INFLUENCE OF COYOTES ON MESO-PREDATOR OCCURRENCE, RESOURCE SELECTION, AND ACTIVITY PATTERNS IN HUMAN-DOMINATED LANDSCAPES, FORT DRUM, NEW YORK

by

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ABSTRACT

C.P. Low. Influence of Coyotes on Meso-predators Occurrence, Resource Selection, and Activity Patterns in Human-Dominated Landscapes, Fort Drum, New York. 109 Pages, 6 Tables, 12 Figures, 8 Appendices, 2017. Journal of Wildlife Management style guide used.

Presence of coyotes remains an underappreciated driver of meso-predator behavior, potentially with implications for effective predator management in human-dominated landscapes. Using camera trap and GPS-collar data, I assessed the potentially interacting effects of coyotes and anthropogenic landscape features on the activity and space use patterns of meso-predators on Fort Drum. In contrast to other meso-predators, foxes markedly structured their space use in response to both coyotes and humans. Foxes restricted their distribution largely to areas of high human activity that provide enhanced foraging opportunity (maintained grassland), ready escape and denning cover (culverts), and potentially lower direct interaction with coyotes (given lower detection probability). Moreover, peak periods of fox activity were offset from that of coyotes, another means supporting their coexistence with the more dominant predator. Whereas direct control measures may be difficult in human-dominated landscapes, my results indicate opportunities for habitat manipulation to favorably influence fox distribution and activity.

Key Words: Fort Drum, coyote, red fox, gray fox, fisher, bobcat, occupancy, two-species occupancy model, activity pattern, resource selection, stable isotope, diet, anthropogenic features

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INTRODUCTION

Carnivores play a vital role in ecological communities by cascading trophic effects, energy and nutrient transfer, stabilizing or destabilizing food webs, and indirectly affecting the abundance and diversity of low trophic-level species (Crooks and Soulé 1999). Given their importance in the broader ecological community, understanding the mechanisms by which predators might exploit human-dominated systems is critical to mitigating conflict while maintaining functional ecosystems in increasingly human-dominated landscapes. In anthropogenic landscapes, predator activity patterns and space use are modulated by interactions among factors that affect reproductive rates, such as food availability, and those that affect survival such as inter-specific competition or human activity (Llaneza et al. 2012). However, in human-dominated landscapes the relative importance of each factor on the occurrence and activity of predators, and the strength of interactions among factors, remains poorly understood.

An under-appreciated but growing driver of predator space use across North and Central America is the coyote (*Canis latrans*). Native to the prairies of the southwestern U.S., coyotes recently achieved a massive range expansion, occurring now across the entirety of the U.S. and Mexico, and much of Canada (Parker 1995*a*, IUCN Canid Specialist Group 2018). Owing to their relatively large body size, gregarious social structure, and ecological plasticity coyotes are likely to compete with a broad range of meso-predators and, potentially, have instigated a top-down trophic cascade in northeastern forests through their direct or indirect influences on smaller predators such as red fox (*Vulpes vulpes*), gray fox (*Urocyon cinereoargenteus*), bobcat (*Lynx rufus*), and fisher (*Pekania pennanti*, formerly *Martes pennanti)*. Coyotes have been observed to kill foxes and fishers (Dekker 1983, Sargeant and Allen 1989, Fedriani et al. 2000, Farias et al. 2005, Aubry and Raley 2006, Wengert et al. 2014) and suppress the numbers and distribution of

smaller predators (Major and Sherburne 1987, Fedriani et al. 2000, Levi and Wilmers 2012, Lesmeister et al. 2015). Although inter-specific predation by coyotes may be rare (Palomares and Caro 1999), the risk perceived by meso-predators may be sufficient to drive their avoidance of areas regularly used by coyotes (Lima and Dill 1990). For instance, as coyotes increased in the Hudson Highlands of southeastern New York, red fox density declined (Brady1994). In more urbanized landscapes, coyotes preferentially selected habitat to minimize contact with humans (Riley 2006, Gehrt et al. 2009) and rarely made direct use of human-derived structures for shelter (Atwood et al. 2004), potentially providing smaller carnivores with refugia from inter-specific competition (Gosselink 1999, Fedriani et al. 2000, Gosselink et al. 2003, Randa and Yunger 2006). As a result, red fox selected human-dominated habitats (residential, urban grass and urban land) that coyotes were either less willing to exploit or in which coyotes, in contrast to fox, were less tolerated by humans (Gosselink et al., 2003; Gehrt et al., 2009). Such a coyote-mediated shift in the distribution of predators across the landscape likely has implications both for ecosystem function and human-wildlife conflict. However, other studies found no effect of coyotes on the space use patterns of meso-predators (Litvaitis and Harrison 1989, Chamberlain and Leopold 2005, Gehrt and Prange 2006). Lesmeister et al. (2015) showed that red foxes co-occurred randomly with coyotes with no apparent large-scale spatial adjustment to coyote presence. Synanthropic species, such as red fox, raccoons (*Procyon lotor*) and to some degree coyotes, not only occupy but seemingly thrive in human-dominated landscapes (Atwood 2006, Randa and Yunger 2006, Bateman and Fleming 2012) where they exploit refuse as food and man-made structures as shelter, and benefit from anthropogenic habitat modifications and associated reductions in predation or hunting pressure (McKinney 2002, Bateman and Fleming 2012). As a result, in human-dominated landscapes effective meso-predator management

requires greater understanding of the relative and interactive effects of environmental, biological and anthropogenic drivers of animal space use and behavior.

The northeastern states represent the most densely populated region of the United States, with 85% of the population residing in urban areas (U.S. Census Bureau 2010). The high intensity of human disturbances and urban land use may strongly structure interactions between coyotes and native predators, resulting in spatio-temporal activity patterns different from other regions (Gosselink et al. 2003, Chamberlain and Leopold 2005, Lesmeister et al. 2015). Yet, to date little work on the effects of coyotes on other species has been carried out in the Northeast (Major and Sherburne 1987, Litvaitis and Harrison 1989). Fort Drum Military Installation in northern New York provides a useful model system for investigating meso-predator responses to the presence of coyotes in areas of high- versus low-human use intensity given the immediate juxtaposition of an urbanized landscape, where residential and administrative activities are concentrated (cantonment areas), and relatively wild and natural landscape (training areas). The adjacency of these two landscapes helps control for large-scale gradients in productivity so as to better isolate the direct influence of human activities on animal distribution patterns. In Chapter 1, I documented the spatial occurrence and temporal activity patterns of meso-predators using motion-sensitive cameras over a period of two years (2015-2016). I explored the independent or interactive influence of coyotes and anthropogenic landscape features on the space use patterns of meso-predators using two-species occupancy models. Further, I compared temporal activity patterns to investigate if meso-predators alter the timing of their activities to reduce direct competition with humans or coyotes. In Chapter 2, I investigated the degree to which local or landscape-level food and cover resources, human disturbances and structures, in addition to space use by coyote (predator) and gray fox (competitor), influenced red fox resource selection

using GPS collars. In this chapter, I also documented the diets of meso- predators using stable isotopes to explore whether foxes differed from coyotes on Fort Drum in their use of anthropogenic food sources.

This thesis is organized into two chapters, with both conforming to the style requirements of the Journal of Wildlife Management. At the end of this thesis is a synthesis of my studies with recommendations for management and further investigations.

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CHAPTER 1

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RH: Low • Meso-predator occupancy and activity pattern

Influence of Coyotes on the Occurrence and Activity Patterns of Meso-predators across a Gradient of Human Use Intensity, Fort Drum, New York

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ABSTRACT

Following range expansion in the 1900s, coyotes (*Canis latrans*) today are widespread, abundant, and potentially out-competing smaller native carnivores across North America. The degree to which coyotes influence meso-predator activity in human-dominated landscapes remains uncertain but may be nontrivial with respect to options for managing human-wildlife conflict. Using camera trap data, I quantified the degree to which meso-predators segregated their activities spatially or temporally from coyotes across a landscape gradient from high to low human use intensity. Coyotes were widespread across the study area but exhibited a lower probability of detection, lower probability of occupancy, and more concentrated activity pattern in human-dominated areas. In contrast, gray fox were detected predominantly in human-

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dominated areas with their probability of occupancy positively related to the density of culverts, which may provide ready escape and denning cover from coyotes, and their activity peaks offset from that of coyotes. Fisher temporal activity and space use appeared independent of coyotes, with their probability of occupancy increasing with forest productivity (measured by NDVI). Our study indicates that, due to reduced pressure from coyotes, gray fox may thrive in human-dominated landscapes where conflicts with humans and pets will be likely. Where direct predator control may be challenging, manipulation of cover via access to culverts might be used to favorably influence space use by gray fox.

KEY WORDS activity pattern, coyote, fisher, gray fox, New York, occupancy, single-species, two-species.

INTRODUCTION

Niche segregation in space or time is one of the fundamental mechanisms supporting the coexistence of sympatric species that share common resources (Garneau et al. 2007, Sollmann et al. 2012, Vanak et al. 2013, Zhong et al. 2016, Karanth et al. 2017). Among sympatric carnivores, the risk of inter-specific predation likely motivates smaller, less aggressive, or otherwise less dominant species to seek geographic locations or environmental features seldom used by more dominant species (Polis et al. 1989, Durant 1998, Ritchie and Johnson 2009). Given predators of differing body sizes or competitive abilities, we might expect the distribution of more ‘dominant’ predators to be driven primarily by food availability whereas subordinate predators should select habitats that balance foraging opportunity with safety from inter-specific predation (Heithaus 2001). However, populations of large predators are also structured by anthropogenic subsidies

and risks, making the outcome of competitive interactions more nuanced, especially in human-dominated environments (Prugh et al. 2009).

Anthropogenic land uses lead to abrupt habitat boundaries (edges), reduction, fragmentation and degradation of natural habitat, increased availability of anthropogenic food sources, and elevation of perceived and real mortality risks from humans (Randa and Yunger 2006), each of which may profoundly influence the distribution and abundance of mammalian predators (Cardillo et al. 2004, Bateman and Fleming 2012). Large-bodied carnivores, such as cougars (*Puma concolor*), grizzly bears (*Ursus arctos*) and wolves (*Canis lupus*) require large contiguous areas to fulfill their life requisites (Litvaitis and Villafuerte 1996) and are usually negatively impacted by the disruption of dispersal processes (Lande 1988, Proctor et al. 2005, Kojola et al. 2009), persecution by humans (Mattson and Merrill 2002, Musiani and Paquet 2004, Proctor et al. 2005, Cooley et al. 2009), and vehicle collisions (Fuller 1989, Vickers et al. 2015) prevalent in more human-dominated landscapes. In contrast, medium-sized carnivores (so-called meso-predators) are typically dietary and habitat generalists that readily capitalize on edges between land cover types as well as anthropogenic food sources and human structures (Harrison 1997, Ordeñana et al. 2010). In fact, meso-predators, such as gray fox (*Urocyon cinereoargenteus*) and red fox (*Vulpes vulpes*), often attain higher population densities in suburban landscapes compared to more rural settings (Atwood 2006, Randa and Yunger 2006). The coyote (*Canis latrans*) is intermediate between these meso- and large-carnivores in body size and adaptability to human-modified landscapes, and is likely an increasingly important player in the structuring of contemporary meso-predator communities across North America.

Coyotes expanded their range into the northeastern United States in the 1920s where today they are widespread and abundant (Gompper 2002*a*). Coyotes directly compete with

smaller carnivores such as red fox, gray fox, bobcat (*Felis rufus*) and possibly fisher (*Pekania pennanti*, formerly *Martes pennanti*), species with whom their diets substantially overlap (Cypher 1993, Warsen 2012). Given their larger body size, coyotes are likely the superior competitor, and they have been observed to kill foxes and fishers (Dekker 1983, Sargeant and Allen 1989, Fedriani et al. 2000, Farias et al. 2005, Aubry and Raley 2006, Wengert et al. 2014). Although such inter-specific killing may occur infrequently (Palomares and Caro 1999), the risk of inter-specific predation may remain a strong driver of meso-predator space use and activity patterns (Voigt and Earle 1983, Sargeant et al. 1987, Harrison et al. 1989, Crooks and Soulé 1999). Indeed, an inverse relationship has been observed between the abundance of coyotes and meso-predators (Sargeant et al. 1993), and in some cases coyote control has been related to increases in the abundance of red foxes, bobcats, raccoons (*Procyon lotor*), and skunks (*Mephitis mephitis;* Robinson 1961, Linhart and Robinson 1972). Yet, variation in a species' tolerance for human presence is also a strong driver of the spatio-temporal distribution of sympatric predators, an important consideration in the northeastern U.S., which contains the most densely populated rural and urban areas within the United States (U.S. Census Bureau 2010).

Avoidance of human-dominated areas and highly fragmented habitats by coyotes is expected to provide smaller predators with refugia from inter-specific competition (Gosselink 1999, Fedriani et al. 2000, Gosselink et al. 2003, Randa and Yunger 2006). However, as coyotes expanded their range across North America, they too have shown a remarkable plasticity in adapting to urban areas (Prugh et al. 2009). As a result, the 'coyote effect' on meso-predators may extend over a much broader gradient of landscape conditions than the effects of larger-bodied carnivores. Importantly, meso-predators such as red fox, gray fox, and bobcat have been shown to use habitat features differently depending on whether they share the landscape with

coyotes, most markedly with respect to their use of anthropogenic landscape features (Tigas et al. 2002, Lesmeister et al. 2015, Rota et al. 2016). As a result, greater understanding of the environmental, biological, and anthropogenic drivers of meso-predator activity in human-dominated environments is needed to guide effective management actions.

My objective was to gain insight into the relative and potentially interacting influence of coyotes and anthropogenic landscape features on the space use and activity patterns of meso-predators. My study location was Fort Drum, NY, USA, an area with clearly distinct areas of high versus low levels of human influence and disturbance. Anticipating coyotes to demonstrate greater avoidance of areas of high human use, I expected detection probabilities of coyotes and meso-predators to differ in areas of high versus low human use. Moreover, given that a species detection rate is to some degree related to population density (Royle and Nichols 2003), I expected an inverse relationship between the detection probabilities of coyotes and meso-predators across the landscape. I further expected meso-predators to use fine-scale habitat features differently depending on the presence of coyotes, foregoing ready access to food for greater security in landscapes they share with coyotes. I expected all carnivores to exhibit more nocturnal behavior in areas of high versus low human use (Riley et al. 2003, Way et al. 2004, Baker and Harris 2007), and, in areas of low human use, for smaller meso-predators to shift their activity patterns to potentially reduce their encounters with coyotes. Importantly, my analyses control for landscape context, and species-specific scales of response, while exploring variables that managers might capitalize on to potentially manipulate the outcomes of meso-predator space use and activity patterns in human-dominated landscapes.

STUDY AREA

This study was conducted on Fort Drum, a 434-km^2 U.S. Army installation located in northwestern New York State, USA (Fig 1.1). Fort Drum had a primarily humid, continental climate with long, cold winters and short, warm summers (USAGFD 2011). Rainfall was well distributed throughout the year with an average annual rainfall of 104 cm. In contrast, snowfall varied considerably among years, with an annual average of 277 cm. Elevations on Fort Drum range from 125 to 278 m.

My study area encompassed 360 km^2 of the installation, which I divided into two regions based on the type and intensity of human uses. The 'High Use' area (i.e., the ~36 km^2 cantonment area) consisted of a network of two or four-lane paved roads, residential housing, and support facilities (e.g. headquarters, barracks, and vehicle maintenance facilities). As of the 2010 census, there were 12,955 people residing in the cantonment, with a population density of 353.14 people/km^2 and housing unit density of 91.40 houses/km^2 (U.S. Census Bureau 2010). About half of the High Use area was 'undeveloped' forest, shrubland and grassland used as urban parks and local training areas. In contrast, the 'Low Use' area (i.e., accessible portions of the training area) had no permanent human habitation although soldiers routinely established temporary bivouac areas during trainings. The Low Use area was dominated by forest (61% of the area) interspersed with grassland (15%), shrubland (14%), and water (5%) with 5% of the area consisting of gravel or unimproved roads along with tank and jeep trails. Forest types on the base included northern mixed stands consisting predominantly of sugar maple (*Acer saccharin*), hemlock (*Tsuga canadensis*), quaking (*Populus tremuloides*) and bigtooth aspen (*Populus grandidentata*), and deciduous lowland stands consisting predominantly of sugar maple, oak (*Quercus* spp.) and American beech (*Fagus grandifolia*). Much of the southern half of Fort

Drum was agricultural land until the 1940s, and as a result forest stands during my study were still in the early stages of natural succession. Timber and wildlife were both managed for sustainable harvest within the Low Use area, with hunting seasons on coyote, red and gray fox and also trapping seasons for these species in addition to fisher. Hunting and trapping of carnivores was not permitted within the High Use area.

METHODS

Field Methods

I collected detection/non-detection data of terrestrial mammals using passive infrared cameras equipped with motion detectors (Moultrie Game Spy M-990i Gen 2, Moultrie Feeders, LLC, Alabaster, Alabama, USA). In 2015, I established 30 survey locations (10 and 20 in the High and Low Use Areas, respectively) arranged into a 2 × 2 km systematic grid (Fig 1.1), with a single camera deployed at each site from 8 August (after the denning period) to 24 September (before the hunting and trapping seasons). In 2016, I expanded the survey in both time and space with traps deployed continuously from 23 May to 29 September with 30 sites surveyed during the denning season (May-July) and 41 sites surveyed post-denning (August-September). In contrast to the uniform sampling grid in 2015, in 2016 sites were selected based on a stratified-random design that accounted for variation in road density and proportion of forest cover. Overlaying 5 equal-interval classes for each variable, I randomly chose 3 survey locations within each of the 25 resulting strata with 4 sites excluded due to accessibility constraints (N = 71 survey locations). At all sites, cameras were placed ~1-2 m from a trail and attached to trees or poles 30-40 cm above the ground. I applied commercial lures (Gusto, Canine Force, Minnesota Brand Predator Bait, Caven's, Minnesota Trapline Products, Pennock, Minnesota; Big Cheese, Milligan

Brand, Chama, New Mexico; TriNitro, Dobbin's Product, Goldsboro, North Carolina) on the animal trails in front of each camera, and reapplied lure every 10 to 15 days.

Temporal activity patterns of meso-predators

I generated a probability density distribution for each species' activity pattern by fitting a kernel density model to photo time stamps following Ridout and Linkie (2009). To minimize issues of temporal autocorrelation, photos taken within 30 minutes of another photo of the same species at the same location were excluded. I compared the shape of the probability density distributions generated using photos taken within either the High or Low Use areas to evaluate if the species altered their activities patterns, such as shifting peak periods of activity, in response to high levels of human activity. To quantify temporal overlap in the activity distribution for a given pair of species, I calculated a coefficient of overlap ($\hat{\Delta}$) which ranged from 0 (no overlap) to 1 (perfect overlap). Confidence intervals were calculated using 10,000 bootstrap samples. All analyses were conducted using the overlap package (Meredith and Ridout 2017) for Program R version 3.3.2 (R Core Development Team 2016).

Occupancy modeling

Detection/non-detection data were combined into five-day sampling occasions such that a species was considered detected at a given location if at least one photograph of the species was obtained during the 5-day occasion, and was otherwise considered undetected. Occasions having less than five active camera days due to camera malfunction were discarded. Because cameras have a limited effective detection range, I assumed that each species moved in and out of each site in a random manner following MacKenzie et al. (2004). Hence, "occupied locations" were interpreted as "used locations" such that the species was within the site at some time during the sampling frame, but not necessarily all the time, and the probability of detection was interpreted

as the “probability that the species was present and detected” (MacKenzie et al. 2004). I combined the detection/non-detection data from the two annual sampling sessions by matching the month and day of surveys across years, considering the 101 locations as independent sites to generate site-specific detection histories for each species. ‘Year’ (2015, 2016) and ‘Region’ (Low Use, High Use) were included as detection covariates to account for potential differences in animal density over time or space. Trap placement, on or off trail, was also included as a detection covariate (Cusack et al. 2015). Lastly, a covariate for ‘Season’ divided the annual sampling sessions into denning (May-July) and post-denning (August-September) periods to account for potential changes in either detectability or occupancy during these two pup development stages.

To understand the factors driving site use patterns by each species, I selected occupancy covariates related to food resources, cover/shelter, and human disturbances at varying spatial scales (George and Zack 2001). Variables were quantified within three hierarchical levels – the immediate vicinity of each site (local level), the larger spatial context surrounding each site (landscape level), and the regional context of each site in terms of coarse-scale differences in the type and intensity of human activities (regional level). At the local level, the distance between each camera and the nearest road, building, culvert and dumpster were quantified using spatial data provided by the Fort Drum GIS Program and the 2015 New York State Street and Address Maintenance Program data (NYS ITS 2015). National Land Cover Data (NLCD, Homer et al. 2015) were reclassified into four classes: forest (deciduous, evergreen, mixed forest, and woody wetlands), shrubland (evergreen dwarf-shrubland, evergreen shrubland, deciduous shrubland, and mixed shrubland), grassland (perennial graminoid vegetation, perennial forb vegetation, and emergent herbaceous wetlands), and developed area (open space, developed area of low,

medium, and high intensity), with the local land cover extracted for each survey site. Local site productivity was quantified using the Normalized Difference Vegetation Index (NDVI) which was presumed related to the population density of rodent prey (Pettorelli et al. 2011). NDVI was calculated from Moderate-resolution Imaging Spectroradiometer (MODIS, MOD13Q1 Version 6, retrieved from https://lpdaac.usgs.gov) images acquired every 16 days, with values averaged across multiple images within a given sampling season and extracted for each camera trap location. At the landscape level, proportional land cover, mean NDVI and the density of forest edges (Šálek et al. 2010) and anthropogenic features (roads, dumpsters, culverts, houses) were quantified within circular buffers around each camera trap having radii of 0.5, 1, 2, 3, and 4 km, corresponding to the range of daily-monthly movements by foxes and coyotes recorded from GPS-collar data (Chapter 2). At the regional level, each camera trap was designated as occurring within the High Use or Low Use areas. Management and analyses of spatial data were achieved using ArcGIS 10.2 (Environmental Systems Research Institute, Inc., Redlands, CA, 2012).

I applied the conditional two-species occupancy model developed by Richmond et al. (2010), which estimated the occupancy and detection probabilities of a presumed subordinate species as a function of the occupancy and detection status of a presumed dominant species. Models were fit using Program MARK 8.0 (White and Burnham 1999). The models estimated 4-8 parameters depending on whether occupancy and/or detection probabilities were modeled conditionally or unconditionally (Appendix 1.1). Each parameter can be modeled as a function of covariates, allowing us to test the simultaneous role of landscape variables and coyote occurrence on the detectability and habitat use by meso-carnivores. Given the high number of potential parameter and covariate combinations, I employed a multi-stage modeling approach following Richmond et al. (2010). At each model selection stage, candidate models were

compared using Akaike's Information Criterion with a small sample bias adjustment (AICc) and covariates were retained in models only when their inclusion yielded an improvement in AICc by more than 2 units (Burnham and Anderson 2002). The most parsimonious model identified at a given stage was carried forward to the next stage of analysis.

First, detection covariates were screened by fitting single-species, single-season occupancy models while holding occupancy probability constant over space and time. Candidate models included year (2015, 2016), trap placement (on trail, off trail), region (High Use, Low Use), season (denning, post-denning), and two-way interactions between covariates. Next, expanding on the best detection model, I added landscape variables potentially affecting site occupancy (food resources, cover/shelter, and human disturbance). This stage involved first determining the appropriate level of measurement for each covariate by species (1 local and 5 landscape contexts), whether the species responded to covariates similarly between the two regions and years, and whether species responses were linear or nonlinear (quadratic). Once the optimal scale was identified for each variable, candidate models were expanded to sets of uncorrelated covariates (all covariate pairs having $r < 0.7$ when $P < 0.05$; Dormann et al. 2013) representing a single habitat category (e.g., food resources, cover/shelter, or human disturbance). Lastly, the best sets of covariates across habitat categories were combined into candidate models along with season and interaction terms between season and landscape covariates. For each species I calculated goodness-of-fit for the most parsimonious model using 1,000 parametric bootstraps (MacKenzie and Bailey 2004).

Ultimately, I combined covariates from the best single-species models into conditional two-species models assuming coyote to be the dominant species. Candidate models tested whether occupancy probability was driven by: 1) habitat only (i.e., same intercepts, $\Psi^{BA} = \Psi^{Ba}$,

with same landscape influences on each); 2) habitat + coyote (i.e. different intercepts, $\Psi^{BA} \neq \Psi^{Ba}$, but same effects of landscape covariates on each), and 3) habitat × coyote (i.e. different intercepts and different landscape influences on Ψ^{BA} and Ψ^{Ba}), with the last model indicating the sub-dominant species responded differently to landscape covariates conditional on the presence of coyotes. Using the best models as identified by AICc, I calculated the species interaction factor (SIF; Richmond et al. 2010) as a function of the corresponding habitat variables, with SIF=1 indicating independence, >1 indicating aggregation and <1 indicating avoidance (Richmond et al. 2010).

RESULTS

Over 5519 camera-days, coyote, gray fox, red fox, fisher, and bobcat demonstrated different distributional patterns with respect to areas of high versus low human use on the base (Table 1.1, Appendix 1.2). Coyotes were widespread and common, being readily detected in areas of High Use and Low Use, albeit with a lower number of detections in the Low Use region. In contrast, gray fox were detected predominantly, and red fox exclusively, within the High Use region. Fishers were detected in both areas, but limited to the largest forest patches within the High Use region. Bobcats were detected in the Low Use region only in both years. With the exception of red fox, all species had more detections in 2016 than 2015 (Table 1.1), potentially due to the greater spatio-temporal sampling effort in the second year of study. Red fox suffered an apparent population collapse between 2015 and 2016, potentially due to an outbreak of mange with 2 of 3 foxes captured in 2016 exhibiting symptoms of mange (R. Rainbolt, Fort Drum Fish and Wildlife Management Program, pers. comm.).

Temporal activity patterns

The activity patterns of coyotes, red foxes, and gray foxes were generally consistent across years, with peaks in activity between 18:00 and 06:00 (Fig 1.2). In areas of high human activity on the base, meso-predator activity increased sharply ~18:00 and dropped sharply between ~06:00 - 08:00 (Fig 1.2), coincident with expected spikes in vehicle traffic before and after routine training and business activities. Coefficients of overlap indicated a higher degree of correspondence in activity patterns between coyotes and red foxes ($\hat{\Delta}$ = 0.85, 0.71-0.96 95% CI) compared to coyotes and gray foxes (0.76 [0.67-0.90] and 0.79 [0.63-0.88] in the High Use versus Low Use region). However, both red and gray foxes exhibited peaks in activity that were offset from peaks in coyote activity, with the pattern being consistent for gray fox across both the High and Low Use areas (Fig 1.2). Further, in both regions, gray fox initiated and terminated their period of activity earlier than coyotes (Fig 1.2). Fisher and bobcat exhibited irregular peaks in activity (Appendix 1.3), with records being too sparse to compare between years or across space, and with lower overall coefficients of overlap with coyotes than observed for foxes (coyote-fisher = 0.73 [0.57-0.87], coyote-bobcat = 0.69 [0.45-0.85]).

Occupancy models

Given data limitations, occupancy and co-occurrence models were restricted to coyote, gray fox, and fisher. The most parsimonious detection models for coyote and gray fox included covariates representing year and region (Table 1.2). Both coyote and gray fox had higher mean probability of detection in 2016 (coyote: 0.18 ± 0.02 SE, gray fox: 0.15 ± 0.03 SE) than in 2015 (coyote: 0.09 ± 0.02 SE, gray fox: 0.07 ± 0.02 SE). Coyotes were also more detectable in areas of lower human use (0.18 ± 0.02 SE) compared to the High Use region (0.11 ± 0.02 SE). In contrast, gray fox detection probability was considerably higher in the High Use region (0.36 ± 0.03 SE)

compared to the Low Use region (0.05 ± 0.02 SE). The detection probability of fisher (0.08 ± 0.03 SE) appeared to be unaffected by covariates (Table 1.2), although sample size may have been limiting (*n* = 27 detections).

Factors affecting the probability of occupancy differed among species (Table 1.2). For coyote, the most parsimonious model included a non-linear response to road proximity, indicating the probability of occupancy peaked at ~250 m from the nearest road, and declined to zero ~700 m (Fig 1.3). The probability of occupancy was lower during the denning season (May-Jul) than post-denning (Aug-Sep) for both gray fox (0.07 ± 0.05 SE and 0.64 ± 0.12 SE, respectively) and fisher (0.03 ± 0.04 SE and 0.23 ± 0.12 SE, respectively). Further, probability of occupancy increased for gray fox given an increasing density of culverts (within a 2-km radius), and increased for fisher given an increasing mean NDVI (within a 500-m radius).

Coyote influence on gray fox - Candidate two-species models included year and region as covariates affecting detection probability for both coyote and gray fox, with distance to road (quadratic form) affecting coyote occupancy and season and culvert density affecting gray fox occupancy. Strong support was observed for models that included an effect of coyote presence, with the null model (including Culvert Density and Season effects on gray fox occupancy but no effect of coyotes on either detection or occupancy) yielding $\Delta AIC_c = 5.90$ compared to the highest ranked model that included an effect of coyote presence on gray fox occupancy (Table 1.3). Contrary to expectations, the best model indicated a positive association between these two species, with gray fox being more likely to occupy areas where coyotes were present ($\hat{\psi}^{\mathrm{BA}}_{May-Jul}$= 0.21 ± 0.13 SE, $\hat{\psi}^{\mathrm{BA}}_{Aug-Sep}$ = 0.79 ± 0.12 SE) compared to where they were absent ($\hat{\psi}^{\mathrm{Ba}}_{May-Jul}$ = 0.01 ± 0.02 SE, $\hat{\psi}^{\mathrm{Ba}}_{Aug-Sep}$ = 0.14 ± 0.12 SE). The species interaction factor calculated from the most parsimonious model indicated spatial aggregation between species in both seasons (May –

July: 1.30 ± 0.12 SE, August – September: 1.25 ± 0.11 SE). Consistent with single species models, the top models further indicated that the probability of occupancy by gray fox was higher later in summer and in areas having a higher density of culverts (Appendix 1.4), responses that did not vary with the presence or absence of coyotes.

Coyote influence on fisher – Candidate models included year and region as covariates affecting detection probability for coyotes whereas no covariates were included for fisher detection. Models also included distance to road (quadratic form) as a covariate affecting coyote occupancy and mean NDVI within 500 m affecting fisher occupancy. Little support was observed for probability of occupancy by fisher being conditional on the presence of coyote (Table 1.3; Appendix 1.5), with the best-supported model yielding SIF = 1, and indicating independence in the space use patterns of these two species.

DISCUSSION

Meso-carnivores in the eastern United States have thrived largely free of the top-down pressures exerted by larger carnivores since the mid-nineteenth century (Gompper 2002*b*). Yet over the past several decades, eastern meso-carnivores such as red and gray foxes, fisher and bobcat have experienced competition from a novel and potentially dominant predator following range expansion by coyotes (Parker 1995*a*, Gompper 2002*a*). Coyotes have long been shown to suppress the abundance and distribution of fox species, primarily in arid and non-forested regions where sufficient cover seems to be a limiting factor (Cypher and Spencer 1998, Kamler et al. 2003, Arjo et al. 2007, Nelson et al. 2007, Robinson et al. 2014). But in the forest-dominated eastern states cover should be more readily accessible, and gray fox in particular may climb trees to avoid interactions with coyotes (Wooding 1984, Cypher 1993). Nevertheless, this

study provides evidence that secure denning cover may be limiting for gray fox in the forested landscapes they share with coyotes. Moreover, I identified multiple advantages to meso-predators in human-dominated landscapes including reduced coyote densities, restricted and more predictable coyote activity patterns, and greater access to secure denning cover in the form of culverts and other manmade structures.

Gray fox may exploit human-dominated landscapes specifically to reduce their exposure to coyotes (Gosselink 1999, Fedriani et al. 2000, Gosselink et al. 2003, Randa and Yunger 2006). Regional-scale differences in human use intensity across Fort Drum drove apparent differences in meso-predator density given greater detection of gray fox and reduced detection of coyotes in areas of high human use (Royle and Nichols 2003, Robinson et al. 2014). Differences in hunting and trapping pressure across Fort Drum is an unlikely alternative explanation for the large-scale differences observed in mesopredator distributions given the low overall harvest rate observed (4 foxes trapped between 2006 and 2011, R. Rainbolt, pers. comm.). Rather, I observed strong positive associations between both gray fox and coyotes and anthropogenic landscape features, specifically areas of higher culvert density for gray fox and areas adjacent to roads for coyotes. Roads provide food directly via carcasses (resulting from vehicle collisions) and indirectly via maintenance of a road margin that provides grassland habitat for small mammals (Rytwinski and Fahrig 2007, Šálek et al. 2010). However, using areas near roads incurs an increased mortality risk from vehicles (Grinder and Krausman 2001, Tigas et al. 2002). The influence of roads as both an attractive force (food source) and repulsive force (mortality risk) explains the nonlinear response exhibited by coyotes, with their highest probability of use predicted to occur ~200-300 m from the nearest road.

The apparent aggregative response between gray fox and coyotes that I observed is more likely a statistical artefact than the result of a facultative or commensal relationship between these species. It is important to recognize that the SIF is calculated in so-called "environmental space", i.e. as a function of the covariate responses, rather than in "geographic space", i.e. in terms of physical geographic coordinates. Consider that the density of culverts, measured within a 2-km radius for gray fox, peaked within 50-300 m of the nearest road (Fig 1.4), coincident with the predicted peak occupancy by coyotes (Fig 1.3). As a result, the SIF indicated aggregation between coyotes and gray fox that was not apparent when the models were applied to the physical landscape on Fort Drum (Fig 1.5). In fact, whereas coyotes were predicted to occur across the base, gray fox were predicted to occur almost exclusively in areas of high human use where culverts, or similar man-made structures, may give fox the ability to avoid coyotes as a finer spatio-temporal scale than our models were able to quantify.

In this study gray fox were strongly associated with all anthropogenic landscape features (roads, buildings, culverts, dumpsters, edge density, and developed areas) and negatively correlated to all variables representing forests, shrub, grassland and greenness (NDVI). However, culvert density consistently received the greatest statistical support in models of gray fox occupancy. Red fox, swift fox (*Vulpes velox*), kit fox (*V. macrotis*) and arctic fox (*V. lagopus*) have each been shown to use culverts as den sites (Egoscue 1956, Eberhardt et al. 1983, Reese et al. 1992, Gosselink 1999, Jackson and Choate 2000, Harrison and Whitaker-Hoagland 2003, Carter et al. 2012), and as a means of avoiding agonistic encounters with coyotes (Scott-Brown et al. 1987, Cypher and Spencer 1998). Kit fox preferentially selected dens having smaller-diameter entrances, presumably because these may not be accessible to larger-bodied carnivores like coyotes (Arjo et al. 2003). An experimental array of artificial escape dens successfully

increased swift fox survival and abundance in a coyote-occupied landscape (Mcgee et al. 2006). Although gray foxes have been reported to maintain their population status in areas co-occupied by coyotes, due in large part to their ability to escape predation by climbing trees (Wooding 1984, Cypher 1993), my results indicate that in areas where gray fox and coyotes overlap, gray fox may be as den-dependent as the non-tree-climbing foxes across North America. During critical pup-rearing periods, gray fox require secure ground-based dens (Sullivan 1956, Nicholson et al. 1985) and likely benefit similarly from culverts as other foxes. My study is the first to indicate a relationship between culvert density and gray fox occurrence, and these findings warrant further investigation to determine the degree to which denning substrates may be limiting gray fox and whether artificial den sites may be used to offset that habitat limitation.

Foxes also may experience an advantage in areas of high human use given that coyotes exhibit more strongly nocturnal behavior in these areas (Quinn 1995, Riley et al. 2003, Atwood et al. 2004, Gehrt et al. 2011, Magle et al. 2014), compared to undisturbed areas (Major and Sherburne 1987, Crabtree and Sheldon 1999, Kitchen et al. 2000), which may make their movements more concentrated and predictable to gray fox. The offset peaks in activity I observed may allow gray and red fox to avoid coyotes temporally if not spatially. For example, gray fox activity peaked at 20:00-22:00, a period within which 24% of their activities were recorded compared to only 11% of coyote activities (coyotes were most active 00:00-02:00, with 21% of their activities recorded during this time period). This temporal segregation of activity patterns, paired with low level of competition and ready cover provided by culverts, may be the primary determinants of successful coexistence between coyotes and foxes on Fort Drum.

Despite a high degree of dietary overlap with coyotes in New York (Warsen 2012), fisher exhibited independence from coyotes in their occupancy patterns on Fort Drum. Fishers avoid

establishing home ranges in areas dominated by non-forested habitats (Weir and Corbould 2010), while coyotes typically use open-canopy forests and edge habitats (Theberge and Wedeles 1989, Fedriani et al. 2000, Kays et al. 2008, Lesmeister et al. 2015). Thus, some degree of habitat segregation, combined with differences in their temporal activity patterns, might reduce potential interactions between coyotes and fishers and facilitate their coexistence. Likewise bobcats exhibited irregular activity patterns, in contrast to the nocturnal patterns exhibited by coyotes in this study, which may provide some degree of temporal segregation from competition by coyotes. These observations are consistent with previous studies in which coyotes did not appear to influence the site use by non-canid, native meso-predators in urban areas (Prange and Gehrt 2004, Gehrt and Prange 2006, Cove et al. 2014). Indeed, in recent years both fisher and bobcat populations have expanded across New York State (A.J. MacDuff, NY State Department of Environmental Conservation, pers. comm.).

MANAGEMENT IMPLICATIONS

As the continuing growth of human population accelerates conversion of agricultural and forested land to residential, commercial, and industrial areas (Nickerson et al. 2011), urban predator populations are also likely to expand (Sargeant et al. 1987). Understanding the spatio-temporal drivers of habitat use and population density of urban predators is critical for managers concerned with mediating human-predator conflict or health concerns related to wild carnivores. Over relatively large spatial scales, coyotes may suppress fox populations (Levi and Wilmers 2012, Newsome and Ripple 2015) but, at relatively finer scales, anthropogenic landscape features help foxes maintain their numbers in landscapes shared by coyotes and also may bring foxes into closer proximity with humans. While urban foxes may be welcomed to some degree as

a means of reducing small mammal abundances, and by extension reducing the risk to humans of tick-borne diseases, their presence poses other risks to humans, pets and livestock (Graham et al. 2005, Cassidy and Mills 2012). Traditional mortality- (e.g. culling) or fecundity-based control strategies (e.g. baits containing abortive compounds) may be difficult to execute or expensive to implement in urbanized landscapes. An alternative method of management is habitat and resource manipulation, which involves reducing habitat quality or the abundance of favored resources (White et al. 2006). This study, in combination with manipulative studies with other fox species in the western U.S. (Mcgee et al. 2006), indicates that manipulation of artificial den sites (culverts) might provide an effective means of managing fox space use and mitigating human-fox conflict in human-dominated landscapes in the eastern U.S..

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Table 0.1. Meso-predators detected on Fort Drum, NY, 2015-16. The percentage of camera locations where the species was detected, with the number of independent photo events shown in parentheses, and the relative abundance index (RAI) are shown separately for the High Use and Low Use areas, as well as for each survey year.

		Percentage of sites where species detected (photo events)		RAI (SE)	
Species	Year	High Use	Low Use	High Use	Low Use
Coyote	2015	30 (4)	45 (15)	0.9 (0.5)	1.7 (0.6)
	2016	48 (27)	61 (142)	1.8 (0.6)	5.6 (1.5)
Gray fox	2015	80 (19)	10 (7)	4.3 (1.1)	0.7 (0.6)
	2016	76 (342)	17 (29)	21.3 (8.2)	1.1 (0.5)
Red fox	2015	60 (52)	0 (0)	11.0 (6.8)	0.0 (0.0)
	2016	12 (11)	0 (0)	0.8 (0.7)	0.0 (0.0)
Fisher	2015	10 (2)	15 (3)	0.5 (0.5)	0.4 (0.2)
	2016	8 (5)	24 (17)	0.3 (0.2)	0.6 (0.2)
Bobcat	2015	0	10 (2)	0.0 (0.0)	0.2 (0.1)
	2016	0	17 (11)	0.0 (0.0)	0.5 (0.2)

Table 0.2. Top supported single-species occupancy models predicting probability of detection (*p*) and occupancy (Ψ) for coyote, gray fox, and fisher on Fort Drum Military Installation, New York, USA, 2015-16. Given for each covariate is the estimated coefficient (β) and 95% confidence interval (CI).

Species	Parameter	Model term	β	LCI	UCI
Coyote	*p*	Intercept	-3.00	-4.20	-1.8
		Year: 2016	0.86	0.23	1.50
		Region: High Use	-0.69	01.24	-0.14
	Ψ	Intercept	0.21	-1.39	1.80
		Distance to nearest road (km)	9.68	-3.47	23.03
		Distance to nearest road squared	-22.53	-45.17	0.11
Gray fox	*p*	Intercept	-2.27	-3.08	-1.46
		Year: 2016	0.93	0.36	1.50
		Region: High Use	1.03	0.34	1.71
	Ψ	Intercept	-5.49	-8.14	-2.85
		Season: Aug - Sep	3.09	0.91	5.27
		Culvert density (per ha, r = 2000 m)	22.93	12.11	33.75
Fisher	*p*	Intercept	-2.50	-3.24	-1.76
	Ψ	Intercept	-20.38	-36.32	-4.43
		Season: Aug - Sep	2.20	-0.25	4.65
		Average NDVI (r = 500 m)	22.57	2.75	42.39

Table 0.3. Conditional two-species occupancy models for interactions between coyotes (presumed dominant species) and either gray foxes or fishers on Fort Drum Military Installation, New York, USA, 2015-16. Models tested whether occupancy (i.e., site use) by the subdominant species was conditional on coyote presence. For each model, the number of estimated parameters (*K*), difference in AIC from the best model (ΔAICc), and AICc model weight (*w*) are indicated.

Subdominant species	Occupancy model	*K*	ΔAICc	*w*
Gray fox	Coyote + CulvDen[a] + Season	13	0.00	0.42
	Coyote × Season + CulvDen	14	0.95	0.26
	Coyote × CulvDen + Season	14	2.65	0.20
	Season + CulvDen	12	5.90	0.11
Fisher	NDVI[b]	9	0.00	0.68
	Coy + NDVI	10	2.14	0.24
	Coy × NDVI	11	4.35	0.08

[a]Culvert density quantified within 2 km radius.

[b]Normalized Differential Vegetation Index averaged within 500 m radius.

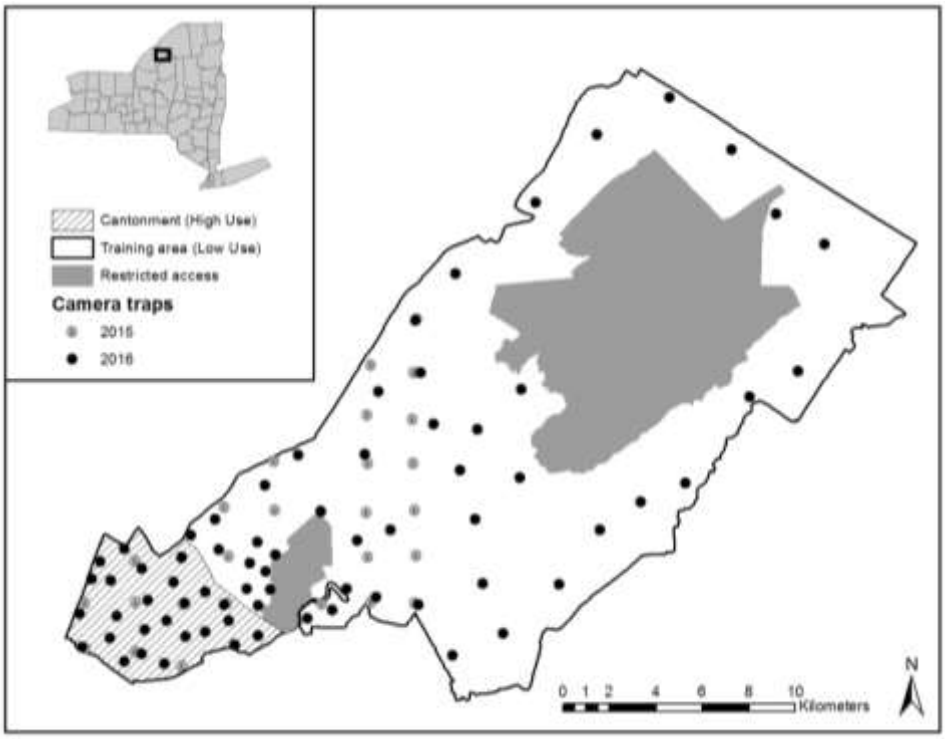

Figure 0.1. Study area on Fort Drum Military Installation, NY, showing camera trap locations in 2015 (gray dots) and 2016 (black dots). Areas with restricted access (gray polygons) were not surveyed.

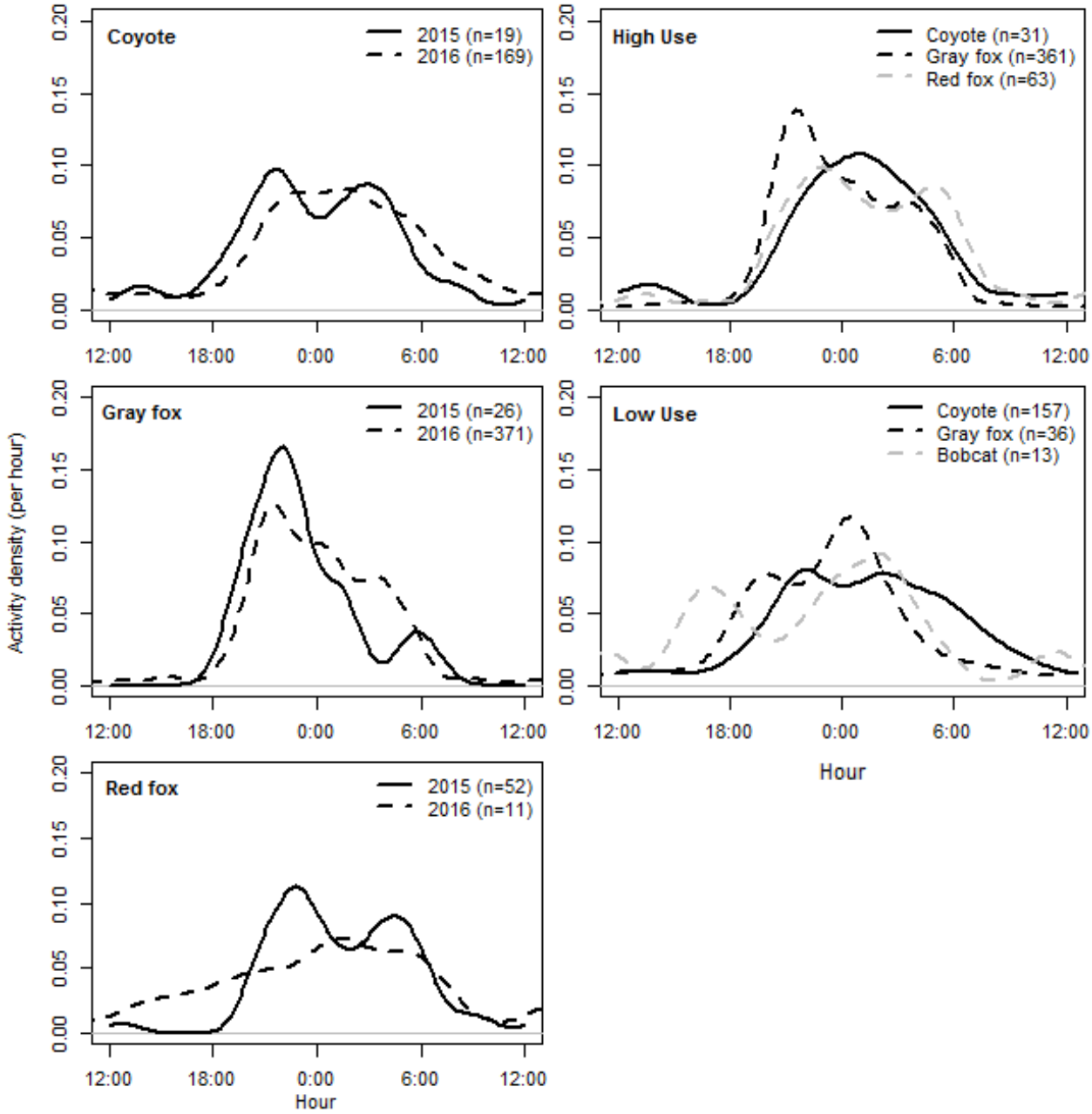

Figure 0.2. Kernel density estimates of temporal activity patterns of meso-carnivores on Fort Drum, NY. Species detections were pooled across the study area to elucidate activity differences between years (left panels) or, alternatively, pooled across years to elucidate differences between areas of high (cantonment) versus low (training) human use on the base (right panels). Numbers in parentheses indicate the total number of photo records used to fit kernel density models.

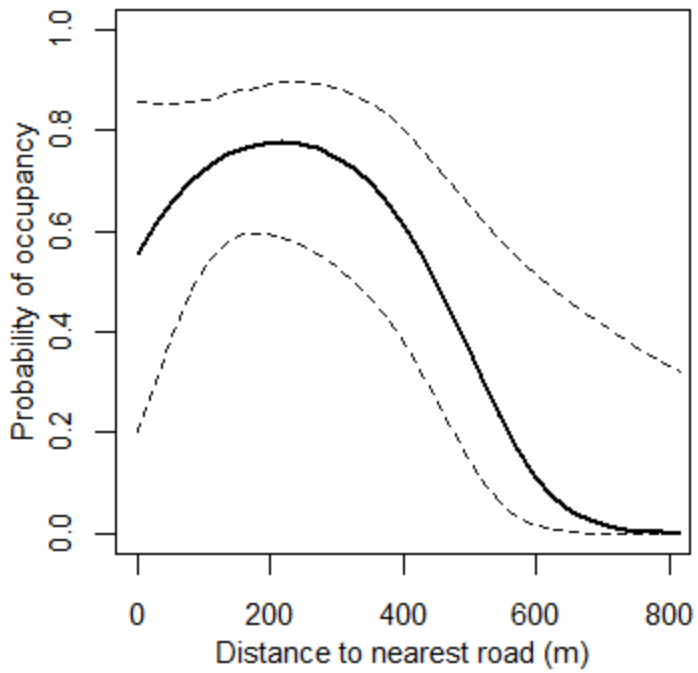

Figure 0.3. Partial slopes with 95% confidence intervals for site occupancy (i.e., site use) probability showing the nonlinear response of coyotes to the proximity of the nearest road as predicted by the best supported single species model.

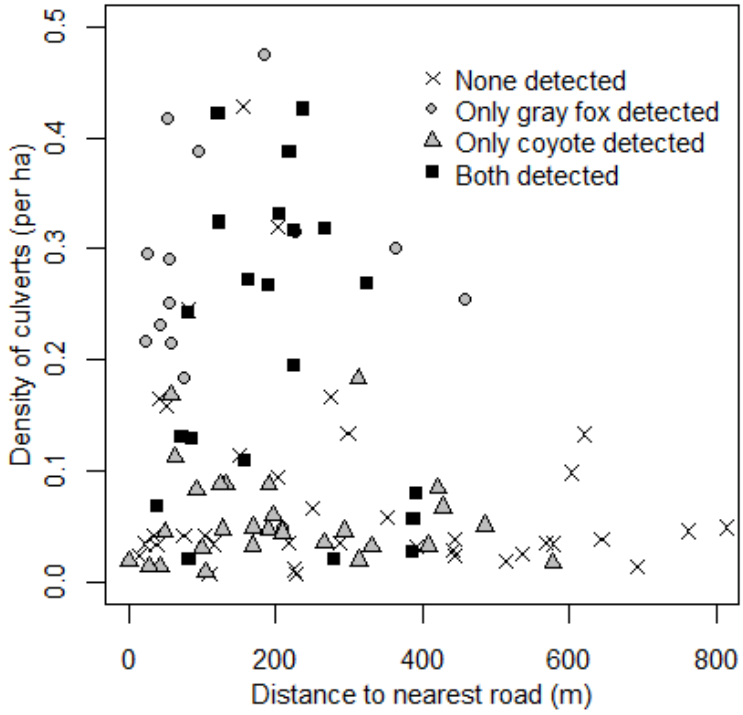

Figure 0.4. Relationship at each camera trap location between the proximity of a road and the density of culverts within a 2-km radius. Whether coyotes (gray triangles), gray fox (gray circles), both species (black squares), or none (×) were detected at each sites is indicated.

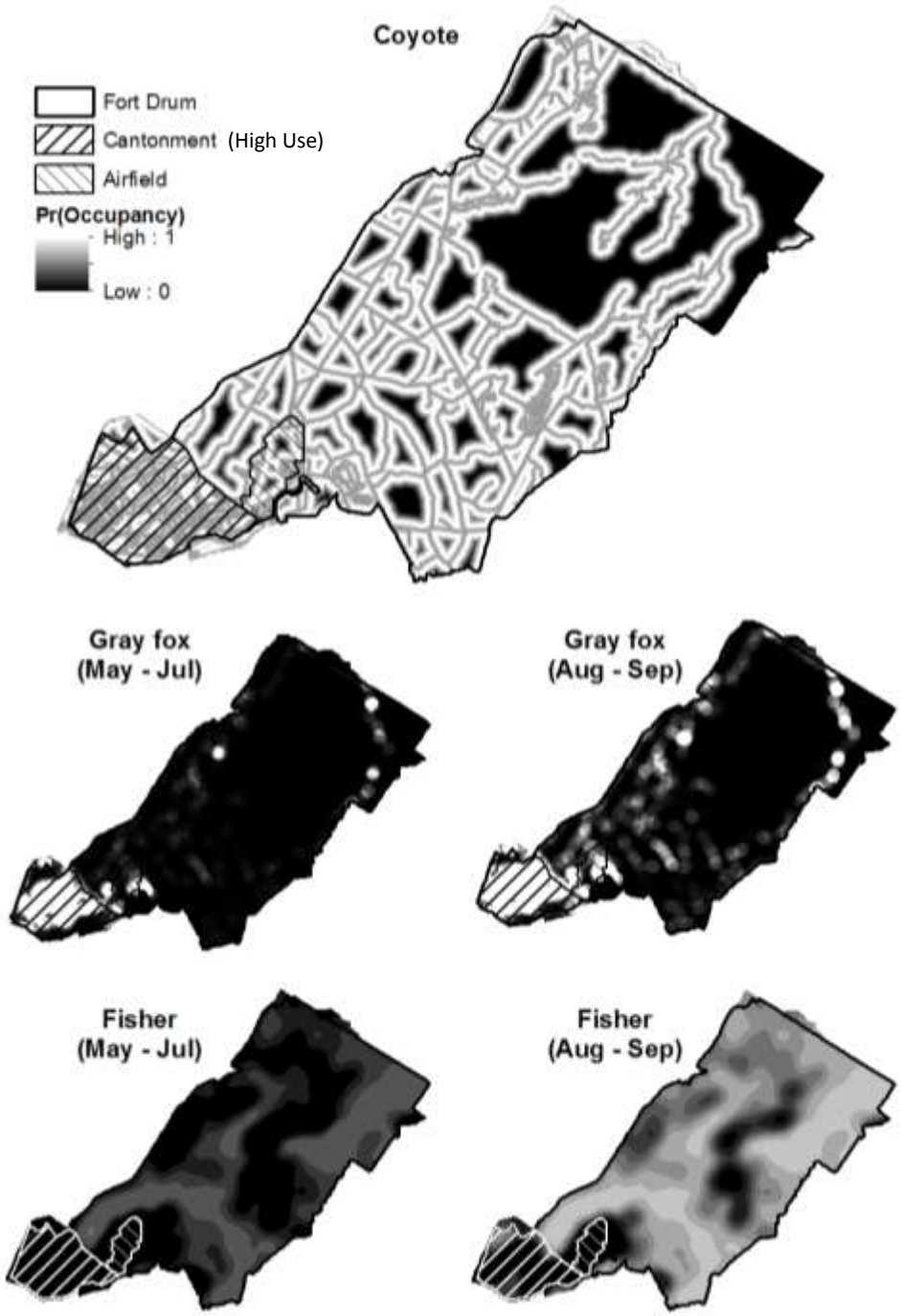

Figure 0.5. Predicted probability of occupancy (i.e., site use) for each 30 x 30 m cell of the landscape based on the best supported single-species models for coyote, gray fox, and fisher. The airfield is indicated, which was demarcated as a Low Use area in terms of human activity but remains subject to high wildlife conflict via air strike hazards.

CHAPTER 2

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RH: Low •Red Fox Resource Selection

Drivers of Red Fox Resource Selection and Diet in a Human-Dominated Environment, Fort Drum, New York

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ABSTRACT

Red fox (*Vulpes vulpes*) are commonly found in urban landscapes across North America where they are an increasing concern for human as well as domestic and wild animal health, and particularly difficult to manage using traditional approaches. To better understand and potentially manage fox use of human-dominated landscapes, I investigated red fox resource selection patterns and diets on the Fort Drum Military Installation, New York. Using radio telemetry data from 8 foxes (Jul 2014 to Nov 2015), I assessed the degree to which local or landscape-level food and cover resources, human disturbances, and space use by coyote (*Canis latrans*; dominant predator) and gray fox (*Urocyon cinereoargenteus*; competitor) influenced red fox responses to

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natural and anthropogenic landscape features. Garbage management on Fort Drum appears to sufficiently limit red fox access to human sources of food, evidenced by the lower carbon isotope signature of red fox diets on Fort Drum compared to their counterparts within the Adirondack Park. Yet, foraging habitat appeared limiting with red fox drawn to human dominated-landscapes given the abundance of preferred foraging habitats (open habitats) they provide compared to the largely forested matrix across the base. Coyotes too may be a driver of fox space use given red fox selection for areas of high culvert density, known to provide secure denning and escape cover for a variety of fox species. Our results indicate that manipulation of foraging habitats (open grasslands) and access to security cover (remnant forest and shrub patches, culverts) within human-dominated landscapes may provide a mechanism for mitigating the risk of human-fox conflict.

KEY WORDS GPS collar, New York, red fox, resource selection function, stable isotope analysis, urban carnivores.

INTRODUCTION

Anthropogenic landscape changes have severely reduced the availability, and altered the quality, of natural habitats for wildlife – remaining the single largest threat to species persistence on a global scale (Randa and Yunger 2006). Yet, a wide range of species have adapted to and even thrived in human-dominated landscapes (McKinney 2002, Bateman and Fleming 2012). A number of predators, including large-bodied species like black bear (*Ursus americanus*) and mountain lion (*Puma concolor*), increasingly have been documented using suburban environments (Kretser et al. 2009*b*, Dellinger et al. 2013, Moss et al. 2016). Carnivores may benefit from higher densities of synanthropic prey species in urbanized environments (e.g. rodents, moles, shrews, and birds) as well as livestock and road-kill (Morey et al. 2007, Bateman

and Fleming 2012, Krauze-Gryz et al. 2012). More omnivorous species like black bear and coyote (*Canis latrans*) may additionally take advantage of increased availability of other anthropogenic food sources such as garbage, compost, and pet food. Spatio-temporal trade-offs between food availability and mortality risk may tip the balance on the attractability of urbanized environments compared to more wild landscapes for wildlife, for example, during periods of natural food scarcity (Aune 1991, Beckmann and Berger 2003, Greenleaf et al. 2009) or perhaps due to changes in the density of a competitor or predator (Newsome and Ripple 2015). Some carnivores themselves have become synanthropic, especially those in the meso-carnivore guild such as raccoon (*Procyon lotor*) and stone marten (*Martes foina*), which behave benefitted from anthropogenic-habitat modifications and associated reductions in predation or hunting pressure in urban environments (McKinney 2006). One synanthropic carnivore, the red fox (*Vulpes vulpes*), has successfully invaded and persisted in cities and suburbs across Europe, Asia, parts of northern Africa, Australia and most of North America (Cavallini and Lovari 1994, Cagnacci et al. 2004, Soulsbury et al. 2010, Krauze-Gryz et al. 2012, Díaz-Ruiz et al. 2016, Walton et al. 2017). Although red fox inhabit a wide range of ecosystems throughout their range, from tundra and prairie to forest, they achieve particularly high densities in farmland and urbanized landscapes (Macdonald and others 1980, Dekker 1983, Adkins and Stott 1998, Van Etten et al. 2007).

Despite their common occurrence in urbanized areas (Soulsbury et al. 2010), urban red fox have been the subject of relatively few studies in North America to date (Sargeant and Allen 1989, Adkins and Stott 1998, Gosselink 2002, Lavin et al. 2003, Gosselink et al. 2007, 2010). Yet, high densities of red fox in urban areas are an increasing concern for human as well as domestic and wild animal health. Red fox are vectors for sarcoptic mange, canine distemper,

rabies, and parasites such as tapeworms and roundworms (Wandeler et al. 2003). Transmission of diseases and parasites may be greater in urban settings owing to high population densities, small and tightly-knit home ranges (Gosselink 1999), and, by extension, higher degrees of social interactions among foxes compared to their more rural counterparts (Gosselink 2002). But red fox presence may to some degree also be valued in human-dominated environments for the role they play in potentially limiting other nuisance wildlife such as rodents, rabbits, and woodchucks (*Marmota monax*; Novak and others 1987), and especially for predating on small mammals that carry the bacteria causing Lyme disease (*Borrelia burgdorferi*). Better understanding of the drivers of space and resource use by urban red fox is needed to effectively manage their ecological impacts and the risks they pose to humans and pets.

The success of urban foxes lies in their ability to exploit human-derived sources of food and cover, which may be more abundant, less seasonal, and easier to obtain in urban versus wild landscapes (Gosselink et al. 2003, Contesse et al. 2004). But one potentially under-appreciated driver of red fox space use is the coyote, which expanded its range into the eastern United States beginning ~1925-1940 and today is both widespread and abundant (Parker 1995*b*). Coyotes are known to displace red fox from preferred habitats directly through killing (Sargeant and Allen 1989) or indirectly by competitive exclusion (Voigt and Earle 1983, Major and Sherburne 1987, Sargeant et al. 1987, Harrison et al. 1989). Although intra-guild predation by coyotes on foxes may be rare (Palomares and Caro 1999), the risk perceived by foxes may be sufficient to drive their avoidance of areas regularly used by coyotes (Lima and Dill 1990). In fact, a large-scale (county-level) study of the eastern United States linked increasing coyote density to increasing incidence of Lyme disease in human populations, with the assumed mechanism being that coyotes suppressed red fox abundance leaving fewer carnivores predating upon the small

mammals that elevate tick and disease prevalence (Levi et al. 2012). However, at a finer-scale red fox may find refugia in human-associated habitats (residential areas, urban 'green' spaces) that coyotes are either less willing to exploit or in which coyotes, in contrast to fox, may be less tolerated by humans (Gosselink et al., 2003; Gehrt et al., 2009). Given the propensity of red fox to use urban environments, finer-scale insights into the drivers of their space use in human-dominated landscapes are needed to better understand how to manage their positive and negative impacts.

Herein, I investigated the resource selection patterns and diets of red fox in and around human-dominated landscapes on the Fort Drum Military Installation, New York, USA. A previous camera trap study (Chapter 1) detected red fox exclusively within the cantonment area, where residential and administrative activities are concentrated. By tracking GPS-collared foxes, I assessed the degree to which local or landscape-level food and cover resources, human disturbances and structures, and space use by coyotes (predator) and gray foxes (*Urocyon cinereoargenteus*; competitor) influenced red fox responses to natural and anthropogenic landscape features – seeking avenues by which fox space use might be effectively manipulated in this human-dominated landscape. I further explored the level of diet augmentation among meso-carnivores with anthropogenic food sources on Fort Drum, expecting red fox to make greater use of anthropogenic sources of food than gray fox or coyotes.

STUDY AREA

I tracked the movements and resource selection patterns of red fox within and around the human-dominated areas of Fort Drum Military Installation, New York, USA (Appendix 2.1), including the ~36 km^2 cantonment, where residential and administrative buildings are contained, and the

~4 km^2 Wheeler-Sack Army Airfield (WSAAF). Although these areas were fenced, collared foxes passed through the fences routinely and roamed to neighboring training areas and private lands, which were unfenced. Approximately 12,955 people resided in the cantonment area (353.14 people/km^2) at a housing unit density of 91.40 houses/km^2 (U.S. Census Bureau 2010). Approximately 45% of the cantonment area was developed with two or four-lane paved roads (~6 km/km^2) separating blocks of industrial properties (headquarters, shops, offices, parking lots, and vehicle maintenance facilities), residential buildings, and landscaped yards (US Army Garrison Fort Drum 2011). The remaining 55% of the area remained 'undeveloped' (forest, shrubland, and grassland) and are used as urban parks and local training areas. The WSAAF consisted of a few buildings, runways, and grassy areas. In order to reduce aircraft collision with wildlife, land cover at the airfield was maintained as uniformly as possible to reduce habitat diversity, and grass is maintained at a uniform height to discourage flocking bird species and rodents. Animal carcasses were removed from the airfield entirely to avoid attracting scavengers.

METHODS

Telemetry data

The Fort Drum Fish and Wildlife Management Program captured nine red foxes (six males, three females; SUNY ESF Animal Care Protocol #130602) in June-Nov 2014 and May-Aug 2015 using foot-hold traps, fitted each animal with a GPS collar (Telemetry Solutions Inc., Quantum 4000E small), and released the animal on site (Appendix 2.1). To maximize GPS battery life, collars were set to alternate schedules daily between a single fix/day at 03:00 and 6 fixes/day at 4-hr intervals. Collared foxes were monitored from capture (summer) through November 2015 or until batteries expired. Three males dispersed off Fort Drum during the study, one within the first

week following its release, leaving eight fox for the modeling exercise. One juvenile male died of unknown causes one month following release, and the remaining animals were monitored 4.5-12 months ($\bar{x}$ = 7.5 months, SD = 2.5, n = 7).

A total of 70-550 GPS locations were acquired per fox ($\bar{x}$ = 342, SD = 127), at a fix rate of 52-75% across animals. To quantify fix rate bias, I deployed test collars (n = 44 sites) that attempted a GPS fix every 4 hours in forest, shrub, grass, and developed land covers, with collars left at a site for 48 hours, and modeled the probability of a collar successfully acquiring a GPS location (P_{fix}) following Frair et al. (2004). P_{fix} did not vary with land cover type, but varied considerably between seasons (leaf-on: P_{fix} = 0.21 [0.09-0.42]; leaf-off: P_{fix} = 0.93 [0.85-0.97]).

Resource selection modeling

Monthly movement rates by red fox were highest Sep-Dec (Fig 2.1a), coincident with the majority of the monitoring data. Strong diurnal differences in movement rates were observed with foxes being active from dusk to dawn and indicating little activity midday (Fig 2.1b). Importantly, the proportion of time foxes spent in each cover type varied between day (08:00-16:00) and night (20:00-04:00; Fig 2.2), thus models were fitted to data pooled across seasons (fitting a single annual model) but separated between day and night.

In each time period, I estimated a population-level resource selection function (RSF) that compared locations used by red fox (GPS fixes) to locations available within the annual range of each animal (i.e. 3rd order selection; Johnson 1980). Annual 95% kernel density home range estimates averaged 6.80 km^2 (4.37 SD, range 0.61 – 13.90 km^2; Appendix 2.1) with no apparent differences between males (n= 5) and females (n = 3, t = 0.38, P = 0.36) or between juveniles (n = 3) and adults (n = 5, t = 1.36, P = 0.12), although sample sizes were small. Within each

animal's home range, I generated randomly available points from a uniform distribution at a ratio of 1 used to 1 random location.

I compared used and available locations based on potential food resources, security cover, anthropogenic disturbance, and competition at each location (local level) and within the area surrounding each location (landscape level; Appendix 2.2). At the local level, I quantified the distances between each point and the nearest road, building, culvert, and dumpster using spatial data provided by the Fort Drum GIS Program and the New York State Street and Address Maintenance Program data from 2015 (NYS ITS 2015). I also identified local cover type as forest (deciduous forest, mixed forest, and evergreen forest), shrubland (deciduous shrubland), grassland (perennial graminoid vegetation, perennial forb vegetation, and hydromorphic rooted vegetation,), or developed (developed and disturbed) after reclassifying polygon land use/land cover data provided by the Fort Drum GIS Program. To account for the effect of potentially dominant meso-carnivores on red fox resource selection, I mapped the predicted probability of occupancy by coyote and gray fox modeled in a camera trap study (Chapter 1) to each 30 × 30-m cell in the landscape. For each red fox location, I extracted the predicted probability of use by coyote and gray fox, assuming that the occupancy status of these species remained largely stationary between 2014-15 (when red foxes were monitored) and 2015-2016 (when the companion study was completed). For each covariate, I also calculated the landscape-level context using circular buffers centered on each fox location having radii of 0.1, 0.25, 0.5, 1, 1.5, and 2 km – radii that corresponded to the range of daily-monthly movements by foxes on Fort Drum. Within each buffer I quantified the density of anthropogenic features, proportion of area covered by each land cover type, and mean occupancy probabilities for coyote and gray fox. Spatial analysis was conducted using ArcGIS 10.2 (Environmental Systems Research Institute,

Inc., Redlands, CA, 2012). Continuous covariates were standardized prior to fitting models (Appendix 2.3).

For each time period, I fit mixed-effects logistic regression models including a random intercept for each fox (Gillies et al. 2006). I included random coefficients to model individual variation in fox responses to anthropogenic features, with the need for random coefficients identified *a priori* by fitting models to each individual fox. To adjust for seasonal fix rate bias, I applied $1/P_{fix}$ as a sample weight to each acquired location and 1 to each available location (Frair et al. 2004). Models were fit using GLLAMM in Stata 11 (StataCorp, College Station, TX, 2009). To identify the best set of fixed effects, I derived maximum-likelihood estimates using adaptive quadrature with 8 integration points (Rabe-Hesketh and Skrondal 2008) while holding the random effects structure constant (random intercept for each fox), and ranked support across candidate models based on Akaike's Information Criterion (AIC, Burnham and Anderson 2002, Bolker et al. 2009, Zuur et al. 2009).

Model selection involved first identifying the best supported set of covariates within each habitat category (food, cover/shelter, human disturbance, or competition; with models including pairs of variables having $r < 0.7$ when $P < 0.05$ following Dormann et al. 2013), and their appropriate scale of analysis (1 local and 6 landscape contexts, and linear versus quadratic fit). Next, a full model included the best set of covariates from each habitat category as well as interaction terms testing for trade-offs between selection for foraging habitats (roads, grasslands, and dumpsters) and security cover (forest, shrub, culverts). Ultimately, covariates and interaction terms were retained only when their inclusion yielded an improvement in AIC by more than 2 units. After selecting the most parsimonious set of fixed effects, I evaluated whether the inclusion of random coefficients explained additional variation in fox resource selection patterns.

For a random coefficient model to be accepted, I required a statistically better fit over the random intercept-only model (based on a Likelihood-Ratio Test; Pinheiro and Bates (2000), Bolker et al. (2009)).

I assessed the predictive capacity of the final model in each time period using 4-fold cross-validation following Johnson et al. (2006). This approach compared the number of fox observations expected (model predicted) versus those observed (withheld data) within 10 equal-interval bins using linear regression, with a good model indicated by a high coefficient of determination (R^2) and slope not different from 1. To understand non-linear responses and interactions among covariates, I mapped the marginal (population) response as:

$$w(x) = \frac{\exp(\beta_1 x_1 + \ \ldots + \beta_i x_i)}{1 + \ \exp(\beta_1 x_1 + \ \ldots + \beta_i x_i)}$$

where $w(\boldsymbol{x})$ is the relative probability of a pixel being selected, and β_i is the coefficient estimate for variable x_i. In the case of random slopes, conditional estimates were computed for each fox and individual responses plotted using the equation above.

Stable isotope analysis of carnivore diets

I performed stable isotope analysis on mammalian guard hair because stable isotope values of hair reflect the diet over a wide range of time. Hair samples were collected opportunistically from animals trapped during our collar deployment efforts, registered trappers, and road kills between 2013-2015. All red fox (n = 14) and gray fox (n = 4) samples were acquired within or immediately adjacent to the cantonment area while all coyotes samples (n = 11) were acquired from the training area and WSAAF. Stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) analyses were conducted by the Cornell University Stable Isotope Laboratory, Ithaca, NY. Stable isotopic ratios are presented using the standard delta (δ) notation in parts per thousand (‰) as:

$$\delta^{13}C \text{ or } \delta^{15}N = [(R_{SAMPLE} / RS_{TANDARD}) -1] \times 1000$$

where R_{SAMPLE} and $R_{STANDARD}$ corresponded to the ratio of heavy to light isotopes in the sample and the international standard, respectively (Vienna PeeDee Belemnite, PDB, for carbon and atmospheric nitrogen, N_2, for nitrogen).

RESULTS

The most parsimonious RSF models, both day and night, included fox responses to food and cover resources and anthropogenic disturbances, but not to coyote or gray fox space use (Table 2.1). Cross-validation indicated that the final model in each time period demonstrated a high predictive capacity (intercept ≈ 0, slope ≈ 1, $R^2 \geq 0.94$; Table 2.2). In the day model, inclusion of random coefficients, which allowed individual fox responses to vary with respect to culvert density and the proportion of area developed, produced a significantly better model compared to fitting these responses using fixed effects only (LRT $\chi^2 = 28.86$, $P < 0.01$), with random slopes explaining 43.1 and 6.7% of the model variance, respectively. In the night model, a random coefficient for the proportion of area developed explained only 1% of the total model variance but improved overall model fit (LRT $\chi^2 = 19.46$, $P < 0.01$).

Red fox selected forest, grassland, and shrubland cover over developed land, with the magnitude of effects reduced during the night when fox were active compared to daylight hours, and with forest being the most highly selected cover class overall (Table 2.3). Moreover, foxes also selected local areas that had a higher proportion of grassland during the night, but avoided such areas during the day. Although models indicated that foxes selected local areas (within 100-m radius) having a higher proportion of developed land, this variable required a random coefficient to account for highly variable individual responses ranging from strong selection to

strong avoidance (Fig 2.3a, b), with differences being most pronounced during the day when human activity on the base was highest, and with females being more likely than males to select for more developed landscapes. A random coefficient was also required during the daytime for fox responses to the density of culverts, however, foxes generally showed moderate to strong selection for the density of culverts with the exception of a single female (Fig 2.3c). Fox selection for areas adjacent to roads was modified by the proximity of forest or shrub cover (Fig 2.4). Fox consistently avoided areas having a high density of buildings at night, but selection during the day peaked at ~200 m from buildings (Fig 2.5).

The $\delta^{13}C$ values of red and gray foxes on Fort Drum overlapped greatly (-22.5 ± 0.6 ‰ and -22.0 ± 0.7 ‰, respectively), and both were higher than coyotes (Fig 2.6) indicating greater use of human food by the foxes than the coyotes in our samples. But we note that, in contrast to the fox samples, our coyote samples were not drawn from animals captured within the cantonment areas.

DISCUSSION

Red fox share the landscape in New York and across North America with coyotes, wiht the larger species expected to competitively displace foxes into lower quality habitat (Voigt and Earle 1983, Major and Sherburne 1987, Sargeant et al. 1987, Harrison et al. 1989). Given that coyotes tend to avoid areas of high human use (Atwood et al. 2004, Kays et al. 2008, Gehrt et al. 2009, Grubbs and Krausman 2009), it follows that red fox might find refuge therein. Although coyotes are increasingly invading and persisting in human-dominated landscapes as well (Ordeñana et al. 2010, Gese et al. 2012), their density may vary with the quality of habitat provided across a gradient from high to low human disturbance. Kays et al. (2008) documented

such a gradient in east-central NY State, observing lower coyote abundance in areas of high human use and increasing coyote abundance in more rural, forested regions. A similar pattern was observed on Fort Drum, with camera traps indicating that coyotes occupy the whole base, but perhaps at lower density in the human-dominated cantonment area compared to the more forested training areas (Chapter 1). Red fox in that camera study exclusively used the cantonment area (Chapter 1), which may indicate large-scale competitive displacement of red fox by coyotes, and further demonstrated peak activity patterns offset from coyotes. This current study of GPS-collared foxes adds to the picture that red fox are strongly tied to areas where foraging habitats are interspersed with substantial cover. Red fox in this study demonstrated the need to balance foraging opportunity with security, utilizing cover in various forms likely to lower the risk of mortality from humans and other predators (Harris and Rayner 1986, Van Deelen and Gosselink 2006). First, fox use of areas near roads occurred only in close proximity to forest and shrub cover, with models indicating that removal of cover within ~400 m of roads might strongly reduce the likelihood of fox use of roadside areas (Fig 2.4). Second, whereas foxes were strongly associated with tree and shrub cover, culverts provided important alternative denning and resting sites during the day where natural cover was either not readily available or provided insufficient protection against coyotes.

Applying my models of fox resource selection to the Fort Drum landscape indicated a much more patchy landscape for fox at night, the period when fox are actively foraging (Fig 2.7), indicating foraging habitat to be potentially more limiting on the base than cover. Yet, even within the human-dominated landscape where foraging habitat was most abundant, I observed spatial variation in resource selection with a higher probability of selection by fox during the day in the core business zones (0.56 ± 0.70 SD culverts/ha) compared to the core residential zones

(0.08 ± 0.23 SD culverts/ha). Although my models included an overall effect of the proximity or density of buildings, I did not discriminate between residential versus administrative or commercial buildings. Yet, housing tracts were consistently avoided by foxes both day and night whereas neighboring business centers switched from a low predicted probability of selection at night to a high probability of selection during the day – and the key variable differentiating these zones was the availability of culverts. Red fox in Illinois used dens as a mechanism to escape from predators, especially coyote (Gosselink 1999, Gosselink et al. 2007). Moreover, swift fox (*Vulpes velox*) and kit fox (*V. macrotis*) in the western U.S. readily used culverts and increasing so in landscapes they shared with coyotes (Egoscue 1956, Reese et al. 1992, Gosselink 1999, Jackson and Choate 2000, Harrison and Whitaker-Hoagland 2003). Even gray fox space use on Fort Drum was predicted best by the density of culverts (Chapter 1), despite their ability to climb trees to escape interactions with coyotes (Wooding 1984, Cypher 1993). Importantly, the seeming reliance of foxes on culverts provides additional opportunities to manage fox use of space and potentially mitigate fox-human conflict in this human dominated landscape. For example, using an experimental array of artificial escape dens, Mcgee et al. (2006) affected a shift in space use and survival by swift fox, with fox moving into previously unoccupied areas after escape dens had been added. Given the difficulties of managing urban carnivore populations through traditional means, specifically hunting and trapping (Thomson et al. 2000, Harding et al. 2001, Berger 2006), habitat manipulation via culverts may provide an effective alternative provided that other attractants for meso-predators, such as food sources, are also well managed (White et al. 2006).

Due to its lack of seasonality and high spatial predictability, anthropogenic food is expected to be readily exploited by meso-predators in urban environments, and has been

purported to be the cause of high densities of coyotes and raccoons in urbanized areas (Fedriani et al. 2001, Prange et al. 2003). Somewhat counterintuitively, red foxes on Fort Drum avoided conditions we expected to provide ready access to human sources of food, namely areas with dumpsters and compost. In fact, red fox on Fort Drum appeared to consume less anthropogenic sources of food than red foxes within the Adirondack Park ($\delta^{13}C$ shift of -1.32 ‰ on Fort Drum compared to observations by Warsen et al. 2014), perhaps owing to more stringent refuse management on Fort Drum than in rural communities. In contrast, gray foxes exhibited similar $\delta^{13}C$ values between Fort Drum and the Adirondacks (shift of 0.23 ‰), indicating that they may be less likely to make use of human sources of food than red fox, and, in turn, to be less drawn into human-dominated areas by the availability of human food. My results indicates that, instead of anthropogenic food, natural foraging opportunities for rodents, birds, invertebrates, and wild fruits may be responsible for the putative increase in red fox numbers in urban landscapes, most especially in otherwise forest-dominated landscapes. Whereas better garbage management may be an important means of mitigating human-fox conflict in rural communities, managers in areas like Fort Drum may need to consider fine-scale habitat management as a means to mitigate potential conflict.

The forces driving animal space use patterns are varied, complex and interacting, and often subtle. Although I did not find a direct response between predicted space use by coyotes and resource selection by red fox in this study, it nonetheless appears that coyotes play a large role in shaping the spatio-temporal movement decisions of red fox on Fort Drum given their largely restricted distribution to the human-dominated cantonment area (Chapter 1 and this study), offset activity patterns (Chapter 1), and demonstrated need for foraging habitat interspersed with suitable cover (this study). The red foxes in this study were captured in and

around the cantonment area, and as such I was unable to detect potential context-sensitive responses to resources along the urban to wild-land gradient. Yet, the presence of coyotes across the landscape may well have shifted the risk-reward ratio perceived by red fox regarding access to foraging habitats in different parts of the base, favoring foraging areas in the more human-dominated landscapes where nearby buildings and culverts provide ready escape cover.

MANAGEMENT IMPLICATIONS

As continuing human population growth drives further conversion of agricultural and forested land to residential, commercial, and industrial areas (Nickerson et al. 2011), urban fox populations are also likely to expand (Sargeant et al. 1987). Understanding the space use and population drivers of red fox is critical for managers concerned with mediating human-predator conflict or health concerns related to wild carnivores. This study demonstrated the importance of anthropogenic modification to the landscape, with respect to food resources and security cover, in the distribution and persistence of red fox in landscapes they share with coyotes. Eliminating access to cover such as remnant forest patches and grating culverts to block entry may discourage fox presence and help reduce the risk of human-fox conflict in areas of concern. Alternatively, shifting fox distribution or enhancing fox numbers might be achieved by increasing foraging opportunity (creating more grassland) along with enhancing cover by adding artificial escape dens to areas where culverts are currently rare. The influence of seasonality of natural prey on persistence and population density of red fox, and the degree to which red foxes may be limited by security cover in forested regions warrants further attention for effective management of these species into the future.

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Table 3.1. Comparison of candidate, day and night models of red fox resource selection on Fort Drum, New York, 2014-2015. Covariates in the best model for each habitat sub-category are indicated (measurement scale in parentheses) along with model log-likelihood (LL), number of estimated parameters (*K*), and difference in Akaike's Information Criterion (ΔAIC) from the final model. The FULL model includes all covariates in the table and an interaction term between distance to forest cover and proximity of road, and the FINAL model represents the most parsimonious combination of covariates across categories, with each variable contributing a ΔAIC > 2 unit change.

Habitat	Daytime model				Nighttime model			
category	Variable	LL	*K*	ΔAIC	Variable	LL	*K*	ΔAIC
Food	Cover type*	-534.46	7	94.05	Cover type*	-1170.09	7	64.93
	Dumpster density (2000 m)*				Dumpster density (500 m)*			
	Proportion grass (100 m)*				Proportion grass (100 m)*			
Cover	Culvert density (100 m)*	-574.30	4	167.73	Culvert density (100 m)	-1185.19	4	89.13
	Distance to forest/shrub cover*				Distance to forest/shrub cover*			
Human	Distance to road*	-540.24	7	105.60	Distance to road*	-1165.94	6	54.61
	Distance to building[a]*				Density of buildings (100 m)*			
	Density of roads (100 m)*				Proportion developed (100 m)[a]*			

	Proportion developed (100 m)*							
Competition	Probability of coyote occupancy	-565.68	3	148.49	Probability of coyote occupancy Probability of gray fox occupancy	-1188.10	4	94.95
FULL	All covariates + Distance to forest/shrub cover × Distance to road*	-478.44	16	0.00	All covariates + Distance to forest/shrub cover × Distance to road*	-1130.29	16	3.33
FINAL	All * covariates	-480.07	15	1.27	All * covariates	-1132.63	12	0.00

[a] Nonlinear response also modeled

Table 3.2. Model validation summary indicating for each data fold the intercept (b_0) and slope (b_1) of a linear regression of predicted against observed and the coefficient of determination (R^2). Given in parentheses are *p*-values of Student's t-tests of whether an intercept was different from 0 and slope was different from 1.

	Daytime model			Nighttime model		
Fold	b_0 (p)	b_1 (p)	R^2	b_0 (p)	b_1 (p)	R^2
1	0.01 (0.25)	0.91 (0.07)	0.98	-0.01 (0.52)	1.09 (0.32)	0.95
2	0.01 (0.66)	0.95 (0.52)	0.95	-0.01 (0.59)	1.08 (0.41)	0.94
3	0.00 (0.57)	0.98 (0.39)	0.99	-0.01 (0.34)	1.12 (0.15)	0.96
4	0.01 (0.41)	0.93 (0.20)	0.98	-0.01 (0.32)	1.13 (0.13)	0.97

Table 3.3. Final models for red fox resource selection during the day and night on Fort Drum, New York, 2014-15. For each variable the estimated coefficient (β) and standard error (SE) are given. An * indicates covariates whose 95% confidence intervals exclude zero. The scale of measurement (radius) of landscape covariates is given in parentheses. Letter superscripts indicate random coefficients.

	Daytime model			Night model		
Variable	Scale	β	SE	Scale	β	SE
Intercept	--	-1.01	0.57	--	-0.68	0.16*
Land cover type	Point					
Forest		1.64	0.40*		0.94	0.25*
Grass		1.41	0.48*		0.62	0.12*
Shrub		1.56	0.59*		0.23	0.57
Developed (reference)		--	--		--	--
Proportion grass	100 m	-0.33	0.16*	100 m	0.29	0.09*
Proportion area developed ^{R}	100 m	0.14	0.35	100 m	0.13	0.17
Distance to forest/shrub cover	Point	-0.43	0.27	Point	-0.20	0.11
Distance to road	Point	-0.49	0.15*	Point	-0.27	0.11*
Distance to road × Distance to cover		0.23	0.09*		0.16	0.05*
Distance to building	Point	0.39	0.18*		--	--
Distance to building^2		-0.37	0.11*		--	--
Density of culverts ^{R}	100 m	1.05	0.73		--	--
Density of roads	100 m	-0.75	0.11*		--	--

Density of buildings	--	--	--	100 m	-0.36	0.06*
Density of dumpsters	2000 m	-0.56	0.45	500 m	-0.13	0.35
Random effects variances (SE)						
Intercept - Fox	0.26 (0.30)			0.01 (0.03)		
Coefficient – Culvert density	0.96 (1.45)			--		
Coefficient – Proportion developed	0.38 (0.51)			0.07 (0.06)		

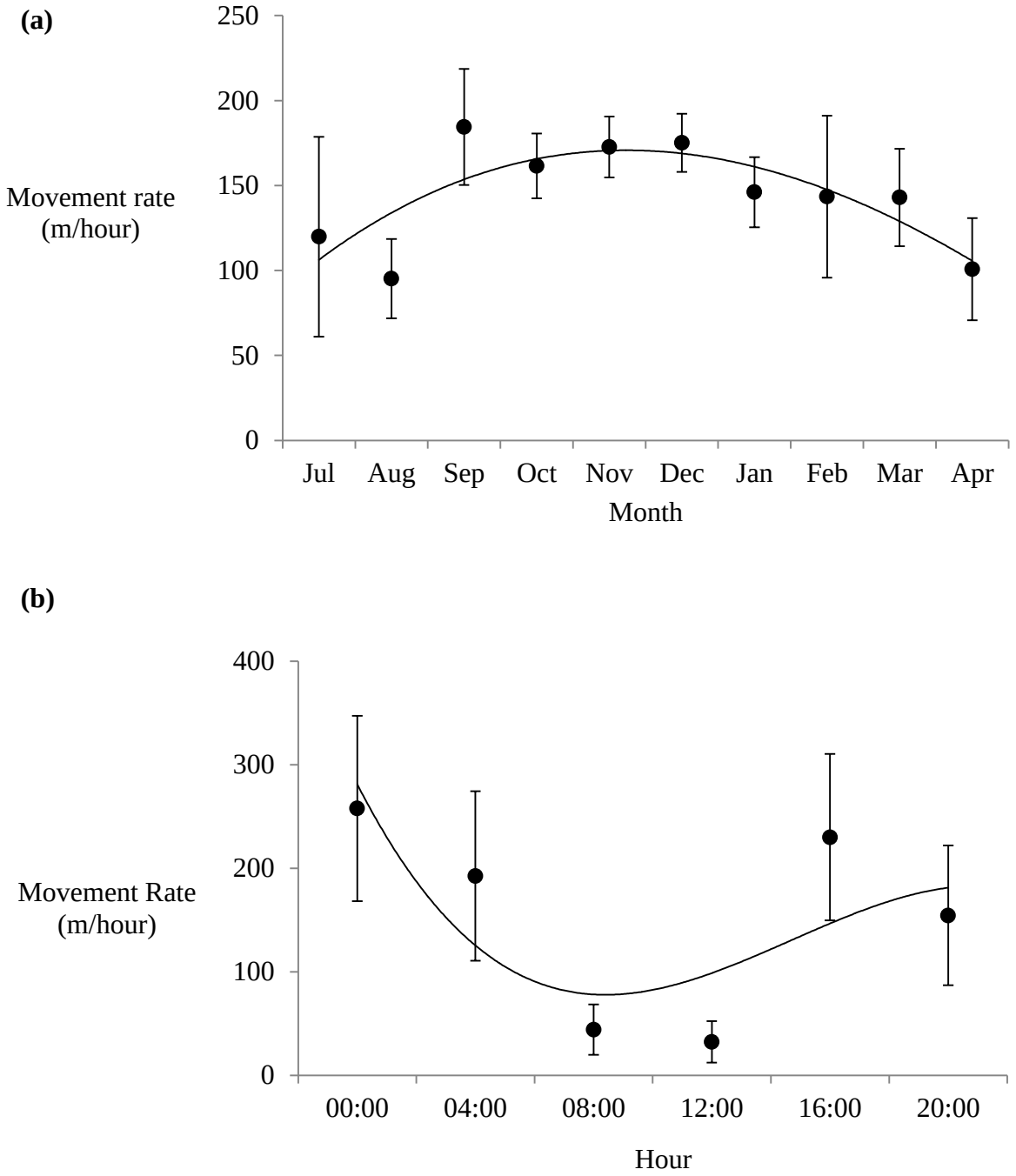

Figure 3.1. Monthly and hourly movement rates (m/hr) by collared red fox on Fort Drum, NY, USA, 2014-2015. Movement rates indicate a grand mean across animals with standard errors. Lines indicate a second or third order polynomial to highlight temporal trends.

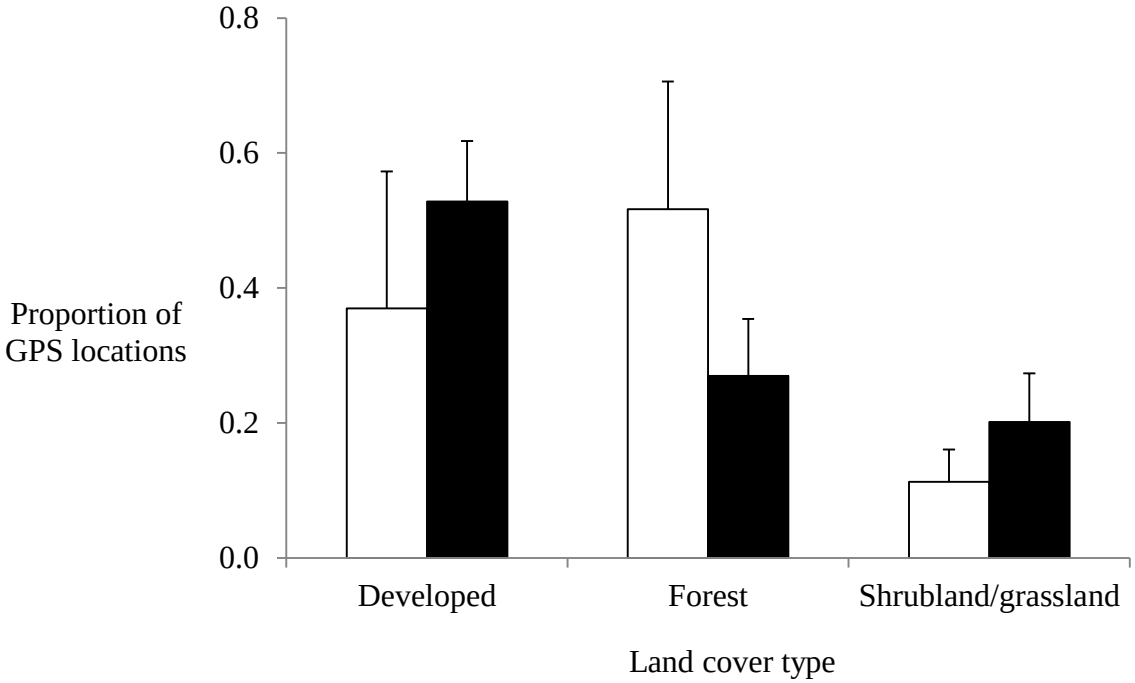

Figure 3.2. Proportion of fox locations within three primary land cover classes in the study area on Fort Drum, NY, USA, 2014-2015. Day-time locations (08:00-16:00; white bars) are shown separately from night-time locations (20:00-04:00; black bars). Proportions indicate a grand mean across foxes with standard errors.

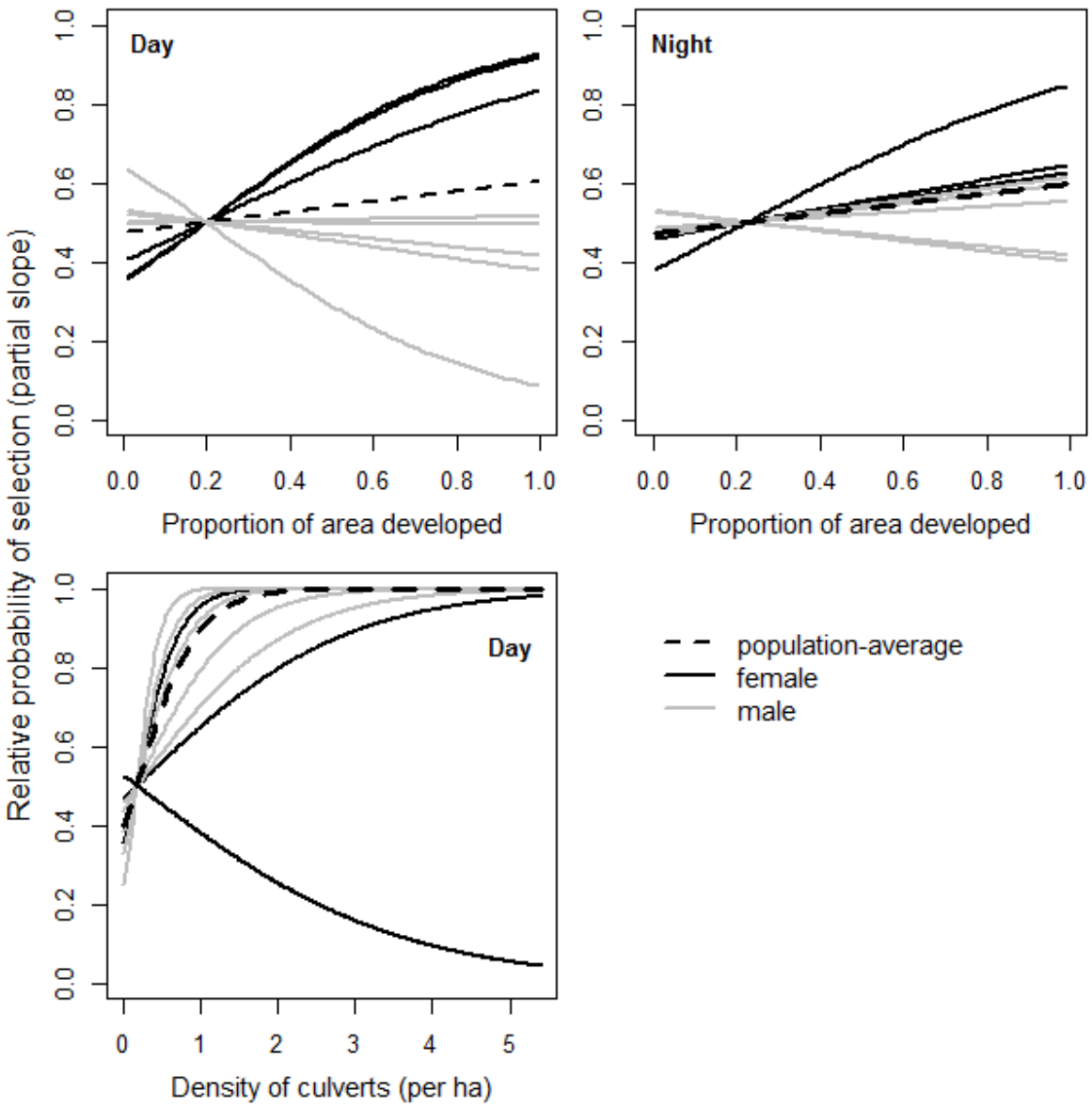

Figure 3.3. Partial slopes for the relative probability of red fox selection of a given location with respect to the proportion of developed area within 0.01 km^2 during day and night (upper panels), and for the density of culverts within a 100-m radius during the day (lower panel), on Fort Drum, NY, USA, 2014-2015. Each line represents the response of a specific individual, with males shown in gray and females in black. The thick dashed line indicated the population-averaged, or marginal, response.

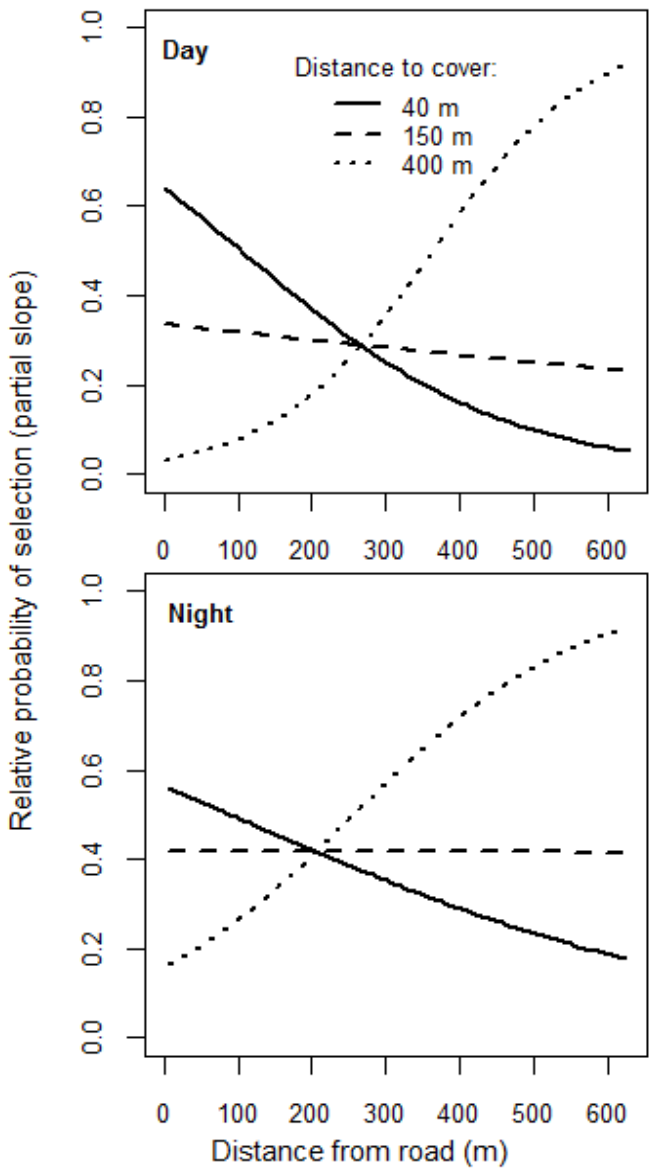

Figure 3.4. Partial slopes for the relative probability of red fox selection of a given location with respect to the distance from nearest road during day and night on Fort Drum, NY, USA, 2014-2015. The three different lines depict the interactive influence of security cover (shrub or forest) on fox responses to road proximity.

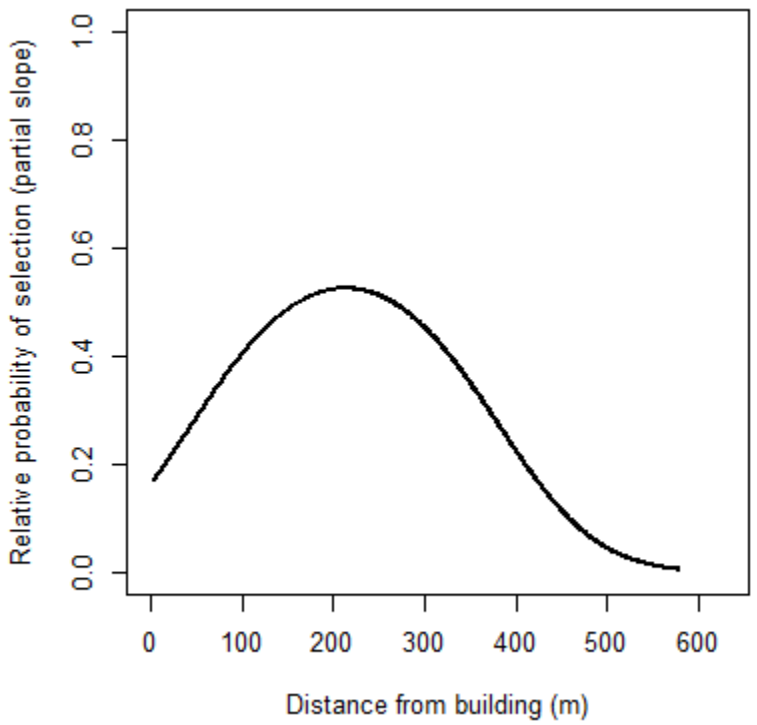

Figure 3.5. Partial slopes for the relative probability of red fox selection of a given location with respect to the distance from nearest building during daytime on Fort Drum, NY, USA, 2014-2015.

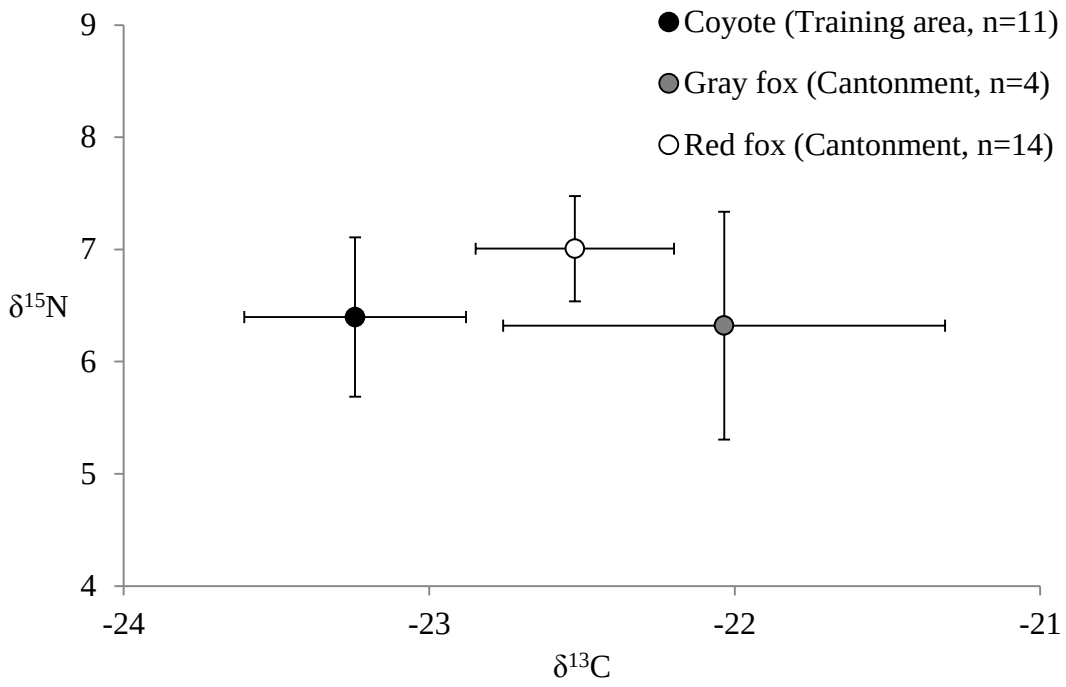

Figure 3.6. Comparison of isotopic niche space among coyotes (black symbols), gray fox (gray symbols) and red fox (white symbols) on Fort Drum, NY, USA, 2013-2015. Plotted values show the mean across sampled individuals (‰) along with 95% confidence intervals for both the nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) stable isotope values.

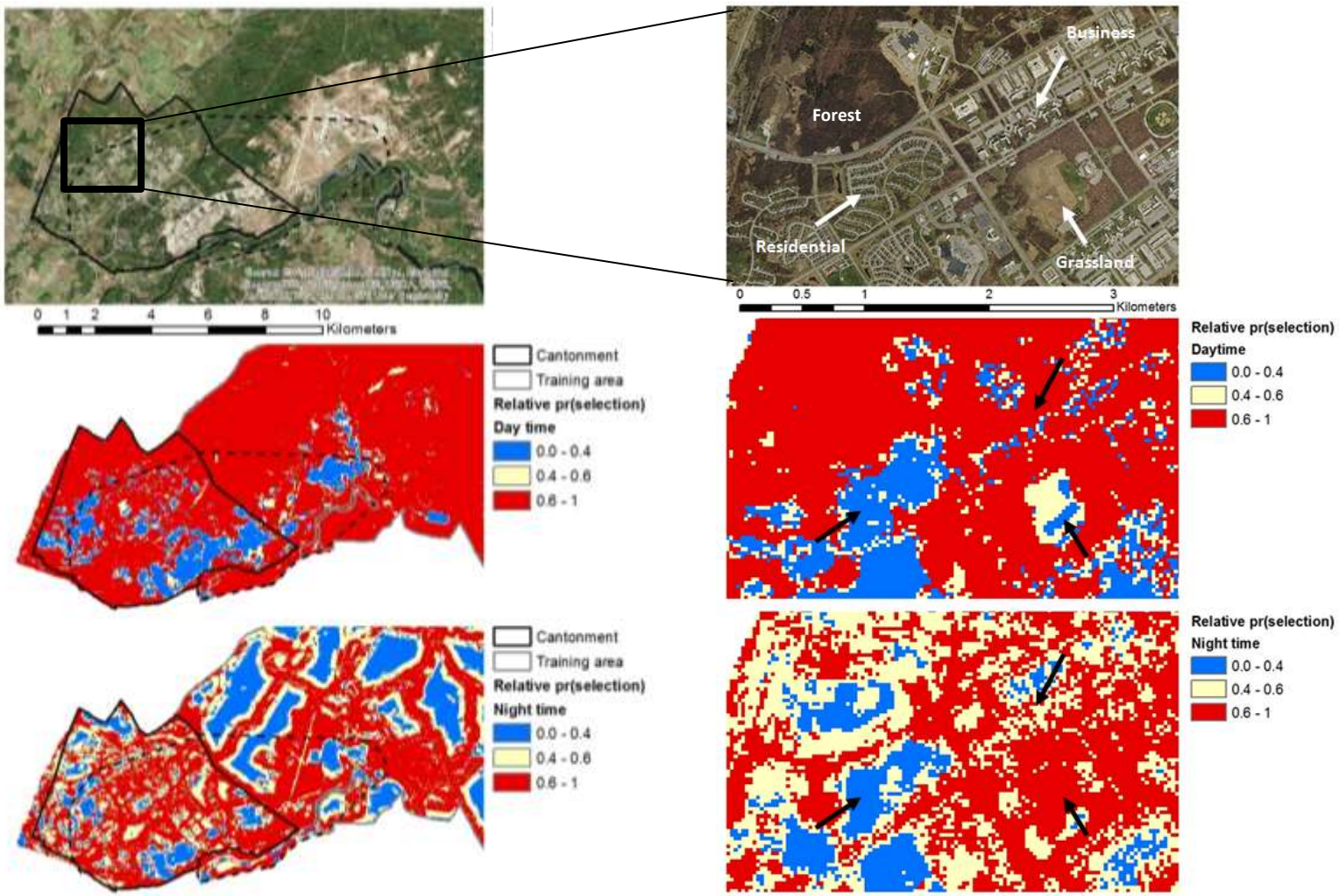

Figure 3.7. Base map of the study area (top left) with inset showing the core cantonment area (top right) on Fort Drum, NY, USA, 2013-2015. Also shown are predictions from the top models in each time period for the relative probability of a fox selecting each 30 × 30 m cell during the day (center) and night (bottom)

CONCLUSION

The presence of coyotes in habitat fragments in has been associated with meso-predator release and dramatically altered rodent and bird communities, leading to a cascade of ecosystem effects (Crooks and Soulé 1999, Henke and Bryant 1999). Despite being widespread and abundant in the Northeast, the impacts of coyotes on native carnivores and their role in structuring wildlife community remain one of the major gaps in our knowledge of coyote ecology (Gompper 2002*a*). This thesis begins to shed light on potential mechanism by which coyotes and anthropogenic factors may impact the occurrence, resource selection and activity patterns of meso-predators and provides insight into possible mechanisms underlying the coexistence of carnivores on Fort Drum.

In both Chapter 1 and 2, I did not find evidence of coyotes directly influencing the space use on other meso-predators. My occupancy and resource selection models quantified either independence from (fisher and red fox) or physical aggregation with (gray fox) coyotes rather than competitive exclusion. Specific to red fox, my study suggested that red foxes on Fort Drum were drawn into human dominated-landscapes by the abundance of preferred foraging habitats (grasslands, road margins), contrary to previous studies that suggested red fox were displaced by coyotes into urban areas (Gosselink 1999, Gosselink et al. 2007). However, I found that coyotes may respond to human-dominated areas on Fort Drum negatively because of the high density of roads and potentially reduced foraging efficiency due to more nocturnal activity pattern. Therefore, red or gray fox may experience lower level of competition in the human-dominated cantonment, due to lower habitat suitability for coyotes, and this, paired with ready escape cover provided by culverts, may facilitate the coexistence of these species. My conclusion relies on the assumed positive relationship between probability of detection and abundance (Royle and

Nichols 2003) instead of direct measurement of coyote density. Future study may be conducted to compare the home range sizes, foraging efficiency, and survival of coyotes between the high and low human use regions in order to widen our knowledge on coyote responses to human activities, and by extension, the strength of competition they exert on other carnivores.

In Chapter 2, I concluded that security cover might not be driving the distribution of red fox on Fort Drum in large part due to the failure to detect (by camera trap) and trap red fox in outside the human-dominated parts of Fort Drum, where natural cover types (forest and shrub) were abundant. Instead, red fox were drawn into the cantonment of Fort Drum due to the availability of foraging habitats. However, without the fox data from the Low Use area, where coyotes are presumed to be more abundant, I was not able to investigate the context-sensitive space use patterns by red fox along the rural-to-wild lands gradient and the potential interaction between various factors (i.e. competition with coyotes, foraging and cover resources). Coyotes may numerically suppress red fox, as well as gray fox, In the Low Use area (Dekker 1983, Cypher 1993, Farias et al. 2005), and security cover may be the limiting factors for the persistence of foxes. Hence, further investigation is warranted to identify factors that are limiting to the fox species in the Low Use area. For instance, experiments can be conducted to investigate whether placement of artificial dens may (Mcgee et al. 2006) or habitat enhancement by creation of grassland in the Low Use area can offset that habitat limitation and encourage them to move into previously unoccupied training area.

The distributions of both red and gray foxes were restricted to High Use area of Fort Drum, and space us by both species were positively correlated to density of culverts. The overlapping distributions and reliance on culverts suggest potential competition between the two fox species for culverts in the High Use area of Fort Drum. Gray fox are believed to be more

aggressive than red fox and may exclude red foxes from some habitatsin areas where they coexist (Cypher 1993). However, I was not able to investigate the influence of gray fox on red fox habitat selection because of the coarser resolution for gray fox space use (determined via camera trap; Chapter 1). Red fox population presumable crashed following a mange outbreak in winter 2015, leading to lower number of sites where red fox were detected and number of independent detection of the species in 2016 (Table 1.3). I also observed an inverse relationship between the numbers of detection of these two species, which may indicate competition between these two species. However, it might be a result of improved overall detectability due to better site selection and longer survey period in 2016. Future study may take advantage of the recovery of red fox population following the mange outbreak and document how increasing red fox population influence gray fox population and space use.

Interestingly, red foxes on Fort Drum avoided sources of anthropogenic food (i.e. dumpsters) and used less human source of food compared to foxes in the Adirondack Park. Future research may explore the impact of seasonality of natural prey on fox persistence in the human-dominated area, and whether red fox switch to anthropogenic food that is easier to obtain in areas where refuse management is less efficient, potentially reducing their role in suppressing small mammals.

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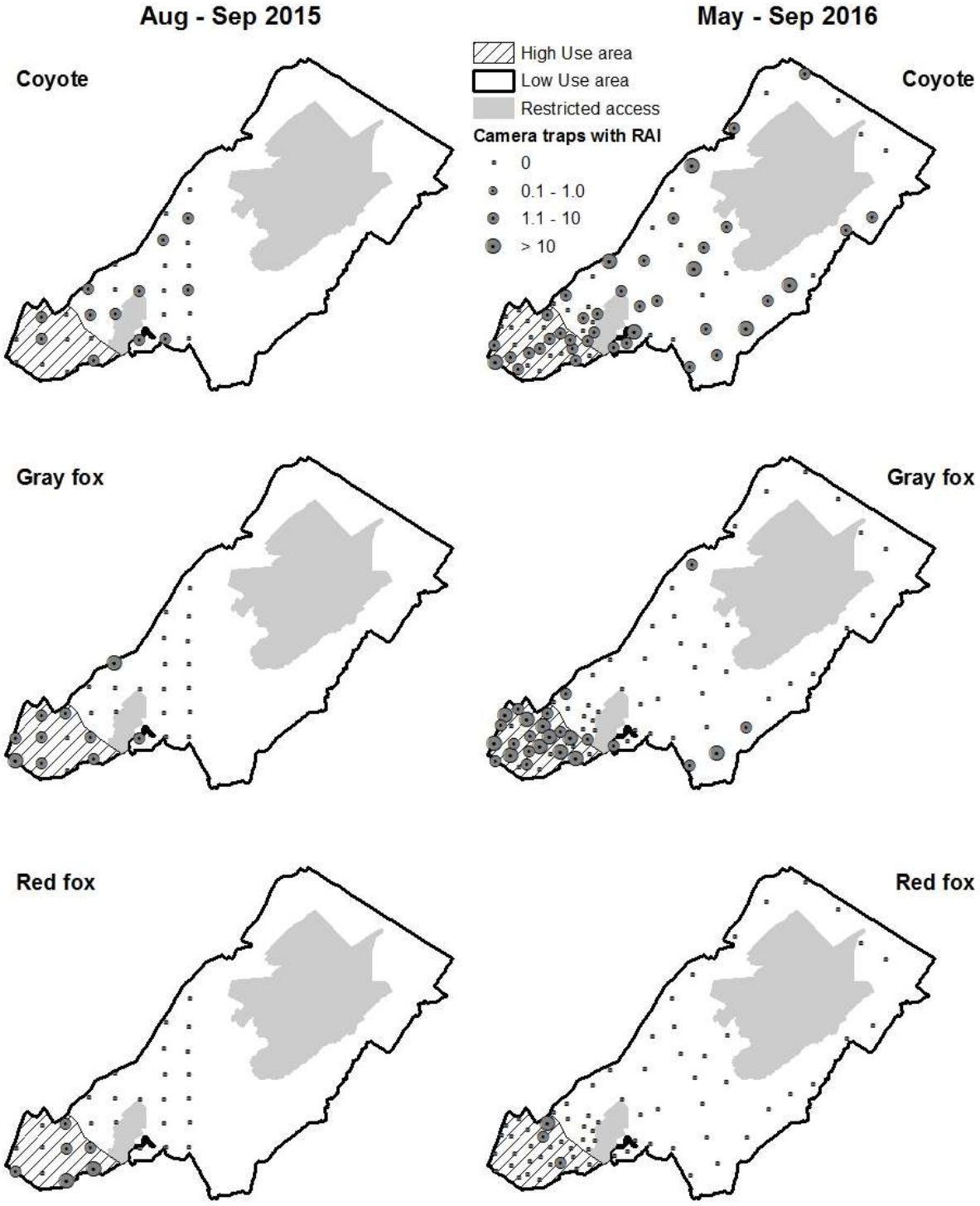
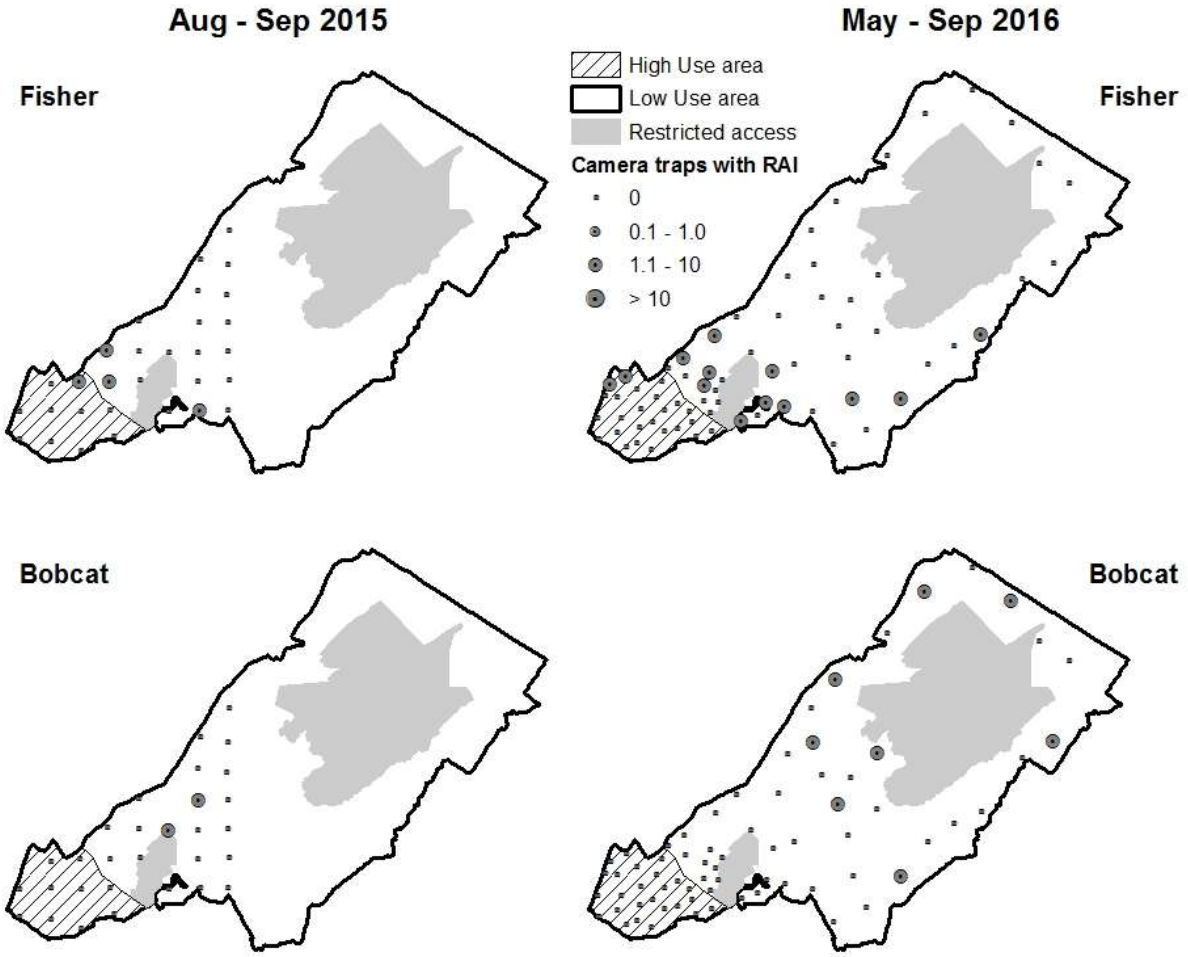
APPENDICES

Appendix 0.1. Descriptions of parameters estimated in the conditional two-species occupancy model; table adapted from Richmond et al. (2010). Species A (coyote) is assumed to be dominant, and species B subordinate.

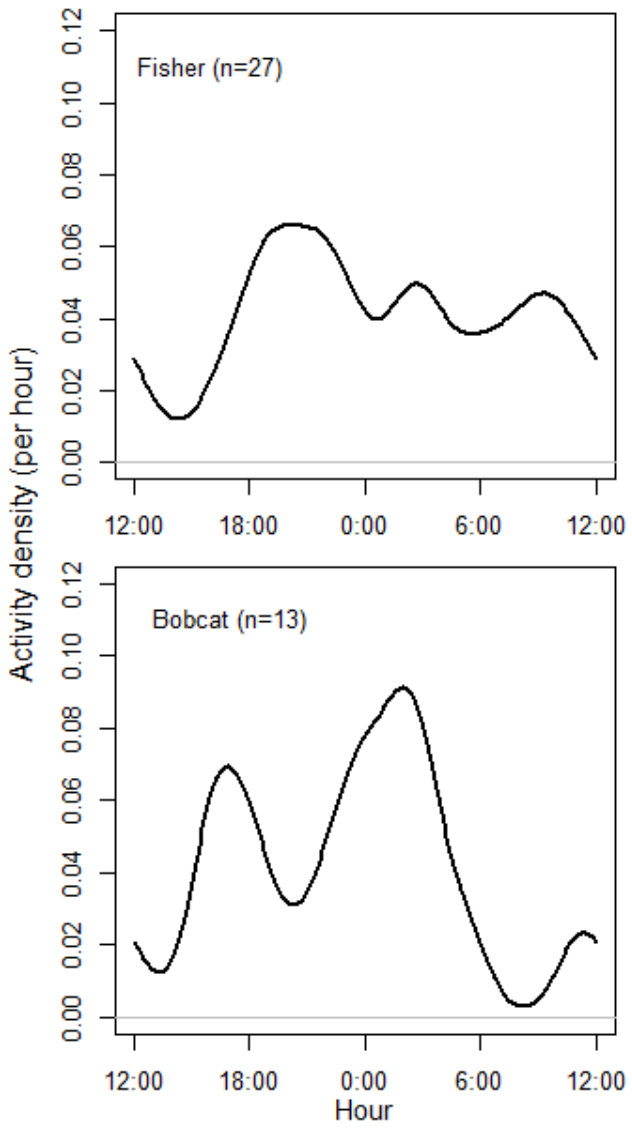
Parameter	Definition
ψ^{A}	Probability of occupancy for species A
ψ^{BA}	Probability of occupancy for species B, given species A is present
ψ^{Ba}	Probability of occupancy for species B, given species A is absent
p^{A}	Probability of detection for species A, given species B is absent
r^{A}	Probability of detection for species A, given both species are present.
p^{B}	Probability of detection for species B, given species A is absent.
r^{BA}	Probability of detection for species B, given both species are present and species A is detected during the sampling occasion.
r^{Ba}	Probability of detection for species B, given both species are present and species A is not detected during the sampling occasion.

Appendix 0.2. Relative abundance index for coyote, gray fox, red fox, fisher and bobcat in 2015 and 2016 on Fort Drum Military Installation, NY.




Aug - Sep 2015
May - Sep 2016
High Use area
Low Use area
Restricted access
Camera traps with RAI
0
0.1 - 1.0
1.1 - 10
> 10
Fisher
Fisher
Bobcat
Bobcat

Appendix 0.3..Kernel density estimates of temporal activity patterns of fisher and bobcat on Fort Drum, NY. Because of the limited numbers of detections records were pooled across the High and Low Use areas for fisher and across years for both species. The total numbers of photo records (n) used to fit kernel density models are also shown.



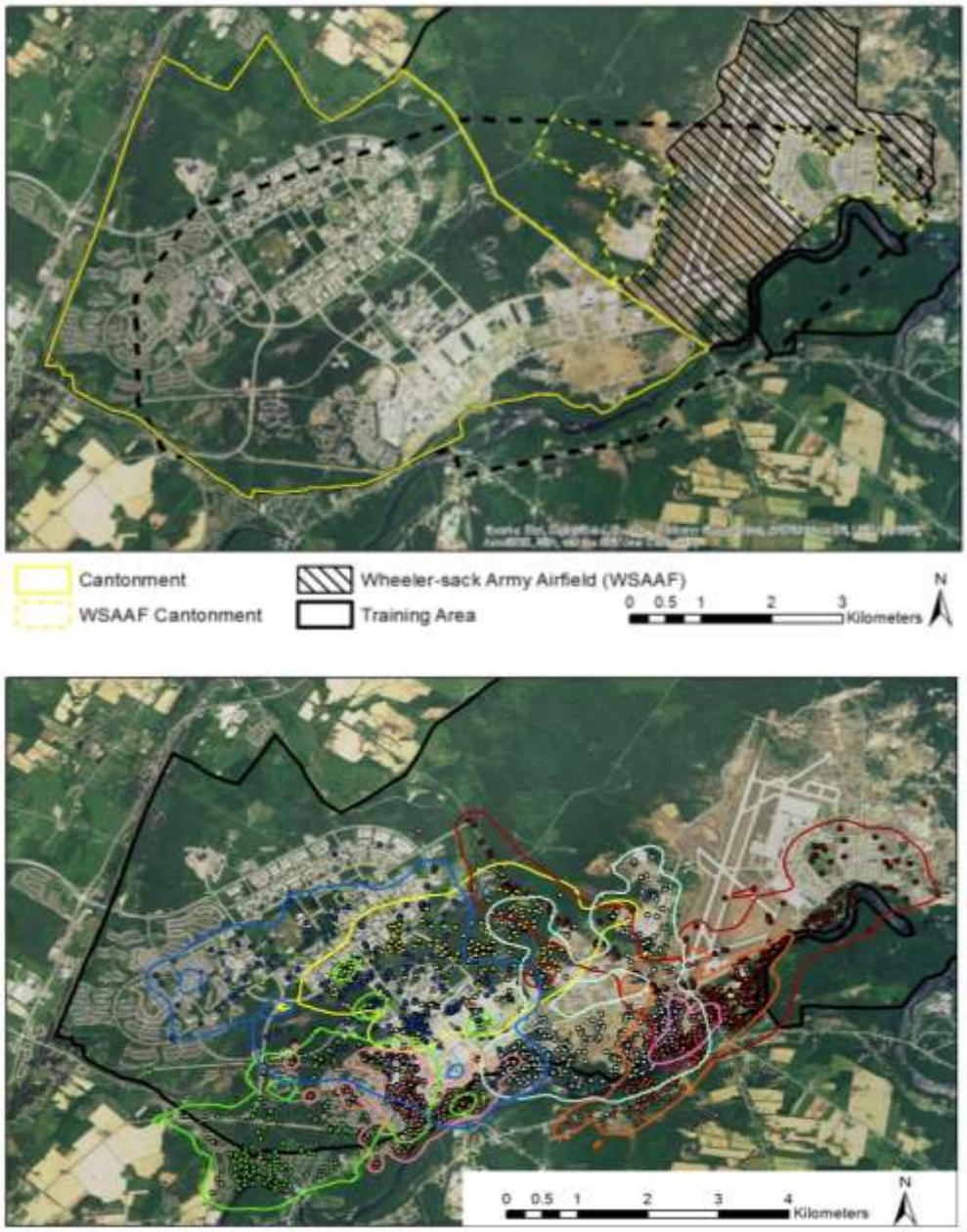
Appendix 0.4. Top supported, conditional two-species occupancy models predicting probability of detection (p) and occupancy (Ψ) of coyotes (COY) and gray foxes (GF) on Fort Drum Military Installation, New York, USA, 2015-16. Given for each covariate is the estimated coefficient (β), standard error (SE), and 95% confidence interval (CI).

Parameter	Model term	β	SE	LCI	UCI
p^{COY}	Intercept	0.15	0.78	-1.38	1.67
	Year: 2016	0.89	0.32	0.27	1.52
	Region: High Use	-0.66	0.28	-1.21	-0.12
p^{GF}	Intercept	-2.05	0.41	-2.86	-1.24
	Year: 2016	0.95	0.29	0.38	1.52
	Region: High Use	0.79	0.35	0.10	1.49
Ψ^{COY}	Intercept	0.15	0.78	-1.38	1.67
	Distance to nearest road (km)	9.41	6.45	-3.24	22.06
	Distance to nearest road squared	-22.00	10.90	-43.40	-0.60
Ψ^{GF}	Intercept	-8.07	2.29	-12.56	-3.58
	Season: Aug - Sep	2.65	1.07	0.55	4.74
	Culvert density (per ha, r = 2000 m)	27.44	7.44	12.86	42.03
	Coyote	3.16	1.37	0.47	5.85

Appendix 0.5. Top supported, conditional two-species occupancy models predicting probability of detection (p) and occupancy (Ψ) of coyotes (COY) and fishers (F) on Fort Drum Military Installation, New York, USA, 2015-16. Given for each covariate is the estimated coefficient (β), standard error (SE), and 95% confidence interval (CI).

Parameter	Model term	β	SE	LCI	UCI
p^{COY}	Intercept	-2.07	0.31	-2.67	-1.47
	Year: 2016	1.08	0.32	0.44	1.71
	Region: High Use	-0.92	0.27	-1.46	-0.39
p^{F}	Intercept	-2.51	0.39	-3.27	-1.76
Ψ^{COY}	Intercept	0.11	0.76	-1.39	1.61
	Distance to nearest road (km)	10.13	6.36	-2.34	22.60
	Distance to nearest road squared	-22.80	10.90	-44.10	-1.60
Ψ^{F}	Intercept	-18.74	7.52	-33.48	-4.00
	Average NDVI (r = 500 m)	22.77	9.65	3.85	41.69

Appendix 0.1. Location of the study area (top, dashed black lines) on Fort Drum, NY, USA, 2014-2015. The study area is a bounding polygon of all collared fox locations (bottom), clipped along the southern boundary of Fort Drum to exclude an off-base community for which detailed GIS data were lacking. The cantonment areas (yellow lines), WSAAF cantonment (dashed yellow lines), and airfield (hashes) indicated areas of concentrated human use. Also shown are the 95% kernel density home ranges of the collared fox.



Appendix 0.2. Variables used to model red fox resource selection on Fort Drum Military Installation, New York, USA. Variables were measured at either local (point-based) or landscape (area-based) levels. Landscape-level variables were summarized around each point within circular buffers having radii of 0.1, 0.25, 0.5, 1, 1.5, and 2 km.

Category	Variable description	Scale
Food resource	Land cover type (forest, shrub, grass, developed)	Local
	Distance to the nearest compost and trash site (m)	Local
	Density of compost and trash dumping sites (sites/ha)	Landscape
	Proportion of area covered by grass	Landscape
Security cover	Distance to nearest culvert (m)	Local
	Density of culverts (culverts/ha) [a]	Landscape
	Distance to forest or shrub (m)	Local
	Proportion of area covered by forest	Landscape
	Proportion of area covered by shrub	Landscape
Anthropogenic disturbance	Distance to the nearest road (m) [a]	Local
	Density of roads (m/ha) [a]	Landscape
	Distance to the nearest building (m) [a]	Local
	Density of buildings (per ha) [a]	Landscape
	Proportion of developed area [a]	Landscape
Competition	Coyote probability of occupancy	Local, landscape
	Gray fox probability of occupancy	Local, landscape

[a] Nonlinear response also modeled

Appendix 0.3. Values used to standardize variables prior to fitting red fox resource selection models.

	Day		Night	
	Mean	SD	Mean	SD
Proportion of area covered by grass (r = 100 m)	0.26	0.27	0.36	0.28
Dumpster density (day: r=2000 m, night: r=500 m; sites/ha)	0.18	0.13	0.35	0.81
Distance to forest or shrub cover (m)	32.93	65.01	40.94	67.43
Culvert density (r=100 m; culverts/ha)	0.17	0.40	--	--
Distance to nearest road (m)	104.42	87.66	89.27	92.21
Distance to nearest building (m)	160.27	98.13	--	--
Density of road (r=100 m; m/ha)	422.02	501.44	--	--
Density of buildings (r=100 m; per ha)	--	--	0.51	1.13
Proportion area developed (r=100 m)	0.20	0.27	0.23	0.26

RESUME

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PRESENTATIONS

"**Anthropogenic drivers of space use among Coyote, Gray Fox, and Fisher on Fort Drum Military Installation, New York",** The Northeast Natural History Conference, Cromwell, CT; April 2017

"**Anthropogenic drivers of space use among Coyote, Gray Fox, and Fisher on Fort Drum Military Installation, New York",** Onondaga Audubon Society, Fayetteville, NY, March 2017

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