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Raccoon Vigilance and Activity Patterns When Sympatric with Coyotes

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Abstract: Nonconsumptive effects of predators potentially have negative fitness consequences on prey species through changes in prey behavior. Coyotes (*Canis latrans*) recently expanded into the eastern United States, and raccoons (*Procyon lotor*) are a common mesocarnivore that potentially serve as competitors and food for coyotes. We used camera traps at baited sites to quantify vigilance behavior of feeding raccoons and used binomial logistic regression to analyze the effects of social and environmental factors. Additionally, we created raccoon and coyote activity patterns from the camera trap data by fitting density functions based on circular statistics and calculating the coefficient of overlap (Δ). Overall, raccoons were vigilant 46% of the time while foraging at baited sites. Raccoons were more vigilant during full moon and diurnal hours but less vigilant as group size increased and when other species were present. Raccoons and coyotes demonstrated nocturnal activity patterns, with coyotes more likely to be active during daylight hours. Overall, raccoons did not appear to exhibit high levels of vigilance. Activity pattern results provided further evidence that raccoons do not appear to fear coyotes, as both species were active at the same time and showed a high degree of overlap ($\Delta = 0.75$) with little evidence of temporal segregation in activity. Thus, our study indicates that nonconsumptive effects of coyotes on raccoons are unlikely, which calls into question the ability of coyotes to initiate strong trophic cascades through some mesocarnivores.

Keywords: activity pattern; camera trap; coyote; fear; mesopredator release; raccoon; trophic cascade; vigilance

1. Introduction

Nonconsumptive effects of predators can alter the interactions that prey species have with their environment, potentially imparting negative fitness consequences [1]. Fear of predation may reduce fitness in a prey species by simplifying decision-making rules, which could hinder optimal resource use (e.g., if foraging areas are separated from escape cover [2]). Thus, predation risk may affect prey populations via changes in prey behaviors [3], including decreases in diel activity [4], changes in group size [5,6], shifts in habitat use [7–10], reductions in feeding time [11,12], or increases in vigilance while foraging [13].

Vigilance while foraging can come at a cost if animals cannot compensate for decreased feeding rates [14–16]. Some species may accept the cost of vigilance during foraging because the reduced intake

is a less important proximal threat to individual fitness compared to increased predation risk [5]. Thus, individual vigilance should be correlated to perceived predation risk [17], though increases in group size when foraging may allow individuals to decrease vigilance without increasing predation risk [6]. Additionally, nocturnal animals may adapt vigilance and foraging time allocation to the amount of light available (e.g., moon phase) as a means of avoiding predation risk [18].

Coyotes (*Canis latrans*) dramatically expanded their range in North America over the past two centuries, potentially allowing them to serve as the top terrestrial predator in many areas [19,20]. Coyote expansion into the southeastern United States has been much more recent [19,21], and coyotes potentially play a role as apex predator by replacing the mountain lions (*Puma concolor*) and red wolves (*Canis rufus*) that were extirpated from the region. Given evidence that coyotes can affect the occupancy of herbivorous mammals, it is possible their presence could have wide-reaching effects on food webs through trophic cascades [22]. Indeed, considering the economic value of white-tailed deer (deer; *Odocoileus virginianus*) and deer hunting in the southeastern U.S., studies of direct [23] and nonconsumptive [24,25] effects of coyotes on deer populations have garnered notable interest recently. However, less attention has been afforded to coyote effects on other taxa, including mesopredators. Mesopredators (e.g., raccoons (*Procyon lotor*)) compete with coyotes for access to some of the same foods, while potentially serving as a coyote food themselves. It is possible that coyotes could function ecologically as a replacement for extirpated red wolves. Red wolves were presumably an important predator of raccoons, as inferred from red wolf scat contents (e.g., [26,27]). Thus, if coyotes depredate raccoons, then raccoons should fear coyotes and respond behaviorally in ways that mitigate predation risk from coyotes (e.g., with high levels of vigilance; with temporal shifts in diel activity). For example, Suraci et al. [28] demonstrated that in an area where domestic dogs (*Canis lupus familiaris*) are known to harass and kill raccoons, playbacks of recorded dog vocalizations altered raccoon foraging and led to cascading effects at lower trophic levels.

Activity patterns provide information on basic decision rules, given tradeoffs associated with forage acquisition, thermoregulation, and predator avoidance [29]. Further, activity patterns have been used to address hypotheses regarding interspecific competition and predator-prey interactions [30–33]. Predation rates on radio-tagged raccoons have been consistently low across populations, with coyotes representing only a small proportion of mortality causes [34]. Gehrt and Clark [34] suggested it was unlikely the threat of coyote predation would have a strong effect on raccoon activity. Previous radio-tag-based data have demonstrated that raccoons do not appear to avoid coyotes spatially (e.g., [35]), and other work has shown that mesocarnivores overlap extensively in activity patterns (i.e., temporally) because they are mostly active during nocturnal and crepuscular diel periods [36].

Raccoons may use a combination of antipredator behaviors to mitigate predation risk, such as altering vigilance rates and using fine-scale changes in activity patterns, rather than shifting overall activity or avoiding areas used by coyotes altogether. Combining data on vigilance behavior and activity patterns should provide additional insight into behavioral and temporal effects of predation risk on raccoons. Our study site provides little baseline evidence that coyotes influence raccoons, which is consistent with Gehrt and Clark's [34] hypothesis that coyote–raccoon interactions do not follow the mesopredator release hypothesis. Hence, our objective was to examine raccoon foraging and activity patterns at baited sites by using camera trap data in an area where raccoons and coyotes have been sympatric for over 20 years. We approached this objective in two ways: (1) we quantified vigilance of raccoons and evaluated effects of social (e.g., group size) and environmental (e.g., moon phase) factors; (2) we estimated activity patterns for raccoons and coyotes to evaluate temporal segregation. The first approach was designed to establish a benchmark vigilance value for raccoons at baited sites using a novel camera-based method. Given the lack of published values of raccoon vigilance, and given our study design was observational, we hypothesized that if raccoons were fearful of coyotes, they would spend more time vigilant than feeding. The second approach used the same photo dataset to address temporal activity of raccoons and coyotes simultaneously. Similarly, assuming raccoons were fearful

of coyotes, we hypothesized raccoon activity patterns would demonstrate temporal differences with coyotes, most likely by departing from expected nocturnality.

2. Materials and Methods

We conducted our study at Fort Bragg Military Installation (Fort Bragg), which was located in the Sandhills physiographic region of central North Carolina, USA. Fort Bragg was owned by the U.S. Department of Defense, and the area we used for this study comprised ~40,500 ha. Fort Bragg was part of the longleaf pine (*Pinus palustris*) ecosystem, with uplands dominated by longleaf pine forests that were managed with growing-season prescribed fire on a 3-year fire-return interval [37]. Interspersed drainages were dominated by blackgum (*Nyssa sylvatica*), with a densely vegetated understory composed primarily of *Lyonia* spp. and *Ilex* spp.

Raccoons were common at Fort Bragg and had been hunted annually, following statewide regulations set by the North Carolina Wildlife Resources Commission (season: mid-October–28 February). At Fort Bragg, raccoons were hunted only at night with the use of dogs, and overall hunter effort ranged from 126 to 624 attempts per season (average: 185) for the 11 years prior to this study (i.e., 2000–2010; Fort Bragg Wildlife Branch, unpublished data). Most raccoon hunters were more concerned with running and listening to their dogs than actually killing raccoons (J. Jones, Fort Bragg Wildlife Branch, personal communication), which explains the relatively low harvest rate during the same time period (i.e., average of 65 raccoons per season; ~0.18 raccoons per attempt; Fort Bragg Wildlife Branch, unpublished data).

Coyotes first arrived at Fort Bragg in 1989 and were common by the mid-1990s [23]. Coyotes and bobcats (*Lynx rufus*) were the only potential raccoon predators present during our study. Moreover, coyotes were a documented source of neonatal and adult female deer mortality [38,39] and had effects on deer population dynamics [23], highlighting their potential as apex predators in the ecosystem. Fort Bragg did not allow trapping for any species, though trapping for coyotes was common on adjacent private land. Coyote hunting was suspended during 2011 and 2012 to accommodate collar-based research efforts (i.e., [40–42]); otherwise, coyotes could be harvested during any other open hunting season (~September–February). Hunter effort and harvest rates were low (i.e., a few coyotes killed per year) and usually associated with opportunistic shooting by deer hunters [39].

To assess effects of social and environmental factors on vigilance of raccoons, we used photographs collected from camera traps deployed systematically and baited with dried, whole kernel corn. Research was approved by the North Carolina State University Institutional Animal Care and Use Committee (10-143-O). We deployed 100 camera traps (Reconyx [model PC800], Holmen, WI) at a density of 1 per 500 hectares during August 2011–2013. Following Jacobson et al. ([43]; designed to survey deer), we used 14-day pre-baiting and survey periods, and we set cameras to a 3-min delay between photographs. For each image, we recorded the number, age (juvenile or adult), and vigilance level of raccoons, as well as the time and date, presence of other wildlife species, and the moon phase. We assigned vigilance level by adapting the approach used on deer (see [44]). We considered a raccoon to be in a feeding posture (i.e., non-vigilant) if its head was down and its silhouette (i.e., its back, neck, and head) was sloped smoothly; we classified it as non-feeding posture (i.e., vigilant) when it was standing on hind legs or its head was up, creating a crook in its silhouette between the head and back (Figure 1; similar to [28]). We determined age based on the relative body size; thus, raccoons could be classified as adult, juvenile, or unknown (if no size comparison could be made). If a raccoon was not fully visible (i.e., posture could not be determined), we discarded that raccoon from the vigilance analysis. Each image contained a time and date stamp, which we used to assign a moon phase (i.e., new, first quarter, full, third quarter) and lighting conditions (i.e., nocturnal, crepuscular, diurnal; based on sunrise and sunset times for that date). We defined each moon phase as a 5-day window centered on the particular phase; thus, days that were in between phases were lumped together in an “other” category. We defined crepuscular lighting conditions as being within 1 h of sunrise or sunset. We used binomial logistic regression in JMP Pro 10 (SAS Institute Inc., Cary, North Carolina) to analyze

the effects of social and environmental factors on raccoon vigilance. We assigned vigilance level as the binary response variable (i.e., vigilant = 1 and non-vigilant = 0) and used group size, age, presence of other species, moon phase, and lighting conditions as explanatory variables ($\alpha = 0.05$). We used the percent of raccoons in a vigilant posture as a proxy for time budget; thus, we report time spent vigilant based on the proportion of vigilant raccoons appearing in the photo sample.



Figure 1. Vigilant raccoons had a crook where the neck meets the body and may have been standing on hind legs; they were classified “head up” (A). Foraging raccoons had a characteristically sloping back and neck and were classified “head down” (B).

Camera traps provide a useful way to monitor activity patterns [45], provided enough detections (≥ 100 ; [46,47]). Camera traps record the date and time for each photograph of an animal, so they are assumed to provide a dataset useful for estimating activity pattern curves of the species detected, which can also be compared among individuals and sexes and across species [48]. Thus, we created raccoon and coyote activity patterns and calculated the coefficient of overlap (Δ) from the camera trap data by fitting density functions based on circular statistics [48] using package `overlap` [49] in R (R Development Core Team 2011). We tested for significant differences in activity patterns using Watson’s 2-sample test for homogeneity in package `CircStats` [50] in R.

3. Results

During 4200 trap nights, camera traps recorded 5248 photographs of raccoons. Raccoons occurred in group sizes from one to seven, though smaller group sizes were more common. We obtained 3199 photographs with a group size of one, and 1140 photographs with a group size of two, 577 with a group size of three, and the remainder ($n = 332$) with group sizes of four or greater. On average, there were 1.67 (SE = 0.015) raccoons per group (i.e., photograph). Overall, raccoons were vigilant 46% of the time while foraging at baited sites (i.e., 46% of sampled raccoons were in the vigilant posture). Raccoons were more vigilant during full moon ($\beta = 0.22$, SE = 0.05, $p < 0.0001$) and diurnal hours ($\beta = 0.40$, SE = 0.15, $p = 0.0091$; Figure 2) but less vigilant as group size increased ($\beta = -0.05$, SE = 0.02, $p = 0.0163$) and when other species were present ($\beta = -0.28$, SE = 0.05, $p < 0.0001$; Figure 3). Age and other lighting conditions and moon phases were not significant predictors of vigilance ($p > 0.05$). We recorded 306 photos of coyotes of which three were with a raccoon present. Other species detected in photographs with raccoons were deer, southern flying squirrel (*Glaucomys volans*), eastern cottontail (*Sylvilagus floridanus*), gray fox (*Urocyon cinereoargenteus*), wild turkey (*Meleagris gallopavo*), and Virginia opossum (*Didelphis virginiana*).

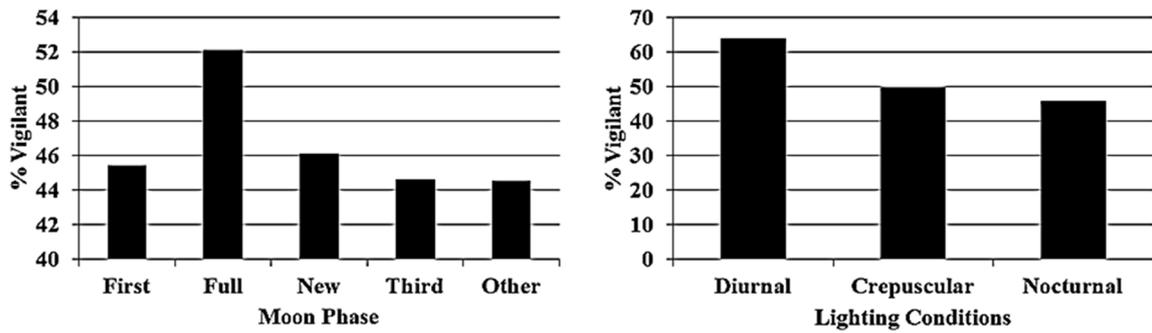


Figure 2. Raccoons were more vigilant at baited sites during full moon and diurnal hours. The “other” moon phase corresponded to days outside the 5-day window around each named phase. We defined crepuscular lighting conditions as being within 1 h of sunrise or sunset.

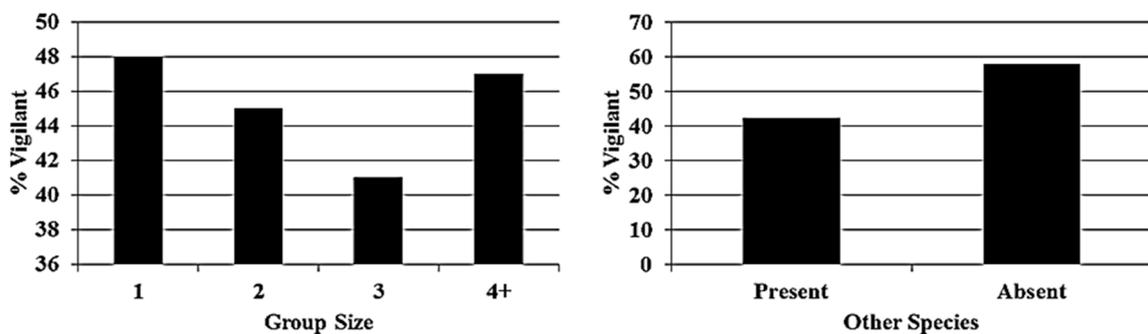


Figure 3. Raccoons were less vigilant at baited sites as group size increased and when in the presence of other species. Group sizes of 4 or more were pooled. Other species detected with raccoons included white-tailed deer, coyote, southern flying squirrel, eastern cottontail, gray fox, wild turkey, and Virginia opossum.

Raccoons and coyotes demonstrated similar nocturnal activity patterns. The coefficient of overlap was 0.75, suggesting a high level of overlap. However, raccoon and coyote activity patterns were different statistically (Watson’s $U_2 = 1.406, p < 0.001$), driven by the fact that coyotes were more likely than raccoons to be active during daylight hours (Figure 4).

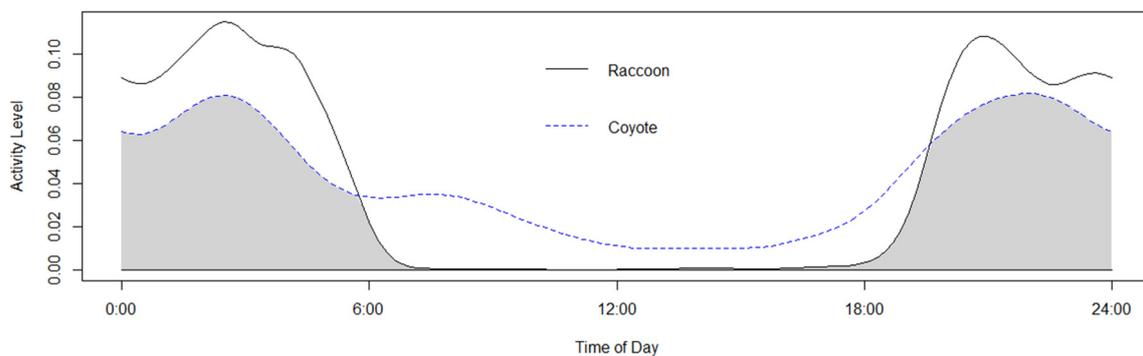


Figure 4. Daily activity patterns for raccoons (solid line) and coyotes (dashed line) at Fort Bragg Military Installation, North Carolina, USA. The coefficient of overlap (Δ ; represented by the shaded area) was 0.75.

4. Discussion

Raccoons did not appear to exhibit high levels of vigilance at baited sites, as indicated by spending more time in a foraging posture. The vigilance level we observed (46%) was lower than the range of vigilance values reported by Etheredge [51]. Etheredge [51] used coyote scat treatments in arena and feeding trials to determine that raccoon vigilance ranged from 47.69% to 61.26%, though treatment effect was not statistically significant. Suraci et al. [28] reported raccoon foraging times of ~54% (i.e., ~46% vigilance) over their long-term timescale (1 month) in areas without predator playbacks. Suraci et al. [28] showed that dog vocalizations reduced raccoon foraging time; however, in the absence of dog vocalizations, the foraging and vigilance times appear similar to those reported here. Similar to Etheredge [51], we conclude that raccoons do not appear to be overly fearful of coyotes, or if they are, they are not expressing it in a way that is detectable using our methodology. Furthermore, raccoon vigilance rates likely are even lower than those we reported, as photographs should overestimate vigilance because the raccoons in a head-up posture could be handling or chewing food items, looking at conspecifics, or simply resting or walking in a way that is confounded with actively scanning for risks. Overall, our study provides a new camera-based method for assessing vigilance in raccoons and establishes a baseline vigilance value for comparison to future work; ideally, future studies will incorporate experimental manipulation to tease apart effects that might be masked by our observational approach.

Vigilance in raccoons varied based on social and environmental factors. Increased vigilance during full moon and diurnal hours likely reflects their comfort with being active and foraging in darkness. Indeed, raccoons are adapted to and most active during crepuscular and nocturnal hours [36, this study], potentially leading to increased need for risk perception during lighted conditions. Many studies have concluded that moonlight avoidance is an adaptation to reduce predation risk from visually oriented nocturnal predators [52–54]. However, Biebow and Blumstein [55] suggested that some species may associate increased illumination with safety. Future work could evaluate how fine-scale changes in prey vigilance behavior might be connected not just to the amount of light itself but to how light interacts with the associated predator community (e.g., functional role of predator, body size of predator).

Reduced vigilance as group size increased is consistent with the idea that aggregating with conspecifics almost universally reduces vigilance [56]; however, aggregating can increase intraspecific competition, as well as the detection or likelihood of attack by a predator [56]. Additionally, increased intraspecific competition could manifest as increased vigilance (e.g., Figure 3), simply as an artifact of the methodology we used. For example, raccoons in head-up posture in a photo could be vigilant to predators or in intraspecific conflict. As a potentially complementary result, our data indicated that raccoons reduced vigilance in the presence of other species, which might imply that raccoons share vigilance with other species or simply benefit from “many eyes” (even when the eyes do not belong to conspecifics). Future work could evaluate the extent to which raccoons and other taxa might share vigilance to mitigate the risk from a common predator species such as the coyote. Likewise, future work could explore how measures of vigilance might be biased by behaviors that actually stem from interspecific competition rather than fear of predation (e.g., raccoons appear to be vigilant because coyotes are competing for the same resources).

Activity pattern results provide further evidence that raccoons do not appear to fear coyotes, at least not enough to deviate in diel distribution of activity. Both species demonstrated nocturnal activity patterns as expected, and descriptively, they showed a high degree of overlap with little evidence of temporal segregation in activity. These results are consistent with Lesmeister et al. [36], who showed no evidence that raccoons spatially or temporally avoided the presence or amount of activity of other carnivores. However, we were able to detect a statistical difference in our raccoon and coyote activity curves, which appeared to be driven by the fact that coyotes showed movement during daylight hours. Raccoons at Fort Bragg showed little diurnal activity, which was similarly reported by a recent photograph-based study of mesocarnivore activity [36]. Biologically, we do not believe the statistical

difference we detected in the curves is relevant, as both species clearly had nocturnal peaks of activity, with movement during crepuscular hours as well. If raccoons were deviating from a nocturnal pattern to avoid coyotes, we would expect to see movement during diurnal hours. Indeed, a recent study suggested that domestic cats (*Felis catus*) increased their diurnal activity as a strategy (by the cats or their owners) to avoid nocturnal coyotes [57].

The idea that raccoons should fear coyotes is grounded in the mesopredator release hypothesis (MRH). The MRH predicts an inverse relationship in population sizes between predator species, as well as spatial or temporal antipredator responses of smaller-bodied predators (to avoid larger ones [58–60]). Though the MRH is supported in a variety of predator guilds [60,61], it may not fit with some systems where the top predator is also considered a mesopredator or where strong competition between predator species is lacking [62]. Gehrt and Clark [34] suggested the MRH was supported within Canidae but argued there was limited support for coyotes as top predators influencing other mesopredators, particularly raccoons. Subsequent work with radio-tags on sympatric raccoons and coyotes [35] and striped skunks (*Mephitis mephitis*) and coyotes [63] discovered little spatial avoidance of coyotes and little evidence of coyote-caused mortality. Based on coyote diet composition at our study site, there is no evidence of direct predation on raccoons by coyotes [64], and it appears to be minimally important in other studies from our region (e.g., [65–68]). Thus, behavioral and temporal activity results from this study are consistent with previous work that suggests the MRH might not hold with some species outside Canidae [34–36,51,62,63], though exceptions exist, e.g., [69].

Understanding potential nonconsumptive effects of predators is important because of cascading effects to other trophic levels (e.g., raccoon fear of dog vocalizations reduced predation pressure on lower trophic levels [28]). Raccoons at our study site have been sympatric with coyotes for the past 20–30 years yet demonstrate an apparent lack of fear based on vigilance behavior and activity pattern. Thus, our study indicates that nonconsumptive effects of coyotes on raccoons are unlikely, which calls into question the ability of coyotes to initiate strong trophic cascades through raccoons directly. Though nonconsumptive effects could manifest themselves through other raccoon behaviors that we did not measure, results from our study combined with raccoon mortality and spatial data (e.g., [34,35]) indicate that coyotes do not induce strong behavioral changes in raccoons via predation risk. Future work should examine the extent to which this holds for other mammalian mesocarnivores and lower trophic levels. Additionally, our results suggest that coyotes may serve simply as another mesopredator rather than an apex predator. Future research could explore how potential trophic cascades might occur through coyotes and raccoons via the competitor release effect [70,71].

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