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Active Humans, Inactive Carnivores, and Hiking Trails within a Suburban Preserve

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Cover Page Footnote

We are grateful to the following people and groups who contributed to the development of this research: Pace University for their generous financial contributions and the staff at Ward Pound Ridge Reservation for allowing us to conduct our research within their park. Special thanks to Roland Kays (Fisheries, Wildlife & Conservation Program, NC State University) who volunteered his time and expertise in aiding the development and design of this research. Lastly, we thank Daniel DiTieri, Thaddeus Cook, David Spillo, Bryan Hogan, Stephanie Fattizzi, Jay Blaze, and Peter Ruggiero for their contributions in the field.

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Habitat fragmentation caused by suburban sprawl is a major threat to wildlife populations in the United States (DeStefano and DeGraaf 2003; Marzluff 2002; Radeloff et al. 2005). Spatial distribution of carnivores in suburban areas, as in natural areas, is influenced by prey abundance, habitat quality, breeding opportunities, and intraguild competition (Lynch et al. 2008). As a result, carnivores in suburban areas are patchily distributed within a matrix of “habitat islands” including preserves, public parks, land easements, and private backyards (Gehrt et al. 2009, Riley et al. 2010). In many of these habitat islands, roads and hiking trails have been established for human travel and recreation. Carnivores often utilize trails and lightly-used roads to facilitate travel (Carbone et al. 2001; Donovan et al. 2011; George & Crooks 2006; Harmsen et al. 2010; Kays et al. 2011; Kays et al. 2016; Weckel et al. 2006); species that use hiking trails include Panthera tigris sumatrae (Pocock) (Tiger) (Carbone et al. 2001), Panthera onca (Linnaeus) (Jaguar) (Weckel et al. 2006), Puma concolor (Linnaeus) (Puma) (Dickson et al. 2005, Harmsen et al. 2010), Leopardus pardalis (Linnaeus) (Ocelot) (Kays et al. 2011), Canis lupus (Linnaeus) (Gray wolf) (Whittington et al. 2005), and Canis latrans (Say) (coyote) (Kays et al. 2008). In contrast, Lynx rufus (Schreber) (bobcat), while known to utilize low-traffic hiking trails (Kays et al. 2017), have displayed less elasticity in their ability to tolerate human presence (Ordenana et al. 2010) and avoid both roads and trails with high human activity.
Avoidance of interspecific competitors and predators may limit the flexibility of species’ responses to human activity. Indeed, avoidance of larger carnivores by smaller carnivores is well documented within the canids (Fedriani et al. 2000; Harrison et al. 1989; Robinson et al. 2014) and has been observed between other carnivore taxa as well (Allen et al. 2015; Mukherjee et al. 2009). Coyote aggression towards foxes (Fedriani et al. 2000; Robinson et al. 2014; Sargeant & Allen 1989) is likely the reason fox territories are largely outside of coyote territories (Harrison et al. 1989; Major & Sherburne 1987; Voigt & Earle 1983). Palomares and Caro (1999) documented intraguild predation of red fox and raccoon (Procyon lotor) by coyotes and of red foxes by Spanish lynx (Lynx pardinus). On a landscape scale, intraguild predation results in shifts in space use by small and mid-sized carnivores (Ripple et al. 2013; Robinson et al. 2014). Whether intraguild predation promotes avoidance at a finer scale in fragmented suburban habitats remains unknown.

Understanding how hiking trails are utilized by both large and small carnivores is important to conserving and managing these species in multi-use systems. Therefore, the goal of this study was to investigate the relationship between human recreation and carnivore activity on hiking trails, and the impact of large carnivore activity on relatively smaller carnivores. Based on prior studies by Kays et al. (2011) and (2017), we predicted that larger carnivores (i.e. bobcats and coyotes) would be detected predominantly on trails during times of low human activity. We further predicted that mesocarnivores (i.e. raccoons and red foxes) would be detected most frequently off-trail, as these species are expected to avoid areas frequented by coyotes and bobcats (Crooks and Soule 1999; Palomares and Caro 1999, Wang et al. 2015).

FIELD-SITE DESCRIPTION

The study was conducted in Ward Pound Ridge Reservation (WPRR), located in Westchester County, New York (Figure 1, 41°15’25''N, 73°35’50''E). WPRR is situated between suburban and natural landscapes. Assembled from over 30 farms in 1938, much of the 17.5 km² reservation is comprised of regenerated second-growth hardwood forest, with a variety of tree species including Eastern hemlock (Tsuga canadensis), hickories (Carya spp.), maples (Acer spp.), oaks (Quercus spp.), pines (Pinus spp.) and spruces (Picea spp.) (Barnard 2002, Herr and Koehl 2013).

A network of man-made trails is maintained by park employees year-round. Trails at WPRR were commonly used for human recreation during set hours, which produced a good opportunity to analyze spatio-temporal activity of carnivores in relation to human activity levels. ‘Primary’ trails are used mostly for hiking, while designated areas permit horseback riding and biking. Motorized vehicles are prohibited on park trails although park employees use slow-moving all-terrain vehicles for trail maintenance. Trail density is 2.6 km/km² for a total of 52 km of trails that provide access to the majority of the park.

Figure 1. Location of Ward Pound Ridge Reservation (WPRR), Pound Ridge, New York
The park receives an average of 100,000 visitors annually and is open year-round from 8am to dusk (J. Main, personal communication, 13 October 2011). Temperatures vary from -12.2°C—35.5°C throughout the study. Annual rainfall averages are approximately 1.24 m, and snowfall averages are approximately 0.75 m.

**METHODS**

**Field Methods**

Unbaited Reconyx RC55 Rapidfire® and HC500 Hyperfire® (Holmen, WI) cameras were deployed from 01 August 2011—30 September 2012 at 236 locations within WPRR. Between eight and 16 cameras were deployed simultaneously and were divided evenly between ‘trail’, ‘buffer’ and ‘core’ areas of the reserve (Figure 2). ‘Trail’ camera-traps were deployed on any suitable tree within one meter of a ‘primary’ trails (as designated by official WPRR trail map) and were set to face the width of the trail (Weckel et al. 2006). ‘Buffer’ cameras were deployed between 20 and 150 m from a ‘primary’ trail. The average distance of buffer cameras from any trail was 86.6 m (± 31.56 SD). ‘Core’ cameras were deployed greater than 150 m from any given trail. The average distance of core cameras from any trail was 226.23 m (± 59.64 SD). The maximum distance of any camera from the trail was 402.8 m. A 150 m buffer was selected as the likely distance from which trail activities would be out of the visual range of carnivores, based on the vegetation and topography of WPRR, and based on a previous study of the alert distances of wildlife to pedestrians in another suburban preserve (Miller et al. 2001). Locations were randomly generated using the ‘Randbetween’ function in Microsoft Excel 2010 (Redmond, WA).

A total of 236 remote cameras were assigned to random locations throughout WPRR’s trail (n = 82), buffer (n = 73), and core (n = 81) areas. Cameras were bound to trees using cable locks and were secured between 20-30 cm above ground, a height found by previous studies to be optimal for detecting carnivores (Kays et al. 2011; Reed 2011; Trolle & Kéry 2003). This camera height was selected to enable camera traps to photograph carnivores of all sizes in our study area. We selected a deployment duration of two weeks (mean/station = 14.4 days; SD = 2.4) in order to balance camera trap deployment duration with the number of camera sites (Kays et al. 2011; Rowcliffe et al. 2008). All procedures followed taxon-specific guidelines approved by the American Society of Mammalogists (ASM) (Sikes et al. 2011).

Relatively short deployment durations and high camera densities were used in order to monitor a wide range of microhabitats and trail types to reduce bias regarding variation in habitat use by species. To reduce inflation of abundance indices through multiple sightings of the same individual, sightings of the same species within 30 minutes of one another were excluded from analysis unless a physical distinction between individuals could be made, a convention that follows Kelly et al. (2008) and Weckel et al. (2006).

**Statistical Methods**

We used Relative Abundance Indices (RAIs) as a measure of species activity at each site to compensate for varying trap efforts amongst the three location types; the core cameras yielded 1336 trap nights (TNs), the trail cameras yielded 1336 trap nights and the buffer cameras yielded 1208 TNs. Furthermore, camera trap deployment durations varied as it was not always possible to collect or redeploy cameras exactly every two weeks. Therefore, camera stations were treated as independent point-count surveys of local abundance, replicated over the number of days deployed (O’Connel...
et al. 2011; Rovero & Marshall 2009) then averaged across the total number of deployments throughout the study for each location type. This number was multiplied by 100 TN to produce a detectability-corrected relative abundance estimate or RAI (George & Crooks 2006; Rovero & Marshall 2009; Weckel et al. 2006).

We used a Generalized Linear Model (GLM) with Poisson error (due to number of captures fitting a Poisson rather than a Gaussian distribution) to describe the relationship between distance of camera (in meters) from any trail and number of captures. In order to avoid possible bias caused by variation in species detectability and trail-use habits (Harmsen et al. 2010; Sollmann et al. 2013) we performed independent GLM’s for each species. All tests were performed using IBM SPSS Statistics 21 (Armonk, NY) and were considered significant at P < 0.05. We utilized the Akaike Information Criterion (AIC) for model selection (Kays et al. 2011). We used number of animal captures during each of the 236 deployments as the dependent variable, subplot in which cameras were placed as the independent variable, and distance from trail was treated as a covariate. A log of the deployment duration was used as an offset in this model to account for slight variations in deployment durations throughout the study. The test was repeated using data collected from off-trail cameras only (i.e. buffer and core) to assess the relationship between distance to trail and carnivore detection rates.

Carnivore detections were categorized as either diurnal, nocturnal, or crepuscular. Crepuscular activity was defined as 45 minutes before and after sunrise and sunset, totaling three hours per day (Table 1), which is consistent with Tigas et al. (2002) and Weckel et al. (2006). A chi-square test of independence was used to determine if the relationship between spatial and temporal distribution was significant (P ≤ 0.05). Time of day (diurnal, nocturnal, or crepuscular) and camera location (trail, buffer, or core) were set as categorical variables. All field and statistical methods in this study conform to published American Society of Mammalogists guidelines (Sikes et al. 2011).

RESULTS

Carnivore Activity

A total of 16 mammalian species were detected, 7 of which were carnivores. Over 3880 trap nights 890 photos were taken of mammalian carnivores. Overall detection success for mammalian carnivores was 22.9/100TN. RAIs were calculated for all carnivores over the duration of the study. Raccoons were detected most frequently (10.25±1.1/100TN), followed by coyotes (9.6±1.4/100TN), red foxes (4.9 ±1.1/100TN), and bobcats (2.1 ±0.4/100TN) (Table 2).

Spatial Distribution

Coyote detection rates were 15-fold higher on trails than off-trails (Wald χ² = 163, df = 1, P < 0.001; Table 1). Bobcat (Wald χ² = 28.5, df = 1, P < 0.001) and red fox (Wald χ² = 28.1, df = 1, P < 0.001) detection rates were over 5-fold higher on trails than off trails. Raccoon captures were equal between trails and off trails (Wald χ² = 0.836, df = 1, P = 0.361). Detection rates did not vary significantly between ‘buffer’ and ‘core’ areas for coyotes (Wald χ² = 0.476, df = 1, P = 0.337), bobcats (Wald χ² = 0.614, df = 1, P = 0.135), red foxes (Wald χ² = 0.047, df = 1, P = 0.543), or raccoons (Wald χ² = 1.992, df = 1, P = 0.540).

Table 1. Time ranges used to categorize detections (diurnal, nocturnal, or crepuscular) for camera trap data collected in Ward Pound Ridge Reservation, NY (2011-2012). Time ranges were discerned from mean sunrise and sunset times throughout winter, spring, summer and fall.

| Season | Diurnal | Nocturnal | Crepuscular |
|--------|---------|-----------|-------------|
| Spring | 6:16-19:35 | 21:06-4:44 | 4:45-6:15 ; 19:36-21:05 |
| Summer | 6:36-19:30 | 21:01-5:04 | 5:05-6:35 ; 19:31-21:00 |
| Fall   | 7:46-15:45 | 17:16-6:14 | 6:15-7:45 ; 15:46-17:15 |
| Winter | 7:16-17:00 | 18:31-5:45 | 5:46-7:15 ; 17:01-18:30 |
Temporal Distribution

Temporal distribution of carnivore activity was markedly different between trail and non-trail camera locations. The percentage of diurnal detections was higher off trails then on trails for all species (Figure 3). The percentage of diurnal detections for bobcats and coyotes was 4-fold and 6-fold higher off-trail than on, respectively. The relationship between spatial and temporal distribution was significant for coyotes ($X^2_{4} = 20.50, df = 4, P < 0.001$) and bobcats ($X^2_{4} = 24.56, df = 4, P < 0.001$), but not for raccoons ($X^2_{4} = 8.55, df = 4, P = 0.07$) or red foxes ($X^2_{4} = 2.57, df = 4, P = 0.632$). Coyotes, red fox, and raccoons exhibited similar activity patterns overall. All three species were largely active at night with a small percentage (< 10%) of diurnal detections. Approximately 67% of bobcat detections occurred nocturnally and 29% occurred diurnally.

DISCUSSION

Coyotes, and to a lesser extent, bobcats, used trails more often at night when the park was closed to visitors, thus supporting our hypothesis that larger carnivores would be detected on trails more frequently than off-trails at night. However, the hypothesis that smaller carnivores would avoid trails due to coyote and bobcat activity was not supported. There was no significant difference between trail and non-trail RAIs for raccoons, while red foxes utilized trails similarly to coyotes and bobcats. Thus, we reject our hypothesis that spatial disassociation by subordinate species would occur in a suburban park.

Our data suggest that coyotes, bobcats, and red foxes all display an affinity for hiking trails. One potential explanation is that these carnivores use trails as least-cost corridors to circumvent thick understory commonly found in deciduous forests (Whittington et al. 2005). Trails may also serve to demarcate territorial boundaries (Major & Sherburne 1987) and would therefore be patrolled frequently. Trails may also be a source of food scraps left by humans (Ciach et al. 2016). For red foxes, the benefits of trail-use appear to outweigh the risk of interspecific killing by coyotes (Palomares and Caro 1999). This was not true for raccoons which did not show a preference for using trails over non-trail areas. This could be attributed to their ability to travel arboreally, which may reduce both their vulnerability to larger predators and make travelling along a cleared path less appealing. There was

Table 2. Summary of carnivore abundance indices (RAIs) from camera trap data collected in Ward Pound Ridge Reservation, NY (2011-2012). RAIs are calculated for varying distances from trails (trail = 0m, buffer 20-150m, core > 150m).

|        | Coyote | Bobcat | Red fox | Raccoon |
|--------|--------|--------|---------|---------|
| Set Type | Mean    | SE     | Mean    | SE      | Mean    | SE      | Mean    | SE      |
| Trail (n = 82) | 24.72   | 3.58   | 4.6     | 0.89    | 10.5    | 2.76    | 12.3    | 1.97    |
| Buffer (n = 73) | 1.99    | 0.55   | 1.31    | 0.55    | 1.34    | 0.64    | 7.77    | 1.5     |
| Core (n = 81)  | 1.29    | 0.35   | 0.5     | 0.24    | 2.69    | 1.09    | 10.4    | 1.95    |

Figure 3. Comparison of carnivore activity levels between trail and off-trail cameras in Ward Pound Ridge Reservation, NY (2011-2012). Detections are categorized as diurnal, nocturnal, or crepuscular. Asterisk indicates a significant difference between habitats in temporal activity patterns.
no association between carnivore capture rates and distance to trail observed, suggesting that the main distinction carnivores make is between trail and non-trail areas rather than distance to trails, a trend also observed with Gray wolves (Whittington et al. 2005).

After comparing carnivore capture rates in trail and non-trail areas during various time periods (nocturnal, diurnal, and crepuscular), we found that bobcats and coyotes used trails significantly less during the day when the park was open to visitors, than at night. This behavior was more prevalent amongst bobcats than coyotes, likely due to their prolonged activity periods that extend into daytime hours (Ordeñana et al. 2010) and their intolerance of humans (Tigas et al. 2002). Indeed, George and Crooks (2006), Riley et al. (2003), and Tigas et al. (2002) also found that coyotes and bobcats became more nocturnal in high human-use areas. We conclude that trail-based recreation in the park is causing carnivores to alter their activity to become more nocturnal on trails.

A recurring trend of human avoidance by bobcats and coyotes suggests that both species respond similarly to fragmented or developed areas as they do to hiking trails and recreation (George & Crooks 2006; Ordeñana et al. 2010; Reed & Merenlender 2008; Riley et al. 2003; Tigas et al. 2002). Thus, we propose that trail-based human recreation in suburban parks may have similar effects on bobcats and coyotes as do urbanization and habitat fragmentation, albeit on a finer scale. Carnivores have had to habituate to human use of trails through behavioral changes, in particular diurnal avoidance of trails. In the Northeastern U.S. coyotes have assumed the role of apex predator and therefore have a major impact on ecosystem function and biodiversity (Gompper 2002). Removal of coyotes from a region can release red fox populations, which may lead to declines in species preyed upon by foxes (Crooks and Soule 1999; Newsome and Ripple 2015; Ripple et al. 2013). Disruption of coyote activity patterns may have a similar effect to outright removal, as larger carnivores often suppress mesocarnivore populations more through prompting avoidance behaviors then through direct predation (Mukherjee et al. 2009; Prugh et al. 2009; Roemer et al. 2009; Salo et al. 2008).

Several adjustments could be made to minimize the impacts of human recreation on carnivores. These include limiting visitor frequency through a permit system, restricting public access to areas of the park during certain times of the year—namely breeding and parturition (Reed & Merenlender 2008), greater enforcement of off-trail trespassing regulations, limiting the hours in which reserves are open to dog walking (George & Crooks 2006), and reducing food subsidies to wildlife through community outreach and education.

A greater understanding of the effects of human recreation and hiking trails on carnivores is important for conservation efforts and management in multi-use systems. Spatio-temporal displacement may increase energetic costs and stress levels of carnivores, possibly affecting survival and reproduction (George & Crooks 2006). Therefore in multi-use systems species, more tolerant to human presence (e.g. coyotes, red foxes, and raccoons) may have a competitive advantage over less adaptable species, such as bobcats. However, for species that habituate easily to human presence, vulnerability to mortality from hunting and vehicle collisions increases with increasing habituation, as do the chances of coming into conflict with humans (Gehrt 2007; Poessel et al. 2013; Weckel et al. 2010). Coyotes, in particular, often come into conflict with humans, especially in suburban parks and preserves (Poessel et al. 2013). Understanding how coyote activity is influenced by human recreation is vital to developing plans to mitigate conflict. As the demand for trail-based recreation grows in suburban areas (Reed & Merenlender 2008), research and monitoring programs should be implemented to better understand the long-term effects that hiking trails and various types of recreation have on carnivores.

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