Identifying and Understanding the Spatial Distribution of Bobcat and Coyote Behavior

Ryan Radford Wilson
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IDENTIFYING AND UNDERSTANDING THE SPATIAL DISTRIBUTION OF
BOBCAT AND COYOTE BEHAVIOR

by

Ryan Radford Wilson

A dissertation submitted in partial fulfillment
of the requirements for the degree
of
DOCTOR OF PHILOSOPHY
in
Wildlife Biology

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UTAH STATE UNIVERSITY
Logan, Utah

2010
ABSTRACT

Identifying and Understanding the Spatial Distribution of Bobcat and Coyote Behavior

by

Ryan R. Wilson, Doctor of Philosophy

Utah State University, 2010

Major Professor: Dr. John A. Shivik
Department: Wildland Resources

A common observation in animal space use studies is that animals do not use space uniformly, but rather use some areas of their home ranges and territories with much higher intensity than others. Numerous methods have been developed to estimate these “core areas”; however, all of the current methods available are based on arbitrary rules. Additionally, most studies do not attempt to understand what behavioral processes lead to the observed patterns of non-uniform space use. This study has four main objectives: 1) to develop an objective and more precise method for estimating core areas, 2) to understand the processes leading to unequal coyote capture probabilities across territories, 3) to understand the biological mechanisms that influence the location of bobcat core areas, and 4) to determine how differences in territory size affect coyote movement patterns. The core area estimation method I developed consistently performed better than methods using arbitrary values to define core areas. Using this method to estimate coyote core areas, I determined that coyote capture locations were not actually
biased towards low use areas because of low familiarity with those areas, but rather because of a higher probability of encountering traps there. Intensity of coyote use did, however, influence the location of bobcat core areas. When prey abundance was high, bobcat core areas were located in areas of low coyote use but occurred in areas of high coyote use when prey abundance was low, indicating bobcat core areas are the result of at least two processes: foraging conditions and avoidance of intraguild predation. Lastly, coyote movement behavior changed significantly as territory size increased, leading to faster and straighter movement patterns. However, even though coyotes in larger territories moved twice as fast as those in small territories, they took significantly longer to traverse their territories compared to those in small territories. This might be the result of coyotes occupying large territories being less constrained by defense due to lower conspecific density compared to coyotes occupying small territories. Overall, my research reveals the importance of using more precise methods to delineate animal space use patterns, and the greater information researchers can obtain when they attempt to understand the processes underlying space use patterns.
ACKNOWLEDGMENTS

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Ryan R. Wilson
PREFACE

Some chapters in this dissertation are written in the required format of the journal to which they will be submitted. Although I am the first author on each manuscript within this dissertation, each has co-authors as well. Chapter 2 has been accepted by the *Journal of Wildlife Management*. The order of authorship is: Ryan R. Wilson, Mevin B. Hooten, Bradley N. Strobel, and John A. Shivik. Chapter 3 has been submitted to the *Journal of Wildlife Management*. The order of authorship is: Ryan R. Wilson, Julie K. Young, and John A. Shivik. Chapter 4 will be submitted to the *Journal of Animal Ecology*. The order of authorship is: Ryan R. Wilson, Terry L. Blankenship, Mevin B. Hooten, and John A. Shivik. Chapter 5 will be submitted to the *Journal of Mammalogy*. The order of authorship is: Ryan R. Wilson and John A. Shivik.
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CHAPTER 1

INTRODUCTION

Understanding animal space use patterns, and the processes underlying those patterns, may help to improve management and conservation of wildlife species. However, even though better and more sophisticated methods have been developed for collecting and analyzing animal space use data, researchers often ignore the underlying ecological mechanisms that lead to the observed patterns (Marzluff et al. 2001). Failure to apply improved methods and incorporate ecological mechanisms is apparent in current methods used to estimate animal space use patterns, which have been built on unfounded assumptions, or subjective decision rules with little or no biological relevance (Shivik and Gese 2000, Powell 2000). Studies of animal space use patterns can be improved by increasing our understanding of why animals differentially use various areas within their ranges (Marzluff et al. 2001, Horne et al. 2008). Understanding the underlying behavioral processes, however, is only possible if we use precise methods (McIntire and Fajardo 2009).

Core areas are frequently reported as an animal space use metric that is used to answer a variety of ecological questions in areas such as interspecific competition (Neale and Sacks 2001), habitat selection (Chamberlain et al. 2003), and territorial defense (Darden and Dabelsteen 2008). Most methods for estimating core areas rely on arbitrary rules that are invariant to intra and interspecific differences in space use patterns (Laver and Kelly 2008). For recent studies employing kernel density estimates (Worton 1989), 89% of authors defined a core area by the 50% density isopleth (Laver and Kelly 2008). Given that different processes underlie space use patterns for different individuals and
species, one should not assume that an arbitrary rule will adequately define a core area. Obtaining imprecise core area estimates, or ignoring variation among animals, could affect conclusions drawn from studies relying on core areas as a parameter.

Methods used to delineate animal space use patterns should have a biological underpinning (Shivik and Gese 2000), but even with precise core area estimates, most studies lack an understanding of the behavioral and overall biological processes that lead to the formation of core areas. A failure to understand underlying mechanisms can be problematic for both research and management. Consider the proposition that animal core areas represent the most critical habitat and that its conservation can be used to mitigate the take of other “less important” areas (Bingham and Noon 1997). This proposition was immediately met with criticism because of the possible negative effects it could have on the populations it was intended to protect given that the level of use an area receives is not necessarily related to its importance (Buchanan et al. 1998).

Assuming greater importance for areas receiving more intense use is problematic, especially without considering fitness-related consequences, how an animal behaves there, or how much it needs an area that it does not spend much time in (Van Horne 1983, Garshellis 2000). For example, although a bedding area likely receives more intense use by an animal, this does not make it more important than a water source that is essential for survival but used infrequently. A movement corridor may be used only once in an individual’s life, yet may also be essential for survival. This is not to say that bedding areas are not important to an individual’s survival and fitness (e.g., Cain et al. 2008), but rather, that one cannot evaluate the importance of an area by only considering the intensity with which that area is used or its size. Few studies have attempted to evaluate
the importance of areas by determining the behaviors that occur inside core areas (e.g., Barg et al. 2006), but rather, researchers usually assume that high-use areas represent primary foraging areas, even without any supporting evidence (e.g., Plowman et al. 2006).

Biologists have similarly assumed a direct relationship between the intensity with which an area is used and an individual’s familiarity with that area. This assumption mostly stems from captive studies, which have convincingly shown that animals behave differently towards novel objects when encountered in an area they are familiar with than in an area they have never visited (Windberg 1996, Harris and Knowlton 2001). Field studies on coyotes have shown a similar pattern, with coyotes tending to be captured disproportionately more in areas receiving lower use, typically on the periphery of territories (Woodruff and Keller 1982, Windberg and Knowlton 1990, Sacks et al. 1999, Harris and Knowlton 2001, Gipson and Kamler 2003). Almost all field studies searching for this pattern, however, have not considered the distribution of traps in relation to space use patterns. When the distribution of traps is taken into account, no location bias in captures occurs (Laundré and Keller 1983). Thus, factors other than time spent in an area are likely to influence an animal’s degree of familiarity with an area.

Because we cannot manipulate an animal’s familiarity with its environment in field settings, determining how environmental familiarity affects behavior is difficult. We can, however, attempt to determine how free-ranging animals maintain familiarity with their environment and factors that influence information acquisition. Specifically, we can use existing variation in territory sizes between populations of coyotes (Gompper and Gittleman 1991, Nilsen et al. 2005) to test for differences in rates of territory
exploration and how coyotes alter their movement patterns in relation to larger areas to explore.

As a means of understanding the underlying behaviors leading to observed animal space use patterns, Marzluff et al. (2001) recommended obtaining spatially-explicit behavioral observations and then calculating the utility distribution for each behavior of interest. This then provides a map of behaviors across an individual’s range. Indeed this method would be extremely useful for understanding underlying processes of observed space use patterns, but is restricted to readily observable species. For more cryptic species, such as coyotes and bobcats, or animals living in heavily vegetated areas, obtaining a sufficient number of unbiased behavioral observations is usually not possible. Therefore, if we are to understand what behaviors underlie animal space use patterns, we must employ a different technique.

Goals and Objectives

The overall goal of my research is to better understand factors that influence the distribution of bobcat and coyote behaviors across their home ranges and territories; I will evaluate underlying factors by testing among competing hypotheses that may cause observed behavioral patterns. My desire is to move beyond a simple description of the intensity of space use patterns and assumptions of underlying behaviors, and infer what behavioral processes lead to the development of observed space use patterns. To accomplish my goals, I first develop a new method for estimating core areas that is objective and precise, and which extracts considerably more information from point patterns than previously used methods. I use my novel method to estimate coyote core
areas and to test among competing hypotheses regarding factors influencing the capture location of coyotes inside their territories. Next, I estimate bobcat core areas and determine if and how the distribution of prey and intensity of coyote use interact to influence the spatial distribution of bobcat core areas. Lastly, I use natural variation in coyote territory sizes between two populations to determine if movement patterns differ as a function of the size of territory occupied.

Literature Cited


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CHAPTER 2
ACCOUNTING FOR INDIVIDUALS, UNCERTAINTY, AND MULTI-SCALE CLUSTERING IN CORE AREA ESTIMATION\textsuperscript{1}

Abstract

Core areas are important descriptors of animal space use patterns, but current estimation methods rely on arbitrary rules and potentially lead to imprecise or erroneous area estimates. We propose a Bayesian statistical model that incorporates an individual-based method for estimating core area boundaries. The model accounts for boundary uncertainty and multiple scales of clustering by partitioning a home range into \( \geq 2 \) completely spatially random point patterns defined by a kernel density isopleth. We use data from coyotes (\textit{Canis latrans}), bobcats (\textit{Lynx rufus}), and red-shouldered hawks (\textit{Buteo lineatus}) to estimate core areas for individual animals. We also estimated core areas from simulated point patterns with known boundaries, varying the numbers of points and relative densities of points inside core areas and compared estimates to those obtained using the 50% isopleth. Optimal isopleths for the empirical data ranged between 18.7 and 71.5%. We found no species-specific range of core area isopleths. Across all simulated scenarios, our method outperformed the 50% isopleth-based estimate which consistently overestimated core areas. Minta overlap values were 20-40\% higher across all scenarios for our method compared to the 50% isopleth and were >75\% in 90\% of scenarios. Objectively estimating core areas using our individual-based method may lead

\textsuperscript{1} Coauthored by Ryan R. Wilson, Mevin B. Hooten, Bradley N. Strobel, and John A. Shivik.
to improved inference about which behavioral and ecological processes underlie observed space use patterns because of greater estimate precision.

Introduction

Landscapes are used and perceived differently by different animals (Haila 2002, Manning et al. 2004). Furthermore, space use patterns vary not only by species, but by individuals within species, and within individuals during different life history periods (Addicott et al. 1987). Individual specialization and behavioral syndromes could also influence how individuals view and use landscapes (Estes et al. 2003, Sih et al. 2004). Yet, in many aspects of spatial ecology, analytical techniques continue to treat individual animals identically, both within and between species.

Core areas are defined as any area of the home range receiving greater intensity of use (i.e., a clustered point pattern; Kaufman 1962, Powell et al. 1997) and are frequently used to answer ecological questions in areas such as interspecific competition (Neale and Sacks 2001), habitat selection (Chamberlain et al. 2003), and territorial defense (Darden and Dabelsteen 2008). Most methods for estimating core areas rely on arbitrary rules that are invariant to intra and interspecific differences in space use patterns (Laver and Kelly 2008). Obtaining imprecise core area estimates, or ignoring variation among animals, could affect conclusions drawn in studies relying on core areas as a parameter. Precise spatial analysis is required if we are to infer underlying behavioral processes from observed point patterns (McIntire and Fajardo 2009).

For recent studies employing kernel density estimates (KDE; Worton 1989), 89% of authors defined a core area by the 50% density isopleth (Laver and Kelly 2008).
Given that different processes underlie space use patterns for different individuals and species, it is probably not valid to assume that an arbitrary rule will adequately define a core area. Rather, methods used to delineate animal space use patterns should have a biological underpinning (Shivik and Gese 2000). The arbitrary choice in isopleth is also problematic because it always estimates a core area, even if one does not exist (Fig. 2.1). It is important that a core area actually be a place of greater intensity use and not a mathematical artifact (Powell et al. 1997).

Many of the features suggested by others as being ideal for core area estimation remain unaddressed. For example, no density-based method is available to objectively choose which isopleth best captures the core area for a given point pattern and a formal definition and ability to account for the internal structure of core areas is lacking (Kenward et al. 2001). Additionally, no core area estimation method exists that accounts for the precision of the core area estimate.

Our objective is to increase objectivity in core area estimation by introducing a novel statistical method that addresses many of the features considered ideal when estimating core areas. We use the method and data from bobcats (*Lynx rufus*), coyotes (*Canis latrans*), and red-shoerded hawks (*Buteo lineatus*), to show how the method works for real data and the types of inference that can drawn from more precise core area estimates. We then show, through simulation, how the model performs under varying conditions compared to the 50% isopleth.
Figure 2.1 - Home range analysis based on two separate point patterns; a completely spatial random (CSR) point pattern and a clustered point pattern from a coyote. The outer boundaries for each home range were defined by the 95% isopleth with fixed kernel methods using reference bandwidth. Axes for graphs in the left column are based on universal transverse mercator. Both point patterns occur on the same spatial scale and with the same number of points. The shaded area within each home range represents the 50% isopleth. The L-functions for each point pattern (right column) indicate whether either pattern departs significantly from CSR (as indicated by the observed L-hat rising above the shaded bounds) bounded by their respective home range boundaries (with no boundary correction). The shaded regions for the L-function graphs represents the minimum and maximum L-hat values from 1,000 Monte Carlo simulations of a CSR point pattern on the respective home range boundary.
Methods

Core area model

The standard definition of a core area indicates that animals behave in such a manner that they occupy regions of their home range with differing intensities (Powell et al. 1997). Therefore, when significant clustering of relocations is indicated in an animal’s home range (through a formal hypothesis test using the L-function; Ripley 1976), we assume that a core area exists and that the temporally independent observed point pattern can be partitioned into \( \nu \) separate completely spatially random (CSR) point patterns. We also assume that the partition(s) is random rather than fixed. This assumption can be intuitively justified by considering that animals are likely unaware of some fixed polygon in their home range that denotes “core” space use. It seems unlikely that a definitive core area boundary even exists, especially given thresholds in resource quality are often indistinct in nature and that boundaries may not be perceived precisely by animals (Powell 2000). Thus core areas might be more appropriately thought of as exhibiting soft boundaries (St-Louis et al. 2004). In the simplest case (i.e., \( \nu = 2 \)), animals use core areas and non-core areas with different intensity, but use is uniform within each area. This implies that the observed set of spatial locations should arise from two independent multivariate uniform probability distributions with irregular boundaries. We begin by describing the model for the simplest case where \( \nu = 2 \), then show how the model can be easily modified to account for situations where \( \nu > 2 \).

The uniform model is difficult to fit, thus, as a discrete approximation, the first step is to transform the relocation data by dividing the home range into a finite number
(m) of square grid cells or bins, and then summing the number of observed animal locations that fall within each bin resulting in an m-dimensional set of counts, N. The appropriate number of bins (m) will vary depending on the total number of animal locations and their distribution within the home range. We found that partitioning the home range into 500 - 2000 bins worked well in most of the situations we considered. Ideally, the number of bins, m, should not influence results, though a sensitivity analysis can verify this if the user wishes to evaluate certain situations. The cell counts, N = \{N_1, \ldots, N_i, \ldots, N_m\} represent the number of observed points in each region of the home range. We can then partition N into core bin counts N(C) and non-core bin counts N(C') (where, C and C' are the core and non-core areas, respectively). If the corresponding animal locations are CSR in C and C', then we expect the sets of counts to have multinomial distributions with equal multinomial cell probabilities (i.e., \(p_C = \{1/m_C, \ldots, 1/m_C\}\) and \(p_{C'} = \{1/m_{C'}, \ldots, 1/m_{C'}\}\)) in each region; where \(m = m_C + m_{C'}\) are the numbers of bins. Then, if we let \(n_C\) and \(n_{C'}\) denote the total number of points inside and outside the core area, respectively, we will have the following likelihood:

\[N|C \sim \text{Multinomial}(n_C, p_C) \times \text{Multinomial}(n_{C'}, p_{C'})\]  

Equivalently, we could use a Poisson likelihood with intensities equal to \(n_C/m_C\), and \(n_{C'}/m_{C'}\), though it makes no difference in terms of implementation in this case.

We assume the boundary can be well-described by an isopleth of a KDE of the observed point pattern. There are other methods for delineating polygons (e.g., convex hull, wombling), however, because KDE is frequently used in animal space use studies (Laver & Kelly 2008) we employ it here. Any application of the model will also be contingent on the choice of bandwidth parameter which should be biologically
meaningful. In developing a core area model, the KDE isopleth ($\phi$) is especially attractive because it is bounded between zero and one and can be treated as a statistical parameter to estimate. Once estimated, $\phi$ completely determines the core area partition $C$. Thus, the likelihood (1) can be conditioned on $\phi$.

A statistical model can be easily constructed using Bayesian methods that incorporates the likelihood (1), any prior knowledge about $\phi$, and accommodates the uncertainty in the boundary estimate. Here, we only assume that $\phi$ should not be too near zero nor too near one, thus we specify a vague Beta distribution as a model for $\phi$ with hyperpriors both equal to 1.1. The model is relatively simple to implement as a one-parameter Bayesian model and although there is non-conjugacy induced through the nonlinearity of $\phi$ in the likelihood, this can be addressed using an accept-reject style algorithm such as Metropolis-Hastings (Gelman et al. 2004). In doing so, we seek to find the posterior distribution for $\phi$ given the multinomial count data $N$:

$$[\phi|N] \propto \text{Multinomial}(N_C|n_C, p_C, \phi) \times \text{Multinomial}(N_C|n_C, p_C, \phi) \times \text{Beta}(\phi|1.1, 1.1) \quad (2)$$

where, the square bracket notation refers to a conditional probability distribution.

The method presented thus far is suitable when the data exhibit only two distinct partitions of the home range. In cases where multiple scales of clustering occur within the home range, we need to allow for the possibility of multiple scales of core areas. We let these $\nu$ partitions of the home range be denoted as $C_1, C_2, \ldots, C_\nu$. Assuming that each of the sets of points falling within the given optimal partitions are independent and CSR, we can obtain the following posterior distribution using another approximate likelihood in terms of a product of multinomial distributions and $N$:
[\phi|\mathbf{N}] \propto \text{Multinomial}(N_{CI}|n_{CI}, p_{CI}, \phi_I) \times \cdots \times \text{Multinomial}(N_{CV}|n_{CV}, p_{CV}, \phi_v) \times \text{Dirichlet} (\phi|\alpha) \tag{3}

where, \( \phi = (\phi_I, \phi_2, \ldots, \phi_V) \)' is a parameter vector containing the kernel density isopleth parameters. The natural constraint on the vector \( \phi \) is such that each of its elements must fall between zero and one and also sum to one. The Dirichlet model is an excellent probability distribution for this multivariate parameter and thus is chosen to serve as a prior distribution for \( \phi \). Again we specify a vague prior for the multi-scale clustering model by setting the elements of the hyperprior vector \( \alpha \) equal to small values (i.e., \( \alpha = (0.1, 0.1, \ldots, 0.1) \)').

**Empirical core area analysis**

We captured and fitted VHF-transmitters to bobcats (\( n = 7 \)), coyotes (\( n = 8 \)), and red-shouldered hawks (\( n = 7 \)) on the Welder Wildlife Foundation Refuge (WWFR; San Patricio County, Texas) between April 2007 and May 2008. We obtained relocations on each individual 4-5 days per week during a 6-month period between April and November 2008. We used triangulation and the maximum likelihood estimator in program Locate II (Nams 2006) to estimate animal locations. We used \( \geq 3 \) bearings collected within 20 minutes, between 20-160º of each other, to estimate locations. We randomly chose start times and animals for telemetry sessions and tested to ensure the data were not autocorrelated (Swihart and Slade 1985). We collected both diurnal and nocturnal locations for bobcats and coyotes as they are active during both periods (Neale and Sacks 2001). Data on red-shouldered hawks are limited to diurnal locations to correspond to their primary period of activity (Dykstra et al. 2008).
We defined home ranges by the 95% density isopleth with reference bandwidth as the smoothing parameter (Venables and Ripley 2002:130). The 95% density isopleth produces unbiased and robust home range estimates for species of largely different life histories (Börger et al. 2006), thus it meets our requirement of having a well-defined home range.

We initially tested each animal’s space use data (using the home range as the spatial domain) for clustering using the L-function (Ripley 1976). For each individual that exhibited clustering in their space use pattern, we estimated the isopleth that optimally partitioned the home range into 2 CSR regions. We again used the L-function to test each partition for departure from CSR. If there was still evidence of clustering, we estimated the 2 isopleths that optimally partitioned the home range into 3 CSR regions. We continued this iterative procedure until all partitioned regions did not differ from CSR so that our model assumptions were met.

We used R (R Development Core Team 2008) and functions within libraries splancs (Rowlingson and Diggle 1993), spatstat (Baddeley and Turner 2005), adehabitat (Calenge 2006), MASS (Venables and Ripley 2002), and MCMCpack (Martin and Quinn 2006), for all modeling and analysis.

**Simulations**

We tested how well the modeled performed with different sample sizes and relative densities of points between the core area and non-core area with known home range and core boundaries. We constrained simulations by choosing a representative home range and core area boundary from the bobcat data sets. Within these bounded
areas we simulated point patterns with 50, 75, 100, 125, and 150 points and with the intensities of points inside the core area being 5, 6, 7, 8, 9, and 10 times as intense as outside the core area. These relative intensities matched the range observed for our empirical estimates. We simulated 10 realizations for each combination of intensity and number of points and estimated the isopleth that best partitioned the home range into 2 regions (i.e., core and non-core). We used the Minta index (Minta 1992) to determine the percent each estimated core area overlapped with the true core area. The Minta index has the ideal feature of accounting for both under and overestimating overlap with the known core area. We also determined the mean percent of points correctly classified as being inside or outside core areas. We determined the Minta overlap values and the percent of points correctly classified using the 50% isopleth to partition each simulated home range into core and non-core areas.

Results

Empirical data

We collected a mean (SD) of 85 (27.5), 83 (22.6), and 108 (22.1) locations for each bobcat, coyote, and red-shouldered hawk, respectively. There was significant interspecific overlap in space use patterns on WWFR, although home ranges for each species occurred at different scales (Fig. 2.2). Every individual exhibited clustering in their spatial point patterns, but the scale of clustering differed between species (Fig. 2.3). Optimal isopleths for delineating the core area ranged between 18.7 and 71.5% for individuals across species. There was significant interspecific overlap in the optimal isopleths that delineated the core area with no obvious species-specific pattern (Fig. 2.4).
Figure 2.2 - Distribution of home ranges of bobcats, coyotes, and red-shouldered hawks (defined by the 95% fixed kernel density isopleth using reference bandwidth) on the Welder Wildlife Foundation Refuge, San Patricio County, Texas) from April-October 2008. Axes for graphs are based on universal transverse mercator.
Figure 2.3 - Examples (left column) of each species used for core area analysis. Home range boundaries are defined by the 95% fixed kernel density isopleth using reference bandwidth. Axes for graphs in the left column are based on universal transverse mercator. The L-functions for each point pattern (right column) indicate whether each pattern departs significantly from completely spatial random (CSR; as indicated by the observed L-hat rising above the shaded bounds) bounded by their respective home range boundaries (with no boundary correction). The shaded regions for the L-function graphs represents the minimum and maximum L-hat values from 1,000 Monte Carlo simulations of a CSR point pattern on the respective home range boundary.
The majority of bobcats (6 of 7) were adequately modeled by partitioning the home range into 2 CSR regions, while only 1 bobcat required the home range to be partitioned into 3 CSR regions (Fig. 2.5). Half of the coyotes studied had home ranges that were partitioned into 2 CSR regions, while the other half required the home range to be partitioned into 3 CSR regions. Four of 7 red-shouldered hawks had home ranges that were partitioned into 2 CSR regions (Fig. 2.5), whereas the other 3 were partitioned into 3 CSR regions. Optimal isopleths delineating inner core areas ranged from 5.0 to 31.7%, with no apparent interspecific differences (Fig. 2.4). There was no systematic difference in the mean number of points within home ranges partitioned into 2 (84.2 [25.9]) and 3 (96.9 [21.28]) CSR regions.

**Simulations**

Our method consistently estimated core area boundaries that coincided with the real boundary (Fig. 2.6) and had high overlap with known core areas in all simulated scenarios (Table 2.1). The 50% isopleth always overestimated the core area (Fig. 2.6) and had Minta index values 20-40% lower than estimates based on our method in all scenarios (Table 2.1). Overlap increased with increasing sample size and relative density of points inside of core areas for both methods (Table 2.1). Across all simulations, the Bayesian method correctly identified 93.5% (5.2) of locations as being inside or outside core areas, whereas the 50% isopleth only correctly identified 82.5% (4.1). The percentage of points correctly classified by the Bayesian method generally increased with increasing numbers of points but not with increasing density of points within the core area (Table 2.2). The percentage of points correctly classified increased with increasing
numbers of points and with the relative density of points inside the core area (Table 2.2). In all but three scenarios (i.e., points and density combinations), the Bayesian method correctly classified a mean of >90% of points, whereas the 50% isopleth was never able to achieve that level of accuracy (Table 2.2). The mean isopleth value estimated for the point patterns by the Bayesian method was 21.7% (7.2).

Figure 2.4 - Optimal isopleth values estimated for each individual of each species. Optimal values are the mode of the posterior distribution of the isopleth parameter (± 95% Credible Interval). Solid bars are the optimal isopleths for the outer core area estimates and hashed bars are the optimal isopleths for the inner core area estimates.
Figure 2.5 - An example of bobcat (left) and red shouldered hawk (right) home ranges showing uncertainty in the partitioning of home ranges (defined by the 95% isopleth and reference bandwidth) into core and non-core areas. The bobcat’s home range is partitioned into 3 complete spatial random (CSR) point pattern (i.e., multi-scale core area model) and the red-shouldered hawk’s is partitioned into 2 CSR point patterns (i.e., single-scale core area model). The darker the shading of the core area boundary (or inner core area boundary) indicates those isopleths with the highest probability of delineating the core area. The level of shading is indicated by the posterior distribution of the isopleth parameter. The width of the shaded boundary indicates the level of uncertainty in the estimate. Axes for graphs are based on universal transverse Mercator grid projections.
Figure 2.6 - Four realizations of simulated point processes on a realistic home range and core area where density of points are seven times greater inside core areas than outside. True core area boundaries are denoted as a light solid line, whereas the dark bold solid line, and dashed lines represent the core area boundary estimated with the Bayesian method and the 50% isopleth, respectively. The simulations contained the following number of points and estimated core area isopleths; A) 50 points, 15.0% isopleth, B) 75 points, 13.1% isopleth, C) 100 points, 18.9% isopleth, and D) 150 points, 22.5% isopleth.
Table 2.1 - Summary of overlap between known and estimated core areas based on boundary estimates from Bayesian techniques or the 50% isopleth. Overlap was measured by Minta index which varies from 0 (no overlap) to 100 (complete overlap). We used a representative home range and core area boundary estimated from a bobcat data set to simulate points in. We simulated point patterns with 50, 75, 100, 125, and 150 points and with the densities of points inside the core area 5, 6, 7, 8, 9, and 10 times that outside the core area. For each point and density combination, we simulated 10 point patterns, and obtained the mean Minta index value.
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Table 2.2 - Summary of the percent of points correctly classified as occurring inside or outside of known core areas based on core area boundary estimates from Bayesian techniques or the 50% isopleth. We used a representative home range and core area boundary estimated from a bobcat data set to simulate points in. We simulated point patterns with 50, 75, 100, 125, and 150 points and with the densities of points inside the core area 5, 6, 7, 8, 9, and 10 times that outside the core area. For each point and density combination, we simulated 10 point patterns, and obtained the average percent of points correctly classified.
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Discussion

We have presented a new core area estimation method that implements many of the features expressed as ideal by Kenward et al. (2001). Specifically, our model formally accounts for the “inner focal areas” (Kenward et al. 2001:1917), provides an objective kernel-based technique for finding the optimal isopleth for estimating core areas (Kenward et al. 2001:1918), is the first to account for uncertainty in the core area boundary estimate, and allows for the visualization of which segment(s) of the boundary are most uncertain. Other approaches exist for partitioning heterogeneous point patterns into homogeneous regions (Wiegand and Moloney 2004) but do not have the benefit of being implemented in a kernel density framework or with the benefits provided by Bayesian analysis.

Through simulation, we found that the model performs very well in a variety of scenarios and is relatively robust to small sample sizes. The method also always outperformed the 50% isopleth in estimating the core area. Although the accuracy of the 50% isopleth core area estimate increased with increasing numbers of points and density of points in the core area, this was the result of the optimal isopleth value delineating the simulated point patterns moving closer to 50%. Thus, the only time the 50% would be equivalent to the Bayesian estimate would be when the Bayesian estimate is around 50%. This result does not imply that if a researcher has a sufficiently large data set (e.g., >150 relocations) that the 50% isopleth would be just as precise as our approach. Given that the optimal isopleth value delineating the core area is a function of both the number of relocations, the relative density of points inside the core area, and likely the proportion of
the home range the core area occupies, it would be unlikely to always converge to 50%. Additionally, these simulations were only of a simple, single-scale core (i.e., 2 CSR processes) example, thus if multiple scales of clustering are present, the 50% isopleth will never be able to partition the home range into >2 regions. The results of these simulations also show how using arbitrary isopleths to delineate core areas could lead to problems in studies investigating habitat selection due to the large overestimation of core areas.

We used fixed KDE methods to implement our model because of their wide use in home range and core area analysis (Laver and Kelly 2008). Our method is not restricted to one bandwidth selection procedure, definition of home range boundary, or home range estimation methodology. The successful implementation of the model is contingent on the assumption that the home range is well-defined and the chosen home range estimation procedure can adequately characterize the core area. This assumption likely excludes the use of our core area model with the minimum convex polygon method (Hayne 1949) due to the numerous biases and inabilities to accurately estimate animal space use patterns (Harris et al. 1990). As long as there is a way to link the parameters (i.e., isopleths in our case) to the boundary definition, our model can easily be extended to other home range estimation procedures (e.g., Getz and Wilmers 2004; Horne et al. 2007). Flexibility in home range estimation method is useful because although KDE methods perform well in many instances (Börger et al. 2006), in some situations they can lead to biased space use estimates (Getz and Wilmers 2004) which would also bias the resulting core area characterization.
Relative to the application of the model, we suggest that core areas be defined iteratively as we did, working upward from one core area to multi-scaled cores incrementally as needed. We recommend checking for additional clustering in each home range partition after fitting the single core model (using the highest posterior mode isopleth as the partitioning polygon). If no additional clustering is evident, then the single core area model results will be used. If additional clustering is evident, then a model with two scales (i.e., \( \nu = 3 \)) of clustering should be fit. Each of the three home range partitions should then be checked for any remaining clustering, at which point the process concludes if none exists. The iterative assumption-checking process also serves as a means of model evaluation. That is, if after fitting the single core area model, evidence of clustering remains in either of the partitioned home range regions, the single core model is inappropriate for the data. Likewise, when all of the clustering tests for the home range partitions indicate no significant deviation from CSR, then the model is appropriately characterizing the space use.

In many instances, researchers might only be interested in the core area boundary estimate, and not on the internal structure of the core area to meet their study objectives. To accurately estimate the core area with our model, however, one would still need to account for the clustering that occurs within the core area, because the estimation of the outer core area boundary is based on the optimal partitioning of the home range into CSR processes. Thus, if three CSR processes exist, but only two are accounted for, the estimated isopleth delineating the core area would be incorrect. Once the three CSR processes are accounted for, the isopleth delineating the outer core area boundary can be used.
An advantage of our model is that it can be informed with prior information about the distribution of optimal isopleths for species or social classes to produce more precise estimates. In the application discussed here we used vague priors for isopleth values. At present we think there is insufficient information in the literature to inform the model with prior distributions for isopleths given that very few studies have objectively estimated isopleths for individuals. More complex models can also be built from our basic model to link other covariates (e.g., environmental, behavioral, temporal) to the estimation of core areas.

Although non-trivial in its implementation, our method is intuitive in principle and uses techniques familiar to those studying animal space use patterns. In addition to being able to accommodate other home range methods, our method can easily be generalized to situations other than analyzing animal space use patterns (e.g., epidemiology).

Estimates of core areas using our method varied widely between individuals. Similarly, we found no evidence for species-specific rules as there was considerable interspecific overlap in the optimal isopleth estimates. That there would be no species-specific optimal isopleth and such large variation among individuals is expected given the myriad factors affecting animal space use. For example, while subordinate coyotes participate in territorial defense and pup-rearing, they do so at lower levels than dominant individuals (Gese 2001). Thus, we would expect differences in what areas of the home range they use most intensively, and in the intensity they use those areas; both factors which would affect the optimal isopleth for delineating a core area. If foraging is a dominant behavioral process leading to the formation of a core area, then the distribution
and density of prey could similarly affect the optimal isopleth for delineating core areas. This is especially true when one considers individual specialization in prey types (Estes et al. 2003). An individual’s behavioral syndrome has also been shown to influence its movement patterns (Bremmer-Harrison et al. 2004), thereby potentially affecting the optimal choice in isopleths for delineating a core area.

Describing a home range only in terms of its boundary ignores information about the internal structure of the home range (Horner and Powell 1990). The same can be said of ignoring the internal structure of core areas. While it is often assumed that a core area is the result of one behavioral process (e.g., foraging), numerous behavioral processes could lead to the formation of a core area. Kenward et al. (2001) alluded to the possibility that non-random space use patterns within the core areas might be related to a different behavioral process. Results from our core area estimates suggest this is true.

While no male red-shouldered hawks showed evidence for multi-scale core areas, all breeding females did (i.e., home range partitioned into 3 CSR regions). An additional female’s nest failed early in the breeding season and showed no evidence of a multi-scale core area. Breeding season behavior of red-shouldered hawks is sex-specific; breeding females devote more time to incubation and brood rearing while males forage widely throughout their home range (Dykstra et al. 2008). Thus, core areas for female hawks likely represent a combination of nesting, hunting, and nest defense behavior, whereas male core areas likely represent preferred areas for hunting to provision nestlings. Only one bobcat showed evidence of multi-scale core areas; a female with a litter of four kittens and a known den site within one of the sub-core areas. We analyzed data for another female, but she showed no evidence of multi-scale core areas. Given her young
age during the study period, however, it is unlikely that she raised a litter of kittens.

Patterns in coyote core area analysis are less clear because of unknown social statuses. The number of individuals that exhibited multi-scale core areas and the patterns that emerge, suggest the life history of an individual, or the ecological neighborhood it currently occupies might be better predictors of the internal structure of the home range than simply considering the individual’s species.

Management Implications

Regardless of the specific method chosen, based on our findings, we advocate the use of a data-based method for estimating core areas rather than an arbitrary rule since the latter can lead to misidentification of areas of high use. Increased precision in animal space use patterns will improve our ability to detect differences between experimental treatments, infer behavioral processes that lead to the formation of core areas, and determine wildlife habitat associations. This can have important implications for setting priorities for conservation and management areas.

Literature Cited


CHAPTER 3

COYOTE CAPTURE VULNERABILITY RELATIVE TO TERRITORY USE AND TRAP DENSITY

Abstract

Coyotes are reported to be less vulnerable to capture in familiar areas of home ranges, however, most studies do not control for trap density across the home range. We determined if accounting for trap density provided a better explanation of observed capture rates. Based on a sample of 25 captured coyotes (6 inside core areas and 19 on home range peripheries) the best fitting model describing capture location only accounted for trap density and not relative time spent in each region. Our results suggest that coyote capture rates are a function of trap density in an area and not novelty avoidance.

Introduction

Understanding movement patterns of resident coyotes is important for predation management because residents are most often responsible for livestock depredation (Andelt 1985, Sacks et al. 1999b, Blejwas et al. 2002). If coyotes are more vulnerable to capture in some parts of their territories than others, predation management may be improved with more efficient removal of specific animals (Sacks et al. 1999b, Blejwas et al. 2002).

Presumably, resident coyotes are familiar with the areas of their home range they use regularly and will avoid points of disturbance such as those caused by the placement

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2 Coauthored by Ryan R. Wilson, Julie K. Young, and John A. Shivik.
of traps; it is generally accepted that coyotes are less vulnerable to capture devices within core areas of their home range (Knowlton et al. 1999). Indeed, multiple studies in captivity have found a strong neophobic response of coyotes to novel objects in familiar areas (Windberg 1996, Harris and Knowlton 2001).

Of those studies looking at spatial bias in coyote captures, most concluded that coyotes were less vulnerable to capture within frequently used areas of their home range (Rucker 1975, Hibler 1977, Woodruff and Keller 1982, Roy and Dorrance 1985, Windberg and Knowlton 1990, Sacks et al. 1999a, Gipson and Kamler 2003). In the one study that controlled for differences in trap density between core and peripheral areas, however, the authors found no capture bias (Laundré and Keller 1983). Thus, the question arises: are coyotes truly less vulnerable to capture in core areas because of increased wariness, or is the widely held conclusion of differential coyote capture vulnerability an artifact of methodological biases?

One of the most common methods for analyzing capture data involves contingency tables, which require accurate expectancies for comparison to observed results (e.g., Gipson and Kamler 2003). Not accounting for different trap densities in core and peripheral areas could affect the calculation of expectancies and thus bias results. Therefore, to reliably assess spatial effects in coyote capture probabilities it is essential to account for differences in trap density across an individual’s territory.

Our objectives were to determine if coyotes are less vulnerable to capture in their core areas or if the methodological problem of not properly accounting for differences in trap density between core and peripheral areas bias results. Specifically, we used
empirical data and Akaike Information Criteria (AIC) to test if models that account for
trap density fit observed core and periphery capture rates better than those that did not.

Methods

Our study was on the Welder Wildlife Foundation Refuge (~3,150 ha) and a
portion of the McFadden Enterprises Ranch (~ 8,000 ha), which are approximately 10 km
north of Sinton, Texas. The study area was located in a transition zone between the gulf
prairies and marshes and south Texas plains, and vegetation consisted mainly of mixed
grasslands and shrubs (Young et al. 2008).

We captured coyotes with a combination of padded leg-hold traps (Victor #3 Softcatch,
Lititz, PA) and collarums (Wildlife Control Supplies, East Granby, CT) during 2003-
2005 and 2007-2008 study seasons. Each captured coyote was fitted with a radio-collars.

We obtained relocations on each individual 4-5 days per week for the first 3
months post-capture (Windberg and Knowlton 1990). We used triangulation and the
maximum likelihood estimator in program Locate II (Nams 2006) to estimate animal
locations. We used ≥ 3 bearings collected within 20 minutes, between 20-160º of each
other, to estimate locations. We chose random start times and animals for telemetry
sessions to avoid problems of serial autocorrelation (Fieberg 2007). We collected both
diurnal and nocturnal locations for coyotes as they are active during both time periods
(Young et al. 2006).

We estimated home ranges for those individuals with ≥ 30 locations to ensure that
we obtained a sufficient number of relocations to estimate home ranges (Seaman et al.
1999). We used the fixed kernel method (Worton 1989) with the ad hoc bandwidth
selection procedure (see Berger and Gese 2007). We defined the home range as the area encompassed by the 100% isopleth. To define core areas, we analyzed home ranges for clusters of locations and used Bayesian methods to identify core area isopleths that best fit the observed animal’s dataset (Wilson et al. 2010). We calculated the percent of time an individual spent in the core area and periphery (i.e., the area between the core area boundary and 100% isopleth) of their home range by determining the relative percent of relocations in each region. We also determined the relative trap density in the periphery and core area for each individual by dividing the number of traps open in each region during the night the coyote was captured by the respective area of each region.

We determined latency to capture by determining how many nights a trap was set before it captured a coyote.

Trap densities could only be calculated within defined core and periphery boundaries of home ranges, and thus only animals that were captured within a defined home range area were used in analyses.

To determine if coyote capture location was related to relative trap density inside the core area, relative use of core area, or both, we parameterized 3 binomial distributions with the expected values for each hypothesis. For the hypothesis that capture location is only related to relative trap density inside the core area, we used the mean relative trap density inside coyote core areas as the mean for the distribution. For the hypothesis that capture location is only related to the relative time spent in the core area, we used the mean proportion of time coyotes spent in their core areas as the mean. Lastly, for the hypothesis that both trap density and time spent in core area explained capture location, we used the average geometric mean of the product of relative trap density and relative
time spent in the core area. We then obtained the likelihoods of the different
glome (Burnham and Anderson 1998) to determine which of the
parameterizations was the best model for the observed data.

Results

We captured 28 resident coyotes, but were only able to use 25 in analyses; 3 were
captured outside of their home ranges, including 2 that had no traps set within their home
ranges. A disproportionate majority of coyotes, however, were captured within their
home ranges ($\chi^2_1 = 12.0, P < 0.001$).

All 25 study coyotes had a core area and the mean isopleth that delineated core
areas was 38.2% (range 10.2 - 70.0%, SD = 15.9 %). Mean percent of time spent (i.e.,
number of locations) within the core area was 53.0 (SD = 15.5). Mean size of core areas
and peripheries were 0.85 (SD = 0.80) and 8.03 km$^2$ (SD = 4.32), respectively. Mean
trap density (traps/km$^2$) inside core areas and the periphery were 0.87 (SD = 1.83) and
0.85 (SD = 0.95), respectively. Relative trap density inside core areas ranged from 0 (18
coyotes) to 100% with a mean relative trap density of 23.9% (SD = 39.9). Traps that
captured coyotes in core areas were open for fewer nights prior to capture (2.8 ± 2.8 d)
than traps that captured coyotes in peripheral areas (4.3 ± 4.2 d). The geometric mean of
the product of the percent of locations inside location areas and the relative trap
density inside the core areas was 20.2% (SD = 33.2).

We captured 6 coyotes in their respective core areas (24% of captures) and 19
coyotes in the peripheries of their home ranges (76%). Six of 7 (86%) coyotes that had
traps set in their core area were captured in their core area; the 7th coyote was captured 31 m from the core area boundary.

Of the 3 models we tested, the model based on relative trap density as a predictor of capture success was best. The additive model (i.e., traps + time spent in area) did not perform as well but was close to being within 2 ΔAIC from the best model (Table 3.1). The model based on time spent in the core area only was the worst fit (Table 3.1).

Table 3.1 - Results of three separate binomial models parameterized with different means based on three separate hypotheses: 1) Capture location is influenced by relative trap density (Trap), 2) Capture location is influenced by relative time spent in an area (Time), or 3) Capture location is influenced by both time spent and relative trap density in an area. Results are based on the capture locations of coyotes (n = 25) relative to time spent and trap density in their core area and territory periphery in South Texas from 2003-2005 and 2007-2008. The number of parameters (k) and Akaike weights (w) are provided.

<table>
<thead>
<tr>
<th>Model</th>
<th>AIC</th>
<th>ΔAIC</th>
<th>k_i</th>
<th>w_i</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trap</td>
<td>3.47</td>
<td>0</td>
<td>1</td>
<td>0.667</td>
</tr>
<tr>
<td>Trap + Time</td>
<td>5.56</td>
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<td>Time</td>
<td>7.28</td>
<td>3.81</td>
<td>1</td>
<td>0.069</td>
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</tbody>
</table>
Discussion

In our analysis, the two top models that accounted for 90% of AIC weights were the trap density only model and the model that incorporated both intensity of coyote space use and trap density. That intensity of coyote use was positively correlated with capture probability indicates that coyotes tend to be more vulnerable to capture in core areas, the opposite pattern observed in studies not controlling for trap density. It is also especially important to note that all but one coyote with traps in its core area was captured in its core area and the one coyote that was not captured in the core area was captured very close to the core area boundary.

Thus, we conclude that the more time a coyote spends in an area with traps in it, the more vulnerable the coyote is to capture due to the increased likelihood of encountering a trap. Our conclusion is further supported by the observed trend that latency to capture in the periphery was twice as long as latency to capture in core areas. Black bears (*Ursus americanus*) are similarly more vulnerable to capture with increasing time spent in an area; bears in the study area >50% of the time were captured more often than those spending <50% of time in the area (Noyce et al. 2001).

Regarding coyotes, our results were similar to those of Laundré and Keller (1983) who also controlled for trap density. Conversely, 66% of capture location bias studies (*n* = 12) that did not control for trap density found a bias towards capture in peripheral areas (Rucker 1975, Hibbler 1977, Woodruff and Keller 1982, Roy and Dorrance 1985, Windberg and Knowlton 1990, Travaini et al. 1993b, Bubela et al. 1998, Sacks et al. 1999a, Harris and Knowlton 2001, Gipson and Kamler 2003). The apparent bias in
previous studies is likely due to an artifact of not accounting for individual differences in trap density between core and peripheral areas rather than a coyote’s familiarity with a core area. Additionally, results of capture location bias studies for other carnivore species show that when trap density is controlled for, a capture bias is not present (Travaini et al. 1993a, Baker et al. 2001).

Many of the studies that did not control for trap density assumed that traps were evenly distributed across the study regions (e.g., Sacks et al. 1999a). Researchers, however, usually do not know a priori where territory or core area boundaries are in the landscape (Laundré and Keller 1983) and because core areas occupy a smaller area than the rest of the territory, by chance alone, researchers would tend to place more traps on the periphery than inside the core area. In our study system, peripheral areas were nearly 10x larger than core areas. Finally, researchers usually place traps along trails, roads, or other linear features in the environment (e.g., Harris and Knowlton 2001). These same features are often used by coyotes to form territory boundaries (Knowlton et al. 1999, Harris and Knowlton 2001).

Had we not controlled for trap density and only used the model based on time spent in core and peripheral areas to address the question of capture bias, we would have come to the same conclusion as the majority of other coyote capture bias studies (i.e., disproportionate capture on the periphery). Especially important is controlling for trap density by individual, rather than across the population. As our results show, when viewed across a population, trap densities did not differ between periphery and core areas. When viewed for individuals, however, only 7 of 25 coyotes had traps in the core area. Thus, only 28% of the population we studied had an opportunity to be captured in
the core areas. Previous observations of capture bias are understandable, but it is less parsimonious to attribute the mechanism to coyote neophobic behavior than to trap density.

Our results suggest that coyotes are not exhibiting an avoidance of novel objects relative to familiar environments as has been documented in previous studies and contradict previous conclusions. We observed greater vulnerability to capture in areas more intensively used by coyotes. Additionally, coyote traps are usually set with lures that do not evoke a neophobic response but rather elicit investigative behavior from coyotes, thus coyotes likely do not view traps as novel objects. As opposed to a novel object, there is no difference in the response of coyotes to novel or familiar odors when presented in familiar and unfamiliar environments (Windberg 1996). Sequin et al. (2003) used camera traps to “capture” coyotes and accounted for trap density by evenly distributing traps across territories. While their results suggested coyotes were disproportionately captured more on the periphery than in core areas, cameras might actually act as novel stimuli, unlike traditional traps. Also, unequal distribution of movement types across a territory (Laundré and Keller 1981) could lead to “capture” biases in camera-trap related studies if coyotes are more active along peripheries than core areas, and thus more apt to be photographed.

Considering intensity of space use to be equivalent to familiarity with an area is another potential problem with the conclusion that coyotes avoid traps in core areas due to their familiarity with the areas. Familiarity can be directly manipulated in captive studies but it would be difficult to manipulate a wild coyote’s familiarity within a portion of its territory. Just as intensity of use does not necessarily imply quality or importance
of habitat (Van Horne 1983, Garshelis 2000) infrequent use also does not indicate a lack of familiarity (Powell 2000). Additionally, coyote movement types are distributed unequally across territories (Laundré and Keller 1981). If an individual’s perception of the environment differs between behaviors (Olden et al. 2004) then the ability to become familiar with an area might also differ. When an animal’s attention is focused on accomplishing a task (e.g., foraging), its ability to perceive other stimuli is often diminished (Dukas and Kamil 2000). Thus, if one behavior requires a lot of attention, gaining general information about the environment might be diminished. Thus, more time spent foraging, or sleeping, in an area does not necessarily result in more familiarity with the local area.

The preponderance of evidence indicates that factors other than familiarity with an area (e.g., probability of encountering a trap) are more important predictors of capture probability. Our study shows the importance of accounting for trap density in studies of capture vulnerability and also shows the merits of simultaneously testing multiple models in an AIC framework (Burnham and Anderson 1998).

Management Implications

Coyotes from specific home ranges can be effectively targeted by placing traps within core areas of their territories. Because most livestock depredation occurs within the territory boundaries of problem packs (Sacks et al. 1999b, Blejwas et al. 2002), identifying habitats that are likely core areas, or using systematically placed traps may provide a more efficient means of increasing removal rates of problem individuals.
Literature Cited


bears to trap and camera sampling and resulting biases in mark-recapture estimates. Ursus 12:211-225.


CHAPTER 4

PREY-MEDIATED AVOIDANCE OF AN INTRAGUILD PREDATOR
BY ITS INTRAGUILD PREY

Abstract

Intraguild (IG) predation is an important factor influencing community structure, yet factors affecting the magnitude of IG interactions are not well understood. Prey availability is thought to influence IG predation as rates increase when prey abundance is low. Most hypotheses to explain this phenomenon are based on changes in the superior IG predator’s behavior, however, changes in the inferior IG predator’s behavior could also explain the pattern. We used bobcats (*Lynx rufus*, Kerr) and coyotes (*Canis latrans*, Say) as model IG predators to test the hypothesis that increased IG predation during periods of low prey availability is the result of the inferior IG predator leaving spatial refuges for greater access to prey. We obtained relocation data for bobcats and coyotes from fall 2007 to spring 2009 and estimated bobcat home ranges and core areas (day, night, and day+night) seasonally. At each bobcat location, we determined the intensity of coyote use, distance to water (an index of waterbird availability), small mammal biomass (obtained through spatial prediction), and mean small mammal biomass of the home range. We built generalized linear mixed models and used Akaike Information Criteria to determine what factors best predicted point location (i.e., inside or outside bobcat core areas). Intensity of coyote use was a primary determinant of whether a bobcat location

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3 Coauthored by Ryan R. Wilson, Terry L. Blankenship, Mevin B. Hooten, and John A. Shivik.
occurred inside the core area location for day, night, and day-night combined. In bobcat home ranges with high prey biomass, core areas occurred in areas with low coyote use, but bobcats shifted core areas to areas more intensely used by coyotes when prey biomass declined. When bobcats resided in a home range with low prey abundance, bobcats exhibited greater evidence of daytime foraging, both relying on diurnally available waterbirds, and increasing use of areas with abundant small mammal prey, even though risk of coyote predation was greater. Our results support the hypothesis that inferior IG predators (e.g. bobcats) alter their space use patterns during periods of low prey abundance, which possibly increases their vulnerability to IG predation (e.g. by coyotes), but are able to spatially avoid superior IG predators when prey are locally abundant. Small-scale spatial variability in prey abundance likely leads to stability of IG predator communities by allowing some individuals of the inferior IG predator species to follow a safety-matching space use strategy.

Introduction

Intraguild predation is increasingly recognized as an important and frequent factor influencing community structure (Crooks & Soulé 1999). Even in the absence of direct predation, indirect effects of superior IG predators on inferior IG predators can have significant population (Creel & Christianson 2008) and community-level effects (Sergio et al. 2007). Recent studies have suggested that the magnitude of IG relationships likely varies spatially and temporally (Sergio, Marchesi & Pedrini 2003; Prange & Gehrt 2007), and that IG relationships are not consistent across all IG predator pairings (Gehrt & Prange 2006; Donadio & Buskirk 2006). Thus, it is important to understand what factors
influence the magnitude of IG interactions to understand when it will have the strongest effect on shaping community structure (Palomares & Caro 1999; Donadio & Buskirk 2006).

One factor proposed as a determinant of the magnitude of interactions between IG competitors is prey availability, although it has rarely been tested (Sergio et al. 2003). Incidents of IG predation appear to increase when prey availability is low (Polis, Myers & Holt 1989; Palomares & Caro 1999; Sergio et al. 2003). Two hypotheses have been proposed to explain why IG predation increases with decreasing prey abundance. The first is that superior IG predators increase predation of inferior IG predators because of the increased competition for resources (Polis et al. 1989). This hypothesis has some support because the inferior IG predator is rarely consumed by the superior IG predator (Palomares & Caro 1999). However, even in situations where IG predators have pronounced resource partitioning, IG predation still increases with decreasing prey abundance (Sergio et al. 2003). The second hypothesis is that when prey populations decline, the superior IG predator exhibits prey switching towards the inferior IG predator (Polis et al. 1989). This hypothesis also has some support from a few reports of inferior IG predators being consumed when prey abundance is low (reviewed in Palomares & Caro 1999).

There are a growing number of studies showing the importance of spatial refugia for the coexistence of IG predator species (Durrant 1998; Sergio et al. 2003; Sergio et al. 2007). Given that these refuges allow inferior IG predators to remain relatively safe from IG predation, some other mechanism than increased competition or being viewed as food must be acting during periods of low prey abundance. Another hypothesis extends from
existing studies in traditional predator-prey systems and trade-offs faced by prey between safety and access to sufficient forage. When prey must venture out of refuges, they generally do so under conditions where risk of predation is lowest (Lima & Dill 1990). The dynamics of this relationship change, however, when forage availability decreases, leading prey to take greater risks to access forage (e.g. Pettersson & Brömark 1993; Whitham & Mathis 2004). If inferior IG predators behave similarly to “traditional” prey when food resources decline, they should be expected to leave spatial refugia to increase access to prey, thereby potentially suffering greater risk of IG predation. At least two studies have shown inferior IG predators increase their risk of IG predation to meet metabolic demands by using areas with greater presence of superior IG predators (Sergio et al. 2003; Webb, Pringle & Shine 2009). Thus, a third hypothesis for the relationship between IG predation rates and prey abundance is that IG predation rates increase because inferior IG predators leave refuges where they are relatively safe during periods of low prey abundance for greater access to prey, thereby increasing their risk of encountering dominant IG predators.

Very little is known about the effects of superior IG predators on inferior IG predator behavior especially for mammalian carnivores (Thompson & Gese 2007). Additionally, little research has addressed how environmental heterogeneity might influence the magnitude of IG predator interactions (Thompson & Gese 2007). Bobcats (Lynx rufus) and coyotes (Canis latrans) are well-suited to study the interactions between mammalian IG predators. Bobcats and coyotes are sympatric over much of their ranges (Larivière & Walton 1997) and exhibit a clear IG predator-prey relationship, with numerous accounts of bobcats being killed by coyotes (Knick1990; Fedriani et al. 2000;
Gipson & Kamler 2002; T. L. Blankenship unpublished data), and bobcats avoiding coyotes at the core area scale (Neale & Sacks 2001; Thornton, Sunquist & Martin 2004). In addition to bobcat space use patterns being influenced by coyotes, they are also strongly influenced by prey abundance, ranging much more widely during periods of low prey abundance (Knick 1990; Blankenship 2000). Finally, they represent an IG relationship that is not canid-canid in nature, allowing greater inference to differences in the magnitude of IG relationships across different pairings (Gehrt & Prange 2006).

The objective of this study is to determine how coyote space use intensity and local prey abundance interact to influence bobcat space use patterns and how this might lead to greater IG predation during periods of low prey abundance. We predict that during periods of low prey abundance, bobcats will increase their use of areas intensively used by coyotes to access more abundant prey but will avoid these areas when prey abundance is high.

Methods

Study area

Our study was conducted on the Welder Wildlife Foundation Refuge (~3,150 ha) approximately 10 km north of Sinton, Texas. The study area was located in a transition zone between the gulf prairies and marshes and south Texas plains, and vegetation consisted mainly of mixed grasslands and shrubs (Young et al. 2006).

Coyote territories form a continuous patchwork across the refuge, with approximately 7-8 territories always present and exhibiting high spatial stability through time (Young et al. 2006). Pack sizes range between 3-7 adults (Andelt 1985). Bobcats
are less abundant on the refuge (ca. 15; Heilbrun et al. 2006), but show extensive home
range overlap with coyote territories. The dietary overlap of coyotes and bobcats is low
except for the common use of small mammals. Coyotes tend to have more varied diets,
with fruit making up a considerable portion of the diet at many times during the year
(Young et al. 2006). Additionally, larger mammals (e.g., whitetail deer [Odocoileus
virginianus, Douglas] and feral pigs [Sus scrofa, Linnaeus]) are more common in coyote
diets (Young et al. 2006) than in bobcat diets (Blankenship 2000). Preferred prey of
bobcats on the refuge are cotton rats (Sigmodon hispidus, Say and Ord), wood rats
(Neotoma micropus, Baird) and to a lesser extent eastern cottontails (Sylvilagus
floridanus, Allen; Blankenship 2000). However, bobcats switch to a greater proportion
of birds (both passerine and waterfowl) during periods of low small mammal abundance
(Blankenship 2000).

Bobcat and coyote monitoring

We captured bobcats with modified Tomahawk live traps (Tomahawk Live Trap
Co., Tomahawk, WI, USA; 107 x 38 x 51 cm). An extension (51 x 38 x 51 cm) was
added to the trap to house and protect live chickens used as bait (Blankenship 2000). We
immobilized captured bobcats with an intramuscular injection of ketamine (i.e. 10-15
mg/kg body mass) and acepromazine (i.e. 0.05 mg/kg body mass). We captured coyotes
with padded leg hold traps (Victor #3 Softcatch, Lititz, PA, USA), neck snares, or
collarums (Wildlife Control Supplies, East Granby, CT, USA). We did not chemically
immobilize captured coyotes. We fitted bobcats and coyotes with very high frequency
collars (Advanced Telemetry Systems, Isanti, MN, USA, for bobcats; Lotek, Newmarket,
Ontario, Canada, for coyotes). Between April 2007 and November 2008, we captured 7 bobcats (5M, 2F) and 13 coyotes (8M, 5F) with each having a portion of its home range overlapping with the opposite species’ home range. The 13 coyotes captured, resided in 7 distinct territories on the refuge.

We obtained relocations on each bobcat and coyote 4-5 days per week. We used triangulation and the maximum likelihood estimator in program Locate II (Nams 2006) to estimate animal locations. We used ≥ 3 bearings collected within 20 minutes, between 20-160º of each other, to estimate locations. Mean distance between estimated and true locations was 260m (SD = 215). We randomly chose start times and animals for telemetry sessions to ensure the data were not autocorrelated (Fieberg 2007). We collected both diurnal and nocturnal locations for bobcats and coyotes.

Home range analysis

We estimated home ranges of bobcats for individuals with ≥ 30 locations to ensure that we obtained a sufficient number of relocations to estimate home ranges (Seaman et al. 1999). We used the fixed kernel method (Worton 1989) with the ad hoc bandwidth selection procedure (see Berger & Gese 2007). We defined the home range as the area encompassed by the 95% isopleth. To estimate bobcat core areas, we analyzed home ranges for clusters of locations and used Bayesian methods to identify which isopleth partitioned the home range into homogeneous point patterns (Wilson et al. in press). This method is highly precise for characterizing points as occurring inside or outside the core area. We estimated bobcat home ranges and core areas for all relocation data (day and night combined; hereafter full core area), relocation data obtained during
the day (0700 – 1900h; hereafter daytime core area), and relocation data obtained at night (1900 – 0700h; hereafter nighttime core area).

Small mammal trapping

We established 15-45 trapping grids every 6 months from autumn 2007 to spring 2009. We distributed trapping grids among all of the major vegetative communities on the study area (Blankenship 2000). Each trapping grid consisted of 25 Sherman live traps (H. B. Sherman Traps, Inc., Tallahassee, FL, USA) baited with grain (corn-milo mixture), in a 5 x 5 design, with traps spaced 10m apart. We opened traps in each grid for 3 nights and captured small mammals were individually-marked by trimming guard hairs in a unique design. For each grid, we determined the total biomass of all small mammals captured based on average weights found on the study site (Otteni, Bolen & Cottam 1972). This is similar to the approach taken by Randa et al. (2009).

Data analysis

We created kernel intensity maps (Schabenberger & Gotway 2005) of coyote space use based on those territories which had >30 points for a respective season. If multiple coyotes resided in the same territory, we combined their relocations. We created a 100m x 100m grid across the study area, and for each coyote territory, estimated the kernel density (with ad hoc bandwidth) value at each grid cell using the function ‘kde2d’ in the MASS library (Venable & Ripley 2002) in the R Statistical Computing Environment (R Core Development Team 2008). We then extracted the grid cells that fell within the 95% isopleth of each coyote territory. We scaled each territory’s grid cell values to their respective mean value, to control for interterritorial differences in the
number of relocations used for kernel density estimates. If grid cells contained multiple intensity estimates (i.e. the grid cell was contained within multiple territories), we only used the greatest intensity value. We created coyote intensity grids based on day, night, and day and night combined coyote relocations for each season.

We used a statistical approach to spatially predict small mammal biomass across the study area each season and at each observed bobcat location. Our trapping data were zero-inflated (i.e. many grids with no captures), thus, we were unable to use standard optimal spatial prediction methods (e.g., kriging). Instead, we used a hurdle model (e.g., Ver Hoef & Jansen 2007) for the correlated zero process (i.e., locations with no captures) and then a correlated log-Gaussian model at locations with captures. This is essentially a mixture model similar to a zero-inflated model, except that a value of zero can only come from one component of the mixture, rather than two. We used an exponential covariance structure on both the zero and positive processes.

After obtaining spatial prediction maps of small mammal biomass, there appeared to be certain regions of the study area which had higher overall prey biomass than others (Fig. 4.1). Given that the availability of prey can influence the level of risk an animal takes while foraging (e.g. Cooper 2000) we determined the mean small mammal biomass in each bobcat’s home range, each season, as an index of home range quality. Whereas the predicted values of small mammal biomass at each bobcat relocation provide information about the spatial distribution of resources within home range, the mean home range biomass (i.e. home range quality) provides a measure of relative prey availability for each bobcat at a study site scale.
Figure 4.1 - Predictive map of small mammal biomass across the study area in spring 2008. Predicted small mammal biomass ranged from 12 (white) to 2000g (black). The black outline represents the Welder Wildlife Refuge boundary.
For each bobcat relocation, we determined small mammal biomass, intensity of coyote use, and the mean small mammal biomass of the home range where the point occurred. We also determined the distance to water because of the importance of water birds in bobcat diets on the study area during periods of low small mammal abundance (Blankenship 2000). We used the estimated home range and core areas for each bobcat during each season to determine whether a relocation occurred inside or outside the core area (coded as 1 or 0, respectively). We used the distance to water, coyote space use intensity, and small mammal biomass as variables and all 2-way interactions with mean home range small mammal biomass for model selection. We also had repeated measures on individuals, thus, we used a logistic generalized linear mixed model (function ‘lmer’ in R package ‘lme4’ [Bates 2007]) with bobcat as a random factor to determine which explanatory variables best explained whether a relocation was from inside or outside its core area (Zuur et al. 2009). We standardized all variables prior to analysis (Zuur et al. 2009). We used Akaike Information Criteria (AIC; Burnham & Anderson 1998) to determine the most parsimonious model that best fit the observed data. We used the same procedure to determine the best fitting models for day relocations, night relocations, and day and night relocations combined.

Results

We obtained 1201 bobcat locations that overlapped with ≥ 1 coyote territory for bobcat home ranges estimated with day and night locations over all seasons and individuals. Of those locations, 680 were classified as occurring inside core areas, and 521 outside. For daytime bobcat home ranges, we obtained 348 (227 inside, and 121
outside core areas) bobcat locations that overlapped with coyote daytime territory estimates. For nighttime bobcat home ranges, 334 (197 inside, and 137 outside core areas) bobcat locations overlapped with coyote nighttime territory estimates. For day and night combined, individual bobcats had 66.7±5.9 (mean±S.E.) locations that occurred within estimated coyote territories each season (37.8±3.7, and 28.9±4.0 from inside and outside of core areas, respectively). For daytime bobcat home ranges, individual bobcats had 31.6±4.4 locations used for analysis each season (20.6±3.8, and 11.0±2.2, from inside and outside of core areas, respectively). Finally, for nighttime bobcat home ranges, individual bobcats had 27.8±4.1 locations used for analysis each season (16.4±3.0, and 11.4±2.1, from inside and outside of core areas, respectively). Mean small mammal biomass in bobcat home ranges varied from 6.5g to 1199g.

The top-ranked model for the full bobcat core area included intensity of coyote use and distance to water, each interacting with home range quality (Table 4.1). This model accounted for 53.5% of the Akaike weights (Table 4.1). The only other competing model (i.e. ΔAIC<2) included the small mammal biomass term, but the slope was not different from 0 (P = 0.60) and only accounted for 18.4% of the Akaike weights (Table 4.1). Coefficient estimates for the top-ranked model (Table 4.2) indicated that as prey abundance increased in home ranges, core areas increasingly occurred further from water and with lower coyote use (Table 4.2, Fig. 4.2).
Table 4.1 - Results of Akaike Information Criteria (AIC) analysis for top 10 logistic generalized linear mixed models with individual as a random effect explaining the location of core areas within bobcat home ranges based on day and night relocations combined. Variables for models included small mammal biomass (SmMam), coyote space use intensity (Coy), distance to water (D2W), home range quality (HRQ) and all 2-way interactions with HRQ (denoted by \( \times \)). Akaike Information Criteria values, differences from the model with the lowest AIC value (\( \Delta \text{AIC} \)), number of parameters (\( k \)), and Akaike weights (\( w_i \)) are listed for each model.
<table>
<thead>
<tr>
<th>Model</th>
<th>AIC</th>
<th>∆AIC</th>
<th>k</th>
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Table 4.2 - Regression coefficients of best fitting logistic generalized linear mixed models with individual as a random effect and assessed by AIC. Models are for bobcat home range and core area estimates based on day (Day), night (Night), and day and night relocations combined (Day + night). Variables for models included small mammal biomass (SmMam), coyote space use intensity (Coy), distance to water (D2W), home range quality (HRQ) and 2-way interactions with HRQ (denoted by ×).
<table>
<thead>
<tr>
<th>Data</th>
<th>Variables</th>
<th>Coefficient</th>
<th>SE</th>
<th>P-value</th>
</tr>
</thead>
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<td>Intercept</td>
<td>0.205</td>
<td>0.105</td>
<td>0.051</td>
</tr>
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<td></td>
<td>HRQ</td>
<td>-0.119</td>
<td>0.103</td>
<td>0.249</td>
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<td></td>
<td>Coy</td>
<td>0.060</td>
<td>0.062</td>
<td>0.336</td>
</tr>
<tr>
<td></td>
<td>Coy × HRQ</td>
<td>-0.165</td>
<td>0.063</td>
<td>0.009</td>
</tr>
<tr>
<td></td>
<td>D2W</td>
<td>0.070</td>
<td>0.065</td>
<td>0.278</td>
</tr>
<tr>
<td></td>
<td>D2W × HRQ</td>
<td>0.347</td>
<td>0.072</td>
<td>&lt;0.001</td>
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<td>Day</td>
<td>Intercept</td>
<td>0.655</td>
<td>0.371</td>
<td>0.078</td>
</tr>
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<td></td>
<td>HRQ</td>
<td>0.004</td>
<td>0.379</td>
<td>0.992</td>
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<tr>
<td></td>
<td>SmMam</td>
<td>-0.589</td>
<td>0.290</td>
<td>0.042</td>
</tr>
<tr>
<td></td>
<td>D2W</td>
<td>-0.420</td>
<td>0.164</td>
<td>0.010</td>
</tr>
<tr>
<td></td>
<td>D2W × HRQ</td>
<td>0.360</td>
<td>0.155</td>
<td>0.020</td>
</tr>
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<td></td>
<td>Coy</td>
<td>-0.007</td>
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<td>0.968</td>
</tr>
<tr>
<td></td>
<td>Coy × HRQ</td>
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<td>0.196</td>
<td>0.011</td>
</tr>
<tr>
<td>Night</td>
<td>Intercept</td>
<td>0.344</td>
<td>0.242</td>
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<td></td>
<td>HRQ</td>
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<td>0.222</td>
<td>0.298</td>
</tr>
<tr>
<td></td>
<td>Coy</td>
<td>0.380</td>
<td>0.130</td>
<td>0.003</td>
</tr>
<tr>
<td></td>
<td>Coy × HRQ</td>
<td>-0.288</td>
<td>0.106</td>
<td>0.006</td>
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</tbody>
</table>
Figure 4.2 - Estimated logistic functions for the best fitting model for the full bobcat core area (i.e. day and night combined) with changes in standardized values of coyote space use intensity and mean home range prey biomass. Other variables were held constant (e.g. distance to water, and its interaction with mean home range biomass).
The top-ranked model for daytime core areas included the small mammal, coyote, and distance to water covariates, with home range quality interacting with coyote use and distance to water (Table 4.3). Coefficient estimates for this model indicated bobcat core areas were negatively associated with small mammal biomass at the home range scale, and occurred further from water and areas intensely used by coyotes with increasing home range quality (Table 4.2). There were 2 competing models, one which included the interaction between small mammal biomass and home range quality, and the other which excluded any small mammal biomass variables (Table 4.3). Coefficients for the model with the interaction between small mammal biomass and home range quality indicated that as home range quality increased, the probability of the daytime core area occurring in high prey areas decreased.

The top-ranked model for nighttime core areas only included the interaction between coyote intensity and home range quality (Table 4.4). Coefficient estimates indicated that as home range quality increased, core areas had an increased probability of occurring in areas with low coyote use (Table 4.2). There were two additional competing models, which each contained the interaction between coyote and home range quality (Table 4.4). The second-ranked model contained the small mammal biomass covariate, indicating core areas occurred in areas of the home range with greater small mammal biomass. The third-ranked model contained the distance to water variable (Table 4.4) indicating core areas occurred in further from water than areas outside the core area.
Table 4.3 - Results of Akaike Information Criteria (AIC) analysis for 10 logistic generalized linear mixed models with individual as a random effect explaining the location of bobcat core areas within home ranges based on daytime relocations (i.e., 700-1900h).

Variables for models included small mammal biomass (SmMam), coyote space use intensity (Coy), distance to water (D2W), home range quality (HRQ) and all 2-way interactions with HRQ (denoted by ×). Akaike Information Criteria values, differences from the model with the lowest AIC value (ΔAIC), number of parameters (k), and Akaike weights (w_i) are listed for each model.
<table>
<thead>
<tr>
<th>Model</th>
<th>AIC</th>
<th>ΔAIC</th>
<th>k</th>
<th>( w_i )</th>
</tr>
</thead>
<tbody>
<tr>
<td>SmMam, Coy, D2W, HRQ, Coy × HRQ, D2W × HRQ</td>
<td>408.4</td>
<td>0</td>
<td>8</td>
<td>0.359</td>
</tr>
<tr>
<td>SmMam, Coy, D2W, HRQ, SmMam × HRQ, Coy × HRQ, D2W × HRQ</td>
<td>409.7</td>
<td>1.3</td>
<td>9</td>
<td>0.188</td>
</tr>
<tr>
<td>Coy, D2W, HRQ, Coy × HRQ, D2W × HRQ</td>
<td>410.4</td>
<td>2</td>
<td>7</td>
<td>0.0132</td>
</tr>
<tr>
<td>Coy, D2W, HRQ, Coy × HRQ</td>
<td>410.8</td>
<td>2.4</td>
<td>6</td>
<td>0.108</td>
</tr>
<tr>
<td>SmMam, D2W, Coy, HRQ, Coy × HRQ</td>
<td>411.6</td>
<td>3.2</td>
<td>7</td>
<td>0.073</td>
</tr>
<tr>
<td>SmMam, Coy, D2W, HRQ, SmMam × HRQ, Coy × HRQ</td>
<td>413.6</td>
<td>5.2</td>
<td>8</td>
<td>0.027</td>
</tr>
<tr>
<td>SmMam, D2W, HRQ, D2W × HRQ</td>
<td>413.7</td>
<td>5.3</td>
<td>6</td>
<td>0.025</td>
</tr>
<tr>
<td>SmMam, Coy, HRQ, Coy × HRQ</td>
<td>414.4</td>
<td>6</td>
<td>6</td>
<td>0.018</td>
</tr>
<tr>
<td>SmMam, D2W, HRQ, SmMam × HRQ, D2W × HRQ</td>
<td>414.7</td>
<td>6.3</td>
<td>7</td>
<td>0.015</td>
</tr>
<tr>
<td>Coy, HRQ, Coy × HRQ</td>
<td>415.3</td>
<td>6.9</td>
<td>5</td>
<td>0.011</td>
</tr>
</tbody>
</table>
Table 4.4 - Results of Akaike Information Criteria (AIC) analysis for top 10 logistic generalized linear mixed models with individual as a random effect explaining the location of bobcat core areas within home ranges based on nighttime relocations (i.e., 1900-700h). Variables for models included small mammal biomass (SmMam), coyote space use intensity (Coy), distance to water (D2W), home range quality (HRQ) and all 2-way interactions with HRQ (denoted by \( \times \)). Akaike Information Criteria values, differences from the model with the lowest AIC value (\( \Delta \text{AIC} \)), number of parameters \( (k) \), and Akaike weights \( (w_i) \) are listed for each model.
<table>
<thead>
<tr>
<th>Model</th>
<th>AIC</th>
<th>ΔAIC</th>
<th>k</th>
<th>wi</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coy, HRQ, Coy × HRQ</td>
<td>437.1</td>
<td>0.0</td>
<td>5</td>
<td>0.381</td>
</tr>
<tr>
<td>SmMam, Coy, HRQ, Coy × HRQ</td>
<td>439.1</td>
<td>2.0</td>
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<td>0.140</td>
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<tr>
<td>D2W, Coy, HRQ, Coy × HRQ</td>
<td>439.1</td>
<td>2.0</td>
<td>6</td>
<td>0.140</td>
</tr>
<tr>
<td>Coy, D2W, HRQ, Coy × HRQ, D2W × HRQ</td>
<td>440.8</td>
<td>3.7</td>
<td>7</td>
<td>0.060</td>
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<tr>
<td>SmMam, Coy, HRQ, SmMam × HRQ, Coy × HRQ</td>
<td>441.0</td>
<td>3.9</td>
<td>7</td>
<td>0.054</td>
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<tr>
<td>SmMam, D2W, Coy, HRQ, Coy × HRQ</td>
<td>441.1</td>
<td>4.0</td>
<td>7</td>
<td>0.052</td>
</tr>
<tr>
<td>Coy</td>
<td>441.7</td>
<td>4.6</td>
<td>3</td>
<td>0.038</td>
</tr>
<tr>
<td>SmMam, Coy</td>
<td>442.1</td>
<td>5.0</td>
<td>4</td>
<td>0.031</td>
</tr>
<tr>
<td>SmMam, Coy, D2W, HRQ, Coy × HRQ, D2W × HRQ</td>
<td>442.8</td>
<td>5.7</td>
<td>8</td>
<td>0.022</td>
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<tr>
<td>SmMam, Coy, D2W, HRQ, SmMam × HRQ, Coy × HRQ</td>
<td>443.0</td>
<td>5.9</td>
<td>8</td>
<td>0.020</td>
</tr>
</tbody>
</table>
Discussion

A key issue lacking in our understanding of IG predation is what factors affect the dynamics of IG predator interactions (Polis et al. 1989; Palomares & Caro 1999; Donadio & Buskirk 2006; Gehrt & Prange 2006; Thompson & Gese 2007). Our results suggest that the dynamics of sympatric IG predator species are influenced by the relative abundance of prey. Unlike other studies that have suggested that these changes are mediated by a need for the superior IG predator to kill interspecific competitors to reduce competition, or eat (Polis et al. 1989; Palomares & Caro 1999), our results indicate an additional mechanism may mediate the interaction between IG predation and prey abundance. Namely, changes in prey abundance lead inferior IG predators to tradeoff avoidance of superior IG predators for access to sufficient prey. Thus, as prey abundance decreased, bobcats exposed themselves to a higher probability of encountering coyotes.

For all three bobcat core area types (i.e. full, day, and night), the top-ranked models contained the interaction between intensity of coyote use and bobcat home range quality, indicating increased avoidance of coyotes when prey was sufficiently high. The importance of this interaction is further supported by the fact that models with the interaction accounted for 80-92% of the total AIC weights. Bobcats and coyotes on the study site exhibit extensive spatial overlap of home ranges and territories (Blankenship 2000; Young et al. 2006), yet, bobcats still managed to use areas of low coyote use as refugia when prey was abundant. This is especially important because the likelihood of encountering superior IG predators is probably a main factor leading to predation of the inferior IG predator (Moehrenschlager, List & Macdonald 2007).
Previous studies have shown spatial avoidance of coyotes by bobcats even when ranges overlap extensively (Neale & Sacks 2001; Thornton et al. 2004) and spatial avoidance of superior IG predators by inferior IG predators is increasingly documented (Durrant 1998; Crooks & Soulé 1999; Sergio et al. 2003; Thompson & Gese 2007; Berger & Gese 2007). We also found that the relationship between bobcats and coyotes varied between home ranges relative to local (i.e. home range scale) prey abundance, even though the study site was relatively small. This is not surprising given the significant spatial variation in prey abundance across the study area (Fig. 4.1). The different spatial responses of bobcats from home ranges of varying quality to the presence of coyotes might explain why some studies have not found spatial avoidance of bobcats towards coyotes (Litvaitis & Harrison 1989).

Bobcats in high quality home ranges are likely not food stressed and have access to sufficient prey allowing them to restrict space use to areas with lower risk of coyotes. Webb et al. (2009) found a similar relationship with IG predator interactions in snakes. They found that juvenile snakes of the inferior IG predator species took greater risks of IG predation to use areas with favorable microclimates, whereas adults did not take those risks because of their greater thermal tolerance.

Bobcats are generally considered to be nocturnal (Neale & Sacks 2001), but our results suggest that when small mammal abundance decreases, bobcats increase their daytime activity to gain access to waterbirds when they are most active (Brisbin & Mowbray 2002). This is further supported by the fact that the top-ranked nighttime core area models did not include distance to water as a covariate, or if it did, showed that core areas were located further from water. Our top daytime core area models also suggest
that bobcats increased daytime foraging for small mammals when they were low in abundance. This was indicated by a higher probability of core areas occurring where small mammal abundance was higher in the home range during periods of low prey abundance than during periods of high prey abundance. By having to forage during the day, bobcats likely increase their exposure to IG predation, especially because daytime core areas shift to areas with greater coyote use when prey abundance is low.

Most hunting for small mammals by bobcats occurs at night, which is supported by the second-ranked model, showing core areas had a higher probability of occurring in areas with high small mammal abundance. But, like the full and daytime core area models, the overwhelming driver of nighttime core area location was the avoidance of coyotes when they could afford energetically to do so. When prey was abundant, bobcats could afford to greater restrict their foraging to areas with low coyote use. Conversely, when prey abundance was low, bobcats had to venture into the riskier areas to obtain sufficient prey to meet energetic demands.

The strength of coyote avoidance by bobcats is impressive given the limited competition between the two on the study site (Andelt 1985; Blankenship 2000, Young et al. 2006). Sergio et al. (2003) found similar results in the IG interactions between black kites (Milvus migrans, Boddaert; intraguild prey) and eagle owls (Bubo bubo, Linnaeus; intraguild predator). Black kites showed significant spatial avoidance of eagle owls even though the two species had low dietary niche overlap. The relationship we found between bobcats and coyotes is striking given the relative rarity of coyote predation on bobcats. However, even if IG predation occurs infrequently, it still might be acting through indirect effects such as spatial avoidance (Lima & Dill 1990; Palomares & Caro...
Others have also shown that inferior IG predators can exhibit a behavioral response towards superior IG predators, even though predation is rarely observed (Sergio et al. 2007; Zuberogoitia et al. 2008) and indirect predator effects can have an equal or greater effect on prey population dynamics (Creel & Christianson 2008). Bobcats on the study site react negatively to the perceived presence of coyotes. When presented with a coyote call playback at a relatively short distance (~ 20 m), bobcats immediately ran for the closest dense vegetative cover (R. Wilson, personal observation). In >15 years of bobcat research at the study site, only one bobcat has been found with evidence that it was killed by a coyote; interestingly, the bobcat was killed during a period of low prey abundance (T. L. Blankenship, unpublished data).

Our results also support the idea that stability of IG predation in our system is most likely influenced by bobcats “safety matching” (selecting habitat based on reduced risk of predation rather than resource availability; Heithaus 2001) rather than outcompeting coyotes for shared resources; although bobcat safety matching is context dependant. As we have shown, bobcats tend to safety match when prey populations are high inside an individual’s home range, but forego safety matching when prey levels are low. If prey abundance was constant across the entire population this could lead to an unstable system wherein during periods of low prey abundance, all bobcats would be forced to leave spatial refugia, increasing the probability of negative interactions with coyotes. An interesting result of our analysis, however, is that even within a population, prey abundance varies spatially, allowing some individuals to continue safety matching while others are required to use riskier areas to access sufficient prey. Coexistence mechanisms between IG predator species have been suggested to differ when
productivity is high and when it is low (Amarasekare 2008). Yet, our results show that coexistence might actually be mediated by spatial variation in productivity within a population. Thus, during any given time period, some portion of the population remains relatively safe from coyotes.

Finally, our results provide some insight into the underlying behaviors that lead to the development of bobcat core areas. Few studies have tested hypotheses about how animals use core areas (e.g., Barg et al. 2006), and most assume they represent foraging areas (Powell, Zimmerman & Seaman 1997; Plowman et al. 2006). Our results indicate, however, that bobcat core area behavior is not just a function of prey abundance, but a balance between prey abundance and coyote avoidance. Future studies should seek to understand underlying behavioral mechanisms that lead to the development of core areas and also consider how those behavioral mechanisms differ temporally.

In conclusion, we found evidence that dynamics between IG predator species are not consistent in space or time. Increases in the occurrence of IG predation during periods of low prey abundance are likely a result of inferior IG predators switching from a safety matching strategy to more risk-prone foraging behavior. Future research should focus on how local-scale heterogeneity might influence IG predation dynamics within a given community.

Literature Cited


Abstract

While many studies have proposed factors such as resource abundance and territorial defense as causal factors for large interpopulation variation in coyote (*Canis latrans*) territory size, proximal behavioral mechanisms, such as coyote movement patterns within different sized territories, have not been examined. We used global positioning system collars to collect fine-scale (15 min) movement data of coyotes in southeastern Texas and south-central Idaho. We compared the rate of territory and territory boundary visitation, daily speed, distance moved, displacement distance, and mean turn angle for coyotes at each study site. Both populations were active for similar lengths of each day (Idaho 61.8 ± 6.2%, Texas 65.9 ± 8.3%), but coyotes in Idaho had territories 10x larger (41.8 km² ± 16.0 vs. 4.0 km² ± 1.0), moved faster (1 km/h ± 0.2 vs. 0.4 km/h ± 0.2) and traveled further daily (23.6 km ± 5.7 vs. 10.2 km ± 2.0), and exhibited less tortuous movement paths than coyotes in Texas (340.7° ± 54.0 vs. 176.4° ± 53.6). Even with increased movement rates, coyotes in Idaho did not visit all areas of their territories as effectively as coyotes in Texas. Thus, we propose that in regions with high resource abundance, coyote territory size is determined by what coyotes can physically defend from intruding conspecifics, whereas in areas with low resource

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4 Coauthored by Ryan R. Wilson and John A. Shivik.
abundance, territories are larger than can be efficiently defended, because territorial defense is less important due to lower interference from conspecifics.

Introduction

Coyotes (*Canis latrans*) are a widespread predator in North America, with a distribution ranging from Costa Rica to northern Alaska (Bekoff and Gese 2003). Coyote behavior is highly adaptable, which allows them to occupy diverse environments, both urban and wild (Gehrt et al. 2009). There is also substantial variation in coyote territory size, which ranges from 4.5 km$^2$ in southeast Texas (Andelt 1985) to 92.4 km$^2$ in central Washington (Springer 1982). Variation in territory sizes is not random, but rather, shows a general trend for larger territories at higher latitudes (Gompper and Gittleman 1989; Nilsen et al. 2005).

Variation in coyote territory size is generally attributed to the abundance and dispersion of resources (Hidalgo-Mihart et al. 2004; Mills and Knowlton 1991) with latitudinal variation explained by lower productivity at higher latitudes (Gompper and Gittleman 1991). However, because areas of high prey abundance also attract more competitors, the alternative hypothesis that coyotes are constrained from maintaining larger territories due to the greater costs of territorial defense might also explain the observed pattern of territory sizes in coyotes (Myers et al. 1979).

Some studies have found variation in territory size to be better explained by competitor density than prey density (Eberhard and Ewald 1994; Klatt and Paszkowski 2005; Myers et al. 1979; Tricas 1989). Observational studies have shown increases in territory size when conspecific density decreases (Myers et al. 1979) and experimental
increases in intruder pressure have led to smaller territories (Norton et al. 1982). Even
in territories not based on defense of food resources, territory size has been shown to be
negatively associated with rate of conspecific intrusion (Ewald et al. 1980).

Also, recent research on coyotes in Texas suggests that not all of the variation in
territory sizes can be explained by prey abundance and dispersion; Young et al. (2008)
provisioned coyotes with superabundant and spatially clustered food resources, but
coyote territory sizes remained unchanged. Because territory size did not change with the
experimental alteration of food resources, factors other than prey likely influence the
maximum constraint on coyote territory size. The competing hypothesis of conspecific
interference-based regulation of coyote territory size has received little attention and
requires further testing.

If the need for effective territorial defense is a factor regulating territory size,
coyotes with larger territories must increase movement rates in order to effectively patrol
their territories and territorial boundaries. Therefore, the objective of this study is to
determine if movement patterns differ between two coyote populations with significant
differences in territory sizes. We determine if 1) coyotes with large territories increase
their relative travel rates in order to more effectively patrol their territories such that 2)
coyotes with larger territories visit a proportionally equivalent amount of territory in the
same time period as coyotes with smaller territories.

Methods

Study site.—This study occurred at two study sites, one in southeast Texas, and
one in south-central Idaho. The Texas study site was located approximately 50 km north
of Corpus Christi, Texas on the Welder Wildlife Foundation Refuge (~3,150 ha). The Welder Refuge is located in a transition zone between the gulf prairies and marshes and south Texas plains, with vegetation consisting mainly of mixed grasslands and shrubs (Young et al. 2008). The Idaho study site (~50,000 ha) was located approximately 50 km northwest of Idaho Falls, Idaho, on the Idaho National Engineering Laboratory. The Idaho National Engineering Laboratory is located in the northern cold desert biome with the dominant vegetation consisting of a sagebrush (*Artemisia* spp.)-wheatgrass (*Agropyron* spp.) shrub-steppe (Anderson and Holte 1981; Harniss and West 1973).

Coyotes in Texas and in the northern Great Basin near the Idaho study site exhibit similar pack sizes (i.e., 2-6, Andelt 1985; Bromley and Gese 2001). Diets of coyotes at the Texas site are quite varied, exhibit significant seasonal fluctuation, and are composed of large portions of fruit during spring and summer, but mostly small to medium-sized mammals such as white-tailed deer (*Odocoileus virginianus*) fawns and cottontail rabbits during the remainder of the year (*Sylvilagus floridanus*; Andelt 1985; Young et al. 2006). Diets of coyotes at the Idaho study site are composed almost exclusively of black-tailed jackrabbits (*Lepus californicus*) and Nuttal’s cottontails (*Sylvilagus nuttallii*; MacCracken and Hansen 1987).

*Animal tracking.*—We used a variety of methods to capture coyotes. In Idaho, we used aerial net-gunning, however, in Texas, we used padded leg-hold traps (Victor #3 Softcatch, Lititz, PA, USA), collarums (Wildlife Control Supplies, East Granby, CT, USA), and neck snares. Once captured, we physically immobilized all coyotes and fitted each with a global positioning system collar (GPS3300S, Lotek, New Market, Ontario, Canada). We programmed collars to acquire differentially-corrected locations at 15-
minute intervals for 3-8 weeks. We retrieved collars by recapturing coyotes or by locating the collar after the pre-programmed drop-off unit deployed.

*Home range analysis.*—We used the fixed-k local convex hull method (Getz et al. 2007) to estimate territory boundaries for each coyote. This method is better suited for locating fixed boundaries (as would be expected for territorial species) than kernel methods (Worton 1989). Whereas kernel methods always overestimate boundaries, local convex hull methods converge on true boundary with increasing point densities (Getz et al. 2007).

*Data analysis.*—We restricted analyses to territorial coyotes only and omitted transients. Both were easily distinguished by their movement paths, with territorial individuals exhibiting restricted space use and transients exhibiting excursive movement patterns with no clear bounded movement. For each territory estimate, we overlayed a grid of 100 m x 100 m cells using the Hawth’s Tools extension (Beyer 2004) in ArcGIS (Version 9.2, ESRI, Redlands, California). We also created a territory boundary grid which was composed of any territory grid cells that intersected the estimated territory boundary. We determined the number of unique territory cells that each coyote’s path crossed per day. For each coyote we calculated the cumulative proportion of its territory it visited through time, and did the same analysis using territory boundary grid cells. To determine if the cumulative visitation curves differed between coyotes from Texas and Idaho, we used a statistical permutation test with the *mean-t* statistic (Elso et al. 2004). We used the function ‘compareTwoGrowthCurves’ in the ‘statmod’ package (Smyth et al. 2010) within the R Statistical Computing Environment (R Core Development Team.
to perform the permutation test. We restricted the number of days modeled to the minimum number of days that each coyote was sampled (i.e., 20).

For each coyote, we calculated the mean distance traveled per day, mean displacement per day (i.e., straight-line distance between start and end locations of a coyote’s daily movement path), and mean speed. We also calculated the mean turn angle of movement paths using method M proposed by Fisher (1993:120). Lastly, we estimated the percentage of time coyotes in Idaho and Texas were active by determining the proportion of relocations that did not differ by a mean of 20 m over a period of 1 hour using a moving window over the entire movement path. Twenty meters was the average location error of the GPS collars at the Texas study site (19.3 m ± 13.8 [SD]). Because coyotes tend to be more active at night, all parameters of daily activity were calculated from 1200h - 1200h (Jedrzejewski et al. 2001). This helped to ensure that movement paths during the most active periods were not artificially broken and were bounded on either side by periods of inactivity. We used the adehabitat package (Calenge 2006) in R (R Development Core Team 2009) to calculate daily movement path characteristics.

To determine if there were differences in the movement parameters between study sites, we used Welch’s two-sample t-tests (Crawley 2007:296) because we had unequal sample sizes (and variances) between study sites. We arcsine-square root transformed activity data prior to statistical testing to meet normality assumptions (Zar 1999). This research followed the American Society of Mammalogists Guidelines for research on live animals (Gannon et al. 2007) and was approved by the Utah State University and National Wildlife Research Center Animal Care and Use Committees.
Results

We captured 15 coyotes in Idaho between December 2004 and May 2005, and 7 in Texas between April 2007 and March 2009. Mean fix success rate of global positioning system collars was 98.6% (1.34) and 95.0% (4.5) for Idaho and Texas coyotes, respectively. We collected a mean of 4,159 (560) and 2,644 (1061) locations for each coyote in Idaho and Texas, respectively.

Mean territory sizes were 10x larger in Idaho (41.8 km² ± 16.0) than in Texas (4.0 km² ± 1.0; \( t = 8.8, d.f. = 14.2, P < 0.001 \)). Coyotes in Idaho traveled further daily \( (t = 8.1, d.f. = 19.4, P < 0.0001) \), had larger daily displacement distances \( (t = 5.1, d.f. = 17.7, P < 0.0001) \), and moved faster \( (t = 8.48, d.f. = 18.8, P < 0.0001) \) than coyotes in Texas (Table 5.1). Mean turn angles for Coyotes in Texas indicate they had more tortuous movement paths \( (176.4° ± 53.6) \) than coyotes in Idaho \( (340.7° ± 54.0) \). There was no difference in the mean percent of time coyotes were active at the Texas \( (65.9 ± 8.3\%) \) or Idaho \( (61.8 ± 6.2\%) \) study sites \( (t = 1.8, d.f. = 9.1, P = 0.267) \). Coyotes in Idaho, however, were slower to cover their territories \( (mean-t = 4.12, P = 0.0003; \) Fig. 5.1) and territory boundaries \( (mean-t = 6.33, P < 0.0001; \) Fig. 5.2) than coyotes in Texas. After 20 d, coyotes in Idaho covered 64.8% (15.0) of their respective territories and 28.8% (13.0) of their territory boundary compared to 85.7% (7.4) and 68.3% (7.0) for coyotes in Texas, respectively (Figs. 5.1, 5.2).
Table 5.1 - Summary of movement parameters calculated from coyotes in southeastern Texas \((n = 7)\), and south-central Idaho \((n = 15)\). Data are from on global positions system collars that obtained relocations at 15 m intervals over a 3-8 week period. Displacement distance per day represents the mean distance between the start and end of a 24 h movement path.

<table>
<thead>
<tr>
<th>Parameter (d^{-1}) (km)</th>
<th>Texas</th>
<th>Idaho</th>
</tr>
</thead>
<tbody>
<tr>
<td>Distance traveled (d^{-1}) (km)</td>
<td>10.2</td>
<td>23.6</td>
</tr>
<tr>
<td>Displacement (d^{-1}) (km)</td>
<td>0.7</td>
<td>2.6</td>
</tr>
<tr>
<td>Speed (km/h)</td>
<td>0.4</td>
<td>1.0</td>
</tr>
</tbody>
</table>
Figure 5.1 - The cumulative proportion a territory visited with increasing numbers of days. Black circles represent data collected from a population of coyotes 50 km north of Corpus Christi, Texas \((n = 7)\), and open circles from a population of coyotes 50 km west of Idaho Falls, Idaho \((n = 15)\). For each coyote territory estimate, we overlayed a grid of 100 m x 100 m cells and determined the cumulative number of unique territory cells that each coyote’s path crossed daily. We then obtained the mean cumulative proportion of a territory visited each day for each study site. Error bars represent 95% C.I.
Figure 5.2 - The cumulative proportion a territory boundary visited with increasing numbers of days. Black circles represent data collected from a population of coyotes 50 km north of Corpus Christi, Texas ($n = 7$), and open circles from a population of coyotes 50 km west of Idaho Falls, Idaho ($n = 15$). For each coyote territory estimate, we overlaid a grid of 100 m x 100 m cells and determined the cumulative number of unique cells overlapping with the territory boundary that each coyote’s path crossed daily. We then obtained the mean cumulative proportion of a territory boundary visited each day for each study site. Error bars represent 95% C.I.
Discussion

Our results suggest that coyotes inhabiting large territories sped up and made more direct movements than coyotes that occupied smaller territories. However, coyotes occupying large territories remained unable to traverse their territories in the same time frame as coyotes inhabiting smaller territories. Because daily activity was similar between study sites and territories were on average ten times larger in Idaho than in Texas, coyotes in Idaho would have to move approximately 2x faster than observed to maintain similar levels of daily territorial patrolling as coyotes in Texas. Similar relationships between movement parameters and territory size have been shown for other species (Kowalczyk et al. 2006; Righton et al. 1998). However, even though movement was more than twice as fast and better suited for discovering disturbances (Alder and Gordon 1992), coyotes in large territories covered considerably less of their territories and territory boundaries during a similar period of time as coyotes occupying smaller territories.

Territories are only beneficial to coyotes if they can be effectively defended from competitors which requires territory holders to monitor their territory frequently enough to detect and respond to intruders (Mitani and Rodman 1979). The importance of such active defense can be shown by how quickly adjacent packs will usurp territories once active defense declines (Gese 1998). The ability of coyotes to effectively monitor and defend territories, however, becomes more difficult in larger territories unless they compensate by altering their movement patterns (Lowen and Dunbar 1994; Mitani and Rodman 1979). Indeed, coyotes with large territories altered their movement patterns as
predicted, but the increase in movement rate and decrease in tortuosity did not result in equivalent proportions of the territory patrolled as those coyotes occupying smaller territories. Reduced rates of territorial patrolling imply that it would be much more difficult for coyotes in Idaho to detect and respond to territorial intrusions, which is congruent with the results of Mitani and Rodman (1979).

Prey abundance and territory size are different between our two study sites (given the large difference in latitude; Gompper and Gittleman 1991) as is the plasticity of response to changes in prey density at both sites. For example, at the Texas study site, coyote territory boundaries have remained stable for over a quarter of a century (Young et al. 2006) even when supplemented with an abundant, high-quality food source (Young et al. 2008), but a northern population of coyotes with similar territory sizes as those in Idaho (i.e., 30-40 km²) showed significant variation in territory size based on changes in the prey population (Patterson and Messier 2001). Conversely, one coyote pack in Yellowstone expanded its territory when an adjacent territory became available, even though prey was abundant (Gese 1998). Thus, the hypotheses of resource- or conspecific interference-driven territorial size regulation are not mutually exclusive.

Unlike other studies of coyote territoriality, we propose that coyote territory size is influenced by both resource availability and conspecific density, with the importance of each factor varying between populations. In areas of high prey abundance such as for coyotes in Texas, intrusion pressure from conspecifics is likely higher and thus might serve as the proximate regulator of territory size because of the costs associated with defending territories from high rates of intrusion. Indeed, when food availability increased, coyotes in Texas did not decrease territory size but rather increased time spent
actively defending territories (Young et al. 2008). Additionally, at the Texas study site, there was a section built to exclude coyotes in the 1970s, however, when the exclusion was removed, a new territory moved in rather than adjacent ones growing larger (Young et al. 2006). This is further evidence that coyotes in Texas are incapable of maintaining expanded territory boundaries due to high conspecific density. Conversely, when coyote territories are large, their size appears more directly related to prey availability (Mills and Knowlton 1991; Patterson and Messier 2001). Coyotes at the Idaho site still actively patrolled territories, though less efficiently than coyotes occupying smaller territories. However, coyotes in Idaho can afford to defend larger territories which take them longer to patrol due to lower conspecific densities and rates of intrusion.

It is possible that different members of the pack patrolled different portions of the territory and territory boundary in large territories, thus increasing the proportion of the boundary patrolled during a given time. However, this seems unlikely because alpha pairs are the primary individuals to respond to territory intrusions (Gese 2001) and most active in territory marking (Gese and Ruff 1997). Also, pack sizes are similar between study regions (Andelt 1985; Bromley and Gese 2001). We also assumed that coyotes in both populations studied have similar perceptual abilities and detection distances. However, visual detection distances might actually be lower in Texas than in Idaho because of greater vegetative cover in Texas. Given the importance of visual cues for coyote behavior (Wells and Lehner 1978), coyotes in Idaho likely had greater detection distances than in Texas. While this might slightly reduce the discrepancy in territory and...
boundary visitation between coyotes in Texas and Idaho, it is unlikely to account for all of the observed differences.

Mills and Knowlton (1991) identified coyotes in one site in northern Utah as being influenced by prey density, but they did not detect changes in territory sizes of coyotes at our same study site in Idaho. It is important to note, however, that the size of territories Mills and Knowlton (1991) estimated were much smaller (~12 km²) and thus it is possible that higher prey and coyote densities resulted in a conspecific-interference driven system at that time. The dynamics of coyote territory size, especially in higher latitudes, then, should not be thought of as static, especially for such an opportunistic and adaptive species. Alternatively, Mills and Knowlton (1991) used radio telemetry, smaller sample sizes, and less precise methods than ours which could have biased their home range calculations. With our GPS data, it was clear where territory boundaries occurred given the mosaic of territories across the study area and we are confident in our assessment of movement patterns.

In conclusion, we propose that in areas with high resource abundance, coyote territory size is primarily determined by what coyotes can physically defend from intruding conspecifics, whereas in low resource areas, territory sizes are determined more by prey abundance because intrusion rates are reduced given the lower density of conspecifics.

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The goals of my research were to improve the analysis of animal space use data by creating a new method to estimate core areas and to better understand the behavioral mechanisms that underlie observed space use patterns of bobcats and coyotes. Each of these goals was met.

I developed a new method for estimating animal core areas that is based on Bayesian statistics and a data-based definition of a core area (CHAPTER 2). The method not only objectively estimates the isopleth that optimally partitions the home range into core and non-core areas but also accounts for uncertainty in the core area estimate and for multiple scales of clustering in animal space use data. To my knowledge, this is the only method capable of accomplishing each of these tasks.

By more precisely estimating core areas and accounting for additional factors other than time spent in an area, I was able to provide evidence that patterns of coyote captures are better explained by trap density than by a coyote’s apparent familiarity with the area (CHAPTER 3). In fact, my results suggest support for a conclusion that is opposite of that typically described. That is, after accounting for differences in trap density between core and peripheral areas of the territory, captures actually appeared to be more likely to occur in the areas that are more intensively used. Thus, coyote behavior towards traps does not appear to be related to neophobia, but to the probability of encountering a trap.
My research was also able to provide empirical evidence for the behavioral mechanisms underlying bobcat core areas (CHAPTER 4). Unlike other studies which assumed that bobcat core areas occurred in locations with the highest abundance of prey, my results suggest that prey abundance is not the only predictor of bobcat core area location. The spatial distribution of bobcat core areas was strongly influenced by the abundance of prey, but it was mostly at the study site scale, and not at the home range scale. Overall, bobcat core area location was most strongly influenced by the intensity of coyote use in an area. Only when prey was sufficiently low would bobcat core areas occur in areas with high coyote use. Thus, the location of bobcat core areas was a tradeoff between prey abundance and the need to avoid intraguild predation by coyotes.

Finally, my results show that the size of coyote territory significantly influences movement patterns and the ability to effectively patrol the territory. My conclusion was supported by coyotes in Idaho, which had mean territory sizes 10x larger than in Texas and took significantly longer to cover their territories and territory boundaries even though their movement patterns were faster and less tortuous. My results suggest that in areas with high resource abundance, coyote territory size is primarily determined by what coyotes can physically defend from intruding conspecifics, whereas in low resource areas, territories are larger than can be efficiently defended. Coyotes that inhabit large territories are able to be less efficient at patrolling in areas with reduced conspecific interference.

My research shows that even when animals cannot be directly observed, researchers can still make inferences about the underlying behavioral processes of observed space use patterns by testing among competing hypotheses. The results of my
research will aid in the management and conservation of carnivores. By understanding how animals use space, managers will be better able to determine the best location for conservation efforts (e.g., supplemental feeding stations), and what factors that might potentially influence the use of those treatments. My research also helps to inform managers of more effective ways of targeting problem coyotes. As my results show that the most important factor influencing the probability of capturing coyotes is the density of traps in the area, researchers and managers can place traps in those receiving the most damage. This may seem trivial, but counters previous research suggesting that it is difficult to capture carnivores in areas used frequently. Increased precision in animal space use patterns will improve our ability to detect differences between experimental treatments, infer behavioral processes that lead to the formation of core areas, and determine wildlife habitat associations. This can have important implications for setting priorities for conservation and management areas. Additionally, understanding factors that contribute to variation in intraguild predation rates will help inform conservationists of possible mitigation strategies that can limit the community-level effect of high intraguild predation rates.
APPENDICES
Dear Bradley Strobel,

I am in the process of preparing my dissertation in the Department of Wildland Resources at Utah State University. I hope to complete in the spring of 2010. I am requesting your permission to include Chapter 2, Accounting for individuals, uncertainty, and multi-scale clustering in core area estimation, and Prey-mediated avoidance of an intraguild predator by its intraguild prey, in which you are a coauthor. I will include acknowledgments and/or appropriate citations to your work.

Please indicate your approval of this request by signing in the space provided. If you have any questions, please call me at the number above.

I hope you will be able to reply immediately.

Thank you for your cooperation.

Ryan Wilson

I hereby give permission to Ryan Wilson to include Chapter 2, Accounting for individuals, uncertainty, and multi-scale clustering in core area estimation, in which I am coauthor for his dissertation.

12 April 2010

Ryan R. Wilson
945 N.W. Circle Blvd., #38
Corvallis, OR 97330
520-955-3754

Dear Dr. Hooten,

I am in the process of preparing my dissertation in the Department of Wildland Resources at Utah State University. I hope to complete in the spring of 2010. I am requesting your permission to include Chapters 2 and 4, *Accounting for individuals, uncertainty, and multi-scale clustering in core area estimation*, and *Prey-mediated avoidance of an intraguild predator by its intraguild prey*, in which you are a coauthor. I will include acknowledgments and/or appropriate citations to your work.

Please indicate your approval of this request by signing in the space provided. If you have any questions, please call me at the number above.

I hope you will be able to reply immediately.

Thank you for your cooperation,

Ryan Wilson

__________________________________________________________________________

I hereby give permission to Ryan Wilson to include Chapters 2 and 4, *Accounting for individuals, uncertainty, and multi-scale clustering in core area estimation*, and *Prey-mediated avoidance of an intraguild predator by its intraguild prey*, in which I am coauthor for his dissertation.

Signed: [Signature]
Dear Dr. Young,

I am in the process of preparing my dissertation in the Department of Wildland Resources at Utah State University. I hope to complete in the spring of 2010. I am requesting your permission to include Chapters 3, *Coyote capture vulnerability relative to territory use and trap density*, in which you are a coauthor. I will include acknowledgments and/or appropriate citations to your work.

Please indicate your approval of this request by signing in the space provided. If you have any questions, please call me at the number above.

I hope you will be able to reply immediately.

Thank you for your cooperation,

Ryan Wilson

I hereby give permission to Ryan Wilson to include Chapters 3, *Coyote capture vulnerability relative to territory use and trap density*, in which I am coauthor for his dissertation.

Signed: [Signature]

[Signature]

13 April 2010
13 April 2010

Ryan R. Wilson
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Corvallis, OR 97330
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Dear Dr. Blankenship,

I am in the process of preparing my dissertation in the Department of Wildland Resources at Utah State University. I hope to complete in the spring of 2010. I am requesting your permission to include Chapter 4, Prey-mediated avoidance of an intraguild predator by its intraguild prey, in which you are a coauthor. I will include acknowledgments and/or appropriate citations to your work.

Please indicate your approval of this request by signing in the space provided. If you have any questions, please call me at the number above.

I hope you will be able to reply immediately.

Thank you for your cooperation,

Ryan Wilson

I hereby give permission to Ryan Wilson to include Chapter 4, Prey-mediated avoidance of an intraguild predator by its intraguild prey, in which I am coauthor for his dissertation.

Signed: [Signature]
CURRICULUM VITAE

Ryan Radford Wilson
Certified Associate Wildlife Biologist

Education:

UTAH STATE UNIVERSITY, Logan, UT 2010
- Ph.D. Wildlife Biology
- Dissertation Title: Identifying and understanding the spatial distribution of bobcat and coyote behavior.

UNIVERSITY OF ARIZONA, Tucson, AZ 2006
- M.S. Wildlife Ecology
- Thesis Title: Recovery efforts for and behavior of Sonoran Pronghorn

UNIVERSITY OF ALASKA FAIRBANKS, Fairbanks, AK 2003
- B.S. Wildlife Biology
- B.S. Statistics
- Minor in Math
- Cum laude

SIERRA HIGH SCHOOL, Tollhouse, CA 1999
- Valedictorian

Publications:

Wilson, R. R., J. K. Young, and J. A. Shivik. In Review. Coyote capture vulnerability relative to territory boundaries.


Wilson, R. R., P. R. Krausman, and J. R. Morgart. 2008. Behavior and timing of
life-history events in a semi-captive population of the Sonoran pronghorn
(*Antilocapra americana sonoriensis*). Southwestern Naturalist 53:389-393.


*Included in the virtual issue International Year of Biodiversity: Connectivity and Corridors in Conservation Biology as 1 of 10 articles making an important contribution to the study of corridors and connectivity*

**Presentations:**


Wilson, R. R., and B. M. Barnes. 2003. Seasonal changes in supercooling point of blood plasma from hibernating arctic ground squirrels (Spermophilus parryii). American Society of Mammalogists Meeting, Lubbock, Texas

**Invited Presentations:**

2010 Invited Seminar: Lincoln University, Jefferson City, Missouri

2009 International Association for Landscape Ecology Workshop: Bayesian Methods for Landscape Ecologists

**Research Grants**

2008 Does predator avoidance determine bobcat core areas? From: American Society of Mammalogists. Principal Investigator ($1500)

2006 Welder Wildlife Foundation Ph.D. Fellowship ($100,000)

2005 Behavior and recovery of Sonoran pronghorn. From: National Fish and Wildlife Foundation. Principal Investigator ($5000)


2002 Seasonal changes in the supercooling ability of the arctic ground squirrel. From: University of Alaska Fairbanks, Undergraduate Research Grant. Co-principal investigator ($1000).

**Workshops Attended:**

2006 Home Range and Animal Movements Workshop, Pocatello, Idaho

2009 Bayesian Methods for Landscape Ecology, Snowbird, Utah

2009 Adaptive Management of Natural Resources, USGS Webinar

**Professional Meetings Attended:**

2009 Ecology Society of America, Albuquerque, New Mexico

2009 U.S. International Association for Landscape Ecology, Snowbird, Utah

2006 Biennial Pronghorn Workshop, Idaho Falls, Idaho

2006 Conference on Research and Resource Management in the Southwestern Deserts, Tucson Arizona
2006    Arizona, New Mexico Chapters of the Wildlife Society, Annual Meeting, Flagstaff, Arizona
2005    Southwest Section of the Wildlife Society Meeting, Alpine, Texas
2005    Annual Meeting of the Arizona and New Mexico Chapter of the Wildlife Society, Gallop, New Mexico
2004    Sonoran Pronghorn Workshop, Tucson, Arizona
2004    Experimental Biology Meeting, Washington, D.C.
2003    American Society of Mammalogists Meeting, Lubbock, Texas.

Professional Work Experience:
Graduate Research Assistant, Utah State University, Department of Wildland Resources, Logan, UT 84322.
July 2006 – present: I worked on the spatial ecology of bobcats and coyotes in south Texas on the Welder Wildlife Foundation Refuge. My research focused on determining the spatial distribution of behaviors and factors that explain their distribution. I set traps, captured, sedated, and handled animals on my own or with the assistance of a technician. I used both radio telemetry and GPS technology to answer these questions. I also developed a new method to analyze the spatial structure of animal space use patterns obtained from traditional telemetry studies. I was responsible for the hiring and supervision of 6 technicians over a 2 years period. I also worked closely with the staff of the foundation in collaborative efforts.

Graduate Research Assistant, University of Arizona, School of Natural Resources, Tucson, AZ 85721.
August 2004 – June 2006: I worked with the endangered Sonoran pronghorn to determine seasonal, and diurnal activity budgets. I also documented recovery efforts that have so far been initiated. The research occurred on Cabeza Prieta National Wildlife Refuge, in Ajo, Arizona. I worked independently on my own research, but also assisted individuals from the Arizona Game and Fish Department and the wildlife refuge when requested.

Research Assistant, University of Alaska Fairbanks, Institute of Arctic Biology, P.O. Box 757000, Fairbanks, AK 99775.
November 2000- December 2003: I researched the mechanisms responsible for the seasonal change in supercooling ability of arctic ground squirrels. I was responsible for assisting with plasma collection, experimental design, data collection, and analysis.

May 2003-August 2003. I worked on a variety of projects including waterfowl pair counts, waterfowl brood surveys, point counts, hare density sampling, passerine banding, malformed frog surveys and invasive plant surveys. Much of this work was done in remote locations only accessible by floatplane. I was required to accurately identify birds that occur in Alaska for all of the surveys as well as pick birds from mist nests and band them.

Biological Technician GS-486-4, United States Forest Service Pacific Southwest Research Station, 2081 E. Sierra Ave., Fresno, CA 93710. May 2001 - September 2001. I located and monitored bird nests of any species in the Sierra Nevada Mountains. I often worked independently and always with little or no supervision. I also collected vegetation data around nest locations.

Biological Technician GS-486-4, United States Forest Service Pacific Southwest Research Station, 2081 E. Sierra Ave., Fresno, CA 93710. June 2000 - September 2000. I collected vegetation data for the calibration of two remote sensing devices in the Sierra Nevada Mountains. Measurements taken included tree heights with lasers, dbh, canopy heights, tree species, crown shape, partial crown heights and snag class. GPS units were used to locate the plots. I often worked with little supervision and for the last month of the season, I was in charge of the field operations and making sure data were collected properly.

**Editorial Experience:**
2009: Peer-reviewer for *Journal of Wildlife Management*
2007: Peer-reviewer for *Southwestern Naturalist*
2006, 2009: Peer-reviewer for *European Journal of Wildlife Research*
2005: Technical reviewer for *Wildlife Monographs*
2005: Peer-reviewer for *Managing Wildlife in the Southwest*

**Other Skills and Qualifications:**
Knowledge of R, Microsoft Word, Excel and Power Point, CPR and First Aid certified, USFWS Bear Safety Training, USFWS low-flying aircraft training, Oregon Driver’s License, some experience with GIS in ArcGIS, experience with GPS, strong swimmer, avid backpacker and hiker, photography skills, and experience with firearms.

**Membership in Professional Organizations:**
The Wildlife Society 2002-present
American Society of Mammalogists 2003-present
Ecological Society of America 2009
Animal Behaviour Society 2007-2008

**Membership in Other Organizations:**
Golden Key National Honor Society
Awards and Scholarships:

• **E. C. Pielou Student Award**, ESA Statistical Ecology Section, 2009
• **Welder Foundation Fellowship** 2006-2010.
• **Best Student Presentation Award**, Arizona/New Mexico Chapters of the Wildlife Society, Annual Meeting, 2006.
• **Rex Thomas Memorial Award**, University of Alaska Fairbanks, 2003.
• **Chancellor’s Scholarship**, University of Alaska Fairbanks, 1999.
• **Seymour Memorial Scholarship**, California Scholarship Foundation, 1999.