



Activity patterns and temporal predator avoidance of white-tailed deer (*Odocoileus virginianus*) during the fawning season

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Abstract

In the presence of a predator, prey may alter their temporal activity patterns to reduce the risk of an encounter that may induce injury or death. Prey perception of predation risk and antipredator responses may increase in the presence of dependent offspring. We conducted a camera trap study during summer 2015 in North Carolina and Tennessee, USA to evaluate temporal avoidance of a predator (coyote *Canis latrans*) by white-tailed deer (*Odocoileus virginianus*). We analyzed activity patterns of bucks, does, and nursery groups (i.e., groups that included fawns) relative to those of coyotes to determine the coefficient of overlap (Δ) using a kernel density estimator. We found that bucks and does had similar Δ with coyotes [$\Delta_1 = 0.729$ (0.629–0.890) and $\Delta_1 = 0.686$ (0.558–0.816, respectively)] and exhibited crepuscular activity patterns comparable to those of coyotes. However, nursery groups displayed a dramatically different activity pattern: unimodal activity was concentrated in the middle of the day with little overlap with coyote activity [$\Delta_1 = 0.362$ (0.176–0.491)]. Because adult deer are rarely prey for coyotes, whereas fawns are common prey during summer, the shift in activity patterns of nursery groups demonstrates a behavioral shift likely aimed at avoiding coyote predation on fawns.

Keywords Camera traps · *Canis latrans* · Landscape of fear · Reproductive condition · Risky time hypothesis · Prey–predator interaction

Introduction

Interactions between predators and prey are of great interest to ecologists, as predators can affect prey populations directly through mortality (Taylor 1984) and through modification of prey behavior (Lima 1998; Laundré et al. 2001; Grovenburg et al. 2012). Antipredator behaviors can include shifts in spatial patterns of behavior (Sih 1984; Lima and Dill 1990; Creel et al. 2008), habitat selection (Creel et al. 2005; Fortin et al. 2005), and activity patterns (Hudgens and Garcelon 2010; Tambling et al. 2015). Predation risk may influence prey fitness if the cumulative costs of antipredator behaviors result in a nutritional deficit or amplified

physiological stress (e.g., increased glucocorticoid levels) that causes decreased fecundity or maternal investment of the prey (Brown 1999; Laundré et al. 2001; Clinchy et al. 2013; Cherry et al. 2016a). The non-consumptive effects of predators can amount to a substantial portion of their total effects on prey, and therefore are essential to understanding the complexities of predation (Lima and Dill 1990; Creel and Christianson 2008).

The risky time hypothesis suggests that prey increase their antipredator behaviors by altering their temporal activity to reduce the risk of predation rather than changing their spatial activity patterns to reduce that risk (Creel et al. 2008). Individual prey may alter their antipredator responses based on their sex and reproductive condition (Laundré et al. 2001; Childress and Lung 2003; Liley and Creel 2008). For example, prey with herding behavior may respond differently to predation risk depending on factors such as group size and composition [e.g., age and sex of group members (Laundré et al. 2001; Lingle 2001; Stone et al. 2017)]. Additionally, predator absence or removal may result in a reduction of antipredator behaviors, such as decreased vigilance (Cherry et al. 2015).

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An animal's behavior and physiology influence their daily activity patterns, although responses to external stimuli, such as the presence of a predator, can also alter these patterns (Daan and Aschoff 1982; Kronfeld-Schor and Dayan 2003). Prey can reduce their risk of predation by altering their activity patterns to minimize the probability of an encounter with a predator (Sih 1984; Creel et al. 2008). The partitioning of daily activity patterns by prey to avoid predators may have evolved as a mechanism of coexistence (Daan 1981; Stiling 1999); however, novel predators present prey with an unusual situation (Tambling et al. 2015). The impact of a novel predator on prey populations may be mediated or amplified depending on the behavioral response of the prey to the predator's presence in the landscape (Hudgens and Garcelon 2010).

Coyotes are predators of white-tailed deer (*Odocoileus virginianus*), especially their fawns (Kilgo et al. 2012; Chitwood et al. 2015; Nelson et al. 2015; Shuman et al. 2017; Gallagher et al. 2019). Deer are considered highly susceptible to predation during their first months of life (Ballard et al. 1999; Lingle et al. 2005; Rohm et al. 2007; Grovenburg et al. 2011) and fawns are known to be important prey items for coyotes during the summer months (Schrecengost et al. 2008; Swingen et al. 2015; Cherry et al. 2016b). Coyote predation risk induces adult deer to increase their vigilance (Cherry et al. 2015; Gulsby et al. 2018), whereas fawns exhibit complex antipredator defenses that include morphological adaptation in the form of cryptic coloration and physiological responses such as alarm bradycardia (Jacobsen 1979). Yet, beyond hiding during the first months of life, little is known about fawn predator-avoidance behaviors. After the hiding phase when fawns are traveling with their dams, they may display diel activity patterns that maximize avoidance of predators. Only a few studies have examined fawn activity patterns in free-ranging populations (Jackson et al. 1972). These suggest that fawns are diurnal to crepuscular, which may be an antipredator behavioral response used to mitigate predation risk if their predators are primarily nocturnal.

We evaluated activity patterns of deer and coyotes in a grassland-dominated system in the eastern USA. Coyotes are considered a novel predator in this part of the USA (Parker 1995), with recent range expansion and releases during the last century (Hill et al. 1987; Gompper 2002; Ripple et al. 2013; Newsome et al. 2017). In other parts of their range, coyotes evolved in open grassland and semi-arid systems, whereas the majority of the eastern USA comprises temperate deciduous forest. Our study site may more closely represent habitat that coyotes evolved in within their historic range. Additionally, coyotes are considered a nuisance species in the study region and are persecuted year-round there, which influences their activity patterns (Kitchen et al. 2000). Our study site is isolated and one of the few sites where

coyote persecution is minimal. We used camera traps to test the hypothesis that the presence of coyotes would influence the activity patterns of nursery groups of deer (i.e., fawns with does) more than those of bucks or does unaccompanied by fawns. When compared to bucks and does without fawns, we predicted that nursery groups would display altered activity patterns to avoid coyotes.

Materials and methods

Study site

Our study took place in the eastern Roan Mountain Highlands in Mitchell County, North Carolina and Carter County, Tennessee, USA (36°6.34'N, 82°5.96'E). The Roan Mountain Highlands are within the Blue Ridge subphysiographic province of the southern Appalachian Mountains. At higher elevations there are large expanses of open, non-forested habitat unique to the region. Vegetation communities in our study area included open grassy balds dominated by mountain oat grass (*Danthonia compressa*), heath balds dominated by Catawba rhododendron (*Rhododendron catawbiense*), and surrounding northern hardwood forests dominated by yellow birch (*Betula alleghaniensis*), American beech (*Fagus grandifolia*), and sugar maple (*Acer saccharum*). Elevations at our study site range from 1450 to 1675 m. White-tailed deer are the only ungulates at our study site. Although there have been reintroductions of elk (*Cervus canadensis*) in the region, and they were detected at the study site in 2018, they were not known to occur at the study site during the time of the study. Predators of white-tailed deer at the study site include coyotes, black bears (*Ursus americanus*), and bobcats (*Lynx rufus*).

Data collection

Camera trapping is a passive survey method that uses remotely deployed cameras with motion-activated triggers to capture images of free-ranging wildlife species. This technique has increasingly become a widespread method for evaluating mammal behavior over spatial and temporal scales (Rowcliffe and Carbone 2008; Bridges and Noss 2011; McCallum 2012), including in the southern Appalachian Mountains (Diggins et al. 2016; Thorne et al. 2017). Methods for estimating and comparing activity patterns for multiple species using camera traps are clearly defined in the literature (see Ridout and Linkie 2009; Rowcliffe et al. 2014).

We randomly selected 40 camera stations over our 50-km² study area along a gradient between grassy balds and adjacent northern hardwood forests to proportionally represent the study area. On average, we placed camera

stations $2,312 \text{ m} \pm 274 \text{ m}$ SE apart. During June–August 2015, we sampled stations for 28–32 days each. We used Bushnell 6 MP Trophy Trail cameras (Bushnell, Overland Park, KS) set approximately 75 cm off the ground on trunks of trees or, for grassy bald locations, on stakes crafted from polyvinyl chloride piping. We directed cameras toward areas with less clutter (i.e., vegetation) in the understory or along wildlife trails to increase our detection probability. The cameras took a three-photo burst separated by 30 s when triggered remotely by heat and motion. We programmed cameras to stay on throughout the day and night. To avoid a biased over-attraction of predators, we did not bait camera sites. During the study, sunrise and sunset occurred between 0615–0645 hours and 2010–2040 hours, respectively.

We collected and tallied photos with deer or coyotes present. For all deer and coyote photos, we recorded date and time using the time stamp available on individual photos. For photos with deer, we also recorded sex and age. We determined sex based on the presence or absence of antlers. If the head was not visible or the individual was a fawn, we recorded sex as ‘unknown.’ We classified deer into two age groups: fawns (< 1 year old) and adults (> 1 year old). We determined fawns by their spotted coat pattern and relatively smaller body size compared to adult deer in the same photo. For each species at each camera station, we considered photo captures of the same age-sex class separated by ≥ 30 min as independent capture events (Kelly and Holub 2008). We categorized independent observations into three classes: bucks, does, and nursery groups. Since it is difficult to determine if a doe is lactating using camera trap photos, we defined does as any adult female deer where a fawn was not detected in any photographs recorded during single detection event (i.e., consecutive photos of the same group). This group included non-reproductively active females and reproductively active females during solitary feeding forays. We defined nursery groups as those in any photograph with a fawn regardless as to whether a doe was detected because fawns are usually mobile only when their dams are nearby (within 50 m) throughout the first couple months of life (Hirth 1985). For photos containing both does and bucks, we counted that photo as an observation for both groups. Photos containing does and fawns were counted as nursery group observations.

Data analysis

We converted time stamps between 0000 and 2359 hours to radial time for all capture events (Meredith and Ridout 2017). Although two other predators of fawns, black bears and bobcats, occurred at our study site, capture events for these two species were too low (18 capture events and 9 capture events for black bears and bobcats, respectively) to evaluate if nursery groups were temporally avoiding these species. To determine whether nursery groups avoided

coyotes by shifting their activity patterns, we measured the coefficient of overlap (Δ) for three groups: (1) coyotes and does (CD), (2) coyotes and nursery groups (CNG), and (3) coyotes and bucks (CB). The coefficient of overlap uses a kernel density estimator to determine the probability density function of temporal activity and ranges between 0 (no overlap in activity patterns) and 1 (complete overlap in activity patterns) (Ridout and Linkie 2009). We used estimator Δ_1 for CD, CB, and CNG since sample sizes for coyotes and nursery groups were < 75 observations (Meredith and Ridout 2017). To determine if Δ_1 significantly varied between CD, CB, and CNG, we obtained 95% confidence intervals for Δ_{1CD} , Δ_{1CB} , and Δ_{1CNG} by running a smoothed bootstrap with 10,000 iterations (Meredith and Ridout 2017). Using the function `resample`, a kernel density estimator creates a matrix of bootstrapped samples for each data set, which generates confidence intervals for each Δ_1 , allowing for comparisons of activity patterns between groups. We used package `overlap` in Program R 3.1.2 (R Core Development Team 2016; Meredith and Ridout 2017) for all analyses.

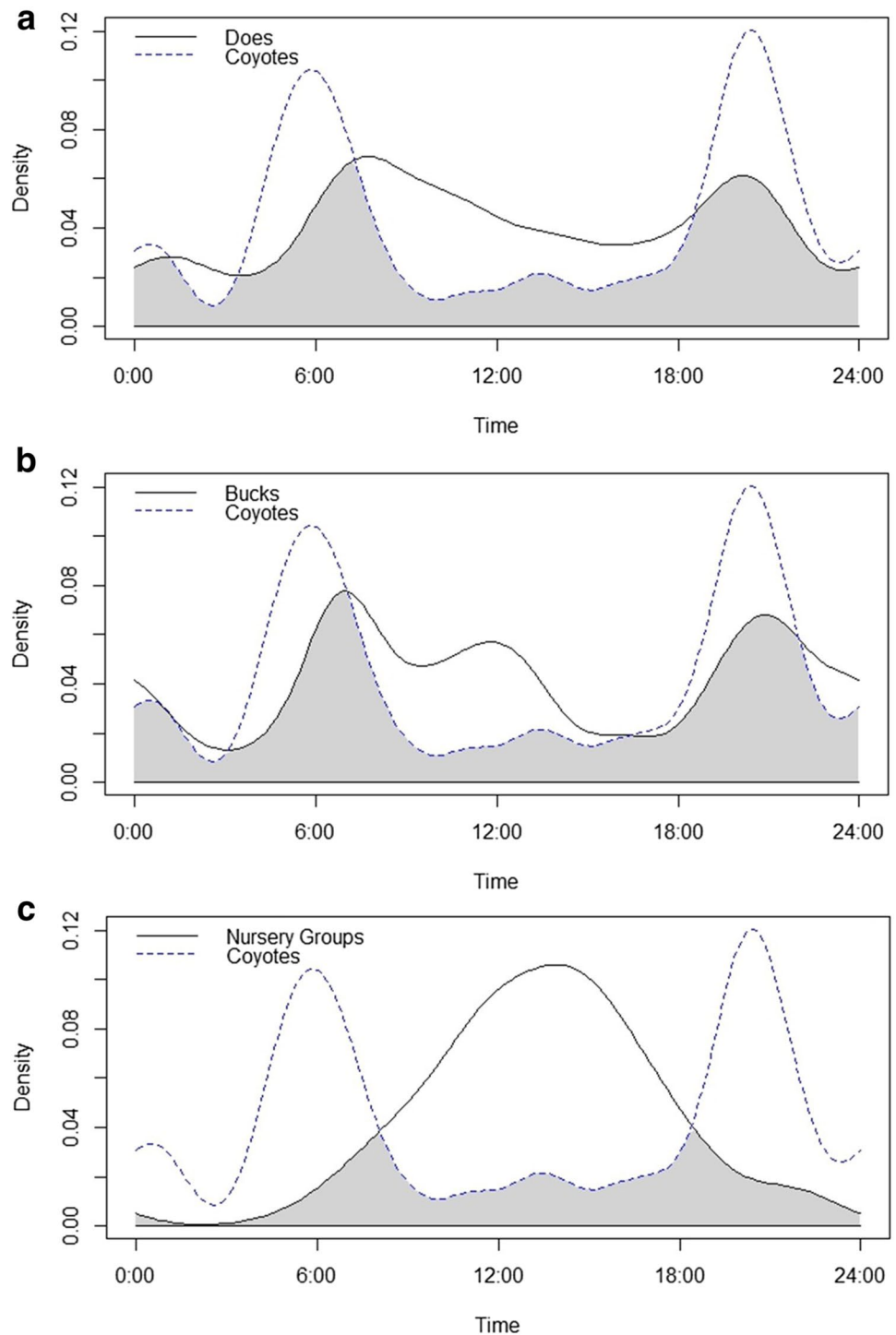
Results

We collected 35 capture events for coyotes at 15 sites (2.4 ± 0.5 SE observations/site; range = 1–7), 36 for nursery groups at 13 sites (2.8 ± 0.5 SE, range = 1–6), 93 for bucks at 27 sites (3.5 ± 0.7 SE, range = 1–14), and 262 for does at 34 sites (8 ± 1.6 SE; range = 1–36) over 1,107 camera days. Coyote activity was crepuscular, with peaks around 0530 and 2000 hours (Fig. 1). Does and bucks exhibited similar activity patterns: activity was crepuscular with greater activity around dawn than dusk (Fig. 1a, b). Nursery groups were diurnal, with unimodal activity peaking between 1200 and 1300 hours (Fig. 1c). Activity overlap for CNG ($\Delta_{1CNG} = 0.317$, LCI = 0.176, UCI = 0.491) was significantly lower than that for CD ($\Delta_{1CD} = 0.686$, LCI = 0.558, UCI = 0.816). Δ_{1CNG} was also significantly lower than Δ_{1CB} (0.729, LCI = 0.629, UCI = 0.890), whereas Δ_{1CD} was similar to Δ_{1CB} (Fig. 2).

Discussion

Our study reports differences in the activity patterns of deer nursery groups and coyotes during the same space and time. Other studies have shown that deer modify their foraging behavior (Cherry et al. 2015) and space use related to the presence of fawns (Conner et al. 2015) to avoid predators, while our study shows a potential temporal variation of nursery group activity to reduce interactions with coyotes. Fawns are primarily diurnal (Jackson et al. 1972); however, telemetry and captivity studies have noted higher fawn activity

Fig. 1 Activity patterns of coyotes (*Canis latrans*) and white-tailed deer (*Odocoileus virginianus*) in the Roan Mountain Highlands in North Carolina and Tennessee, USA in summer 2015. Sunrise occurred between 0615 and 0645 h and sunset between 2010 and 2040 h



around dawn and dusk (Schwede et al. 1992). As fawns age, their activity patterns may shift towards those of adult deer (Jackson et al. 1972), but we lacked sufficient data to investigate this. However, it is not surprising that nursery groups exhibited activity patterns that differed from those of coyotes more drastically than those of other demographic groups. Circadian rhythms and behaviors of juvenile ungulates

are, in part, driven by antipredator strategies (Ralls et al. 1986; Schwede et al. 1992). Lingle et al. (2005) observed that the majority (65%) of fawn-coyote encounters occurred when fawns were active and accompanied by their mothers, whereas a smaller number of encounters occurred when the fawns were bedded down without a female present. Fawn activity during the middle of the day may be important to

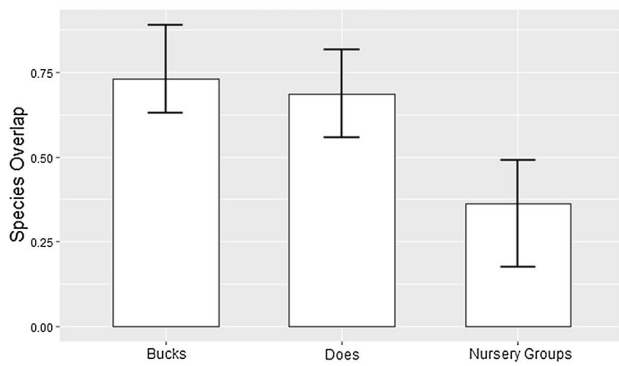


Fig. 2 Activity pattern overlap of coyotes (*C. latrans*) and white-tailed deer (*O. virginianus*) in the Roan Mountain Highlands in North Carolina and Tennessee, USA in summer 2015. Species overlap is indicated by the coefficient of overlap (0=no overlap between species, 1=complete overlap) and confidence intervals are represented by error bars

reducing encounters with coyotes. Therefore, the ability of nursery groups to adapt to coyote presence (e.g., increasing activity when predators are less active) may be important for fawn survival, recruitment, and long-term population growth (Lingle et al. 2008; Kilgo et al. 2010; Grovenburg et al. 2012; Conner et al. 2015; Gulsby et al. 2015; Cherry et al. 2016a).

Fawns represent a reproductive investment that imposes an energetic cost to does during gestation (Pekins et al. 1998) and lactation (Clutton-Brock et al. 1989; Verme 1989). However, lactating does often spend energy on increased anti-predator behaviors to protect fawns (Laundré et al. 2001; Lashley et al. 2014), which could decrease foraging time, resulting in an energetic deficit during the high energetic demands of reproduction (Brown 1999; Fortin et al. 2004). Accordingly, lactating does may forage during riskier times, leaving fawns bedded in concealed areas to increase foraging opportunity and decrease time spent on vigilance if fawns are present during foraging bouts when coyotes are more active.

Hunting pressure can shift coyote activity patterns away from diurnal movements (Kitchen et al. 2000). Although legal persecution of coyotes occurs in the region, hunting pressure on coyotes at our site is minimal due to its relative isolation. In areas where coyotes are not persecuted by humans, they are known to hunt for fawns during crepuscular times of the day (Lingle 2000). By concentrating nursery group activity during the middle of the day, lactating does may provide increased protection for fawns by reducing the probability of an encounter with coyotes and minimizing fawn mortality, whilst also meeting their own energetic needs. Furthermore, restricting movements to safer times of the day may reduce the need for other costly reactive antipredator behaviors, such as aggression or fleeing (Brown

1999; Lingle et al. 2005; Grovenburg et al. 2012). Additionally, does tend to reduce their home ranges and select areas with greater amounts of cover when their fawns are young, allowing for mothers to forage while still close to their bedded-down fawns (Bertrand et al. 1996; Lashley et al. 2015; Cherry et al. 2017).

The coyote diet is plastic (Andelt et al. 1987; Schrecengost et al. 2008; Swingen et al. 2015), and fawns are readily available as prey during the summer months. If fawns were a significant food source for coyotes at our site, we would expect coyote activity patterns to mimic those of nursery groups, unless coyotes primarily hunt for bedded fawns during periods of inactivity. Although fawns are a major dietary item for coyotes and consumption of deer by coyotes increases during the fawning season (Schrecengost et al. 2008; Swingen et al. 2015; Cherry et al. 2016b), the availability of other prey items at our study site may also influence when coyotes are active. These prey items include numerous rodent species and lagomorphs (*Sylvilagus* spp.) (Kitchen et al. 2000; Crimmins et al. 2012; McVey et al. 2013) and may provide sufficient food that coyotes do not alter the timing of their foraging activity to target fawns. Although coyotes are generalist predators, lagomorphs are their primary prey in the grasslands and plains of the western USA (Ripple et al. 2013). Lagomorphs are abundant throughout our study area and have crepuscular activity patterns similar to those of coyotes, where activity is higher in the evenings than in the mornings (Moser et al. 2016). Therefore, the temporal avoidance of nursery groups of deer coupled with the abundance of alternative prey species may account for the dramatic difference we observed in activity patterns between nursery groups and coyotes.

Although our study demonstrates differences in activity patterns of coyotes and deer nursery groups, it does not account for deer activity patterns in areas without coyotes. Since other known predators of fawns (i.e., black bears and bobcats) occur at the study site, deer daytime activity may be a strategy used to decrease encounters with multiple predators, including coyotes. Understanding the effects of multiple predators on a prey species is critical to determining how behavioral shifts reduce predation risks by those predators. However, studies on the effects of multiple predators on prey activity are rare, which limits our understanding of activity shifts of prey species (Dröge et al. 2017). More information on black bear and bobcat behavior at our study site, for example, could help to explain the activity shift that we observed in nursery groups. Bobcats also prey on fawns during the summer (Nelson et al. 2015), but they are largely nocturnal and crepuscular (Thornton et al. 2004), which may further explain the diurnal shift we observed. Conversely, black bears are primarily diurnal during the summer (Bridges et al. 2004) and depredate fawns during this time of year (Bastille-Rousseau et al. 2011). However,

bear predation is largely restricted to the fawns' first few weeks of life when they remain bedded down between lactation bouts (Shuman et al. 2017).

Cover may affect movements of nursery groups (Cherry et al. 2017); however, we did not assess if grassy versus forested cover types influenced temporal movement of deer due to a lack of sufficient data. Movement data on coyotes and deer would inform if and how deer use the available cover types to avoid interactions with coyotes and other predators. Additionally, other factors such as weather and resource availability may influence the activity patterns of wildlife (Beier and McCullough 1990; Brivio et al. 2016). Within our study site, we do not believe that certain resources, such as forage, were limiting since our study was conducted during the growing season. Although there may be other factors (e.g., other predators, weather, and alternative prey available to coyotes) that influenced the differentiation in activity patterns between the two groups, we believe our findings merit further investigation for a better understanding of the activity patterns of deer in relation to predation risk, particularly during the fawning season. Future research on antipredator behavior in deer and other ungulates should seek to evaluate the effect of individual condition, other predators (i.e., black bears and bobcats), seasonality, resource availability, and herding behavior on activity patterns and ultimately the fitness consequence of these antipredator behaviors.

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