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ARTICLE

Resource selection by coyotes (*Canis latrans*) in a longleaf pine (*Pinus palustris*) ecosystem: effects of anthropogenic fires and landscape features

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Abstract: Prescribed fire is used to restore and maintain fire-dependent forest communities. Because fire affects food and cover resources, fire-mediated resource selection has been documented for many wildlife species. The first step in understanding these interactions is to understand resource selection of the predators in a fire-maintained system. We attached GPS radio collars to 27 coyotes (*Canis latrans* Say, 1823) and examined resource selection relative to fire-maintained vegetation types, years since fire, anthropogenic features that facilitate prescribed burning, and other landscape features likely to affect coyote resource selection. Coyote home ranges were characterized by more open vegetation types and more recently burned forest (i.e., burned 0–1 year prior) than available on the study area. Within their home ranges, coyotes avoided areas close to densely vegetated drainages and paved roads. Coyote selection of more recently burned forest likely was in response to greater prey density or increased ability to detect prey soon after vegetation cover was reduced by fires; similarly, coyotes likely avoided drainages due to decreased hunting efficiency. Coyote resource selection was linked to prescribed fire, suggesting the interaction between fire and coyotes may influence ecosystem function in fire-dependent forests.

Key words: Canis latrans, coyote, longleaf pine, *Pinus palustris*, prescribed fire, resource selection.

Résumé : Le brûlage dirigé est utilisé pour restaurer et maintenir des communautés forestières qui dépendent du feu. Comme le feu a une incidence sur les ressources de nourriture et de couverture, la sélection de ressources modulée par le feu est documentée pour de nombreuses espèces sauvages. La première étape vers une compréhension de ces interactions consiste à comprendre la sélection des ressources par les prédateurs dans un système entretenu par le feu. Nous avons fixé des colliers émetteurs GPS à 27 coyotes (*Canis latrans* Say, 1823) et examiné leur sélection de ressources en fonction des types de végétation maintenue par le feu, du nombre d'années écoulées depuis un feu, d'éléments d'origine humaine qui facilitent le brûlage dirigé et d'autres éléments du paysage qui auraient vraisemblablement une incidence sur la sélection de ressources par les coyotes. Les domaines vitaux des coyotes étaient caractérisés par des types de végétation plus ouverts et des forêts plus récemment brûlées (c.-à-d. de 0 à 1 an auparavant) que ce qui était disponible dans la région à l'étude. Dans leurs domaines vitaux, les coyotes évitaient les zones situées près de cours d'eau présentant une végétation dense et de routes revêtues. La sélection par les coyotes de forêts brûlées plus récemment était probablement une réaction à la plus grande densité de proies ou la capacité accrue de déceler des proies peu après la réduction de la couverture végétale par le feu; de même, les coyotes évitaient probablement les cours d'eau en raison d'une moins grande efficacité de la chasse dans ces milieux. La sélection de ressources par les coyotes était reliée au brûlage dirigé, ce qui indiquerait que les interactions entre le feu et les coyotes pourraient influencer la fonction écosystémique dans les forêts dépendant du feu. [Traduit par la Rédaction]

Mots-clés : Canis latrans, coyote, pin des marais, *Pinus palustris*, brûlage dirigé, sélection des ressources.

Introduction

Fire is a dominant disturbance that occurs globally and regulates many terrestrial plant and animal communities. Influences of fire on the function and structure of ecosystems are well studied and research on the topic has revealed complex interactions among plant and animal species and fire (e.g., Bradstock et al. 2005; Russell et al. 1999, 2009). For example, biodiversity may be greater within a few years following fire due to fire-induced vegetative regrowth and increased availability of fruits and seeds (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 can mimic those of naturally occurring lightning-caused fire. Therefore, the application of prescribed fire provides opportunity to study community-level interactions among plant and animal species and fire.

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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 impact 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., quaking aspen (*Populus tremuloides* Michx.), willow (species of the genus *Salix* L.), cottonwood (species of the genus *Populus* L.)) occurred following gray wolf (*Canis lupus* Linnaeus, 1758) reintroduction, highlighting the important effects of predators on ungulates. Thus, because predators and fire function to shape ecosystems independently, it is likely they interact to form a novel disturbance when paired.

A growing body of literature examining the effects of fire on resource selection of apex predator species suggests that these species alter their space use in response to prescribed fire, perhaps as a cascading response to post-fire changes in vegetation. Examples of predator attraction to recently burned areas have been documented in felids (e.g., Dees et al. 2001; McGregor et al. 2014, 2015), raptors (e.g., Bond et al. 2009; Hovick et al 2017), and canids (e.g., Thompson et al. 2008; Hradsky et al. 2017). Fire temporarily decreases vegetative cover and may allow for greater hunting efficiency in recently burned open areas due to decreased prey crypticity (e.g., Wilgers and Horne 2007; Hradsky et al. 2017). Also, post-fire decreases in vegetative structure could permit easier movement for predators and facilitate use of a variety of vegetation types (Lyon et al. 2000), potentially making prey more vulnerable to predation (Chitwood et al. 2017). Furthermore, fire-caused numerical increases of prey species (e.g., deer mice (species of the genus *Peromyscus* Gloger, 1841)) may attract predators to more recently burned areas (Lyon et al. 2000). Conversely, fire-induced decreases in vegetative cover could reduce predator hunting success and lead to predator avoidance of recently burned areas (e.g., Eby et al. 2013).

The recent expansion of coyotes (*Canis latrans* Say, 1823) into the eastern United States (Parker 1995) provides unique opportunity to investigate how fire affects coyote resource selection. Coyotes recently became established in the region through anthropogenic means and natural movements (Hill et al. 1987; Hody and Kays 2018), and traits such as high fecundity and generalist diet may allow coyotes to play key functional roles by influencing trophic cascades in forested ecosystems (Gompper 2002; Jones et al. 2016). Recent evidence indicates that coyotes are affecting wildlife populations directly in the southeastern United States (e.g., Kilgo et al. 2010; Chitwood et al. 2015) and may cause non-consumptive effects on prey populations in the longleaf pine (*Pinus palustris* Mill.) ecosystem (e.g., antipredator responses in white-tailed deer (*Odocoileus virginianus* (Zimmerman, 1780)); 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, 2015, 2017; Cherry et al. 2015), which exert strong effects on plant communities (Waller and Alverson 1997). To understand the relationship between fire and coyotes, we investigated multi-scale, seasonal resource selection by coyotes in relation to fire-maintained vegetation types, years since fire, and several landscape features, including those that facilitate prescribed burning. Because coyotes evolved to hunt in grasslands and other open vegetation types, we hypothesized that coyotes would select resources associated with early succession vegetation and more recently burned forests (i.e., within 1–2 years prior). Furthermore, we hypothesized that coyote resource selection would vary in relation to seasonal changes in availability of prey and forage.

Materials and methods

Study site

Our study was conducted on the 735 km² Fort Bragg Military Installation (Fort Bragg) located in the Sandhills physiographic region of the southeastern United States (Fig. 1). Fort Bragg maintains one of the largest contiguous blocks of the threatened longleaf pine ecosystem. Prescribed fire is applied primarily during the growing season and on a 3-year fire return interval. Forest stands are divided by streams and fire breaks (i.e., drivable sand roads used by military and forest management personnel) into prescribed fire management units about 0.43 km² in size. To limit hardwood encroachment into the mid-story and to maintain vegetation structure appropriate for the federally endangered Red-cockaded Woodpecker (*Leuconotopicus borealis* (Vieillot, 1809); also known as *Dendrocopos borealis* (Vieillot, 1809) and *Picoides borealis* (Vieillot, 1809)), approximately one-third of Fort Bragg is burned annually (Cantrell et al. 1995; Garabedian et al. 2017). Backing fires (i.e., slow moving, low-intensity fires that back into the wind) are used initially to light the stand, followed by strip head fires (i.e., several head fires lit in parallel) (Wade and Lundsford 1990). Prescribed fire ignition, largely for backing fires, most commonly occurs along fire breaks at Fort Bragg, creating fire shadows that are characterized by a higher density of hardwood stems and greater fruit availability than farther from fire breaks (Lashley et al. 2014).

Primary vegetation types are upland pine forest (67%), drainages and ecotone (9%), and unforested (24%). Upland pine forest is primarily longleaf pine overstory with an understory of oak (species of the genus *Quercus* L.) and wiregrass (species of the genus *Aristida* L.). We defined drainages as moist areas near streams that generally do not burn and contain a dense understory of ericaceous shrubs and trees not common to upland forested areas. Ecotones are transition areas between drainages and upland pine that consist of plant species common to both vegetation types (Kilburg et al. 2014). Unforested areas include drop zones (mean size = 3.05 km²) and managed wildlife openings (mean size = 0.003 km²). Drop zones are open areas maintained as grasslands for military use. Managed wildlife openings are maintained by Fort Bragg 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 that were radio-collared for research, but coyote hunting was legal on adjacent private lands year-round.

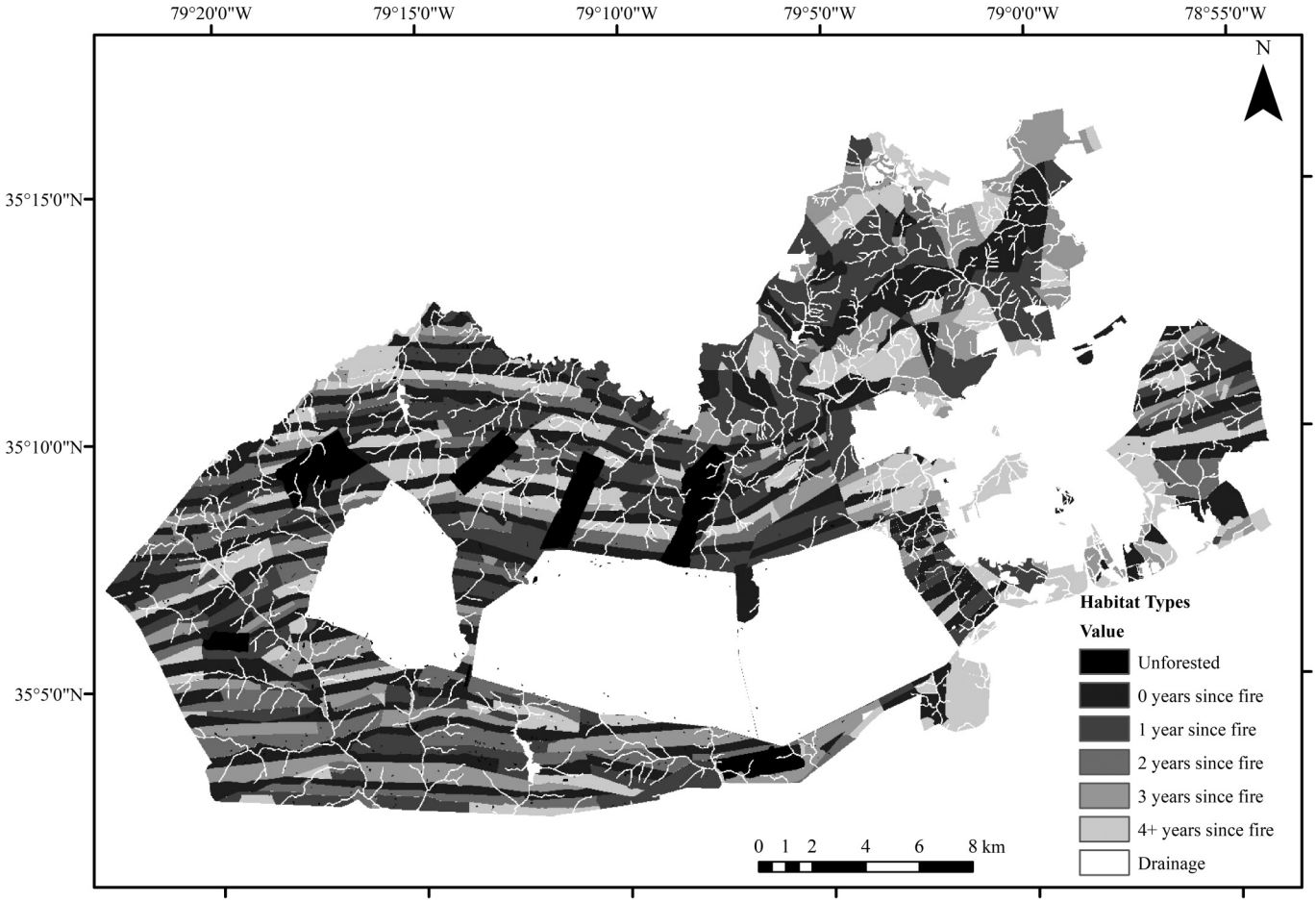
Field methods

From February to May 2011, we captured coyotes throughout Fort Bragg using MB-550 foothold traps (Minnesota Trapline Products Inc., Pennock, Minnesota, USA). For all captured coyotes, we recorded sex, mass, and age class. We determined age using tooth wear and placed each into one of three classes: (juvenile (≤1 year), subadult (between 1 and 2 years), adult (≥2 years); Gier 1968). We fitted each with a Wildcell SG GPS radio collar (Lotek Wireless Inc., Newmarket, Ontario, Canada). Radio collars were programmed to record locations every 3 h for up to 70 weeks with a pre-programmed release. All coyote trapping and handling methods were conducted according to the guidelines of the American Society of Mammalogists (Sikes and The Animal Care and Use Committee of the American Society of Mammalogists 2016) and approved by the North Carolina Wildlife Resources Commission and the North Carolina State University Institutional Animal Care and Use Committee (Protocol: 11-005-O).

Second-order resource selection

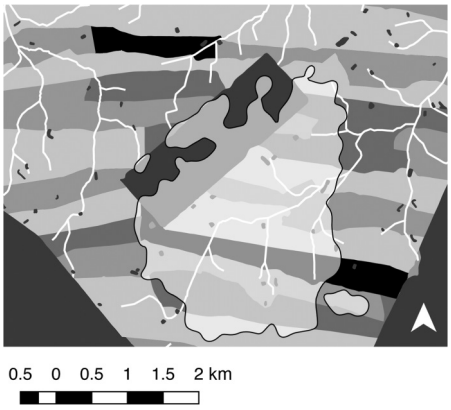
We used compositional analysis to investigate second-order (selection of home range within the study area; Johnson 1980) resource selection by coyotes (Aebischer et al. 1993). Composi-

Fig. 1. Example of habitat variables used in a second-order compositional analysis of coyote (*Canis latrans*) (n = 27) resource selection during 2012, Fort Bragg Military Installation, North Carolina, USA.



tional analysis uses log-ratios to compare proportions of used resources to available resources and subsequently determine the ranked selection for each vegetation type. Compositional analysis treats the individual animal as a sampling unit rather than the relocations (Aebischer et al. 1993). For each year, 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 (Fig. 2; Seaman and Powell 1996). Using a geographic information system (GIS) and yearly fire-history data provided by Fort Bragg, we identified seven discrete vegetation types as potentially important predictors of coyote vegetation type selection (Fig. 1). We categorized land cover as drainage area, unforested, and upland forest. For each year, we subcategorized upland forest into five vegetation types 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 (Fig. 2) and availability as the proportion of each vegetation type within the study area (i.e., Fort Bragg). We considered the entire study area to be available for use by each coyote because of their capability for wide-ranging movements beyond the boundaries of Fort Bragg, and we defined transient individuals as those coyotes that dispersed beyond the boundaries of Fort Bragg (Elfelt 2014). 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 paired t tests (Aebischer et al. 1993).

Fig. 2. Example of a coyote (*Canis latrans*) home range, Fort Bragg Military Installation, North Carolina, USA. The white shaded areas outlined in black represent the boundaries of the 95% fixed-kernel home range. The shades of gray in the background represent differing years since fire and the white lines represent drainages.



Third-order resource selection

We estimated third-order resource selection (Johnson 1980) in coyotes by examining intensity of use within the home range, fitted using a negative binomial generalized linear mixed-effects model (Boyce and McDonald 1999; Zuur et al. 2009). This approach treats the response as a continuous measure of intensity of use

Table 1. Pairwise comparisons of selection index values based on compositional analysis of second-order selection for coyotes (*Canis latrans*) (n = 27) at Fort Bragg Military Installation, North Carolina, USA, 2011.

	Unforested	0 YSF	1 YSF	2 YSF	3 YSF	4+ YSF	Drainage	Rank
Unforested		+++	+	+++	+++	+++	+	1
0 YSF	−−−		−−−	−	−	+++	−	6
1 YSF	−	+++		+++	+	+++	+	2
2 YSF	−−−	+	−−−		−	+++	−	5
3 YSF	−−−	+	−	+		+++	−	4
4+ YSF	−−−	−−−	−−−	−−−	−−−		−−−	7
Drainage	−	+	−	+	+	+++		3

Note: A triple plus sign indicates that the vegetative type in the row was selected over the type in the column, whereas a triple minus sign indicates that the vegetation type in the row was selected less than the type in the column at $\alpha = 0.05$. Single signs indicate the relationship was not significant. Rank indicates the sum of "+" for each habitat type and denotes the order that selection of vegetation type occurred. YSF is years since fire.

rather than the binary response traditionally estimated by resource selection functions. Furthermore, this model implicitly accounts for temporal autocorrelation because the response variable is the count of locations within a sampling unit rather than locations collected from an individual animal (Nielson and Sawyer 2013). We measured coyote locations by systematically sampling non-overlapping circular 200 m radii sampling units within the 95% fixed-kernel home-range boundaries of each individual. The 200 m radii of circular sampling units were appropriately scaled for coyote movements (i.e., small enough to detect changes in coyote distribution and large enough to include multiple locations) (Millspaugh et al. 2006; Nielson and Sawyer 2013). We measured five potentially important covariates of coyote resource selection: (1) distance to nearest fire break, (2) distance to paved road, (3) distance to nearest drainage, (4) distance to nearest wildlife opening, and (5) distance to nearest drop zone. We measured distance covariates in metres (m) from the center of each circular sampling unit. Prior to modeling, we standardized all distance covariates to improve model convergence (Zuur et al. 2009). We used Pearson correlations to assess collinearity of potential distance covariates and considered distance covariates to be collinear when $|r| > 0.60$.

We fit the relative frequency of coyote locations within each non-overlapping sample unit as the response variable. We included the total counts for each coyote as an offset term to transform observed counts of coyote locations within each sample unit to relative frequency of use (Nielson and Sawyer 2013). To assess coyote selection relative to seasonal phenology, we divided the year into four seasons: spring (1 March – 31 May), summer (1 June – 31 August), fall (1 September – 30 November), and winter (1 December – 28 February). We fit year, sex, age class, season, standardized distance covariates, and interactions between season and each distance covariate as fixed effects and evaluated precision of fixed effects with 95% confidence intervals constructed using 500 bootstrap samples. To account for variation in baseline selection due to individual differences in behavior among sampled coyotes, we fit individual coyote ID as a random intercept term. We used Tukey's multiple comparisons to determine whether the rate of selection for each distance covariate varied across seasons. We conducted spatial analyses in ArcGIS version 10.2 (Environmental Systems Research Institute (ESRI), Inc., Redlands, California, USA) and statistical analyses in R version 3.4.0 (R Core Team 2017) using the contributed packages adehabitatHS (Calenge 2006), lme4 (Bates et al. 2016), and lsmeans (Lenth 2016).

Results

From February to May 2011, we captured and attached GPS radio collars to 31 coyotes, including 12 females (4 juveniles, 5 subadults, and 3 adults) and 19 males (4 juveniles, 3 subadults, and 12 adults). We monitored coyotes from February 2011 to October 2012. For the analysis of second-order coyote resource selection, we excluded four transient individuals (2 females and 2 males) that dispersed outside the boundary of Fort Bragg. For the analysis of third-order coyote resource selection, we excluded two individuals with <50 relocations, in addition to the four transient individuals that dispersed outside the site boundary. The 95% fixed-kernel mean home-range size of coyotes that remained near or within the boundaries of Fort Bragg was 85.04 ± 14.17 km^2. Although home-range size generally was larger for males (103.94 ± 18.93 km^2) than females (47.25 ± 12.98 km^2), this relationship was statistically weak (t = –1.99, P = 0.06). The 95% fixed-kernel home-range size did not differ among age classes ($F_{[2,24]}$ = 0.77, P = 0.47) (Elfelt 2014).

Compositional analysis

We used relocations from 27 coyotes (10 females and 17 males) to evaluate second-order selection using compositional analysis. Mean number of relocations per individual used was 2 812 (SE = 236.49) and the number of relocations per individual ranged from 320 to 4 883 (85 385 total relocations). Coyotes strongly selected unforested areas in 2011 (Wilks' $\lambda_{[6]}$ = 0.26, p < 0.0001) and 2012 (Wilks' $\lambda_{[6]}$ = 0.27, 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 $\alpha = 0.05$ (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.

Third-order selection

Third-order resource selection by coyotes (n = 25) varied with year (χ^2 = 349.1, p < 0.001), season (χ^2 = 183.3, p < 0.001), distance to drop zone (χ^2 = 3115.0, p < 0.001), distance to wildlife opening (χ^2 = 146.5, p < 0.001), distance to drainage (χ^2 = 44.8, p < 0.001), and distance to paved road (χ^2 = 51.0, p < 0.001). We detected significant interaction effects between season and distance to drop zone (χ^2 = 479.1, p < 0.001), distance to wildlife opening (χ^2 = 48.3, p < 0.001), distance to drainage (χ^2 = 73.0, p < 0.001), distance to fire break (χ^2 = 9.6, p = 0.023), and distance to paved road (χ^2 = 38.8, p < 0.001). We failed to detect significant effects of age and sex on selection. On average, the among-coyote standard deviation in intercept estimates was 0.577 (i.e., <10% of the population intercept), suggesting differences among sample sizes and individual coyote behavior accounted for relatively small changes in baseline selection.

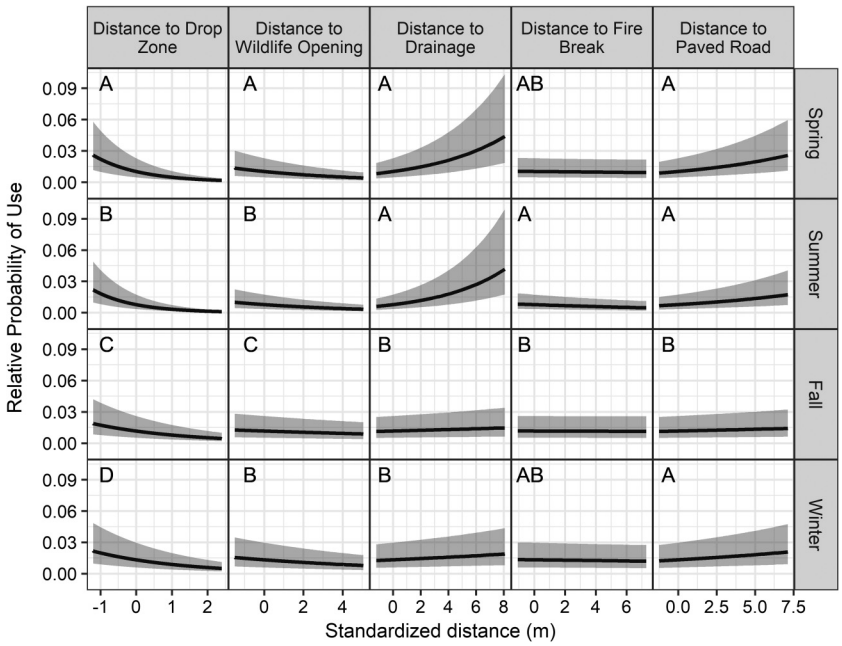
Overall, coyotes selected areas close to drop zones and wildlife openings and away from drainages and paved roads, but the direction and magnitude of selection varied among seasons and

Table 2. Pairwise comparisons of selection index values based on compositional analysis of second-order selection for coyotes (*Canis latrans*) (n = 27) at Fort Bragg Military Installation, North Carolina, USA, 2012.

	Unforested	0 YSF	1 YSF	2 YSF	3 YSF	4+ YSF	Drainage	Rank
Unforested		+	+++	+	+	+++	+++	1
0 YSF	−		+	−	+	+++	+	3
1 YSF	−−−	−		−	+	+	−	5
2 YSF	−	+	+		+++	+++	+	2
3 YSF	−	−	−	−−−		+	−	6
4+ YSF	−−−	−−−	−	−−−	−		−	7
Drainage	−−−	−	+	−	+	+		4

Note: A triple plus sign indicates that the vegetative type in the row was selected over the type in the column, whereas a triple minus sign indicates that the vegetation type in the row was selected less than the type in the column at α = 0.05. Single signs indicate the relationship was not significant. Rank indicates the sum of "+" for each habitat type and denotes the order that selection of vegetation type occurred. YSF is years since fire.

Fig. 3. Predicted effects of distance on selection for drop zones, wildlife openings, drainages, fire breaks, and paved roads across seasons for radio-collared coyotes (*Canis latrans*) (n = 25) at Fort Bragg, North Carolina, USA, averaged across 2011–2012. Black lines represent predicted rate of use within each season and gray shaded areas represent 95% confidence bands. Letters within columns denote Tukey groupings from simultaneous pairwise comparisons of effects for each distance covariate across seasons using α = 0.05. Panels exhibiting the same letters indicate similar predicted selection.



between years (Supplementary Table S1).[1] Coyotes selected areas closer to drop zones during spring and summer but avoided drop zones during fall and winter (Fig. 3). Coyotes selected areas closer to wildlife openings during spring but avoided wildlife openings during summer and fall (Fig. 3). Coyotes showed marginal selection for areas closer to drainages during fall and winter but avoided drainages during spring and summer (Fig. 3). Coyotes selected areas closer to fire breaks during summer (Fig. 3). Coyotes selected areas closer to paved roads during fall, but they avoided paved roads during spring and summer (Fig. 3).

Discussion

Coyotes at Fort Bragg selected open areas at multiple spatial scales, probably because of high food availability and understory vegetation that provided cover, two factors commonly reported as determinants of resource selection in other parts of the species' range (Litvaitis and Shaw 1980; Andelt et al. 1987; Guevara et al. 2005). Coyote selection of areas closer to wildlife openings and drop zones varied seasonally, with coyotes selecting most strongly for open areas in spring and avoiding them most strongly during fall. Some small rodents (e.g., hispid cotton rat (*Sigmodon hispidus* Say and Ord, 1825)) occur in high densities within vegetation types similar to those occurring within drop zones, so rodent prey density may have been high in drop zones (Stokes 1995). Because small rodents form 13.7% of coyote diet at Fort Bragg and small rodents were most abundant in coyote diet during spring (32.4%) (Swingen et al. 2015), our results indicate that coyotes may be selecting drop zones and small wildlife openings during spring because of the abundance of small mammals. Also, insects (e.g., grasshoppers) are common in grasslands (Branson et al. 2006) and are an important coyote prey item at Fort Bragg, comprising 35.3% of coyote diet during summer months (Swingen et al. 2015). Lastly, vegetation in drop zones and wildlife openings primarily was perennial grasses and forbs, which enter dormancy and thereby lose

[1]Supplementary table is available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2018-0150.

their value as cover during the late fall through winter; however, the ericaceous shrubs in the drainages are evergreen and likely provided critical cover for coyotes and other wildlife during the winter months.

Within forested areas, coyote selection of more recently burned areas (i.e., areas burned 0–1 years prior) and avoidance of areas burned 4 or more years prior may have been driven by food availability. Although upland pines burned 2 years prior have more soft mast (i.e., fruits and seeds, a major component of coyote diets at Fort Bragg; Swingen et al. 2015) than areas burned during the same or previous year (Allred et al. 2011; Lashley et al. 2015*b*, 2017), production of fruits and seeds often declines 3+ years following fire (Stransky and Harlow 1981). Moreover, Sasmal et al. (2017) reported small mammals (e.g., *Peromyscus* spp.) tended to be in greater abundance in forest stands burned during the previous year than in stands burned 2 or 3 years prior. Thus, selection of forested areas likely was driven by individual coyotes selecting areas where their foods were most abundant.

Coyotes selected areas away from drainages, though selection varied seasonally; coyotes selected areas closer to drainages during fall and winter and areas away from drainages in spring and summer. At Fort Bragg, drainages experienced infrequent fire due to high moisture levels and were composed of dense ericaceous vegetation, especially during the spring and summer growing seasons. Although the opportunistic nature of coyotes has allowed them to expand from their native range into more forested areas, coyotes inhabiting mixed forest – agricultural landscapes demonstrate improved hunting efficiency over coyotes inhabiting more densely vegetated areas (Richer et al. 2002). At Fort Bragg, *Peromyscus* spp. occur in greater abundance in drainages, possibly due to higher quality nesting and escape cover (Sasmal et al. 2017). Coyote avoidance of areas close to drainages despite higher prey abundance may indicate limited hunting efficiency in these areas. Other predator species have been documented avoiding areas with high prey abundance and low hunting success (e.g., Eby et al. 2013) and are less successful when hunting prey in areas with complex vegetation structure (e.g., McGregor et al. 2015). Therefore, drainages at Fort Bragg may serve as a refuge for prey species from coyotes. Furthermore, vegetation cover was more abundant across the study area during the spring and summer months, so coyotes likely were able to forage and hide across a greater portion of the landscape then. Conversely, as the herbaceous vegetation in the drop zones and upland pine forest entered dormancy in the fall and winter, the cover in the drainages may have become more important.

The negative ecological impacts of roads are well documented and range from direct (e.g., mortality from vehicle collisions: Trombulak and Frissell 2000) to indirect (e.g., behavioral modifications: Jaeger et al. 2005; population fragmentation: Bennett 2017). Indeed, road mortalities accounted for 29% of mortality among collared individuals during our study (Stevenson et al. 2016). Herein, we documented coyote avoidance of areas closer to paved roads, but we did not record positive or negative coyote selection for fire breaks. Because paved roads experienced greater, faster, and more consistent traffic at Fort Bragg, and fire breaks were sandy tertiary roads that experienced relatively little traffic, coyotes may be adjusting their space use to avoid roads with greater traffic.

Coyote presence may have indirect cascading effects associated with predation risk on other wildlife species. For example, lactating female 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 they avoided those areas at Fort Bragg, likely due to increased predation risk associated with decreased cover (Lashley et al. 2015*a*). 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). It has been well established that predators can shape ecosystems via their direct and indirect effects on populations and behavior of prey (Beschta and Ripple 2012), and coyote selection of areas reported to be avoided by the major herbivore in this system suggests that coyotes may regulate interactions between fire and herbivory to shape ecosystem functions at Fort Bragg. Thus, because coyotes have the potential to influence prey population dynamics via direct and indirect effects, managers concerned with prey abundance should consider possible interactions between coyotes and fire. Future research is needed on how predators may interact with fire to shape plant and animal communities through predation and the dispersal of plant seeds.

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