SHORT COMMUNICATION

Nocturnal light-specific temporal partitioning facilitates coexistence for a small mesopredator, the eastern spotted skunk

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Abstract

Eastern spotted skunks are of conservation concern, where competition and predation are possible causes of their decline. Using camera traps at a food subsidy, we investigated nocturnal temporal overlap of spotted skunks with co-occurring predators. Spotted skunks were more active during dark nights, when their activity overlapped with the largest predator (coyotes), but not with other mesopredators, thus possibly avoiding interspecific competition. Spotted skunk activity shifted during moonlit nights, where overlap with all predators was reduced, suggesting avoidance of both predators and competitors. This implies that both predation and interspecific competition could limit spotted skunk populations, and one mechanism they apply to coexist is nocturnal light-specific temporal partitioning.

Introduction

Scavenging is a common foraging strategy during winter in temperate systems, where many facultatively scavenging species alter their diet to include more carrion when other food is difficult to find (Dell'Arte et al. 2007; Robbins et al. 2007; Van Dijk et al. 2008; Swingen et al. 2015). However, interspecific interactions at carcasses can lead to increased competition that may not occur other times of the year when food is more readily available and carrion is not as heavily utilized. Anthropogenically provided and reliable food sources can increase competition between carnivores and also increase interactions, such as predation (Newsome et al. 2015). So, by providing a valuable food subsidy when naturally occurring food sources are scarce (i.e., winter), we can test behavioral mechanisms of species coexistence that may influence predation events and interspecific competition.

The eastern spotted skunk (*Spilogale putorius*; hereafter spotted skunk) is a small (~ 400 g; Kinlaw 1995) mesopredator currently listed as Vulnerable on the IUCN Red List (Gompper and Jachowski 2016). Spotted skunks were once widely distributed throughout the eastern and southern United States (Gompper and Hackett 2005) but, in the 1940s, the spotted skunk population decreased rapidly and significantly, has since never recovered, and continues to decline (Gompper and Hackett 2005; Gompper and Jachowski 2016). The reason behind the population decline and limited subsequent recovery is unknown (Gompper and Hackett 2005). Furthermore, little is known about the activity patterns of spotted skunks (Eastern Spotted Skunk Cooperative Study Group 2020). Predation {for example, by bobcats [*Lynx rufus*], coyotes [*Canis latrans*], and great horned owls [*Bubo virginianus*]}, and interspecific competition {e.g., with striped skunks [*Mephitis mephitis*]} could be limiting factors on spotted skunk populations (Kinlaw 1995; Lesmeister et al. 2010; Legrand and Howard 2013). Therefore, any insight into spotted skunk behavior and their ability to coexist with other predators could assist in their conservation.

Moonlight suppresses the activity of mesocarnivores and insectivores (Prugh and Golden 2014). Similarly, spotted skunks are more active during darker nights (Thorne et al. 2017; Benson et al. 2019), which is suggested to be

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a predator avoidance strategy. However, small carnivores must also avoid interspecific competition. Small carnivores undergo strong competitive pressure (interference and exploitation; de Satgé et al. 2017), and so must balance avoiding predation and competition with gaining sufficient resources. This is especially relevant during winter when food is scarce and competition is increased.

To explore the coexistence strategy of spotted skunks we used winter carcass provisioning to evaluate potential mechanisms of coexistence. Based on prior research, we first hypothesized that spotted skunks would be less active on moonlit nights when they are more visible to nocturnal predators (Thorne et al. 2017; Benson et al. 2019). Next, we evaluated support for two competing hypotheses about the influence of predator avoidance or interspecific competition on spotted skunk activity patterns regardless of nocturnal light. We first hypothesized that spotted skunks might adopt a predator avoidance (PA) strategy regardless of moonlight, where we expected that they would avoid temporal overlap with their primary predators (barred owls, bobcats, and coyotes) and overlap temporally with other mesopredators. In contrast, if spotted skunks were adopting an interspecific competition avoidance (ICA) strategy, then we expected that they would overlap temporally with their primary predators and avoid temporal overlap with other mesopredators (i.e., the enemy of my enemy is my friend; Sheehy et al. 2018).

Materials and methods

In 2008, a winter camera trap study was initiated across eastern United States to monitor overwintering eagles at carcasses of white-tailed deer (*Odocoileus virginianus*) (Jachowski et al. 2015). Between 2008 and 2013, many more sites were added, making a vast and long-term monitoring network. As a result of the bait at these sites, considerable 'by-catch' data of terrestrial mammalian carnivores were collected (e.g., Marneweck et al. 2021). We used data from this camera trap study to investigate the temporal activity patterns of spotted skunks (specifically, the subspecies Appalachian spotted skunk, *S. p. putorius*) during winter seasons (i.e., December–February). Each site was equipped with a non-invasive, motion-sensitive camera trap (multiple brands were used) that was set to record an image with a delay of ≤ 1 min before taking a successive image. Each site was baited with at least one carcass in one location that was secured to the ground and replaced as needed to ensure constant access to carrion at each site. Site managers visited sites at least weekly to check cameras and replace carcasses that were largely consumed, following the same protocol (for more details on this study, see Jachowski et al. 2015). The sites were located in areas of low human population density and were heavily forested, except for the small clearings in

which cameras were placed (for more details see Marneweck et al. 2021).

We focused our analysis on two sites in West Virginia where we recorded spotted skunks. These sites were ~ 30 km apart in (1) Grant County (latitude 38.90), and (2) Pendleton County (latitude 38.75). We identified and added the species name to the default image metadata (i.e., date and time) using the desktop program digiKam v.6.2.0 (KDE applications, Berlin, Germany) or the web-based program Wildlife Insights (Ahumada et al. 2020). For images processed in digiKam, we used the R package *camtrapR* (Niedballa et al. 2016) to extract metadata from all photographs taken ≥ 10 min apart, a time interval chosen to ensure that observations were independent. We chose this time interval based on previous spotted skunk studies, which show revisitation rates after 10 min are low (S Harris pers. comm.). For images processed through Wildlife Insights, we created a function in R to ensure that the metadata from images of the same species were similarly separated by 10 min. We identified each species as a potential predator or mesopredator (i.e., competitor) for spotted skunks based on their body size, diet, and ecology, where we considered coyotes, bobcats, and barred owls (*Strix varia*) as primary predators (Korschgen 1957; Kinlaw 1995; Schwartz and Schwartz 2001; Lesmeister et al. 2010; Hassler et al. 2021), and gray foxes (*Urocyon cinereoargenteus*), Virginia opossums (*Didelphis virginiana*; hereafter opossums), northern raccoons (*Procyon lotor*; hereafter raccoons), and striped skunks as potential competitors. While we acknowledge that great horned owls are a primary predator of spotted skunks (Kinlaw 1995; Lesmeister et al. 2010), we did not obtain a sufficient number of detections to include them ($n = 13$).

We used the R package *suncalc* (Thieurmel and Elmarhraoui 2019) to assign the sunrise and sunset time according to the date and location at the camera trap site. We then converted the sunrise and sunset time to radians and filtered our data to include only images that were taken after sunset and before sunrise (i.e., creating a dataset of nocturnal images that we could relate to moonlight) and for which there were > 15 images for each species. Next, we used the *suncalc* package to assign the proportion of moon illumination as per the image date. From here, we subset the moon illumination into high (i.e., proportion potential illumination ≥ 0.75; hereafter moonlit nights) and low (i.e., proportion of potential illumination ≤ 0.25; hereafter dark nights) to contrast activity between these two periods.

We calculated the proportion of detections of spotted skunks during moonlit and dark nights as a proportion of the total number of detections for this species (i.e., number of spotted skunk detections during moonlit nights/total number of nocturnal spotted skunk detections). We then compared these proportions using the *prop.test* function in R to investigate during which nights (moonlit or dark) spotted skunks

were more active. To investigate if spotted skunk temporal activity changed between moonlit and dark nights, we conducted a Watson's two-sample test (a test for homogeneity of two samples of circular data). We repeated this for each species to investigate activity change with nocturnal light. Next, to investigate if spotted skunk temporal activity overlapped with other predators, we calculated the coefficient of overlap using the *overlap* package (Ridout and Linkie 2009) for all pairs of co-occurring predators to assess the degree of overlap during moonlit and dark nights, followed by a Watson's two-sample test. When estimating the overlap coefficient {Δ; ranging from 0 [no overlap] to 1 [complete overlap]}, we performed a smoothed bootstrap generating 1000 bootstrap samples and obtained 95% confidence intervals. We performed all analyses in R version 4.0.1 (R Core Team 2021).

Results

In total, the two sites yielded 28,601 images over 262 trap days during winters of January 2013–February 2017. After filtering to focus on nighttime images and on species that met our sample size inclusion criteria, we were left with 8,767 images containing three primary predators (barred owls, bobcats, and coyotes) and five mesopredators (gray foxes, opossums, raccoons, spotted skunks, and striped skunks). Of these 8767 images, 2936 images occurred over 88 dark nights, and 2848 occurred over 89 moonlit nights.

We collected 365 independent detections of spotted skunks at our two sites in West Virginia, of which 195 occurred during dark nights and 60 during moonlit nights. Spotted skunk activity differed between dark and moonlit nights ($W = 0.61$, $p < 0.01$; Table 1, Fig. 1), where we detected them more than twice as frequently during dark nights ($\chi_1 = 108.22$, $p < 0.01$). During moonlit nights, there was a large peak in activity (18:00–23:00; Fig. 1), whereas during dark nights, spotted skunks were active more consistently throughout the night (Fig. 1). Of the primary predators, bobcats were the only species that showed differing activity patterns for moonlit and dark nights, where, during moonlit nights, bobcats were most active 03:00–07:00 (Table 1; Fig. 1a, b).

We found differences in spotted skunk overlap with co-occurring predators in response to nocturnal light (Table 1; Fig. 1). During dark nights, the activity overlap of spotted skunks with other predators was high ($\Delta = 0.74$–0.89), in particular with coyotes and raccoons (Table 1, Fig. 1f, j). During moonlit nights, spotted skunk activity changed and overlap with all co-occurring predators was reduced ($\Delta = 0.54$–0.67) and became particularly low for barred owls; Table 1, Fig. 1c).

Discussion

Consistent with other studies suggesting that nocturnal light increases the vulnerability and thus predation risk of small mammals to nocturnal predators (Orrock et al. 2004; Prugh

Table 1 Species pairwise comparisons of activity overlap during moonlit (white) and dark (gray) nights in the eastern USA

Species	Bobcat	Barred owl	Coyote	Gray fox	Opossum	Raccoon	Spotted skunk	Striped skunk
Bobcat	W0.32 **	Δ0.72 (0.58-0.85) W0.36 **	Δ0.75 (0.63-0.86) W0.17	Δ0.77 (0.70-0.83) W0.77 ***	Δ0.77 (0.66-0.87) W0.17	Δ0.75 (0.67-0.83) W0.54 ***	Δ0.82 (0.75-0.89) W0.28 **	Δ0.86 (0.78-0.92) W0.11
Barred owl	Δ0.65 (0.54-0.77) W0.64 ***	W0.06	Δ0.77 (0.61-0.89) W0.17	Δ0.76 (0.65-0.86) W0.30 **	Δ0.69 (0.54-0.84) W0.34 **	Δ0.74 (0.61-0.84) W0.25 **	Δ0.78 (0.66-0.88) W0.21 *	Δ0.69 (0.56-0.82) W0.40 ***
Coyote	Δ0.82 (0.72-0.90) W0.09	Δ0.71 (0.57-0.85) W0.40 ***	W0.09	Δ0.87 (0.79-0.94) W0.07	Δ0.80 (0.67-0.91) W0.10	Δ0.83 (0.73-0.90) W0.08	Δ0.89 (0.80-0.96) W0.04	Δ0.83 (0.69-0.93) W0.09
Gray fox	Δ0.79 (0.70-0.87) W0.35 **	Δ0.78 (0.69-0.86) W0.30 **	Δ0.80 (0.70-0.89) W0.20 *	W0.10	Δ0.76 (0.65-0.85) W0.22**	Δ0.89 (0.83-0.94) W0.14	Δ0.88 (0.82-0.93) W0.25 *	Δ0.80 (0.73-0.87) W0.60 ***
Opossum	Δ0.66 (0.55-0.77) W0.53 ***	Δ0.84 (0.72-0.93) W0.17	Δ0.67 (0.53-0.80) W0.45 ***	Δ0.83 (0.77-0.91) W0.30 **	W0.30 **	Δ0.71 (0.60-0.81) W0.21 *	Δ0.74 (0.63-0.83) W0.22 *	Δ0.79 (0.68-0.88) W0.11
Raccoon	Δ0.84 (0.75-0.92 W0.25 **	Δ0.76 (0.65-0.86) W0.31 **	Δ0.90 (0.81-0.97) W0.08	Δ0.85 (0.79-0.90) W0.19 *	Δ0.72 (0.63-0.82) W0.47 ***	W0.22 *	Δ0.89 (0.81-0.96) W0.13	Δ0.77 (0.68-0.85) W0.47 ***
Spotted skunk	Δ0.64 (0.51-0.77) W0.48 ***	Δ0.54 (0.40-0.67) W0.62 ***	Δ0.57 (0.43-0.71) W0.52 ***	Δ0.67 (0.56-0.78) W0.57 ***	Δ0.66 (0.54-0.78) W0.32 **	Δ0.59 (0.46-0.72) W0.60 ***	W0.61 ***	Δ0.83 (0.74-0.91) W0.24 *
Striped skunk	Δ0.78 (0.70-0.87) W0.30 **	Δ0.64 (0.55-0.74) W0.55 ***	Δ0.79 (0.70-0.89) W0.11	Δ0.78 (0.71-0.85) W0.51 ***	Δ0.66 (0.58-0.75) W0.78 ***	Δ0.79 (0.70-0.87) W0.24 *	Δ0.63 (0.50-0.74) W0.70 ***	W0.11

Icons obtained from BioRender.com

Δ = overlap coefficient (where 1 = total overlap and 0 = no overlap) with 95% confidence interval in parentheses. *W* Watson's two-sample test statistic, where ***$p < 0.001$, **$p < 0.01$, and *$p < 0.05$. *W* test statistic for one species' activity between moonlit and dark nights is under its icon

Icons obtained from https://www.BioRender.com

Fig. 1 Eastern spotted skunk activity overlap with co-occurring predators over moonlit and dark nights as measured by camera traps baited with white-tailed deer over winter seasons. The shaded area represents the overlap in activity. Δ = overlap coefficient
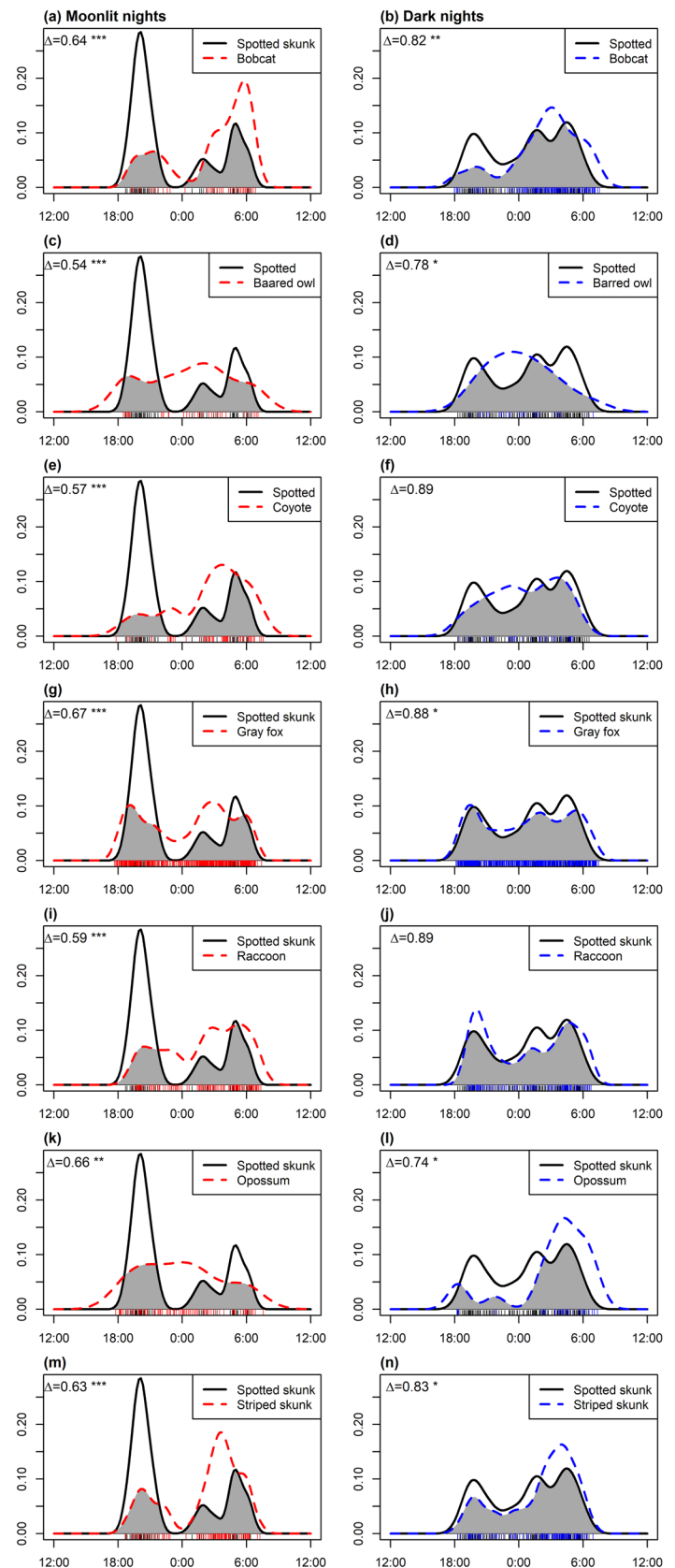
and Golden 2014), and previous findings on spotted skunks (Thorne et al. 2017; Benson et al. 2019), we found that spotted skunks were more active on dark nights. On these dark winter nights, spotted skunk activity did not show any defined peaks and there was high activity overlap with co-occurring predators. On moonlit winter nights, overlap with all co-occurring predators was reduced and there was a peak in activity at the beginning of the night (20:00–23:00). This peak in activity on moonlit nights occurred during a period when most other predators were less active (e.g., barred owls and bobcats), supporting the hypothesis that predation risk is higher during moonlit nights (Orrock et al. 2004; Prugh and Golden 2014).

Rather than adhering to a solely predator avoidance (PA) strategy or a solely interspecific competition avoidance (ICA) strategy, spotted skunks aligned partially with both PA and ICA hypotheses, where they avoided overlap with all other predators which was most apparent on moonlit nights. Mephitids are under strong predation pressure given their small size and that they are less likely to out-run predators due to their plantigrade foot posture (Hunter and Caro 2008). Considering that bobcats and owls have been cited as the primary predators of spotted skunks (Kinlaw 1995; Lesmeister et al. 2010; Hassler et al. 2021), and nocturnal light can increase predation success (Pratas-Santiago et al. 2016), it is likely spotted skunks reduce activity during moonlit nights when bobcats prefer to hunt and owl hunting success increases (Clarke 1983; Rockhill et al. 2013).

Our findings highlight that nocturnal light may increase vulnerability to competition as well as predation, because spotted skunks also avoided competitors on moonlit nights. While literature on the sympatric competitors of spotted skunks is limited (Kinlaw 1995), being the lowest ranking carnivore in our system, spotted skunks are likely avoiding competition from multiple sympatric carnivores during moonlit nights when they are more easily detected. As the largest predator in the system, coyotes can suppress second ranking mesocarnivores (Egan et al. 2021). Thus, by increasing overlap with coyotes on dark nights when spotted skunks are more active, competition may be decreased and carrion acquisition facilitated for this small carnivore (Allen et al. 2015).

Our findings represent a significant contribution to spotted skunk literature as they extend beyond previous findings on the negative influence of moon illumination on spotted skunk activity (Thorne et al. 2017; Benson et al. 2019). We illustrate that, during moonlit nights, vulnerability to both predation and competition are higher but, during dark nights, overlap in timing of foraging with the largest predator could be a useful competition avoidance strategy. This suggests that nocturnal light-specific temporal partitioning may facilitate coexistence between smaller and larger predators and allow the smaller to avoid both predation and competition. We encourage research into other factors that could influence this light-dependent relationship in the behavior of spotted skunks and other nocturnal small carnivores. Specifically, in this study we classified light and dark nights coarsely and, as such, there is likely a limited influence of cloud cover on our classification of moonlit nights (≥ 0.75 proportion moon illumination) versus dark nights (≤ 0.25 proportion moon illumination). Given interactions of moonlight and cloud cover can have implications on nocturnal animal activity (Linley et al. 2020), we encourage future studies to assess how fine-scale differences in cloud cover could influence the nocturnal light available and subsequent overlap. The amount of food available may also impact species co-occurrence when scavenging and competitive interactions (Newsome et al. 2015). Accordingly, it would be valuable to compare different amounts of food subsidies to investigate if the findings differ from our study, where the food source was plentiful.

Ultimately, we show data that illustrates the complexity of interactions spotted skunks experience and need to balance in order to persist. With increasing concern over the declining populations of spotted skunks (Gompper and Hackett 2005; Gompper 2017), this study provides important insight into potential mechanisms of coexistence for the species. Temporal avoidance is prevalent for small carnivores subject to high predation pressure (Hunter and Caro 2008), and additional behavioral and demographic studies on this species are needed to understand how predation and interspecific competition could be imposing limitations on spotted skunks. More broadly, our use of experimental food subsidies and remotely activated cameras has provided a starting point for subsequent investigations into factors structuring the dynamics that influence the structure of carnivore communities in our study area and could be replicated to begin understanding other systems with interacting predators and mesopredators.

Declarations

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