ABSTRACT

STEVENSON, ELIZABETH ROSE. Coyote Survival and Habitat Selection in a Longleaf Pine Ecosystem. (Under the direction of Drs. Christopher E. Moorman and Christopher S. DePerno).

The Coyote (*Canis latrans*) is a novel predator in the southeastern United States and facilitates ecologically novel interactions with other wildlife species. Though coyotes recently expanded to the southeastern United States, little data exist on vital rates of southeastern coyotes. Furthermore, knowledge of survival rates where coyotes are protected from hunting and trapping is lacking. To estimate annual survival where coyote harvest was restricted, we captured and radiocollared 31 coyotes during 2011 at Fort Bragg Military Installation, North Carolina. We used a 12-month period (Feb 2011 – Feb 2012) and known-fate modeling in Program MARK to create monthly and annual survival estimates. The model where survival varied with time ($S(t)$) was the most parsimonious model according to model selection results. Annual survival from February 2011 – February 2012 was 0.80 (95% CI = 0.60 – 0.91). Seven mortalities occurred during the study period, including two from vehicles, two from off-site trapping, and three from unknown causes. Though hunting and trapping were restricted, anthropogenic causes of mortality were predominant and coyote survival rates at Fort Bragg were similar to other reported estimates from the southeastern US.

Fire is a disturbance that shapes plant and animal community composition around the globe, and apex predators may have cascading effects on these communities. However, scant empirical data describe how fire and predators may interact to collectively affect ecosystem processes. We examined resource selection of coyotes in a fire-maintained ecosystem to

understand how fire and predators may interact to shape ecosystems. Our objective was to examine resource selection relative to fire-maintained vegetation types, years-since-fire, and manmade features that facilitate prescribed burning (i.e., roads). Coyotes selected open, grass-forb areas over forested areas when selecting a home range. Coyotes avoided areas burned 4 or more years prior but selected upland forest burned 1 and 2 years prior. Coyotes selected open areas year round, probably because of high prey availability and dense understory vegetation that provided cover. Coyote selection of more recently burned areas likely was in response to increased ability to detect prey soon after vegetation cover was reduced by fires. In ecosystems where prescribed fire is used to maintain fire-dependent plant communities, coyote resource selection may be linked to prescribed fire. Coyote habitat selection related to fire regimes may indicate an interaction with fire that could influence ecosystem function.

Coyote Survival and Habitat Selection in a Longleaf Pine Ecosystem

by
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DEDICATION

To Wishbone, my first and best canid.

BIOGRAPHY

Elizabeth Stevenson was born in Jacksonville, Florida and grew up in coastal Maryland. She developed her love for all things wild on her grandparents' farm in upstate New York, a passion nurtured by numerous outdoor experiences with her parents. After years of exploring the woods alongside her sister, she formally pursued her ecological interests at the University of Maryland, where she graduated with a Bachelor's degree in Ecology and Evolution in 2013. During this time, several professional experiences lead her to develop an interest in wildlife ecology and management. Prior to the completion of her Master's degree, Elizabeth moved to Florida and is currently a Mammal Biologist with the Florida Fish and Wildlife Conservation Commission.

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CHAPTER 1

SURVIVAL AND CAUSE-SPECIFIC MORTALITY OF COYOTES IN A PROTECTED POPULATION

ABSTRACT

Canis latrans (Coyote) recently expanded into the southeastern United States, creating ecologically novel interactions with other species. However, relatively few studies have examined vital rates of southeastern coyotes or estimated vital rates where individuals are protected from hunting and trapping. In 2011, we captured and radiocollared 31 coyotes at Fort Bragg Military Installation, North Carolina where coyote harvest was restricted. We used a 12-month period (Feb 2011 – Feb 2012) and known-fate modeling in Program MARK to estimate annual survival. Model selection results indicated the time-varying model (S(t)) was the most parsimonious model. Annual survival from February 2011 – February 2012 was 0.80 (95% CI = 0.60 – 0.91). We documented seven mortalities including two from vehicles, two from off-site trapping, and three from unknown causes. Estimated coyote survival rates at Fort Bragg were similar to most other estimates from the southeastern US. Anthropogenic causes of mortality were important even though hunting and trapping were restricted locally.

INTRODUCTION

Prior to the 1940s, *Canis latrans* (coyote) was restricted to western North America (Nowak 1978). However, coyotes now occur throughout the eastern United States (Parker 1995), including the most recent expansion into the southeastern United States (Hill et al. 1987). For example, Lovell et al. (1998) documented a 7.5-fold increase in coyote population size since 1980 in Mississippi. Similarly, Main et al. (2000) reported that coyote distribution continued to expand southward in Florida and the rate of spread increased over the most recent decade. In North Carolina, coyotes were reported in all counties by 1998 (Debow et al. 1998) and other states in the southeastern U.S. have reported similar trends in recent coyote expansion and population growth (Houben 2004).

As coyote populations continue to expand in range and abundance, wildlife managers have expressed concerns about the ecological impact of coyotes, especially related to prey populations. Ample evidence suggests the effects of coyotes on community structure may be far reaching (Gompper 2002); effects may be indirect (e.g., resource competition with species such as *Lynx rufus* Kerr [Bobcat]; Litvaitis and Harrison 1989) or direct (e.g., predation). For example, numerous studies in the Southeast have documented direct effects of coyotes on *Odocoileus virginianus* Zimmermann (White-tailed Deer) (e.g., Chitwood et al. 2015, Kilgo et al. 2010). Though recent focus has been directed toward negative effects of expanding coyote populations on prey species and competitors, other evidence suggests positive implications of coyote presence. For instance, Brady (1994) reported eradication of feral dogs following coyote establishment in southeastern New York. Similarly, because coyotes compete with and depredate *Vulpes vulpes* Linnaeus (Red Fox) and *Procyon lotor*

Linnaeus (Raccoon), coyote presence has resulted in increased nesting success of *Anas.* spp (Duck) and *Melospiza melodia* Baird (Song Sparrow) (Rogers and Caro 1998, Sovada et al. 1995). Also, increases in songbird diversity have been associated with coyote predation on feral cats (Crooks and Soulé 1999). The complex ecological effects of coyotes highlight the need for a comprehensive understanding of coyote vital rates throughout their new range.

Despite increased interest in the community-level effects of coyote expansion, relatively few studies have examined vital rates of southeastern coyotes or estimated vital rates in unexploited populations (i.e., those protected from hunting and trapping). Though demographic responses of coyotes to increased exploitation have been explored (e.g., Knowlton et al. 1999, Gese 2005, Pitt et al. 2001), estimating population-specific vital rates such as annual survival in unexploited populations is needed to inform management decisions. Because coyote vital rates vary widely across their range (Gommper 2002), more study in areas where they are protected from harvest is warranted, particularly in the southeastern United States where their presence is novel. Therefore, we quantified survival and determined causes of mortality for a population of coyotes protected from hunting and trapping at Fort Bragg NC. Specifically, our objectives were to: 1) estimate annual survival, 2) determine potential effects of sex and age on survival, and 3) determine causes of mortality.

STUDY AREA

Fort Bragg Military Installation (hereafter Fort Bragg) was located in south-central North Carolina, USA, in the Sandhills ecoregion (Fig. 1). Fort Bragg consisted of 73,469 ha and

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was one of the largest contiguous blocks of the threatened *Pinus palustris* Mill (Longleaf

Pine) ecosystem in the southeastern United States. The Pine/Scrub Oak sandhill community

described by Sorrie et al. (2006) was widespread and abundant within Fort Bragg and was

dominated by Longleaf Pine, *Quercus laevis* Walter (Turkey Oak), and *Aristida stricta*

Michx (Wiregrass). Upland forests were managed with growing-season prescribed fire on a

3-year fire-return interval (Lashley et al. 2014). Historically, Fort Bragg allowed coyote

hunting when other game seasons were open; however, trapping has never been permitted on

the base. According to Fort Bragg estimates, <10 coyotes were removed each year through

hunter harvest (J. Jones, Fort Bragg Wildlife Branch, Fort Bragg, NC, pers. comm.). During

our study period, Fort Bragg suspended coyote hunting.

METHODS

Coyote capture and monitoring

We captured coyotes throughout Fort Bragg using MB-550 foothold traps (Minnesota

Trapline Products Inc., Pennock, MN, USA) from February – May 2011. We manually

restrained trapped coyotes and recorded sex and weight for each. We determined age

(juvenile [≤ 1 year], subadult [between 1 and 2 years], adult [≥ 2 years]; Gier 1968) based on

tooth wear. We fitted each with a GPS radiocollar (Lotek Wireless Inc., Ontario, Canada) and

programmed radiocollars to obtain relocation data at 3-hour intervals and to transmit all data

to a remote site until a collar was no longer being monitored due to coyote mortality, loss of

signal, or pre-programmed collar release (70 weeks following deployment). We determined

cause of death by locating collars which were transmitting a mortality signal and performing

subsequent field necropsy. We classified mortalities as unknown when field evidence was

not sufficient to identify cause. All coyote trapping and handling methods were approved by the North Carolina Wildlife Resources Commission and the North Carolina State University Institutional Animal Care and Use Committee (Protocol: 11-005-O) (Elfelt 2014).

Data analysis

We used a Kaplan-Meier known-fate model (Kaplan and Meier 1958) in Program MARK (White and Burnham 1999) following a staggered entry procedure (Pollock et al. 1989) to estimate monthly survival for the 21-month study period. We estimated annual survival for February 2011 to February 2012 by truncating the 21-month study period.

To determine the importance of sex and age on survival, we used an information theoretic approach to select from *a priori* models (Burnham and Anderson 2013). We first compared time-varying (S(t)) and time-constant (S(.)) survival models. We then determined the relationship of survival estimates to age and sex covariates by using the best time-predicted model. We used Akaike's Information Criterion adjusted for small sample size (AIC_c) and compared ΔAIC_c values and model weights (w_i) to determine the most parsimonious model. Models that had ΔAIC_c values ≤ 2 units from the top model were considered candidate models (Burnham and Anderson 2013).

RESULTS

We captured 31 coyotes, including 19 males (4 juveniles, 3 subadults, and 12 adults) and 12 females (4 juveniles, 5 subadults, and 3 adults). We monitored coyotes from February 2011 – October 2012. Three (1 subadult male, 1 subadult female, and 1 juvenile female) dispersed from the study area, established home ranges elsewhere, and were excluded from

analyses. We documented 7 mortalities, including two from vehicle collisions, two from off-site trapping, and three from unknown causes (Table 1). Vehicle collisions occurred in March and April, whereas both trapping mortalities occurred in January. The best model indicated survival varied monthly (i.e., S(t); Table 2). Though time-varying models that included age and sex as covariates fell within 2 ΔAIC_c, the relative weight of these models was low and we did not consider them as competing models. Combined juvenile and subadult survival (0.75; 95% CI = 0.45 − 0.92) was not significantly less than adult survival (0.86, 95% CI = 0.59 − 0.97). Monthly survival ranged from 0.86 (January 2012) to 1.00 (Table 3). Annual survival from February 2011 through February 2012 was 0.80 (95% CI = 0.60 − 0.91).

DISCUSSION

Annual coyote survival rates at Fort Bragg were greater than those reported in Georgia (0.50; Holzman et al. 1992), but other estimates from the southeastern U.S. were similar (i.e., included within our 95% confidence interval [South Carolina; 0.67 (Schrecengost et al. 2009) and Mississippi; 0.73 (Chamberlain and Leopold 2001)]). Known causes within the boundaries of Fort Bragg were limited to vehicle collisions; however, two coyotes that left Fort Bragg were legally trapped, highlighting the influence of anthropogenic effects (i.e., hunting, trapping, vehicles) on coyote survival. The proportion of coyote mortalities that are anthropogenic vary throughout the Southeast and range from 22% in Georgia (Holzman et al. 1992) to 60% in South Carolina (Schrecengost et al. 2009). We provide evidence that anthropogenic sources of mortality appear to be important even on large areas where coyote hunting and trapping is prohibited.

Despite Fort Bragg being protected from hunting and trapping, two coyotes were trapped during the study period. This was likely due to wide-ranging movement, as both trapping events occurred on private lands just outside the boundary of Fort Bragg. Elfelt (2014) documented large home ranges and apparently high numbers of transient coyotes at Fort Bragg, a phenomenon possibly attributed to high coyote population density, increased territoriality among older adults, and low resource availability (Conner et al. 2008, Gese et al. 1996). Other studies reported larger coyote home ranges and younger age structure when the coyote population was protected from human persecution (Sacks et al. 1999, Springer 1982, Windberg and Knowlton 1990). Because transient coyotes are usually young (Harrison 1992, Way et al. 2002), a younger age structure may lead to greater numbers of transient coyotes. During our study, 15 coyotes left the boundaries of Fort Bragg at least once (E. Stevenson, North Carolina State University, Raleigh, NC, unpubl. data), which predisposed them to hunting and trapping on adjacent private land. Thus, unexploited coyote populations may remain vulnerable to hunting and trapping mortality despite their protected status because wide-ranging individuals frequently move into unprotected areas.

Two mortalities during the study period were caused by vehicles. The majority of roads at Fort Bragg are low-traffic sandy roads that are used for military training and function as firebreaks for prescribed fire. However, several paved and gravel roads experience greater amounts of military and civilian vehicle traffic. During our study, 1 coyote was killed on a paved high-traffic road, while another was killed on a relatively low-traffic gravel road. Coyote mortality rates due to vehicle fatalities vary throughout their range and appear to be largely dependent on level of urbanization and road density (Gehrt 2007). No other coyote

survival studies in the southeastern United States have reported vehicle-related mortalities (Chamberlain and Leopold 2001, Holzman et al. 1992, Schrecengost et al. 2009), but these studies had small numbers of coyote mortalities, low road density, or few paved roads.

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Table 1. Causes of mortality among 28 *Canis latrans* captured at Fort Bragg Military

Installation, North Carolina, 2011-2012.

Age at mortality	Trapping		Vehicle		Unknown	
	Male	Female	Male	Female	Male	Female
Juvenile (<1 year)	0	0	0	0	0	0
Subadult (1-2 years)	0	1	0	2	1	0
Adult (>2 years)	1	0	0	0	2	0

Table 2. Candidate models, number of parameters (k), Akaike's Information Criterion values corrected for small sample size (AIC$_c$), ΔAIC$_c$, and AIC weights (w_i) for estimating *Canis latrans* monthly survival, Fort Bragg Military Installation, North Carolina, 2011-2012.

Model	k	AIC$_c$	ΔAIC$_c$	w_i
S(t)	21	59.8814	0.0000	0.50399
S(t + age)	22	61.5460	1.6646	0.21926
S(t + sex)	22	61.7690	1.8876	0.19613
S(t + age + sex)	23	63.5863	3.7049	0.07905
S(.)	11	71.4239	11.5425	0.00157

Table 3. Monthly *Canis latrans* survival estimates for a 21-month period at Fort Bragg Military Installation, North Carolina, 2011-2012.

Month / Year	Survival estimate	SE
February 2011	1.0000	0.0000
March 2011	1.0000	0.0000
April 2011	0.9615	0.0377
May 2011	1.0000	0.0000
June 2011	0.9615	0.0377
July 2011	1.0000	0.0000
August 2011	1.0000	0.0000
September 2011	1.0000	0.0000
October 2011	1.0000	0.0000
November 2011	1.0000	0.0000
December 2011	1.0000	0.0000
January 2012	0.8636	0.0732
February 2012	0.9444	0.0540
March 2012	0.9412	0.0571
April 2012	1.0000	0.0000
May 2012	1.0000	0.0000
June 2012	1.0000	0.0000
July 2012	1.0000	0.0000
August 2012	1.0000	0.0000
September 2012	1.0000	0.0000
October 2012	1.0000	0.0000
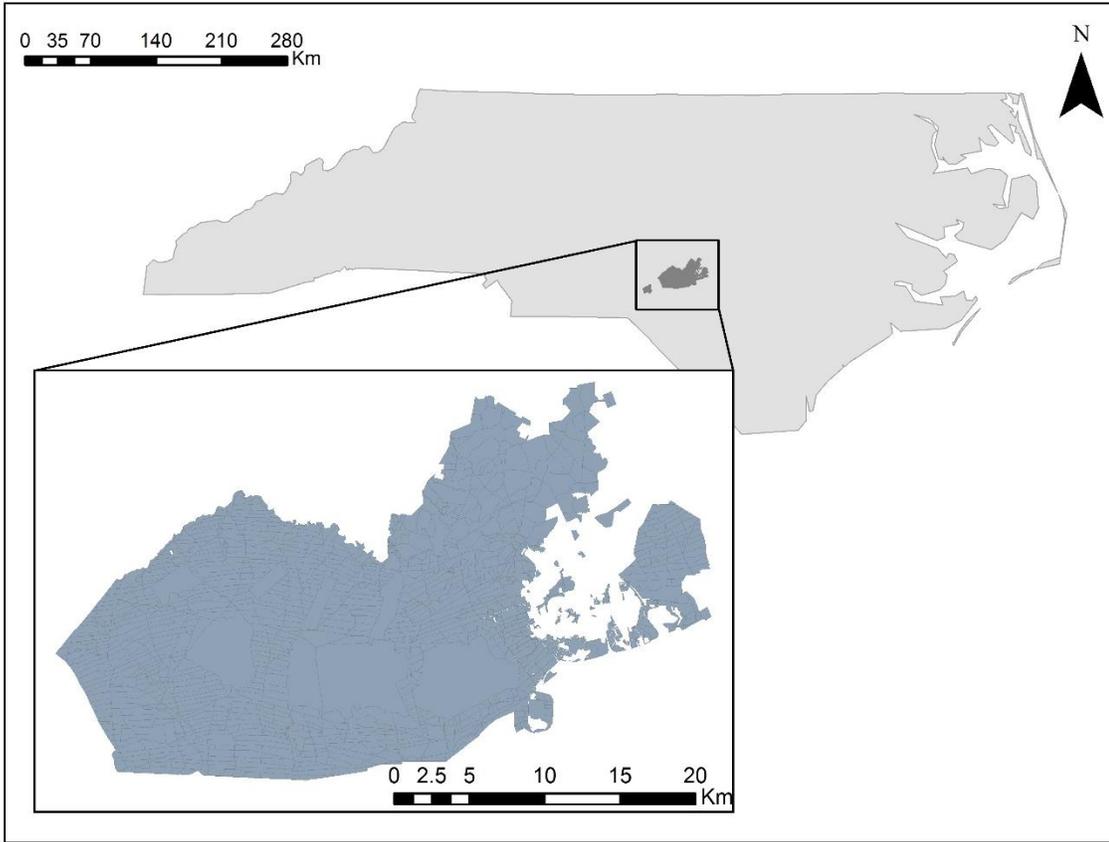
Figure 1. Location of Fort Bragg Military Installation, south-central North Carolina.

CHAPTER 2

HABITAT SELECTION OF COYOTES IN A LONGLEAF PINE ECOSYSTEM

ABSTRACT

Prescribed fire is used to restore and maintain fire-dependent forest communities, and its effects on these ecosystems are well studied. Likewise, apex predators may affect the function of ecological systems. However, scant empirical data describe the potential interactions of fire and predators or how they may collectively affect ecosystem processes. The first step in understanding how fire and predators may interact to shape ecosystems is to understand resource selection of the predator in a fire-maintained system. To take advantage of the recent expansion of coyotes (*Canis latrans*) into the longleaf pine (*Pinus palustris*) ecosystem of the southeastern United States, we radiotagged 27 coyotes and examined resource selection relative to fire-maintained vegetation types, years-since-fire, and manmade features that facilitate prescribed burning (i.e., roads). Coyotes selected open, grass-forb types over several forest vegetation types when selecting a home range. Coyotes selected upland forest burned 1 and 2 years prior, while avoiding areas burned 4 or more years prior. Coyote selection of more recently burned areas likely was in response to increased ability to detect prey soon after vegetation cover was reduced by fires. Our results demonstrate that coyote resource selection may be linked to prescribed fire, suggesting the interaction between fire and apex predators may influence the ecosystem function of fire-dependent forests.

INTRODUCTION

Fire occurs globally and shapes plant and animal communities. Influences of fire on the function and structure of ecosystems are well studied and have revealed complex interactions among plant and animal species and fire (e.g., Russell et al. 1999, Bradstock et al. 2005, Russell et al. 2009). Species diversity is greater within a few years following fire due to fire-induced vegetative regrowth, increased soft mast availability, and structure changes (Brockway and Lewis 1997). Prescribed fire frequently is used to restore and maintain fire-dependent forest communities (Van Lear et al. 2005), and its effects on ecosystem function mimic those of natural fire regimes. Therefore, the application of prescribed fire provides opportunity to study community-level interactions among plant and animal species and fire.

Like fire, apex predators may shape ecosystem processes through their effects on prey species. Predators directly affect prey populations from the top-down via predation (Paine 1980) and indirectly through non-consumptive effects of predation risks (Lima and Dill 1990). As a result, direct and indirect effects may cascade into other trophic levels ("trophic cascade"; Paine 1980) and even affect geological processes (e.g., Beschta and Ripple 2012). For example, Beschta and Ripple (2009) documented several trophic cascades where recovery of woody browse species (e.g., aspen [*Populus tremuloides*], willow [*Salix* spp.], cottonwood [*Populus* spp.]) occurred following wolf reintroduction, highlighting the importance of predator control of ungulates. Thus, because predators and fire function to shape ecosystems independently, it is likely they interact to form a novel disturbance when paired.

Reports of the effects of fire on predators are scant, though researchers have evaluated the effects of prescribed fire on other wildlife species (e.g., wild turkey [*Meleagris gallopavo*; Kilburg et al. 2014], Bachman's sparrow [*Aimophila aestivalis*; Tucker et al. 2004, Tucker et al. 2006, Shriver and Vickery 2001], and red-cockaded woodpecker [*Leuconotopicus borealis*; James et al. 1997, Sparks et al. 1999]). Additionally, Lashley et al. (2015) provided evidence that white-tailed deer (*Odocoileus virginianus*) increased selection of burned areas as years-since-fire increased. Similarly, others have described a relationship where herbivores may interact with fire to collectively affect plant communities in a shifting mosaic of disturbance that shapes ecosystem functions (Fuhlendorf et al. 2009).

The recent expansion of coyotes into the eastern United States (Parker 1995) provides unique opportunity to investigate how coyotes may interact with fire to affect ecosystem processes. Coyotes recently became established in the region through anthropogenic means and natural movements (Hill et al. 1987), and traits such as high fecundity rates and generalist diet may allow coyotes to play key functional roles in influencing trophic cascades in forested ecosystems (Gompper 2002). Recent evidence indicates that coyotes are affecting wildlife populations directly in the southeastern U.S. (e.g., Kilgo et al. 2010, Chitwood et al. 2015). Furthermore, coyotes may incur non-consumptive effects on prey populations in the longleaf pine ecosystem (e.g., antipredator responses in deer; Cherry et al. 2015). Also, coyotes may interact with prescribed fire to indirectly influence ecosystem processes given their influences over white-tailed deer (Chitwood et al. 2014, Chitwood et al. 2015, Cherry et al. 2015), which exert strong influences over plant distribution and abundance (Waller and Alverson 1997). To understand the complex feedback mechanisms between fire, vegetation,

and coyotes, we investigated multiscale resource selection by coyotes in relation to fire maintained vegetation types, years-since-fire, and manmade features that facilitate prescribe burning. Because coyotes evolved to hunt in grasslands and other open vegetation types, we hypothesized coyotes would select resources associated with early succession vegetation types and recently burned forests.

MATERIALS AND METHODS

Study site

Our study was conducted on the 73,469-ha Fort Bragg Military Installation (Fort Bragg) located in the Sandhills physiographic region of the southeastern United States (Fig. 1). Fort Bragg maintained one of the largest contiguous blocks of the threatened longleaf pine ecosystem. Prescribed fire was applied primarily during the growing season and on a 3-year fire return interval. Forest stands were divided by streams and firebreaks into prescribed fire management units about 43 ha in size (Lashley et al. 2014). Primary vegetation types were upland pine forest (67%), bottomland hardwood and ecotone (9%), and non-forested (24%). Upland pine forest was primarily longleaf pine overstory with an understory of oak (*Quercus* spp*.*) and wiregrass (*Aristida* spp.). We defined drainages as moist areas near streams that generally did not burn and contained a dense understory of ericaceous shrubs and trees not common to upland forested areas. Ecotones were transition areas between drainages and upland pine that consisted of plant species common to both vegetation types (Kilburg et al. 2014). Non-forested areas included drop zones (mean size = 305 ha) and managed forest openings (mean size = 0.003 km^2). Drop zones were open areas maintained as grasslands.

Fort Bragg maintained forest openings by disking annually and by planting agricultural crops.

Coyote trapping was not permitted at Fort Bragg but was common on adjacent private land. Also, coyote hunting on Fort Bragg was suspended during 2011 and 2012 to protect individuals radiocollared for research, but coyote hunting was legal on adjacent private lands year round (J. Jones, Fort Bragg Wildlife Branch, Fort Bragg, NC, pers. comm.).

Field methods

From February – May 2011, we captured coyotes throughout Fort Bragg using MB-550 foothold traps (Minnesota Trapline Products Inc., Pennock, MN, USA). For all captured coyotes we recorded sex, weight, and age (juvenile [≤ 1 year], subadult [between 1 and 2 years], adult [≥ 2 years]; Gier 1968), and fitted each with a Wildcell SG GPS radiocollar (Lotek Wireless Inc., Ontario, Canada). Radiocollars were programmed to record locations every 3 hours for up to 70 weeks with a pre-programmed release (Elfelt 2014). All coyote trapping and handling methods were approved by the North Carolina Wildlife Resources Commission and the North Carolina State University Institutional Animal Care and Use Committee (Protocol: 11-005-O).

Data analysis

We used Geospatial Modeling Environment (GME, Version 0.7.3.0, Hawthorne L. Beyer 2009 – 2012) to calculate 95% fixed-kernel home range boundaries for each coyote and used the least square cross-validation (LSCV) plug-in option to estimate the bandwidth for each individual's kernel density estimate (Seaman and Powell 1996).

To determine vegetation type selection (Johnson 1980) by coyotes, we used a compositional analysis (Aebischer et al. 1993) that treated the individual animal as the sample unit using the R package adehabitatHS (Calenge 2006). Using a Geographic Information System (GIS) and land cover data provided by Fort Bragg, we identified 7 discrete vegetation types as potentially important predictors of coyote vegetation type selection. We categorized land cover as drainage area, unforested, and upland forest. Unforested areas were managed forest openings and military drop zones. We subcategorized upland forest based on fire history (0, 1, 2, 3, and 4+ years-since-fire). We defined use as the proportion of each vegetation type in a home range and availability as the proportion of each vegetation type within the study area. We ranked each vegetation type according to the mean and standard deviation of log-ratio differences and compared the pairwise relationship between vegetation types using *t*-tests (Aebischer et al. 1993).

We evaluated finer-scale coyote habitat selection using a negative binomial resource selection probability function (RSPF; Boyce and McDonald 1999) implemented in R using package MASS (Venables and Ripley 2002). We measured relative frequency of use by systematically sampling 2,013 nonoverlapping circular sampling units across the study area and determining the number of coyote locations within each unit. The 200-m radii of circular sampling units were small enough to detect changes in coyote distribution and large enough to include multiple locations (Nielson and Sawyer 2013). We identified 5 variables as potentially important predictors of coyote habitat selection: (1) distance to nearest firebreak, (2) distance to road, (3) distance to nearest stream, (4) distance to nearest forest opening, and (5) distance to nearest drop zone. We measured each predictor variable in meters (m) from

the center of each sampling unit and tested for multicollinearities among variables using a Pearson's pairwise correlation analysis to determine whether any variables should be excluded from analysis ($|r| > 0.60$).

We modeled the relative frequency of locations measured for each sampling unit as a continuous response variable in a generalized linear model (GLM). We included an offset term to scale the response variable from counts of coyote locations within each sampling unit to relative frequency of use (i.e., probability of use) and modeled the response as a function of predictor variables, plus or minus an error term assumed to have a negative binomial distribution (McCullagh and Nelder 1989, White and Bennetts 1996).

To create a population-level model, we estimated coefficients by fitting a negative binomial GLM for each individual GPS-collared coyote, which correctly treated each coyote as the experimental unit. We excluded coyotes lacking the sufficient amount of locations required for model convergence. To create a seasonal population-level model, we defined seasons according to calendar time (i.e., spring [March 1 − May 31], summer [June 1 − August 21], fall [September 1 − November 30], and winter [December 1 − February 28]). Because we lacked the number of locations by season to reach convergence for some individual coyotes, we pooled data across animals to develop a population-level seasonal model. For all models, we used a forward-stepwise model-building procedure (Neter et al. 1996) where a *t*-statistic determined variable entry ($\alpha \leq 0.15$) and variable exit ($\alpha > 0.20$) (Hosmer and Lemshow 2000). We conducted spatial analyses in ArcGIS 10.2

(Environmental Systems Research Institute, Redlands, California) and statistical analyses in R 3.1.1 (R Development Core Team, 2012).

RESULTS

From February – May 2011, we captured and equipped 31 coyotes (12 females and 19 males) with GPS collars (Elfelt 2014). We monitored coyotes from February 2011 – October 2012. For all analyses, we excluded 4 individuals (2 females and 2 males) that dispersed outside the boundary of Fort Bragg.

Compositional analysis

For compositional analysis, we used locations from 27 coyotes (10 females and 17 males). Mean number of locations per individual used in compositional analysis was 2,812 (SE = 236.49), and number of relocations per individual ranged from 320 to 4,883 (85,385 total relocations). Coyotes showed strong selection for unforested areas in 2011 (Wilks' Λ = 0.26, $df = 6$, $p < 0.0001$) and 2012 (Wilks' Λ = 0.27, $df = 6$, $p = 0.0001$). In 2011, coyotes selected vegetation types in the following order: unforested > 1 year-since-fire > drainage > 3 years-since-fire > 2 years-since-fire > 0 years-since-fire > 4+ years-since-fire, though some differences in selection were not significant at α = 0.05 (Table 1). In 2012, coyotes selected vegetation types in the following order: unforested > 2 years-since-fire > 0 years-since-fire > drainage > 1 year-since-fire > 3 years-since-fire > 4 + years-since-fire (Table 2). Coyotes avoided upland pine forest burned 4+ years prior in 2011 and 2012.

Individual-based RSPF models

Of the 27 collared coyotes, 10 individuals lacked locations for models to converge. Therefore, we developed individual RSPF models for 17 GPS-collared coyotes (39,385 locations). Most coyotes selected areas close to firebreaks (12 out of 17), close to streams (10 out of 17), close to small forest openings (10 out of 17), close to drop zones (13 out of 17), and away from roads (10 out of 17). We estimated a population-level RSPF model (Table 3) that included 4 predictor variables. Distance to roads did not enter the models because it was not significant ($\alpha > 0.15$) at the population level. Coyotes selected areas closer to firebreaks, streams, small forest openings, and drop zones.

Seasonal RSPF models

In spring, coyotes (n=27; 13,749 relocations) selected areas close to firebreaks, forest openings, and drop zones (Table 4). In summer, coyotes (n=26; 10,023 relocations) selected areas close to firebreaks, away from streams, and close to drop zones (Table 4). In fall, coyotes (n=24; 8,391 relocations) selected areas away from streams and close to drop zones (Table 4). In winter, coyotes (n=27; 7,222 relocations) selected areas close to forest openings and close to drop zones (Table 4).

DISCUSSION

Coyotes selected open areas year round, probably because of high food availability and dense understory vegetation that provided cover, two factors commonly reported as determinants of habitat selection in other parts of their range (Litvais and Shaw 1980, Andelt et al. 1987, Guevara et al. 2005). Coyotes expanded into eastern North American from the

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midwestern United States, where they evolved in grassland vegetation (Nowak 1978, Gese et al. 1996). Small rodents (e.g., hispid cotton rat (*Sigmodon hispidus*)) occur in high densities within vegetation types similar to those occurring within drop zones, so rodent density may have been high in drop zones (Stokes 1995). Because small rodents form 13.7% of coyote diet at Fort Bragg (Swingen et al. 2015), our results indicate that coyotes may be selecting drop zones and small forest openings because of the abundance of small mammals. Also, insects such as grasshoppers are common in grasslands (Branson et al. 2006) and are an important coyote prey item at Fort Brag, comprising 72.7% of coyote diet during summer months (Swingen et al. 2015).

Within forested areas, coyote selection of burned areas likely was driven by prey availability. Upland pines burned 1 and 2 years prior have more soft mast (i.e., a major component of coyote diets at Fort Bragg [Swingen et al. 2015]) than areas burned during the same year (Lashley 2014, Allred et al. 2011). Also, Elfelt (2014) reported greater small mammal (e.g., *Peromyscus* spp.) abundance in more recently burned forest stands than in less recently burned forest stands, though the differences were not significant.

Coyotes likely used firebreaks year round to facilitate movement across the base, but American persimmon (*Diospyros virginiana*; hereafter, persimmon), which comprised 59.7% of coyote diet at Fort Bragg (Swingen et al. 2015), was most abundant within 25 m of firebreaks (Lashley et al. 2014). Persimmon may be especially important at Fort Bragg where other mammalian prey items occur in low densities (Chitwood et al. 2015; Elfelt 2014).

Although coyote habitat selection largely was consistent across seasons, selection of some habitat features varied seasonally, which may reflect a seasonally variable diet. Seasonal variation in coyote diet is well documented (e.g., Gese et al. 1988; Dumond et al. 2001; Schrecengost et al. 2008; Turner et al. 2011) and is linked to temporal fluctuations in food availability (e.g., MacCracken and Hansen 1987, Schrecengost et al. 2008). For example, coyotes at Fort Bragg selected small forest openings during spring and winter when rodents (e.g., hispid cotton rat [*Sigmodon hispidus*] and eastern cottontail [*Sylvilagus floridanus*]) formed a large component of coyote diets (Swingen et al. 2015). Similar to drop zones, small forest openings may harbor relatively high numbers of rodents (Stokes 1995). However, drop zones experienced less human activity at Fort Bragg and may be more important year-round due to their potential function as coyote cover and prey habitat.

Coyote habitat selection related to fire regimes may indicate an interaction with fire that could influence ecosystem function. For example, coyote selection of areas with greater soft mast availability induced by prescribed fire (i.e., firebreaks and areas burned 1 and 2 years prior) could facilitate seed dispersal of fruit-bearing plant species. Because coyotes are effective dispersers of seeds (Roehm and Moran 2013) and coyote home ranges at Fort Bragg are large (Elfelt 2014), coyotes may interact with fire to shape plant communities through dispersal (Nadakavukaren and McCracken 1985). Also, coyote presence may have cascading effects associated with predation risk on other wildlife species. For example, white-tailed deer should benefit from using areas burned the same year because of increased forage nutritive quality and palatability immediately following fire (Wood 1988), yet deer avoided those areas likely due to increased predation risk associated with decreased cover (Lashley et

al. 2015). Therefore, coyotes may alter interactions between deer and fire, which could have cascading effects on the plant communities via changes to pyric herbivory dynamics (Fuhlendorf et al. 2009).

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Table 1. Pairwise comparisons of selection index values based on compositional analysis of vegetation type selection for coyotes at Fort Bragg Military Installation, North Carolina, USA, 2011. A triple plus or minus sign indicates significant deviation from random at $p < 0.05$. Rank indicates the sum of "+" for each habitat type. Rank indicates the order that vegetation type selection occurred.

	Open	0 YSF	1 YSF	2 YSF	3 YSF	4+ YSF	Drain	Rank
Open	•	+++	+	+++	+++	+++	+	1
0 YSF	---	•	---	-	-	+++	-	6
1 YSF	-	+++	•	+++	+	+++	+	2
2 YSF	---	+	---	•	-	+++	-	5
3 YSF	---	+	-	+	•	+++	-	4
4 + YSF	---	---	---	---	---	•	---	7
Drain	-	+	-	+	+	+++	•	3

Table 2. Pairwise comparisons of selection index values based on compositional analysis of vegetation type selection for coyotes at Fort Bragg Military Installation, North Carolina, USA, 2012. A triple sign indicates significant deviation from random at p < 0.05. Rank indicates the sum of "+" for each habitat type. Rank indicates the order in which vegetation type selection occurred.

	Open	0 YSF	1 YSF	2 YSF	3 YSF	4+ YSF	Drain	Rank
Open	•	+	+++	+	+	+++	+++	1
0 YSF	-	•	+	-	+	+++	+	3
1 YSF	---	-	•	-	+	+	-	5
2 YSF	-	+	+	•	+++	+++	+	2
3 YSF	-	-	-	---	•	+	-	6
4 + YSF	---	---	-	---	-	•	-	7
Drain	---	-	+	-	+	+	•	4

Table 3. Coefficients for a population-level model resource selection probability function for coyotes at Fort Bragg Military Installation, North Carolina, USA, 2011 and 2012. Distance metrics are measured in meters from the predictor variable.

Predictor	β	SE	p
(Intercept)	-6.6040	0.0795	$p < 0.001$
Roads	NS[a]		
Firebreaks	-0.0015	0.0020	0.1093
Streams	-0.0003	0.0007	0.0005
Forest openings	-0.0010	0.0006	$p < 0.001$
Drop zones	-0.0009	0.0001	$p < 0.001$

[a] Not significant.

Table 4. Coefficients for a seasonal population-level resource selection probability function for coyotes at Fort Bragg Military Installation, North Carolina, USA, 2011 and 2012. Distance metrics are measured in meters from the predictor variable.

Predictor	Spring			Summer			Fall			Winter		
	β	SE	p	β	SE	p	β	SE	p	β	SE	p
(Intercept)	-6.2310	0.1050	$p < 0.001$	-6.9430	0.0945	$p < 0.001$	-6.9735	0.0722	$p < 0.001$	-6.539	0.0857	$p < 0.001$
Roads	NS[a]			NS			NS			NS		
Firebreaks	-0.0014	0.0006	0.0208	-0.0018	0.0006	0.0046	NS			NS		
Streams	NS			0.0006	0.0002	0.0015	0.0006	0.0002	0.0002	NS		
Forest openings	-0.0011	0.0002	$p < 0.001$	NS			NS			-0.0007	0.0002	$p < 0.001$
Drop zones	-0.0004	0.0000	$p < 0.001$	-0.0003	0.0000	$p < 0.001$	-0.0004	0.0000	$p < 0.001$	-0.0004	0.0000	$p < 0.001$

[a] Not significant.