sub-adult's first litter of cubs, it was always either chased long distances or was highly subordinate to the adult lioness (M. W. Hayward pers. obs.). We suspect that the adult lioness also killed the sub-adult lioness' first litter after it located the lair and remained in its vicinity for 2 weeks, during which time several fights were observed while the adult lioness attempted to enter the lair.

While nomadism in female lions is not unheard of, it is uncommon (Schaller, 1972). A lone sub-adult lioness in a nomadic phase, without the help of pride mates, is probably on par with a leopard *Panthera pardus* or cheetah *Acinonyx jubatus* in the dominance hierarchy existing among African predators. One way to minimize interactions with dominant competitors, each of which is largely nocturnal, is to become diurnal. Morphological features of lionesses facilitate this. The pale pelage of lionesses, particularly sub-adults, in comparison with male lions, reflects heat thereby reducing heat load (West & Packer, 2002). The lack of a mane further facilitates lioness activity in hotter temperatures (West & Packer, 2002). Similarly, the pelage of lions is shorter than the coats of all but the oldest spotted hyaenas, facilitating activity by lions during hotter temperatures than hyaenas prefer to be active in. We know of no other study that has documented the activity of sub-adult females that are essentially living a nomadic lifestyle given that they do not have the support of a pride to assist and protect them. We hypothesize that this is a strategy that young lions expelled from natal prides and forced into a solitary, nomadic existence employ to survive. The absence or reduced mane size of sub-adult lions and females is also likely to increase the hunting success of these nomads.

The dominance shift amongst the two male coalitions resulted in a reduced level of activity for both (Table 1). Although not significant, there is some evidence that the shift in dominance hierarchy altered their activity patterns with the dominant coalition reaching peak activity between midnight and dawn and the subordinate coalition reaching their peak activity immediately after sunset (Fig. 4). The dominant coalition was also active throughout the day (Fig. 4). It seems likely that this pair would choose when to be active and the subordinate coalition would attempt to avoid agonistic interactions by temporally partitioning their activity times. Moreover, given the importance of advertizing a territory via roaring for territorial male lions (Schaller, 1972; Grinnell & McComb, 2001), it seems the dominant coalition are likely to perform this activity in optimal conditions. Wind and temperature substantially affect the transmission of sound in the frequency range of lion roars with ideal conditions occurring in the still, cooler conditions of the early morning (Garstang *et al.*, 1995). This is when the dominant coalition are most active (Fig. 4) and is also when they roar most (M. W. Hayward unpubl. data).

It is a popular misconception that lions sleep for 22 h day^{-1}, but in Addo they were active 41% of the time. We hypothesize that the lack of a pride increased the amount of activity that Addo's lions performed compared with lions elsewhere, where in large prides individuals reduce their vigil (looking for megaherbivores that may trample or gore them and conspecifics or competitors that may attack and maul them) by gaining the same advantages that prey species do in larger herds (Hamilton, 1971). The small group sizes in Addo prevented such safety mechanisms.

Lion movements occur throughout the day (Fig. 1). Some of the diurnal activity of lions is a result of the random location of their resting sites. Addo has a high density of elephants (Gough & Kerley, 2006) and buffalo, and they frequently encounter lions. When they do, they often chase the lions and this happened on several occasions during our 96-h follows, once during the day when elephants chased the dominant male coalition for 600 m. Tourists are another cause of diurnal movements by lions when they drive too close or harass them. Tourists and megaherbivores are less problematic for spotted hyaenas in Addo, as they remain in or near the refuge of well marked and remote den sites.

The activity pattern of spotted hyaenas might be expected to follow that of lions given the potential for commensal relationships to exist by way of scavenging lion kills. Hyaena activity in Addo appears to be more influenced by the climate as they obtained the majority of their food from their own kills (M. W. Hayward unpubl. data). All but the oldest individuals have a thicker, longer and darker coat than lions, probably causing an increased thermal load during the day. Consequently, they are inactive during the hottest parts of the day and only start becoming active at or after sunset. Hyaenas use behavioural mechanisms, such as bathing and denning, to reduce their thermal load (M. W. Hayward pers. obs.) and neither of these activities are performed by extant lions which seek shade and pant to reduce heat stress.

Definitions of activity differ between studies. The activity pattern of lions in Etosha has been intimated from the timing of roars (Stander & Stander, 1988). We have observed lions roaring without raising themselves from a lying position and returning to sleep immediately afterwards, and so avoided this definition. Cheetah activity patterns have been elucidated from the timing of kills (Bissett, 2004), but this requires a large sample size and ignores unsuccessful hunts during which the animal was likely to be highly active and is further biased by opportunistic kills where prey are captured without prior active search periods. Our definition of activity that required a physical movement of 100 m or more seems satisfactory to discriminate between brief, small-scale movements like seeking shade on hot days before returning to inactivity, while maintaining adequate sensitivity. Clearly, the distance moved should be determined with cognisance of the distances that a study species can move.

We have shown that lions and spotted hyaenas exhibit very similar activity patterns in Addo, increasing their potential for competition. At low densities with abundant prey these two top predators can avoid competition by partitioning themselves spatially. The difference in activity between lions and hyaenas in Addo was probably caused by the choice of lions to be active throughout the day, and morphological limitations on hyaenas that limited their activity during the hottest part of the day. Sub-adult, nomadic lions may avoid competition and conflict with larger competitors by becoming diurnal, in a fashion similar to that employed by the cheetah *A. jubatus* and the African wild dog *Lycaon pictus* (Mills & Harvey, 2001).

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