Temporal partitioning of carcasses by mammalian scavengers in Etosha National Park, Namibia

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ABSTRACT

The mechanisms behind the partitioning of sympatric species' ecological niches are highly debated, and few studies have explored how a community temporally partitions a single resource. My study investigated how a mammalian scavenger community in Etosha National Park (ENP) temporally partitioned carcasses that died from natural causes, hypothesizing that the presence of a dominant scavenger (lions (*Panthera leo*)) will affect the probability of observing subordinate scavenger species (spotted hyenas (*Crocuta crocuta*) and black-backed jackals (*Canis mesomelas*)). Remote camera trap data was collected at 32 carcass sites in ENP from February to June 2010, and histograms of the general activity patterns for each species over 24-hour time periods were created. The parameters of day versus night, lion presence within six hours and the state of carcass degradation were included in a logistic regression model used to predict the probability of observing a species on a smaller, interaction-based time scale. When qualitatively comparing the general activity patterns of each species, all species had similar nocturnal activity patterns. However, when analyzing specific interactions on a smaller time scale, lion presence negatively affected the probability of observing hyenas and positively affected the probability of observing jackals. The results confirm that lion presence does affect the probability of observing hyenas and jackals at a carcass site. Temporal partitioning of a resource like carcasses that occur heterogeneously in space and time should be considered in terms of individual-level interactions rather than comparing generalized activity patterns of sympatric species.

KEYWORDS

competition avoidance, black-backed jackal, lion, niche partitioning, spotted hyena

INTRODUCTION

The ecological niche, defined as the resources a species utilizes, encompasses three main dimensions – habitat, food type and time (Schoener, 1974a). These dimensions are often divided by sympatric species in a concept known as niche partitioning (Schoener, 1974a). Habitat preference has the strongest influence on niche partitioning, followed by food type and finally time (Schoener, 1974a). Schoener (1974a, 1974b) hypothesized that temporal partitioning occurs infrequently in nature because the benefits of using the resource outweigh the costs of not using the resource at a particular point in time. However, temporal partitioning is usually observed in communities where intraguild predation is common (Hayword & Slotow, 2009). Among African carnivores temporal partitioning is primarily caused by intraspecific competition avoidance of the subordinate species (Hayword & Slotow, 2009). The mechanism behind temporal partitioning is often ascribed to competition, specifically avoidance of interference competition (Carothers & Jaksic, 1984). Studies examining temporal niche partitioning among African carnivores (Hayword & Slotow, 2009) and between two vulture species in Spain (Jaksic, 1982) have attributed interference competition as the primary cause of resource partitioning. Yet the exact mechanisms behind temporal partitioning and how it relates to the other two dimensions of niche partitioning are highly debated.

Studies on temporal niche partitioning have generally focused on diet and habitat overlap in sympatric species of mammals (Ridout & Linkie, 2009). Among wild felids in the neotropics, species that have a similar morphology have a higher dietary overlap and greater inter-species variation in activity patterns than other, less morphologically similar species (Di Bitetti, De Angelo, Di Blanco, & Paviolo, 2010). In central Mexico, pumas (*Puma concolor*) were found to alter their activity patterns based on that of the jaguar (*Panthera onca*; Monroy-Vilchis, Rodriquez-Soto, Zarco-Gonzalez & Urios, 2009). However, among canids in South America there was little difference among species' activity patterns, although there was high overlap in their diet and habitat use (de Almeida Jacomo; Silveira, & Diniz-Filho, 2004). Studies often focus on species of similar morphology and the amount of overlap in their diet and habitat; few studies have observed how mammalian communities temporally partition one particular food source.

Mammalian scavenger species are an excellent community to use in temporal partitioning research due to a common food source (Wilmers, Stahler, Crabtree, Smith & Getz, 2003). Mammalian scavengers are a diverse and paraphyletic species assemblage and those that are morphologically dissimilar often do not have extensive dietary overlap besides carrion (DeVault, Rhodes & Shivik, 2003). Temporal partitioning has been observed among avian scavengers (Jaksic 1984). In Spain, the Golden Eagle (*Aquila chrysaetos*) and the Common Raven (*Corvus corax*), temporally partition carcasses depending on the time of year but otherwise have limited dietary overlap (Blazquez, Sánchez-Zapata, Botella, Carrete & Eguía, 2009). Little is known how time affects the niche partitioning of a naturally occurring, finite resource such as carcasses among a mammalian scavenger community.

My study aimed to assess the theory of resource partitioning based on time within the framework of a mammalian scavenging community in Etosha National Park (ENP), Namibia. I hypothesized that temporal partitioning does occur among scavengers. Specifically, I expected to find that the dominant scavenger species in this system (e.g. lion (*Panthera leo*)) would not alter its activity patterns at a carcass site due to the presence of subordinate species. However, I expected that the presence of a dominant scavenger would lower the probability of viewing smaller, subordinate scavengers, such as black-backed jackals (*Canis mesomelas*) and spotted hyenas (*Crocuta crocuta*).

METHODS

Study System

The study was conducted in ENP (18° 56’ 43” S, 15° 53’ 52” E), a wildlife reserve which covers 22,270 km^2 and is located in northwestern Namibia, Africa. ENP experiences two main seasons - the wet season, January-April, and the dry season, May-early December (Lindque & Turnbull, 1994). Anthrax occurs seasonally in ENP with incidence among plains ungulates such as Burchell’s Zebra (*Equus quagga*) peaking at the end of the wet season (Lindque & Turnbull, 1994).

Data Collection

To monitor an ungulate carcass for an extended period of time, motion-sensor camera traps (Reconyx RC55) were set up near zebra carcasses by S. Bellan and colleagues in ENP. The cameras were programmed so that once triggered, a series of 10 photographs at 1 second intervals (photographic burst) were taken. Camera sites were selected based on the state of the carcass and the proximity of the carcass to the road. Additional site selection factors included logistical limitations such as camera availability and time of day. Only zebra carcasses were considered in this analysis as they are by far the most frequent anthrax carcasses observed in ENP. Cameras were deployed at a total of 32 sites from February to June 2010.

The photographs were organized into 15 minute intervals starting at the time the camera was first triggered. All species were recorded as present or absent within that 15 minute interval. For every interval I identified the carcass visibility (Table 1) in the frame as well as the state of the carcass (Table 2). If the carcass visibility or state of the carcass was altered within the interval, I used the most current visibility and state for the following interval.

Table 1. Carcass Visibility Coding Scheme

Code	Carcass Visibility
0	Not in frame
1	Partially in frame
2	Fully/partially in frame but cannot observe state because obstructed by scavengers
3	Fully in frame

Table 2. State of Carcass Degradation Coding Scheme

Code	State of Carcass
0	Unknown
1	Untouched
2	Fresh – scavenging just started
3	Fresh – but mouth, guts and/or anus eaten at
4	Muscle and organs largely eaten at
5	Skin and bones only
6	Bones and little skin or flesh

7	Just bones
8	Nothing left

Data Analysis

I created histograms of activity patterns over a 24 hour period using the presence of jackals, hyenas and lions recorded during the fifteen minute intervals for all 32 carcass sites. To determine the carcass states that were frequented most often by scavengers, I created a graph of the percentage of individual observations each species was observed at for each carcass state. I used multiple logistic regression to examine how the state of the carcass, day versus night and presence of lions at a carcass site affected the probability of observing a specific scavenger species. Carcass state was considered an unordered categorical variable. The presence of lions at a carcass within six hours of observation was also included as an explanatory variable in models of jackal or hyena occurrence. Lions are the dominant predator and have been known to kill hyenas (Trinkel & Kastberger, 2002). I considered lion presence to include 6 hours after the time a lion was sited, as lions remained at the carcass for extended periods of time, even if not always in view of the camera trap. A binary variable indicating daytime (between 7:00 and 19:00) or nighttime (between 19:00 and 7:00) was incorporated as an explanatory variable for all species models, as all three species are considered primarily nocturnal. I assessed the support of each parameter in predicting the probability of observing each species using Akaike's Information Criterion (AIC; Burnham & Anderson 2004). The MASS package in the statistical program R was used for all data analyses (Venables & Ripley, 2002).

RESULTS

Scavenger Composition and Activity Patterns

Three mammalian scavenger species appeared consistently throughout all 32 study sites – black-backed jackals, spotted hyenas, and lions. Jackals were the most commonly seen species (seen at 32/32 sites), followed by hyenas (seen at 29/32 sites), while lions appeared infrequently (seen at 17/32 sites). All three species were most active at night, although jackal activity was observed throughout the day (Figure 1). I observed a spike in activity for all three species from 0:00 to 1:00.

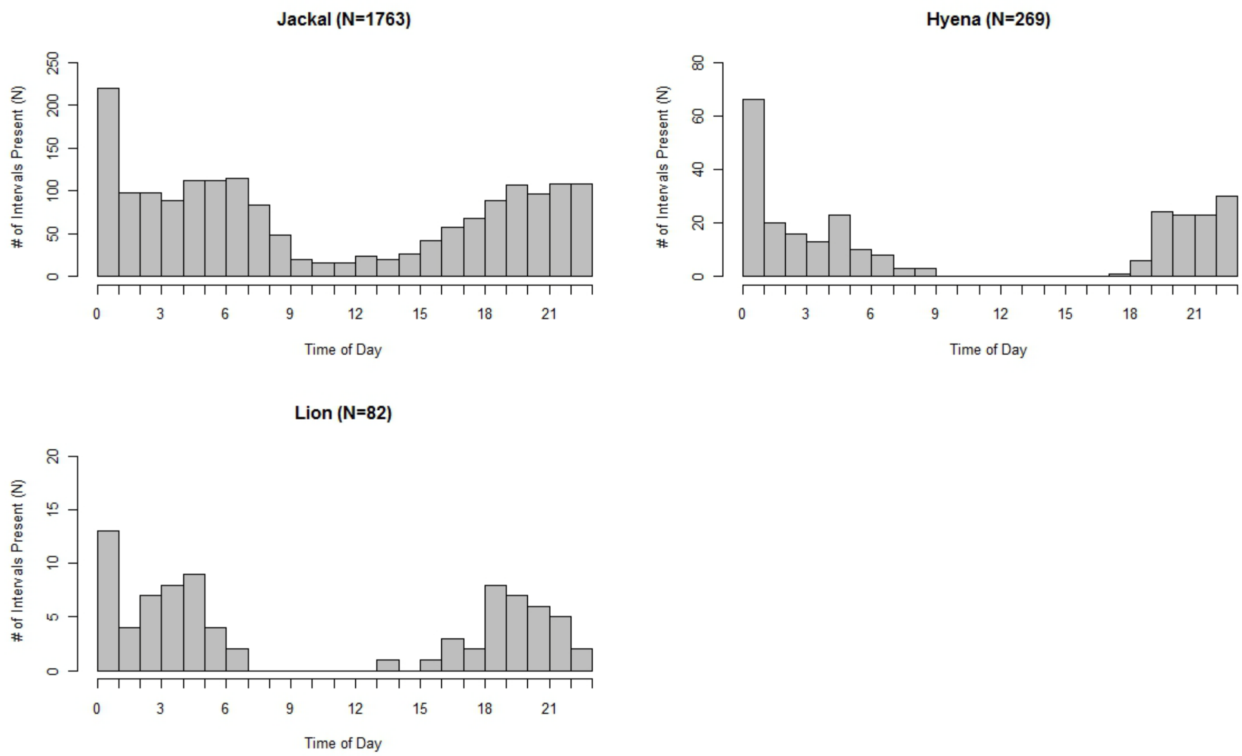

Figure 1. Activity patterns for three common mammalian scavengers: black-backed jackal, spotted hyena, and lion. Activity patterns were based on the presence of a species recorded in 15 minute intervals. The total number of intervals each species was observed in is indicated in parentheses.

Scavenger occurrence at carcass sites

Jackals, lions and hyenas were observed most often at carcass states 3, 4 and 5, with jackals being present at all eight stages of carcass degradation (Figure 2). The peak in the probability of observing a jackal at a carcass state occurred at carcass state 4. The top AIC logistic regression model included the effects of all parameters - carcass state, daytime, and lion presence for jackals and hyenas and carcass state and daytime for lions (Table 3). The presence of lions within the past six hours was significant in predicting the probability of jackals and hyenas at a site (Table 4). However, the presence of lions caused an increase in the probability of observing jackals, while lion presence caused a decrease in the probability of observing hyenas. Daytime was a significant factor for all three species, with a decrease in the probability of observing any of the three species.

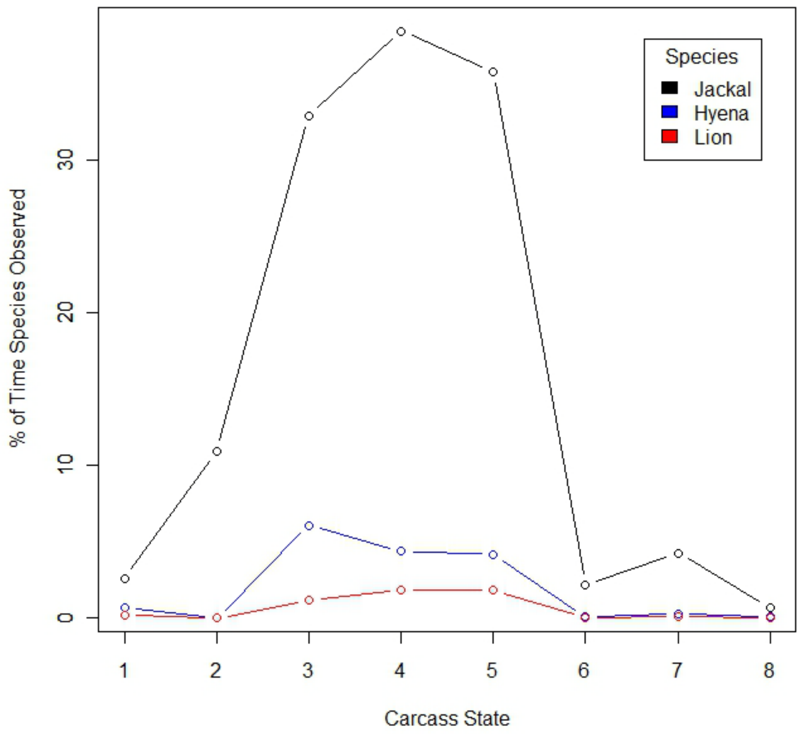

Figure 2. Percentage of time each species was observed at each carcass state. Percentages are based on the presence of observed species occurring in 15 minute interval periods. For a list of the coding scheme of each carcass state refer to Table 2.

Table 3. Carcass state, daytime, and lion presence affecting the probability of observing a specific species at a carcass site.

Species	Model	No. Parameters	AIC	ΔAIC	*w*
Jackal	Carcass state, day, lion presence	9	8017.6	0.0	0.766
	Carcass state, day	8	8020.0	2.4	0.234
	Carcass state, lion presence	8	8139.1	121.4	0.000
	Day, lion presence	2	11017.3	2999.6	0.000
Hyena	Carcass state, day, lion presence	9	1310.3	0.0	0.877
	Carcass state, day	8	1410.2	3.9	0.123
	Carcass state, lion presence	8	1314.3	99.9	0.000
	Day, lion presence	2	1651.9	342.6	0.000
Lion	Carcass state, day	8	507.1	0.0	0.816
	Carcass state	7	510.1	3.0	0.183
	Day	1	667.2	160.0	0.000

Table 4. Results of the multiple logistic regression model determining the probability of observing a given species.

	Odds Ratio (95% CI)		
	Jackal	Hyena	Lion
Parameter			
Lion observed within 6 hours	1.43 (1.02 - 2.00)*	0.25 (0.04 - 0.79)*	NA
Daytime	0.49 (0.43 - 0.55)*	0.10 (0.05 - 0.17)*	0.49 (0.25 - 0.92)*

* Odds Ratio significant

DISCUSSION

Sympatric species activity patterns

Black-backed jackals, lions, and hyenas had similar nocturnal activity patterns consistent with other findings in the literature (Figure 1; Haas, Hayssen & Krausman, 2005; Kaunda & Skinner 2003). It is not likely that hyenas and jackals are altering their activity patterns based on general lion activity patterns that occur on a daily basis, in contrast to sympatric species that have similar morphology (Di Bitetti, De Angelo, Di Blanco, & Paviolo, 2010; Romero-Munoz, Maffei, Cuellar & Noss, 2010). Lack of differing activity patterns on a generalized time scale could be due to variation in diet if there is little dietary overlap besides scavenging activities at carcasses. However, other studies have observed that lions and hyenas do experience a high amount of dietary overlap in addition to opportunistic scavenging of carcasses that they did not kill. For example, kleptoparasitism has been observed, with both species stealing each other's kills. In ENP, lions are the dominant predator and often steal hyena kills (Hayword, 2006; Trinkel & Kastberger, 2005). In my analysis, lion presence within six hours at a carcass decreased the probability of observing a hyena at the carcass site, but as previously mentioned hyenas did not appear to be avoiding lions based on a qualitative comparison of the two species' general temporal activity patterns (Figure 1). Thus lion presence at a carcass may act as a deterrent for hyena presence on a relatively small time scale.

Lion presence at a carcass was associated with higher probabilities of jackal presence based on specific interactions on a smaller time scale (lion presence within six hours) rather than generalized activity patterns. Instead of resource partitioning occurring, jackals may actually use lion presence as a way of finding food. Jackals that live in areas where other, larger predators, including lions, predominate tend to be mostly scavengers rather than active predators (Kaunda & Skinner, 2003). Kaunda and Skinner (2003) described jackals in Botswana as opportunistic predators that subsist mainly on animal matter, but they were not able to differentiate whether the animal matter was obtained through predation or scavenging. Jackals occur in higher numbers than lions and hyenas in ENP and were observed feeding at carcasses in later states more frequently than the other two species (Figure 2). This provides some evidence that jackals may be more dependent on these types of carcasses (i.e. carcasses not killed by predation) as a source of animal matter than lions or hyenas in ENP.

The temporal partitioning of carcasses between hyenas and lions and the lack of such partitioning between jackals and lions provides insight into the nature of competitive interactions between these species in ENP. The temporal partitioning observed between lions and hyenas in regards to carcasses can be explained by competition avoidance, namely avoidance of intra-guild predation on behalf of hyenas. However among several study sites in Africa, including ENP, Hayword and Slotow (2009) found that lions and hyenas do not alter their behavior to avoid competition, but other less dominate predators, such as cheetahs and wild dogs, do avoid interference competition through temporal partitioning.

Temporal Partitioning

Temporal partitioning does occur among hyenas and lions based on competition avoidance; however, this partitioning should not be framed in terms of a comparison of general activity patterns of sympatric species, but rather in terms of avoidance that occurs based on specific interactions in a specific place and time. Hyena activity patterns at the observed carcasses are not affected by lion activity patterns on a long-term time scale, but may be affected on a more immediate time scale (i.e. lion presence within six hours). The carcasses observed had died of natural causes or disease, causing the lions and hyenas to come across the carcasses opportunistically. Because carcasses are a finite resource that occur heterogeneously in time and space, general activity patterns are not an effective method of determining temporal partitioning among scavengers. Analyzing how the presence of a dominant species affects the presence of a subordinate species is more effectual with a resource as heterogeneously distributed in space and time as carcasses. This analysis will allow for a more accurate depiction of the ecological interactions that occur between sympatric species.

Limitations

ENP is a fenced preserve and has a lower density of hyenas than other parks elsewhere in Africa. This may affect hyena-lion interactions, allowing for increased dominance of lions compared to other ecosystems (Trinkel, 2009). So although the methodology and analysis may be applicable to other systems, the populations and clan/pride size of both lions and hyenas in those systems may affect their competitive interactions, resulting in a different dynamic than that found in ENP. Another limitation when using the original data set is the large number of jackal photos compared to lion and hyena photos. Jackals have a larger population and are much more common than lions and hyenas in ENP, causing them to be observed more frequently (S. Bellan, pers. comm.). This is an important consideration when qualitatively comparing the general activity patterns of the three species.

Future Research

Further research should include additional camera traps and all vertebrate scavengers, including avian scavengers. This will provide a better overall description of how the food web works not only in ENP, but also other ecosystems throughout Africa with a similar food web. Additional work should also focus on animal behavior and interactions at a carcass, to observe if there is explicit competition at a carcass or if a hierarchical structure exists for all species present at a carcass. Including avian scavengers may affect diurnal competitive interactions, as white-backed vultures (*Gyps africanus*) and lappet-face vultures (*Torgos tracheliotus*) were observed frequently in the earlier carcass states. These scavengers may impact the current hierarchical structure at carcasses presented in this study.

Conclusion

In conclusion, my data suggests that there is a high degree of overlap among the three species in terms of nocturnal visitation and that resource partitioning does occur among lions and hyenas. This partitioning may be associated with hyenas avoiding direct competition with lions due to dietary overlap. However when examining the partitioning of carcasses that have died from natural causes, temporal partitioning should be investigated in terms of competition avoidance at specific carcasses, rather than general differences in activity patterns as these carcasses are a heterogeneously distributed resource in space and time. Jackals do not appear to temporally partition carcasses with lions, but instead may follow lions to food resources. Additional research on key predators, such as lions, hyenas and jackals, would improve our understanding of their ecological interactions both intra- and inter-specifically.

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