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Abstract. Africa is home to the last intact guild of large carnivores and thus provides the only opportunity to investigate mechanisms of coexistence among large predator species. Strong asymmetric dominance hierarchies typically characterize guilds of large carnivores; but despite this asymmetry, subdominant species may persist alongside their stronger counterparts through temporal partitioning of habitat and resources. In the African guild, the subdominant African wild dogs and cheetahs are routinely described as diurnal and crepuscular. These activity patterns have been interpreted to result from the need to avoid encounters with the stronger, nocturnal spotted hyenas and lions. However, the idea that diel activity patterns of carnivore species are strongly shaped by competition and predation has recently been challenged by new observations. In a three-year study in the Okavango Delta, we investigated daily activity patterns and temporal partitioning for wild dogs, cheetahs, spotted hyenas and lions by fitting radio collars that continuously recorded activity bursts, to a total of 25 individuals. Analysis of activity patterns throughout the 24-h cycle revealed an unexpectedly high degree of temporal overlap among the four species. This was mainly due to the extensive and previously undescribed nocturnal activity of wild dogs and cheetahs. Their nocturnal activity fluctuated with the lunar cycle, represented up to 40% of the diel activity budget and was primarily constrained by moonlight availability. In contrast, the nocturnal activity patterns of lions and hyenas were unaffected by moonlight and remained constant over the lunar cycle. Our results suggest that other ecological factors such as optimal hunting conditions have shaped the diel activity patterns of subdominant, large predators. We suggest that they are "starvation driven" and must exploit every opportunity to obtain a meal. The benefits of activity on moonlit nights therefore offset the risks of encountering night-active predators and competitors.

Key words: activity data-loggers; African carnivore guild; coexistence; costs-benefits; moonlight; nocturnal activity; predator–predator relationships; temporal niche.

Introduction

Intraguild competition and predation have been recognized as important ecological factors influencing the population dynamics of carnivores (Palomares and Caro 1999, Linnell and Strand 2000, Caro and Stoner 2003). For example, interactions with dominant species could be responsible for the general rarity of competitively inferior carnivore species (Palomares and Caro 1999, Caro and Stoner 2003) and may push some species, such as the African wild dog (*Lycaon pictus*), to the edge of extinction (Vucetich and Creel 1999). Understanding the relationships among the members of a guild is particularly important for large carnivores as they tend to be extinction prone, due to low

population densities and low reproductive rates (Purvis et al. 2000). Furthermore, human-induced habitat loss and fragmentation are forcing carnivores to inhabit ever-smaller areas, increasing the frequency of antagonistic interactions and hence potentially accelerating extinction rates (Creel 2001, Caro and Stoner 2003).

Prior to a wave of extinctions during the Late Pleistocene and the modern era, guilds of large predators were widespread on all five continents (Barnosky et al. 2004, Koch and Barnosky 2006, Turvey and Fritz 2011). Today, however, an intact guild of large predator species can be found only in Africa (Valkenburgh 1988, Dalerum et al. 2009). The African guild, which consists of the African wild dog, the cheetah (*Acinonyx jubatus*), the leopard (*Panthera pardus*), the spotted hyena (*Crocuta crocuta*), and the lion (*P. leo*), thus offers the last opportunity to investigate a complete range of interactions among large predators. Large predators in extant and extinct guilds are known to compete for

similar prey species, despite the variation in body size among guild members (Sinclair et al. 2003, Radloff and Du Toit 2004). This body-size variation has led to strong interspecific dominance hierarchies, resulting in larger members of the guild dominating the smaller ones (Rosenzweig 1966, Maynard-Smith and Parker 1976, Polis and Holt 1992, Carbone et al. 1997, Palomares and Caro 1999, Woodward and Hildrew 2002). Lions and hyenas are, for example, known to kill wild dogs and cheetahs, steal their food, and exclude them from prey-rich areas, whereas wild dogs and cheetahs have little or no influence on the dominant members of the guild (Laurenson et al. 1995, Mills and Gorman 1997, Durant 1998, Gorman et al. 1998, Creel and Creel 2002).

It has been suggested that smaller, subdominant species coexist with their larger and more dominant counterparts through temporal partitioning of habitats and resources (Pianka 1974, Schoener 1974a, Durant 1998, Linnell and Strand 2000, Harrington et al. 2009). Temporal partitioning as a mechanism to reduce competition or predation has been suggested, for example, between predators and prey (Sih 1980, Kotler et al. 1993, Ziv et al. 1993) and between the early mammals and the dominant dinosaurs (Crompton et al. 1978, but see Schmitz and Motani 2011). Accordingly, it is widely accepted that lions and hyenas have strongly shaped the temporal niches of wild dogs and cheetahs. In particular, the previously described diurnal and crepuscular activity pattern of wild dogs and cheetahs has commonly been interpreted as a behavioral adaptation to avoid encounters with the predominantly night-active lions and hyenas (Hayward and Slotow 2009).

Direct field evidence for temporal partitioning in African large predators is, however, lacking, and there has been no detailed study of activity patterns conducted on all species of the guild at the same time and in the same place. In the only published paper dealing with the topic, Hayward and Slotow (2009) conclude that "top-down effects appear to drive temporal partitioning within the [African] large-predator guild" and that "the remaining members of the guild probably evolved to become active in periods that limit their potential for interaction with lions." In fact, anecdotal observations (Schaller 1972, Creel and Creel 2002) and a more recent study (Rasmussen and Macdonald 2011) suggest that light availability at night may influence activity patterns of wild dogs and cheetahs, and that nocturnal activity may be more pronounced than previously thought, thus questioning the real role of lions and hyenas in influencing the activity patterns of the two subdominant species.

While a critical test of the temporal partitioning hypothesis would involve removing the dominant predators and looking for a change in the behavior of the subdominant species, such a study is clearly impractical. Instead, by carrying out a detailed study of activity patterns of a population of sympatric large predators, we aimed to test whether the activity patterns of wild dogs and cheetahs appear to have been primarily shaped by light availability, rather than by avoidance of lions and spotted hyenas. For this purpose, we attached radio collars equipped with activity sensors to a total of 25 individuals of the four species, in a region of the Okavango Delta in northern Botswana. We first investigated how activity was distributed throughout the 24-h cycle for all species. Second, we tested if the nocturnal activity patterns were correlated with moonlight availability. A strong positive relationship would suggest that light availability plays an important role in determining activity at night. Third, for wild dogs and cheetahs, we investigated whether there were trade-offs in activity during different periods of the 24-h cycle. Specifically, we investigated whether increased nocturnal activity resulted in reduced activity on the following day. Trade-offs in activity within the 24-h cycle would suggest that, when moonlight is sufficient, subdominant predators shift their diurnal activities to the night hours, despite the risk associated with a higher likelihood of encountering more dominant members of the guild.

METHODS

The African large predator guild

The African large predator guild consists of five species: the African wild dog, the cheetah, the leopard, the spotted hyena, and the lion (Hayward and Slotow 2009), which are characterized by a pronounced predatory behavior. The members of the guild vary in body mass ranging from 200 kg (lion) to 25 kg (wild dog), giving rise to a dominance hierarchy where the larger lions and hyenas clearly dominate the smaller wild dogs and cheetahs. In contrast to lions and hyenas, the outcome of interactions between leopards vs. wild dogs and cheetahs is less unidirectional. Leopards have furthermore been shown to be almost equally active during day- and nighttime and therefore not unequivocally categorized as nocturnal/crepuscular or as diurnal/crepuscular (Hayward and Slotow 2009, McManus 2009). Because leopards are active throughout the 24-h cycle, they are not likely to bias the behavior of the other species toward or away from any particular time of the day. For this reason, they were not included in the study.

Field work

Radio collars equipped with sensors (Vectronic Aerospace GmbH, Berlin, Germany) specifically designed to record activity data (more detail follows) were fitted to the study animals (following Osofsky et al. 1995, Kock et al. 2006) by a registered veterinarian in compliance with Botswana law. After immobilization, the collared individuals safely rejoined their group showing no signs of distress. Between 2008 and 2010, we monitored the activity of a total of seven wild dogs in five packs, six cheetahs, six hyenas in five clans, and six lions in five prides. All four species were found throughout the entire study area. The collared animals ranged over an area of approximately 4000 km^2 and

their territories largely overlapped (Appendix A). Throughout the duration of this study, at least two individuals of each species were collared at any time. However, no more than one individual per social group was collared at any given time to avoid data duplication owing to the collective movement of group members. Data were recorded for a mean of 329 d for cheetahs (range, 217–472 d); 368 d for wild dogs (range, 217–448 d); 416 d for lions (range, 328–486 d); and 432 d for hyenas (range, 310–587 d).

Subdivision of a 24-h cycle

To investigate activity patterns, we divided each 24-h cycle into five periods: night, morning twilight, morning, afternoon, and evening twilight. These periods reflect the main activity periods for wild dogs and cheetahs (day and twilight) and for lions and hyenas (night and twilight) as currently described in the literature (Hayward and Slotow 2009). Night stretched between the astronomical dusk and dawn, when the sun is 18° below the horizon and sunlight contribution to overall luminosity is nil. The morning twilight started at dawn and ended at sunrise; the evening twilight started at sunset and ended at dusk. The day lasted from sunrise to sunset and the division between morning and afternoon occurred around noon each day (Appendix C).

Nighttime was further divided into seven periods: three periods before midnight, one period across the midnight hour, and three periods after midnight. Each period (apart from the midnight period) had an exact duration of 1.2 h and was therefore directly comparable to the duration of the morning and afternoon twilight periods. Because the overall night length slightly changes over time, we had to adjust the length of the period spanning midnight, which therefore varied slightly in length (±30 minutes).

Light availability and environmental factors

Moonlight intensity, our main predictor variable, was taken as a measure of light availability at night and was defined as the percentage of the lunar disc illuminated (United States Naval Observatory 2011). Full-moon nights and new-moon nights were defined when respectively ≥95% and ≤5% of the lunar disc was illuminated, giving four or five full-moon and four or five new-moon nights per lunar cycle. First-quarter and third-quarter moon (i.e., half of the moon visible from the Earth's surface) were defined when the percentage of the lunar disc illuminated was between 45% and 55%. We refer to these phases of the lunar cycle as half-moon waning and half-moon waxing. Since cloud cover reduces available moonlight during the wet season, we only considered data collected during the dry season (April–October) when cloud cover was negligible. Because temperature has been shown to influence activity patterns of carnivore species (Theuerkauf 2009), we obtained records for the study area and used temperature as a covariate in our statistical models. For each day,

average temperatures for the five periods of the 24-h cycle were calculated using the data recorded at 15-minute intervals by a fixed weather station situated in Maun, the town closest to the study area (Jacana raw weather data for 2006–2011 are *available online*).[5] Maun lies at the southern edge of the Okavango Delta and is part of the same geo-ecological system as the study site.

Data analysis

The activity data used in our analyses were systematically collected by radio collars equipped with two motion sensors mounted on the study animals. The two motion sensors continuously recorded activity bursts and summed them over 5-minute intervals; a raw data point consisted of the number of activity bursts per 5 minutes (thus the data are continuous, not categorical). To control for the highly pseudo-replicated nature of the raw data, we averaged, for each day, the activity data recorded by each collar over the five periods of the 24-h cycle. Thus, the data set consisted of one activity value for night, morning twilight, morning, afternoon, and evening twilight, for each day and for each individual. Study animals were followed during daytime and the observed behavior matched with the data collected by the collars at the time of observation. Resting animals usually showed activity levels of about 5–15 counts per 5 minutes depending on the species, and we include this threshold line in some of our graphs to help visual interpretation of the results.

For the four species, we calculated mean activity values during each period of the 24-h cycle during full-moon and new-moon days, as well as mean activity values for the seven periods of the night during full-moon, half-moon (waning and waxing), and new-moon days. Periodicity in the nocturnal activity of the four species was analyzed using Fourier spectral analysis, performed using the statistical software R (R Development Core Team 2011). The Fourier algorithm isolates the period of a sinusoidal waveform (e.g., Polansky et al. 2010), and was applied to nocturnal activity values of each individual separately. Because Fourier analysis does not reveal the directionality and strength of the relationship between variables, we analyzed nocturnal activity using linear mixed-effects models (performed using the statistical software GenStat [VSN International, Hemel Hempstead, UK]) with moonlight intensity as an explanatory variable. Nocturnal activity, the response variable, was log-transformed to meet the assumptions of normality and homoscedasticity. Animal identity was treated as a fixed effect; night temperature and activity during the previous day time were entered as covariates; moon cycles and days nested within moon cycles were treated as random effects. We included a first-order auto-regressive error structure when necessary, based on diagnostic plots of residuals.

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[5] http://www.jacananet.com/Weather.htm

To further investigate the effects of nocturnal activity on the activity levels during the following day and to understand how activity was partitioned across the 24-h cycle, we constructed four additional mixed-effects models with, respectively, morning twilight activity, morning activity, afternoon activity, and evening twilight activity as response variables. The activity variables were log-transformed to meet the assumptions of normality and homoscedasticity. For each model, animal identity, moonlight intensity, activity during the previous periods of the 24-h cycle (e.g., morning twilight activity when analyzing morning activity), and temperature of the respective period were treated as fixed effects. For both models, moon cycles and days nested within moon cycles were treated as random effects. Model simplification started from a full model and followed a backward selection procedure based on the Akaike Information Criterion (Zuur et al. 2009). Denominator degrees of freedom reported in the text were rounded to the nearest integer. Significance was assessed at $P = 0.01$. Throughout the *Results*, central tendency values are expressed as mean ± SE.

RESULTS

Nocturnal activity of wild dogs and cheetahs comprised, respectively, 25.9% ± 2.1% (mean ± SE) and 25.6% ± 3.5% of the overall diel activity budget, a high value for two species currently described as day active. In contrast, for lions and hyenas, nocturnal activity made up 60% ± 2.7% and 67.9% ± 2.6% of their respective activity budgets (Table 1). In addition, wild dogs and cheetahs conducted roughly half of their total activity (wild dogs, 51.3% ± 1.3% and cheetahs, 43.8% ± 1.9%; Table 1) during the main activity periods of lions and hyenas (night and twilight). This rather extensive and unexpected overlap between the activity patterns of the subordinate and the dominant predators is inconsistent with the idea of strict temporal partitioning.

Mean activity values over the five periods of the 24-h cycle (night, morning twilight, morning, afternoon, and evening twilight) showed significant differences between full-moon days and new-moon days for wild dogs and cheetahs but not for lions and hyenas (Fig. 1 and Table 1). This suggests that the activity pattern of wild dogs and cheetahs changes over a lunar cycle, while the activity pattern of lions and hyenas remains constant and is thus uncoupled from the phases of the moon (Fig. 1 and Table 1). On full-moon days, about 40% (wild dogs, 40.4% ± 3.8%; cheetahs, 39.7% ± 4.4%) of the total diel activity of wild dogs and cheetahs occurred at night while this figure dropped to approximately 15% (wild dogs, 15.9% ± 2.2%; cheetahs, 13.8% ± 2.4%) during new-moon days (Table 1). In contrast, the nighttime activity of lions and hyenas did not change between the different phases of the lunar cycle (Table 1).

The Fourier spectral analysis showed that the nocturnal activity of six of the seven wild dogs had a main period of 29.17 ± 0.75 d (mean ± SE) corresponding very closely with the lunar cycle of 29.53 d (Figs. 2 and 3); one wild dog (#4) did not show any periodicity (Fig. 3b). Five of the cheetahs exhibited a main period of 30.45 ± 0.49 d (Figs. 2 and 3), while one individual (#3) showed little signature at this wavelength (Fig. 3c). In contrast to wild dogs and cheetahs, the nocturnal activity of lions and hyenas showed no relationship with the lunar cycle, although they exhibited shorter activity cycles of a few days (Fig. 2). A fine-scale investigation of the nighttime activity between different phases of the lunar cycle showed that wild dogs and cheetahs adjusted their nocturnal behavior according to the presence of the moon in the sky. For example, during a waning moon, when the moon is in the sky during the first half of the night, both species were highly active during the hours preceding midnight (Appendices D and E). With sufficient moonlight, the night activity levels of wild dogs and cheetahs was comparable with activity levels exhibited during the morning twilight on full-moon days (compare Fig. 1 with Appendices D and E). In contrast, the activity of lions and hyenas was not related to the presence of the moon in the sky and remained generally constant during the night (Appendices F and G). This further supports our prediction that moonlight intensity, rather than the activity of lions and hyenas, is a major driver influencing the nocturnal activity of wild dogs and cheetahs.

In the linear mixed-effects models, the nocturnal activity of lions and hyenas showed no relationship with moonlight intensity, despite reports that the hunting success of lions increases when the moon is absent or obscured by clouds (Funston et al. 2001, Packer et al. 2011). In contrast, there was a strong positive relationship between wild dogs' nocturnal activity and moonlight intensity ($F_{1, 571} = 231.06$, $P < 0.001$), although one individual (#4) showed no nocturnal activity (interaction term individual by moonlight, $F_{6,1020} = 4.33$, $P < 0.001$; Fig. 3). For cheetahs, there was a similar positive relationship between nocturnal activity and moonlight intensity ($F_{1, 981} = 164.02$, $P < 0.001$) although one male (#3) showed consistently high levels of activity at night (interaction term individual by moonlight, $F_{5, 981} = 6.38$, $P < 0.001$; Fig. 3). For both wild dogs and cheetahs, the total diel activity remained roughly constant over a lunar cycle and hence showed no relationship with moonlight intensity (wild dog, $F_{1, 512} = 0.69$, $P = 0.41$; cheetah, $F_{1, 980} = 1.37$, $P = 0.24$). This suggests that wild dogs and cheetahs trade off and partition nocturnal and diurnal activity according to available moonlight.

To further investigate this suggestion and understand how diel activity was partitioned, we carried out additional analyses for each period of the 24-h cycle. For both wild dogs and cheetahs, high levels of moonlight intensity negatively influenced the activity during each period of the following day, with the exclusion of the evening twilight activity of cheetahs (all

Table 1. Portion of activity during the five periods of the 24-h cycle over an entire lunar cycle and for two different phases of the lunar cycle.

| Time period | Portion of activity (%) | | | |
	Wild dog	Cheetah	Spotted hyena	Lion
Overall				
Night	25.9 ± 2.1	25.6 ± 3.5	67.9 ± 2.6	60.0 ± 2.7
Morning twilight	11.0 ± 0.9	9.9 ± 1.4	8.1 ± 0.8	7.4 ± 0.7
Morning	28.7 ± 1.6	34.3 ± 2.1	10.4 ± 1.7	16.3 ± 1.4
Afternoon	19.9 ± 1.5	21.9 ± 1.5	5.0 ± 1.1	9.3 ± 1.8
Evening twilight	14.4 ± 0.8	8.3 ± 0.7	8.6 ± 0.5	7.9 ± 0.8
Partial overlap	51.3	43.8	84.6	75.3
Full moon				
Night	40.4 ± 3.8	39.7 ± 4.4	66.7 ± 2.3	57.7 ± 4.0
Morning twilight	8.5 ± 0.5	7.1 ± 1.6	9.3 ± 0.4	7.7 ± 0.5
Morning	21.2 ± 2.4	28.1 ± 2.1	10.5 ± 1.7	16.9 ± 2.1
Afternoon	16.9 ± 1.8	17.2 ± 1.0	4.9 ± 1.2	9.8 ± 2.0
Evening twilight	13.1 ± 1.3	7.8 ± 0.7	8.6 ± 0.6	8.0 ± 0.9
Partial overlap	62.0	54.6	84.6	73.4
New moon				
Night	15.9 ± 2.2	13.8 ± 2.4	67.7 ± 2.9	60.9 ± 2.4
Morning twilight	13.6 ± 1.0	12.3 ± 1.2	7.6 ± 1.3	7.4 ± 0.8
Morning	32.2 ± 1.9	40.1 ± 2.0	10.8 ± 1.6	14.5 ± 1.4
Afternoon	21.9 ± 1.9	24.7 ± 1.8	5.0 ± 1.1	9.2 ± 1.4
Evening twilight	16.3 ± 1.3	9.1 ± 0.7	8.9 ± 0.5	8.0 ± 0.8
Partial overlap	45.8	35.2	84.2	76.3

Notes: Values are means ± SE. Partial overlap is the sum of the activities recorded during the three periods of major lion and hyena activity (night, morning twilight, and evening twilight) and shows how much of the diel activity of wild dogs and cheetahs takes place during times of overlapping activity with their two stronger competitors.

P values <0.001; Appendix B). For wild dogs, high activity levels during moonlit nights led to decreased activity the following day (except for the evening twilight activity, which was independent of the activity during the previous night; Fig. 1 and Appendix B). Morning twilight and morning activity showed a positive relationship as did afternoon and evening twilight activity (Appendix B). Wild dogs thus show three distinct activity periods (night; morning twilight and morning; afternoon and evening twilight) clearly separated by phases of inactivity. The patterns for cheetahs were different: after correcting for differences in activity due to differences in moonlight intensity (Fig. 1 and Appendix B), we found that levels of activity in adjacent periods showed a positive relationship; hence it seems that, once active, cheetahs remain active over long periods (Appendix B). For both species, temperature negatively influenced activity only during the hottest part of the day (i.e., morning and afternoon periods; Appendix B).

Discussion

In contrast to previous studies suggesting a high degree of temporal partitioning among African large predators (Hayward and Slotow 2009), our study in the Okavango Delta revealed extensive temporal overlap. This was mainly due to the unexpected nocturnal activity of wild dogs and cheetahs, the two species

previously regarded as diurnal, and the partly diurnal habits of lions and hyenas. Only for wild dogs and cheetahs was nocturnal activity correlated with the lunar cycle: with sufficient moonlight, both species were considerably active at night and nocturnal activity constituted almost half of the total diel activity on full-moon days. It therefore seems that activity patterns of these subdominant species are primarily constrained by light availability, rather than by the activities of the larger, dominant species. Our findings support the idea that, at the diel level, temporal niche partitioning may be a relatively rare event (Schoener 1974b).

Our results conflict with those from the meta-analysis carried out by Hayward and Slotow (2009) who concluded that available studies did not support nocturnal behavior for wild dogs and cheetahs. However, the authors used data from different sites that had been collected opportunistically using a range of different methodologies for different species. In addition, they often assumed that the timing of sunrise and sunset were constant through the year and along a latitudinal gradient. These assumptions can lead to incorrect conclusions, as pointed out by Nouvellet et al. (2011). Although our results are not consistent with the hypothesis that activity patterns of dominant competitors have been the main force shaping the temporal niches of wild dogs and cheetahs, we nonetheless acknowledge that lions and hyenas pose a real threat
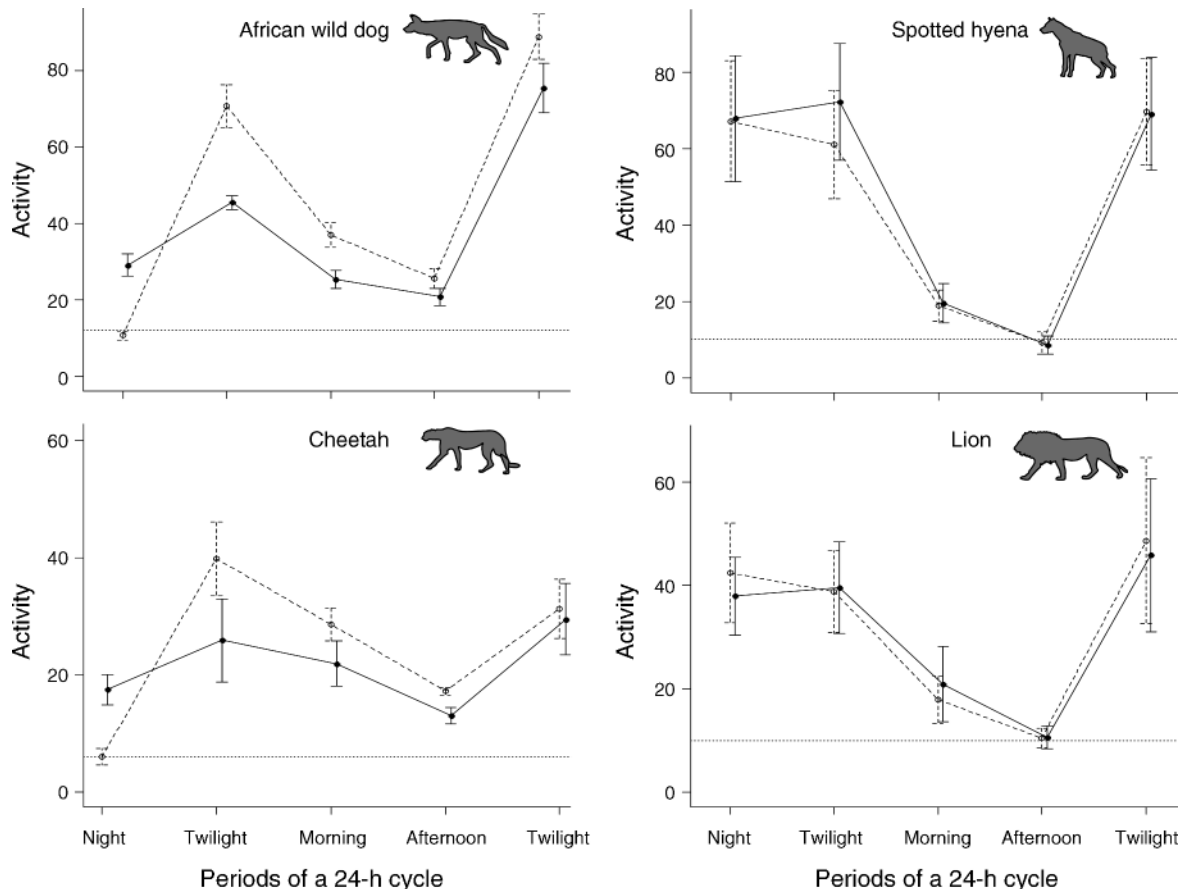
FIG. 1. Mean activity values (defined in *Methods: Data analysis*) during five periods of the 24-h cycle for full-moon days (solid lines) and new-moon days (dashed lines). Error bars represent standard errors of the mean. Connecting lines between mean values have been added for visualization purposes. The horizontal dotted line shows the inactivity threshold.

(Laurenson et al. 1995, Mills and Gorman 1997, Gorman et al. 1998). Playback experiments have for example revealed short-term behavioral modifications in response to the presence of lions and hyenas such as reduced hunting activity and fleeing behavior (Durant 2000, Webster et al. 2011), and simulation models revealed the sensitivity of wild dog populations to lion predation (Vucetich and Creel 1999).

Only wild dogs and cheetahs showed nocturnal activity patterns that were correlated with the availability of moonlight while the nocturnal activity of hyenas and lions did not vary over the lunar cycle. This raises the question of why good light is a key requirement for activity in wild dogs and cheetahs but not in lions and hyenas. Both wild dogs and cheetahs hunt small and medium-sized antelopes, e.g., impala (*Aepyceros melampus*), and conduct high-speed chases over relatively long distances. During such chases, wild dogs can pursue their prey at 40–60 km/h for more than 1 km and cheetahs reach speeds of over 100 km/h for several hundred meters. Such long, high-speed chases are inherently risky and good light conditions (i.e., during

the day and on moonlit nights) and sufficient visibility are likely to be essential to maintain contact with the prey, avoid fatal injuries, and increase hunting success (Schaller 1972, Bertram 1979, Creel and Creel 2002, Rasmussen and Macdonald 2011). This cursorial hunting technique is in clear opposition to the ambush hunting technique of lions, whose success increases when the moon is absent or obscured by clouds (Funston et al. 2001, Packer et al. 2011). Different foraging techniques may thus explain the different activity patterns among the species of the guild, and stress the evolutionary importance of bottom-up forces (e.g., prey acquisition) in shaping the behavior of large predators.

If lions and hyenas pose a threat to wild dogs and cheetahs, why do they not completely avoid nocturnal activity? One possibility is that they must take every opportunity to catch prey and that they cannot afford to miss exploiting nights with sufficient moonlight. Thus, wild dogs and cheetahs may have evolved short-term visual, auditory, and olfactory cues, e.g., fleeing on hearing lion calls, to avoid potentially dangerous situations, rather than completely avoiding being night
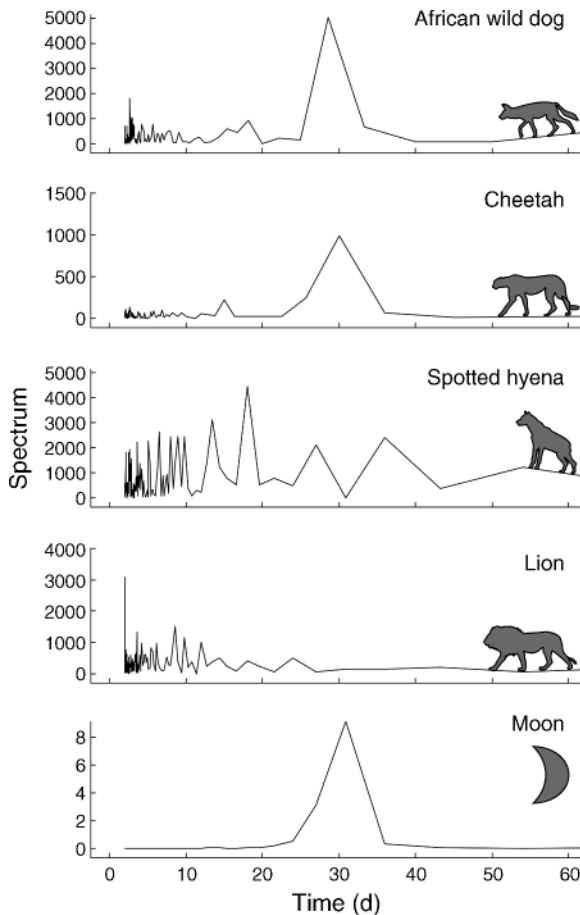
FIG. 2. Spectrogram showing periodicity in the nocturnal activity pattern of a typical African wild dog, cheetah, spotted hyena, and lion. Activity data recorded by the collars were averaged per night and investigated using Fourier spectral analysis. For comparison, the spectrogram of the moon is shown. While the activity of wild dogs and cheetahs shows a main period of 30 days (similarly to the period of the lunar cycle), the activity of spotted hyenas and lions show cyclicity every few days. The width of each peak is a measure of accuracy.

active. Neither wild dogs nor cheetahs showed any cyclical pattern in their total diel activity over the course of a lunar cycle, suggesting that nocturnal activity was not a strategy to increase the overall activity budget. Instead, wild dogs showed clear trade-offs in activity between adjacent periods within a 24-h cycle. For example, a night with high activity was followed by a morning with reduced activity, implying that nocturnal activity allowed or forced subdominant species to rest the next day. We therefore assume that the benefits of nocturnal activity offset the risks of encountering night-active predators and competitors. Indeed, we might expect hunting success to be higher at night because prey animals have a reduced chance of spotting predators under dim light conditions. For example, it is known that hunting success in cheetahs is higher when they can

stalk undetected very close to intended prey (FitzGibbon and Fanshawe 1988) and that wolves (*Canis lupus*) are almost twice as successful when hunting on moonlit nights (Theuerkauf et al. 2003). To the contrary, the high levels of activity during early mornings that followed moonless nights, when activity was limited, suggest a behavioral response to an increasing hunger risk.

The influence of moonlight on the hunting behavior of predator species has been widely described for nocturnal species (Horning and Trillmich 1999, Lang et al. 2006), and our results suggest that moonlight can equally influence (allegedly) diurnal species. Understanding and quantifying the energetic budget of single species based on patterns of activity is beyond the scope of this study; nevertheless, on the basis of our findings, it is evident that wild dogs and cheetahs have more time to fulfill their energetic requirements than just a few hours in the morning and in the late afternoon as currently assumed. Further research is thus required to understand the role of each period of the 24-h cycle for the diel energetic budget as compared to the diel activity budget.

Our findings suggest that the temporal niches of subdominant large predator species are only moderately shaped by the need to avoid predation and competition (Schoener 1974b, Lima and Dill 1990, Theuerkauf 2009). This is in contrast to findings at other trophic levels, for example, in guilds of herbivore species (Sinclair et al. 2003, Chesson and Kuang 2008). Subdominant large predators must trade off the risk of encountering dominant species against the risk of starvation (e.g., Lima 1988, Roth and Lima 2007) and subdominant large predators appear to be mainly "starvation driven." The well-documented positive relationship between the distribution and density of prey species and their predators (e.g., Carbone and Gittleman 2002) further suggests a tight casual association between bottom-up forces and communities of large predators. Additional research in ecosystems characterized by different densities of competitors and prey species will be necessary to better understand the role of top-down and bottom-up forces in shaping animal communities and facilitating coexistence. In contrast to herbivores, large carnivores must invest a lot of energy finding and catching food, as prey are widely scattered, often rare, and difficult to catch, and hunting is energy-intensive, time-consuming, and often unsuccessful (e.g., Carbone et al. 1999). Given the relative difficulty of catching a meal vs. the relatively low likelihood of encountering a dominant species (large predators live at relatively low densities [Carbone and Gittleman 2002]), we conclude that, on moonlit nights, wild dogs and cheetahs prioritize hunting opportunities and success over the need to avoid been hunted and over the possibility of losing their kill. In conclusion, it appears that under favorable light conditions, the benefits of nocturnal activity outweigh the costs of encountering stronger competitors and predators.
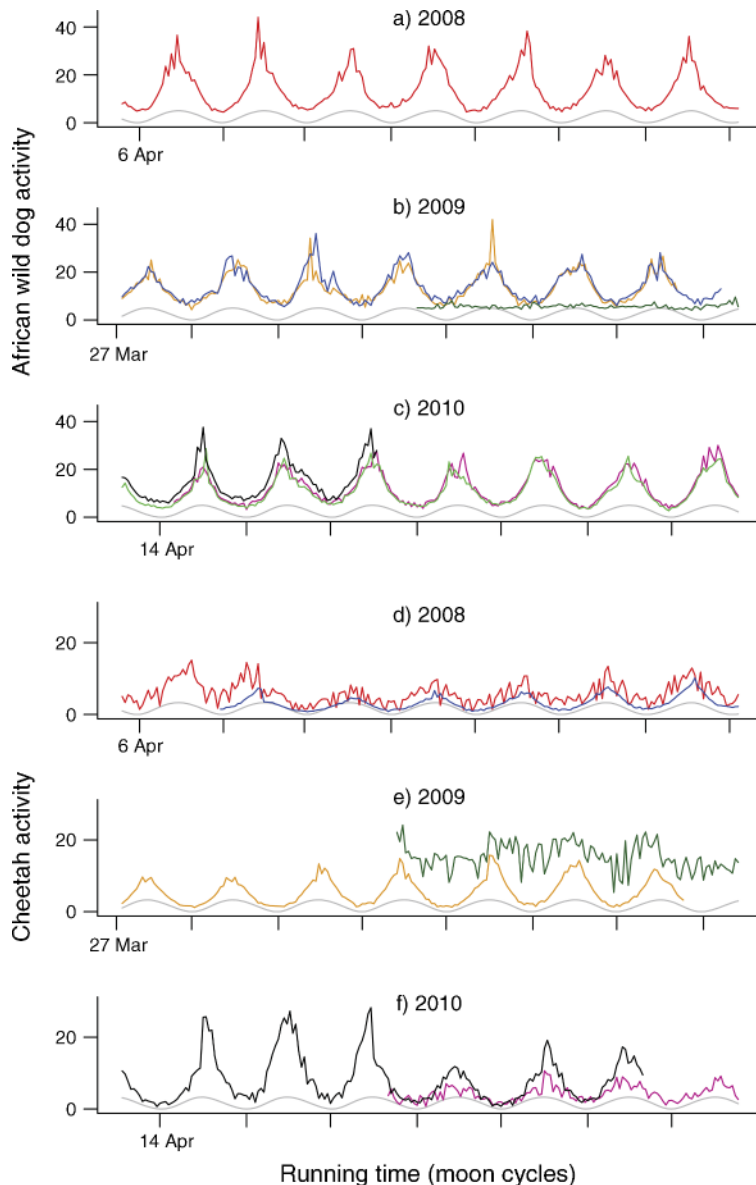
FIG. 3. Fitted values from mixed-effects models showing the nocturnal activity patterns of (a–c) African wild dogs ($n = 7$ individuals) and (d–f) cheetahs ($n = 6$ individuals) during the dry season in three consecutive years. Each color represents a different individual. Tick marks on the x-axis represent the beginning of a moon cycle (new moon). The beginning dates of moon cycles change from year to year; thus the x-axes are not aligned between years. The date of the first new moon for each year's data is shown under the first tick. Only data collected beginning 1 April of each year (the beginning of the dry season) have been considered for analysis, and the fitted (colored) lines all start on 1 April. Variation in moonlight intensity is depicted for comparison in each panel (gray line; not to scale) and highlights the strong positive relationship between animals' activity and moonlight availability. One wild dog [panel (b), green line] shows no nocturnal activity, while one male cheetah [panel (e), green line] shows consistently high nocturnal activity.

LITERATURE CITED

Barnosky, A. D., P. L. Kock, R. S. Feranec, S. L. Wing, and A. B. Shabel. 2004. Assessing the causes of Late Pleistocene extinctions on the continents. Science 306:70–75.

Bertram, B. C. R. 1979. Serengeti predators and their social systems. Pages 221–248 in A. R. E. Sinclair and M. Norton-

Griffiths. editors. Serengeti: dynamics of an ecosystem. University of Chicago Press, Chicago, Illinois, USA.

Carbone, C., J. T. Du Toit, and I. J. Gordon. 1997. Feeding success in African wild dogs: does kleptoparasitism by spotted hyenas influence hunting group size? Journal of animal Ecology 66:318–326.

Carbone, C., and J. L. A. Gittleman. 2002. Common rule for the scaling of carnivore density. Science 295:2273–2276.

Carbone, C., G. M. Mace, S. C. Roberts, and D. W. Macdonald. 1999. Energetic constraints on the diet of terrestrial carnivores. Nature 402:286–288.

Caro, T. M., and C. Stoner. 2003. The potential for interspecific competition among African carnivores. Biological Conservation 110:67–75.

Chesson, P., and J. J. Kuang. 2008. The interaction between predation and competition. Nature 456:235–238.

Creel, S. 2001. Four factors modifying the effect of competition on carnivore population dynamics as illustrated by African wild dogs. Conservation Biology 15:271–274.

Creel, S., and N. M. Creel. 2002. The African wild dog: behavior, ecology and conservation. Princeton University Press, Princeton, New Jersey, USA.

Crompton, A. W., C. R. Taylor, and J. A. Jagger. 1978. Evolution of homeothermy in mammals. Nature 272:333–336.

Dalerum, F., E. Z. Cameron, K. Kunkel, and M. J. Somers. 2009. Diversity and depletions in continental carnivore guilds: implications for prioritizing global carnivore conservation. Biology Letters 5:35–38.

Durant, S. M. 1998. Competition refuge and coexistence: an example from Serengeti carnivores. Journal of Animal Ecology 67:370–386.

Durant, S. M. 2000. Living with the enemy: avoidance of hyenas and lions by cheetahs in the Serengeti. Behavioral Ecology 11:624–632.

FitzGibbon, C. D., and J. H. Fanshawe. 1988. Stotting in Thomson's gazelles: an honest signal of condition. Behavioral Ecology and Sociobiology 23:69–74.

Funston, P. J., M. G. L. Mills, and H. C. Biggs. 2001. Factors affecting the hunting success of male and female lions in the Kruger National Park. Journal of Zoology 253:419–431.

Gorman, M. L., M. G. L. Mills, J. P. Raath, and J. R. Speakman. 1998. High hunting costs make African wild dogs vulnerable to kleptoparasitism by hyenas. Nature 391:479–481.

Harrington, L. A., A. L. Harrington, N. Yamaguchi, M. D. Thom, P. Ferreras, T. R. Windham, and D. W. Macdonald. 2009. The impact of native competitors on an alien invasive: temporal niche shifts to avoid interspecific aggression? Ecology 90:1207–1216.

Hayward, M. W., and R. Slotow. 2009. Temporal partitioning of activity in large African carnivores: tests of multiple hypotheses. South African Journal of Wildlife Research 39:109–125.

Horning, M., and F. Trillmich. 1999. Lunar cycles in diel prey migrations exert a stronger effect on the diving of juveniles than adult Galapagos fur seals. Proceedings of the Royal Society B 266:1127–1132.

Koch, P. L., and A. D. Barnosky. 2006. Late quaternary extinctions: state of the debate. Annual Review of Ecology, Evolution, and Systematics 37:215–250.

Kock, M., D. Meltzer, and R. Burroughs. 2006. Chemical and physical restraint of wild animals: a training and field manual for African species. International Wildlife Veterinary Services, Johannesburg, South Africa.

Kotler, B. P., J. S. Brown, and A. Subach. 1993. Mechanisms of species coexistence of optimal foragers: temporal partitioning by two species of sand dune gerbils. Oikos 67:548–556.

Lang, A. B., E. K. V. Kalko, H. Römer, C. Bockholdt, and D. K. Dechmann. 2006. Activity levels of bats and katydids in relation to the lunar cycle. Oecologia 146:659–666.

Laurenson, M. K., N. Wielebnowski, and T. M. Caro. 1995. Extrinsic factors and juvenile mortality in cheetahs. Conservation Biology 9:1329–1331.

Lima, S. L. 1988. Initiation and termination of daily feeding in dark-eyed juncos: influences of predation risk and energy reserves. Oikos 53:3–11.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619–640.

Linnell, J., and O. Strand. 2000. Interference interactions, coexistence and conservation of mammalian carnivores. Diversity and Distribution 6:169–176.

Maynard-Smith, J., and G. A. Parker. 1976. The logic of asymmetric contest. Animal Behaviour 24:159–175.

McManus, J. S. 2009. The spatial ecology and activity patterns of leopards (Panthera pardus) in the Baviaanskloof and Greater Addo Elephant National Park, Eastern Cape Province, South Africa. Thesis. Rhodes University, Grahamstown, South Africa.

Mills, M. G. L., and M. L. Gorman. 1997. Factors affecting the density and distribution of wild dogs in the Kruger National Park. Conservation Biology 11:1397–1406.

Nouvellet, P., G. S. A. Rasmussen, D. W. Macdonald, and F. Courchamp. 2011. Noisy clocks and silent sunrises: measurement methods of daily activity pattern. Journal of Zoology 286:179–184.

Osofsky, S. A., J. W. McNutt, and K. J. Hirsch. 1995. Immobilization of free-ranging African wild dogs (Lycaon pictus) using a ketamine/xilazine/atropin combination. Journal of Zoology and Wildlife Medicine 27:528–532.

Packer, C., A. Swanson, D. Ikanda, and H. Kushnir. 2011. Fear of darkness, the full moon and the nocturnal ecology of African lions. PLoS ONE 6(7):e22285.

Palomares, F., and T. M. Caro. 1999. Interspecific killing among mammalian carnivores. American Naturalist 153:492–508.

Pianka, E. R. 1974. Niche overlap and diffuse competition. Proceedings of the National Academy of Sciences USA 71:2141–2145.

Polansky, L., G. Wittemeyer, P. C. Cross, C. J. Tambling, and W. M. Getz. 2010. From moonlight to movement and synchronized randomness: Fourier and wavelet analyses of animal location time series data. Ecology 91:1506–1518.

Polis, G. A., and R. D. Holt. 1992. Intraguild predation: the dynamics of complex trophic interactions. Trends in Ecology and Evolution 7:151–154.

Purvis, A., J. L. Gittleman, G. Cowlishaw, and G. M. Mace. 2000. Predicting extinction risk in declining species. Proceedings of the Royal Society B 1456:1947–1952.

R Development Core Team. 2011. R: a language and environment for statistical computing. R Project for Statistical Computing, Vienna, Austria. http://www.R-project.org

Radloff, F. G. T., and J. T. Du Toit. 2004. Large predators and their prey in a southern African savanna: a predator's size determines its prey size range. Journal of Animal Ecology 73:410–423.

Rasmussen, G. S. A., and D. W. Macdonald. 2011. Masking the zeitgeber: African wild dogs mitigate persecution by balancing time. Journal of Zoology 286:232–242.

Rosenzweig, M. L. 1966. Community structure in sympatric Carnivora. Journal of Mammalogy 47:602–612.

Roth, T. C., and S. L. Lima. 2007. The predatory behaviour of wintering Accipiter hawks: temporal patterns in activity of predators and prey. Oecologia 152:169–178.

Schaller, G. B. 1972. The Serengeti lion: a study of predator–prey relations. University of Chicago Press, Chicago, Illinois, USA.

Schmitz, L., and R. Motani. 2011. Nocturnality in dinosaurs inferred from scleral ring and orbit morphology. Science 332:705–708.

Schoener, T. W. 1974a. Resource partitioning in ecological communities. Science 185:27–39.

Schoener, T. W. 1974b. The compression hypothesis and temporal resource partitioning. Proceedings of the National Academy of Sciences USA 71:4169–4172.

Sih, A. 1980. Optimal behaviour: can foragers balance two conflicting demands? Science 210:1041–1043.

Sinclair, A. R. E., S. Mduma, and J. Brashares. 2003. Patterns of predation in a diverse predator–prey system. Nature 425:288–290.

Theuerkauf, J. 2009. What drives wolves: fear or hunger? Humans, diet, climate and wolf activity patterns. Ethology 115:649–657.

Theuerkauf, J., W. Jedrzejewski, K. Schmidt, H. Okarma, I. Ruczynski, S. Sniezko, and R. Gula. 2003. Daily patterns and duration of wolf activity in the Bialowieza forest, Poland. Journal of Mammalogy 84:243–253.

Turvey, S. T., and S. A. Fritz. 2011. The ghosts of mammals past: biological and geographical patterns of global mammalian extinction across the Holocene. Philosophical Transactions of the Royal Society B 365:2564–2576.

United States Naval Observatory. 2011. Phases of the moon and percent of the moon illuminated. United States Naval Observatory, Washington, D.C., USA. http://aa.usno.navy.mil/faq/docs/moon_phases.php

Valkenburgh, B. V. 1988. Trophic diversity in past and present guilds of large predatory mammals. Paleobiology 14:155–173.

Vucetich, J. A., and S. Creel. 1999. Ecological interactions, social organization, and extinction risk in African wild dogs. Conservation Biology 13:1172–1182.

Webster, H., J. W. McNutt, and K. McComb. 2011. African wild dogs as a fugitive species: playback experiments investigate how wild dogs respond to their major competitors. Ethology 117:1–10.

Woodward, G., and A. G. Hildrew. 2002. Body-size determinants of niche overlap and intraguild predation within a complex food web. Journal of Animal Ecology 71:1063–1074.

Ziv, J., Z. Abramsky, B. P. Kotler, and A. Subach. 1993. Interference competition and temporal and habitat partitioning in two gerbil species. Oikos 66:237–246.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York, New York, USA.

SUPPLEMENTAL MATERIAL

Appendix A

A table showing the spatial range and overlap of the studied animals (*Ecological Archives* E093-242-A1).

Appendix B

A table including the detailed mixed-effect models used to investigate partitioning of activity within the 24-h cycle (*Ecological Archives* E093-242-A2).

Appendix C

A figure depicting the division of the 24-h cycle into five periods: morning twilight, morning, afternoon, evening twilight, and night (*Ecological Archives* E093-242-A3).

Appendix D

Mean activity values for African wild dogs during seven periods of the night for four phases of the lunar cycle: full moon, half moon (waning), half moon (waxing), and new moon (*Ecological Archives* E093-242-A4).

Appendix E

Mean activity values for cheetahs during seven periods of the night for four phases of the lunar cycle: full moon, half moon (waning), half moon (waxing), and new moon (*Ecological Archives* E093-242-A5).

Appendix F

Mean activity values for spotted hyenas during seven periods of the night for four phases of the lunar cycle: full moon, half moon (waning), half moon (waxing), and new moon (*Ecological Archives* E093-242-A6).

Appendix G

Mean activity values for lions during seven periods of the night for four phases of the lunar cycle: full moon, half moon (waning), half moon (waxing), and new moon (*Ecological Archives* E093-242-A7).