Home Range, Habitat Use, and Movement Patterns of Female Coyotes in Georgia: Implications for Fawn Predation

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Abstract: Coyote (*Canis latrans*) depredation rates on white-tailed deer (*Odocoileus virginianus*) fawns are variable across the southeastern United States, perhaps due to varying dispersion of coyotes as related to social behavior and habitat preferences. To evaluate fawn predation risk related to coyote distribution, we studied home range patterns and habitat use of 15 female coyotes during the 2012–2013 fawning periods. Seasonal home range sizes varied but followed two general patterns. Small home range coyotes (SHR; likely breeding females) had a mean home range area of 7.4 km^2 (CL = 5.4–9.5 km^2), whereas large home range coyotes (LHR; transients) had a mean home range area of 47.1 km^2 (CL = 27.5–66.8 km^2). We measured consistency of space use as a gauge for predation risk by examining revisitation rates of core areas and quantified movements by calculating residence time along paths. Coyotes avoided pine habitats within core areas, avoided developed areas during the day, and selected open areas at night. SHR coyotes had greater core area revisitation rates than LHR coyotes. Residence time estimates suggested considerable variation in patterns of patch residence. Because of greater revisitation of fewer core areas, SHR females may have disproportionate impacts on fawn survival within their respective home ranges. Future research addressing interactions between coyotes and fawns should focus on improving understanding of how coyote spatial ecology affects fawn predation within an area.

Increasing concern surrounding impacts of coyotes (*Canis latrans*) on white-tailed deer (*Odocoileus virginianus*) recruitment in the southeastern United States has prompted a series of studies on coyote food habits (Schrecengost et al. 2008, Kelly 2012) and cause-specific mortality of fawns (Saalfeld and Ditchkoff 2007, Kilgo et al. 2012, McCoy et al. 2013). Although coyotes can significantly impact local deer populations, predation rates and impacts on fawn recruitment are variable. For example, coyotes were responsible for depredating 7% of radio-collared fawns on one South Carolina site (McCoy et al. 2013), and 62% on another (Kilgo et al. 2012). Likewise, recruitment rates at two locations in Georgia separated by only 8 km and with similar coyote abundance differed by almost 0.3 fawns/doe (Gulsby et al. 2014).

Although several hypotheses have been offered to explain differences in fawn predation among studies, recent evidence suggests that fawn predation risk may be associated with habitat characteristics and coyote distribution across the landscape (Kelly 2012, Kilgo et al. 2012, Gulsby et al. 2014). Coyote space use appears to be highly variable across the southeastern United States (Holzman et al. 1992, Thornton et al. 2004), but coyotes consistently select edges, early successional habitats, and agricultural/open areas (Holzman et al. 1992, Chamberlain et al. 2000, Kays et al. 2008, Schrecengost et al. 2009) which are often associated with increased prey abundance (Atkeson and Johnson 1979). Therefore, areas containing greater amounts of preferred habitats may support greater coyote abundance or concentrate coyote movements, leading to increased local fawn predation (Gulsby et al. 2014).

Coyote space use is influenced by season, sex, energy requirements, habitat composition, prey distribution, and physiographic characteristics (Bekoff and Gese 2003). Coyotes are known to ex-

hibit two patterns of space use, with some adults exhibiting resident behaviors and others appearing to be transients. Resident coyotes exhibit high site fidelity and maintain relatively small home ranges, whereas transients exhibit low site fidelity and do not maintain consistent home ranges (Messier and Barrett 1982, Andelt 1985, Gese et al. 1988). Presumably, resident coyotes use smaller areas containing specific habitat or landscape characteristics. Therefore, areas containing these characteristics may harbor greater numbers of resident coyotes and be subject to greater rates of fawn predation. Conversely, the effects of transient coyotes on prey populations are likely more evenly distributed across the landscape. Although previous work has noted the existence of resident and transient coyotes in southeastern populations (Hinton et al. 2012), methods of quantitatively defining these behaviors are ambiguous.

Resident animals exhibit home range behavior and tend to disproportionately revisit or remain in particular patches within their ranges (Benhamou and Riotte-Lambert 2012). The resulting heterogeneous use of space means that merely defining the range of a coyote is insufficient to accurately assess spatial patterns of predation risk. A more complete picture can be gained by using techniques to estimate utilization distributions (UD) conditioned on the movements of individuals as well as by quantifying behavioral characteristics such as patch revisitation rates and residence times. Additionally, an understanding of habitat selection in a given landscape allows for further inference on spatial patterns of predation risk. Therefore, we investigated the spatial ecology of female coyotes during the deer fawning season with the objective of characterizing the spatial distribution and habitat selection of coyotes when fawns are most vulnerable to predation. Our primary objective was to document the possibility of differential coyote predation risk for fawns across the landscape and characterize habitat selection of female coyotes.

Study Area

We captured coyotes on 7,200 ha of privately-owned land consisting of multiple tracts in Harris County, Georgia. Topography consisted of gently rolling hills approximately 200 m above sea level. The area was mostly forested and contained both natural and planted pine (*Pinus taeda* and *P. palustris*) stands in upland areas. Remaining forest types included hardwood ridges and bottomlands. Hardwood forests primarily included white oak (*Quercus alba*), northern red oak (*Q. rubra*), southern red oak (*Q. falcata*), chestnut oak (*Q. prinus*), and hickories (*Carya* spp.) Wildlife openings of various sizes (approximate range = 0.4 – 4 ha) were interspersed throughout the area and were planted in agronomic crops including alfalfa (*Medicago sativa*), corn (*Zea mays*), and soybeans (*Glycine max*). Approximately 15% of the study area was inten-

sively managed for white-tailed deer hunting and included open loblolly pine stands burned on 3-yr rotations. Most of the area surrounding the study site was rural except for a 526-ha subdivision located adjacent to the northern end.

Methods

We captured female coyotes during January–April 2012 and 2013 using #1.75 and #2 offset-modified coil-spring traps (Minnesota Trapline Products, Pennock, MN). Coyotes were restrained using a 1.5-m catch pole, removed from the trap, and their hind legs and rostrum secured using electrical tape. We equipped female coyotes with Tellus Light global system of mobile communications (GSM; Followit AB, Lindesberg, Sweden) GPS-equipped collars. Animal handling procedures were approved by the University of Georgia Institutional Animal Care and Use Committee (#A2012 01-016-Y3-AO).

Collars were programmed to collect and store GPS locations on their nonvolatile memory. During 2012, collars collected 12 locations/day (120-min intervals) from deployment until 30 April and 36 locations/day (40-min intervals) from 1 May until collar failure or recovery using a remotely-activated release mechanism during the last week of July. During 2013, collars were programmed to collect 6 locations/day (240-min intervals) from deployment until 30 April and 24 locations/day (60-min intervals) from 1 May until collar failure or recovery during the last week of July.

We estimated UD's during 1 May–4 July 2012 and 2013 using a dynamic Brownian Bridge Movement Model (dBBMM; Kranstauber et al. 2012) implemented in Program R 3.01 (R Core Team 2013), using the package move (Kranstauber and Smolla 2013). Because dBBMMs are based on the movement characteristics of the animal path as opposed to the spatial distribution of relocations, Brownian bridge based UD estimations perform well with high volume GPS datasets for which many of the assumptions underlying kernel density analyses are violated (Horne et al. 2007). The dBBMM further incorporates variation in movement behavior along a path into UD estimation, which is measured by sweeping a moving window along the path using a modified version of the behavioral change point analysis (Guararie et al. 2009). As such, implementation of the analysis requires the researcher to specify three parameters: the telemetry error associated with relocations, the size of the moving window, and the margin size bounding the window (Kranstauber et al. 2012). Based on static tests of transmitter accuracy in representative habitats, we determined that mean telemetry error was 18 m. We selected a window and margin size of 31 and 9 steps respectively, which appeared to provide the best overall combination for detecting relevant changes in movement behavior. We quantified coyote home ranges and core areas based

on the 95% and 50% UD contours, respectively. For the purpose of comparing our home range estimates to those of prior studies, we calculated 95% minimum convex polygon (MCP) home ranges for each individual using the Geospatial Modelling Environment (GME) version 0.7.2.0 (Beyer 2012).

We used revisitation rates and residence time analysis (RT, Barraquand and Benhamou 2008) to quantify use intensity and characterize resident and transient behaviors. We examined consistency of space use for each coyote by calculating revisitation rates of core areas. We considered more than one 48-h visit to a core area as a revisitation; high revisitation rates suggested coyotes intensively and consistently used these areas.

Residence time is the amount of time an animal spends within a circle of a given radius centered on a specific point along a movement trajectory. It is measured by computing the sum of the durations of all portions of the movement path that intersect the circle during a predefined cut-off time (Barraquand and Benhamou 2008). The mean RT along a path allows inferences regarding the exploitation intensity exhibited by each animal. Coyotes with high mean RT likely exploit profitable habitat patches intensively, whereas coyotes with low mean RT generally make frequent moves between patches. Residence time calculations were performed using functions available in the R package adehabitatLT (Calenge 2006). To further evaluate movement patterns we examined step length distributions of individual movement paths. Datasets were filtered to include only time-steps associated with time intervals of 2 h to address issues with missed GPS fixes and different data collection schedules.

We created density maps of point locations to further evaluate how intensively coyotes used certain areas within their home range. First, we overlaid a grid consisting of 1-ha cells on the study area using the fishnet tool in ArcMap 10.1 (Environmental Systems Research Institute, Inc., Redlands, CA). We then used the countpntsinpolys function in GME to count the number of coyote point locations occurring within each 1-ha cell. We depicted results as a temperature gradient map.

We developed a land cover map based on the 2006 USGS National Land Cover Database (NLCD, Fry et al. 2011). We reclassified data into five habitat classes: developed, open, early successional, pine, and hardwood. Developed areas included constructed materials, unpaved roads, and impervious surfaces such as buildings and paved roads. Open habitats primarily consisted of maintained pastures, wildlife food plots, and agricultural fields. Early successional habitats consisted of scrub/shrub, <5-yr-old clear cuts, and overgrown pastures or old fields. Pine habitats consisted of upland pine stands >5 yr old. Hardwoods consisted mostly of bottomland hardwoods with occasional upland hardwood ridges.

We used the isectpolyrst function in GME to obtain the percentage of each habitat type within each home range and core area as well as throughout the study area. We then used compositional analysis (Aebischer et al. 1993) to identify habitat selection at three spatial scales as described by Chamberlain et al. (2003). The first order compared habitat composition within home ranges versus the study area, the second order compared habitat composition within core areas versus the home range, and the third order compared habitat composition at individual locations versus within the home range. We evaluated habitat selection at the third order during diurnal (0700–1900 hours) and nocturnal (2000–0600 hours) periods. We substituted a value of 0.7% for areas with zero use as recommended by Bingham and Brennan (2004). We examined differences in habitat selection using the Wilkes lambda test statistic. When significant differences between habitat use and availability existed, we used a ranking matrix of *t*-tests to assess the order of preference.

Results

We collared 20 female coyotes during January–April 2012 and 2013. Two coyotes suffered mortality and collar malfunctions resulted in incomplete datasets for five coyotes. Therefore, we quantified space use and habitat selection for 13 female coyotes based on an average of 2,271 locations/animal (range = 1,245–3,017 locations/animal). Fix success rates of GPS units averaged 84.9% (range = 65.1%–98.3%). We used partial datasets obtained from two coyotes with malfunctioning collars to generate MCP home range estimates for a total of 15 coyotes.

We observed distinct differences in spatial behaviors among coyotes. Eight of 13 females revisited 100% of their core areas, whereas five revisited ≤50% of core areas for ≥48 h (Figure 1). Females with 100% core area revisitation rates had smaller home ranges than those with lower core area revisitation rates. As a result, we defined coyotes with 100% revisitation rates as small home range coyotes (SHR, likely residents) and coyotes with revisitation rates ≤50% as large home range coyotes (LHR, likely transients). Generally, SHR coyotes had fewer core areas ($\bar{x} = 2$, range = 1–3) than LHR coyotes ($\bar{x} = 6$, range = 2–10).

Mean 95% dBBMM home range area for all coyotes was 22.7 km^2 (CL = 9.7–35.8 km^2), but varied widely among individuals. Mean 95% MCP home range area was 112.7 km^2 (CL = 53.1–172.4 km^2), and similarly varied among individuals. Mean dBBMM home range area for SHR and LHR coyotes was 7.4 km^2 (CL = 5.4–9.5 km^2) and 47.1 km^2 (CL = 27.5–66.8 km^2), respectively. Mean MCP home range area for SHR and LHR coyotes was 33.7 km^2 (CL = −2.1–69.4) and 203.1 km^2 (CL = 123.9–282.3 km^2), respectively.

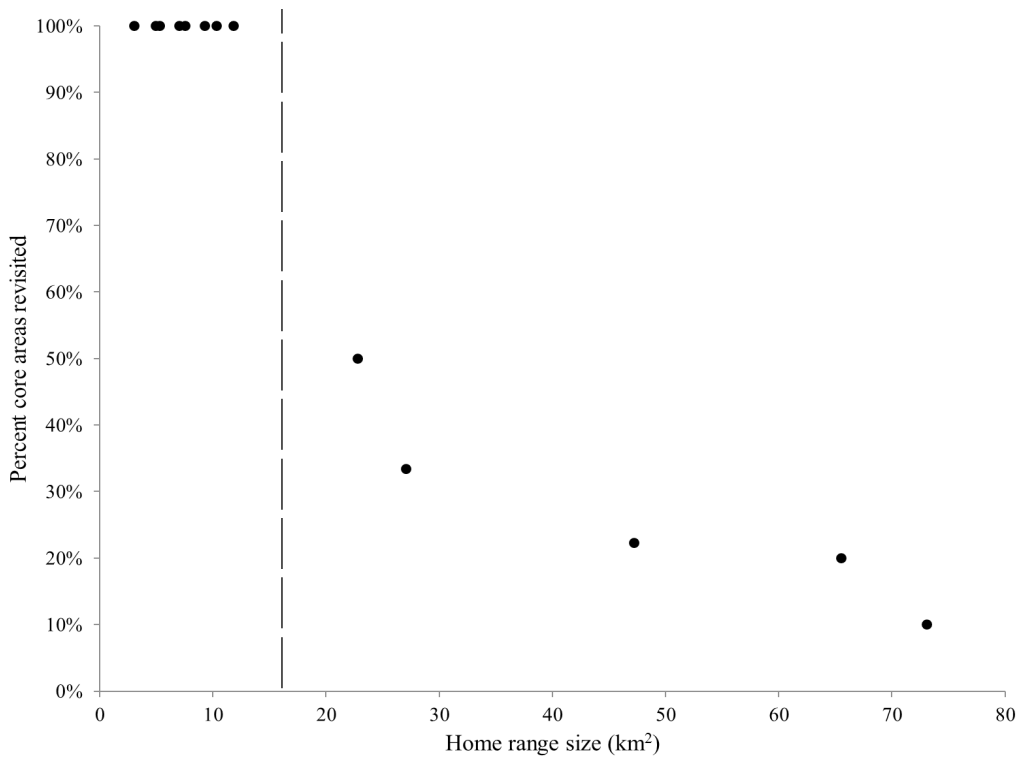There was a high degree of individual variability in movement

Figure 1. Percentage of core areas (50% dBBMM) revisited by individual female coyotes for ≥48 h during May–June 2012 and 2013 in west-central Georgia. Small home range females revisited 100% of their core areas while large home range females revisited ≤50% of their core areas.
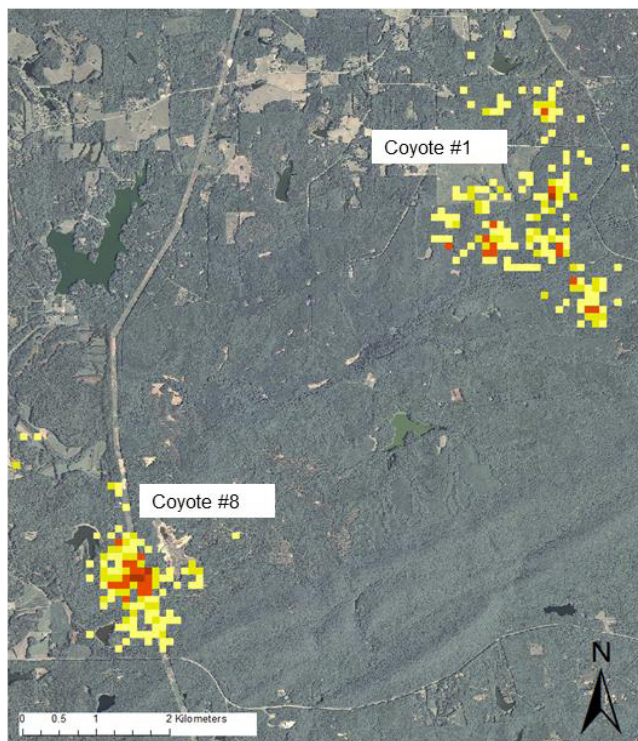

Figure 2. A comparison of home range use patterns between two small home range (likely resident) female coyotes in Harris County, Georgia, during May–June 2012 and 2013. Coyote #8 had a relatively small area of intensive use within its home range while Coyote #1's intensively used areas were more evenly dispersed throughout its home range. Heat map is scaled from light yellow (3–8 locations/pixel) to dark red (47-80 locations/pixel).

patterns and there was no clear correlation between RT and home range area. Mean step lengths also varied widely among individuals and showed little relationship to home range area. Graphical representations of high-use areas within SHRs also indicated variability, even within this spatial class. Whereas some SHR coyotes ($n = 5$) almost exclusively used small, restricted areas within their home ranges, movements of others were more evenly distributed throughout the entire home range ($n = 3$; Figure 2).

The composition of habitats within home ranges was similar to the availability of habitats across the study area (first order habitat selection). However, the composition of habitats within core areas differed relative to the availability of habitats within the home

Table 1. Multi-scale habitat selection for 8 female, resident coyotes in west-central Georgia during May–June 2012 and 2013. Rankings are on a scale from 1 (most preferred)–5 (least preferred) and values with the same upper case letter were not significantly different at $P < 0.05$.

Cover type	First order [a]	Second Order [b]	Third order [c]	
			day	night
Developed	4ABC	4C	5C	5B
Open	5C	1A	1A	1A
Early Successional	2ABC	2AC	3AB	3B
Hardwood	1ABC	3B	2A	2B
Pine	3AB	5ABC	4B	4B

a. Selection of home range habitats in proportion to their availability within the study area
b. Selection of core area habitats in proportion to their availability within the home range
c. Selection of diurnal and nocturnal habitats in proportion to their availability within the home range

range (second order habitat selection), with coyotes selecting core areas with more open habitat (Table 1). Coyotes used all habitats within home ranges similarly during the day, except they avoided developed areas. Coyotes disproportionately used open habitats at night (third order habitat selection).

Discussion

Although some natural variation in coyote space use across their range is expected (Bekoff and Gese 2003), the lack of standardization among studies further contributes to the reported variation. Variable sampling methods (Laundre and Keller 1984), use of different home range estimators (Woodruff and Keller 1982), and perhaps more importantly inclusion of transient coyotes with large home ranges in calculations, all contribute to high variability among studies. Classification of a resident coyote is intuitive, but classifying a transient is more ambiguous. As a result, we described a discrete, quantitative method that classified coyotes based on consistency of space use, rather than overall space use (i.e., home range area). Five of 13 female coyotes in our study were classified as LHR coyotes, similar to a previous report in southern Texas (Windberg and Knowlton 1988). Although incomplete datasets for two additional females precluded our ability to estimate space use using the dBBMM, their 95% MCP home ranges were comparable to those of other LHR individuals. Therefore, nearly 50% of our coyotes were potentially transient individuals during spring and summer when our monitoring occurred, which is higher than what has been reported elsewhere (Gese et al. 1988, Chamberlain et al. 2000, Hinton 2014). To understand differences in spatial distribution among coyotes, we urge standardization of methods for classifying spatially distinct behaviors in future research.

Comparison of the number of core areas and core area revisitation rates indicated that SHR coyotes intensively used a smaller number of areas than LHR coyotes. Although intensive use of small areas likely increases coyote encounter rates with fawns, and thus predation risk within those areas, these intensively-used areas were not evenly distributed across the landscape. Therefore, patchy distribution of high use areas likely results in a similar patchy pattern with regards to predation risk of fawns across the landscape.

In our study, SHR coyotes selected open habitats at the second and third orders of selection, which is not surprising given that other studies have reported general preferences for open, treeless environments by coyotes across their range (Gosselink et al. 2003, Van Deelen and Gosselink 2006). Additionally, open habitats are preferred by a variety of coyote prey and therefore are highly attractive (Holzman et al. 1992, Chamberlain et al. 2000, Kays et al. 2008, Schrecengost et al. 2009).

Although coyotes exhibit similar habitat preferences within re-

gions (Gese et al. 1988), residents often occupy more productive (i.e., early successional areas with greater prey abundance) habitats (Kamler and Gipson 2000, Hinton 2014), and transients avoid encounters with residents by restricting their movements to areas between or on the margins of resident home ranges (Witham 1977, Hinton 2014). Because productive habitat types are generally attractive to deer as well, resident coyotes likely have a disproportionate effect on fawn recruitment in these areas. For example, on two sites in central Georgia, fawns occurred in a greater percentage of coyote scats on the site with a greater proportion of habitat preferred by both coyotes and deer (Kelly 2012). Despite greater deer abundance on the site and similar coyote abundance between sites, recruitment was lower on the site with more deer and preferred habitat, suggesting that coyotes may have used the site more intensively during the fawning season (Gulsby et al. 2014).

Our results regarding coyote space use may also hold important implications for predation management through coyote removal. Because transients cover large areas over relatively short time intervals, these animals may serve as population founders in areas vacated by coyotes following removal efforts. Thus, in areas where transient coyotes are abundant removal efforts may yield marginal or temporary results. For example, in South Carolina annual coyote removal rates remained constant among three sites for three consecutive years (Kilgo et al. 2014), and in central Georgia coyote abundance decreased following the first year of removal, but increased to nearly pretreatment levels after year two (Gulsby et al. 2014). These results demonstrate how quickly coyotes, perhaps transients, can occupy vacant areas.

The scattered distribution of transient coyotes is likely an adaptation for coyote populations to persist where they are heavily exploited. In other words, transient behaviors increase the probability of quickly locating and occupying areas containing preferred habitat where resident animals are removed. Transient home range patterns in our study were similar to those reported in North Carolina where coyotes established biding areas, which are temporary localized movements analogous to home ranges (Hinton et al. 2012). A three-year study in North Carolina revealed that 88% of transient coyotes eventually established permanent home ranges in or near their biding areas, suggesting this was a strategy used to familiarize themselves with areas they roam. Further, these biding areas may also be a result of extended foraging needs for traversing long distances (Hinton 2014).

Management Implications

Our results indicate that wildlife managers should consider coyote spatial ecology as an important indicator of local fawn predation risk. Resident coyotes had fewer core areas which they re-

visited frequently, whereas transient coyotes had more core areas which they infrequently revisited. However, even among individual residents, the distribution of intensively-used areas throughout the home range was sometimes patchy, likely resulting in variable predation risk across the landscape. Additionally, because transient coyotes serve as a source population, removal efforts in areas containing preferred coyote habitat may yield marginal, temporary results. Although we acknowledge that our study was limited in sample size and duration, the variability in intensity of use patterns, even among resident animals, offers a reasonable hypothesis to explain differences in fawn predation across small spatial scales.

Acknowledgments

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