MOVEMENT AND BEHAVIORAL ECOLOGY OF COYOTES IN SOUTHERN TEXAS

A Dissertation

by

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ABSTRACT

Coyotes (*Canis latrans*) are a ubiquitous and successful predator species across North America. This success stems from their generalist diet, adaptable behavior, and cognitive abilities, and leads to many management and conservation issues. Despite a century of scientific research, effective coyote management practices remain elusive. This is caused, in part, by limited scientific understanding of the relationships between their behavior and their disease transmission, population dynamics, and effects on prey. These topics were difficult to study until the recent advent of GPS telemetry technologies and appropriate techniques to analyze the large, and complex data sets they produce.

This work leverages these methodological advances to examine links between coyote movement behavior, sociality, disease transmission dynamics, population dynamics, and predator-prey relationships. I utilize recent advances in copula regression to examine the effects of carrion deposition on joint space use of coyotes, which is linked to contact rates in disease transmission models. I then compare competing explanations of coyote social and dispersal behavior, and obtain a behaviorally informed estimate local emigration rate. Finally, I examine inter-individual variation in the dynamics of coyote activity cycles, utilizing a new adaptation of autocorrelation functions, to test a common assumption underlying studies of dynamic predator-prey interactions.

I found that copula regression methods gave asymptotically unbiased estimates of changes in coyote interactions. This study also suggests that social perturbations caused by carrion availability may have impacts that last longer than the resource. I found that the common resident-transient paradigm of coyote sociality is insufficient. The results of this work suggest that biding is an important dispersal behavior that influences coyote population dynamics, and that 88% of adult, territorial coyotes disperse annually. Finally, coyote activity cycles were more dynamic than previous work suggests. Activity was consistently acyclic across individuals in winter. Cycles were strongest in summer, but individuals diverged between crepuscular and nocturnal behavior. This work carries implications for the study of predator-prey dynamics in a landscape of fear context, suggesting not only are predator activity patterns seasonally dynamic, but the population average of activity cycles may be a poor predictor of risk to a given prey species.

Overall, these three studies suggest that researchers should exercise caution with simplistic assumptions of coyote behavior. A more detailed understanding of both behavioral processes, and their implications is necessary to achieve effective strategies for managing coyote impacts.

DEDICATION

To Ernesto "Neto, El Tejon Chingón" Garcia-Ortega and Robert "Trapper-Bob" Allcorn.

Siempre Chocobos.

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I. INTRODUCTION AND LITERATURE REVIEW

Introduction

Conflict between carnivores and human interests are as old as civilization itself (Frank and Conover 2015). Whether for personal safety, or protecting livestock, humans have attempted to manage carnivore issues with the same operational goal of reducing carnivore numbers for millennia (Reynolds and Tapper 1996). As civilization expanded, agriculture intensified to provide stable food and fiber resources, and human-carnivore issues intensified in kind. Public policies of predator elimination date back to ancient Greece (Dannenfeldt 1985), and grown more common and broader in scope since the middle ages (Reynolds and Tapper 1996). Such policies resulted in the wide extirpation of many large carnivores across much of the globe (Clark et al. 1996). Smaller species proved more resilient and have persisted in the face of persecution in areas where larger members of the guild have vanished (Sillero-Zubiri et al. 2004, Ripple et al. 2013). Thus, human–carnivore conflict is as relevant today as it was in antiquity.

Scientific inquiry into predator management is comparatively new, however, originating in the early 20th century (Goldman 1930, Henderson 1930, Errington 1935, Jacobsen 1962). Reliable inferences on the subject are few (Treves et al. 2016). Trapping and opportunistic shooting are long-standing, lethal management practices that are still commonly used to manage coyote issues (Knowlton et al. 1999). However, the limited information available suggests that these practices are unreliable at best in achieving desired management outcomes of reduced livestock loss (Allen 2000, Berger 2006), enhanced productivity of wildlife populations (Baines 1996, Bodey et al. 2011, Ellis-Felege et al. 2012), or, excepting the largest apex predators, predator population reduction (Lieury et al. 2015, Minnie et al. 2016, Treves et al. 2016). Nonlethal methods have shown mixed results as well (Treves et al. 2016), but the use of livestock protection dogs appears promising at reducing sheep losses (Gehring et al. 2010). Difficulty in finding effective management solutions resulted in several calls for better understanding of carnivore behavioral ecology to better frame research on management strategies (Knowlton et al. 1999, Mitchell et al. 2004).

Coyotes (*Canis latrans*) are a model species for the study of predator ecology with an eye to effective management. Their generalist habits, behavioral adaptability, and cognitive abilities allow them to persist in the face of intense persecution. Indeed, management issues surrounding coyotes have received scientific attention for a century (Henderson 1930), yet effective practices to reduce their negative impacts remain elusive (Kilgo et al. 2014). Despite a substantial body of research, our understanding of coyote behavior, dispersal, and population dynamics is simplistic and relies on untested foundational assumptions. Carnivores in general, and coyotes in particular, are difficult to study due to their elusive nature and wariness towards humans (Bekoff and Wells 1986, Gese et al. 1996). Radio telemetry revolutionized the study of carnivore behavior (Craighead and Craighead 1972), allowing researchers to track an individuals' position from a distance. These methods provided rigorously quantifiable data on animal movement (White and Garrott 1990), but were still time intensive, subject to observer influences on movement, and limited in temporal resolution, as well as spatial precision (Kochanny et al. 2007).

The advent of GPS telemetry in the 1990s revolutionized the study of animal movement behavior, allowing researchers to collect frequent, highly precise location estimates while minimizing observer influence on behavior (Tomkiewicz et al. 2010). GPS technology is maturing rapidly, making the study of animal movement behavior a truly data intensive field (Urbano et al. 2010). However, analytic methodologies to link these data to ecological questions have only recently begun to catch up to telemetry technology (Hooten et al. 2017*b*). Research into analysis of telemetry data is beginning to flourish, and there are now appropriate methods for many complex, previously intractable ecological questions (Nathan 2008, Hebblewhite and Haydon 2010, Hooten et al. 2017*b*). However, many opportunities for developing methodologies linking GPS data to both ecological and management oriented questions.

The goal of this dissertation is to leverage GPS technology and recent analytical advances to better understand the nature, complexity, and implications of coyote movement behaviors for management issues. In this work, I present: 1) a new analytical approach to capture and explain the dynamics of coyote interactions using joint space use measures, with implications for transmission of infectious diseases; 2) the first objective assessment of the nature and dynamics of coyote territoriality, with implications for local population dynamics, and thus lethal management; and 3) an analysis of coyote activity patterns through time, with implications for the study predator-prey dynamics, a key theoretical underpinning of carnivore management.

Literature Review

Coyotes

Evolution, taxonomy, and range.— Coyotes are 1 of 8 species in the genus *Canis* (Bekoff and Gese 2003). There are 19 recognized subspecies (Bekoff and Gese 2003), 3 of which are found in Texas; *C. l. frustor*, *C.l. texensis*, and *C. l. microdon* (Bailey 1905). They are believed to have descended from an ancestral species *C. lepophagus*, from which they differ slightly in cranial and mandibular morphology (Bever 2005).

Coyotes historically range through the western half of North America, from northern Alaska to Costa Rica (Bekoff and Gese 2003). They expanded their geographic range north and eastward into eastern Canada in the 20th century (Hilton 1978, Boisjoly et al. 2010). Competing hypotheses of the drivers of this expansion are the eradication of gray wolves (*Canis lupus*) from much of their former range, human alteration of the landscape, and active relocation by humans (Hill et al. 1987, Gompper 2002).

Life history and behavior.— Coyotes are medium-sized dietary generalists (Bekoff and Gese 2003), which affords them a great deal of trophic flexibility. They are able to meet energetic requirements from vertebrates, invertebrates, and vegetation more effectively than smaller or larger canids (Carbone et al. 1999). They adapt dietarily to a wider range of foraging conditions that larger canids, which are considered carnivore specialists, or smaller canids, which are not capable of taking large prey species (Bekoff et al. 1981). There is evidence to suggest that coyotes exhibit optimal foraging (MacCracken and Hansen 1987, Hernandez et al. 2002), adapting their diets to the most energetically profitable prey under the conditions they experience, though this is contested in the literature (Boutin and Cluff 1989).

They are socially subordinate to, and persecuted by, wolves *Canis lupus* where they coexist (Arjo and Pletscher 1999, Atwood and Gese 2010), though they exert similar dominance behaviors on foxes and other meso-mammals (Levi and Wilmers 2012). Coyotes have replaced wolves as an apex predator where the latter have been extirpated (Crooks and Soule 1999), but do not perform the same ecological functions. Wolves specialize on large ungulate prey, compared to the generalist diet discussed in coyotes above, thus coyotes exert different effects on predator prey systems (Berger et al. 2008, Benson et al. 2017).

Coyote life history is characterized by territorial behavior, where social groups defend well-defined, non-overlapping territories from neighboring groups and dispersing individuals (Bekoff and Wells 1986, Gese 2001). Groups maintain territory boundaries with scent-marking behavior (Barrette and Messier 1980) and, to a lesser extent, direct confrontation (Gese 2001). Unlike confrontations between wolves, or wolves and coyotes, escalations rarely result in injury or death to either party (Bekoff and Wells 1982, Mech 1993, Gese 2001). Territory boundaries are stable over several generations of occupants (Andelt 1985, Young et al. 2006), and are partially conterminous, with appreciable interstitial space (Windberg and Knowlton 1988). Coyotes that do not belong to a territorial group move through these spaces, presumably with the intent of gaining access to a territory (Bekoff and Wells 1986, Gese 2001). This has led to a binary consideration of coyotes as resident (sometimes termed 'territorial') or transient (Gese et al. 1988*a*). recent work suggests that coyote space use behavior is more nuanced that a simplistic binary treatment, suggesting that multiple space use strategies during dispersal contribute to coyote population persistence (Morin and Kelly 2017).

Territorial behavior in canids is believed to be an adaptation to their unique breeding strategy (Asa and Valdespino 1998). At high population densities, only the highest ranking male and female coyotes (the alpha pair; Bekoff and Wells 1986) within a territorial group breed (Windberg 1995), thus breeding opportunities are tied to territorial status. Females are seasonally monestrous, with a 10-day estrous period occurring in mid-March (Kennelly and Johns 1976). Gestation lasts approximately 63 days (Bekoff and Wells 1986). Females may be reproductively viable for as many as 8 years (Green et al. 2002). Coyotes give birth to altricial young, which are completely dependent on their parents for the first 5–7 weeks (Snow 1967). Coyotes exhibit alloparental care, where subordinate (beta) territory members care for pups along with the alpha pair (Bekoff and Wells 1986). Beta females exhibit pseudo-pregnancy and lactate, but typically do not bear young (Bekoff and Wells 1986, Montgomery et al. 2018). Pups born to beta females typically do not survive to disperse (Bekoff and Wells 1986). The average litter size across their range is 6 (Bekoff and Gese 2003), but has been shown to vary with population density, resource availability, nutrition, and human persecution (Knowlton 1972, Todd and Kieth 1983, Windberg 1995, Gese et al. 2016). Fecundity may increase during eradication efforts as females release more eggs during ovulation, litter sizes increase, and more females breed in the face of persecution (Knowlton 1972). These compensating mechanisms lead to the hypothesis that coyote populations are self regulating (Wallach et al. 2015).

Coyote management issues and methods.— Their broad range and generalist, predatory habits have lead to to numerous conflicts between coyotes and human economic and conservation issues. Coyotes are commonly implicated in livestock losses (Pearson and Caroline 1981), particularly in sheep and goat operations where losses are concentrated on kids and lambs (**?**Sacks and Neale 2007). Predation by coyotes is commonly implicated as a primary cause of the decline of the sheep and goat industry, however, while declines in U.S. sheep numbers were correlated with federal spending on predator management, market cost explained most variation in industry decline (Johnson and Gartner 1975, Berger 2006).

Wildlife management issues involving coyotes are numerous. Coyotes impact the survival and recruitment of several endangered species, including San Joaquin kit foxes (*Vulpes macrotis mutica*;Cypher and Scrivner 1992), Gaspé caribou (Rangifer tarandus caribou; Boisjoly et al. 2010), and red wolves (*Canis rufus*; Hinton et al. 2018). Expansion into the southeast led to recent concerns for the viability of white-tailed deer (*Odocoileus virginianus*) populations through reduced reproductive output and fawn survival (Cherry et al. 2016, Gulsby et al. 2017). In the west, they are a concern for the recruitment of both mule deer (*Odocoileus hemionus*) and pronghorn (*Antilocapra americana*) populations (Hamlin et al. 1984, Brown and Connover 2011, Hurley et al. 2011).

Methods of reducing coyote impacts on both livestock and wildlife are an area of active research. Early research focused on methods of lethal removal through trapping and shooting (Henderson 1930, Casto and Presnall 1944, Alcorn 1946), or chemical compounds, such as sodium fluoroacetate (compound 1080;Robinson 1948). However, the use of 1080 bait stations was federally banned in 1972 (Wagner 1975). Lethal control has long been scrutinized by both scientists (Adams 1925, Redington 1928, Anthony 1931, Reese 1937) and the public (Slagle et al. 2017), and links between lethal predator removal and reduction of predator impact are equivocal (Conner et al. 1998, Allen 2000, Bodey et al. 2011, Ellis-Felege et al. 2012, Treves et al. 2016). Relationships between coyotes and other sympatric predators are complex and control efforts may be confounded by compensatory effects of mesopredators (Crooks and Soule 1999, Henke and Bryant 1999, Prugh and Arthur 2015). Further, lethal management of coyotes is unreliable at sustainably reducing population sizes (Wagner and Conover 1999, Karki et al. 2007, Mosnier et al. 2008). Thus, there is considerable interest in both nonlethal and indirect means of reducing coyote impacts.

Coyote population reduction is rarely, if ever, the motivating goal of control efforts. Rather, it is an operational goal to achieve a management objective. In the case of livestock depredation the objective is usually to minimize losses to predators (Conner et al. 1998, Sacks et al. 1999*a*), while in wildlife management it is commonly to increase the survival or recruitment of another target species (Brown and Connover 2011, Gulsby et al. 2015). In the case of reducing livestock losses, livestock protection dogs are a promising management tool (van Bommel and Johnson 2012). Other methods received considerable research attention, but proved ineffective or impractical, such as conditioned taste aversion by lithium-chloride (Bourne and Dorrance 1982, Connover and Kessler 1994), optical and sonic frightening devices (Darrow and Shivik 2009), pyrotechnics

(Pfeifer and Goos 1982), surgical sterilization (Bromley and Gese 2001), and even electronic dog training collars (Andelt et al. 1999). Nonlethal management alternatives for wildlife-related objectives are more elusive, however recent work suggests that habitat structural complexity mediates predator impacts on prey species by providing refugia for prey (Lichtenstein et al. 2019). Indeed, coyote effects on white-tailed deer fawn in the southeastern U.S. are reduced with increasing landscape heterogeneity (Gulsby et al. 2017). Thus, effective habitat management may be an important tool in buffering prey populations.

Developments in the Analysis of Telemetry Data

Recent advances in computing power, in both GPS-based telemetry devices and desktop computers, revolutionized the collection, visualization, and analysis of animal movement data (**?**). However, technological advancement outpaced the development of scientific concepts linking detailed individual movements to population-level questions (Hebblewhite and Haydon 2010). Despite the proliferation of statistical descriptions of movement data, scientists and statisticians have been slow to link these advances to ecological problems (Borger 2015). A chronic problem is the focus on rote methodologies, rather than scientific hypotheses (Fieberg and Borger 2012). Despite this slow start, many new tools have emerged that provide insight to the ecological mechanisms and implications of animal movement behavior (Hooten et al. 2017*a*). In this dissertation, I utilize and expand on several recent statistical developments, which are reviewed below.

Copulae and beta regression.— Copulae are mathematical structures used to convey complex correlation structures, particularly when variables are modeled as different distributions (Nelsen 2006). The fundamental basis for copulae is Sklar's theorem, which states that for any joint distribution can be represented as a set of marginal (univariate) distributions and a copula, represented with containing the correlation structure using an arbitrary, convenient distribution (Parsa and Klugman 2011). In a 2-dimensional case, this is represented formally as

$$H(x, y) = C(F(x), G(y)) \tag{I.1}$$

where, $H(x, y)$ is the joint distribution of variables x and y (including their correlation), $F(x)$ is the marginal distribution function of variable x, $G(y)$ is the marginal distribution function of variable y, and $C(\cdot)$ is the copula function containing the correlation structure that links x and y (Nelsen 2006). This works by using the probability integral transform to translate the parent distribution to a uniform distribution with correlation, then into the appropriate mixture.

The practical benefit is that intricate correlations can be modeled between variables of any distribution using a well known distribution, such as a Gaussian (normal) or t-distribution. One important application is in quantifying the autocorrelation of a non-Gaussian time series. For example, many ecological data are measured as percentages or proportions (Legendre and Legendre 1998), which are not well approximated with conventional statistical procedures that assume a normal distribution. An appropriate alternative is to model these data as arising from a beta distribution, which is bounded on the interval $[0, 1]$ (Ferrari and Cribari-Neto 2004). If the measurements are in a sequence, such as percent herbaceous cover through time, the serial autocorrelation in such a data set can be addressed using familiar $ARMA(p, q)$ errors from a linear model, linked to the beta distribution by a copula (Guolo and Varin 2014). In such a scenario, the time series is considered to be *marginally* beta distributed. This approach has important advantages, including straightforward interpretation of regression coefficients and computational speed.

Hidden Markov models.— Hidden Markov models (HMMs) are a class of state-space model that treats observed values of a (potentially multivariate) time series as arising from distributions that depend on underlying states (Langrock et al. 2012). The states are not directly observable, but rather inferred from the measured time series (Patterson et al. 2017). This allows the researcher to detect behavioral changes that affect the series. The typical application is to model the step length and turning angles between successive GPS locations of an animal (Patterson et al. 2009). This treats the movement trajectory as a mixture of random walk models, where the distribution of lengths and angles are random draws from a pair of distributions whose parameters change with the underlying state (Zucchini et al. 2016). The most common example is a track composed of ‘travelling’ and ‘encamped’ behaviors (McClintock and Michelot 2018). When in a travelling state, step lengths will be long, and turning angles shallow. This produces directed movement that results in large spatial displacement of the individual. Encamped behavior, on the other hand, is characterized by short steps and large turning angles. This results in tortuous paths and a restricted area of movement.

While it would be desirable to assign specific behaviors to the states, such as migration and foraging, that is typically discouraged without sound justification of why such a behavior would produce the observed pattern exclusively of other behaviors (Zucchini et al. 2016; p. 231). This is particularly difficult in the typical step length and turning angle scenario, as foraging, social, or other relevant behaviors may produce similar patterns in the two variables.

II. DYNAMICS OF ANIMAL JOINT SPACE USE: A NOVEL APPLICATION OF A TIME SERIES APPROACH

Introduction

Quantifying spatial overlap, or joint space, use between individual animals is of interest in many branches of ecology. How animals utilize space is a function of many factors, including resource availability (Beyer et al. 2010), risk (Kohl et al. 2018), and competition (Berger and Gese 2007). How these factors affect interactions between individuals is of key importance for many ecological issues. For example, joint space use has been linked to animal contact rates, and thus disease transmission (Schauber et al. 2007, Magle et al. 2013), animal social behavior (Carter et al. 2013, Elbroch et al. 2016), as well as population genetics (Roffler et al. 2012). Though a common procedure, the analysis of joint space use remains problematic (Winner et al. 2018).

Ecologists commonly analyze space use in terms of an animal's utilization distribution (hereafter UD), the 2-dimensional relative frequency (probability) distribution of animal locations in space (Van Winkle 1975). UDs provide a continuous representation of the relative amount of time an animal spent at a given location, or the intensity of space use, facilitating easy interpretation (Figure 1). The probabilistic nature of UDs provides attractive properties that make them useful for home range estimation. For example, taking the isopleth contour at a given probability density can provide a demarcation of where an animal spent an arbitrary proportion of its time (Van Winkle 1975). However, utilizing the parent distribution in further analyses permits deeper inference into the spatial interactions between individuals.

Quantifying the degree of joint space use between 2 individuals permits the testing of a variety of hypotheses about inter-individual interactions (Fieberg and Kochanny 2005). The 3-dimensional intersection of 2 UDs provides an estimate of spatial overlap that incorporates information about the relative intensity of space use by each individual (Figure 1). This provides a more robust estimate of joint space use compared to 2-dimensional approaches that use

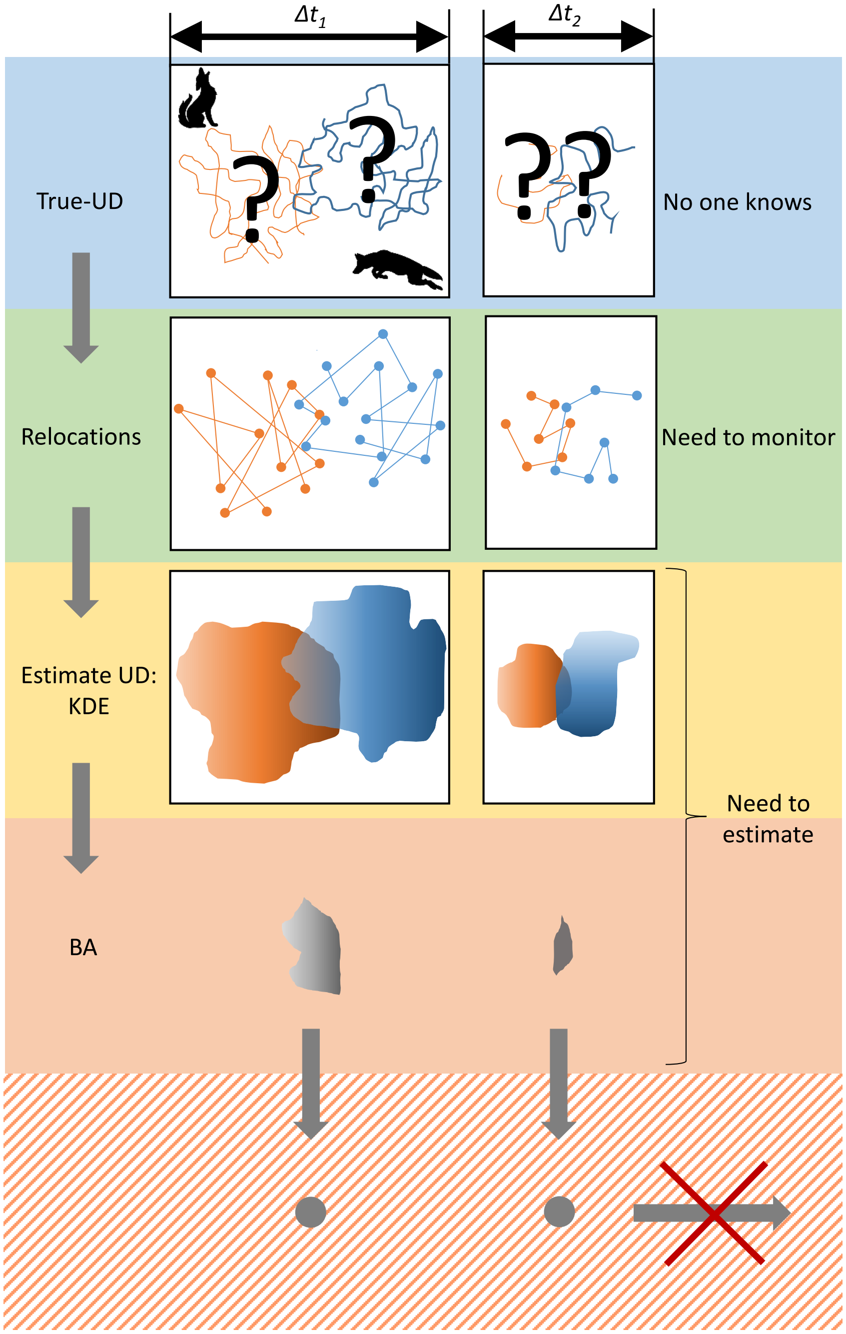

Figure II.1: Conceptual representation of previous approaches to analyzing joint space use by estimating the intersection of utilization distributions (UDs). This figure follows the sampling process and underlying idea of sampling from a true, but unknown, UD with GPS collars, to estimating the UD with kernel density estimators (KDEs), to finally deriving a measure of their 3-dimensional intersection with Bhattacharyya's Affinity (BA). These methods estimate joint space use over few, long blocks of time for further analyses.

the shared area of UD isopleths. This joint volume can be measured using several indices, however Bhattacharyya's Affinity (BA; Bhattacharrya 1943) has been shown to be minimally biased and has attractive properties that lend interpretability (Fieberg and Kochanny 2005). BA scales from 0 to 1, where 0 represents no spatial overlap and 1 represents identical space use. Theoretical bounds on behavioral metrics greatly facilitate ecological interpretation (Joo et al. 2018). Several authors have utilized these pairwise comparisons to examine changes in joint space use between blocks of time (*sensu* Schauber et al. 2007, Bauder et al. 2016, McColgin et al. 2018; Figure 1).

Though a common procedure in ecological literature, such an analysis oversimplifies temporal variation in joint space use. These interactions are dynamic in both time and space, making analysis of interactions inherently high-dimensional. Comparisons between few, relatively long time blocks provide limited insight into these processes, and overlook considerable temporal detail. Furthermore, they implicitly assume that animal space use patterns are stationary, or unchanging within the time period over which UDs are estimated (Lichti and Swihart 2011). This is unlikely to be the case for long periods of time, but such an assumption is much more reasonable over shorter intervals. Comparing UDs over finer, regular intervals (e.g. week or month) would reveal considerably more detail in patterns of spatial interactions, and permit statistical analysis of interaction dynamics, which was previously elusive (Kie et al. 2010).

I achieve such an analysis with a novel approach that synthesizes tools already familiar to ecologists and applies an appropriate regression framework. Abrahms et al. (2017) derived a UD-based index of space use stability by measuring the intersections of successive monthly UD estimates for an individual. Though they did not consider trends in the sequence of measurements, their approach is readily extendable to examine dynamic interactions using a time series framework (Kie et al. 2010, Shumway and Stoffer 2011), a logical avenue for the analysis of space use dynamics. When coupled, existing UD intersection metrics and time series analyses provide a simple, interpretable, and rigorously testable summary of complex dynamics of joint space use. This reduces a 5-dimensional problem (latitude, longitude, use intensity of 2 individuals, and time) to 2 manageable dimensions (spatial overlap and time). However, the bounded nature of BA precludes the use of standard regression procedures, such as normal linear regression or generalized linear models (GLMs). This is because members of the exponential family of distributions, for which GLMs are suited, do not accommodate continuous variables with an upper limit (Guolo and Varin 2014). Other, analogous methods are needed to link the index to covariates.

Copula regression methods are a commonly used alternative to traditional GLMs in the financial and actuarial sectors (Patton 2012) though, to my knowledge, their use in ecology is limited to one example (Eskelson et al. 2011). They accommodate any response distribution and are used to model complex correlation structures (Parsa and Klugman 2011). Recent work extends these methods to bounded time series (Guolo and Varin 2014), providing a link between the intersection index and explanatory variables.

Extending UD intersection metrics to a time series framework provides a flexible and interpretable approach to the analysis of space use interactions between individuals (Figure 2). Modeling joint space use in this way shows how the proportion of time 2 individuals use the same places changes through time, which is not only mathematically tractable, but intuitively understandable. This makes the results of my approach simple to communicate to both peers and non-scientists alike.

The success of this framework depends on the precision with which BA can be estimated with current GPS technology, which will affect both the sampling distribution of BA itself and the estimates of the effect of covariates on BA. Therefore, the goals of this work are: 1) To determine the precision with which BA could be estimated over reasonable sampling intensities; 2) to evaluate the accuracy and precision of effect size estimates of a covariate; and 3) to demonstrate the application of my methodology to a real data set. I simulated GPS data sets arising from known UDs at varying sampling intensities, then examined the precision of BA estimates from these simulations at high and low true values. I then evaluated the accuracy and precision of effect size estimates as sampling intensity increases. Finally, as an example, I examined the change in

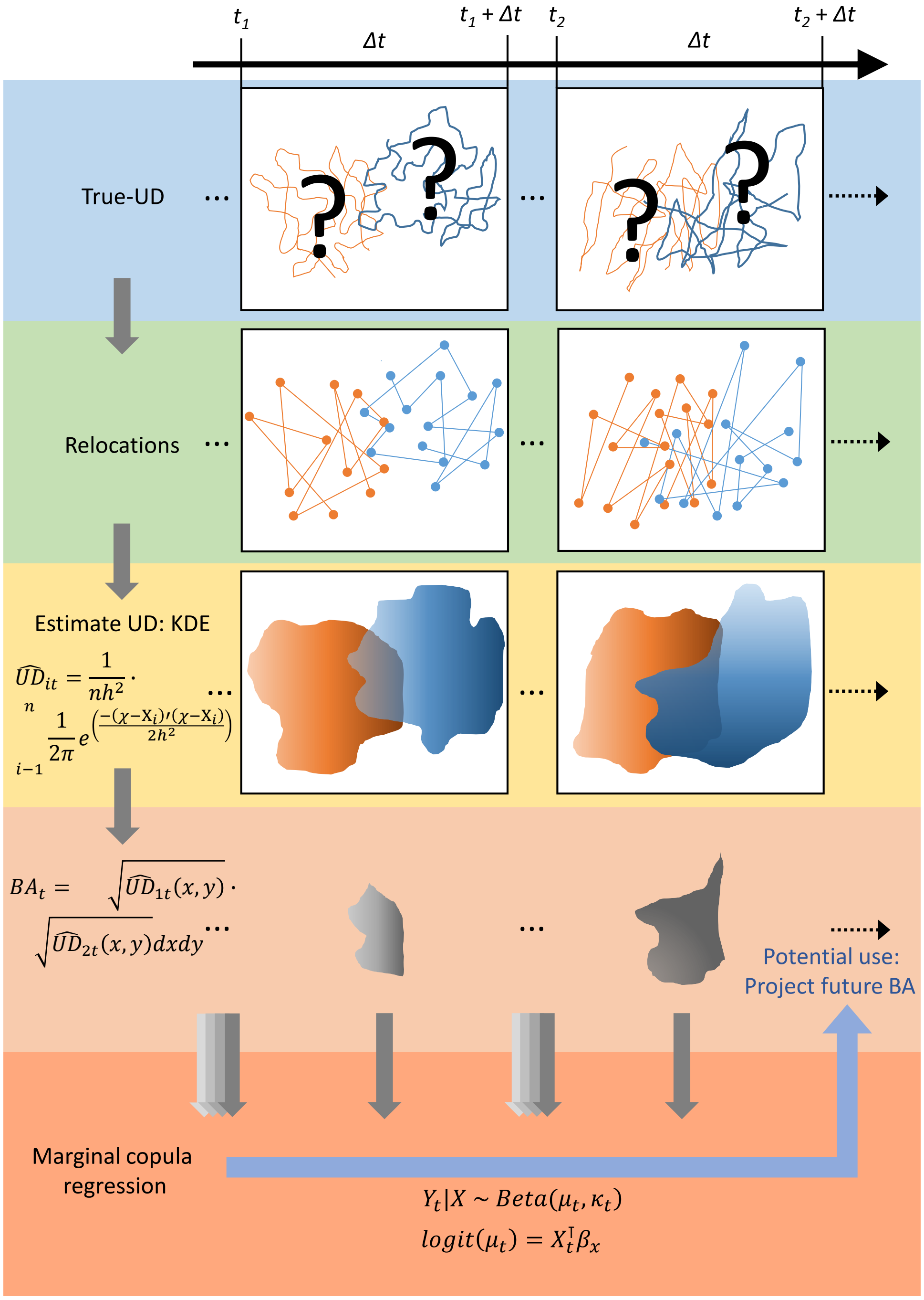

Figure II.2: My method extends previous approaches by adopting a short, consistent time interval (Δt) for estimating utilization distributions (UDs) and Bhattacharyya's Affinity (BA). This short Δt leads to a time series of BA values that captures much more information on the dynamics of joint space use.

spatial interaction of 2 coyotes (*Canis latrans*) in southern Texas in response to a carrion deposition event.

Material and Methods

Simulation Study

I expanded simulation methods previously developed to evaluate kernel density estimator (KDE; Worton 1989) performance as home range estimators (Seaman et al. 1999, Fieberg 2007). I used these simulations to a produce a known series of BA values with which I could compare estimates (Figure 2). Each series consisted of 100 time windows (t). The true UD of each individual was held constant for the first half of the series, shifted to produce a known change in BA at $t = 50$, and then held constant throughout the remainder of the series. I drew a specified number of locations from the true UD of each individual at each time window, representing artificial GPS location data, to examine bias and precision as sampling intensity increases. I used simple bivariate normal (BVN) UDs with equal, unit variances with means separated by a fixed distance. I induced a 0.60 change in BA at $t = 50$ by changing the distances between means from 3.580 to 1.319 (Figure 3).

I used a fixed KDE to fit a UD estimate for each individual at each time window. I used a bivariate normal kernel according to

$$\widehat{UD}_{it} = \frac{1}{nh^2}\sum_{i-1}^{n}\frac{1}{2\pi}exp\left(\frac{-(\mathbf{x}-\mathbf{X}_i)'(\mathbf{x}-\mathbf{X}_i)}{2h^2}\right) \tag{II.1}$$

where $\widehat{UD}_{it}$ is the estimated UD surface of animal i at time t, $\mathbf{x}$ is any location in 2-d space, $\mathbf{X}_i$ is the i^{th} observation of the animal's location, n is the number of observations, and h is a smoothing parameter (Worton 1989). I used the reference smoothing parameter for computational simplicity, calculated as

$$h = \sqrt{\frac{s_x^2 + s_y^2}{2}} \cdot n^{-1/6} \tag{II.2}$$

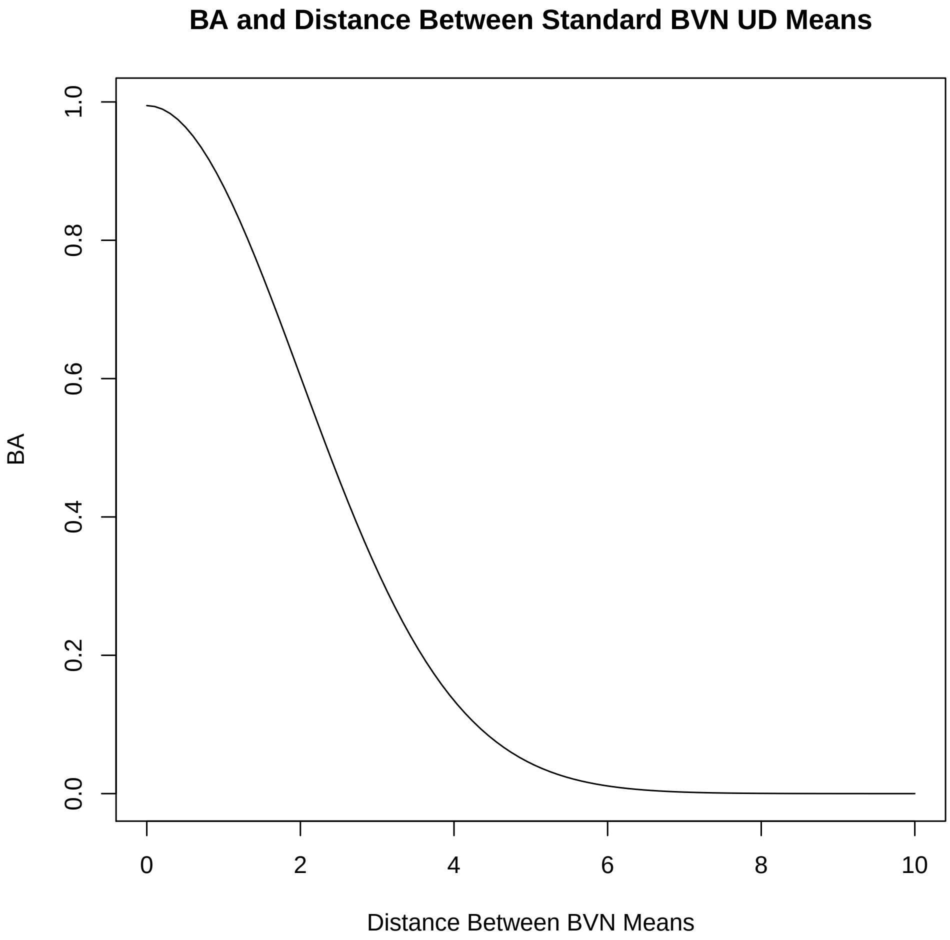

Figure II.3: Relationship between Bhattacharyya's Affinity (BA) of bivariate normal (BVN) distributions with unit variance and the distance between the BVN means.

where s_x^2 and s_y^2 are the variances of the x and y coordinates, respectively (Worton 1995).

I then calculated BA between the 2 simulated individuals at each time window to obtain a series of BA estimates,

$$BA_t = \iint \sqrt{\widehat{UD_{1t}}(x,y)} * \sqrt{\widehat{UD_{2t}}(x,y)}dxdy \tag{II.3}$$

where $\widehat{UD_{1t}}$ and $\widehat{UD_{2t}}$ are the UD estimates of individuals 1 and 2, respectively, at time t. I evaluated the bias and precision of BA estimates for sampling intensities of 50–1000 locations per temporal window, at increments of 50. I fit KDEs and calculated BA using the *adehabitatHR* package (Calenge 2006) in R (R Core Team 2017).

I then evaluated how well I could estimate the effect size (magnitude of change) in BA due to my simulated disturbance at $t = 50$. I used a marginal beta regression with a Gaussian copula (Guolo and Varin 2014) of the form

$$\begin{aligned} Y_t|X &\sim Beta(\mu_t, \kappa_t) \\ logit(\mu_t) &= X_t^\top \beta \end{aligned} \tag{II.4}$$

where $Y_t|X$ is the value of the BA series at time t, given covariates X, μ_t and κ_t are the mean and precision of the beta distribution at time t, respectively, and β is the vector of regression coefficients. Copula methods exploit the probability integral transformation to relate the beta distributed response Y_t to covariates X_t,

$$Y_t = F_t^{-1}\{\Phi(\epsilon_t); \beta\} \tag{II.5}$$

where Y_t is assumed to be marginally beta distributed, $F_t^{-1}\{\cdot; \beta\}$ represents the appropriate cumulative density function linking the density to covariates (see Guolo and Varin 2014), and $\Phi(\epsilon_t)$ is the cumulative distribution function of the normal distribution with mean 0 and variance ϵ_t. Residual serial dependence is addressed using stationary autoreggresive and moving average ($ARMA(p, q)$) terms

$$\epsilon_t = \sum_{i=1}^{p} \psi_i \epsilon_{t-i} + \sum_{j=1}^{q} \lambda_j \eta_{t-j} + \eta_t \tag{II.6}$$

where ϵ_{t-i} is the error of the previous observation, ψ_i is an autoregressive parameter vector, λ_j is a moving average parameter vector, and η_t are independent zero-mean normal variables (Guolo and Varin 2014). Parameters are estimated with maximum likelihood. The copula-based approach separates the linear predictor from the correlated error structure, meaning the regression coefficients are interpreted in the same manner as a GLM and not confounded by the

$ARMA(p,q)$ term (Guolo and Varin 2014).

I fit marginal beta regression models using a binary covariate corresponding to the known change in UDs at $t = 50$ using the *gcmr* package (Masarotto and Varin 2017). In ecological terms, this is analogous to estimating the effect of the presence of a resource, the implementation of some disturbance, a hypothesized season, or some other relevant binary variable, on the degree of spatial interaction between two individuals. I replicated the entire process 100 times for each level of sampling intensity to obtain the sampling distribution of my effect size as a function of sampling intensity.

Application to Empirical Data

I then used field data representing 2 coyotes to demonstrate the practical utility of my approach in describing the dynamics of animal space use (Figure 4). I collected these data on the East Foundations 61,000 ha San Antonio Viejo Ranch (SAVR) in Jim Hogg and Starr counties in southern Texas. The East Foundations ranches are managed as a living laboratory to promote the advancement of land stewardship through ranching, science, and education. The area is dominated by shrub savannas, primarily composed of honey mesquite (*Prosopis glandulosa*), prickly pear (*Opuntia* spp.), cat-claw acacia (*Acacia greggii*), blackbrush (*Acacia rigidula*), whitebrush (*Alloysia gratissima*), and granjeño (*Celtis palida*), with early to mid-successional grasses, including three-awns (*Aristida* spp.), little bluestem (*Schizachyrium scoparium*) and windmill grasses (*Chloris* spp.).

I captured individuals by helicopter using a net gun (Gese et al. 1987), fitted them with a Vertex Plus or Vertex Lite GPS collar (Vectronic Aerospace GmbH, Berlin), and released them at the site of capture on 10 December 2016 (n = 1) and 1 April 2017 (n = 1) as part of an ongoing study of coyote space use. These collars collected location data every 2 hours until 31 December 2017, when they automatically released from the animal. While my collars collected location data synchronously, this is not strictly necessary for my analysis, provided the sampling intensity is the same. To standardize across collars, I omitted data prior to 1 April 2017 from the analyses presented below. Both coyotes were considered territorial (Kamler and Gipson 2000), and

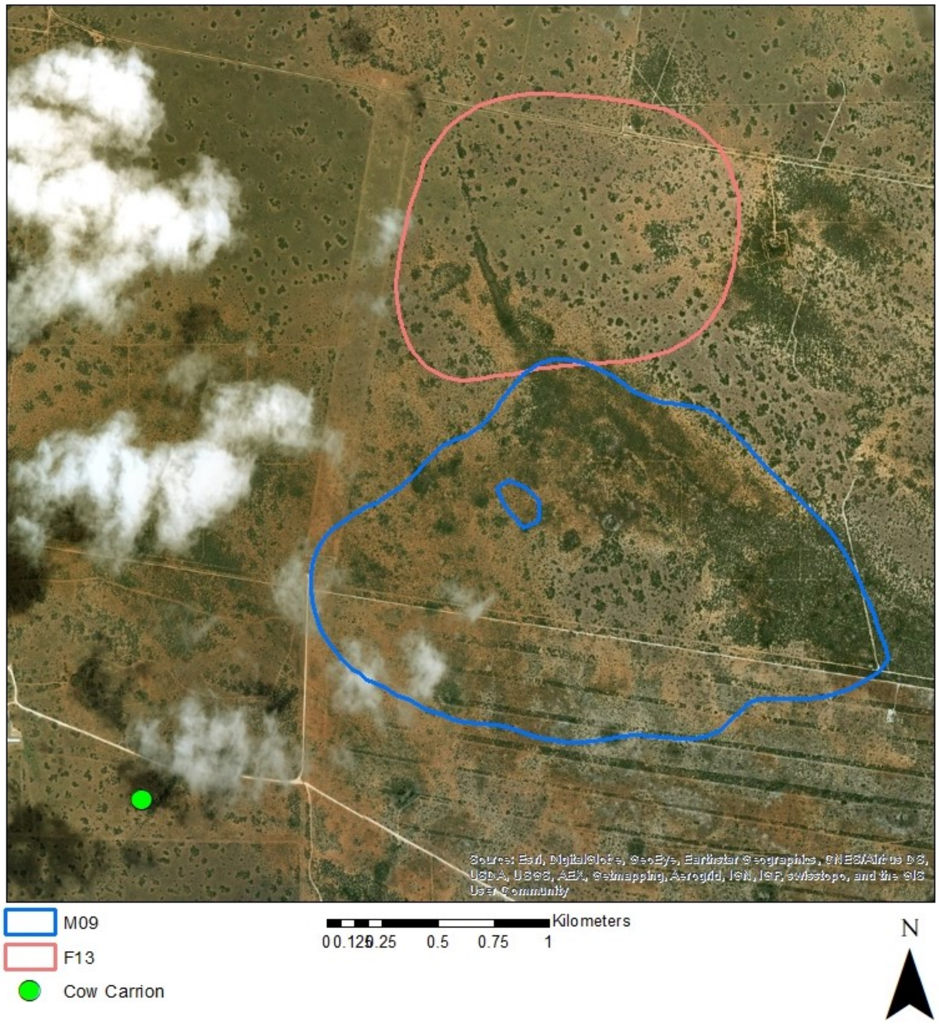

Figure II.4: Territories of the 2 GPS-collared, coyotes M09 and F13, used in my example from the East Foundation's San Antonio Viejo Ranch. Territories were delineated using the 75% isopleth of a fixed kernel density estimate of all locations for each individual. Note the location of the carrion resource near, but outside, both territories.

occupied distinct, non-overlapping territories. A domestic cow (*Bos taurus x B. indicus*) died of unknown causes in an area well outside both territories (Figure 4) during the week of 23 September 2017. Coyotes alter their patterns of space use to utilize carrion resources (Hein and Andelt 1996), so this event afforded me the opportunity to evaluate whether my methods would detect a change in spatial overlap between the coyotes in response to the presence of carrion.

I included time relative to death of the cow (before or after) as a dummy coded variable

$$x_t \in \{0, 1\}$$
$$x_t = \begin{cases} 0, & \text{if } t < t_{carrion} \\ 1, & \text{if } t \geq t_{carrion} \end{cases} \tag{II.7}$$

where $t_{carrion}$ is the week of carrion deposition, to test whether that event had a persistent effect on the mean BA. Autocorrelation was modeled with $ARMA(1, 1)$ terms. This model is consistent with an interrupted time series design (Bernal et al. 2017) and is analogous to an ANOVA for a beta-distributed variable with serial dependence. The resulting regression form consists of the marginal model

$$\begin{gathered} BA_t | x_t \sim Beta(\mu_t, \kappa_t) \\ logit(\mu_t) = x_t\beta_1 + \beta_0 \end{gathered} \tag{II.8}$$

and copula

$$\begin{gathered} \Phi(\epsilon_t) \\ \epsilon_t \sim ARMA(1, 1) \end{gathered} \tag{II.9}$$

Succinctly, this model tests for a persistent change in spatial interaction between 2 coyotes following the carrion deposition event, and estimates its magnitude.

Results

Simulation Study

My simulation showed that reasonably precise estimates of BA can be achieved with 150 sampled locations per time window at both high and low values of BA ($s.e. = 0.029$; Figure 5). Estimates based on as few as 50 relocations per window could be useful if the hypothesized effect of some covariate is sufficiently large. These results also suggest a slight positive bias at low BA values, which decreases with sampling intensity. At 50 locations per window, the average bias at a true

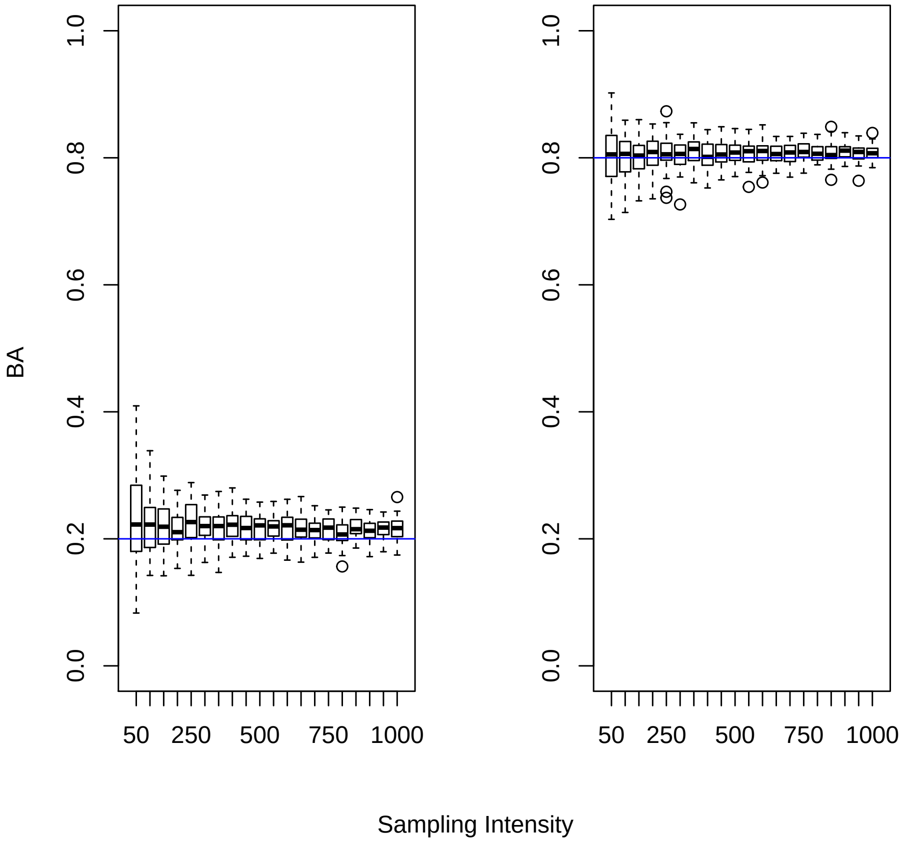

Figure II.5: Estimated effect size of binary covariate on Bhattacharyya's Affinity (BA) as a function of sampling intensity (sampled locations per time window). The blue line represents the true effect size.

BA of 0.20 was 0.0311 ($SE =$ 0.00919), while at a true BA of 0.80 the average bias was -0.00077 ($SE =$ 0.00641). The bias at low BA declined with increasing sampling intensity to 0.0155 ($SE =$ 0.00253). The average bias at high true BA values never exceeded 0.0105 ($SE =$ 0.00342).

Parameter estimates from regression models stabilized quickly at 150 relocations, while error around the prediction slowly contracts beyond that point (Figure 6). These estimates were slightly negatively biased, with an average bias of -0.0427 ($se =$ 0.00106) at 50 locations/window,

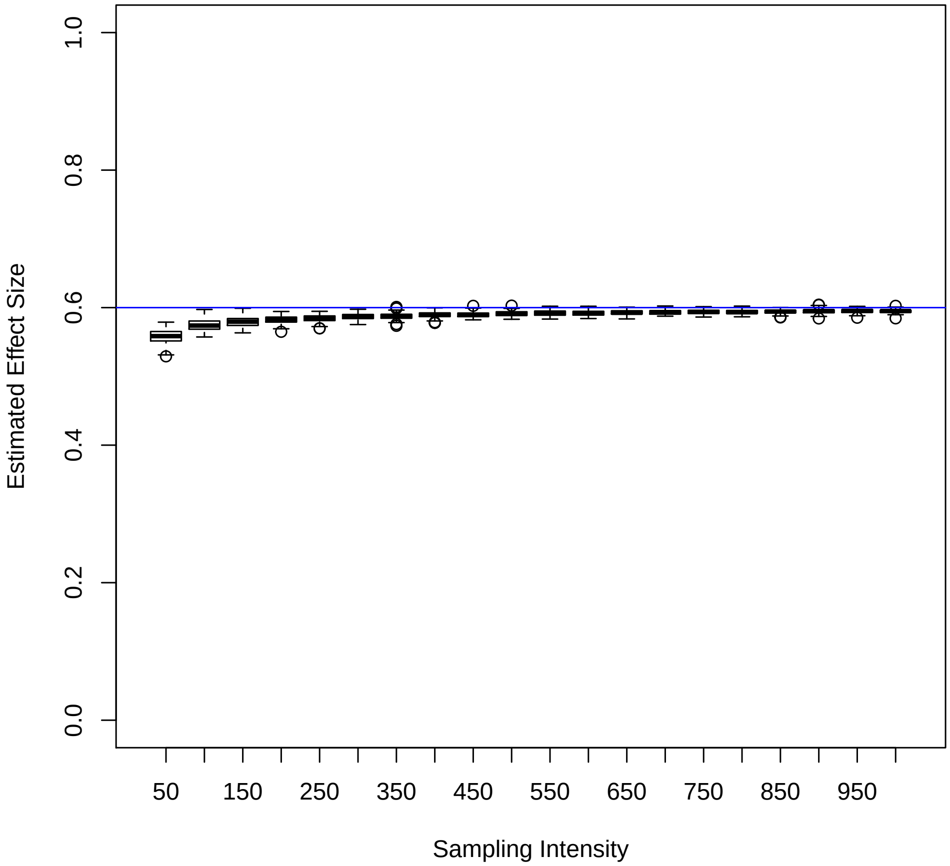

Figure II.6: Distribution of estimated Bhattacharyya's Affinity (BA) values as sampling intensity increases. Blue lines represent the true BA values of the parent utilization distributions.

decreasing to a minimum of -0.00508 ($se = 0.00106$) as sampling intensity increased. This is likely due to the slight positive biases of low-valued BA estimates as these biases were strongly negatively correlated ($r =$ -0.784).

Application to Coyote Data

The time series of BA values between the two coyotes indicated an obvious change in behavior following the appearance of the carrion resource (Figure 7) and the beta regression model showed a significant effect of the carrion event ($P < 0.001$; Figure 7). The average UD intersection increased by 0.246, meaning that, on average, the 2 coyotes spent approximately 25% more time in the same places following the carrion deposition event. Upper and lower 95% CIs of this effect were 0.437 and 0.092, respectively. The graphs of observed and fitted values (Figure 7), and the residuals (Figure 8A) showed unaccounted structural differences between weeks 0-9 and weeks 10-24. Weeks 20, 27, 29, and 36 were identified as potential outliers (Figure 8B), but overall the distributional form was appropriate. The $ARMA(1,1)$ terms were significant ($P < 0.001$ for both). Autocorrelation diagnostic plots supported the appropriateness of the assumed autocorrelation structure (Figure 8C-D).

Discussion

My results are a proof of concept for the use of sequential measurements of UD intersections in a time series framework to capture dynamics of spatial interactions between 2 individuals. Results with simulated data reveal slight positive biases in low-valued BA estimates leading to slight negative biases in effect size estimates. However, the effect of such small biases on the ecological interpretation of results likely would be negligible in most cases. Further, sampling error is reasonable at achievable sample sizes with current GPS technology. My framework is based on familiar analytic tools and results are readily interpretable. The framework also provides a much more detailed view of interactions through time compared to existing methods, as I demonstrated with the coyote example.

Practical Application and Performance

Various authors have reported minimum numbers of locations required to obtain a reliable UD estimate with the methods I used (Worton 1995, Seaman et al. 1999, Borger et al. 2006). My simulations show acceptable results using a first-generation estimator with 150 samples per UD

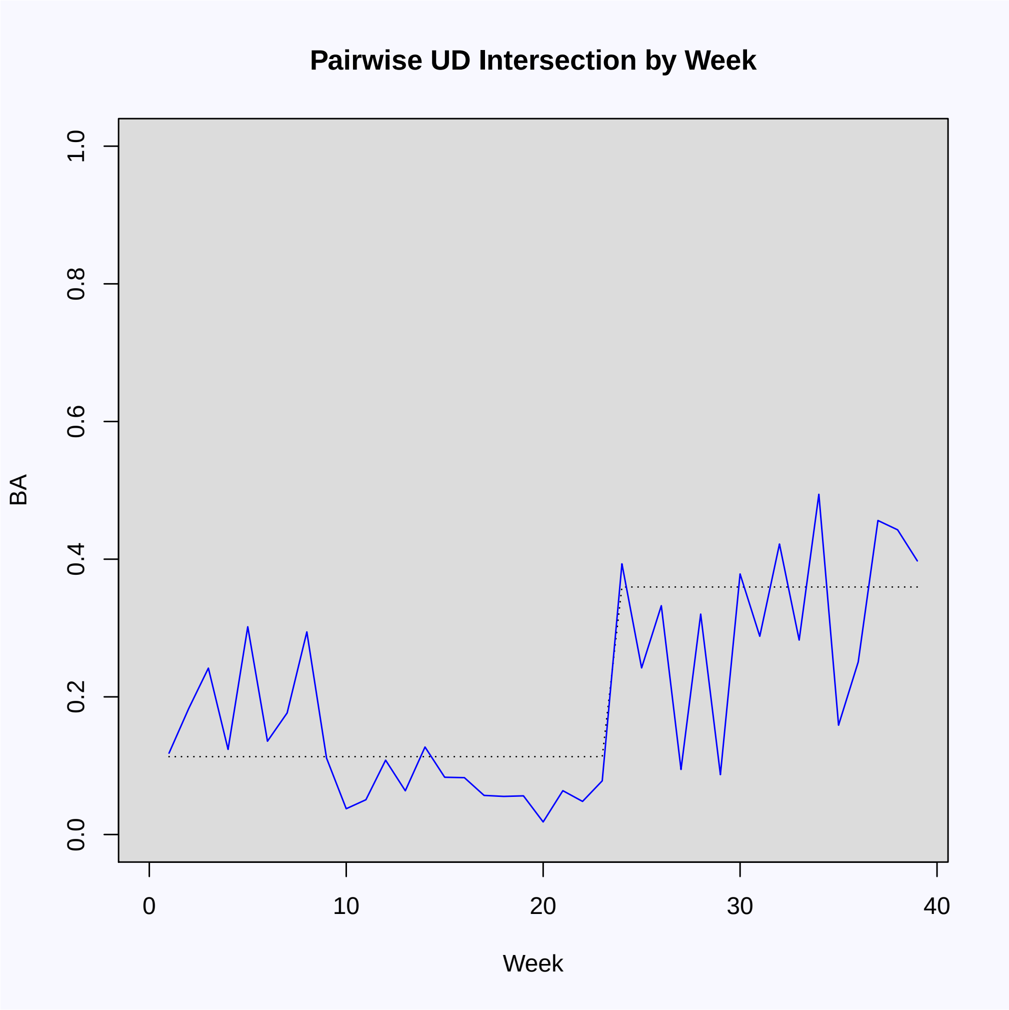

Figure II.7: Time series of joint space use between the 2 GPS-collared coyotes from the East Foundation's San Antonio Viejo Ranch, measured by Bhattacharyya's Affinity (BA; blue line) and fitted values of the copula regression model (black, dashed line).

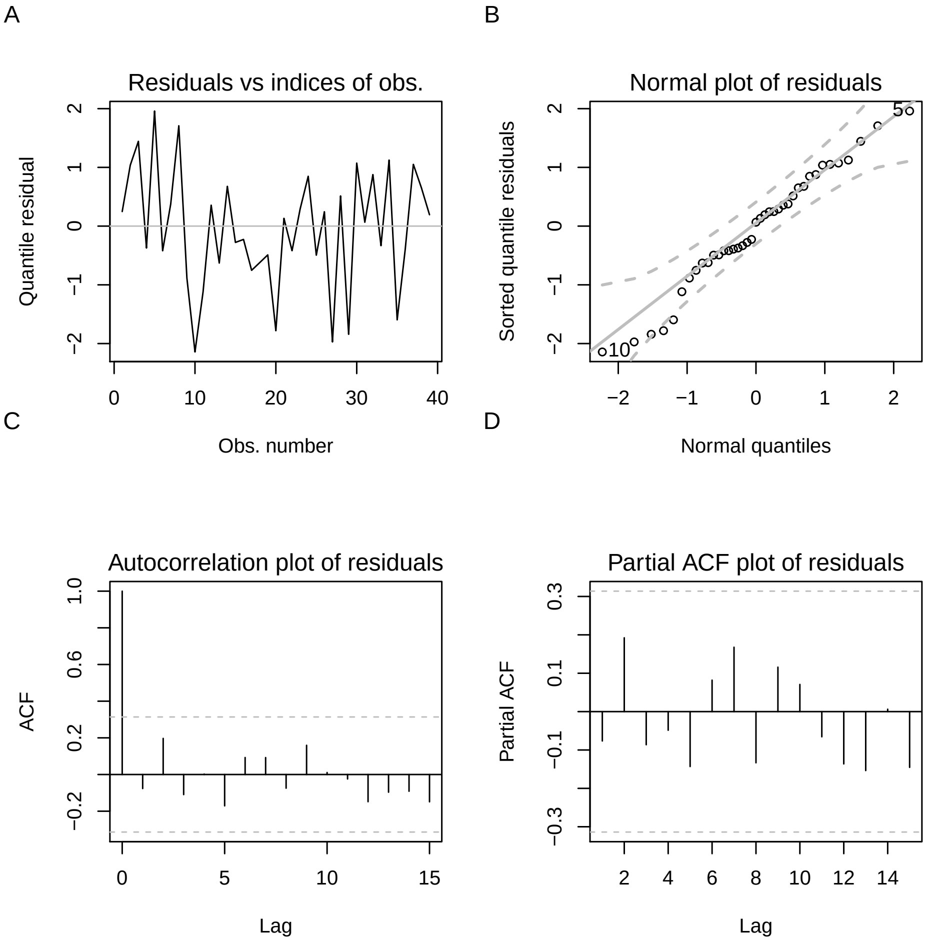

Figure II.8: Residual diagnostics of beta regression model of two coyotes from the East Foundation's San Antonio Viejo Ranch. A) The plot of residuals through time shows an unaccounted for structural difference between weeks 0-9 and subsequent weeks, as well as potential outliers at weeks 20, 27, 29, and 36. B) The Q-Q plot shows reasonable model performance, again suggesting possible outliers at weeks 20 and 36. C-D) Autocorrelation and partial autocorrelation plots show no significant residual autocorrelation, meaning the $ARMA(1,1)$ term adequately captured the dependence structure.

window and 100 windows, approximating hourly collection intervals over a a 2-year period. This sampling regime is common for larger species (Bar-David et al. 2009, Gautestad et al. 2013, Bohrer et al. 2014), yielding 168 locations per week. This sampling intensity is sufficient to generate reliable UDs, given the inherently unbiased design of sampling at regular time intervals

(Worton 1995, Seaman et al. 1999), and gave adequate performance in my simulations. This sampling intensity is relatively easy to achieve for large species, but presently unattainable for smaller species incapable of carrying large batteries. These constraints may be alleviated by improvements in battery technology and efficiency of GPS collar circuits, as well as more efficient UD estimators.

The precision of BA estimates is a function of the performance of the KDE method used. While I utilized a first-generation estimator for simplicity and computational speed, any KDE method is suitable for this approach and the appropriate estimator will depend on the particular research question (Steury et al. 2010, Lichti and Swihart 2011). Given that the true UDs in my simulations were bivariate normal, my use of the reference parameter is justified in the literature (Worton 1989, Seaman et al. 1999). However, this procedure is known to overestimate the 95% isopleth area of more complex UDs (Naef-Daenzer 1993, Seaman and Powell 1996, Seaman et al. 1999), suggesting that the density in the tails of the UD is overestimated. This may also be the case in my simulations, which would explain the greater degree of bias when the UDs intersect mainly in their tails (at low true BA values). This greater positive bias at low values would compress effect size estimates in cases when BA increased following disturbance, as in my simulations. On the other hand, if the effect was negative following the disturbance, its magnitude would be slightly overestimated. The magnitude of the bias is small in either case, as indicated at my lowest sampling intensity. A bias of 3% (my largest average bias) is unlikely to affect ecological interpretation of results, and may be safely considered negligible in most cases. More sophisticated methods may be less biased in the tails of the UD, reducing bias in parameter estimates. The relative performance of various KDE procedures within this context is an open question that warrants further research.

Further Development

Beyond technological improvements, there are analytical limitations to overcome to realize the full potential of my approach. My techniques provide pair-level series, permitting analysis at the dyad level. Population level inference will require multivariate time series methodologies that accommodate potentially non-independent, beta-distributed response variables, which to my knowledge are currently unavailable. However, such methods do exist for short, non-stationary, Gaussian series that could serve as a conceptual basis for similar approaches with beta-distributed response variables (Zuur et al. 2003). Additionally, the approach I demonstrate here treats BA measurements as fixed values, though I show that they are estimated with error. Recent work provides a potential means to handle this source of error (Winner et al. 2018), and an appropriate hierarchical structure could be derived.

Advantages of this Approach

The residual analysis of the beta regression model of coyote interactions reveals an important advantage of my approach; there is another period of interaction early in the series that I have captured, but failed to explain (Figure 8). This early period of interaction would have been masked in a simple analysis of UD intersections before and after the death of the cow, as would be done using previous methods. Assuming space use itself to be stationary over these time blocks is unwarranted. The time series framework I propose captures the nonstationary dynamics of space use patterns and provides a means to explain them. Additionally, my methodology yields a statistical test of the effect that until now was not possible. Although (Winner et al. 2018) produced a method to test the significance of a single BA estimate, my framework permits modeling the influence of 1 or more variables on the dynamics of joint space use in an interpretable way.

Each stage of my framework was selected for straightforward interpretability (Figure 9). The probabilistic nature of UDs, and their widespread use by ecologists make them an attractive starting point. The intuitive interpretation of BA as a symmetric index of how much 2 individuals use the same space makes it a natural choice. More subtly, the choice of marginal copula regression over other appropriate time series methods also aids interpretability. The separation of the regression component from the correlated error structure allows straightforward interpretation of model coefficients, which is not possible with other available methods (Guolo and Varin 2014). Despite the substantially different mathematical architecture, this means that interpretation of

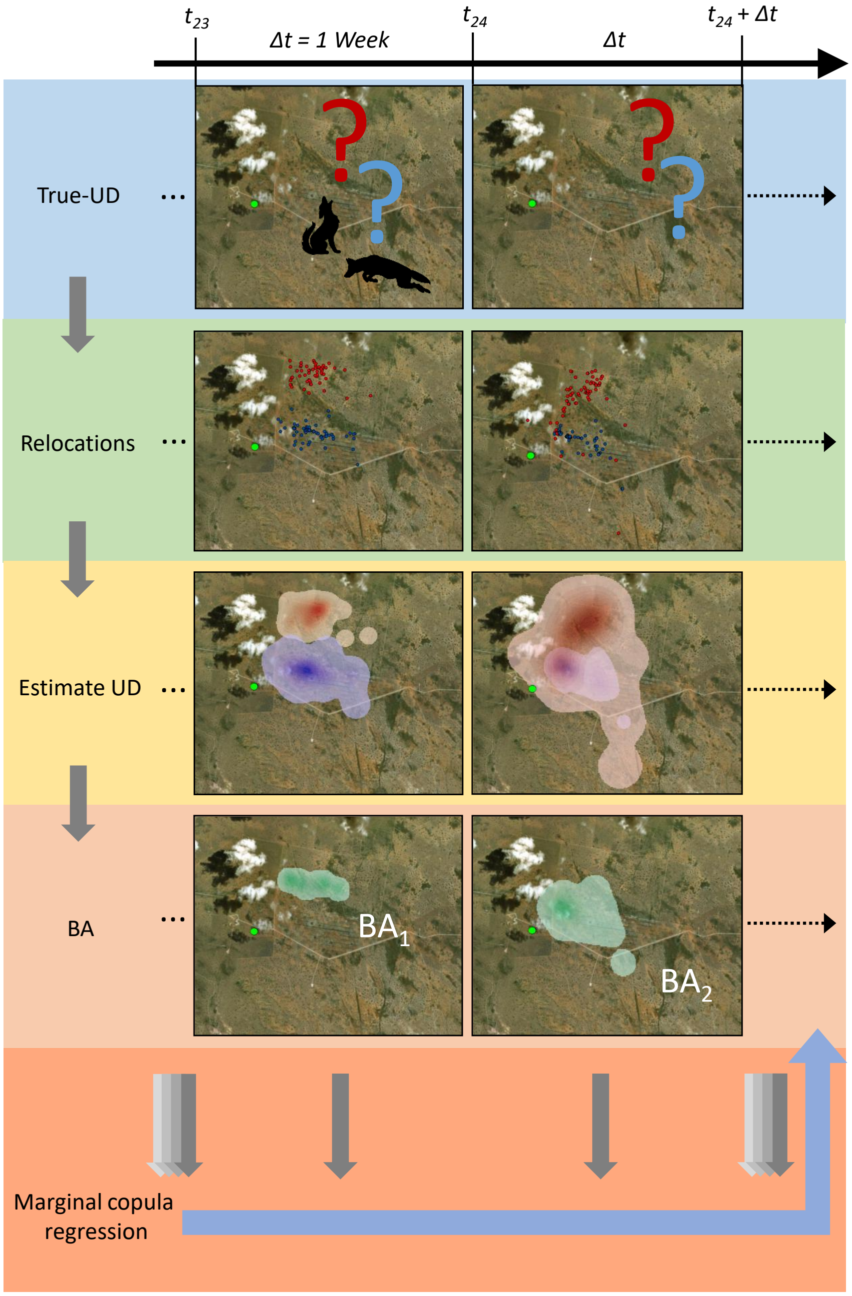

Figure II.9: Visualization of the quantification of joint space use by the 2 coyotes from the East Foundation's San Antonio Viejo Ranch during the week prior to the carrion deposition event (t_{23}: carrion location marked with green dot) and during the week in which the event occurred (t_{24}). Relocation data are analyzed to estimate the 2 individual space utilization distributions (UD; red dots and shading for the female, blue for the male), from which the joint UD volume is calculated (the integral of which is BA), which indicates the area of joint space use (green shading).

model coefficients is done in the same manner as GLMs, which are common in ecological literature. This familiarity makes my approach easily accessible to ecologists.

The results of my approach are also readily visualized, which is of great heuristic value and lends intuitive context to the quantitative results. For example, I can visualize the change in joint space use by the 2 coyotes immediately before and after the carrion deposition event (Figure 9). Mapping the UDs and the joint UD volume (the integral of which is BA) shows that joint space use before the event was concentrated along the boundary between the 2 territories. After the event, joint space use increased markedly as the female expanded her activity range toward the southeast, engulfing the activity range of the male, which also shifted slightly toward the southeast. Interestingly, both individuals moved synchronously away from the carrion initially, and did not converge on it until the following week. The cause of these movements remains unknown, but their identification provides important contextual information that aids interpretation and the generation of ecologically-based hypotheses.

I argue that these properties also simplify communication of results to scientific peers and non-scientist stakeholders alike. The statement “on average, the 2 coyotes spent 25% more time in the same places each week after the carrion resource became available" is an accurate and meaningful interpretation of my results. An important caveat is that the individuals were not necessarily in those places at the same time within the week. Thus, the temporal grain and scale used in the analysis will affect interpretation. Nonetheless, such a statement carries implications for a variety of disciplines.

This work represents a marked advance towards informative, tenable analysis linking variables to the dynamics of joint space use that is also communicable to non-scientists. This methodology has applications in many areas of applied ecology where the dynamics of animal interactions are of interest. Given limited time, money, and material resources, successful management requires focused efforts. My methodology provides needed information that is intuitively understood by stakeholders. This facilitates effective communication between scientists and decision makers, ideally leading to efficient, spatio-temporally targeted management actions supported by valid analyses.

III. BEHAVIOR AND DISPERSAL CHARACTERISTICS OF A LARGE, UNHARASSED COYOTE POPULATION

Introduction

Mammalian carnivores are commonly implicated in conservation issues around the world, (Sinclair et al. 1998, Bodey et al. 2011, Marolla et al. 2018) and their impacts on humans are as old as civilization itself (Frank and Conover 2015). Despite this long history, effective management and conservation strategies for minimizing the negative effects of carnivores remain elusive (Karki et al. 2007, Lavers et al. 2010, Mahoney et al. 2018).

Carnivore management is currently limited by our understanding of how behavior is linked to population processes. Individual animal movement and space use are believed to drive population processes, but empirical linkages between individual behavior and population processes remain rare (Morales et al. 2010). Dispersal is a key behavior driving population dynamics over space. The frequency at which individuals disperse, and the movement capacity of dispersing individuals are key factors affecting persistence of spatially structured populations (Bowne and Bowers 2004, Revilla and Wiegand 2008). Though complex, animal dispersal traditionally has been treated simplistically as a fixed process represented by a single emigration parameter, despite poor predictive performance of this approach (del Mar-Delgado and Penteriani 2008). Heterogeneity in animal dispersal behavior has been linked to the dynamics of spatially structured populations in model systems (Clobert et al. 2009). Much of carnivore management focuses on influencing local population dynamics, by excluding or eliminating individuals from focal areas (Bjorge and Gunson 1985, Boisjoly et al. 2010, DeCesare et al. 2018). However, managers rarely consider the influence of population processes on the cost effectiveness of management actions (Engeman et al. 2002, Baxter et al. 2008, Engeman et al. 2010).

Historically, carnivore management focused on livestock protection through both lethal and nonlethal means. Studies of the effectiveness of nonlethal methods have shown mixed results, thus carnivore management efforts still commonly focus on lethal control (Doherty and Ritchie 2017, Moreira-Arce et al. 2018). These methods are subject to public scrutiny, (Schwartz et al. 2003, Slagle et al. 2017) and are not reliably effective at achieving management goals (Beauchamp et al. 1996, Bolton et al. 2007, DeCesare et al. 2018). Compensatory immigration leads to short lived effects of population reduction as dispersing individuals recolonize newly vacant areas (Frey and Connover 2007, Lieury et al. 2015). Thus, effective carnivore management requires better understanding of dispersal behavior.

Coyotes (*Canis latrans*) are an ideal species for studying the management implications of dispersal behavior, and are a widespread species of economic and public health concern. They remain difficult to manage, despite a century of scientific inquiry (Goldman 1930, Kilgo et al. 2014). Management efforts focus on lethal approaches to solve livestock depredation (Pearson and Caroline 1981, Conner et al. 1998, Knowlton et al. 1999, Blejwas et al. 2006, Harrington and Connover 2007), conservation (Boisjoly et al. 2010, Brown and Connover 2011, Orning and Young 2017), and disease (Knowlton 1972) issues. Such efforts are usually ineffective at producing desired management outcomes, such as reducing livestock losses, or increasing survival or recruitment of wildlife species (Cypher and Scrivner 1992, Hurley et al. 2011, Kilgo et al. 2014), or achieving sustained population reduction (Knowlton 1972, Mosnier et al. 2008). As with other carnivores, these failures are largely attributed to compensatory immigration (Windberg and Knowlton 1988, Conner et al. 1998, Wagner and Conover 1999, Mosnier et al. 2008). Scientific understanding of this process remains limited.

Coyote life history is characterized by territorial behavior, a land-tenure system where residents defend territories from neighboring or transient individuals (Bekoff and Wells 1986, Kamler and Gipson 2000). Most studies of coyote behavioral ecology are predicated on a binary classification of individual coyotes (e.g. territorial-transient or resident-transient; Bowen 1982, Gese et al. 1988*c*, Windberg and Knowlton 1988, Windberg et al. 1997, Kamler and Gipson 2000, Gese 2001, Sequin et al. 2003, Hinton et al. 2015, Sasmal et al. 2019). Territory occupancy is linked to individual survival (Gese et al. 1988*b*) and reproductive success (Windberg 1995).

Theoretical work suggests that territory occupancy should confer foraging benefits as well, including better access to food and thus less energy expended foraging (Peres 1989). Transient strategies, conversely, are thought to contribute to the resilience of coyote populations by allowing rapid colonization of vacant habitats (Hinton et al. 2012, 2015), which undermines traditional lethal management techniques through compensatory immigration (Windberg and Knowlton 1988). Coyote territorial boundaries are stable in space through time, even over several generations of occupants (Andelt 1985, Young et al. 2006), thus the dynamics of occupant turnover may be an important factor in coyote population dynamics (Windberg and Knowlton 1988). Such a spatially structured population (Sample et al. 2017), where social groups occupying a territory represent sub-populations, is connected by transient dispersal. In this scenario, emigration is defined as the act of a territorial resident departing into a transient state, while immigration represents an individual gaining access to a territory and absorbing into the social group within it.

Resident and transient behaviors lead to differential patterns in space use (Kamler and Gipson 2000), thus space use is the most common criterion for differentiating between resident and transient coyotes (Andelt and Gipson 1979, Mitchell et al. 2015, Ward et al. 2019). Residents display small, stable ranges while transients have large ranges that shift through time. Behaviors of transients are also thought to be more variable than behaviors of residents. For instance, transient coyote range sizes may vary seasonally, while resident ranges are consistent across seasons (Sasmal et al. 2019). Methods used to differentiate these behaviors are usually simplistic, typically focusing on asymptotic home range size (*e.g.* Bowen 1982) or relative range size between individuals for the duration of the study (*e.g.* Kamler and Gipson 2000), both of which fail to capture changes in behavior through time and may mask other important behaviors.

Summarizing dispersal as simply ‘transience’ fails to capture important variation in behavior that contributes to coyote survival. Variation in dispersal can be the result of individuals choosing between a fixed set of behavioral strategies through time (del Mar-Delgado and Penteriani 2008). By treating dispersing individuals homogeneously as transients, the coyote literature has effectively ignored the possibility of multiple strategies with different implications for mortality risk, population connectivity, and ultimately population persistence (Revilla and Wiegand 2008). However, some authors recognize additional classes, such as biding individuals that move between relatively small, temporary ranges (Morin and Kelly 2017), or dispersers that travel long distances to new areas (Gese et al. 1988*b*). These additional strategies may carry different costs to the individual, which ultimately affect population dynamics. Indeed, neglecting effects of multiple dispersal strategies and individualistic combinations of behaviors leads to poor predictions of population dynamics (del Mar-Delgado and Penteriani 2008). Only a few studies have expressly acknowledged the dynamic nature of these strategies (Morin and Kelly 2017), whereas others have reported observations of behavioral changes but ignored them in their analyses (Sasmal et al. 2019). Thus, dispersal strategies and their temporal dynamics remain poorly studied.

The recent maturation of state-space models has provided an opportunity to examine dispersal dynamics, giving researchers the power to formally confront complex hypotheses with empirical data (Patterson et al. 2017). Hidden Markov models (HMMs), a class of state-space models that treats observed values of a time series as arising from distributions that depend on underlying states (Langrock et al. 2012), are one such approach. Generally, HMMs focus on modeling step length and turning angles of the movement process sampled by GPS collars, where interpretation of the underlying states is limited by a lack of ecological context (Zucchini et al. 2016; p. 231). Despite the limitations of previous studies, patterns of space use are a logical avenue for identifying territorial behavior. The defensible links between coyote behavior and space use lend interperetability to the latent states. For coyotes, small, stable ranges would indicate residence, while large unstable ranges would be consistent with transience (Kamler and Gipson 2000). Given that their activity focuses on the periphery of one or a few territories, biding coyotes would exhibit range sizes larger than those of resident individuals but smaller than those of transients (Morin and Kelly 2017). Stability should also be intermediate as they itteratively move between interstitial spaces between territories. HMMs naturally fit the idea of individuals changing between a set of behavioral strategies which manifest themselves in different patterns of space use through time (Bowler and Benton 2005).

The validity of any binary or trinary scheme has never been expressly tested. This represents an opportunity to examine the complexity evident in coyote social systems and evaluate the common, but untested, resident–transient assumption of coyote behavior. In this paper I studied an unharassed coyote population in southern Texas, a region with consistently high coyote densities (Knowlton 1972, Andelt 1985, Windberg 1995, Bekoff and Gese 2003). I evaluated competing binary and trinary characterizations of territoriality and examined the dynamic nature of territorial status using hidden Markov models. I also evaluated whether sex or time of year influenced the probability of coyotes changing behavioral states, reflecting sex-biased and seasonal dispersal, respectively. Finally, I examined whether transient or biding coyotes exhibited seasonal patterns in range sizes, which would indicate seasonal pattern in the spatial extent of dispersal. This study is the first to explicitly examine these dynamics within a coyote population in an objective way.

Methods

Study Area

This study was conducted on the East Foundations 61,000 ha San Antonio Viejo Ranch (SAVR) in Jim Hogg and Starr counties in southern Texas. The East Foundations ranches are managed as a living laboratory to promote the advancement of land stewardship through ranching, science, and education. The area is dominated by shrub savannas, primarily composed of honey mesquite (*Prosopis glandulosa*), prickly pear (*Opuntia* spp.), cat-claw acacia (*Acacia greggii*), blackbrush (*Acacia rigidula*), whitebrush (*Alloysia gratissima*), and granjeño (*Celtis palida*), with early to mid-successional grasses, including three-awns (*Aristida* spp.), little bluestem (*Schizachyrium scoparium*) and windmill grasses (*Chloris* spp.). Given the East Foundation's mission of wildlife research and stewardship, lethal harvest and harassment of native animals, including coyotes, has been prohibited on SAVR since the East Foundation's inception in 2007. This region persistently features high coyote densities (Knowlton 1972, Andelt 1985, Windberg 1995, Bekoff and Gese 2003).

Coyote Capture

I captured individuals by helicopter using a net gun (Gese et al. 1987), fitted them with a Vertex Plus or Vertex Lite GPS collar (Vectronic Aerospace GmbH, Berlin), and released them at the site of capture on 10 December 2016 (n = 10), 1 April 2017 (n = 6), and 25-26 January 2018 (n = 24) as part of an ongoing study of coyote space use. Collars deployed in 2016-17 collected location data every 2 hours until 31 December 2017, while collars deployed in 2018 recorded locations hourly until 31 January 2019 when they automatically released from the animal. I subset the data from the 2018 collars to 2-hour intervals to attain congruence with the previous year's collars.

Analyses

I derived 2 time series based on coyote space use. The first series represented range stability, based on a modification of a utilization distribution (UD)-based index proposed by Abrahms et al. (2017). Their index measured the intersections of successive monthly UD estimates for an individual. Though they did not consider patterns in the sequence of measurements, their approach is readily extendable to a time series framework. I used a fixed kernel density estimator with reference smoothing (Worton 1989) to fit a UD estimate for each individual each week. I then measured the similarity of the UDs of each individual at times t and $t-1$ using Bhattacharyya's affinity (BA; Bhattacharrya 1943),

$$BA_{i,t} = \iint \sqrt{\widehat{UD_{i,t}}(x,y)} * \sqrt{\widehat{UD_{i,t-1}}(x,y)} dxdy \tag{III.1}$$

where $\widehat{UD_{i,t}}$ and $\widehat{UD_{i,t-1}}$ are the UD estimates of individual i at week t and $t-1$, respectively, to obtain a series for each individual. I extracted the area of the 75% isopleth contour to obtain a second series of weekly range size for each individual. The range size estimates at week 1 was omitted to maintain congruence with the stability series, which has a start up loss at week 1. I emphasized space use instead of the underlying movement process for 2 reasons; 1) coyote territoriality is justifiably based on patterns that are apparent at the space use level and 2) this permits simultaneous testing of hypotheses about covariates that affect range sizes deferentially between behavioral states.

I used HMMs to evaluate competing hypotheses of coyote territorial behavior. These models treat time series as arising from state-dependent distributions of the (potentially multiple) response variables (Zucchini et al. 2016). The sequence of states is an unobservable (hidden) process underlying the observed series and assumed to change according to a matrix of transition probabilities at each time step (Patterson et al. 2017; Figure III.1). In our case, behavioral states are represented by characteristic distributions of weekly range size and stability. For example, a resident state would be characterized as highly stable, but exhibiting relatively small ranges, whereas a transient state would be characterized by larger, unstable ranges (Kamler and Gipson 2000; Figure III.2). BA is bounded between 0 and 1 and treated as beta-distributed while range size is strictly positive and treated as gamma-distributed (McClintock and Michelot 2018). Thus, the initial model is stated as

$$\begin{gathered} BA_t|(S_t = i) \sim Beta(\nu_i, \phi_i) \\ RS_t|(S_t = i) \sim Gamma(\mu_i, \sigma_i) \end{gathered} \tag{III.2}$$

where BA_t and RS_t are the range stability and size, respectively, at week t, ν_i is the mean BA of state i, ϕ_i is the precision of BA in state i, μ_i is the mean range size of state i, and σ_i is the range size standard deviation in state i (Figure III.1). Transitions between states are governed by the transition matrix Γ where the rows represent the state at time $t-1$, and the columns represent the state at time t. For a resident-transient model,

$$\Gamma = \begin{bmatrix} \gamma_{RR} & \gamma_{RT} \\ \gamma_{TR} & \gamma_{TT} \end{bmatrix} \tag{III.3}$$

where γ_{RR} and γ_{TT} are the probabilities of remaining in resident and transient states, respectively, γ_{RT} is the probability of switching from a resident state to a transient state, and γ_{TR} is the probability of switching from a transient state to a resident state. This would expand to a 3 x 3

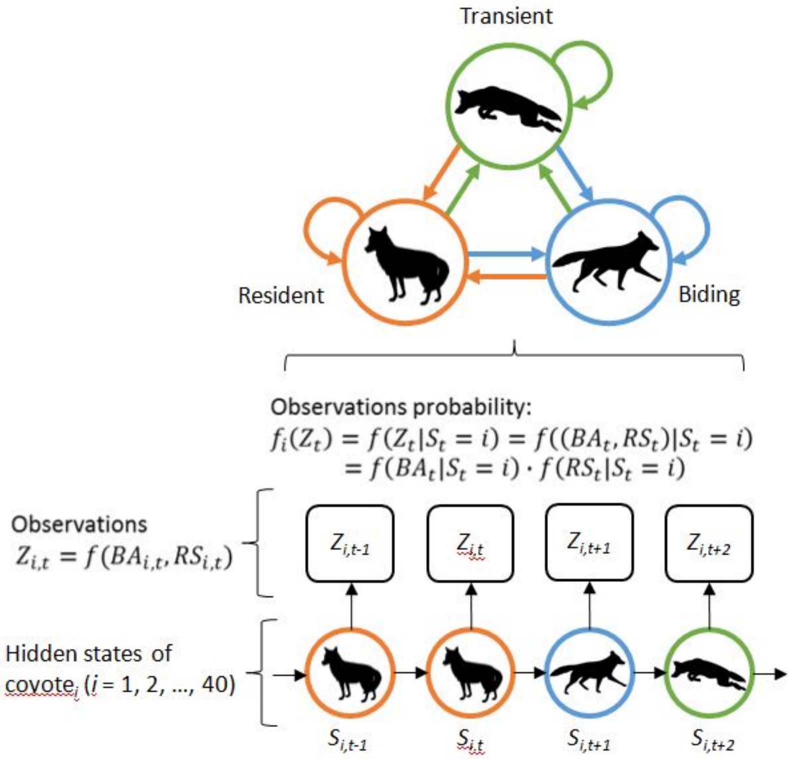

Figure III.1: Conceptual representation of applying a HMM to coyote dispersal. The probability of observed range stability (BA) and range size (RS) depend on the underlying behavioral state of the coyote, which represents territorial status (resident, transient, or biding).

matrix in a 3-state case, with the diagonal elements representing the probabilities of remaining in the initial state.

The basic HMM can be used to investigate the long-term probability of state switching among the population, but these models easily incorporate covariates in multiple ways. For instance, the elements of the transition matrix can be related to environmental or individual-level characteristics to evaluate the influence of these factors on the probability of switching from one state to another. This is stated as

$$\begin{aligned} \gamma_{ij}|\mathbf{X} &\sim Bin(\lambda) \\ logit(\lambda) &= \boldsymbol{\beta}\mathbf{X} \end{aligned} \tag{III.4}$$

where $\gamma_{ij}|\mathbf{X}$ is the probability of switching from state i to state j, given covariate matrix $\mathbf{X}$, λ is the expected value of a binomial distribution, $logit(\cdot)$ represents the logit link function, and $\boldsymbol{\beta}$ is a parameter vector. Parameters of the response distributions can also be conditioned on covariates, in a manner analogous to that used with generalized linear models, but embedded within a single analysis (McClintock and Michelot 2018). For example, a model explaining variation in range size within a given state would be stated as

$$\begin{gathered} RS_t|(S_t = i) \sim Gamma(\mu_i, \sigma_i) \\ log(\mu_i) = \boldsymbol{\theta}\mathbf{Z} \end{gathered} \tag{III.5}$$

where $log(\cdot)$ is the log link function, $\boldsymbol{\theta}$ is a parameter vector, and $\mathbf{Z}$ is a matrix of range size covariates.

I specified 14 models reflecting each of our competing hypotheses (Table III.1). Seven models reflect a binary (resident-transient) paradigm and seven models represent a trinary paradigm (resident-transient-biding; Figure III.2). I included sex and time of year (using cosine terms; see McClintock and Michelot 2018) as transition matrix covariates, and time of year as a covariate of range size mean and standard deviation in non-resident states. I used two global models reflecting 2- and 3-state hypotheses, and selected 6 sub-models of each. For both 2- and 3-state hypotheses, I included: 1) a model with no transition matrix covariates, but time of year as a covariate of range size and variation; 2) a model with time of year and sex as covariates of the transition matrix; 3) a model with time of year, sex, and their interaction as covariates of the transition matrix; 4) a model with sex as a covariate of the transition matrix; 5) a model with time of year as a covariate of the transition matrix; 6) a null model, in the sense that I included no covariates of range size or the transition matrix. I compared models using standard AIC procedures and model weights (Burnham and Anderson 2002, McClintock and Michelot 2018), and assessed model fit and performance with pseudo-residuals (Zucchini et al. 2016).

Model	Transition Covariates	Range Size Covariates
2-state, stationary [null model]	–	–
2-state, sex biased dispersal	sex	–
2-state, seasonal dispersal	cosinor(week)	–
2-state, seasonal ranges	–	cosinor(week)
2-state, seasonal sex-biased dispersal	sex + cosinor(week)	–
2-state, seasonal sex-biased dispersal, seasonal ranges	sex + cosinor(week)	cosinor(week)
2-state, sex dependent seasonality of dispersal	sex ∗ cosinor(week)	–
3-state, stationary [null model]	–	–
3-state, sex biased dispersal	sex	–
3-state, seasonal dispersal	cosinor(week)	–
3-state, seasonal ranges	–	cosinor(week)
3-state, seasonal sex-biased dispersal	sex + cosinor(week)	–
3-state, seasonal sex-biased dispersal, seasonal ranges	sex + cosinor(week)	cosinor(week)
3-state, sex dependent seasonality of dispersal	sex ∗ cosinor(week)	–

Table III.1: Candidate models describing the dispersal process of coyotes on SAVR. Two-state models reflect a resident-transient paradigm, while 3-state models reflect a resident-transient-biding paradigm. Transition covariates were applied to all transition probabilities. Range size covariates were applied to transient and biding states only.

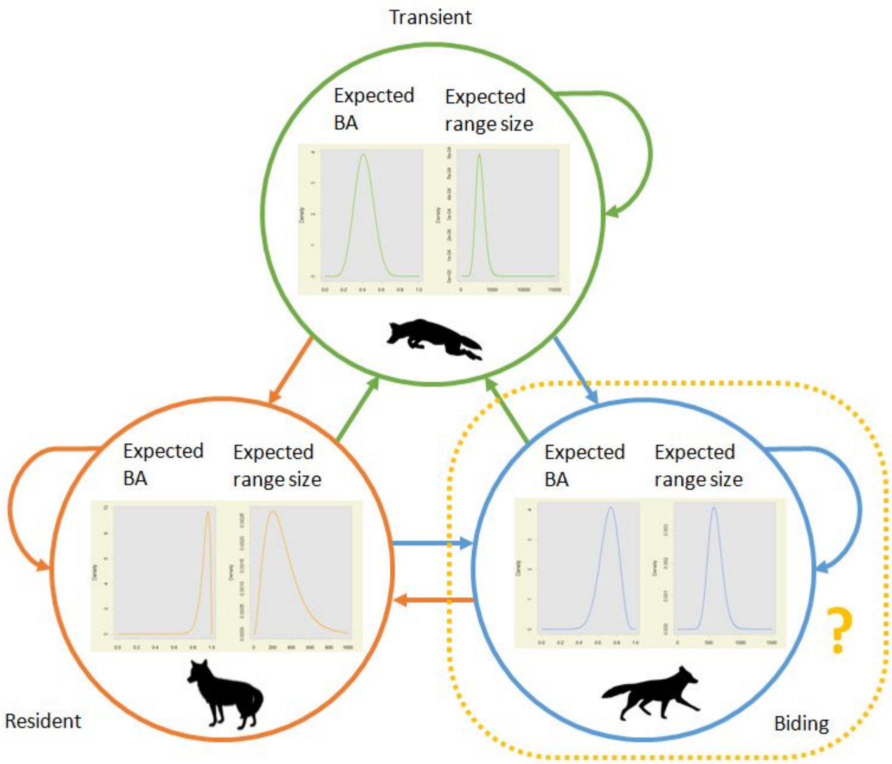

Figure III.2: Conceptual representation of competing hypothesized dispersal behaviors of coyotes. Researchers commonly assume a binary, resident-transient system underlies coyote dispersal, while recent evidence suggests the importance of biding behavior.

Results

Models incorporating 3 behavioral states consistently out-performed 2-state models. ΔAIC between our best performing 2-state and worst performing 3-state model was 392.7. The top performing model considered the influence of time of year on the mean and standard deviation of range sizes for states 2 and 3. AIC of this model was 27.58 lower than the next lowest model and received essentially all model weight (Table III.2), thus it is the only one considered below.

Pseudo-residual diagnostics show slight kurtosis in BA residuals and 2 potential outliers in range size, but overall they indicate acceptable model performance (Figure III.3). There was appreciable residual autocorrelation in range sizes, indicating that there are other trends to explain. Autocorrelation does not affect the quality of the estimates in a HMM as they do not

Model	AIC	weight	ΔAIC
3-state, seasonal ranges	19565.07	1.00	0.00
3-state, seasonal sex-biased dispersal, seasonal ranges	19592.65	0.00	27.58
3-state, seasonal sex-biased dispersal	19635.91	0.00	70.84
3-state, seasonal dispersal	19644.46	0.00	79.39
3-state, sex biased dispersal	19651.79	0.00	86.72
3-state, stationary [null model]	19671.13	0.00	106.06
3-state, sex dependent seasonality of dispersal	19674.04	0.00	108.97
2-state, seasonal sex-biased dispersal, seasonal ranges	20066.77	0.00	501.70
2-state, seasonal ranges	20084.61	0.00	519.54
2-state, seasonal sex-biased dispersal	20108.32	0.00	543.25
2-state, sex biased dispersal	20115.52	0.00	550.45
2-state, sex dependent seasonality of dispersal	20116.12	0.00	551.05
2-state, seasonal dispersal	20121.07	0.00	556.00
2-state, stationary [null model]	20127.62	0.00	562.55

Table III.2: Comparison of competing models of coyote dispersal behavior using Akaike's information criterion (AIC), associated model weights, and ΔAIC, relative to the top model. A three state model incorporating seasonality of non-resident range sizes was clearly the top model based on ΔAIC, and received essentially all model weight.

assume uncorrelated errors (Zucchini et al. 2016).

State 1 was consistent with resident behavior characterized by high range stability ($\bar{X}$ =0.928, $\hat{\phi}$ = 61; note that $\hat{\phi}$ represents precision and is inversely related to variance [Ferrari and Cribari-Neto 2004]) and relatively small ranges ($\bar{X} = 95.7$ ha, $\hat{\sigma} = 46.8$ ha). Range stability was lower in state 2 ($\bar{X}$ = 0.268; Figure III.4) and highly variable ($\hat{\phi}$ = 5.32). Range sizes varied from a peak average size of 3257 ha ($\hat{\sigma}$ =2870 at week 52) and a minimum of 1463 ha at week 26 ($\hat{\sigma}$ =1388 ha; Figure III.5). This state was consistent with transient behavior. Stability was slightly lower in state 3 than state 1 ($\bar{X}$ = 0.88) but considerably more variable ($\hat{\phi}$ = 22.9; Figure III.4). Range sizes were an order of magnitude smaller than state 2, but followed an analogous pattern (Figure III.5). They ranged from a peak average of 390 ha ($\hat{\sigma}$ =390 ha) at week 52 to a minimum of 152 ha at week 27 ($\hat{\sigma}$ =152 ha). These results were consistent with our expectations of biding behavior. I hereafter refer to states 1, 2, and 3 as resident, transient, and biding, respectively.

The top model was homogeneous (Zucchini et al. 2016), thus transition probabilities may be

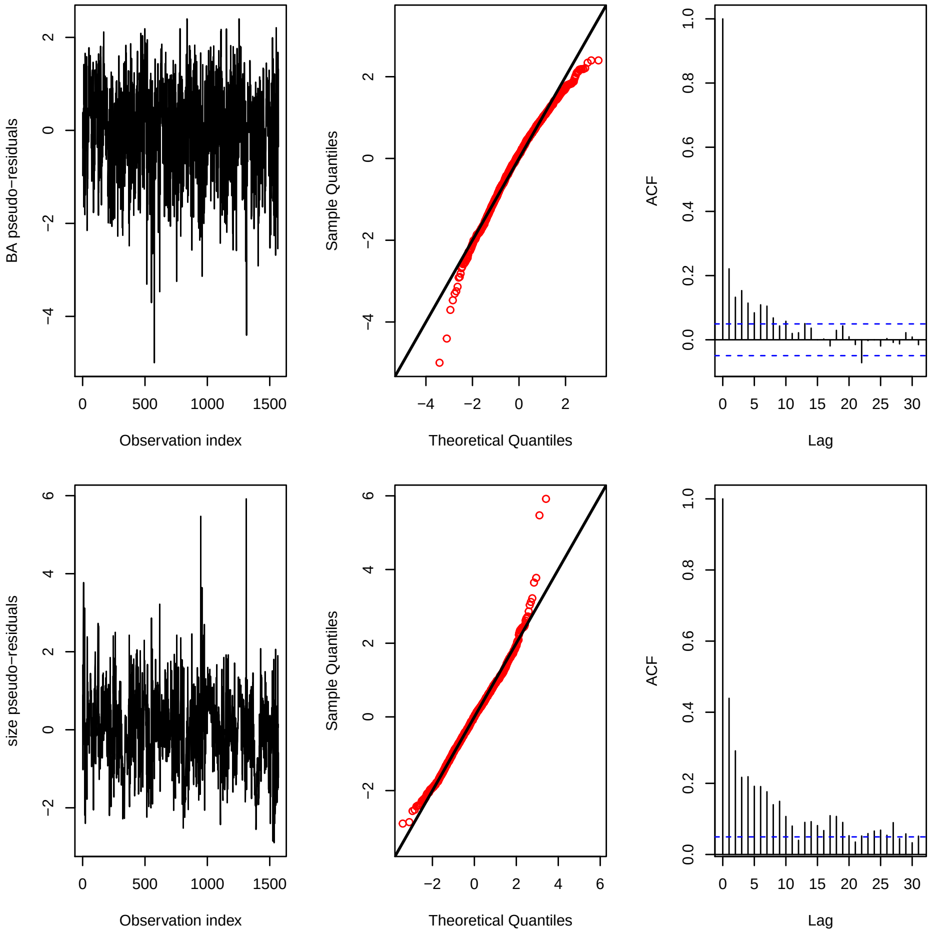

Figure III.3: Pseudo-residual diagnostics of my top model. Q-Q plots (center) of range stability (BA; top) and range size (RS; bottom) suggest slight kurtosis in BA, and 2 outliers in RS. There is appreciable autocorrelation in RS residuals (lower right), which indicates additional pattern in range size dynamics but does not affect model performance. Overall, diagnostics suggest good model performance.

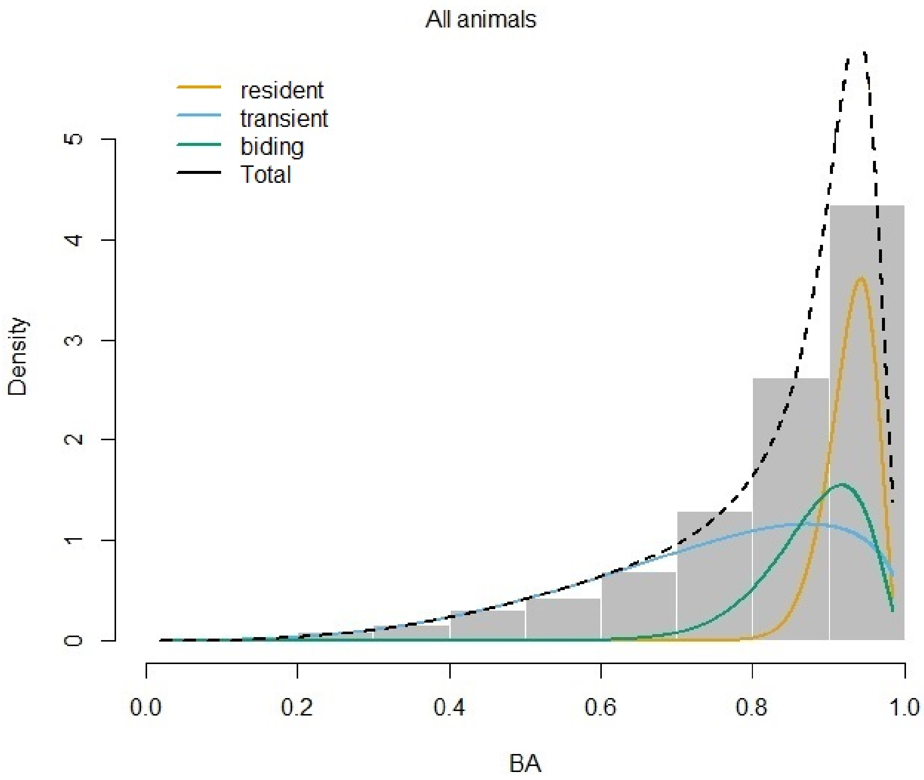

Figure III.4: Distribution of range stability values by state, measured by Bhattachyarra's Affinity (BA). Residents (orange) exhibited highly stable ranges, with little variability in BA ($\bar{X} = 0.928$, $\hat{\phi} = 61$). Transients (blue) exhibited lower average, but highly variable range stability ($\bar{X} = 0.268$, $\hat{\phi} = 5.32$). Biding coyotes (green) were intermediate in both average stability and variation ($\bar{X} = 0.880$, $\hat{\phi} = 22.9$).

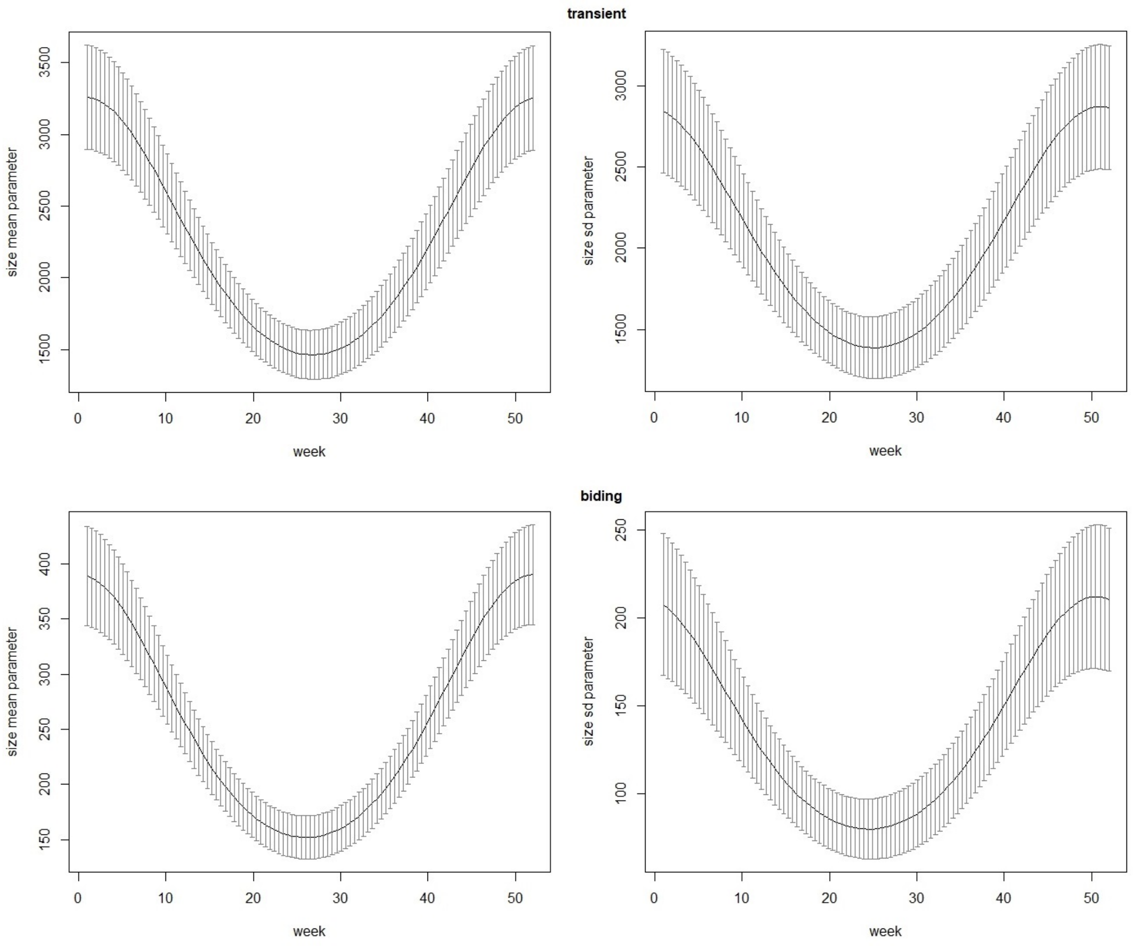

Figure III.5: Average (left) and standard deviation (right) of transient (top) and biding (bottom) range sizes (ha) through the year, with 95% confidence intervals. Both transients and biding coyote ranges were largest and most variable in the winter, while smallest and least variable in the summer. Transient ranges are an order of magnitude larger than those of biding coyotes, regardless of the time of year (note differences in scale on y-axes).

considered stationary, meaning time of year and sex did not provide competitive explanations of transition probabilities. States were generally persistent, represented by high probabilities along the diagonal of the transition matrix (Figure III.6). While the probability of switching states at a given week was low, switching was common over the course of the study. Transitions from transient to resident behavior and from resident to transient behavior were an order of magnitude less probable than transitions from resident to biding, biding to resident, and biding to transient.

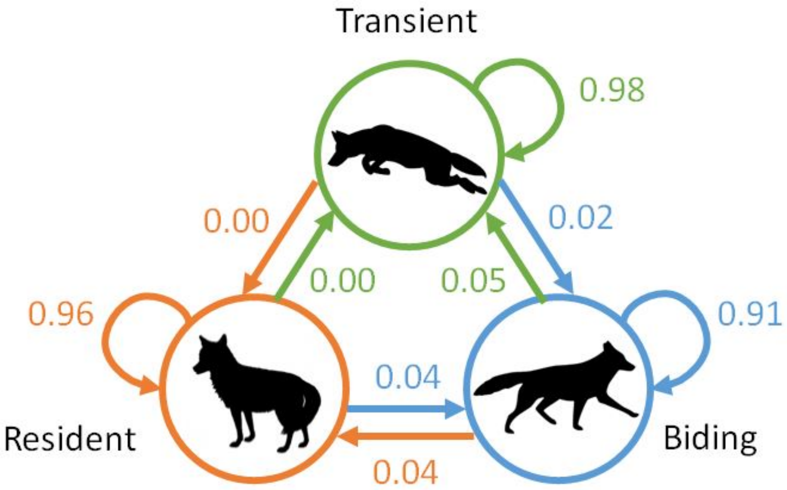

Figure III.6: Weekly transition probabilities between resident, transient, and biding states. Transitions between resident and biding, as well as biding and transient states were considerably more probable than transitions directly between resident and transient states (which are non-zero at 4 decimal places). This indicates that biding is an important intermediate behavior between residence and transience.

Since emigration is defined as leaving an occupied territory, the probability of leaving a resident state represents a weekly emigration rate of residents. Because the transition probabilities of the top model can be considered stationary, the weekly emigration rate can be transformed to an annual *conditional* emigration rate by

$$E|R = 1 - {\gamma_{RR}}^{52} \tag{III.6}$$

where $E|R$ represents the emigration rate, given the individual is in the resident state. This yields an estimate of 0.88 (Upper and lower 95% CIs = 0.98, 0.7, respectively). Because this rate applies conditionally to residents, it cannot be considered a *per capita* rate representing the entire population.

Discussion

I found overwhelming support for a trinary behavior system in coyotes, supporting the importance of biding, in addition to transience, during dispersal. A binary treatment was insufficient to explain coyote spatial behavior. Emigration of residents was common. I found no evidence of seasonal variation or sex bias in emigration, though I did observe seasonality in transient and biding range sizes. These results support recent findings that coyote dispersal behavior is more nuanced than a single transient life history phase (Morin and Kelly 2017). Clobert et al. (2009) discussed 3 stages of dispersal, including departure, transience, and settlement. Our results suggest biding is an important intermediate behavior between territory departure, transience, and (perhaps to a lesser degree) settlement. The scale of transient space use suggests that localized population reduction through lethal management is unsustainable. A cursory examination of mortality of our collared individuals while in the different states suggests different levels of risk between biding and transience, with implications for understanding the population dynamics of coyotes, and potentially other territorial canids.

Resident coyotes exhibited relatively small, highly stable ranges, as I expected. Meaningful comparisons with other studies are difficult due not only to differences in sampling design and estimator methodology (Laundre and Keller 1984, Fieberg and Borger 2012), but also to underlying assumptions about coyote behavior. Unrecognized biding behavior may have been incorporated into estimates based on subjective, post-hoc classification of resident and transient individuals. However, the resident range sizes I observed were superficially similar to those reported in Kansas (Kamler and Gipson 2000), northwestern Texas (Kamler et al. 2005) and the Welder Wildlife Foundation in southern Texas (Young et al. 2006). Territories were near circular, non-overlapping, and partially conterminous, with appreciable interstitial spaces. Our estimated emigration rate was quite high, suggesting that almost 90% of resident coyotes emigrate over the course of a year. This result is similar to previous observations in Maine, where 87.5% of pups dispersed in the first year (Harrison 1992), though it is unlikely that the coyotes I observed were pups based on the time of capture (Bekoff and Gese 2003).

Biding is clearly an ecologically relevant transitional behavior, as revealed by the transition matrix (Figure III.6). This behavior may reduce the risk of dispersal mortality by permitting the individual to gain familiarity with an area before attempting to occupy a territory. This is consistent with observations of increased mortality risk in transient coyotes (Harrison 1992), and the notion that mortality risk decreases with familiarity of an area (Woodruff and Keller 1982, Windberg and Knowlton 1990). Indeed, of the 6 mortalities observed in our study, 3 occurred in the transient state according to our model. One of the 6 was excluded from the analysis due to the short duration for which it was collared, but its pattern of space use was consistent with that of a transient according to our model. Though not formally included in our analyses, this does offer circumstantial evidence supporting higher mortality risk during transient behavior. Transience has been shown to increase direct mortality risk in unfamiliar areas (Sacks et al. 1999*a*). Extra-territorial movement has also been shown to increase stress levels, leading to multiple physiological consequences over long periods of transience (Young and Monfort 2009). Biding likely provides a reduction in both risk and physiological costs prior to attempting to gain access to a territory once a potential settling area has been located.

While there was no pattern in the initiation of dispersal, there was evidence of annual cyclicity in the range of dispersed individuals. This was evident in the range sizes of both biding and transient states, though the mean weekly range size of transients was an order of magnitude larger than that of biders consistently through the year. The winter peak in range sizes may be a function of prey and forage availability (Springer 1982, Mills and Knowlton 1991) or perhaps maturation of dispersing pups (Andelt 1985, Harrison 1992). These results suggest that dispersal in coyotes not only includes 2 behavioral modes, but 2 stages in the dispersal process. While there is no seasonality in departure, there is seasonality in the spread of dispersed individuals (of both behavioral states) into new areas. The scale of transient movements in particular was quite large. The maximum observed weekly range of a transient was 50,989 ha and the maximum displacement of an individual occurred when a transient male moved 41.7 km west to the eastern city limits of Zapata, TX. Our results are consistent with observations of transients in South

Carolina (Hinton et al. 2012).

The combination of a high emigration rate and large-scale transient movements suggests that traditional, localized lethal control methods are unlikely to be effective at reducing coyote density at reasonable intensities. Localized control is ineffective at producing sustained population reduction in red foxes (*Vulpes vulpes*) due to compensatory effects of immigration (Lieury et al. 2015, Porteus et al. 2018) and similar behaviors have been suggested to undermine such efforts in black-backed jackals (*Canis mesomelas*; Minnie et al. 2016). Furthermore, reduction of predator populations itself is rarely the motivating goal of predator management. Rather, increasing the survival or fecundity of a target prey species is a much more common goal (Mosnier et al. 2008, Boisjoly et al. 2010). Recent work suggests that structural complexity of habitat is strongly linked to prey survival in the face of predation (Lichtenstein et al. 2019), and has been linked to increased survival of neonate ungulates in the presence of coyotes (Gulsby et al. 2017). Thus habitat management efforts may be more effective in achieving such management goals than reducing predator population densities, particularly when there are multiple, interacting predator species (Prugh and Arthur 2015, Curveira-Santos et al. 2019).

In the case of depredation management, targeted lethal control of offending individuals may be appropriate in some cases, if difficult in application (Sacks et al. 1999*a*). Non-selective lethal removal may result in reduced livestock losses in the short term when applied strategically, but is unlikely to result in sustained population reduction or other lasting effects (Wagner and Conover 1999, Harding et al. 2001). Our results suggest that, as with other species, the effects of such efforts would be quickly overcome by compensatory immigration (Windberg and Knowlton 1988, Conner et al. 1998). Given the large scale of transient movements, lethal control efforts would have to be sustained at a large spatial scale for extended periods (Harding et al. 2001). The logistical requirements of broad-scale efforts (Lieury et al. 2015, Krull et al. 2016), and the questionable link between non-selective removal and reduction of livestock losses (Allen 2000, Berger 2006), suggest that they are unlikely to be cost-effective compared to more targeted methods. Management techniques that alter coyote behavior or space use may be more cost-effective at reducing depredation loss than population reduction (Shivik 2004, van Bommel and Johnson 2012, Conner et al. 2016, Moreira-Arce et al. 2018).

In a basic ecological context, our results add empirical evidence to the notion that summarizing dispersal via use of a single parameter is insufficient (del Mar-Delgado and Penteriani 2008, Benton and Bowler 2012). The 2 non-resident behavior modes I observed carry different levels of risk, with implications for population processes. Ignoring changes in individual behavior during dispersal has been linked to shortcomings in spatially-structured population models (del Mar-Delgado and Penteriani 2008). Quantifying dispersal rates empirically is difficult (Abadi et al. 2010), particularly for carnivore species (Porteus et al. 2018). I was able to derive a behaviorally-informed estimate of the emigration rate within a spatially structured population from telemetry data using readily accessible methods (McClintock and Michelot 2018). Given the behavioral similarities between coyotes and other territorial, generalist canids (Minnie et al. 2016), our resident-transient-biding model of coyote behavior could provide a tractable basis for relating telemetry data of canids to their population dynamics. While I produced useful results, our model is presently limited by a lack of state-specific mortality estimates. Telemetry data generally include information on individual survival that is broadly useful. A HMM formulation that leverages this information to produce state-specific mortality rate estimates would greatly expand the inferential power of our model, and would be useful for the analysis of telemetry data in general (Morales et al. 2010). Such a model would allow for empirical evaluation of the effects of management and environmental factors on the population dynamics of carnivore populations.

By melding theoretical, technological, and analytical advances in this way, we can gain a much better understanding of carnivore population dynamics. The knowledge gained will provide a basis for evaluating the effects and effectiveness of carnivore management strategies, whether for agricultural damage control or wildlife recovery efforts. This will allow scientists to obtain objective answers to questions about both the ecology and management of carnivores, leading to better management on-the-ground.

IV. DIVERGENT PREDATOR ACTIVITY MUDDIES THE DYNAMIC LANDSCAPE OF FEAR

Introduction

The landscape of fear (LOF; Laundre et al. 2001) hypothesis suggests that prey species perceive spatial variation in predation risk and navigate this landscape to balance foraging requirements and risk. This phenomenon is thought to underlie trophic cascades (Bliecher 2017), and explain non-consumptive effects of predators on prey species (Preisser et al. 2005). However, empirical evidence of LOFs has been mixed in the literature (Palmer et al. 2017). Recent work suggests that this landscape is dynamic at multiple time scales, and is influenced by the activity patterns of predators (Palmer et al. 2017, Kohl et al. 2018). Because of this dynamism, spatial segregation of predators and prey changes through time, masking LOF predictions if time were not considered. Thus, predator diel cycles are linked to trophic cascades, and may have reaching impacts on communities and ecosystems (Bliecher 2017).

The underlying assumption of a dynamic LOF is strong predictability of predator cycles (Dodson 1990, Smith et al. 2019). Behavioral differences among predator species in multi-predator systems can impact the predictability of predation risk (Schmidt and Kuijper 2015). For example, Morosinotto et al. (2010) observed differential behavioral responses of pied flycatchers (*Ficedula hypoleuca*) to two superficially similar species of owl (Family strigidae) with different activity patterns. One would not accurately predict prey response by considering only one predator behavior. I posit that the same may be true of different behaviors across individuals within a predator species.

Most studies of the temporal dynamics of a LOF implicitly assume that cycles in activity, such as nocturnal or crepuscular behavior, are similar across individuals within predator populations (Eriksen et al. 2011, Palmer et al. 2017). However, this may not be true in generalist species (Kohl et al. 2018, Smith et al. 2019). Many predators exhibit dietary and behavioral plasticity, which contributes to the broad distribution of many species (Slayter et al. 2013). Although some studies consider behavioral variation of a predator species across regions (e.g. Yang et al. 2018), variation within a local population has not been considered. Predators vary daily activity cycles to reduce both inter- and intraspecific competition (Alanara et al. 2001, Lucherini et al. 2009), which are in turn linked to foraging strategies (Polansky et al. 2013). Thus not all individuals within a predator population necessarily represent the same risk to a given prey species.

Prey species may perceive differences in risk between individual predators directly, or by recognizing spatio-temporal variation in risk of predation events rather than risk of encountering predators *per se* (Lank and Ydenberg 2003, Palmer et al. 2017). Ungulates appear able to distinguish differences in risk posed by predators of the same species (Gese 1998). If indeed prey can distinguish threatening from non-threatening predators, regardless of the mechanism, the activity cycles *of threatening predators* are of interest. If threatening individuals exhibit different activity cycles than non-threatening ones, the overall pattern of the predator species will reflect a combination of distinct, component behaviors. Failing to account for these differences will bias parameter estimates, add unmodeled statistical noise to analyses. Thus, inference into the effects of predator activity on their prey may be confounded by differential behavior, foraging, and perceived threat to prey among predators in the same population. Ignoring this variation could cloud inference in LOF settings but is difficult to address, given the small sample sizes and capture biases typical of carnivore studies (Thompson et al. 2012, Kohl et al. 2018). Researchers need information on the dynamics of the activity cycles of individuals in order to explicitly account for their effects, or control for them in study designs.

As a model, I examined the degree and nature of behavioral variation within a population of a generalist carnivore: the coyote (*Canis latrans*). Coyotes are a ubiquitous species in North America that exhibits a great deal of behavioral variation (Bekoff and Wells 1986, Bekoff and Gese 2003). Their wide range and generalist, predatory habits have led to many conservation and management issues; ranging from impacts on endangered species through predation (Boisjoly et al. 2010) or hybridization (Hinton et al. 2018), to agricultural impacts on crops (Holzman et al.

1992) and livestock (Sacks and Neale 2007), to the spread of zoonotic diseases (Way and White 2013). Despite the numerous issues associated with coyotes, and the importance of animal behavior in effective conservation and management (Berger-Tal et al. 2011), factors affecting coyote activity cycles are poorly understood.

If individual coyotes choose between alternative activity strategies, researchers will need reliable predictors to differentiate individuals exhibiting similar patterns. Carnivore studies sometimes identify focal classes of individuals as a design assumption, such as residents and transients (e.g. Hinton et al. 2015). For this to work, simple, repeatable predictors of behavior are needed. Few studies examine individual variation in coyote activity cycles, but scientists recognize some tendencies. For example, coyotes tend to exhibit nocturnal (Holzman et al. 1992) or crepuscular behavior (Gipson and Sealander 1972, Woodruff and Keller 1982, Andelt 1985, Arias-Del Razo et al. 2011). Which strategy an individual adopts may depend on straightforward predictors, such as sex, habitat characteristics, or resident status. Male and female activity patterns may diverge during the breeding season, when females are thought to exhibit less evening activity than males (Andelt 1985, Way et al. 2004). This relationship could potentially guide the timing of sex-targeted management actions to reach conservation goals. Coyotes may also adapt their hunting strategies to the structure of their habitats, where the success of a particular hunting strategy will depend on vegetation density and visibility (Thibault and Ouellet 2005, Arias-Del Razo et al. 2012, Ward et al. 2019). Thus vegetation density may be linked to activity cycles (Kitchen et al. 2000), and could be manipulated to achieve conservation goals. Finally, Andelt (1985) reported limited evidence that diel activity cycles varied by territorial residency status, which manifests in individual range sizes (Kamler and Gipson 2000) and may be related to body mass (Bekoff and Wells 1986). Lethal management efforts disproportionately target non-resident coyotes (Sacks et al. 1999*b*), which may bias them towards a particular activity pattern if this relationship holds.

I examined variation in the dynamics of coyote activity patterns within an unharvested coyote population in southern Texas. I quantified activity cycles through time to examine seasonal trends and inter-individual variation in activity dynamics. I then checked for evidence of multiple, simultaneous patterns of activity dynamics, which would undermine the appropriateness of population-level activity patterns for LOF studies. I then related their variation to simple predictors to determine whether they could serve as reliable indicators of activity dynamics. Finally, I evaluated the implications of my results for inference in LOF dynamics.

Methods

Study Area

This study was conducted on the East Foundations San Antonio Viejo Ranch (SAVR), approximately 61,000 Ha of Jim Hogg and Starr counties in southern Texas. The East Foundations ranches are managed as a living laboratory to promote the advancement of land stewardship through ranching, science, and education. The area is dominated by shrub savannas, primarily composed of honey mesquite (*Prosopis glandulosa*), prickly pear (*Opuntia* spp.), cat-claw acacia (*Acacia greggii*), blackbrush (*Acacia rigidula*), whitebrush (*Alloysia gratissima*), and granjeño (*Celtis palida*), with early to mid-successional grasses, including three-awns (*Aristida* spp.), little bluestem (*Schizachyrium scoparium*) and windmill grasses (*Chloris* spp.). Given the East Foundation mission of wildlife research and stewardship, lethal harvest and harassment of native animals, including coyotes, has been prohibited on SAVR since the East Foundation's inception in 2007. This region persistently features high coyote densities (Knowlton 1972, Andelt 1985, Windberg 1995, Bekoff and Gese 2003). These characteristics provide a unique opportunity to study activity dynamics in an unharassed, saturated coyote population.

Coyote Capture and Telemetry

I captured a total of 40 coyotes across 3 capture events by helicopter using a net gun (Gese et al. 1987). Captures occurred 10 December 2016 (n = 10) and 1 April 2017 (n = 6), and 25-26 January 2018 (n = 24). I fitted each coyote with a Vertex Plus or Vertex Lite satellite GPS collar (Vectronic Aerospace GmbH, Berlin), and released it at the site of capture. Collars deployed in 2016-17 were programmed to release from the animal on 1 January 2018, while those deployed in

2018 were programmed to release on 31 January 2019. These collars were programmed to collect location data every 1 (n = 24) or 2 (n = 16) hours. I filtered hourly data to 2-hour intervals to standardize across all collars. Three coyotes died within 3 months of their respective capture dates and were excluded from these analyses. An additional 4 collars failed over the course of the study, leaving n = 31 coyotes considered in this study.

Statistical Analyses

Except where indicated, all analyses were performed in R (R Core Team 2017). I estimated individual range size as the area of the 75% isopleth of a fixed kernel density estimate of each individual's utilization distribution (Worton 1989) using the *adehabitatHR* package (Calenge et al. 2009).

To estimate the percentage of woody canopy cover in coyote ranges, I obtained 2016 1 Meter resolution, National Agricultural Imagery Program, natural color and color infrared imagery (https://tnris.org/; Accessed 24 April 2017). These images were merged and color matched in ArcGIS 10.4 (ESRI, Redlands, CA). Pixels were classified as woody canopy cover or non-cover using an interactive supervised classification (Campbell and Wynne 2011). I used a roving window to calculate percent canopy cover at 10 m resolution. I calculated the average canopy cover within each coyotes' range using zonal statistics tools in the spatial analyst toolbox, within ArcGIS.

I converted each series of locations to a trajectory of movement vectors, defined in terms of step lengths and turning angles, using the *adehabitatLT* package (Calenge et al. 2009). Since locations were collected on a regular time interval, I took the sequence of step lengths as a a measure of net movement activity through time (Turchin 1998). Missing values resulting from missed GPS fixes were interpolated using the weighted moving average procedure implemented in the *imputeTS* package (Moritz and Bartz-Beielstein 2017).

I adapted the analytic approach of Cushman et al. (2005) to analysis of nonstationary animal activity patterns. I used 15-day, non-overlapping windows beginning on 10 December and advancing by 15 days until 31 January of each collar year. I estimated the ACF for each individual over 50 lags (100 hours) for each window as

$$\rho_\tau = \frac{\frac{1}{n}\sum(X_{t-\tau} - \bar{X})(X_t - \bar{X})}{S_0} \tag{IV.1}$$

where ρ_τ is autocorrelation at lag τ, X_t is the the value of the time series of coyote velocity at time t, $\bar{X}$, and S_0 is the variance of the series (Venables and Ripley 2002). The result is an autocorrelation surface (ACS) with lags on the x-axis, the window sequence on the y-axis, and autocorrelation on the z-axis. The surface is interperetable visually, with variation on the x-axis reflecting the periodicities in activity cycles (*sensu* Boyce et al. 2010) and variation along the y-axis representing changes in activity cycles through time. More generally, the ACS is a bivariate function representing the maximal amount of information about the individual's activity patterns, and serves as the sample unit in further analysis (Ramsay and Silverman 2002).

I took the cell-wise mean and standard deviation across surfaces to produce a mean and standard deviation surface, respectively. These are analogous to the mean and standard deviation of numeric data, but cannot be reduced to a single value and are represented graphically. The mean surface represents the population-level trend in coyote behavior dynamics while the standard deviation surface identifies the regions of the surface that are most variable across individuals.

Next I centered the ACS of each coyote by subtracting the mean surface from each. I then calculated the cell-wise L^2 Minkowski distance between centered surfaces (equivalent to Euclidean distance; Montero and Vilar 2014) to produce a $n * n$ distance matrix. I checked for behavioral clusters with complete linkage clustering (Lance and Williams 1967). This method is robust to noise and produces maximally linked clusters with clear discontinuities (Legendre and Legendre 1998). I then used PERMANOVA (Anderson 2001) to assess whether overall similarity in coyote behavior dynamics could be explained by sex, initial body mass, range size, brush canopy cover within ranges, or year with the *vegan* package (Oksanen et al. 2019).

Results

I collected an average of 4,189 locations per coyote (*sd* = 465) during the study period. The average fix success rate was 0.98 (*sd* = 0.015), thus any effects of missed fixes or the interpolation of the step length series may safely be considered negligible. Box plots of step lengths by hour of day revealed a pronounced lull in activity in the afternoon, thus I consider daily periodicity in activity to represent nocturnal behavior for all coyotes (Figure IV.1).

The mean ACS showed pronounced peaks in autocorrelation at daily lag intervals (multiples of 12), corresponding to a strong daily cycle in movements (Figure IV.2). The overall magnitude of autocorrelation was largest in the summer, meaning this was when coyote activity was most strongly cyclic. Autocorrelation was weak in the winter, indicating weakly cyclic or acyclic activity patterns. This suggests that temporal variation in coyote activity is least predictable by prey in winter. The standard deviation surface revealed that the vast majority of variation in autocorrelation was at crepuscular intervals from mid-April through July, punctuated by a lull in early June (Figure IV.3). There was also a general negative trend in variation as lag interval increased. In combination, these surfaces reveal that the dominant, and least variable characteristic in coyote activity is a circadian rhythm while crepuscular behavior is the most variable behavior aspect across individuals, particularly in summer.

Complete linkage clustering revealed at least 3 distinct groups of activity dynamics (Figure IV.4). One group consisted of 5 individuals collared in 2016-17, one contained 6 individuals collared in 2018, and the third contained 21 representing both years. PERMANOVA results show no evidence of sex or size bias in behavior patterns (Table IV.1). Range size and habitat complexity were not related to similarity in behavior cycles, but study year explained 10.0% of the variance in the distance matrix ($P = 0.001$; Table IV.1). At a minimum, these results indicate the existence of at least 2 distinct patterns of activity dynamics in each year within the same population.

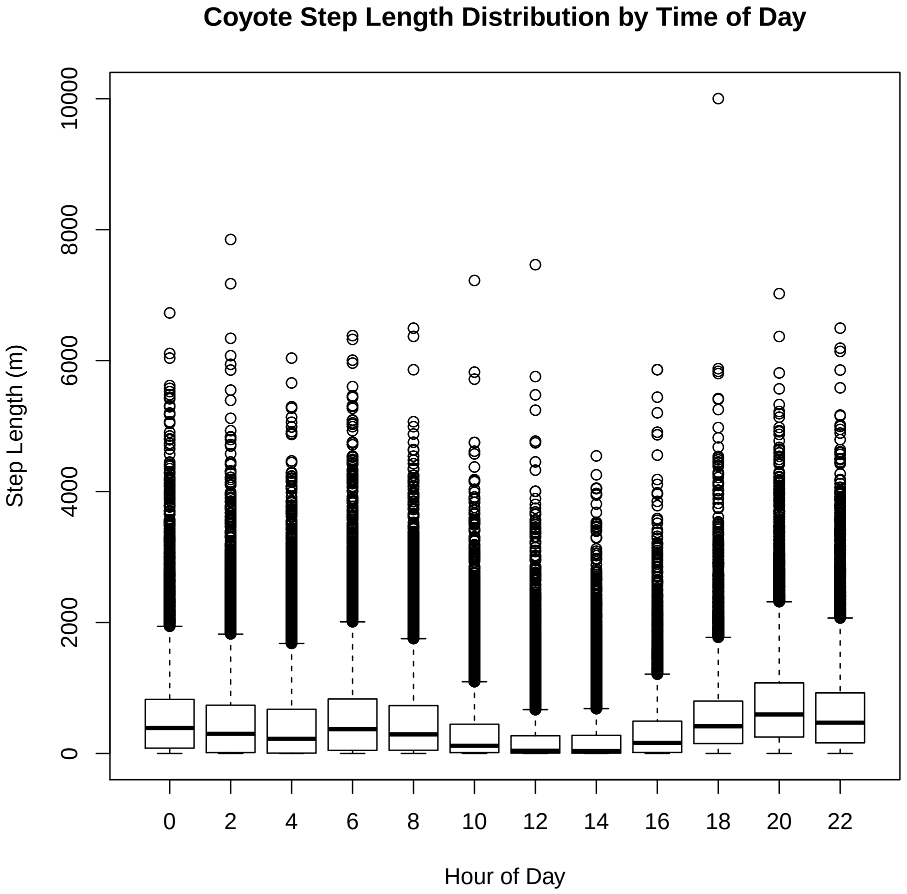

Figure IV.1: Overall distribution of coyote step lengths by hour of day. Note the pronounced lull in activity in the afternoon, despite high variability.

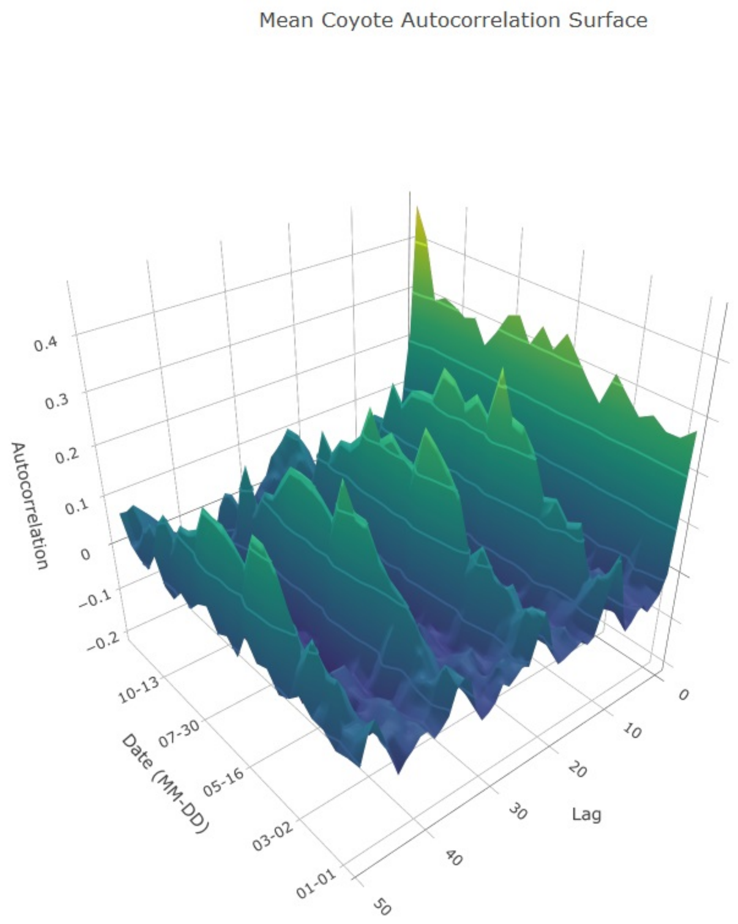

Figure IV.2: The mean coyote autocorrelation surface shows a pronounced circadian rhythm in coyote activity, with positive autocorrelation spikes at 12-lag (24-hour) intervals. The strength of autocorrelation peaks in mid-May and is weakest in mid-January.

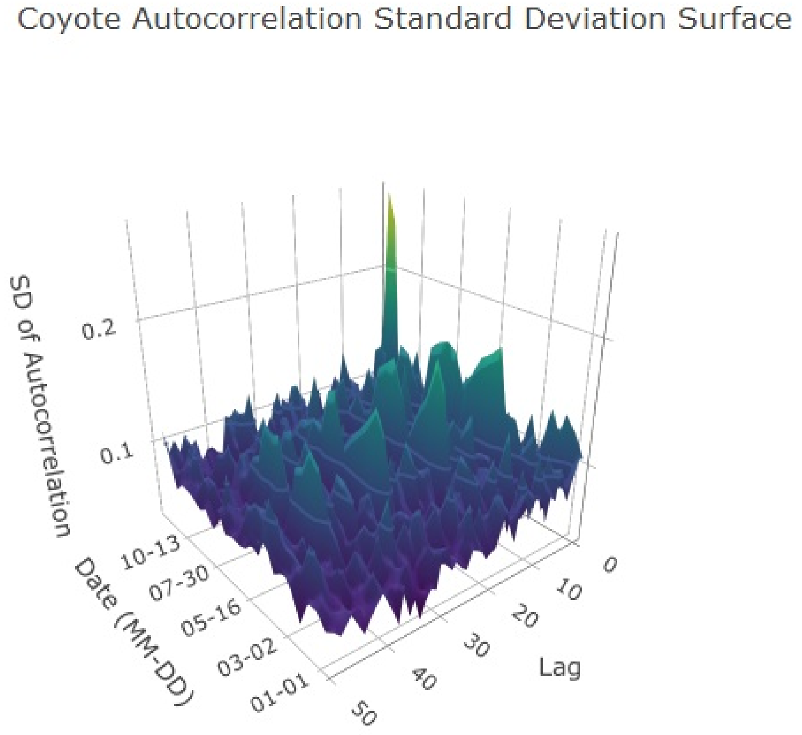

Figure IV.3: The autocorrelation standard deviation surface shows 2 pronounced spikes in variation at crepuscular intervals (6-,18-,30-lags, and so on) in early and late summer, respectively. This is evidence of coyotes diverging between nocturnal and crepuscular activity patterns across individuals.

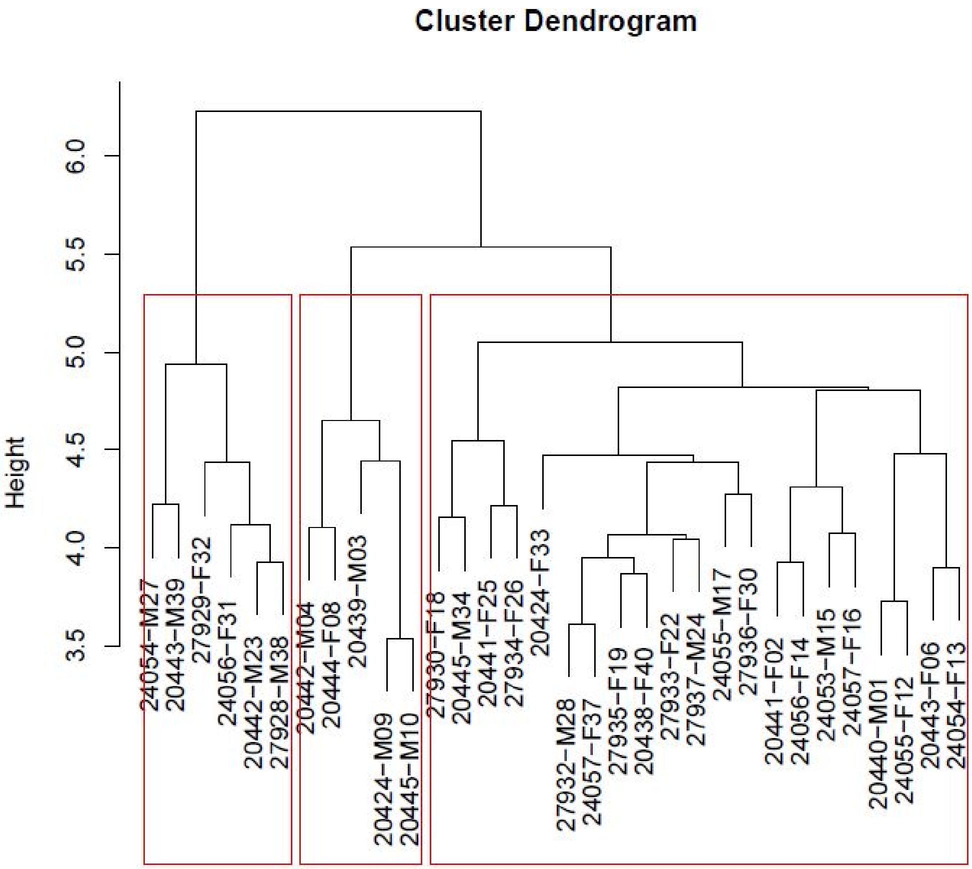

Figure IV.4: Dendrogram of complete linkage clustering of coyote autocorrelation surfaces. The left group contains only coyotes from the second study year while the middle group contains only individuals from the first. The right group contains individuals from both study years. This indicates the existence of at least 2 patterns of activity dynamics in each year.

	Df	SumOfSqs	R^2	F	Pr(>F)
Range Size	1	10.26	0.03	1.05	0.3320
Sex	1	9.66	0.03	0.99	0.4380
Body Mass	1	11.20	0.03	1.14	0.2240
Canopy cover	1	11.90	0.04	1.21	0.1550
Year	1	34.90	0.10	3.56	0.0010
Residual	26	254.73	0.77		
Total	31	332.64	1.00		

Table IV.1: PERMANOVA results indicate none of the hypothesized predictors of activity dynamics explained appreciable variation in the similarity between autocorrelation surfaces. Year did explain 10.0% of the variation, suggesting at least some coyotes adapted their activity to annual conditions.

Discussion

My results indicate the dynamics of activity cycles within an unharvested population of coyotes varied by individual. Individuals exhibited divergent nocturnal and crepuscular strategies simultaneously within the study area (Figure IV.3). Consideration of such variation is lacking in LOF research, despite the recent focus of ethology on inter-individual variation and animal personalities (Dingemanse et al. 2009). Overall, autocorrelation was weakest in winter and strongest in the summer (Figure IV.2). Thus, if I had searched for a dynamic LOF in the winter, I would have been unlikely to find it since predator activity showed no evidence of a predictable temporal cycle. In such a case, the dominant variation in the LOF would be spatial and consistent with early predictions (Laundre et al. 2001). However, failing to account for temporal variation in risk during the summer would mask real spatial variation in risk that that depended on activity cycles (Kohl et al. 2018).

Previous studies suggest that the divergent dynamics I observed may carry different implications for different prey species. Coyote diets in southern Texas are most consistent in winter, focusing on lagomorphs and white-tailed deer (*Odocoileus virginianus*) carrion (Andelt

1985, Andelt et al. 1987). Activity cycles were consistently weak in the winter, when food resources are likely most limited (Figures IV.2 and IV.3). Thus, the intensity of a LOF may peak in the winter for lagomorphs, but also be relatively constant at daily time scales. This would result in clear spatial patterns of risk because prey would not perceive predator down-times (*sensu* Smith et al. 2019) during which they could utilize otherwise risky habitats. Indeed, Arias-Del Razo et al. (2012) observed space use patterns consistent with a LOF with coyotes and lagomorphs in northern Mexico during winter, though their design controlled for cyclicity in risk rather than evaluating it.

Conversely, white-tailed deer fawns are a key component of coyote diets in summer (Andelt 1985, Andelt et al. 1987), when I observed coyotes diverging between nocturnal and crepuscular behaviors. Given strong cyclicity in coyote activity, variation in risk throughout the day would be most predictable by deer during this period. However, if crepuscular or nocturnal hunting strategies are more effective at catching fawns, the risk posed by a coyote to the fawn will vary by which strategy they use. This is a key question in both predator-prey dynamics, and management literature. The latter provides insight relevant to our example. Deer nursery groups minimize activity overlap with coyotes at crepuscular hours (Higdon et al. 2019). Further, fawns in southern Texas were shown to avoid activity at crepuscular hours, but not during the day or at night (Jackson et al. 1972). This would minimize activity overlap with crepuscular coyotes, but not nocturnal ones. If ungulates can distinguish differences in risk posed by different coyotes (Gese 1998), despite their predictability, the overall patterns of summer coyote activity would poorly reflect daily risk dynamics from the perspective of a fawn.

Disentangling which coyotes pose particular risks to certain prey requires reliable predictors of activity cycles. However, I found no evidence of simplistic associations between sex, range size, body size, or woody canopy cover with patterns of activity (Table IV.1). Thus, commonly hypothesized, simple predictors of activity patterns appear unreliable. Without a way to distinguish drivers of activity patterns, one cannot use convenient activity proxies (*e.g.* game camera capture rates) to assess perceived risk times if not all predators within a species pose the same risk to a given prey. This makes disentangling activity patterns, and isolating particular predators contributing to a dynamic LOF difficult. Interestingly, I found no relationship between range size, which is linked to territory residency (Kamler and Gipson 2000), and similarity in activity dynamics. Residency is linked to breeding opportunities, and reduced mortality risk (Gese et al. 1988*b*, Windberg 1995), indicating no strong linkages between this host of variables and activity dynamics. This suggests that any influences of territoriality on activity may depend on the dynamic nature of space use (Chapter III), as well as that of activity cycles.

Other factors that I did not capture, however, may drive activity dynamics. Social rank is believed to affect behavioral responses of individuals to resource limitation (Polansky et al. 2013), which is known to influence several aspects of coyote behavior (Bekoff and Wells 1982). However social rank is difficult to study in semi-cryptic carnivores, particularly habitats with dense vegetation, due to limited visibility and confounding effects of observer presence (Bekoff and Wells 1986). Thus, I was unable to evaluate the effect of coyote social rank within a social group on behavior. Further, while I was able to show that individuals within a population diverged in activity patterns, I could not directly assess whether this was related to their choice of prey or their mode of hunting in this study. Both of these constraints may be alleviated with rapidly developing video bio-logging technology (de la Rosa 2019). Video data would provide needed information on social interactions as well as prey choice without biases associated with human observers. This information could be used in conjunction with my methodology to evaluate relationships between activity dynamics, social rank, and foraging strategy.

Using species-level activity patterns as a proxy for temporal variation in predation risk assumes that the mean activity pattern is representative of individuals that prey on the prey species of interest. However, the mean activity pattern will poorly predict dynamics if behavior patterns diverge across individuals. This has long been recognized in carnivore behavior research (Gittleman and Harvey 1982), and is relevant to LOFs when the groups of activity patterns represent predators with different foraging strategies. My results suggest that trends and intraspecific variation in predator activity cycles should be taken into account in LOF research.

The LOF concept is a unifying idea, bridging animal behavior, habitat selection, movement, and population dynamics. It has great potential as both a theoretical, and heuristic tool, as well as implications for generating spatio-temporally targeted management solutions to predator issues. However, to realize the potential of the LOF, we must not overlook critical aspects of predator ecology with simple assumptions. Acknowledging the role of differential behavior within predator populations further advances the concepts utility. I demonstrated the complexity and inter-individual variation in coyote behavior, and argue that its explicit consideration will further aid the LOF concept in explaining the complexity of predator-prey dynamics. Acknowledging and accounting for intraspecific differences in activity will reduce unmodeled error in studies of LOF dynamics, perhaps clarifying equivocal support in previous work. By considering intraspecific behavioral variation explicitly, we can gain a much clearer picture of the complexity, drivers, and ecological effects of fear.

V. SUMMARY AND CONCLUSIONS

The results of the three studies I presented suggest we must further consider the complexities of coyote behavior in order to better understand the internal mechanics of their interactions, population dynamics, and impacts on prey. Commonly used, simplistic dichotomies of coyote behavior are inadequate to guide management because they do not consider the nature of coyote dispersal, which affects the resilience of local sub-populations (Chapter III). The same is true for a static view of their behavior and space use, because coyote behaviors are temporally dynamic over a large spatial scale relative to that of management efforts (Chapters II and III). I provided evidence that population-level aggregations of their activity patterns may not adequately represent risk dynamics to particular prey species (Chapter IV). This may affect predator-prey dynamics and carry implications for how we assess the impacts of coyotes on other species. In the aggregate, my work demonstrates that these simplistic assumptions, commonly relied upon in coyote research (Kamler and Gipson 2000, Hinton et al. 2015), must be set aside if we are to make defensible conclusions about their ecology, which lead to effective management. Defensible conclusions to complex questions require appropriate tools to extract them from data. Those using the tools must recognize what is appropriate for the question to achieve direct inference (Fieberg and Borger 2012). This requires bridging ecological knowledge and statistics.

Assumptions simplify analyses, not the system under study. Unwarranted assumptions act as blinders, limiting our perception and comprehension of the world around us, or in this case, coyotes. The vast majority of coyote studies focusing on movement used scant data from manual radio-tracking to address complex questions (e.g. Andelt 1985, Gese et al. 1988*a*, Windberg and Knowlton 1988, Kitchen et al. 2000). They then relied on simple parametric statistics for inference. While many of these researchers were simply doing the best with what was available, these approaches required strong assumptions, many implicit, that varied by study. Newer studies using GPS telemetry used considerably more data, but similar approaches to older studies (Hinton et al. 2015, Sasmal et al. 2019, Ward et al. 2019; but see Moorcroft et al. 2006). Detail is a commonly cited advantage of GPS telemetry (Cagnacci et al. 2010), but this detail is lost without appropriate analytic methods. The chosen analysis should capture, not mask, this detail if we are to learn from it.

Capturing this detail begins with our *a priori* assumptions. Much of the coyote literature is based on the assumption that coyote territoriality is characterized by 2 groups; resident coyotes that occupy and defend discrete, non-overlapping territories, and transients that move individually or in small groups outside of them (Kamler and Gipson 2000). This assumption originated as an explanation of observed territorial behavior (Camenzind 1978), but was not formally questioned until recently (Morin and Kelly 2017). Binary schemes underlie key studies of coyote behavior (Andelt 1985) and population dynamics (Windberg and Knowlton 1988), among many others. By comparing competing explanations explicitly, I showed that this pervasive assumption is unjustified, undermining the basis for a considerable body of work.

Methodological assumptions have implications for ecological interpretation, which affect our understanding of coyote behavior. Perhaps the most pervasive, unrecognized assumption is stationarity, or constancy of parameters through time (Benhamou 2014). So called “home range" estimates used in numerous coyote studies are a key example (e.g. Andelt and Gipson (1979), Gese et al. (1988*a*), Ward et al. (2019). Regardless of the methodology chosen, these estimates were made over relatively long time blocks, such as years or seasons, which assumes that the pattern of space use does not change within the given time window, or at least such changes are not relevant to the question. However, I showed that coyote space use patterns can change rapidly (Chapters II and III), which carries implications for coyote population dynamics. Previous work considering the implications of coyote space use on population dynamics simulated 2 time periods (before and after the imposition of a control effort) that were otherwise temporally static (Windberg and Knowlton 1988). Though my work supports the speculation of these authors, their analytical treatment neglects the longevity of management effects, which are key to determining their efficacy, thus limiting their scope of inference. The approach I took captures the temporal dynamics (nonstationarity) of coyote space use, permitting not only empirical estimates of space use and emigration parameters, but with further development can be used to make informed projections of coyote population responses to management efforts.

The final common assumption is internal homogeneity of samples, otherwise stated as no unmodeled groups within a data-set. Violation of this assumption can result in non-normal, even multimodal distributions of residuals, non-constancy of variance, and biased parameter estimates, invalidating simple parametric tests (Zar 2010). Like stationarity, internal homogeneity is a common assumption underlying many analyses of coyote behavior (e.g. Arias-Del Razo et al. 2011). This is a common assumption in many studies of coyote activity patterns, particularly those based on camera-trapping, where activity differences between individuals are difficult to estimate Rowcliffe et al. 2008, 2014. This imposes an assumption of internal consistency of activity patterns that is likely unjustified, given even the limited evidence of divergent activity patterns between individual coyotes (Andelt 1985, Gese et al. 1989, Kitchen et al. 2000). I provided evidence of group effects in both coyote activity cycles, and their dynamics through time (Chapter IV). Simple predictors were not related to group membership, including those potentially determined from images. These results highlight the need to critically evaluate whether internal homogeneity is a reasonable assumption when choosing not only statistical procedures, but also field methodology.

Moving forward, researchers should acknowledge the complexity of coyote sociality and territoriality, how they influence the spatial structure of populations, and their temporal dynamics explicitly in their studies. Researchers should be aware of the assumptions imposed by their choice of analysis, particularly the implicit assumptions, and how they relate to the question at hand.

Challenges and Further Study

Each of the 3 preceding studies will benefit from continued conceptual and analytic development in order to extract more relevant inference from the data. The methods presented in chapter II are adequate for examining pair-level interactions, but methods of comparing parameters across pairs, that incorporate spatial information and higher level covariates, are required for population-level inference. Two potential solutions are expanding the copula to incorporate covariance among overlap time series, and a random effects approach where inter-individual variation is modeled as a distribution. The first approach would model similarity among series explicitly, and would be easy to estimate with standard maximum likelihood procedures (Nelsen 2006). However, the covariance terms would be difficult to interpret except in relative terms (Parsa and Klugman 2011), and may be difficult to link with covariates due to the geometric increase in parameters in the covariance matrix with the number of series. Alternatively, a random effects approach would allow straightforward incorporation of pair-level covariates, but may require Bayesian methods to estimate parameters (Lele and Dennis 2009). Further research is warranted to compare these alternatives.

Chapter III provides important information and an explicit process for modeling dispersal parameters (emigration and immigration) of an open, spatially structured coyote population, but is limited by the lack of straightforward estimates of state-specific mortality. HMMs are used population dynamics models (Newman et al. 2006), but have not been integrated with other HMMs describing movement or space use processes. An *as hoc* solution may be to use dummy state with fixed parameters representing mortality. Series values would be coded with the fixed parameters following mortality such that transition to the dummy state represents death. Thus, transition probabilities between other states would account for mortality, we would obtain direct estimates of state-specific mortality rates, and not estimate superfluous parameters describing the space use and stability of the dummy state. Whether this approach is statistically tractable requires further investigation.

Finally, the collection of autocorrelation surfaces in chapter IV contains much more ecologically interpretable information than could be extracted with the present methods. Multivariate functional principal components analysis (MFPCA; Happ and Greven 2018) appears to be a viable option for separating variation into distinct patterns. This method is used to compare magnetic resonance images in multiple sclerosis research, breaking variation into distinct, interpretable components . In the context of autocorrelation surfaces, this would break variation in coyote activity dynamics into distinct component surfaces, analogous to numeric principal components in traditional multivariate analysis. This is a developing methodology and the performance of current algorithms in the presence of missing data is questionable (C. Happ, Department of Statistics, Ludwig Maximilian University of Munich, personal communication).

Moving forward, researchers should acknowledge the complexity of coyote sociality and territoriality, how they influence the spatial structure of populations, and their temporal dynamics explicitly in their studies. Researchers should be aware of the assumptions imposed by their choice of analysis, particularly the implicit assumptions, and how they relate to the question at hand. Otherwise, researchers blind themselves to potentially critical aspects of the questions they seek to answer. Testing assumptions can shed light on important behavioral processes, as I showed in Chapters III and IV. Continued reevaluation of longheld assumptions provides new insight into ecological processes. This is particularly important in predator management, which perenially relied on simple assumptions (Treves et al. 2016). Only, by better understanding the processes underlying predator ecology can we achieve effective and sustainable management solutions to the issues that surround them.

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