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Indrani Sasmal (IS)*, Christopher E. Moorman (CEM), Morgan B. Swingen (MBS)¹, Shubham Datta (SD), and Christopher S. DePerno (CSD)

Fisheries, Wildlife, and Conservation Biology Program, Department of Forestry and Environmental Resources, North Carolina State University, Raleigh, NC, USA.

isasmal@ncsu.edu

Fisheries, Wildlife, and Conservation Biology Program, Department of Forestry and Environmental Resources, North Carolina State University, Raleigh, NC, USA.

chris_moorman@ncsu.edu

Fisheries, Wildlife, and Conservation Biology Program, Department of Forestry and Environmental Resources, North Carolina State University, Raleigh, NC, USA.

mbelfelt@ncsu.edu

Biology Department, Dakota College at Bottineau, Bottineau, ND, USA.

shubham.datta@dakotacollege.edu

Fisheries, Wildlife, and Conservation Biology Program, Department of Forestry and Environmental Resources, North Carolina State University, Raleigh, NC, USA.

chris_deperno@ncsu.edu

Indrani Sasmal

North Carolina State University, Raleigh, NC 27695, USA

Phone number: (605)592-0683

¹ Natural Resources Research Institute, University of Minnesota Duluth, Duluth, MN, USA

Email: bulirchithi@gmail.com

Draft

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Carolina

Indrani Sasmal (IS), Christopher E. Moorman (CEM), Morgan B. Swingen (MBS), Shubham Datta (SD), and Christopher S. DePerno (CSD)

Abstract:

Coyote (*Canis latrans* Say, 1823) is a recent immigrant into eastern United States, and little is known about the species' space use and movement in the region. We compared space use and movement of radio-collared coyotes among biological seasons. We captured and collared 30 coyotes from February through May 2011 and collected 85,386 GPS locations through October 2012 at Fort Bragg Military Installation. We defined 4 biological seasons according to coyote life history: breeding (December–February), gestation (March–May), pup-rearing (June–August), and dispersal (September–November). Out of 27 radio-collared individuals, we identified 10 as transient and 11 as resident based on home range size and variability across seasons; 6 switched their status and were classified as intermediate. We observed low variability of core area size across seasons for resident males and females, whereas we documented high variability for transient males. Movement rate of resident coyotes during spring (449.75 m/hr) was greater than summer (295.33 m/hr), whereas movement rates did not differ between any other seasons. For transient coyotes, movement rate during summer (283 m/hr) was less than fall (374.73 m/hr), spring (479.85 m/hr), and winter (488.5 m/hr). Some coyotes adjusted their residency status seasonally and other individuals dispersed large distances (> 200 km).

Key Words: biological seasons, *Canis latrans*, coyote, dispersal, GPS telemetry, home range, movement, radio-collar.

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Introduction

During the late 20th and early 21st centuries, the coyote (*Canis latrans*) 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 et al. 2014; Chitwood et al. 2015; Hody and Kays 2018). Following extirpation of gray wolves (*Canis lupus* Linnaeus, 1758) 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; Hody and Kays 2018). 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 by altering 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 are wide-ranging carnivores that can change their space use to better adapt to the environment (Andelt 1985; Gese et al. 1988; Kamler and Gipson 2000; Hinton et al. 2012a; Morin 2015). Coyotes aggressively defend small, mutually exclusive territories when adequate resources are available, but may use large territories which overlap with other individuals when resources are limited (Andelt 1985; Kamler and Gipson 2000; Hinton et al. 2012b; Morin 2015). Coyotes can 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. 2008; Mitchel et al. 2015). High movement rates and large home ranges may indicate 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 and Gipson 1979; Gese et al. 1989; Shivik et al. 1997). Previous research has classified individual coyotes as either “resident” or “transient” based on their seasonal space use; the home-range sizes of resident coyotes vary little among biological seasons, whereas seasonal home-range sizes of transient coyotes can vary significantly due to their instability in defending a defined territorial boundary (Kamler and Gipson 2000; Gehrt et al. 2009; Hinton et al. 2012*b*; Morin 2015). Moreover, resident coyotes aggressively maintain mutually exclusive home ranges within each biological season, but transient home ranges may overlap with the home ranges of multiple resident or transient coyotes in each biological season (Gese et al. 1988; Kamler and Gipson 2000; Gehrt et al. 2009; Hinton et al. 2012*b*; Morin 2015). Thus, space use studies conducted at a broad temporal scale without particular emphasis on the biological seasons may fail to provide adequate information about the vagile response of the coyote to its environment.

Although many studies have been conducted to document space use of resident and transient coyotes (Gese et al. 1988; Kamler and Gipson 2000; Gehrt et al. 2009; Hinton et al. 2012*b*, Mitchel et al. 2015), no research has evaluated space use of resident and transient coyotes across different biological seasons. Gese et al. (1988) examined space use of 2 distinct groups of coyotes in different biological cycles; however, they did not document the seasonal space use of transient individuals due to a limited number of location points in different biological seasons. Therefore, our objective was to determine space use and movement ecology of radio-collared coyotes in different biological seasons using GPS location data collected over a contiguous period of time. Based on previous studies, we hypothesized the home-range size of resident

coyotes would not differ across biological seasons as they tend to maintain a stable home range boundary, whereas home ranges of transient coyotes would vary significantly due to their instability in defending a defined territorial boundary (Kamler and Gipson 2000; Gehrt et al. 2009; Hinton et al. 2012b; Morin et al. 2015). Also, we hypothesized that residents would maintain a small, mutually exclusive home range in each biological season, whereas transient home ranges would vary in size and overlap with home ranges of multiple resident or transient coyotes in each biological season.

Materials and Methods

Study area

Fort Bragg Military Installation (FBMI) encompasses approximately 65,000 ha in the Sandhills physiographic region of south-central North Carolina, and contains one of the largest contiguous remnants of the longleaf pine-wiregrass (*Pinus palustris*-*Aristida stricta* Mill.) ecosystem. Average yearly rainfall was 120 cm, average yearly snowfall was 7.5 cm, and average frost-free days were 175 (Sorrie et al. 2006). The most abundant plant community type present at FBMI was the pine/scrub oak (*Quercus* spp. Schaeffer) sandhill, which consisted mainly of a longleaf pine canopy, oak subcanopy, and wiregrass ground layer (Sorrie et al. 2006). Other common plant communities included streamhead pocosin and ruderal areas, which were highly disturbed military training areas with no canopy (Sorrie et al. 2006).

Land management at FBMI was driven by efforts to support military training activities and to restore and maintain habitat for the federally endangered red-cockaded woodpecker (*Leuconotopicus borealis* Vieillot, 1809), which requires the open, mature longleaf pine communities maintained by frequent fire (U.S. Fish and Wildlife Service 2003). Since 1989, early, growing-season burns (March-April) on a 3-year return interval composed most of planned

burns to control woody stem encroachment into the forest midstory and to maintain a diverse herbaceous layer. However, due to logistical constraints, some forest stands were managed with dormant-season (January-February) prescribed fire, and some non-forested areas (e.g., open military drop zones) were burned annually or biennially to limit woody growth. Lowland areas were subjected to the same fire regime as uplands but often burned less frequently or less completely because of greater soil moisture levels.

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 gender, mass, and age class. We aged coyotes based on tooth wear and placed each into one of 3 categories: juvenile (≤ 1 year), subadult (between 1 and 2 years), or adult (≥ 2 years of age) (Gier 1968). 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 field methods were consistent with the wild mammal use guidelines of the American Society of Mammalogists (Sikes et al. 2011), and were approved by the North Carolina State University Institutional Animal Care and Use Committee (Protocol: 11-005-O). We monitored all radiocollared coyotes until mortality, loss of collar signal (battery expiration), or programmed collar release (70 weeks after deployment).

Data Analysis

Space Use - We divided location data collected over the entire study period (February 2011 – October 2012) into 4 biological seasons according to coyote life history (Gese et al. 1988): breeding (December-February), gestation (March-May), pup-rearing (June-August), and

dispersal (September-November). We calculated the 50% (core use) and 95% (home range) isopleth of each individual animal within each season using the fixed-kernel method using the home range tool (HRT) in ArcGIS 10.3.1 (Rodgers et al. 2015). We used the default smoothing parameter (h) provided in the HRT after rescaling the data to unit variance because variances of the x and y coordinates of the points were highly unequal.

Based on space use, we separated individual coyotes into 3 groups: residents, transients, and intermediates. We evaluated the core area size of each individual in each biological season, and designated transients as individuals with core area size that varied (standard error ≥ 7) most among seasons. We defined resident individuals as those with: 1) core areas that did not vary among seasons; and 2) comparatively small core area and home range (core area size $\leq 12 \text{ km}^2$ and home range size $\leq 57 \text{ km}^2$) where the seasonal home ranges overlapped by 80% or more for each individual (Hinton et al. 2016) for at least 3 biological seasons. We identified those individuals which changed their status within the study period from resident to transient and vice versa as intermediates and did not include them for any analysis comparing transients and residents. We used the fixed kernel method for determining seasonal isopleth because kernel has been the primary analytical method of coyote home range studies (Andelt 1985; Gese et al. 1988; Kamler and Gipson 2000; Gehrt et al. 2009).

Seasonal Movement Rate – We calculated distances traveled and movement rates by converting sequential point locations to line segments using Geospatial Modeling Environment (Beyer 2012). We divided length of each segment by time interval between those locations to determine movement rate in m/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 movement rates by calendar seasons:

summer (May-July), fall (August – October), winter (November – January), and spring (February – April). Calendar seasons were defined differently than the previously described biological seasons and were based on coyote seasonal food availability cycles, including white-tailed deer (*Odocoileus virginianus* Zimmermann, 1980) fawns and insects in summer, soft mast (e.g., persimmon [*Diospyros virginiana* L.]) in fall, white-tailed deer and soft mast in winter, and white-tailed deer, eastern cottontail (*Sylvilagus floridanus* J.A. Allen, 1890), and hispid cotton rat (*Sigmodon hispidus* Say and Ord, 1825) during spring (Swingen et al. 2015). We tested for difference in seasonal movement rates between residents and transients, residents and intermediates, and transients and intermediates using 2-tailed unequal variance t-tests (Ott and Longnecker 2008). Also, we compared movement rates between seasons within each residency class using the 2-tailed unequal variance t-test (Ott and Longnecker 2008).

Results

We captured and radiocollared 30 coyotes (19 male and 11 female) from February through May 2011. We collected 85,386 GPS locations through October 2012, with between 797 and 4,883 locations per individual. Three coyotes dispersed from FBMI, and traveled considerable distances (> 192 km) before establishing new home ranges: one subadult male, one subadult female, and one juvenile female. The data from these 3 individuals that dispersed permanently from the study site were not included in home range or movement rate analyses.

Space Use

We identified 10 transients (2 females and 8 males), 11 resident (4 females and 7 males), and 6 intermediate (3 females and 3 males) coyotes among the 27 collared animals based on variability in 50% and 95% fixed kernel home-range sizes across biological seasons (Table). The seasonal 50% core area sizes (Table) of resident females (breeding ≤ 6 km², gestation ≤ 2

km², pup-rearing ≤ 4 km², dispersal ≤ 9 km²) and resident males (breeding ≤ 12 km², gestation ≤ 10 km², pup-rearing ≤ 8 km², dispersal ≤ 11 km²) were comparatively smaller ($P \leq 0.05$) than the 50% core area sizes (Table) of transient females (breeding = 24 km², gestation ≥ 20 km², pup-rearing = 24 km², dispersal = 16 km²) and transient males (breeding ≥ 31 km², gestation ≥ 28 km², pup-rearing ≥ 31 km², dispersal ≥ 24 km²). We observed low variability of 50% fixed kernel core area sizes (Table) among seasons for resident males (standard error ≤ 2.5) and resident females (standard error ≤ 1.5), whereas we documented high variability (Table) for transient males (standard error ≥ 7) except for 2 individuals that we classified as transient males due to large 50% fixed kernel core area sizes in different biological seasons (50% fixed kernel core area size ≥ 28 km²). Among the 2 female coyotes that we classified as transients, one individual had data only for March (gestation); although we could not compare variability in core area sizes among seasons, we classified the individual as transient because of the large core area size (20 km²). The other transient female coyote showed comparatively low variability (SE = 2.9) of 50% fixed kernel core area sizes across different biological seasons, but we classified it as transient because it had a large core area in multiple biological seasons (≥ 15 km²). Core areas of resident males and females, except paired male and female, did not overlap in any season. Conversely, transient individuals exhibited more than 80% overlap in each season. One juvenile male, 2 adult males, 2 juvenile females, and 1 adult female changed status between resident and transient in different seasons based on core area and home range sizes and were classified as intermediates (Table).

Seasonal Movement Rate

The average movement rate of resident coyotes during spring (449.75 m/hr) was greater ($P = 0.03$) than during summer (295.33 m/hr), whereas movement rates did not differ ($P > 0.05$) between fall (328.9 m/hr) and winter (332.38 m/hr), or between any other seasons. For transient

coyotes, average movement rate during summer (283 m/hr) was less ($P=0.02$) than fall (374.73 m/hr), less ($P=0.05$) than spring (479.85 m/hr), and less ($P=0.01$) than winter (488.5 m/hr). Movement rates did not differ between fall and spring ($P=0.28$), between fall and winter ($P=0.12$), nor between spring and winter ($P=0.93$) for transient coyotes. Winter movement rates were greater ($P=0.04$) for transients (488.5 m/hr) than residents (332.38 m/hr). However, movement rates of transients and residents did not differ during fall ($P=0.2$), spring ($P=0.4$), or summer ($P=0.7$). Movement rates did not differ between resident male and female coyotes during any season.

Long Distance Dispersal

All 3 dispersing coyotes left FBMI in March 2011, within 1 month of their capture, and traveled considerable distances before establishing new home ranges (Fig.1). The subadult male 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, total distance traveled from FBMI before reaching the new location was at least 729 km. The subadult female 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 point of capture to the new location was 221 km, with the furthest location 356 km from the capture location. Total distance traveled was at least 557 km. The juvenile female 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 new location was at least 668 km.

Discussion

Similar to previous studies, core areas of resident individuals, except those that were paired, did not overlap in any season during our study (Andelt 1985; Gese et al. 1988; Gehrt et al. 2009). Conversely, transient individuals exhibited substantial overlap in each season. Resident or breeding pairs of coyotes maintained small home ranges in all biological seasons with affinity to 1 particular area, whereas transient or non-breeding individuals maintained varied sizes of home ranges in different seasons and did not show affinity towards a particular area for more than 1 biological season. Transient core areas showed substantial overlap with other resident and transient core areas in different seasons, which could be used as a characteristic to distinguish between resident and transient coyotes (Andelt 1985; Gese et al. 1988; Gehrt et al. 2009). However, resident coyotes may exclude transients from core areas in other regions or types of landscapes (Mitchell et al. 2015).

Coyotes are extremely adaptable and adjusted their residency status during different biological seasons, which may aid in their movement and expansion across their range (Kamler and Gipson 2000; Hinton et al. 2012b; Morin 2015). One adult male and 1 juvenile female changed status from transient to resident, possibly to compensate for the loss of resident individuals and availability of undefended space (Gese et al. 1988; Gehrt et al. 2009). Also, 1 juvenile and 1 adult female, and 1 juvenile and 1 adult male, changed their status from resident to transient, possibly because of the loss of a mate or because of departure from an existing family unit (Kamler and Gipson 2000).

Movements of resident and transient coyotes differed seasonally, likely in response to varied prey availability and changed physiological demands. Resident coyotes at FBMI had lesser movement rates in summer than in spring, possibly because individuals travel less during the pup-rearing season (Lkaundre and Keller 1981) which corresponded to summer in our study.

However, transient movement rates were similarly low in summer, suggesting that factors in addition to pup-rearing contributed to low movement rates during this period. Temperatures and related heat indices on FBMI commonly exceed 34°C, so individuals, regardless of residency status, may have limited movements to limit thermoregulatory costs (Hidalgo-Mihart et al. 2009). Although we did not document any difference between resident male and female seasonal movement rates, Chamberlain et al. (2000) observed greater movement rates of male residents during winter. Home ranges differed among resident and transient coyotes in our study, but seasonal movement rates differed between resident and transient coyotes only during winter, when rates of transients were greater than that of residents. In winter, transient coyotes may have moved more in search of limited foods because resident coyote home ranges were in higher quality habitat with better food availability in winter (Swingen et al. 2015).

Our study documented 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 (Rosatte 2002). It is possible the dispersal distances we recorded are common for coyotes, and GPS collars were better able to detect and record these movements compared to traditional VHF-tracking methods. Also, Hinton et al. (2012b) documented coyote dispersal movements of >50km using GPS collars, although straight-line distances were not reported. Many previous records of long-distance dispersals were the result of a marked animal being privately trapped or harvested and then reported (Carbyn and Paquet 1986; Rosatte 2002; Kolbe and 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). Additionally, long-distance dispersal by coyotes has

implications for spread and management of zoonotic diseases (e.g., rabies, canine distemper virus).

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Figure. Map of long distance dispersal of coyotes from Fort Bragg Military Installation, NC, USA, 2011-2012.

[County boundary data were obtained from www.census.gov]

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Table. Sizes (km²) of 50% fixed kernel core area in different biological cycles of 11 resident, 10 transient, and 6 intermediate coyotes and the standard error of 50% core area size for different biological seasons of individual coyotes at Fort Bragg Military Installation, North Carolina, USA, 2011-2012 [F- Female, M-Male, J-Juvenile, SA-Sub-adult, A-Adult].

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Coyote	Gender	Age	Status	50% Fixed Kernel Home Range (km ²) in Different Biological Season				SE among biological seasons
				Breeding	Gestation	Pup-rearing	Dispersal	
38	M	A	Resident	-	4.151	6.916	7.947	1.133
40	M	SA	Resident	3.685	4.649	1.472	3.361	0.665
41	M	A	Resident	3.560	3.125	3.198	4.038	0.295
43	M	A	Resident	9.907	10.537	7.992	11.354	0.716
48	M	A	Resident	12.359	1.517	2.494	7.878	2.522
52	M	A	Resident	-	3.661	4.162	3.870	0.145
53	M	A	Resident	4.088	2	3.582	5.481	0.719
11	F	SA	Resident	6.387	-	4.168	9.104	1.427
20	F	SA	Resident	3.192	1.809	3.064	4.130	0.477
35	F	J	Resident	4.099	1.953	3.686	9.166	1.551
37	F	A	Resident	2.297	1.107	1.629	2.655	0.344
8	M	J	Transient	-	53.649	105.588	-	25.969
18	M	A	Transient	88.938	51.993	37.843	25.519	13.732
21	M	J	Transient	138.281	52.985	38.649	96.391	22.537
36	M	A	Transient		28.204	38.307	31.206	2.995
39	M	J	Transient	72.872	49.666	55.859	23.89446	10.156
42	M	A	Transient	65.31	45.459	30.96	47.015	7.0401
45	M	A	Transient	42.931	43.33	44.854	37.923	1.504
51	M	SA	Transient	30.624	60.585	49.119	54.899	6.497
44	F	A	Transient	-	20.152	-	-	-
49	F	SA	Transient	24.449	29.508	24.067	15.457	2.914
34	M	A	Intermediate	56.111	10.820	5.483	67.603	15.718
46	M	A	Intermediate	31.220	58.751	6.286	15.919	11.451
47	M	J	Intermediate	91.811	10.746	3.720	8.152	21.118
12	F	A	Intermediate	85.279	9.211	1.287	8.335	19.830
22	F	J	Intermediate	37.786	2.462	0.682	1.791	0.519
54	F	J	Intermediate	26.043	1.431	2.965	7.619	1.860

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Map of long distance dispersal of coyotes from Fort Bragg Military Installation, NC, USA, 2011-2012.
[County boundary data were obtained from www.census.gov]

304x190mm (96 x 96 DPI)