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ORIGINAL ARTICLE

Spatio-temporal niche partitioning between the African lion (*Panthera leo leo*) and spotted hyena (*Crocuta crocuta*) in western African savannas

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Abstract
Large predators in West Africa are threatened with extinction mainly by direct and indirect effects of human activities. Within this context, intraguild competition can limit populations of some species and even play a role in extinction. In this study, we used camera trapping to assess the spatial and temporal patterns of niche partitioning between the African lion *Panthera leo leo* and the spotted hyena *Crocuta crocuta* in Pendjari Biosphere Reserve, Benin. We found that these predators are more nocturnal in the hunting zone than in the national park of the biosphere reserve. The temporal overlap between lion and hyena was high in the national park (Pianka overlap index 0.88) and low in the hunting zones (0.39). The spatial overlap was low (0.40 in the national park and 0.38 in the hunting zones). The two predators were distributed independently in the national park, but showed significant positive association (co-occurrence) in the hunting zones. We suggest that anthropogenic activities leading to depletion of predators and their prey limit lion and hyena distribution in the hunting zones to some safety areas which are strongly selected by both predators. We recommend to significantly improve conservation efforts in the hunting zones of Pendjari Biosphere Reserve and to expand research of lion-hyena intraguild relationships to improve predator survival in West Africa.

Keywords Apex predators · Coexistence · Activity patterns · Anthropogenic impacts · Conservation · Benin

Introduction

Interspecific competition among predators determines the structure and dynamics of habitats, landscapes, and whole ecosystems (Caro and Stoner 2003; Linnell and Strand 2000). This competition can take the form of exploitation competition where species compete for the same resource and interference competition where they interact directly with each other (Mills 1991). Competition can not only affect the subordinate species of the guild (Swanson et al. 2014) but also produce cascading effects on lower trophic levels (Crooks and Soulé 1999; Palomares et al. 1995; Ripple et al. 2014). The patterns of predator coexistence vary across ecosystems and respective research helps to understand the reasons of global declines of predator populations. Subordinate species develop temporal and spatial partitioning of resource use in order to minimize competition with dominant species by avoiding the periods of time and habitats preferred by dominant competitors (Fedriani et al. 1999; Hayward and Slotow 2009; Swanson et al. 2014). Coexistence between subordinate and apex predators is well documented (Caro and Stoner 2003; Cozzi et al. 2012; Dröge et al. 2017; Swanson et al. 2014).

Lion *Panthera leo leo* and spotted hyena *Crocuta crocuta* are the top predators in African savannas. Situated atop the trophic niches, they share several characteristics and have a similar diet (Hayward and Kerley 2005, 2008; Hayward 2006; Periquet et al. 2015) but differ in hunting strategies (Kruuk 1972; Schaller 1972). They reciprocally harass and exert kleptoparasitism on each other (Höner et al. 2002; Periquet et al. 2015). Usually, lions dominate hyenas which can lead to the suppression of hyena populations through food stealing (Watts and Holekamp 2008) and direct killing (Kruuk 1972; Trinkel and Kastberger 2005; Watts and Holekamp 2008).

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However, when living in large groups, hyenas may outcompete lions (Höner et al. 2002; Watts and Holekamp 2008). Despite this intense competition between the two species, they do not avoid each other (Watts et al. 2010) and have a significant overlap in diets and activity patterns (Hayward and Slotow 2009). This could explain why their densities are positively correlated in African protected areas (Creel and Creel 1996).

In West Africa, as other large predators, lion and hyena are mainly confined to protected areas and are threatened with extinction. While population estimates are available for lion (Henschel et al. 2015, 2016), these data are lacking for hyena. However, the Red List status of the two species suggests that hyena densities are higher than lion densities (Bohm and Höner 2015; Henschel et al. 2015). Few available studies show that in West and Central Africa, lions tend to consume more medium-sized prey than in other parts of the continent (Bauer et al. 2008; Di Silvestre et al. 2000; Sogbohossou 2011). Furthermore, lions in West Africa live in smaller groups than elsewhere (Bauer et al. 2003; Sogbohossou et al. 2014). In line with that, a very high dietary overlap between lion and hyena and, consequently, high competition compared to other parts of Africa is to be expected, being aggravated by prey scarcity provoked by poaching and habitat loss (Lindsey et al. 2017). According to Bauer et al. (2015), the lion population in West and Central Africa is likely to drop by about 30% in the next 5 years and about 50% in 20 years. The lion population in West Africa is already categorized as Critically Endangered but only as Vulnerable in other parts of Africa (Henschel et al. 2015). The urgency to protect this species is reinforced by the genetic distinctiveness of the species in West and Central Africa (Bertola et al. 2015). Therefore, an understanding of the interactions and mechanisms between these top predators of West African savannas is an essential component of their conservation and management.

In this study, we used camera trapping to assess spatial and temporal niche partitioning between lion and hyena in Pendjari Biosphere Reserve, Benin, which hosts one of the largest and most stable lion population in West Africa (Bauer et al. 2015). We expected high competition between the two species due to higher density of hyenas compared to lions in the reserve, but low overall density of both species (Di Silvestre and Bauer 2013; Sogbohossou 2007; Sogbohossou and Tehou 2009, unpublished reports). Since temporal niche partitioning (Cozzi et al. 2012; Schoener 1974) is rare, we hypothesized that lion and hyena would have either a high temporal overlap but a lower spatial overlap to facilitate their co-existence in the study area.

Methodology

Study area

We conducted this study in Pendjari Biosphere Reserve (PBR), northern Benin. PBR spans on about 4800 km^2 between 11° 40–11° 28 N and 00° 57–2° 10 E. It is composed of Pendjari National Park (2660 km^2) and two hunting zones: Pendjari (about 1600 km^2) and Konkombri (250 km^2). It is part of the larger protected ecosystem that includes W Transboundary Biosphere Reserve in Benin, Burkina Faso, and Niger; Arly-Pama-Singou protected areas in Burkina Faso; and Oti-Keran-Mandouri in Togo and called WAPOK or WAP when the Togolese part is not considered (Fig. 1). The WAPOK ecosystem shelters the largest population of predators in West Africa (Riggio et al. 2013), except for wild dog *Lycaon pictus*. The PBR with the Arly complex is the best protected part of this ecosystem (Henschel et al. 2016).

Data collection and analysis

Originally, the camera trapping surveys were focused on cheetah *Acinonyx jubatus* and then on wildlife monitoring in general. We deployed cameras randomly on 99 stations during a first period from December 2014 to July 2015 and then on 89 stations during a second period from November 2015 to July 2016. We sampled a total of 147 stations, with at least 2 km between stations and one camera per station. We placed camera traps mainly along trails or roads actively used by the studied predators based on ranger records. We used Bushnell Trophy Cam 11-9636, Browning Dark Ops HD, and Moultrie M880i and M-990i passive infrared cameras. Cameras were attached to a tree at about 40 cm above the ground. They operated 24 h a day with a delay of 30 s and were checked every 10 to 14 days to change memory cards or batteries and to ensure that cameras were functioning properly.

To investigate the spatial and temporal activity pattern of lion and hyena, we considered only independent captures that were taken from different stations or at least 30 min apart from the same station, or depicted unambiguously different individuals in the same station (Farris et al. 2015).

To describe the species' distribution in the area, we calculated occupancy as the proportion of stations at which a species was detected from all stations (Schuette et al. 2013).

To assess temporal and spatial overlap, we calculated the Pianka's overlap index (O), which is extensively used to assess niche overlap between species (Pianka 1973; Glen and Dickman 2008; Farris et al. 2015):

$$O = \frac{\sum P_{ij} P_{ik}}{\sum {P_{ij}}^2 \sum {P_{ik}}^2}$$

where P_{ij} and P_{ik} are the proportions of the item i used by the species j and k, respectively. The index ranges from 0 (no overlap) to 1 (complete overlap). We estimated this coefficient for the whole biosphere reserve, and the hunting zones and the national park.

We also estimated the temporal activity patterns in the entire biosphere reserve and in its different parts—hunting zones

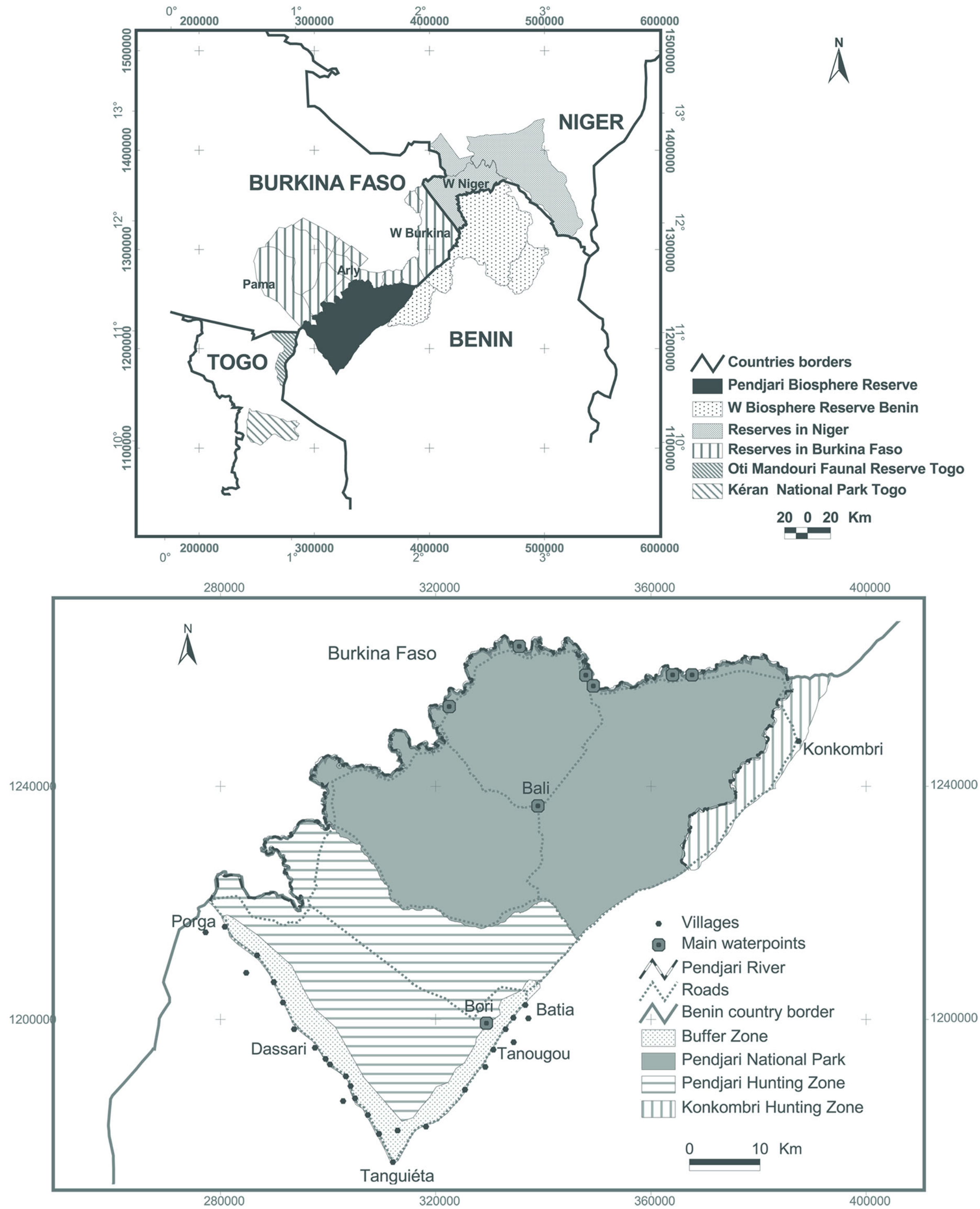

Fig. 1 Location of Pendjari Biosphere Reserve in Benin and the W-Arly-Pendjari-Oti-Kéran-Mandouri (WAPOK) protected ecosystem

and the national park—through the probability density function using the kernel density estimate of overlap (Ridout and Linkie 2009; Foster et al. 2013). We estimated the coefficient of overlap (Δ), which varies from 0 (no overlap) to 1 (complete overlap). We estimated Δ_4 for the reserve and the national park as the sample sizes were large enough in these two areas and Δ_1 which is more suitable for small samples for the hunting zones. We calculated the 95% confidence interval (95% CI) of Δ using 10,000 bootstrap samples and compared it between the national park and the hunting zones. We tested differences between stations used by lion and hyena, using Pearson's chi-square (χ^2), and Spearman's rho to examine correlation between lion and hyena records. We considered relationships with two-tailed $p < 0.05$ as significant and $p < 0.001$ as strongly significant. We implemented statistical analyses with R 3.3.3 (R Development Core Team 2017) and SPSS 24.0 (SPSS IBM Corp.).

Results

From the 88 camera traps stations in the national park and 59 stations in the hunting zones, a sampling effort of 9325 trap-nights was accumulated, yielding 87 captures of lions and 185 of hyenas. Overall occupancy was 23.1% for lion and 33.3% for hyena. The two species were sampled together in 14.8% of stations in the national park and 5.1% in the hunting zones.

Temporal overlap

Lion and hyena were both found being nocturnal as only 14.9% of lion captures and 10.7% of hyena captures were taken between 6:00 and 18:00 (Fig. 2). However, the two species were more nocturnal in the hunting zones (7.7% of lion captures and 0% of hyena captures taken from 6:00 to 18:00) than in the national park (16.2 and 12.0%, respectively). Lion activities concentrated between 18:00 and 8:00 while hyenas had two crepuscular peaks at 18:00–24:00 and 4:00–8:00. In the national park, lions stayed active longer during the daytime than in the hunting zones. In the hunting zones, both predators became active after the sunset until the beginning of the sunrise. The Pianka's overlap index was high in the national park (0.88, $n = 241$ captures) and low in the hunting zones (0.39, $n = 32$ captures).

The kernel density estimation confirmed the significant overlap between lion and hyena as $\Delta_4 = 0.83$ (95% CI = 0.74–0.91) in the national park and $\Delta_1 = 0.79$ in the hunting zone (95% CI = 0.49–0.90) (Fig. 3). Additionally, there was a strong correlation between temporal records of lion and hyena (Spearman's rho = 0.77, $p < 0.001$).

Spatial overlap

The Pianka's overlap index was low, 0.40 in the national park and 0.38 in the hunting zones. There was no correlation between the presence of the two species in stations (Spearman's rho = 0.159, $p = 0.05$).

In the national park, hyenas were equally likely to be present and absent in stations ($\chi^2 = 0.727$, $p = 0.394$), but lions were significantly more likely to be absent ($\chi^2 = 13.136$, $p < 0.001$). Here, both species were captured randomly as expected and did not show signs of positive or negative relationships ($\chi^2 = 0.114$, $p = 0.736$). In the hunting zones, both hyena and lion were significantly more likely to be absent in stations ($\chi^2 = 28.492$, $p < 0.001$ and $\chi^2 = 34.322$, $p < 0.001$, respectively). Here, when one or the other predator was present, they were significantly more likely to be present together ($\chi^2 = 4.681$, $p = 0.030$).

Discussion

Our study showed that lion and hyena are both nocturnal in Pendjari Biosphere Reserve, but the lion is more diurnal than hyena. This is consistent with findings from other parts of Africa where lion exhibits a predominantly crepuscular and nocturnal activity but can be active throughout the day while the spotted hyena is the most nocturnal of Africa's large carnivores (Hayward and Hayward 2007; Hayward and Slotow 2009; Swanson et al. 2016). Despite the two species being nocturnal, in the national park, their activities are spread over the night, mainly between 20:00 and 6:00 with no real peak. However, in the hunting zones, the lion is active earlier and concentrated its activities between 18:00 and 4:00 while hyena has two peaks in its activities: one around 20:00 after sunset and another one before sunrise. This situation in the hunting zone corresponds to Schuette et al. (2013) who found that—in contrast to lions which can be active throughout the night—hyenas are more likely to be more active after sunset and before sunrise.

However, with less than 15% of captures during the day between 6:00 and 18:00, the two species are more nocturnal in Pendjari than elsewhere (Cozzi et al. 2012; Hayward and Hayward 2007; Schuette et al. 2013). Lions are usually more active during the day in cooler autumn and winter months (Hayward and Hayward 2007) and also the nocturnal life of hyenas is explained by avoidance of high temperatures and not by their need for darkness to hunt successfully (Cooper 1990; Hayward and Hayward 2007). Daytime air temperatures in Pendjari typically vary from 18° to 35° and can reach 40° during the dry season when we conducted this study. These temperatures are usually higher than the ones in Southern and Eastern Africa where most large predator studies have been conducted. This can explain, at least partly, why the two predators are more nocturnal in Pendjari than elsewhere.

However, in our study, lion and hyena were more nocturnal in the hunting zones than in the national park of Pendjari. Most parts of the hunting zones are close to villages and serve as a buffer zone between human settlements and the national park. Thus, the hunting zones are prone to high pressure of hunting and other human activities. Strict nocturnal life of both predators in the hunting zones can be considered as an adaptation to minimize contacts with humans (Frank and Woodroffe 2001; Boydston et al. 2003; Kolowski et al. 2007).

While the distribution of lions and hyenas is not mutually correlated in the national park, they tend to co-occur in the hunting zones. We hypothesize that this can be caused by

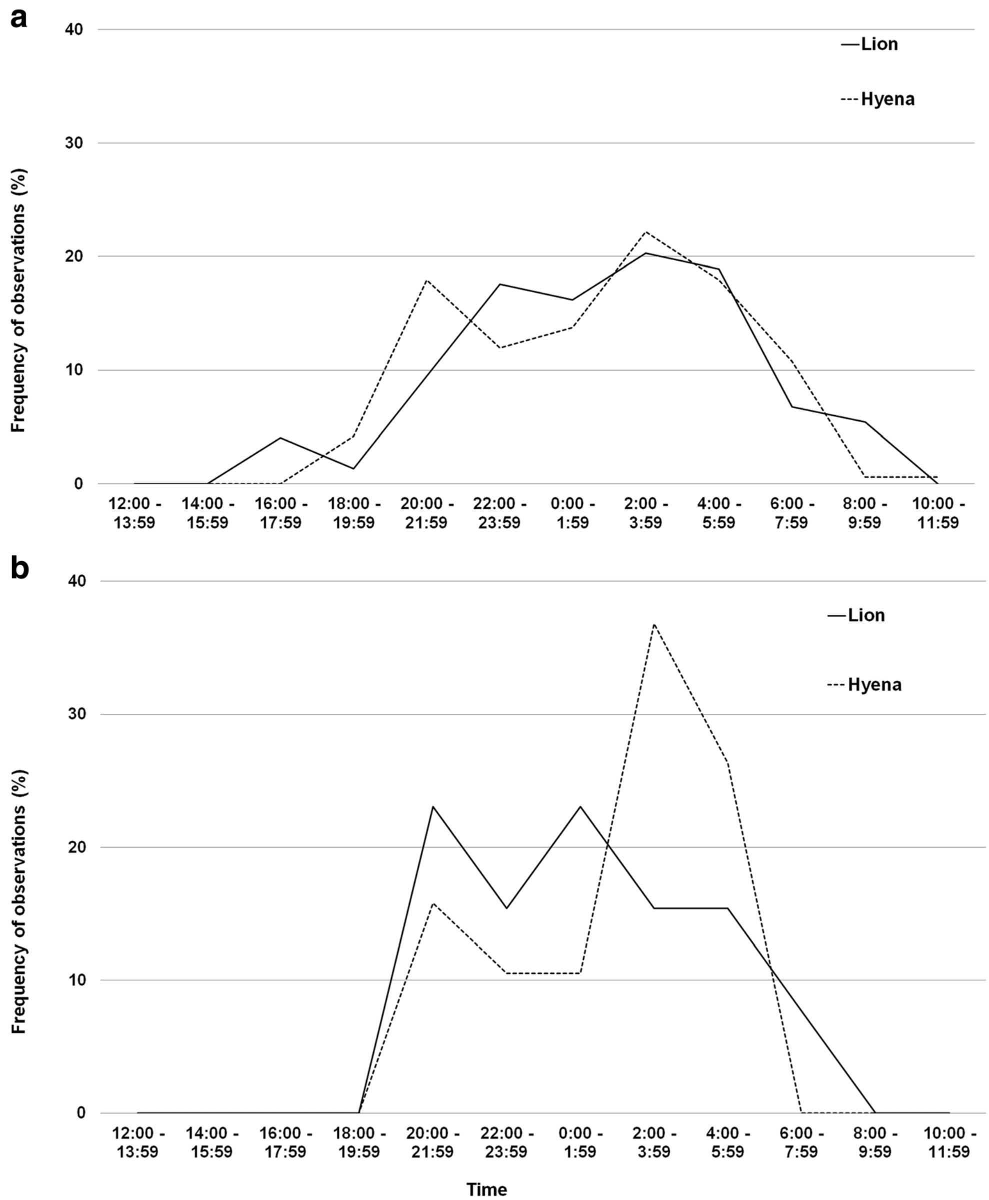

Fig. 2 The distribution of lion and hyena captures across time periods in **a** Pendjari National Park and **b** hunting zones

human pressure that leads to uneven distribution and low densities of predators and their prey in the hunting zones. A previous wildlife census in Pendjari showed that many parts of the hunting zones, especially those adjacent to villages, are almost empty from wildlife (WAP 2014, unpublished report) due to the edge effect (Balme et al. 2010). This means that prey species may be irregularly distributed across the hunting zones, concentrating in some safety areas. Prey abundance may determine habitat use by lion and hyena more strongly than competition, leading to their co-occurrence (Hayward et al. 2007; Périquet et al. 2015; Swanson et al. 2016). We expect that lion and hyena follow their prey and become spatially restricted to the same habitats in safety areas where they may not avoid each other and why their spatial distribution may be correlated (Boydston et al. 2003; Dröge et al. 2017; Périquet et al. 2015; Swanson et al. 2016).

In the hunting zones, lions and hyenas co-occur in such safety areas, but show strong temporal partitioning. As our results suggest a comparably low hyena and lion density in the hunting zones because the two species are more likely to be absent than present, lions are more likely to outcompete hyenas here (Trinkel and Kastberger 2005; Watts and Holekamp 2008). To avoid this, hyenas become even more nocturnal in the hunting zones. In contrast, in the national park with low human disturbance and high prey abundance, both predators are distributed independently from each other with a high level of temporal overlap.

The fact that we could not capture lions and hyenas in most stations in the hunting zones indicates a low density of both

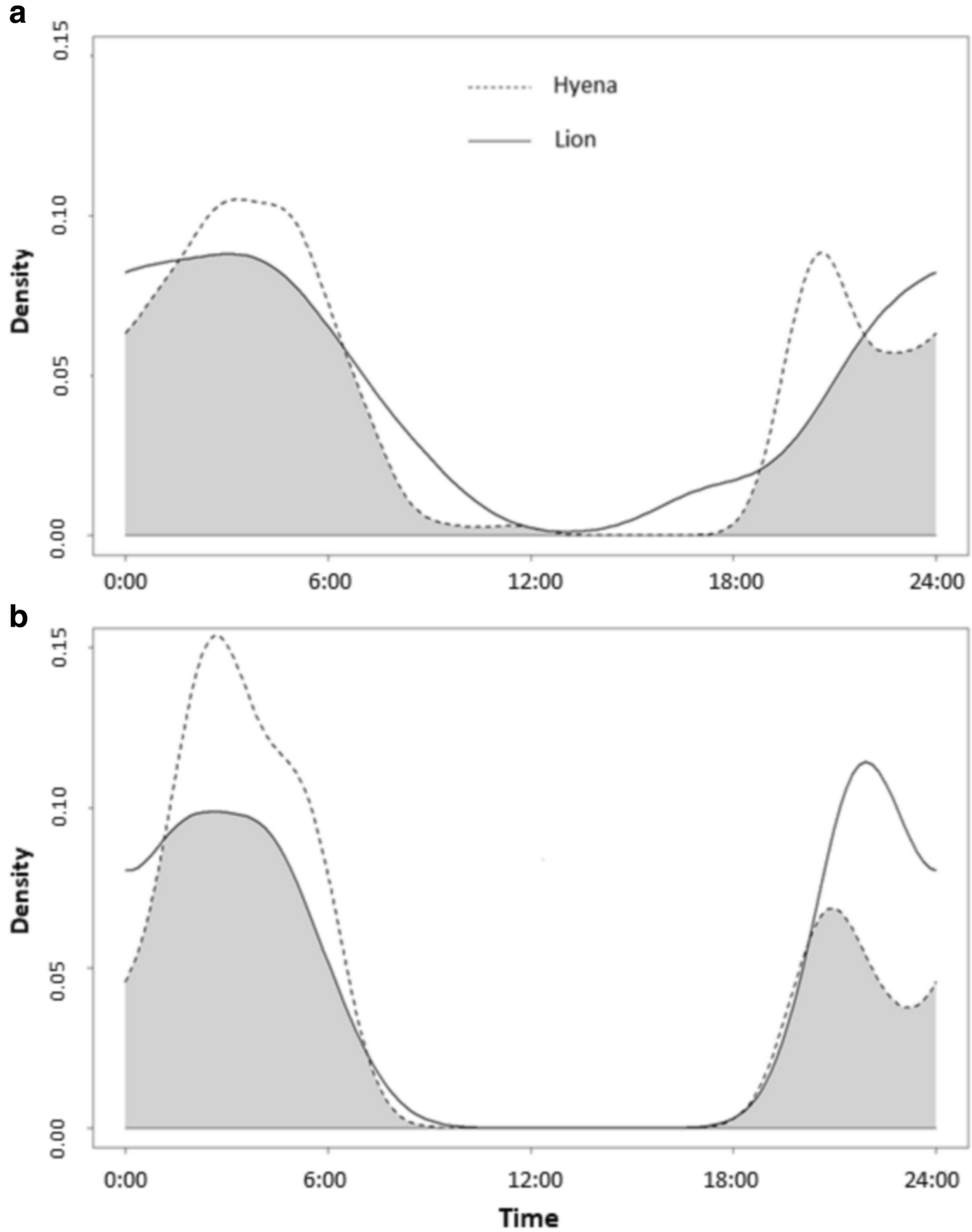

Fig. 3 Density estimates of daily activity patterns of lion and hyena in **a** Pendjari National Park and **b** hunting zones. The overlap is represented by the shaded area

predators in these zones. Obviously, anthropogenic activities and their consequences exert a strong effect not only on predator numbers but also on their distribution, behavior, and interspecific relationships. This is in line with other studies showing a complex negative impact of humans on carnivore populations (Boydston et al. 2003; Lindsey et al. 2017; Schuette et al. 2013). However, Pendjari is in a unique position to be part of the large protected WAPOK ecosystem which is arguably the best West African area to guarantee the survival of large predators due to its large transboundary coverage and relative ecological integrity in most areas (Riggio et al. 2013). To take advantage of this opportunity, much more effort should be undertaken to promote efficient control of hunting and other human activities in the hunting zones of Pendjari. More research is required to understand how predators co-exist and predator-prey systems function under anthropogenic activities. Studies of predator diets and feeding ecology are important to understand spatio-temporal partitioning and to assess the chances of cheetah and wild dog to survive in the area.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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