

ABSTRACT

ELFELT, MORGAN BRIANNA. Coyote Movement Ecology and Food Habits at Fort Bragg Military Installation. (Under the direction of Drs. Christopher E. Moorman and Christopher S. DePerno.)

The coyote (*Canis latrans*) recently expanded its range into the eastern United States following the extirpation of other large carnivores. Coyote diet and movement ecology vary regionally and temporally, and local data are important to understanding the impacts of this novel predator on southeastern ecosystems. In the fire-dependent longleaf pine (*Pinus palustris*) ecosystem, low prey density may contribute to larger home-range size and greater movement rates than in other areas of the Southeast. Also, low food availability could cause coyotes to have an amplified impact on energetically beneficial prey items such as white-tailed deer (*Odocoileus virginianus*). To determine the diet of coyotes in the longleaf pine ecosystem, we analyzed scat samples collected from Fort Bragg Military Installation (FBMI), North Carolina. White-tailed deer were the most common mammalian food item, occurring in 14.9% of all scats. However, white-tailed deer occurrence in scats was lowest in fall, when soft mast occurred in most coyote scats (98.2%), suggesting the widespread availability of soft mast during the fall may decrease predation pressure on white-tailed deer.

To investigate the abundance of small mammals, an important coyote food item, we established live-trapping grids in five vegetation types: open, lowland hardwood, upland pine 1-year post burn, upland pine 2-yrs post burn, and upland pine 3-yrs post burn. We captured 243 individuals in 12,250 trap-nights, including 208 *Peromyscus* spp. We used closed capture models to estimate the abundance of *Peromyscus* spp. in each of the five vegetation types. We did not detect differences in abundance among the 1-, 2-, and 3-years post burn upland pine vegetation types, suggesting no effect of time since burn. However, the open

and lowland hardwood vegetation types differed from each other, with open having the lowest and lowland hardwood having the greatest *Peromyscus* abundance. Greater abundance in the lowland cover type likely was attributable to greater ground-level vegetation complexity, which provided more food and cover resources.

Little is known about coyote movement ecology in the southeastern United States; therefore, we determined home-range size, movement rates, and dispersal distances for coyotes at FBMI using GPS technology. We captured 30 coyotes and attached radiocollars programmed to record locations every 3 hours for 70 weeks. Home-range size (95% fixed-kernel) averaged 85.04 km², with males marginally larger than females ($t = -1.99$, $P = 0.06$), and no difference among age classes ($F_{2,24} = 0.77$, $P = 0.47$). Movement rates (m/hr) differed among seasons ($F_{3,73} = 19.18$, $P < 0.001$) and between time periods (night vs. day; $F_{1,26} = 236.54$, $P < 0.001$). Movement rates did not differ between sexes ($t = -1.44$, $P = 0.16$) or among age classes ($F_{2,24} = 0.97$, $P = 0.39$). Also, we observed three collared coyotes which dispersed from FBMI, traveling straight-line distances of 192km, 221km, and 345km before establishing new home ranges. The large home-range sizes and long dispersal distances recorded in our study may be attributable to low food availability at our study site. Our results highlight the ability of coyotes to travel long distances and colonize new areas, which suggests an extended geographic and temporal scale should be considered when managing local coyote populations.

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Coyote Movement Ecology and Food Habits at Fort Bragg Military Installation

by
Morgan Brianna Elfelt

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APPROVED BY:

Christopher E. Moorman
Committee Co-Chair

Christopher S. DePerno
Committee Co-Chair

Brian J. Reich

DEDICATION

To Donna Stockrahm, who encouraged and inspired me to start this degree, and never doubted my ability to finish it.

BIOGRAPHY

Morgan Elfelt was born and raised in Andover, MN, spending the majority of her childhood in the great outdoors. After the encouragement of her undergraduate advisor, she chose to major in Biology at Minnesota State University Moorhead. After several summers of catching turtles, bears, and degus, Morgan decided to pursue a master's degree at North Carolina State University. She was married in August 2014 to Jason Swingen and now works as an Assistant Scientist at the Natural Resources Research Institute in Duluth, Minnesota.

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CHAPTER 1

Seasonal Coyote Diet Composition at a Low-Productivity Site

ABSTRACT

Coyotes (*Canis latrans*) are considered optimal foragers, consuming energetically beneficial (high-ranking) prey items whenever encountered. We studied coyote diet to examine the species' potential impact on energetically beneficial species, such as White-tailed deer (*Odocoileus virginianus*), in a low-productivity area where alternate food resources may be scarce. We determined coyote diet composition through analysis of 315 scats collected at Fort Bragg Military Installation between May 2011 and July 2012. White-tailed deer were the most common mammalian food item, occurring in 14.9% of all scats, and 42.5% of winter scats. White-tailed deer occurrence in coyote diet was lowest in fall, when Persimmon (*Diospyros virginiana*) occurred in most coyote scats (95.7%). Our results indicate that availability of persimmon during the fall may lessen predation pressure on white-tailed deer during this time period.

INTRODUCTION

The ability of *Canis latrans* (coyote) to adapt foraging strategies to spatial and temporal variation in food resources likely facilitated their expansion into the eastern United States (Parker 1995). Coyotes are omnivorous with primary food items including mammals,

insects, and fruit, but relative proportions of these items vary regionally (Wooding et al. 1984, Stratman and Pelton 1997, Chamberlain and Leopold 1999, Hidalgo-Milhart et al. 2001, Schrecengost et al. 2008, Turner et al. 2011, McVey et al. 2013). For example, in south Texas, Lagomorphs were the most common food item, whereas in West Virginia, *Odocoileus virginianus* (white-tailed deer) and rodents were the most commonly occurring food items (Crimmins *et al.* 2012, Windberg and Mitchell 2013). Also, coyote diets vary seasonally as the availability of food items change (e.g., Stratman and Pelton 1997, O'Donoghue et al. 1998, Hidalgo-Milhart et al. 2001, Morey et al. 2007, Schrecengost et al. 2008). Generally, white-tailed deer occurrence in coyote diets is greatest during the fawning period (Wooding et al. 1984, Blanton and Hill 1989, Schrecengost et al. 2008), and soft mast occurrence often follows local fruiting phenology (Andelt et al. 1987, Stratman and Pelton 1997, Chamberlain and Leopold 1999, Schrecengost et al. 2008).

Although coyotes often are categorized as generalist predators, their foraging strategy is debated in the literature (Patterson et al. 1998, Sacks and Neale 2002, McKinney and Smith 2007, Randa et al. 2009), with more recent studies supporting optimal foraging theory, where food items are selected based on an energetic benefit/cost ratio (MacCracken and Hanson 1987, Hernández 2002). Theoretically, the optimal selection of each food item incorporates the “value” in terms of energy and nutrition and the expenditure of time and energy required to search for, pursue, and consume each item into a relative ranking (see Norberg 1977, Pyke et al. 1977). According to the theory, energetically beneficial foods always are consumed when encountered, and the proportion of lower-quality foods should decrease with increasing

availability of more energetically beneficial foods (Pyke et al. 1977, MacCracken and Hanson 1987).

Under the optimal foraging theory, the effects of coyote predation on highly-ranked prey species (e.g., white-tailed deer) are unknown in low-productivity areas where availability of energetically beneficial food sources may be lower than at sites with greater site productivity. Previous research quantifying food value concluded that white-tailed deer is high in gross energy and crude protein (Davison et al. 1978, Litvaitis and Mautz 1980, MacCracken and Hansen 1986). We believe that due to their high energetic value and large size, white-tailed deer are an energetically beneficial food item for coyotes in the southeastern United States (Pekins and Mautz 1990). The optimal foraging theory predicts that coyotes should consume energetically beneficial food items when encountered; however, as availability of energetically beneficial items decreases, diets should become more diverse and include more lower-ranking food items (Pyke et al. 1977). Hence, the prevalence of white-tailed deer in coyote diets may be relatively low in low-productivity regions such as the Sandhills of the southeastern United States. Conversely, a high proportion of white-tailed deer in coyote diets in low productivity regions could suggest greater impact on deer populations, especially given the lower reproductive potential in these regions (Shea and Osbourne 1995).

Therefore, our objectives were to determine the seasonal composition of coyote diets, and investigate the impact of coyotes on prey species at a low productivity site. We expected

seasonal changes in coyote diets to follow regional phenology, and diets to contain a higher diversity of food items than on higher productivity sites.

METHODS

Study Area – Our study was conducted at Fort Bragg Military Installation (FBMI), which is in the Sandhills region of central North Carolina. The Sandhills are considered low in productivity, because of the well-drained sandy soils (Shea and Osbourne 1995, Sorrie et al. 2006). FBMI covers approximately 65,000 hectares and contains one of the largest contiguous remnants of the *Pinus palustris* (longleaf pine)- *Aristida stricta* (wiregrass) ecosystem in the Southeast. The most abundant plant community type at FBMI is the pine/scrub oak sandhill (as described by Sorrie et al. 2006) which consists mainly of a longleaf pine canopy, oak (*Quercus* spp.) subcanopy and wiregrass ground layer, with open canopy structure maintained by fire. The understory in longleaf pine forests has been shown to have especially low production compared to other grasslands due to competition with trees in this water limited forest system (Mitchell et al. 1999). Other common plant communities at FBMI include riparian areas dominated by shrubs and trees, and disturbed areas with ruderal plants, mainly in open drop zones for parachuting and other military training activities (Sorrie et al. 2006).

Land management at FBMI is driven by efforts to restore and maintain habitat for the federally endangered *Picoides borealis* (red-cockaded woodpecker). Prescribed burns are conducted on a three-year return interval to maintain open longleaf pine forest required by this species. Prior to 1989, burning was conducted exclusively during the dormant season,

but growing-season burns now make up the majority of planned burns in forested cover types on FBMI (Lashley et al. 2014).

Scat Analysis – At FBMI, we opportunistically collected coyote scat samples determined to be <1 week old along roads and firebreaks from May 2011 through June 2012. Scats were identified based on size, shape, odor, and associated tracks. *Canis lupus familiaris* (domestic dogs), *Vulpes vulpes* (red fox), and *Urocyon cinereoargenteus* (gray fox) were uncommon in the areas we collected scats, as evidenced by a concurrent camera trap study at FBMI (B. Will, North Carolina State University, Raleigh, NC, unpubl. data). We placed coyote scats in zip-top plastic bags and stored them in a -30°C freezer until analysis. We categorized the scats into four seasons based on food availability cycles: summer (May – July), fall (August – October), winter (November – January), and spring (February – April). We hand-washed the scats in nylon mesh, dried them for ≥48 hours at 50°C, and manually separated and identified the components. To avoid over-representation of food items, components making up <5% of the total volume of a scat were not included in the analysis. We compared bone, tooth, and nail fragments to specimens housed in the Naturalist Center at the North Carolina Museum of Natural Sciences. We identified hairs using macroscopic color patterns and by microscopically comparing patterns in the medulla to known hair samples (Moore et al. 1974, McVey et al. 2013). We classified remains from white-tailed deer as fawn rather than adult only if small hooves were present in the scat. We identified insects to Order when possible and categorized feathers as avian. We identified soft mast food items by comparing seeds to known samples. We assumed any non-mast vegetative components or inorganic items (e.g., sticks, pine needles, sand, and rocks) were

either ingested incidentally by the coyote or collected incidentally with the scat sample and excluded them from the analysis.

We calculated “percent of scats” as the proportion of all samples which contained a particular item and “percent of occurrence” as the proportion of occurrences out of the total number of food items (Schrecengost et al. 2008, Turner et al. 2011). Also, we recorded the number of unique food items contained in each scat, which we defined as diet diversity (Grigione et al. 2011). We used an analysis of variance (ANOVA) to test for differences in diet diversity among seasons.

RESULTS

We analyzed 315 scats containing 590 food items. Seventy-seven scats were from summer, 164 from fall, 40 from winter, and 34 from spring. The majority of scats contained two food items (44.1%) or one food item (36.2%), and 19.7% of scats contained ≥ 3 food items. Diet diversity varied among seasons ($F_{(2,311)}=5.69$, $p=0.001$), with summer having the greatest mean number of food items per scat (2.14 ± 0.09), and spring the lowest (1.65 ± 0.13 ; Table 1).

Soft mast was the most common food item detected, followed by mammals and insects (Tables 2, 3). Trash, avian, and “other” categories composed the smallest proportions of percent of scats and percent of occurrence. *Diospyros virginiana* (common persimmon; hereafter “persimmon”) accounted for 77.7% of scats containing soft mast and occurred in 59.7% of scats overall. White-tailed deer, *Sylvilagus floridanus* (eastern cottontail), and

Sigmodon hispidus (hispid cotton rat) were the most common mammalian food items, occurring in 14.9%, 9.8%, and 7.3% of scats, respectively (Table 2).

We detected seasonal variation in percent of scats and percent of occurrence for the three most common categories of food items: soft mast, mammals, and insects. Soft mast prevalence was greatest in fall (98.2% of scats, 60.4% of occurrence) and lowest in spring (0% of scats, 0% of occurrence). Insects were most common in diets in summer (72.7% of scats, 33.9% of occurrence) and lowest in winter (12.5% of scats, 6.0% of occurrence). Insect Orders identified were Orthoptera, Coleoptera, and Hemiptera, composing 55.17%, 43.10% and 1.72% of insects identified, respectively. Occurrence of mammals in diets was greatest in spring (76.5% of scats, 58.2% of occurrence) and lowest in fall (26.2% % of scats, 16.0% of occurrence). White-tailed deer were detected in 14.9% of scats and most commonly in winter (42.5% of scats, 20.5% of occurrence). During summer, fawn white-tailed deer remains were detected in 9 scats and composed 11.7% of scats and 5.5% of occurrence.

DISCUSSION

Coyote diet diversity at FBMI was similar to other reported studies in the southeastern United States, indicating site productivity has relatively little influence on coyote diet diversity. In a Florida suburb, Grigione et al. (2011) reported diet diversity (1.69) similar to our results (1.65 – 2.14 mean items per scat), although coyote diet diversity in wildland areas was greater (3.18). Schrecengost et al. (2008) reported that in over half of coyote scats collected in South Carolina, 90% or more of the volume was composed of a single food item,

indicating low diversity. Similarly, McVey (2013) noted that a single food item composed >95% of dry volume in 55% of coyote scats collected in eastern North Carolina. Other studies in the Southeast did not report mean number of food items per scat as a metric of diet diversity, but instead have used a Shannon Diversity Index (e.g., Chamberlain and Leopold 1999). However, we believe the Shannon Diversity Index is not useful for comparisons among studies, as many studies, including our own, identify some food items to broader taxonomic groups rather than to species level (e.g. Patterson et al. 1998, Rose and Polis 1998, Hidalgo-Milhart et al. 2001, Grigione et al. 2011).

Coyote diets showed high plasticity and reliance on seasonally available foods. Soft mast was important in coyote diets in the fall when persimmon fruits were most abundant. Insects were consumed most in summer (May-July), which coincided with the emergence of many Orthopteran nymphs (Squitier and Capinera 2002). Mammals were the most common food item from November to April, when soft mast and other seasonal foods were least abundant. The low availability of alternate food items, such as soft mast, in winter and spring likely increased pressure on mammalian prey during this period.

In our study, white-tailed deer were the most common mammalian food item and were detected in every season; white-tailed deer were most commonly detected during winter rather than during the fawning period as many other studies have noted (Wooding et al. 1984, Blanton and Hill 1989, Patterson et al. 1998, Hidalgo-Milhart et al. 2001, Schrecengost et al. 2008). However, Chitwood (2014) showed that coyotes depredate ~50% of all fawns born at FBMI (30 of 65 fawns monitored during 2011 and 2012), so neonate deer are an important

component of coyote diets at FBMI. High occurrence of white-tailed deer in winter coyote diets could be attributed to hunter-killed or vehicle-killed carcasses, as coyote predation on adult white-tailed deer in the Southeast is uncommon (Blanton and Hill 1989, Kilgo et al. 2010), although Chitwood et al. (2014) documented multiple instances of coyote predation on adult white-tailed deer at FBMI.

Our study documented high consumption of soft mast by coyotes, which may lessen predation pressure on alternate prey. Persimmon fruits were more common in coyote diets in our study (95.7% of scats in Aug.-Oct.) than other published studies in the Southeast, with Schrecengost et al. (2008) reporting that 81% of coyote scats during October contained persimmon. Additionally, the Aug.-Oct. period in our study was the season with lowest occurrence of white-tailed deer in scats (1.2% of scats, 0.7% of occurrence). Schrecengost et al. (2008) noted a similar trend, with white-tailed deer occurring in 8%, 3% and 0% of scats from August, September, and October, respectively. Previous studies have suggested that soft mast may be highly selected when available, as coyotes may expend less energy foraging, and may be more efficient (Chamberlain and Leopold 1999). This may be the case at FBMI, where white-tailed deer, rodent, and Lagomorph densities all are low (Chitwood 2014; M. Elfelt, unpubl. data; E. Stevenson, unpubl. data). Although rarely discussed, food item rankings are dynamic, changing with shifts in availability of all food resources due to changes in foraging energy requirements. Our data indicate the increased availability of persimmon in the fall lessens coyote predation pressure on mammals, especially white-tailed deer.

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Table 1. Seasonal diversity (mean # of food items per scat) of coyote diets at Fort Bragg Military Installation, North Carolina, May 2011 – June 2012.

Season	Diet Diversity (Mean \pm SE)
Summer (May – July)	2.14 \pm 0.09
Fall (Aug – Oct)	1.76 \pm 0.06
Winter (Nov – Jan)	2.08 \pm 0.15
Spring (Feb – Apr)	1.65 \pm 0.13
Overall	1.88 \pm 0.05

Table 2. Seasonal composition of coyote scats showing “percent of scats,” the proportion of scats that contained each food item, at Fort Bragg Military Installation, North Carolina, May 2011 – June 2012.

Food item	Season				Overall n = 315
	Summer (May-July) n = 77	Fall (Aug-Oct) n = 164	Winter (Nov-Jan) n = 40	Spring (Feb-Apr) n = 34	
Aves^a	6.5	3.1	7.5	11.8	5.4
Insects^b	72.7	32.3	12.5	35.3	40.0
Mammals	58.4	26.2	75.0	76.5	45.7
<i>Didelphis virginiana</i>	2.6	0.6	0	0	1.0
<i>Odocoileus virginianus</i>	26.0	1.2	42.5	23.5	14.9
Adult	14.3	2.6	22.1	10.4	12.1
Fawn	11.7	0	0	0	2.9
<i>Sciurus carolinensis</i>	1.3	0	0	2.9	0.6
<i>Sciurus niger</i>	2.6	1.2	0	0	1.3
Small rodents	7.8	9.2	27.5	32.4	13.6
<i>Scalopus aquaticus</i>	1.3	0.6	0	0	0.6
<i>Sigmodon hispidus</i>	1.3	3.1	17.5	29.4	7.3
Other small rodents ^c	5.2	11.7	5.2	1.3	5.7
<i>Sylvilagus floridanus</i>	6.5	10.4	15.0	8.9	9.8
Other ^d	20.8	6.1	7.5	5.9	10.1
Soft mast	39.0	98.2	75.0	0	70.2
<i>Diospyros americana</i>	1.3	95.7	75.0	0	59.7
<i>Gaylussacia</i> spp.	7.8	1.2	0	0	2.5
<i>Prunus serotina</i>	3.9	0	0	0	1.0
<i>Rubus</i> spp.	27.3	0	0	0	6.7
<i>Vaccinium</i> spp.	2.6	1.2	0	0	1.3
<i>Vitis</i> spp.	0	7.9	2.5	0	4.4
Other fruit ^e	2.6	0	0	0	0.6
Trash^f	18.2	5.5	12.5	20.6	11.1
Other Animal^g	1.3	0.6	2.5	0	1.0

^aIncludes both bird remains (feathers, etc.) and bird eggshell fragments ^bInsects identified were mainly *Coleoptera* and *Othoptera*. ^cIncludes *Reithrodontomys humilis*, *Peromyscus* spp., *Microtus* spp., and unidentified small rodents. ^dOther mammals include: *Castor canadensis*, *Canis latrans*, *Lontra canadensis*, and unidentified mammals. ^eOther fruit includes *Toxicodendron* spp., and *Prunus* spp. (wild plum). ^fTrash includes any anthropogenic materials, e.g., plastic packaging, rope and rubber. ^gIncludes a juvenile turtle, *Pseudemys concinna concinna*, reptile eggshell fragments and snail shell fragments(O:*Gastropoda*).

Table 3. Seasonal composition of coyote scats showing “percent of occurrence,” the proportion of each food item out of the total number of food items, at Fort Bragg Military Installation, North Carolina, May 2011 – June 2012.

Food item	Season				Overall n = 590
	Summer (May-July) n = 164	Fall (Aug-Oct) n = 288	Winter (Nov-Jan) n = 83	Spring (Feb-Apr) n = 55	
Aves^a	3.1	1.7	3.6	7.3	2.9
Insects^b	34.2	18.4	6.0	21.8	21.4
Mammals	32.3	16.0	45.8	58.2	28.6
<i>Didelphis virginiana</i>	1.22	0.4	0	0	0.5
<i>Odocoileus virginianus</i>	12.2	0.7	20.5	14.6	8.0
Adult	6.7	0.7	20.5	14.6	6.4
Fawn	5.5	0	0	0	1.5
<i>Sciurus carolinensis</i>	0.6	0	0	1.8	0.3
<i>Sciurus niger</i>	1.2	0.7	0	0	0.7
Small rodents	3.6	5.2	13.2	23.6	7.6
<i>Scalopus aquaticus</i>	0.6	0.4	0	0	0.3
<i>Sigmodon hispidus</i>	0.6	1.7	8.4	18.2	3.9
Other small rodents ^c	2.4	3.1	4.8	5.5	3.4
<i>Sylvilagus floridanus</i>	3.1	5.9	7.2	5.5	5.3
Other ^d	9.8	2.8	2.4	10.9	5.4
Soft mast	21.3	60.4	37.4	0	40.7
<i>Diospyros americana</i>	0.6	54.5	36.1	0	59.7
<i>Gaylussacia</i> spp.	3.7	0.7	0	0	2.5
<i>Prunus serotina</i>	1.8	0	0	0	1.0
<i>Rubus</i> spp.	12.8	0	0	0	6.7
<i>Vaccinium</i> spp.	1.2	0.7	0	0	1.3
<i>Vitis</i> spp.	0	4.5	1.2	0	4.4
Other fruit ^e	1.2	0	0	0	0.6
Trash^f	8.5	3.1	6.0	12.7	5.9
Other Animal^g	0.6	0.4	1.2	0	0.5

^aIncludes both bird remains (feathers, etc.) and bird eggshell fragments ^bInsects identified were mainly *Coleoptera* and *Othoptera*. ^cIncludes *Reithrodontomys humilis*, *Peromyscus* spp., *Microtus* spp., and unidentified small rodents. ^dOther mammals include: *Castor canadensis*, *Canis latrans*, *Lontra canadensis*, and unidentified mammals. ^eOther fruit includes *Toxicodendron* spp., and *Prunus* spp. (wild plum). ^fTrash includes any anthropogenic materials, e.g., plastic packaging, rope and rubber. ^gIncludes a juvenile turtle, *Pseudemys concinna concinna*, reptile eggshell fragments and snail shell fragments (*O:Gastropoda*).

CHAPTER 2

Influence of Time since Burn and Vegetation Type on *Peromyscus* Abundance in a Longleaf Pine Ecosystem

ABSTRACT

Prescribed fire temporarily alters the ground-level structure of managed forests, and can alter food and cover resources for mice and other ground-dwelling wildlife. We evaluated the effect of time since burn and vegetation type on *Peromyscus* abundance in a longleaf pine (*Pinus palustris*) ecosystem at Fort Bragg Military Installation, North Carolina. During spring 2010 and 2011, we trapped for 12,250 trap-nights in open, lowland hardwood, upland pine 1-year post burn, upland pine 2-yrs post burn, and upland pine 3-yrs post burn vegetation types using Sherman traps and captured 243 individuals, including 208 *Peromyscus* spp. Using closed capture-recapture models, we detected an effect of vegetation type on capture and recapture probabilities of *Peromyscus* but did not detect a year effect. We did not detect differences in *Peromyscus* abundance among the 1-, 2-, and 3-years post burn upland pine vegetation types, but abundance was greater in the lowland hardwood vegetation type than in open areas. The lack of effect of time since burn on *Peromyscus* abundance could be due to the short fire return interval at our study site, which limited the time for post-burn shifts in vegetation composition and structure.

INTRODUCTION

Forest ecosystems in the southeastern United States evolved with frequent lightning-ignited fires, a natural process mimicked with prescribed fire today (Van Lear 1984, Frost 1998, Van Lear and Harlow 2000). The longleaf pine - wiregrass (*Pinus palustris* - *Aristida stricta*) ecosystem once covered over 30 million hectares in the southeastern United States, and was maintained by frequent lightning-ignited fires (Brockway and Lewis 1997, Frost 1998). Native Americans and early European settlers recognized the importance of fire and used burning to clear undergrowth and improve habitat for important grazing species (Van Lear 1984, Frost 1998, Van Lear and Harlow 2000, Oswalt *et al.* 2012). Frequent low-intensity fires prevent encroachment of hardwoods and less fire-tolerant pines (e.g., *Pinus taeda*), while reducing fuel loads and increasing plant diversity (Van Lear 1984, Landers *et al.* 1995, Brockway and Lewis 1997, Frost 1998).

Small mammals (e.g., voles, mice, rats) are an important ecosystem component in many terrestrial communities and depend on the ground-level vegetation most commonly affected by prescribed fire. Small mammals are primary consumers and an important prey source for many larger mammals and raptors (Masters *et al.* 1998, Karmacharya *et al.* 2012). Consumption of plant material and seeds by small mammals can affect succession of plant communities and stability of plant populations (Davidson 1993, Valone and Schutzenhofer 2007). Also, many species of small mammals are important dispersers of seeds and fungal spores (Johnson 1996, Masters *et al.* 1998).

Prescribed burning temporarily decreases cover for small mammals but may concurrently increase food resources, making predictions regarding population-level effects difficult. Prescribed fires consume coarse woody debris and leaf litter (Bock and Bock 1983, Converse et al. 2006a, Amacher et al. 2008, Morris et al. 2011), which provide food and cover for small mammals (Graves et al. 1988, Masters et al. 1998, Bowman et al. 2000, Carey and Harrington 2001, Converse et al. 2006b). Conversely, fire may increase food availability by increasing herbaceous plant production in the first few seasons after burning (Bock and Bock 1983, Outcalt 1994, Masters et al. 1996, Sparks et al. 1998, Converse et al. 2006a). Also, consumption of the litter layer by fire can facilitate navigation and movement on the forest floor and uncover seeds previously inaccessible in deep litter (Kaufman et al. 1988, Clark et al. 1991, Reed et al. 2004, Reed et al. 2005, Zwolak et al. 2012). In a large-scale study, Converse et al. (2006b) reported that small mammal populations generally increased after fuel reduction treatments (prescribed fire and thinning), but noted that results varied by species and study area, making local data and adaptive management strategies important.

In longleaf pine ecosystems, prescribed fire is applied frequently and often occurs during the growing season. The effects of this fairly intensive fire regime on small mammals are unknown. Growing season burns reduce woody vegetation more intensely than dormant season fire, and decrease vegetation complexity (Van Lear and Harlow 2000). Therefore, we compared *Peromyscus* spp. abundance among vegetation types in a longleaf pine-wiregrass ecosystem managed primarily with a 3-year fire return interval.

METHODS

Study area – Fort Bragg Military Installation (FBMI) encompasses approximately 65,000 ha in the coastal plain physiographic region of south-central North Carolina, and contains one of the largest contiguous remnants of the longleaf pine-wiregrass ecosystem in the southeastern US. The most abundant plant community type present at FBMI is the pine/scrub oak (*Quercus* spp.) sandhill, which consists mainly of a longleaf pine canopy, oak subcanopy, and wiregrass ground layer (Sorrie et al. 2006). Other common plant communities present in this ecosystem include streamhead pocosin and ruderal areas, which are described as highly disturbed areas with no canopy (Sorrie et al. 2006).

Land management at FBMI is driven by efforts to restore and maintain habitat for the federally endangered red-cockaded woodpecker (*Picoides borealis*), which requires the open, mature long-leaf pine communities maintained by frequent fire (U.S. Fish and Wildlife Service 2003). Prior to 1989, prescribed burning was conducted exclusively during the dormant season. However, growing season burns have composed the majority of planned burns in forested vegetation types at FBMI since 1989 (J. Jones, pers. comm.). Prescribed burns are scheduled on a three-year rotation for most forested upland areas of FBMI, while some non-forested areas (e.g., open military drop zones) are burned annually to remove all woody growth. Lowland areas are subjected the same fire regime as uplands but generally burn less frequently because of greater soil moisture levels.

Vegetation Classification – We defined five major vegetation types at FBMI using existing GIS cover type and burn history data: 1) upland pine 1 year post burning; 2) upland

pine 2 years post burning; 3) upland pine 3 years post burning; 4) lowland hardwood; and 5) open. We included the lowland hardwood and open vegetation types in addition to the fire-treated vegetation types to better assess the overall small mammal distribution at FBMI. Open areas consisted mainly of drop zones, areas used for military parachuting and supply drops, and portions of the impact areas, which were off-limits zones used for detonating explosives and firing live ammunition. Vegetation in these areas consisted of grasses and forbs with sparse shrubs. Lowland hardwood areas mainly existed along streams and other bodies of water and contained mature hardwoods such as oaks, blackgum (*Nyssa sylvatica*), and sweetgum (*Liquidambar styraciflua*), with a dense understory of ericaceous shrubs and hardwood midstory. Upland pine vegetation types were most commonly mature longleaf pine-dominated communities with patchy oak-dominated hardwood inclusions.

Small Mammal Sampling – We sampled five trapping grids in each of the five vegetation types in 2011 and 2012, for a total of 25 trapping grids per year. Trapping grids were placed in different locations in 2012 than in 2011. We established each trapping grid with one edge abutting a hard edge (i.e., a firebreak), so that sampling was not biased by more edge in smaller stands than in larger stands. We placed 49 Sherman traps (H.B. Sherman Traps, Tallahassee, FL) at each site in a square grid with 10-m spacing between traps. We baited traps with a mixture of oats and peanut butter and placed a cotton ball in each trap for bedding material. At each trap site, we cleared the ground of vegetation and sprayed with a chemical insecticide (Raid Ant & Roach Killer®; S.C. Johnson and Son, Inc., Racine, WI) to reduce bait-stealing and predation by fire ants without affecting small mammal trapping yield (Gettinger 1990). We sampled all 25 trapping grids in April-May of

each year, trapping five grids at a time for five consecutive nights each, before moving traps and sampling the next five sites. We left traps open overnight and closed them during the day to reduce heat stress.

We identified, weighed, and marked all captured small mammals with individually numbered ear tags (Style 1005-1; National Band and Tag Co., Newport, KY) prior to release. For recaptured individuals, we recorded the tag number and trap location and immediately released the animal at the site of capture. We identified captured animals to species, except white-footed mice (*Peromyscus leucopus*) and cotton mice (*Peromyscus gossypinus*), which were difficult to distinguish in the field and may hybridize in some areas (Barko and Feldhammer 2002); we lumped these species as *Peromyscus* spp. All trapping and handling protocols were approved by the North Carolina State University Institutional Animal Care and Use Committee (Protocol: 11-005-O).

Data Analysis – We used closed capture-recapture modelling in Program MARK (White and Burnham 1999) to estimate small mammal abundance for each vegetation type. We used closed capture models M_0 (null) and M_b (behavior) with year and vegetation type as effects on p (capture probability) and c (recapture probability; Otis et al. 1978). The effect of vegetation type was modeled using the five major vegetation type categories previously defined, which included time since burn in upland pine stands. We conducted model selection using Akaike's Information Criterion adjusted for small sample size (AIC_c), and chose the highest-ranked model (minimum AIC_c) to estimate abundance parameters (Akaike

1974). We used z-tests with a Bonferroni adjustment at $\alpha=0.05$ to test for pairwise differences in abundance estimates between vegetation types.

RESULTS

We trapped for 12,250 trap-nights and captured 243 individuals (126 in 2011 and 117 in 2012; Table 1). Total captures including recaptures were similar between years, with 276 and 259 in 2011 and 2012, respectively. Three species were captured in 2011, and five species were captured in 2012 (Table 1). The majority of individuals captured each year were *Peromyscus* spp. (94.5% of captures in 2011 and 84.5% of captures in 2012). Therefore, we analyzed only capture data for *Peromyscus* spp., which consisted of capture histories from 118 individuals in 2011 and 90 in 2012 (Table 2).

Due to low capture rates, we pooled the data from all five trapping grids within each vegetation type in each year. Additionally, we had especially low capture rates in the open vegetation type (Table 2) and excluded those data from preliminary analysis. The top four models from the preliminary analysis included a behavioral effect ($p \neq c$; Model M_b), and the two highest ranked models did not include an effect of year. However, the third-ranked model contained only an effect of year and no effect of vegetation type. The three top-ranking models were within 2 Δ AIC, so we included all 3 models in the final analysis with the full dataset.

We analyzed the full dataset (including the open vegetation type) using the top three models from the initial analysis: the null model, the model with vegetation type as an effect

on p and c , and the model with year as an effect on p and c . For the two models that did not include an effect of year, we combined the two years of data to estimate the abundance value, \hat{N} , for each vegetation type. The best model (lowest AIC) included vegetation type as an effect on p and c , with no year effect. Therefore, we used this model to calculate abundance estimates, \hat{N} , for each vegetation type.

Parameter estimates from the best model varied by vegetation type with lowland hardwood having the greatest abundance of *Peromyscus* spp. and open the lowest (Table 3). Additionally, the best model included a behavioral effect, with $c > p$ for all vegetation types (Table 3), indicating a “trap-happy” response. Estimated abundance in the open vegetation type was lower than in all vegetation types except upland pine 3-years post burn (Table 4). Similarly, abundance in the lowland hardwood vegetation type was greater than all other vegetation types except upland pine 1-year post burn (Figure 1, Table 4). Although abundance estimates in the upland pine vegetation types generally decreased with increasing time since burn, these differences were not significant (i.e., no effect of time since burn; Figure 1, Table 4).

DISCUSSION

Vegetation type, but not time since burn, was an important predictor of *Peromyscus* spp. abundance in the longleaf pine ecosystem, which likely was an artifact of the vegetation structure in the different vegetation types. Because the lowland hardwood vegetation type did not burn as frequently as the uplands and contained more moist soil conditions than the

deep, sandy soils of the uplands, it was characterized by more complex vertical structure and more abundant down coarse woody debris. Understory complexity was reduced by frequent prescribed burning in the upland pine types and by mowing in the open drop zones.

Similarly, other studies have suggested that increased vegetation structure provides food resources, nesting cover, and escape cover for small mammals (Masters et al. 1998, Carey and Harrington 2001, Anderson et al. 2003, Zwolak et al. 2012).

With relatively low small mammal diversity and abundance in the frequently burned upland areas and across the research site as a whole, the lowland hardwood vegetation type may be allowing *Peromyscus* populations to persist in a heavily managed longleaf pine ecosystem. Sharp *et al.* (2009) suggested that bottomland hardwood areas may be serving as source populations for upland habitats at a managed longleaf pine site in Alabama; however, the evidence was circumstantial as they did not directly sample these areas. We believe our results support this hypothesis, and highlight the importance of conserving hardwood areas within longleaf pine ecosystems.

Peromyscus abundance did not vary with time since burn in the upland pine vegetation type, likely due to the short fire prescription interval at our study site. Although differences were not significant, we noted a trend of decreasing abundance as time since burn increased. Kaufman et al. (1988) detected an increase in small mammal captures following fire, but noted the positive response was only evident from approximately 3-11 months following a burn, suggesting that our sampling design may have missed the most significant short-term changes in *Peromyscus* abundance. Additionally, the long-term effects of fire on vegetation

may not have been evident within the first three years following fire. Although ground-level vegetation biomass and complexity generally increase over time following a prescribed fire (see Masters et al. 1996), the interval between fires may have been too short to allow substantial shifts in the composition of vegetation communities (i.e., from herbaceous dominated to woody dominated). It is possible that over longer periods of time following fire, *Peromyscus* may become increasingly rare or vegetation conditions in fire-suppressed uplands may converge with the more favorable conditions in lowland areas. Therefore, we suggest future research in the longleaf pine ecosystem incorporate a wider time frame to assess short- and long-term impacts of fire on small mammal populations.

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Table 1. Small mammals (annual percent of total captures) captured at Fort Bragg Military Installation, North Carolina, 2011 and 2012.

Species	2011		2012	
	Individuals	Captures	Individuals	Captures
<i>Peromyscus</i> spp.	118 (93.6)	261 (94.6)	90 (76.9)	219 (84.6)
<i>Reithrodontomys humulis</i>	7 (5.6)	12 (4.4)	5 (4.3)	5 (1.9)
<i>Microtus pinetorum</i>	1 (0.8)	3 (1.1)	0 (0)	0 (0)
<i>Sigmodon hispidis</i>	0 (0)	0 (0)	7 (6.0)	14 (5.4)
<i>Ochrotomys nuttalli</i>	0 (0)	0 (0)	2 (1.7)	3 (1.2)
<i>Mus musculus</i>	0 (0)	0 (0)	13 (11.1)	18 (7.0)
Total	126 (100)	276 (100)	117 (100)	259 (100)

Table 2. Trapping results (number of individuals and captures) for *Peromyscus* spp. at Fort Bragg Military Installation, North Carolina, 2011 and 2012.

Vegetation Type	2011		2012	
	Individuals	Captures	Individuals	Captures
Open	12	21	2	4
Upland Pine 1-yr post burn	26	57	28	71
Upland Pine 2-yr post burn	22	45	20	47
Upland Pine 3-yr post burn	16	29	17	37
Lowland Hardwood	42	109	23	60
Total	118	261	90	219

Table 3. *Peromyscus* spp. population parameter estimates from the top model: p(vegetation type) c(vegetation type) using data from both years of trapping data combined to estimate abundance at Fort Bragg Military Installation, North Carolina, 2011 and 2012.

Vegetation Type	Capture Probability (p)	Recapture Probability (c)	Abundance Estimate (\hat{N})	SE of (\hat{N})	95% CI of (\hat{N})
Open (non-forested)	0.30	0.34	12.79	1.67	(12.06, 22.19)
Upland Pine 1-yr post burn	0.25	0.56	32.46	5.82	(26.92, 53.99)
Upland Pine 2-yrs post burn	0.27	0.48	27.08	4.53	(23.14, 44.75)
Upland Pine 3-yrs post burn	0.23	0.44	20.48	5.75	(16.01, 44.66)
Lowland Hardwood	0.26	0.65	50.22	5.46	(44.51, 68.89)

Table 4. Pairwise comparison results (z-values) for differences in *Peromyscus* spp. abundance estimates between five vegetation types at Fort Bragg Military Installation, North Carolina, 2011 and 2012. Significant differences are marked with **.

Vegetation Type*	Open	UP 1	UP 2	UP 3	LH
Open (non-forested)	-	-3.23**	-2.96**	-1.28	-6.55**
Upland Pine 1-yr post burn	-	-	0.73	1.46	-2.22
Upland Pine 2-yrs post burn	-	-	-	0.90	-3.26**
Upland Pine 3-yrs post burn	-	-	-	-	3.75**
Lowland Hardwood	-	-	-	-	-

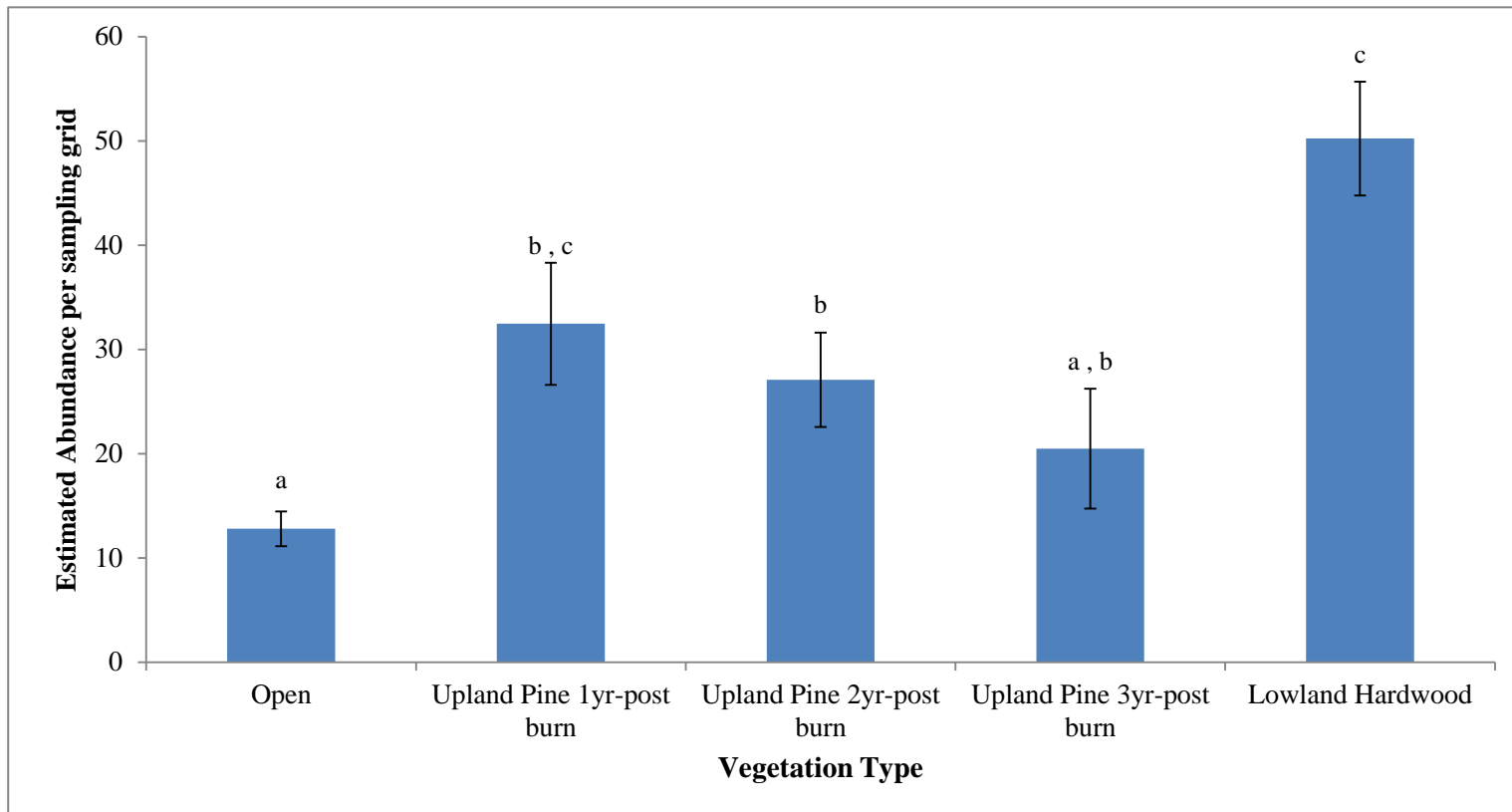


Figure 1. Abundance estimates (SE) for *Peromyscus* spp. in five vegetation types at Fort Bragg Military Installation, North Carolina, 2011 and 2012. Small letters represent pairwise comparisons results, where values with the same letter indicate similarities between estimates ($p < 0.05$, see Table 4).

CHAPTER 3

Home-Range Size and Movement Ecology of Coyotes in an Area of Low Hunting Pressure

ABSTRACT

The coyote (*Canis latrans*) is a relatively recent immigrant into most of the southeastern United States and little is known about the species' movement ecology in the region. Therefore, we determined home-range size, movement rates, and dispersal distances for coyotes at Fort Bragg Military Installation (FBMI), North Carolina, where coyotes largely were protected from hunting and trapping. During the spring of 2011, we captured 30 coyotes and attached GPS collars. Average 95% fixed-kernel home-range size was 85 km², with male home ranges marginally larger than females' ($t = -1.99, P = 0.06$), and no differences among age classes (juvenile/subadult/adult; $F_{2,24} = 0.77, P = 0.47$). Movement rates averaged 295 m/hr, with greatest movement rates observed nocturnally and during fall and winter. Movement rates did not differ between sexes or among age classes ($t = -1.44, P = 0.16$; $F_{2,24} = 0.97, P = 0.39$). Three coyotes dispersed from FBMI and traveled straight-line distances of 192 km, 221 km, and 345 km before establishing new home ranges. The home-range and movement measurements calculated in this study are greater than most reported for the Southeast, which could be due to low prey density connected to the low productivity soils common on the study site.

INTRODUCTION

The coyote (*Canis latrans*) recently expanded its range into the eastern United States and may have altered the trophic dynamics of the region (Kilgo et al. 2010, Kilgo et al. 2012, Chitwood 2014, Chitwood et al. 2014). Prior to 1900, the coyote range was restricted to the prairies of the western United States (Parker 1995, DeBow et al. 1998). However, following extirpation of gray wolves (*Canis lupus*) and other large carnivores east of the Mississippi River, coyotes began to move into the northeastern, and later, the southeastern United States (Hill et al. 1987, DeBow et al. 1998). Range expansion resulted from this natural dispersal and merging of local populations along with local introduction by humans (Hill et al. 1987). As a novel predator, coyotes could have wide-reaching ecological impacts through alteration of prey population dynamics and subsequent trophic cascades (Berger et al. 2008, Gehrt et al. 2009, Kilgo et al. 2010, Crimmins et al. 2012). Ecological impacts of coyotes can be amplified by human activity (Boisjoly et al. 2010), which highlights the need for comprehensive understanding of coyote ecology across a range of landscape conditions.

Coyotes exhibit seasonal and spatial variability in home-range size and movements because of changes in food availability and variation in habitat composition (Andelt and Gipson 1979, Springer 1982, Mills and Knowlton 1991, Schrecengost et al. 2009, Crimmins et al. 2012). High movement rates and large home-ranges may be an indication of low habitat quality and low prey density (Mills and Knowlton 1991, Boisjoly et al. 2010, Turner et al. 2011). Also, seasonal changes in home-range size may correspond with changes in

human activity levels (Gese et al. 1989), or biological activities such as breeding and pup-rearing (Andelt & Gipson 1979, Shivik et al. 1997).

Where they are protected from persecution by humans, coyote home-range size and movement ecology may differ from areas where they are regularly hunted or trapped. For example, Springer (1983) documented larger home-range sizes on relatively undisturbed sites than those reported in other published studies, which the author attributed to social stability, low population density, and low food availability. Conversely, Berger and Gese (2007) noted a positive relationship between coyote population density and protected area status; areas where coyotes could not be legally hunted had greater population densities. In addition, high population density could increase dispersal rates and distances by increasing competition (Matthysen 2005).

We studied home-range size and movement ecology of coyotes in North Carolina using Geographic Positioning System (GPS) technology that allowed us to collect frequent data, even for individuals that dispersed long distances from our study site. Geographic Positioning System technology provided increased precision and frequency of locations and allowed monitoring of dispersing coyotes, information which is unavailable from very high frequency (VHF) technology. Therefore, we were able to conduct detailed analysis of home-range size and movement ecology of coyotes, and quantify coyote movement ecology in a landscape with low hunting and trapping pressure.

METHODS

Study Area – Fort Bragg Military Installation (FBMI) covers approximately 65,000 ha in the Coastal Plain physiographic region of central North Carolina, and contains one of the largest contiguous remnants of the longleaf pine-wiregrass (*Pinus palustris*-*Aristida stricta*) ecosystem. Over 45,000 ha of FBMI are forested lands, almost all of which are burned on a three-year return interval. The most abundant plant community type present at FBMI is the pine (*Pinus* spp.)/scrub oak (*Quercus* spp.) sandhill, which consists mainly of a longleaf pine canopy, oak subcanopy, and wiregrass ground layer, with savanna-like openness maintained by fire (Sorrie et al. 2006). Current prescribed burning regimes and other habitat management practices at FBMI are driven primarily by efforts to restore and maintain habitat for the federally endangered red-cockaded woodpecker (*Picoides borealis*). Public trapping of coyotes is not permitted at FBMI, and coyote hunting was suspended during our study period. Prior to our study, wildlife managers at FBMI estimated that hunters removed <10 individual coyotes per year (J. Jones, personal communication).

Field Methods – From February – May 2011, we captured coyotes with MB-550 foothold traps set throughout FBMI and checked once per day. We manually restrained captured coyotes and recorded sex, weight, and age class. We aged coyotes based on tooth wear and placed each into one of three categories: juvenile (≤ 1 year), subadult (between 1 and 2 years), or adult (≥ 2 years of age). We fitted coyotes weighing ≥ 9 kg with a Wildcell SG GPS radiocollar (Lotek Wireless Inc., Ontario, Canada) programmed to record a GPS location every 3 hours. We released all captured coyotes immediately following processing at the capture location. All trapping and handling protocols were approved by the North

Carolina State University Institutional Animal Care and Use Committee (Protocol: 11-005-O). Coyote radiocollars transmitted GPS locations to a central computer where they were compiled and stored until analysis. We monitored all radiocollared coyotes until mortality, loss of collar signal (battery expiration), or programmed collar release (70 weeks after deployment).

Data Analysis – We calculated home ranges using the Geospatial Modeling Environment software package (Beyer 2012). Home range boundaries were determined using a 95% fixed-kernel method using plug-in methods to select the smoothing factor, h . Gitzen *et al.* (2006) demonstrated the plug-in method for smoothing factors was more accurate than least squares cross validation (LSCV) or reference h -values when dealing with location data that was relatively evenly distributed in space. Also, LSCV methods often fail when multiple locations have similar values, which is common in GPS datasets with large sample sizes (Hemson *et al.* 2005). We calculated 50% fixed-kernel core areas for each coyote using the same methods. We used a student's t -test to compare home-range and core area sizes between sexes and a one-way analysis of variance (ANOVA) to compare among age classes.

We calculated distances traveled and movement rates by converting sequential point locations to line segments using Geospatial Modeling Environment (Beyer 2012). The length of each segment was divided by the time interval between those locations to determine the movement rate in meters per hour. Sequential locations separated by a time interval of less than one hour or more than 24 hours were not used for movement rate analysis; most time intervals were approximately 3 hours. We calculated an average overall movement rate

for each individual and tested for differences in movement rate between sexes using a student's t-test and among age classes using a one-way ANOVA.

We calculated movement rates by seasons: summer (May-July), fall (August – October), winter (November – January), and spring (February – April). Seasons were defined based on seasonal food availability cycles (e.g. white-tailed deer fawns in summer, soft mast in fall). We classified movement by time period (day and night) based on the time of day during which the interval occurred. We categorized intervals beginning between one hour before sunrise and one hour before sunset as day, and the remainder as night (i.e., if sunrise occurred at 0715 hours and sunset at 1700, any time intervals starting between 0615 and 1600 hours on that day would be categorized as “day”). We averaged movement rates in each season and time period for all individuals. We fit generalized linear models with a random effect for coyote to test for an effect of season and time period on movement rate, and used the Tukey-Kramer method for multiple comparisons among seasons. We set $\alpha=0.05$ for all statistical tests.

RESULTS

We captured and collared 30 coyotes (19 male and 11 female) from February through May 2011 (Table 1). We collected 85,386 GPS locations through October 2012, with between 797 and 4,883 locations per individual. Coyote mortality and collar malfunction limited the number of total locations for some coyotes. Three coyotes dispersed from FBMI, and traveled considerable distances before establishing new home ranges: one subadult male, one subadult female, and one juvenile female. The data from these three individuals was not included in home range or movement rate analyses.

Home-range size was highly variable for the 27 collared coyotes which remained on or near FBMI (Table 2). The 95% fixed-kernel home range size was larger for males ($103.94 \pm 18.93 \text{ km}^2$) than females ($47.25 \pm 12.98 \text{ km}^2$), although the difference was statistically weak ($t = -1.99, P = 0.06$). Core area (50% fixed-kernel) size differed between sexes, with males ($16.92 \pm 3.50 \text{ km}^2$) larger than females ($5.12 \text{ km}^2 \pm 1.22$; $t = -2.33, P = 0.03$). Neither 95% nor 50% fixed-kernel size differed among age classes ($F_{2,24} = 0.77, P = 0.47$ and $F_{2,24} = 0.67, P = 0.52$, respectively).

Movement rates differed among seasons ($F_{3,73} = 19.18, P < 0.001$) and between time periods ($F_{1,26} = 236.54, P < 0.001$), with average movement rate of 294.6 m/hr. The maximum movement rate recorded was 5,312 m/hr, when an adult male moved 15.84 km between 2300 and 0200 hours. Movement rates were greater during fall and winter than during spring and summer months (Fig. 2A), and were greater during night than the day (Fig. 2B). The average movement rate for males (303.6 m/hr) was similar to females (271.8 m/hr, $t = -1.44, P = 0.16$). Movement rate did not differ among age classes ($F_{2,24} = 0.97, P = 0.39$).

All three dispersing coyotes left FBMI in March 2011, within one month of their capture, and traveled considerable distances before establishing new home ranges (Fig. 1). The subadult male (Coyote 30810) ranged west and south of FBMI before traveling northeast and establishing a home range in Halifax County, North Carolina, a straight-line distance of 192 km from the capture location. However, the total distance traveled from FBMI before reaching the new home range was 729 km. The subadult female (Coyote 30819) traveled south into South Carolina and west towards the Georgia border, before returning to central South Carolina and establishing a home range in Newberry County. The straight-line

distance from the point of capture to the new home range was 221 km, with the furthest location 356 km from the capture location. The total distance traveled was 557 km. The juvenile female (Coyote 30850) traveled north into Virginia and then east, establishing a home range in Caroline County, Virginia, a straight-line distance of 345 km from the capture location. The total distance traveled between FBMI and the home range location was 668 km.

DISCUSSION

Coyotes on FBMI had relatively large home ranges compared to other published studies, which may have been the result of unique age structure and resident status of the population attributable to limited trapping and hunting pressure. Greater coyote population density resulting from low human-caused mortality could have caused the proportion of transient coyotes in the population to increase due to territoriality by older adults and fewer resources per individual (Gese et al. 1996, Conner et al. 2008). Also, low hunting and trapping pressure could increase the proportion of juvenile coyotes in the population, as young and inexperienced coyotes are most vulnerable to trapping (Windberg and Knowlton 1990, Sacks et al. 1999). Results of previous research on the effect of age and resident status on home-range size of coyotes have been conflicting, and inconsistent analytical methods can make direct comparisons among studies difficult. Two published studies reported smaller home ranges for juveniles than adults (Springer 1982, Holzman et al. 1992) and two others reported similar home range sizes between age classes (Litvaitis and Shaw 1980, Gehrt et al. 2009). Yet, other studies either had small sample sizes of juvenile coyotes, lumped adults and juveniles together for analysis, or purposely excluded juvenile coyotes from analysis

(e.g., Andelt and Gipson 1979, Chamberlain et al. 2000, Schrecengost et al. 2009). Age-specific analysis of coyote home-range size has been further complicated by the fact that juvenile coyotes and “elderly” coyotes are more likely to be transients, without well-established home ranges (Gese et al. 1988, Kamler and Gipson 2000). Often, “transient” coyotes are analyzed separately or excluded from analysis based on somewhat subjective criteria regarding observed spatial affinity, home-range overlap with other coyotes, or simply home-range size; however, these definitions are vague and re-interpreted in each study (see Schrecengost et al. 2009). Also, individual coyotes may transition between transient and resident status, as has been reported in some studies, adding even more complexity to analysis (Gese et al. 1988, Mills & Knowlton 1991, Kamler & Gipson 2000).

Additionally, the large home ranges calculated in our study may have been the result of poor habitat quality in the Sandhills. Previous research similarly reported larger home ranges when prey density was low, an assumed result of increased foraging efforts (Mills and Knowlton 1991). Soft mast and white-tailed deer (*Odocoileus virginianus*) are important components of coyote diets at FBMI and in other areas of the region (Schrecengost et al. 2008, McVey et al. 2013, Chitwood 2014, Chitwood et al. 2014, M. Elfelt, unpubl. data), and white-tailed deer density at FBMI was 2-4 deer/km², lower than most forested ecosystems in the southeastern United States. Also, small mammal densities were low at FBMI (M. Elfelt, unpubl. data). Common persimmon (*Diospyros virginiana*), an important coyote food, was distributed unevenly across FBMI due to the patterns of prescribed fire application (Lashley et al. 2014), which could necessitate larger foraging areas for coyotes.

Thirdly, larger home range size may have resulted from the methods we used to collect locations. Prior to the use of GPS technology for wildlife tracking, most researchers located animals using VHF transmitters and receivers, inferring an animal's location by triangulation of multiple bearings. However, use of VHF has been shown to underestimate movements, especially for animals which can move large distances between locations (Samuel and Kenow 1982, Lee et al. 1985). Also, radiotelemetry of large animals can be time-consuming, often limiting the possible number of locations that can be recorded, which decreases accuracy of home-range size estimates (Girard et al. 2002). A recent study of coyotes in eastern Canada used GPS collars and reported 95% MCP home range of 112km², similar to our estimates and much larger than most other published studies (Boisjoly et al. 2010). Previous estimates of eastern coyote home-range size using VHF tracking range from 10.1 km² in Georgia (Holzman et al. 1992) to 31.85 km² in South Carolina (Schrecengost et al. 2009), although analytical methods differed.

Average movement rates determined in our study were similar to those previously reported in the southeastern United States, with greater movement rates nocturnally (Holzman et al. 1992, Chamberlain et al. 2000). Coyotes generally are accepted as being nocturnal or crepuscular mammals, a behavioral pattern which is likely the result of human activity levels; in areas with greater human activity, coyotes avoid humans by becoming more active during the night (McLennen et al. 2001). Kavanau and Ramos (1975) documented greater coyote activity in low and moderate light than in total darkness, suggesting coyotes are best adapted physically to crepuscular and diurnal rather than nocturnal activity. In relatively undisturbed areas, coyotes show increased diurnal activity,

sometimes even equaling nocturnal activity and movement rates (Tremblay et al. 1998, Patterson et al. 1999, Kitchen et al. 2000).

Greater movement rates in fall and winter could be attributed to mate searching, which usually occurs during January-February. However, other research has documented low activity rates during this time period, suggesting low food availability on our study sites as a more likely driver of high activity levels (Shivik et al. 1997, Chamberlain et al. 2000). In the southeastern United States, coyote diet varies and often includes seasonally available food items such as soft mast, insects, and white-tailed deer fawns (Wooding et al. 1984, Hoerath & Causey 1991, Stratman & Pelton 1997, Schrecengost et al. 2008, McVey et al. 2013, M. Elfelt, unpubl. data). Many of these seasonal food items are unavailable during winter, which could necessitate more extensive foraging efforts by coyotes to meet energy requirements during this season.

Our study documents the longest dispersal distances in the southeastern United States, which highlights coyote ability to colonize new areas while raising concerns for management of local coyote populations and zoonotic diseases. It is possible the dispersal distances we recorded are common for coyotes, and the methods we used were better able to detect and record these movements compared to traditional VHF-tracking methods. Many previous records of long-distance dispersals were the result of a marked animal being privately trapped or harvested and then reported (e.g., Carbyn & Paquet 1996, Rosatte 2002, Kolbe & Squires 2004), as researchers are often unable to continue VHF-tracking of dispersing research animals due to constraints on time and effort. If long-distance dispersals are common, localized management of coyote populations is likely to be ineffective (Harrison

1992). As problem individuals or small populations are targeted with removal, dispersing coyotes could quickly fill these areas, making short-term removals unsuccessful. With long dispersal distances, the coyote population at FBMI or other areas with low hunting pressure could serve as source populations for extensive geographic areas. Additionally, long-distance dispersal by coyotes has implications for the spread and management of zoonotic diseases (e.g., rabies) (Rosatte 2002). Our results indicate that managers may need to consider an extended geographic scale on which coyotes may colonize and spread disease in the southeastern United States, as well as considering longer-term management solutions when dealing with nuisance coyotes.

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Table 1. Age and sex distribution of collared coyotes at Fort Bragg Military Installation, North Carolina, 2011-2012.

Sex	Age Class		
	Juvenile	Subadult	Adult
Male	4	3	12
Female	4	4	3

Table 2. Size (km²) of 95% fixed-kernel home range and 50% fixed-kernel core area for 27 collared coyotes at Fort Bragg Military Installation, North Carolina, 2011-2012.

Coyote	Sex	Age^a	N^b	95% fixed kernel (km²)	50% fixed kernel (km²)
30811	F	SA	798	26.09	6.59
30812	F	A	3693	83.58	5.32
30820	F	SA	4157	10.45	2.07
30822	F	J	2703	18.36	0.93
30835	F	J	3754	20.55	2.97
30837	F	A	3680	7.97	1.33
30844	F	A	893	55.79	5.85
30849	F	SA	4883	98.57	11.34
31754	F	J	3609	103.89	9.67
30808	M	J	950	71.57	14.62
30818	M	A	2600	154.17	22.58
30821	M	J	2561	260.09	45.85
30834	M	A	2978	164.45	12.41
30836	M	A	2243	118.24	25.50
30838	M	A	2082	28.14	4.07
30839	M	J	3810	229.10	44.53
30840	M	SA	922	20.16	2.79
30841	M	A	3884	12.48	2.44
30842	M	A	2743	172.98	33.70
30843	M	A	3915	32.42	8.62
30845	M	A	3731	145.40	28.66
30846	M	A	4041	106.46	10.92
30847	M	J	3103	99.83	8.14
30848	M	A	3908	32.57	1.46
30851	M	SA	3886	194.63	32.01
30852	M	A	1784	12.29	3.36
30853	M	A	2272	15.99	2.96
AVERAGE			2947.52	85.04	12.99

^a Age classes are A=adult, SA=subadult, and J=juvenile.

^b N is the total number of locations used to calculate the home-range polygons.

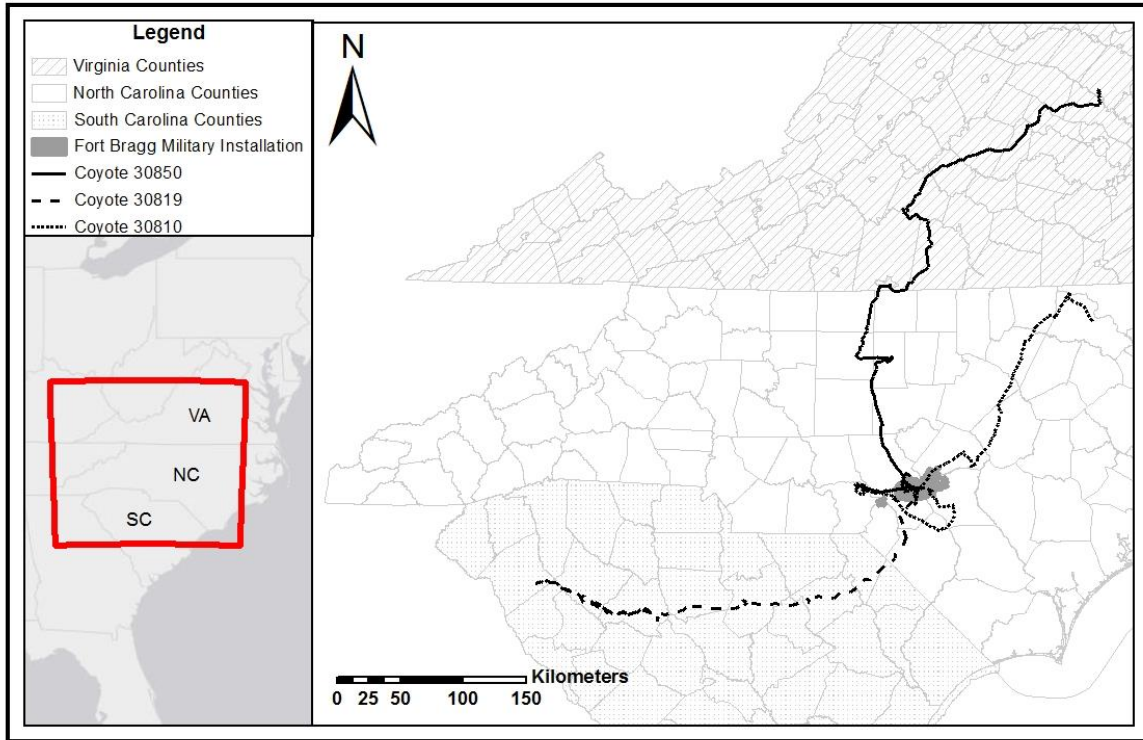
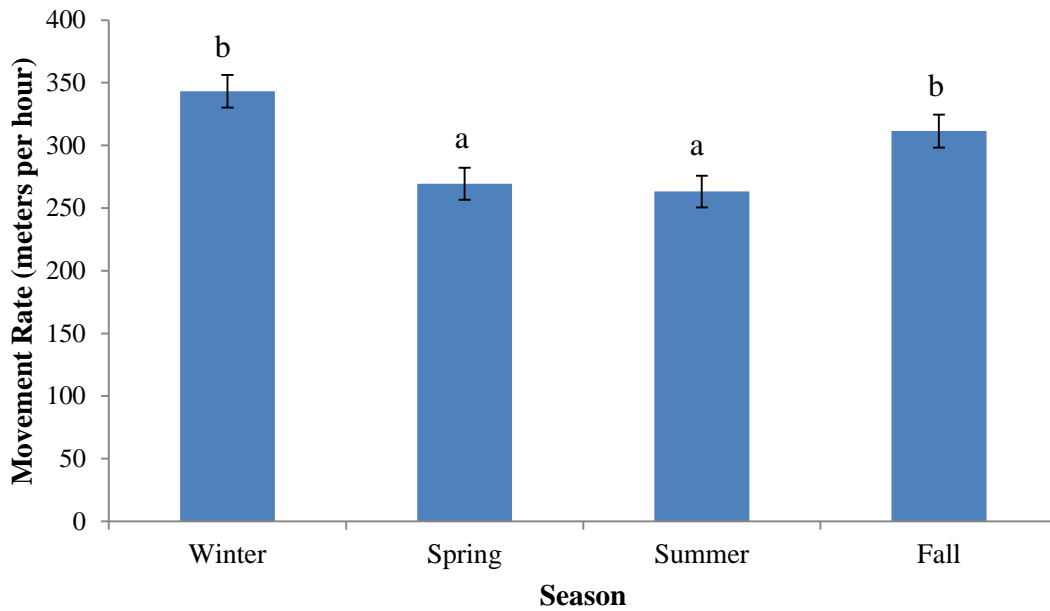


Figure 1. Map of dispersal routes of three coyotes captured at Fort Bragg Military Installation, North Carolina, 2011-2012. Coyote 30810 was a subadult male, coyote 30819 was a subadult female, and coyote 30850 was a juvenile female at the time of capture in spring 2011.

A



B

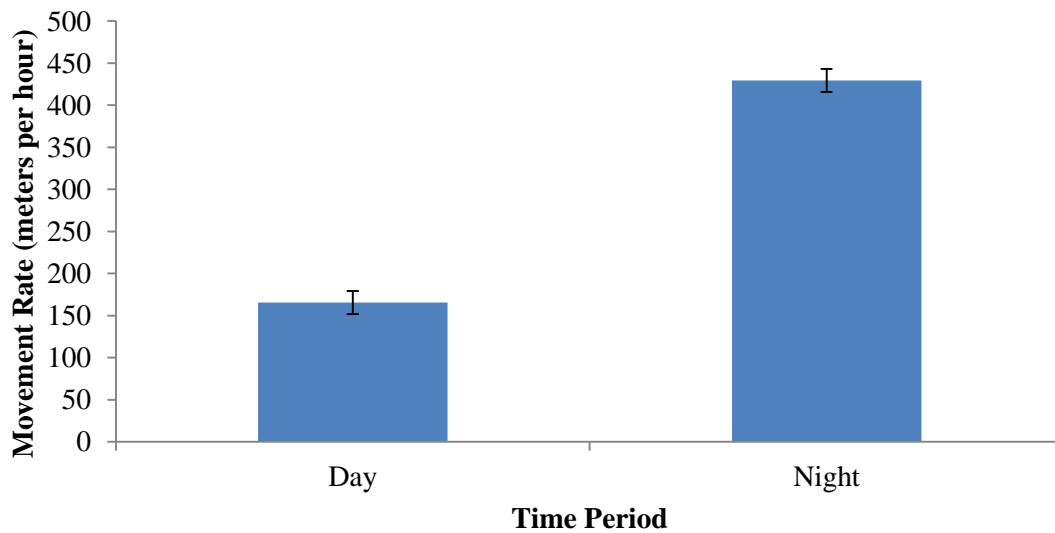


Figure 2. Least squares mean estimates and standard error for average coyote movement rates (m/hr) by season (**A**) and time period (**B**) at Fort Bragg Military Installation, North Carolina, 2011-2012. Seasons were defined as: summer (May – July), fall (Aug. – Oct.), winter (Nov. – Jan.), and spring (Feb. – Apr.). Letters above bars (in **A**) indicate Tukey-Kramer groups for multiple comparisons; bars with the same letter above were not different. Time periods in (**B**) were different ($p < 0.001$).