## DEFINING AND EVALUATING THE SPATIO-TEMPORAL DIMENSIONALITY OF CARNIVORE ECOLOGY

By

Remington J. Moll

#### A DISSERTATION

Submitted to Michigan State University in partial fulfillment of the requirements for the degree of

Fisheries and Wildlife – Doctor of Philosophy Quantitative Biology – Dual Major

#### ABSTRACT

#### DEFINING AND EVALUATING THE SPATIO-TEMPORAL DIMENSIONALITY OF CARNIVORE ECOLOGY

#### By

#### Remington J. Moll

In this dissertation I defined and evaluated the spatio-temporal dimensionality of carnivore ecology via philosophical analysis, literature synthesis, and empirical study. In Chapter 1, I analyzed philosophical and empirical arguments that postulate model section techniques like AIC empirically justify a value for simplicity in statistical modeling of ecological phenomena. My analysis drew upon an extensive case study regarding the reintroduction of wolves into Yellowstone National Park, USA. I showed that assumptions of stationarity required for the epistemic justification of simplicity are generally violated when considering complex ecological phenomena. I concluded that simplicity plays a greater epistemic role in explaining past events than it does in predicting future ones, thereby tempering the value traditionally lauded upon simplicity in ecological study.

In Chapter 2, I evaluated the niche width of a mesocarnivore species commonly assumed to be a forest specialist (the pine marten *Martes martes*). I used a large-scale spatial occupancy model to show that although pine martens were positively associated with forested habitat, they occurred across a remarkable variety of habitats and exhibited no negative association with nonforested areas. I concluded that evaluations of species' niche width should be informed by large scale studies rather than local assessments.

In Chapter 3, I examined the effects of large carnivores on the grouping behavior of African ungulates. I modeled spatial predation risk from two carnivore species in three ways: 1) as a function of habitat, 2) as a function of carnivore occurrence, and 3) as a function of where

carnivores tended to kill prey. I found that prey behavioral response to risk varied across these three expressions in complex ways, highlighting the need for a multi-expressional approach to assessing risk effects in multi-species systems.

In Chapter 4, I coupled a conceptual framework with a formal literature review to synthesize the ways that predation risk was measured and modeled in carnivore-ungulate systems. I found striking variability in methodological approach to measuring and modeling risk. I synthesized our findings into a cohesive framework based upon predator-prey theory and centered around long-term risk, short-term risk, and habitat characteristics. I concluded with a call for risk-related studies to employ a multi-dimensional approach and to evaluate multiple, competing hypotheses. In Chapter 5, I applied the recommendations generated in Chapter 4 in a study of human-carnivore interactions in an expansive semi-urban park system. I employed a multi-dimensional spatio-temporal framework that revealed how humans and carnivores share the city by avoiding one another in space and time.

I conclude the dissertation with a summary of lessons learned and a look ahead to future research. Future studies that critically evaluate ecological phenomena across multiple spatiotemporal dimensions via a variety of variable expressions will be most efficient in separating out ecological signals from noise and locating the characteristic scales upon which such phenomena occur. Such research will bring clarity not only to ecological theory, but will facilitate more efficient conservation and management strategies by providing clear linkages between ecological processes and the scales at which they can be manipulated or influenced. Dedicated to the love of my life, Valerie Ann, and our beloved children, November Iris, Selah Elise, and forthcoming Baby Moll.

#### ACKNOWLEDGEMENTS

I am lucky to be here. My path to the completion of this dissertation has been circuitous and indelibly shaped by mentors, friends, family, and faith. I have been blessed at every step. I first thank my advisor, Dr. Bob Montgomery. Bob is one of those rare individuals who can challenge you to the core while simultaneously empowering you. Bob has shown remarkable flexibility, amazing loyalty, tireless dedication, and piercing insight at every stage of this dissertation. Somehow, Bob has known just what to do at each critical point in my journey and nudged me in a strategic direction. Bob has also been a vigorous champion of family life, encouraging me to put family in its rightful place above research and profession. I could not have asked for a better mentor and I will be ever grateful for Bob's guidance.

I thank my graduate committee, including Drs. Brian Maurer, Kevin Elliot, Scott Peacor, and Josh Millspaugh. My time with Brian was tragically cut short by his passing, and I mourn this loss. I am thankful for the mentorship he provided, especially his ability to think broadly and critically while being exceptionally kind. Discussions with Kevin ranged the map from philosophy to applied science to modeling and ethics. I am thankful for his expansive knowledge of the contextual history of science and the insight he has brought with respect to non-epistemic values in the scientific process. Kevin has inspired me to be thoughtful and empathetic, even in the critical atmosphere of academia. I thank Scott for being extremely flexible and joining my committee so late in the game. I am grateful for Scott's ability to incisively cut to the core of an issue and link empirical questions to prevailing theory. Scott's guidance in understanding the theoretical foundations of risk effects was incredibly enlightening and gave me the confidence to critically tackle Peter Abrams' papers! Josh has been a mentor to me for over a decade. His

v

thoughtful, measured, caring guidance has molded me into the scientist and person I am today. When faced with a difficult situation or challenge, my mind often turns to Josh, wondering what he would do if placed into my situation. Though I certainly have much work to do, I have tried to emulate his rigorous approach to science, his unwavering dedication as a mentor, and the incredible clear-headedness with which he forges ahead in our discipline and in life.

I thank those who funded this research. My primary funding came from the National Science Foundation Graduate Research Fellowship and Michigan State University's (MSU) University Distinguished Fellowship. I also received support from the Au Sable Fellowship from the Au Sable Institute, and the Ambrose Patullo, Vera M. Wallach, and Joseph Laurence Maison Fellowships provided via the Department of Fisheries and Wildlife at MSU. These institutions and individuals believed in and took a chance on me. I am grateful for their support and I hope that I have been a faithful steward of their generosity.

I benefited tremendously from a fantastic group of colleagues at MSU. Many faculty provided training, advice, and mentorship along the way, especially Drs. Jean Tsao, Daniel Steel, Elise Zipkin, Gary Roloff, Jerry Urquhart, and David Williams. My graduate and undergraduate colleagues provided a warm, welcoming community of support. I am grateful to all members of the RECaP lab for their friendship and kindness. I especially thank Steve Gray, Jackie Beck, Herbert Kasozi, Claire Hoffman, Symon Masiaine, Tutilo Mudumba, Dr. Leandro Abade, Arthur Muneza, Kyle Redilla, Clara Lepard, Waldemar Ortiz-Calo, and Jeremiah Eaton for their numerous contributions to my professional development and career. I would be lost without such an inspiring group of collaborators. I also thank Amanda Dolinski, Andrew Dennhardt, Lauren Phillips, Tracy Melvin, Alex Killion, Talesha Dokes, and Sean Sultaire for their friendship.

vi

I was fortunate to work with wonderful collaborators outside of MSU. I am grateful for the deep relationships formed with the Cleveland Metroparks (CMP) research team, including Jon Cepek and Drs. Terry Robison, Pam Dennis, and Pat Lorch. What a great team! I thank others at CMP who invested in me and contributed to the project, especially John Krock, Liz Clingman, Jen Brumfield, Ben Piazza, and Tim Krynak. I also thank many other collaborators with whom I have had the pleasure of working with these last four and a half years, including Drs. Matt Hayward, David MacDonald, Craig Tambling, Kerry Kilshaw, Roo Campbell, Laura Harrington, Johnny Birks, and Shawn Riley. I thank Eric Tans for his friendship and collaborative help. I spent two weeks in Norway with the amazing team at the Norwegian Institute for Wildlife Research. Drs. Bram van Moorter and Manu Panzacchi graciously opened their home to me. Their hospitality was incredible. I am also thankful for the generosity that Dr. Christer Rolandsen, Dr. Erling Solberg, and Dr. John Linnell showed me in Norway.

While writing, I listened extensively to music by Tycho, Kiasmos, Bonobo, Odesza, William Basinski, Heurco S., Deru, Emancipator, Minutes of Sleep, Bon Iver, Chelsea Cutler, Houses, Beach House, and Post Malone. Thanks to these artists for help in creating something new. Likewise, John Wooden, Henri Nouwen, and Ursula K. LeGuin guided me through their writings as I struggled to create beautiful and useful research while living a healthy life.

Finally, thank you to my friends and family for supporting me. Nick McCann was a confidant that helped me navigate the tortuous back alleys of academia. I thank Richard and Becca Shaull, Ben and Michelle Rous, Peter and Renee Hoffman, Scott and Nikki Magie, and all our friends at Liberty for their friendship and spiritual companionship. I thank my family and especially my parents for being an ever-present source of love, affirmation, and generosity. I thank my children for their love and affection. I thank my wife Valerie for being the most

vii

amazing human I have ever known. She always has in mind my greatest good and works tirelessly for our family and for our world. I thank God for the opportunity to pursue a career in ecology

#### PREFACE

The five main chapters of this dissertation have been published in peer-reviewed journals with co-authors. Due to copyrights, the first four chapters could not be reprinted here. Thus, each of the first four chapters are briefly summarized in the main body of this document, followed by a link to the online article. Chapter 5 is reprinted. The citations for these chapters are below.

Chapter 1: Moll, R. J., D. Steel, and R. A. Montgomery. 2016. AIC and the challenge of complexity: A case study from ecology. Studies in History and Philosophy of Biological and Biomedical Sciences 60: 35-43.

Chapter 2: Moll, R. J., K. Kilshaw, R. A. Montgomery, L. Abade, R. D. Campbell, L. A. Harrington, J. J. Millspaugh, J. D. S. Birks, and D. W. Macdonald. 2016. Clarifying habitat niche width using broad-scale, hierarchical occupancy models: A case study with a recovering mesocarnivore. Journal of Zoology 300: 177-185.

Chapter 3: Moll, R. J., A. K. Killion, R. A. Montgomery, C. J. Tambling, and M. W. Hayward. 2016. Spatial patterns of African ungulate group size reveal complex but limited risk effects from reintroduced carnivores. Ecology 97: 1123-1134.

Chapter 4: Moll, R. J., K. M. Redilla, T. Mudumba, A. B. Muneza, S. M. Gray, L. Abade, M. W. Hayward, J. J. Millspaugh, and R. A. Montgomery. 2017. The many faces of fear: A synthesis of methodological variation in characterizing predation risk. Journal of Animal Ecology 86: 749–765.

Chapter 5: Moll, R. J., J. D. Cepek, P. D. Lorch, P. M. Dennis, T. Robison, J. J. Millspaugh, and R. A. Montgomery. 2018. Humans and urban development mediate the sympatry of competing carnivores. Urban Ecosystems 21: 765-778.

#### TABLE OF CONTENTS

LIST OF TABLES	xii
LIST OF FIGURES	xiii
INTRODUCTION	1
CHAPTER 1: THE EPISTEMIC VALUE OF SIMPLICITY IN MODELING COMPL ECOLOGICAL PHENOMENA	EX 5
CHAPTER 2: A SPATIAL EVALUATION OF NICHE WIDTH IN A RECOVERING MESOCARNIVORE	Э б
CHAPTER 3: EVALUATING MULTIPLE SPATIAL EXPRESSIONS OF PREDATION A CANRIVORE-UNGULATE SYSTEM	ON RISK 7
CHAPTER 4: A SYNTHESIS OF METHODS CHARACTERIZING PREDATION RICARNIVORE-UNGULATE SYSTEMS	ISK IN 8
CHAPTER 5: HUMANS AND URBAN DEVELOPMENT MEDIATE THE SYMPAT	TRY OF
COMPETING CARNIVORES	9
Abstract	9
Introduction	10
Methods	13
Study System	13
Dominant-Subordinale Carmvore Pair	18
Study Design	19
Hypothesis 1: Spatial Occupancy and Site-Visitation Modering	
Hypothesis 2: Spatio temporal Modeling	23 24
Results	2 <del>4</del> 25
Occupancy and Site-Visitation Modeling	
Temporal Activity Patterns	
Spatio-temporal Modeling	
Discussion	31
Acknowledgements	
CONCLUSION	
REFERENCES	

#### LIST OF TABLES

Table 1. Descriptions, hypothesized relationships, and references for covariates used in occupancy and site-visitation models for coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*) in the Cleveland Metroparks, December 2015 – May 2016. The range, mean, and standard deviation of covariates across all sites is included below covariate names. Hypotheses and references for coyotes and red foxes are provided in white and gray boxes, respectively......17

#### LIST OF FIGURES

Figure 4. Temporal activity patterns of coyotes (Canis latrans) and red foxes (Vulpes vulpes) based on data from 104 camera-trap sites in the Cleveland Metroparks, December 2015 – May 2016. High and low development sites were determined using k-means clustering. Delta values represent the degree of overlap with bootstrapped confidence intervals shown parenthetically...29

Figure 5. Median times-to-encounter for coyotes (Canis latrans), red foxes (Vulpes vulpes), and humans (Homo sapiens) based on data from 104 camera-trap sites in the Cleveland Metroparks, December 2015 – May 2016. High and low development sites were determined using k-means clustering. The vertical dashed line is the observed median time-to-encounter and the shaded areas are the random expectation of distributions based upon 1000 simulated permutations. P-values depict the proportion of times the observed value exceeded the random expectation......31

#### INTRODUCTION

All ecological phenomena occur in space and time. Although it is clear that both spatial and temporal dimensions are important to consider when studying ecological phenomena (Weins 1989, Levin 1992), one or more of these dimensions is often collapsed or omitted in theory or empirical practice. For example, many foundational equations undergirding population dynamics (e.g., Lotka-Volterra equations) lack an explicit spatial dimension, and many empirical studies of wildlife-habitat relationships lack an explicit temporal dimension (Ramalho and Hobbs 2012). Focusing on one spatio-temporal dimension to the exclusion of the other might be justified on a number of grounds, ranging from the practical constraints of field work to the theoretical relevance of a particular dimension to a given research objective. Whatever the rationale, researchers must decide whether a spatial or temporal dimension will be collapsed or omitted in a given study, or whether some spatio-temporal approach will be taken as a middle road.

Within both spatial and temporal dimensions, particular ecological phenomena tend to manifest on a characteristic scale (Levin 1992). Identifying this characteristic scale within a given dimension for a given phenomenon can be difficult, and is highly contingent upon research questions or objectives. For example, objectives related to defining a species' ecological niche might require evaluation of niche axes across broad spatio-temporal scales to capture the variation that characterizes the species as a whole (Moll et al. 2016a). Conversely, objectives related to the behavior of particular populations or individuals might require data collection on more narrow spatio-temporal scales, with resultant inference constrained to local conditions and organisms (Moll et al. 2017).

Finally, once spatial and temporal dimensions and their associated scales have been chosen, researchers must make decisions regarding multiple, often similar, expressions of a

given variable across a given dimension and at a given scale. For example, a study of the effect of temperature on a species' movement might consider many instantiations of temperature across a landscape, including its mean, maximum, minimum, or variability, each calculated across some spatio-temporal scale. As with dimension determination, finding the most relevant expression of a variable for a given ecological phenomenon of interest can be a challenge, especially in instances where little ecological knowledge exists (Moll et al. 2016b). Moreover, the challenge of multiple expression is magnified for variables that are latent or implicit, such as perceived predation risk or urbanization (Moll et al., 2017, Moll et al. in review). Such latent variables cannot be directly measured in the field in the way that one might measure a quantity like temperature or tree height. Thus, researchers must decide which combination of measurable quantities best represents the concept represented by a given latent variable.

The above examples make clear that there are three important issues to consider when studying ecological phenomena, namely, *i*) considering the spatial, temporal, or spatio-temporal dimensions, *ii*) finding the characteristic scales at which a given ecological phenomenon manifests within those spatial and/or temporal dimensions, and *iii*) identifying suitable expressions of variables of ecological interest at particular spatio-temporal scales. In all cases, the challenge is to properly align the spatio-temporal dimensions, their scales, and the variables measured therein with specific research objectives such that reliable knowledge is achieved. Collectively, I refer to this issue as the *challenge of spatio-temporal dimensionality*.

The challenge of spatio-temporal dimensionality is particularly acute in carnivore ecology research. Studying carnivore ecology across time and space is made difficult by a number of factors, including small sample sizes due to low population densities, logistical field challenges related to these species' extensive movement patterns, and ethical considerations that limit interventions such as removal experiments (Estes 1995). Moreover, the long-lived and wide-ranging nature of many carnivores implies that studies should encompass large spatial scales and numerous years, which is often in tension with logistical constraints such as personnel availability, study timeframes, and funding support. The challenge of spatio-temporal dimensionality is further intensified by carnivores' behavioral flexibility as predators, with dynamic adaptations to fluctuating resources in time and space representing the norm (Lima 2002). This flexibility means that ecologically important variables (e.g., habitat availability, abundance of a given prey species) and their expressions in the field are often moving targets that researchers must try to measure across broad spatial and temporal scales. Taken together, these issues mean that defining and evaluating the spatio-temporal dimensionality of carnivore ecology is often very difficult.

Nonetheless, there has perhaps never been a more important time in history to gain a better understanding of the spatio-temporal dimensionality of carnivore ecology. Increasing human population and associated expansion of urbanization and agriculture means that potential for human-carnivore conflict is extremely high (Woodroffe 2000, Treves and Karanth 2003). Such conflict is just one source of many that are leading to declines in the majority of large carnivore populations worldwide, with numerous species rapidly progressing towards endangerment or extinction (Ripple et al. 2014). At the same time, there has been an increasing recognition of the crucial role that carnivores play in numerous ecological processes, including trophic dynamics and ecosystem functioning (Estes et al. 2011, Ripple et al. 2014). Moreover, there is a persisting societal value for the existence of many charismatic carnivore species, which remain socially and culturally important across the globe (Chapron et al. 2014, Gebresenbet et al. 2018, Hovardas 2018).

Here, I explore the spatio-temporal dimensionality of carnivore ecology via philosophical analysis, literature synthesis, and empirical study. In Chapter 1, I lay the groundwork for the dissertation by analyzing the complexity inherent in broad-scale carnivore-ungulate ecology and its implications for statistical modeling. In Chapter 2, I present a case study of carnivore ecology in space (i.e., temporal dimension collapsed) with an application to niche theory. In Chapter 3, I build upon Chapter 2 by presenting another analysis of carnivore space use that examines multiple expressions of that spatial dimension the context of predator-prey interactions. In Chapter 4, I review and synthesize the carnivore-ungulate literature on risk effects and conclude that studies embracing multi-dimensionality in space and time are needed to move the field forward. In Chapter 5, I apply the framework developed in Chapter 4 to complex human-carnivore interactions across time and space. I conclude the dissertation with a summary of lessons learned and a look ahead to future research.

## CHAPTER 1: THE EPISTEMIC VALUE OF SIMPLICITY IN MODELING COMPLEX ECOLOGICAL PHENOMENA

We analyzed philosophical and empirical arguments that postulate model section techniques like AIC empirically justify a value for simplicity in statistical modeling of ecological phenomena. Our analysis drew extensively upon a case study regarding the reintroduction of wolves into Yellowstone National Park, USA. We showed that assumptions of stationarity required for the epistemic justification of simplicity are generally violated when considering complex ecological phenomena. We concluded that simplicity plays a greater epistemic role in explaining past events than it does in predicting future ones, thereby tempering the value traditionally lauded upon simplicity in ecological study. For a full text of this work, go to:

https://doi.org/10.1016/j.shpsc.2016.09.007

# CHAPTER 2: A SPATIAL EVALUATION OF NICHE WIDTH IN A RECOVERING MESOCARNIVORE

We evaluated the niche width of a mesocarnivore species commonly assumed to be a forest specialist (the pine marten *Martes martes*). We used a large-scale spatial occupancy model to show that although pine martens were positively associated with forested habitat, they occurred across a remarkable variety of habitats and exhibited no negative association with non-forested areas. We concluded that evaluations of species' niche width should be informed by large -scale studies rather than local assessments. For a full text of this work go to:

#### https://doi.org/10.1111/jzo.12369

## CHAPTER 3: EVALUATING MULTIPLE SPATIAL EXPRESSIONS OF PREDATION RISK IN A CANRIVORE-UNGULATE SYSTEM

We examined the effects of large carnivores on the grouping behavior of African ungulates. We modeled spatial predation risk from two carnivore species in three ways: 1) as a function of habitat, 2) as a function of carnivore occurrence, and 3) as a function of where carnivores tended to kill prey. We found that prey behavioral response to risk varied across these three expressions in complex ways, highlighting the need for a multi-expressional approach to assessing risk effects in multi-species systems. For a full text of this work go to: <u>https://doi.org/10.1890/15-</u>

#### <u>0707</u>

## CHAPTER 4: A SYNTHESIS OF METHODS CHARACTERIZING PREDATION RISK IN CARNIVORE-UNGULATE SYSTEMS

We coupled a conceptual framework with a formal literature review to synthesize the ways that predation risk was measured and modeled in carnivore-ungulate systems. We found striking variability in methodological approach to measuring and modeling risk. We synthesized our findings into a cohesive framework based upon predator-prey theory and centered around long-term risk, short-term risk, and habitat characteristics. We concluded with a call for risk-related studies to employ a multi-dimensional approach and to evaluate multiple, competing hypotheses. For a full text of this work go to: <u>https://doi.org/10.1111/1365-2656.12680</u>

## CHAPTER 5: HUMANS AND URBAN DEVELOPMENT MEDIATE THE SYMPATRY OF COMPETING CARNIVORES

#### Abstract

Humans can profoundly shape animal community dynamics, but such effects have rarely been evaluated for terrestrial carnivores. Humans affect carnivores in both spatial and temporal dimensions via the chance of human encounter and alteration of the landscape through urban development. We investigated three hypotheses regarding how humans mediate the sympatry of larger, dominant carnivores with their smaller, subordinate counterparts. We tested these hypotheses by examining the spatio-temporal dynamics of a dominant carnivore (covote *Canis latrans*) and its subordinate competitor (red fox *Vulpes vulpes*) across an extensive urban park system. We found that dominant and subordinate carnivores exhibited strong and often opposing spatio-temporal responses to the probability of human encounter and urban development. Spatially, coyotes visited more highly developed sites less frequently while red foxes exhibited an opposing response. Temporally, both species avoided humans via nocturnal activity. Spatiotemporally, red foxes avoided coyotes at all sites and avoided humans at highly developed sites, whereas covotes showed a positive association with humans at such sites. Our analysis indicates that areas with higher urban development might act as spatial refugia for some subordinate carnivores against interference from larger, dominant carnivores (a "human shield" effect). Our findings also reveal that broad-scale spatial avoidance is likely a crucial component of coexistence between larger, dominant carnivores and humans, whereas finer-scale spatiotemporal avoidance is likely a key feature of coexistence between humans and smaller, subordinate carnivores. Overall, our study underscores the complex and pervasive nature of human influence over the sympatry of competing carnivores inhabiting urban systems.

#### Introduction

Humans exert profound effects on animal communities globally. These effects typically occur via three pathways. First, humans exploit (i.e., harvest, poach, or kill) animals at rates many times higher than non-human predators, a phenomenon known as "superpredation" (Darimont et al. 2015). As superpredators, humans have triggered rapid population-level trait-changes in a variety of animal communities via harvest practices, thereby restructuring trophic dynamics (Darimont et al. 2009). Second, given the lethal threat associated with human encounter, animal communities are also shaped via risk effects whereby animals make behavioral modifications to avoid humans (Oriol-Cotterill et al. 2015). For instance, many species respond to spatio-temporal peaks in human activity by increasing vigilance and selecting habitat with a decreased probability of encountering humans (reviewed by Frid & Dill 2002). Finally, humans affect animal communities by transforming the physical environment (Ellis 2011). For example, habitat loss and fragmentation associated with agricultural land conversion and urbanization have reduced animal biodiversity worldwide (McKinney 2006, Dirzo et al. 2014). Although research attention to these three pathways has increased in the last decade (Magle et al. 2012, Forman 2016), relatively little is known of the ways in which the threat exerted by human superpredators affects animal communities (Oriol-Cotterill et al. 2015). This knowledge gap constitutes a crucial research need given the rapid rate at which natural systems are being shaped by human-related activities globally (Ellis 2011, Dirzo et al. 2014).

Terrestrial, mammalian carnivores are especially vulnerable to human-related effects due to their wide-ranging nature and capacity to kill animals valued by humans (e.g., livestock; Treves & Karanth 2003). Although lethal exploitation affects most carnivore species (Darimont et al. 2015), recent work suggests they also strongly respond to the risk of human encounter

(Smith et al. 2017) and the indirect effects of human-induced landscape development (Ordeñana et al. 2010). For clarity, we hereafter use the term *development* to represent built structures primarily in the form of residential buildings and associated paved surfaces, while acknowledging that other forms of development also affect carnivores (e.g., agricultural land conversion; Dorresteijn et al. 2015). Carnivores often adjust to the dual threats of human encounter and development by modifying their spatial and temporal ranging and activity patterns (Oriol-Cotterill et al. 2015). For example, both large and mesocarnivores avoid areas where the risk of human encounter is high (Dorresteijn et al. 2015, Loveridge et al. 2017) or use such areas only when humans are absent (e.g., at night; Gehr et al. 2017). Similarly, as levels of development increase, carnivores reduce their home ranges (Šálek et al. 2015), increase use of less developed habitat patches (Wilmers et al. 2013), and become more nocturnal (Wang et al. 2015).

The sympatry of competing carnivores is often enabled via species' differentiation in spatial and temporal ranging and activity patterns (Karanth et al. 2017). For example, sympatry in guilds of large African carnivores is borne out via variation in movement behavior among species, whereby larger, dominant species are avoided by smaller, subordinate species across multiple spatio-temporal scales (Vanak et al. 2013). Given humans' potential to alter the behavior of carnivores (Oriol-Cotterill et al. 2015), sympatry among competing carnivores in human-dominated systems is likely shaped by species' differential tolerance of human activity (e.g., frequency of visits to a given site) and development (cf. Polis and Holt 1992). For instance, compared to their smaller counterparts, large carnivores are typically more sensitive to these human-related factors, especially landscape development (Ordeñana et al. 2010, Wang et al. 2015). In this way, higher levels of human activity and development can reduce the occurrence

of larger, dominant carnivores and result in indirect, positive effects on the smaller, subordinate mesocarnivores by reducing interference competition (Dorresteijn et al. 2015, Wang et al. 2015). Beyond these preliminary observations, however, much remains unknown of the role humans play in shaping the sympatry of competing carnivores inhabiting developed landscapes (Dorresteijn et al. 2015, Oriol-Cotterill et al. 2015). Examining this role is crucial for understanding the mechanisms that enable both carnivore sympatry (Karanth et al. 2017) and human–carnivore coexistence (Oriol-Cotterill et al. 2015).

Here, we articulate and test hypotheses that predict how humans might mediate the sympatry of larger, dominant carnivores with their smaller, subordinate counterparts. The spatiotemporal dynamics of wide-ranging carnivores are inherently complex (Vanak et al. 2013, Karanth et al. 2017), and become even more so when considering mediating effects of humans on carnivore interactions. This complexity necessitates an analysis framework that considers multiple spatial and temporal dimensions (Moll et al. 2017). Therefore, we evaluate hypotheses on three distinct, but related, spatio-temporal dimensions. First, we consider spatial patterns of competing carnivore species' occurrence and activity (i.e., site-visitation rates). Previous work has revealed a spatial "human shield" effect in predator-prey systems, whereby prey reduce their predation risk by spatially associating with anthropogenic factors (e.g., developed areas) that are avoided by predators (Berger 2007, Kuijper et al. 2015). In a similar way, smaller, subordinate carnivores might reduce the potential for agonistic encounters with larger, dominant carnivores by spatially associating with anthropogenic factors that their larger counterparts avoid (Crooks et al. 2010, Ordeñana et al. 2010, Kuijper et al. 2016). We refer to this hypothesis as the spatial human shield effect (Fig. 1a). This hypothesis predicts that smaller, subordinate carnivores will indirectly benefit from, and be spatially associated with, both human activity and development

(Fig. 1a). Second, we consider carnivores' overlap in daily activity patterns. Previous work has shown that sympatry among competing carnivores is often facilitated via segregation in daily activity patterns (Frey et al. 2017, Lashley et al. 2018). Given that human activity is primarily constrained to daytime hours, we expect that both dominant and subordinate carnivores will avoid humans by being active at night (Wang et al. 2015, Gehr et al. 2017). Moreover, we hypothesize that such avoidance will intensify at more highly developed sites because such sites are more highly fragmented and surrounded by denser human populations (Wang et al. 2015). As a result, we predict that subordinate and dominant carnivores' temporal activity patterns will demonstrate greater overlap in developed areas due to a concomitant nocturnal shift by both species in such areas (Fig. 1b). We refer to this hypothesis as development-mediated temporal avoidance (Fig. 1b). Third, we consider spatio-temporal avoidance, whereby a subordinate species might not avoid a site occupied by a dominant species altogether (i.e., complete spatial avoidance), but rather avoids a given site for some period of time after it is visited by the dominant species. Such avoidance has been linked to carnivore sympatry and coexistence in guilds of African, Asian, and North American carnivores (Vanak et al. 2013, Wang et al. 2015, Karanth et al. 2017). This phenomenon likely extends to carnivore avoidance of human superpredators, which are dominant over all carnivores (Dorresteijn et al. 2015). In our urban study area, more highly developed sites are surrounded by relatively dense human populations and often contain physical refugia (e.g., culverts) that might enable subordinate carnivores to escape persecution from dominant carnivores (Gosselink et al. 2007). As a result, we predict that dominant carnivore avoidance of humans will be intensified at more highly developed sites, while subordinate carnivore avoidance of dominant carnivores will be reduced at such sites (Fig. 1c). We refer to this hypothesis as *development-mediated spatio-temporal avoidance* (Fig. 1c).

Importantly, these multi-dimensional hypotheses are not mutually exclusive, but rather collectively depict the possible relationships that enable humans and competing carnivores to coexist in space and time throughout an urban landscape.



Figure 1. Conceptual diagrams of hypothesized relationships between human superpredators (yellow circles), a dominant-subordinate carnivore pair (coyote *Canis latrans* and red fox *Vulpes vulpes*; green and blue circles, respectively), and development (i.e., built structures and paved surfaces; gray rectangles). In (a), red arrows indicate a negative effect and dashed blue arrows indicate an indirect, positive effect on carnivore space use. In (c), finely dashed black arrows indicate spatio-temporal avoidance (arrows pointing away from the species being avoided). In all cases, arrow width indicates strength of effect. Circle intersections in (b) represent diel periods of activity overlap. See main text for detailed descriptions of hypotheses.

We tested these hypotheses using a case study of humans, coyotes (*Canis latrans*), and red foxes (*Vulpes vulpes*) across an extensive urban park system that contained substantial variation in both human activity and development. We selected coyotes and red foxes as our focal carnivore species because *i*) both commonly occur in urban areas in North America, *ii*) both avoid humans, and *iii*) the species pair exhibits a clear dominance hierarchy, whereby the dominant carnivore (coyotes) negatively affect the subordinate species (red foxes) via interference competition (Gosselink et al. 2007, Crooks et al. 2010, Levi and Wilmers 2012)

#### Methods

#### Study System

We conducted research in the Cleveland Metroparks (hereafter Metroparks). The Metroparks consist of >9,300 ha (23,000 acres) divided among 18 reservations that have a circum-city distribution around Cleveland, Ohio, USA (population: ~2 million; Fig. 2). Reservations vary in shape, size, and connectivity, ranging from 24 to 1611 ha (mean = 459 ha, sd = 480 ha; Fig. 2). Habitat in the Metroparks primarily consists of mixed deciduous hardwood forest with patches of interspersed grasslands, surrounded by a matrix of residential, industrial, and commercial land. The reservations vary with respect to level of development. Several reservations are surrounded by major industrial development and interstate highways while others are embedded in a suburban-exurban-rural matrix (Fig. 2). Substantial portions of the Metroparks are situated along small to medium rivers (e.g., the Cuyahoga River). Topography across the parks ranges from steep slopes in riverine areas to rolling terrain in smaller urban parks (e.g., slope at study sites ranged from 0.2 to 23.8; Table 1). Human activity in the Metroparks is high, with ~18 million individual recreational visits annually, the majority of which occur in more urbanized parks

(Cleveland Metroparks 2017). Thus, the Metroparks constitutes a heterogeneous urban landscape that contains substantial variation in natural habitat, development, slope, and human activity.



Figure 2. The distribution of 104 camera-trap sites (black dots) deployed from December 2015 to May 2016 in the Cleveland Metroparks (outlined in solid grey).

Table 1. Descriptions, hypothesized relationships, and references for covariates used in occupancy and site-visitation models for coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*) in the Cleveland Metroparks, December 2015 – May 2016. The range, mean, and standard deviation of covariates across all sites is included below covariate names. Hypotheses and references for coyotes and red foxes are provided in white and gray boxes, respectively.

Covariate	Description	Hypothesized	References
		Relationship	
Distance to edge range: 0.3 - 483.4 mean: 110.4	Euclidean distance (m) to the nearest edge, where edge is the boundary between open habitat	negative	Theberge and Wedeles 1989, Randa and Yunger 2006, Kays et al. 2008
sd: 106.7	(shrub/scrub, grassland, cropland, developed open space, and low intensity development) and closed habitat (deciduous, coniferous, and mixed forest and woody wetlands)	neutral or weakly negative	Sargeant et al. 1987, Harrison et al. 1989, Goad et al. 2014, Lesmeister et al. 2015
Distance to park	Euclidean distance (m) to the	positive	Goad et al. 2014
feature range: 9.7 – 2487.3 mean: 450.9 sd: 518.3	nearest park feature commonly used by park visitors, including stables, visitor centers, trail access points, parking lots, picnic areas, ball fields, golf courses, information kiosks, boat launches, observation decks, and playgrounds	neutral or positive	Marks and Bloomfield 2006, Goad et al. 2014
Proportion developed range: 0.0 – 0.86 mean: 0.29 sd: 0.21	Proportion of low, medium, or "open" developed area within a 500 m buffer; mostly consisting of large-lot and single-family residences and mowed areas around development	negative strong positive	Randa and Yunger 2006, Kays et al. 2008, Goad et al. 2014, Lesmeister et al. 2015, Mitchell et al. 2015, Wang et al. 2015 Wapenaar et al. 2012, Goad et al. 2014, Lesmeister et al. 2015, Kays et al. 2016

Table 1 (cont'd)

Proportion grassland or agriculture	Proportion of area within a 500 m buffer characterized by gramanoid or herbaceous vegetation (including grazing land), pasture, or cropland	positive	Theberge and Wedeles 1989, Gosselink et al. 2003, Mitchell et al. 2015
range: 0.0 – 0.31 mean: 0.04 sd: 0.07		neutral or negative	Gosselink et al. 2003, Goad et al. 2014, Mitchell et al. 2015, Kays et al. 2016
Slope range: 0.2 – 23.8	Slope at camera-trap site (30 m resolution)	neutral or negative	Kays et al. 2008, Lesmeister et al. 2015
mean: 5.0 sd: 5.2		positive	Adkins and Stott 1998
Human activity	The average number of	negative	Goad et al. 2014
range: 0.0 – 2.5 mean: 0.2 sd: 0.3	humans detected at a site per day	weakly negative	Marks and Bloomfield 2006, Goad et al. 2014
Coyote activity range: 0.0 – 0.5 mean: 0.06 sd: 0.07	The average number of coyotes detected at a site per day	negative	Harrison et al. 1989, Gosselink et al. 2003, 2007

#### Dominant-Subordinate Carnivore Pair

Like many places in North America, coyotes in Cleveland act as dominant, apex predators, occupying the trophic position formerly held by extirpated gray wolves (*Canis lupus*; Gompper 2002). In this dominant position, coyotes suppress red foxes via interference competition that manifests in the form of agonistic interactions, spatial exclusion, and direct killing (Sargeant and Allen 1989, Gosselink et al. 2003). These interspecific interactions depict the causal mechanisms hypothesized to underlie red fox declines throughout the eastern U.S. (Levi and Wilmers 2012, Lesmeister et al. 2015). Given that coyotes often exhibit a stronger avoidance of human activity and development than foxes, highly urbanized areas are hypothesized to serve as refugia that enable red fox persistence in the presence of coyotes (Gosselink et al. 2007, Wapenaar et al. 2012, Lesmeister et al. 2015).

#### Study Design

We established 104 camera-trap sites (hereafter "sites") throughout the Metroparks using a Generalized Random Tessellation Stratified design, resulting in a spatially random sample balanced across multiple, nested spatial scales (within and among Metroparks reservations; Stevens and Olsen 2003; Fig. 2). We placed camera traps at sites using a consistent protocol (Burton et al. 2015). At each site, we placed a Bushnell Trophy Cam HD Aggressor on trees or, in the rare instances in which trees were not available, posts, ~50 cm above the ground. We used camera settings that maximized animal detectability in a previous pilot study.

#### Hypothesis 1: Spatial Occupancy and Site-Visitation Modeling

#### Modeling Framework

We evaluated Hypothesis 1 (the *spatial human shield effect*) by modeling the site occupancy and visitation dynamics of coyotes and red foxes in the Metroparks. Occupancy models generally use temporally replicated sampling at a given site to estimate detection probability, which is in turn used to estimate site occupancy, with *occupancy* defined as site use during the study period (MacKenzie et al. 2002). Detection probability is the probability of detecting a species at the camera-trap site in a period (e.g., 1 week), given site-occupancy. Detection probability is of ecological interest because it varies with carnivore behavior. For example, a low detection probability of a subordinate carnivore at a given site might result from frequent site-use by a dominant carnivore (Wang et al. 2015). Traditional occupancy models collapse detections within a given temporal replicate into a binary variable, where ones denote detections and zeros, non-detections. This method omits information because a period with numerous detections is coded identically as a period with a single detection. To overcome this limitation, we reparameterized

the traditional occupancy model as a zero-inflated negative binomial model, where the zeroinflated submodel represents a logistic occupancy model and the negative binomial submodel estimates site-visitation rate while accommodating overdispersed count data (Greene 2008).

We collected data from camera traps that were deployed at each of the 104 sites continuously from December 15 2015 to May 2 2016. This period encompassed the breeding and early pup-rearing season for both species. We chose this period because previous work has shown that movement patterns are similar throughout this time for both species, thereby satisfying the seasonal closure assumption required in occupancy modeling (MacKenzie et al. 2002, Gosselink et al. 2007, Morey et al. 2007, Gehrt et al. 2009b). Nonetheless, we included temperature as a "nuisance" covariate (Kays et al. 2016) to accommodate potential variation in canid movement behavior during colder months (i.e., increased foraging movements during cold periods; Gosselink et al. 2003) and/or temperature-induced variation in camera-trap sensor sensitivity (Newey et al. 2015).

We binned detections into 1-week temporal replicates and modeled occupancy as:

$$z_i \sim \text{Bernoulli}(\psi_i),$$
 (1)

where site *i* is occupied (i.e.,  $z_i = 1$ ) with a probability  $\psi_i$ . We modeled the effects of covariates on site-occupancy probability via a logit link:

$$logit(\psi_i) = x_i \boldsymbol{\beta},\tag{2}$$

where  $x_i$  is a vector of covariates (described below; Table 1) at the *i*th site and  $\beta$  is a conformable vector of parameters. We modeled site-visitation, given occupancy, as

$$y_{ij} \sim \text{Poisson}(z_i * \mu_{ij}),$$
 (3)

$$\mu_{ij} = \rho_{ij} * \lambda_{ij}, \text{ and} \tag{4}$$

$$\log(\lambda_{ij}) = x_{ij} \boldsymbol{\alpha},\tag{5}$$

where  $y_{ij}$  is the number of visits to site *i* during week *j*,  $\lambda_{ij}$  is the expected number of visits to site *i* during replicate *j*, given covariates  $x_{ij}$  and site occupancy  $z_i$ , *a* is a conformable vector of parameters, and  $\rho_{ij}$  is a random variable with a 1-parameter gamma distribution ( $\rho_{ij} \sim$  Gamma( $\theta$ , $\theta$ )) that relaxes the equidispersion restriction of traditional Poisson models (Greene 2008). We did not include an offset because we only used data from camera traps that were active for an entire given week, resulting in equal sampling effort for each of the *j* replicates for each camera trap site (mean number of complete weeks recorded per site = 19.02, sd = 3.69). Finally, naïve occupancy for coyotes was extremely high (>95%). Such high levels of occupancy obviate occupancy modeling due to lack of variation (cf. Kays et al. 2008). Therefore, the coyote model was simply a site-visitation model with the form described above.

#### Model Covariates

We modeled the effects of human, habitat and interspecific covariates hypothesized to affect the spatial dynamics of coyotes and red foxes (summarized in Table 1). The covariates represented habitat features (edge, slope, proportion grassland, and proportion developed), human activity (human site-visitation rate and site proximity to park features frequently visited by humans), and coyote site-visitation rate (Table 1). For area-based proportional covariates, we used a 500 m buffer distance for final models because initial comparison of univariate models via AIC suggested that this buffer distance had a superior model fit over others and covariates at this buffer distance have been shown to affect urban carnivores (e.g., Gallo et al. 2017). All

covariates lacked collinearity (variance inflation factors < 3.0; Zuur et al. 2010). We standardized covariates to have a mean of 0 and standard deviation of 1.

#### Model Analysis and Selection

We analyzed models in a Bayesian framework via Markov chain Monte Carlo (MCMC) simulations in RStudio (R version 3.3.2; RStudio Team 2015) and JAGS (Plummer 2003) using the package R2Jags (Su and Yajima 2012). For each model, we used diffuse priors and ran 3 chains of 25,000 iterations following a burn-in of 5,000 and thinned posterior chains by 10.

We used Bayesian indicator variables for model selection (Hooten and Hobbs 2015). Indicator variables (*w*) were Bernoulli distributed with a non-informative prior of 0.5. The posterior of indicator variables represents the probability that a given covariate *N* is included in the best model of of  $2^N$  possible models (Royle and Dorazio 2008). We model-averaged covariates by calculating the posterior of the *N*th parameter where *w* = 1 for the *N*th covariate in the MCMC history (Royle and Dorazio 2008). We based inference on whether posterior means of indicator variables were  $\geq 0.5$  (Barbieri and Berger 2004). We assessed model goodness-of-fit via posterior predictive checks using a chi-square deviance statistic calculated on data simulated by the fitted model to the same statistic calculated on the observed data (Kéry and Royle 2015). We evaluated these statistics using a Bayesian *p*-value, where extreme values (i.e., <0.1 or >0.9) indicate poor fit (Kéry and Royle 2015). We ensured convergence using R-hat statistics (all values <1.1; Gelman and Hill 2007). Finally, we checked for spatial autocorrelation by examining spline correlograms of Pearson residuals summed at each site (Moll et al. 2016a).

For these spatial models to support Hypothesis 1 (the *spatial human shield effect*) we would expect to see *i*) a positive relationship between red foxes and both human activity and

development, and *ii*) a negative relationship between coyotes and both human activity and development (Fig. 1a). The occupancy and site-visitation models described above offer a robust method to determine the presence and strength of these potential relationships.

#### Hypothesis 2: Temporal Activity Patterns

We evaluated Hypothesis 2 (*development-mediated temporal avoidance*) by examining time-ofday activity patterns of humans, coyotes, and red foxes as a function of development. We used the package camtrapR (Niedballa et al. 2016) in RStudio to extract the time of day for each species detection. Following other studies on carnivore activity patterns, we enforced a 30minute temporal independence window between successive detections of the same species (Monterroso et al. 2013, Wang et al. 2015). Given that coyotes and red foxes respond to solar events (e.g., sunset) rather than "clock time" (i.e., based upon a 24-hr clock), and that solar event timing changed throughout the study period, we calculated activity patterns based upon "solar time" rather than clock time (Nouvellet et al. 2012). We converted clock time to solar time by centering 24-hour activity patterns around mean sunrise and sunset times for the study period (07:22 and 18:24).

We used the R package overlap (Meredith and Ridout 2014) to calculate the coefficient of overlap ( $\Delta$ ) in temporal activity patterns between coyotes, red foxes, and humans (Ridout and Linkie 2009) using sample-size appropriate estimates of  $\Delta$  (Meredith and Ridout 2014). This method assumes that temporally-explicit detections arise from an underlying continuous probability density function. Activity patterns are then estimated by a nonparametric kernel density function, and the coefficient of overlap ( $\Delta$ ) quantifies the overlap in these density functions between species. Overlap values range from 0 (no overlap) to 1 (complete overlap), with uncertainty determined via bootstrapping (Ridout and Linkie 2009).

We examined differences in overlap between species at sites categorized into two levels of development (high and low) using the proportion of development within a 500 m buffer of each site (Table 1). We chose this binary description of development because a continuous metric would require a minimum number of species-specific detections at each site (e.g., N  $\approx$ 30); our sample sizes for coyotes and red foxes required binning sites into two categories (cf. Wang et al. 2015). We determined the breakpoint for high and low development sites objectively via *k*-means clustering, which separates data into *k* (here *k* = 2) clusters such that within-cluster variance is optimally minimized (Hartigan and Wong 1979). The *k*-means algorithm separated the 104 sites into clusters of high development (N = 41 sites, mean proportion developed in 500 m buffer = 0.51, sd = 0.14) and low development (N = 63 sites, mean proportion developed in 500 m buffer = 0.15, sd = 0.11). Thus, for each species, activity patterns based on observations pooled across high development sites were compared to those based on observations pooled across low development sites. We based inference on whether 95% bootstrapped confidence intervals of estimates overlapped each other (Ridout and Linkie 2009).

For this temporal activity analysis to support Hypothesis 2 (*development-mediated temporal avoidance*) we would expect to see *i*) a decrease in red fox and human activity overlap at high development sites, *ii*) a decrease in coyote and human activity overlap at high development sites, and *iii*) an increase in coyote and red fox overlap at high development sites (Fig. 1b).

#### Hypothesis 3: Spatio-temporal Modeling

To evaluate Hypothesis 3 (*development-mediated spatio-temporal avoidance*), we followed Karanth et al. (2017) and used a time-to-encounter multi-response permutation approach (Mielke et al. 1976) to analyze the spatio-temporal dynamics of humans, coyotes, and red foxes. We calculated the minimum time between detections of species pairs at the same site, obtaining an observed time-to-encounter for each pair (Karanth et al. 2017). To compare this to a random expectation (i.e., a null model representative of neither avoidance nor association), we permutated the data such that each image received a randomly assigned site. We then used this permutation to re-calculate the time-to-encounter for each site and repeated this process 1000 times (Karanth et al. 2017). Finally, we compared the observed median time-to-encounter to the medians of the random permutations and calculated *p*-values as the proportion of times the observed median was larger than the medians of the permutations (Karanth et al. 2017). A large *p*-value indicates spatio-temporal association (i.e., observed time-to-encounter shorter than the random expectation) while a small value indicates spatio-temproal avoidance (Karanth et al. 2017). As with the temporal activity pattern analysis, we calculated times-to-encounter for each species pair at high and low development sites.

For the spatio-temporal analysis to support Hypothesis 3 (*development-mediated spatio-temporal avoidance*) we would expect to see *i*) red fox avoidance of coyotes at low development sites but not high development sites, and *ii*) red fox and coyote avoidance of humans at high development sites but not low development sites (Fig. 1c).

#### Results

In 14,343 camera-trap nights across 104 sites we recorded 1,011 coyote detections, 360 red fox detections, and 3,043 human detections. Raw data indicated that humans occupied 100% of the sites (N = 104), coyotes occupied 95.2% (N = 99), and red foxes occupied 51.9% (N = 54).

Occupancy and Site-Visitation Modeling

The red fox model fit the data well, with a Bayesian *p*-value of 0.67 and minimal spatial autocorrelation. The occupancy submodel estimated that red foxes occupied 59.6 out of 104 sites (57.3%). Development was the only covariate in the occupancy submodel with an inclusion probability of  $\geq$ 0.5 (0.79) and a model-averaged 95% credible interval (CI) that did not overlap zero (Table 2). As development increased, red fox occupancy probability increased strongly (Fig. 3a). Three covariates in the site-visitation submodel had inclusion probabilities near 1.0 and none of their model-averaged 95% CIs overlapped zero (Table 2). As both development and slope increased, red fox site-visitation increased strongly (Fig. 3b,c). As average human activity at a site increased, red fox site-visitation decreased (Fig. 3d). Of these three covariates, development had the largest effect (i.e., largest magnitude of standardized coefficient), followed by human activity, and then slope (Table 2).



Figure 3. Effects plots of covariates with inclusion probabilities  $\geq 0.5$  from occupancy and sitevisitation models for coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*) fit to data from 104

camera-trap sites in the Cleveland Metroparks, December 2015 – May 2016. Shaded areas display 95% credible intervals.

Table 2. Model-averaged posterior means, standard deviations, 95% credible intervals (CI), and inclusion probabilities for parameters from occupancy and site-visitation models for coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*) fit to data from 104 camera-trap sites in the Cleveland Metroparks, December 2015 – May 2016. Inclusion probabilities  $\geq$ 0.5 are shaded in gray.

Species	Sub-	Covariate	Mean	SD	Lower	Upper	Inclusion Probability
	Occupancy	Intercept	0.36	0.27	-0.12	0.90	N/A
		Dist Edge	-0.7	0.38	-1.41	0.04	0.34
		Dist_Pk_Feat	-0.29	0.26	-0.77	0.23	0.11
		Prop_Develop	0.89	0.31	0.28	1.53	0.79
		Prop_Grass	-0.05	0.39	-0.68	0.78	0.08
		Slope	0.30	0.26	-0.21	0.82	0.10
		Coy_Activity	0.12	0.51	-0.62	1.37	0.09
fox		Hum_Activity	0.37	0.62	-0.61	1.69	0.13
		Sites Occupied	59.60	2.86	55.0	66.0	N/A
Sed	Site-Visitation	Intercept	-1.57	0.1	-1.77	-1.36	N/A
Υ. Υ		Dist_Edge	-0.07	0.15	-0.35	0.23	0.04
		Dist_Pk_Feat	-0.02	0.12	-0.27	0.22	0.03
		Prop_Develop	0.57	0.09	0.39	0.75	1.0
		Prop_Grass	-0.10	0.15	-0.41	0.20	0.05
		Slope	0.32	0.06	0.19	0.45	1.0
		Temp	-0.15	0.09	-0.32	0.02	0.08
		Coy_Activity	-0.27	0.12	-0.51	-0.03	0.25
		Hum_Activity	-0.43	0.12	-0.68	-0.21	0.97
Coyote	Site-Visitation	Intercept	-0.84	0.05	-0.93	-0.74	N/A
		Dist_Edge	-0.31	0.05	-0.41	-0.20	1.0
		Dist_Pk_Feat	0.26	0.04	0.19	0.34	1.0
		Prop_Develop	-0.47	0.06	-0.58	-0.34	1.0
		Prop_Grass	0.11	0.04	0.03	0.20	0.23
		Slope	0.03	0.04	-0.06	0.11	0.01
		Temp	-0.22	0.05	-0.32	-0.12	1.0
		Hum_Activity	-0.09	0.06	-0.22	0.02	0.04

The coyote model also fit the data well, with a Bayesian *p*-value of 0.60 and a lack of spatial autocorrelation. Four covariates had inclusion probabilities of 1.0 and none of their model-averaged 95% CIs overlapped zero (Table 2). As distance to edge, development, and weekly temperature increased, coyote site-visitation decreased (Fig. 3e,g). As the distance to park features frequently used by humans increased, coyote site-visitation increased (Fig. 3f). Development had the strongest effect, followed by distance to edge, distance to park feature, and temperature (Table 2).

#### Temporal Activity Patterns

Coyotes and red foxes showed a high degree of overlap in temporal activity patterns at both high (0.89) and low development sites (0.83; Fig. 4a,b). The confidence intervals (CnIs) of these values overlapped (Fig. 4a,b). The activity patterns of red foxes were highly divergent from those of humans and almost exclusively nocturnal (Fig. 4c,d). Red fox overlap with humans was higher at low development sites, but this result was not statistically significant (Fig 3c,d). Coyotes were also highly nocturnal, but less so than red foxes (Fig. 4e,f). Coyote overlap with humans significantly increased at low development sites (Fig. 4e,f).





#### Spatio-temporal Modeling

Red foxes exhibited spatio-temporal avoidance of coyotes at both high and low development sites, but the distributions varied between the two groups of sites (Fig. 5a,b). The median time-to-encounter for red foxes and coyotes at high development sites (14.9 days) was longer than 98% of the random permutation medians (Fig. 5a). Similarly, the median time-to-encounter for red foxes at low development sites (25.2 days) was longer than 97% of the random permutation medians (Fig. 5b). Red foxes also exhibited spatio-temporal avoidance of humans,

but only at high development sites (Fig. 5c,d). The median time-to-encounter for red foxes and humans at high development sites (31.7 days) was longer than every median of the 1000 simulated permutations (Fig. 5c). Conversely, the median time-to-encounter for red foxes and humans at low development sites (28.2 days) did not differ from the random expectation (Fig. 5d). Finally, coyotes exhibited a positive spatio-temporal association with humans at high development sites; their observed median time-to-encounter (11.8 days) was less than >99% of the random permutation medians (Fig. 5e). In contrast, coyotes at low development sites weakly avoided humans; their observed median time-to-encounter (17.6 days) was higher than >90% of random permutation medians (Fig. 5f).



Figure 5. Median times-to-encounter for coyotes (*Canis latrans*), red foxes (*Vulpes vulpes*), and humans (*Homo sapiens*) based on data from 104 camera-trap sites in the Cleveland Metroparks, December 2015 – May 2016. High and low development sites were determined using k-means clustering. The vertical dashed line is the observed median time-to-encounter and the shaded areas are the random expectation of distributions based upon 1000 simulated permutations. P-values depict the proportion of times the observed value exceeded the random expectation.

#### Discussion

Here we showed that the sympatry of a competing dominant-subordinate carnivore pair inhabiting an extensive urban park system was strongly mediated by both the risk of human encounter and degree of development across spatio-temporal dimensions. Research in a variety of systems conducted on a diversity of taxa has demonstrated the remarkable ability of humans to profoundly alter fundamental ecological processes, from nutrient cycling to community species assemblage (Frid and Dill 2002, McKinney 2006, Ellis 2011, Dirzo et al. 2014, Forman 2016). Our results strongly suggest that human influence over ecological dynamics extends to the top of the food chain by altering the spatio-termporal dynamics of competing terrestrial carnivores (Dorresteijn et al. 2015, Wang et al. 2015, Kuijper et al. 2016).

Our analysis generally supported Hypothesis 1, which predicted that human-related factors would negatively affect larger, dominant carnivores and indirectly benefit smaller, subordinate carnivores via a spatial "human shield" effect (Berger 2007; Fig. 1a). This effect has been documented in mammalian predator-prey systems, whereby prey escape predation risk by spatially associating with anthropogenic factors that predators avoid (Berger 2007, Kuijper et al. 2015). Our study provides evidence that the "human shield" effect extends to dominantsubordinate carnivore interactions. For example, we found strongly opposing responses of covotes and red foxes to development (Fig. 3a,b,g; Table 2). This opposing pattern indicates that development might facilitate the sympatry of competing carnivores, with more highly developed sites acting as a spatial refuge for more development-tolerant, subordinate carnivores against interference competition from larger carnivores (Crooks et al. 2010). Our results add to the body of literature supporting the idea that development enables red foxes to persist in areas occupied by coyotes (Gosselink et al. 2003, 2007, Lesmeister et al. 2015). These conclusions are reinforced by the fact that development had both the largest magnitude of effect and an inclusion probability of 1.0 in both red fox and coyote models (Table 2). Development was a better predictor of spatial carnivore dynamics than long-term human activity at a site (Table 2), highlighting the importance of broader-scale development (i.e., in a 500 m buffer) over site-

specific human visitation rate. While the range of development at our study sites was substantial (i.e., development in a 500 m buffer ranged from 0 - 0.86; Table 1), it primarily consisted of medium- and low-density residential development. Additional studies should investigate whether the opposing responses of larger, dominant and smaller, subordinate carnivores to development extend into more highly developed areas (e.g., downtown commercial districts). Indeed, coyotes can inhabit highly developed areas (Gehrt et al. 2009a), but investigations of coyote - red fox interactions in such locations are lacking. We also found that covotes had lower site-visitation rates at sites closer to park features frequently used by humans (e.g., parking lots, picnic areas; Fig. 3f,g). This result corroborates coyotes' general spatial avoidance of anthropogenic influences in matrices of undeveloped habitat (Gosselink et al. 2003, Lesmeister et al. 2015). Coyote site-visitation rate also increased near edge habitat (Fig. 3e), suggesting such habitat provides access to prey (Theberge and Wedeles 1989) or is associated with movement corridors (e.g., utility line rights-of-way; Gehrt and Riley 2010). The site-visitation rate of red foxes was positively associated with steeper slopes (Fig. 3c; Table 2). This association might represent a strategy to avoid interference competition from coyotes via increased use of energeticallydemanding topography, a tactic sometimes employed by ungulates to escape carnivore predation (e.g., in wolves and elk Cervus elaphus; Mao et al. 2005). The positive association between red foxes and slope might also explain why red fox occupancy was higher in our study system, where steep slopes abound, than in a nearby urban system in Chicago, Illinois, USA, which consists of predominately flat terrain (Gallo et al. 2017). On a broader geographic scale, red foxes are declining in many areas throughout the eastern United States. This trend is thought to be partly attributable to coyote range expansion (Levi and Wilmers 2012, Lesmeister et al. 2015). Our study provides support for the idea that developed areas might facilitate the

coexistence of red foxes and coyotes, as other research has suggested (Gosselink et al. 2007, Mueller et al. 2018).

Our results only marginally supported Hypothesis 2, which predicted that temporal activity overlap between subordinate and dominant carnivores would increase at more highly developed sites due to a concomitant nocturnal shift in both species (Fig. 1b). Temporal activity patterns are an important component of species' niches (Schoener 1974) and the sympatry of competing carnivore guilds is often facilitated by segregation along this temporal niche axis (Frey et al. 2017). Accordingly, a parallel nocturnal shift in activity patterns among carnivores at more highly developed sites could increase agonistic interspecific interactions at such sites. Others have found support for this idea, with increased nocturnal carnivore activity and temporal overlap at more highly developed sites (Wang et al. 2015). In our study, both red foxes and coyotes avoided humans via nocturnal activity (Fig. 4). However, coyote activity only weakly shifted nocturnally at high development sites (Fig. 4e,f) and red fox activity was unaffected by development (Fig. 4a-d). Thus, there is limited support for a nocturnal shift in coyote activity with increasing development, and no support for a nocturnal shift in red foxes. Overall, red foxes in our system exhibited high temporal overlap with coyotes (Fig. 4a,b), which, taken in context with the results of our spatial modeling, suggests that spatial rather than temporal niche partitioning likely facilitates these species' sympatry across our study area (Polis and Holt 1992, Frey et al. 2017; Fig. 3a,b,g). We encourage additional research to determine the generalizability of this result to other systems.

Our spatio-temporal analysis revealed complex avoidance dynamics between humans, red foxes, and coyotes, with some aspects of Hypothesis 3 supported and others contradicted (Fig. 1c, Fig. 5). Carnivore avoidance of humans was mediated by development (as predicted by

Hypothesis 3), but the effect on red foxes (intensification at high development sites) opposed that on coyotes (Fig. 5c-f). In addition, red foxes strongly avoided coyotes at both high and low development sites, contrasting with the prediction of intensified avoidance at less developed sites (Fig. 1c, Fig. 5a,b). Red foxes' avoidance of coyotes at all sites lends further support to the idea that interference competition with coyotes represents an important limiting factor for red foxes (Gosselink et al. 2007, Levi and Wilmers 2012, Lesmeister et al. 2015). Spatio-temporally, covotes only weakly avoided humans at low development sites and showed a positive association with them at high development sites (Fig. 5e,f). This finding suggests that coyotes' primary strategy for mitigating risk of human encounter is broad-scale and spatial (Fig. 3; Table 2) rather than site-specific and spatio-temporal (Fig. 5e,f,). The positive spatio-temporal association between coyotes and humans at high development sites is notable (Fig. 5e). Humans commonly walk domestic dogs at such sites and, given that our study was conducted during the breeding and early-pup rearing season, the positive association between coyotes and humans might arise due to coyotes "following" human dog-walkers as an act of protective territoriality (cf. Poessel et al. 2012). This speculation deserves further study given the potential for human-coyote conflict in urban areas (Poessel et al. 2012). An alternative explanation for the positive spatio-temporal association is that more human-intolerant coyotes avoid highly developed areas altogether while more tolerant individuals remain in such areas, perhaps due to increased resource availability or decreased competition (Bejder et al. 2006). Finally, we found that although red fox site-visitation increased with increasing development, foxes nonetheless strongly avoided humans at high development sites (Fig. 5c). This unique association casts red foxes as a kind of inquiline commensalist (i.e., an innocuous species that lives in the home of another species) that also

avoids its host species, a fascinating ecological role that deserves further elucidation (cf. Gehrt et al. 2011).

Our study has implications for both the multi-dimensional study of risk effects and the degree to which carnivore sympatry in developed areas resemble those in undeveloped systems. Risk effects research has a long history in ecology but has tended to be conducted in microcosms (e.g., invertebrate systems; Werner and Peacor 2003) and has often failed to take a multidimensional approach to characterizing risk (Moll et al. 2017). Nonetheless, much recent work has been carried out in large-scale systems (e.g. carnivore-ungulate systems) and recent calls have been made to place such work in a multi-dimensional framework (Moll et al. 2017, Schmitz et al. 2017). Our results strongly support the notion that risk-related avoidance between humans and carnivores uniquely manifests in spatial, temporal, and spatio-temporal dimensions. Other recent studies have found similar multi-dimensional responses to risk both within carnivore guilds (e.g., Karanth et al. 2017) and between carnivores and ungulates (e.g., Dröge et al. 2017). Our results also relate to the mesopredator release hypothesis (Crooks and Soulé 1999) in that smaller, subordinate red foxes were much more prevalent at more developed sites that larger, dominant covotes visited infrequently. The unique aspect of our study is that a "release" of red foxes in our system appears to be mediated by development associated with humans (and concomitant spatial avoidance by their dominant competitors, coyotes), whereas a broader-scale "release" of coyotes in the less developed areas of our system has been precipitated by historical human extirpation of covotes' natural dominant competitors (i.e., gray wolves). Thus, humans and development have fundamentally altered the trophic dynamics of this carnivore guild and created novel interactions not present in these species' evolutionary histories (Fischer et al. 2012, Dorresteijn et al. 2015). More generally, our study contributes to ongoing debate in the literature

regarding how ecological processes traditionally studied in more "natural" systems (e.g., the predator-prey dynamics of carnivores and ungulates in a national park) manifest in more urbanized contexts (Forman 2016). Whereas this study provides a snapshot into the pervasiveness of human-related factors in mediating such processes, future work should examine them over longer timescales. Indeed, given that our study was conducted during a period of relatively low human park-use (i.e., winter and spring), our results likely represent a conservative estimate of the overall effects of human activity on carnivore sympatry in our study system. Long-term (i.e., multi-year) studies will clarify key, outstanding issues related to carnivore dynamics in human-dominated systems, including whether tolerance of human disturbance constitutes a unique niche axis that enables coexistence between species with differential human tolerance (cf. Polis and Holt 1992) and the degree to which ecological processes in highly developed systems such as cities resemble their counterparts in less developed systems (Forman 2016).

#### Acknowledgements

We are grateful to Cleveland Metroparks and Michigan State University staff, students, and volunteers who contributed to field work and data preparation, especially E. Clingman, T. Krynak, J. Krock, T. Kraft, G. Woodard, W. Ortiz, C. Lepard, and members of the RECaP laboratory. R.J.M. was supported by a National Science Foundation Graduate Research Fellowship. We thank the associate editor and two anonymous reviewers for comments that improved the manuscript.

#### CONCLUSION

In this dissertation, I have used philosophical argument, literature synthesis, and empirical study to examine the challenge of spatio-temporal dimensionality in carnivore ecology research. This challenge consists of three nested components: *i*) considering the spatial, temporal, or spatio-temporal dimensions of an ecological phenomenon, *ii*) finding the characteristic scales at which a given phenomenon manifests within those spatial and/or temporal dimensions, and *iii*) identifying suitable expressions of variables of ecological interest at particular spatio-temporal scales. This challenge generalizes to all ecological research, but is especially acute in studies of terrestrial carnivores due to their wide-ranging nature, their iconic status, their declining populations, and their ability to influence ecosystems via top-down pathways.

Several broad lessons can be learned from the analyses contained within this dissertation. First, there is a clear need to more formally recognize the ways that complexity challenges traditional methods of statistical modeling. In Chapter 1, I showed that most statistical models and model selection techniques carry an assumption of stationarity that is often violated in ecology. The implications of this violation is that although we often strive for generalizable inference in ecological study, this goal is often fundamentally out of reach because the spatiotemporal dimensionality of a given study does not apply in a general way to other systems or species. This work highlights the need to interpret studies in the context of their spatio-temporal dimensionality to correctly align inference with study design, neither over- or under-interpreting research findings. The second lesson learned is that studies conducted across broad spatial scales are crucial to accurately evaluating general categorizations of species' traits, roles, and niches. In Chapter 2, I used a large-scale study design conducted across all seasons to demonstrate that the habitat niche width of pine martens is wider than previously thought. Importantly, the

classification of pine martens as forest specialists was largely borne out of studies conducted on local scales with limited sample sizes. A broader-scale approach elucidated relationships obscured by local variability. The third lesson learned is that decisions regarding how to express and measure latent variables such as predation risk can strongly influence inference. For example, the conclusions of Chapter 3 would have been dramatically different had I limited predation risk to the probability of carnivore encounter (as is commonly done in the literature; Moll et al. 2017) rather than including both this expression of risk and that of the probability of death given encounter. Like the general theme of lesson one above, Chapter 3 underscores the need to carefully interpret results in the context of the spatio-temporal dimensionality of a given study. The fourth lesson learned is that the tremendous variability in research methodologies that examine complex latent variables like predation risk complicates the development of theory because many studies are incommensurable due to contrasting spatio-temporal dimensionality. This observation emphasizes the need for conceptual frameworks and structured literature syntheses to guide emerging areas of research on complex ecological phenomena. Finally, the fifth lesson learned is that a deeper understanding can often be gained regarding complex ecological phenomena when they are evaluated across multiple spatio-temporal dimensions within a given study. In Chapter 5, I examined human-carnivore interactions from spatial, temporal, and spatial-temporal angles and found that each revealed an important insight into how these three species co-inhabit a semi-urban landscape.

The challenge of spatio-temporal dimensionality has been recognized in ecology for decades (e.g., Levin 1992), but conclusions about how to best address this challenge remain elusive, especially with respect to carnivore ecology. Our discipline is increasingly data rich, not least due to technological advancements that enable us to couple near-continuous wildlife

tracking with present and historical satellite data describing the physical landscape. Moving forward, studies that use these rich data to critically evaluate ecological phenomena across multiple spatio-temporal dimensions via a variety of variable expressions will be most efficient in separating out ecological signals from noise and locating the characteristic scales upon which such phenomena occur. Such research will bring clarity not only to ecological theory, but will facilitate more efficient conservation and management strategies by virtue of providing clear linkages between ecological processes and the scales at which they can be manipulated or influence. REFERENCES

#### REFERENCES

- Adkins, C. A., and P. Stott. 1998. Home ranges, movements and habitat associations of red foxes Vulpes vulpes in suburban Toronto, Ontario, Canada. Journal of Zoology 244:335– 346.
- Barbieri, M. M., and J. O. Berger. 2004. Optimal predictive model selection. Annals of Statistics 32:870–897.
- Bejder, L., A. Samuels, H. Whitehead, and N. Gales. 2006. Interpreting short-term behavioral responses to disturbance within a longitudinal perspective. Animal Behaviour 72:1149–1158.
- Berger, J. 2007. Fear, human shields and the redistribution of prey and predators in protected areas. Biology Letters 3:620–623.
- Burton, A. C., E. Neilson, D. Moreira, A. Ladle, R. Steenweg, J. T. Fisher, E. Bayne, and S. Boutin. 2015. Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. Journal of Applied Ecology 52:675–685.
- Chapron, G., P. Kaczensky, J. D. C. Linnell, M. Von Arx, D. Huber, H. Andrén, J. V. López-Bao, M. Adamec, F. Álvares, O. Anders, L. Balečiauskas, V. Balys, P. Bedõ, F. Bego, J. C. Blanco, U. Breitenmoser, H. Brøseth, L. Bufka, R. Bunikyte, P. Ciucci, A. Dutsov, T. Engleder, C. Fuxjäger, C. Groff, K. Holmala, B. Hoxha, Y. Iliopoulos, O. Ionescu, J. Jeremić, K. Jerina, G. Kluth, F. Knauer, I. Kojola, I. Kos, M. Krofel, J. Kubala, S. Kunovac, J. Kusak, M. Kutal, O. Liberg, A. Majić, P. Männil, R. Manz, E. Marboutin, F. Marucco, D. Melovski, K. Mersini, Y. Mertzanis, R. W. Mysłajek, S. Nowak, J. Odden, J. Ozolins, G. Palomero, M. Paunović, J. Persson, H. Potoečnik, P. Y. Quenette, G. Rauer, I. Reinhardt, R. Rigg, A. Ryser, V. Salvatori, T. Skrbinšek, A. Stojanov, J. E. Swenson, L. Szemethy, A. Trajçe, E. Tsingarska-Sedefcheva, M. Váňa, R. Veeroja, P. Wabakken, M. Wölfl, S. Wölfl, F. Zimmermann, D. Zlatanova, and L. Boitani. 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. Science 346:1517–1519.
- Cleveland Metroparks by the numbers. 2017. . https://www.clevelandmetroparks.com/about/cleveland-metroparks-organization/by-thenumbers.
- Crooks, K. R., S. P. D. Riley, S. D. Gehrt, T. E. Gosselink, and T. R. Van Deelen. 2010.
  Community ecology of urban carnivores. Pages 185–200 *in* S. D. Gehrt, S. P. D. Riley, and
  B. L. Cypher, editors. Urban Carnivores: Ecology, Conflict, and Conservation. The Johns Hopkins University Press, Baltimore, Maryland, USA.
- Crooks, K. R., and M. E. Soulé. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400:563–566.

- Darimont, C. T., S. M. Carlson, M. T. Kinnison, P. C. Paquet, T. E. Reimchen, and C. C. Wilmers. 2009. Human predators outpace other agents of trait change in the wild. Proceedings of the National Academy of Sciences 106:8–10.
- Darimont, C. T., C. H. Fox, H. M. Bryan, and T. E. Reimchen. 2015. The unique ecology of human predators. Science 349:858–861.
- Dirzo, R., H. S. Young, M. Galetti, G. Ceballos, N. J. B. Isaac, and B. Collen. 2014. Defaunation in the Anthropocene. Science 345:401–406.
- Dorresteijn, I., J. Schultner, D. G. Nimmo, J. Fischer, J. Hanspach, T. Kuemmerle, L. Kehoe, and E. G. Ritchie. 2015. Incorporating anthropogenic effects into trophic ecology: predator–prey interactions in a human-dominated landscape. Proceedings of the Royal Society B: Biological Sciences 282:20151602.
- Dröge, E., S. Creel, M. S. Becker, and J. M'soka. 2017. Risky times and risky places interact to affect prey behaviour. Nature Ecology & Evolution 1:1123–1128.
- Ellis, E. C. 2011. Anthropogenic transformation of the terrestrial biosphere. Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences 369:1010–1035.
- Estes, J. A. 1995. Top-level carnivores and ecosystem effects: question and approaches. Pages 151–158 *in* C. Jones and J. H. Lawton, editors. Linking Species & Ecosystems. Chapman & Hall, New York.
- Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, T. E. Essington, R. D. Holt, J. B. C. Jackson, R. J. Marquis, L. Oksanen, T. Oksanen, R. T. Paine, E. K. Pikitch, W. J. Ripple, S. a Sandin, M. Scheffer, T. W. Schoener, J. B. Shurin, A. R. E. Sinclair, M. E. Soulé, R. Virtanen, and D. a Wardle. 2011. Trophic downgrading of planet Earth. Science 333:301–306.
- Fischer, J. D., S. H. Cleeton, T. P. Lyons, and J. R. Miller. 2012. Urbanization and the predation paradox: The role of trophic dynamics in structuring vertebrate communities. BioScience 62:809–818.
- Forman, R. T. T. 2016. Urban ecology principles: are urban ecology and natural area ecology really different? Landscape Ecology 31:1653–1662.
- Frey, S., J. T. Fisher, A. C. Burton, and J. P. Volpe. 2017. Investigating animal activity patterns and temporal niche partitioning using camera-trap data: challenges and opportunities. Remote Sensing in Ecology and Conservation:1–10.
- Frid, A., and L. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. Ecology and Society 6:11.

- Gallo, T., M. Fidino, E. W. Lehrer, and S. B. Magle. 2017. Mammal diversity and metacommunity dynamics in urban green spaces: implications for urban wildlife conservation. Ecological Applications 0:1–12.
- Gebresenbet, F., B. Baraki, G. Yirga, C. Sillero-Zubiri, and H. Bauer. 2018. A culture of tolerance: coexisting with large carnivores in the Kafa Highlands, Ethiopia. Oryx 52:751–760.
- Gehr, B., E. J. Hofer, S. Muff, A. Ryser, E. Vimercati, K. Vogt, and L. F. Keller. 2017. A landscape of coexistence for a large predator in a human dominated landscape. Oikos:1–11.
- Gehrt, S. D., C. Anchor, and L. a. White. 2009a. Home range and landscape use of coyotes in a metropolitan landscape: conflict or coexistence? Journal of Mammalogy 90:1045–1057.
- Gehrt, S. D., C. Anchor, and L. A. White. 2009b. Home range and landscape use of coyotes in a metropolitan landscape: conflict or coexistence? Journal of Mammalogy 90:1045–1057.
- Gehrt, S. D., J. L. Brown, and C. Anchor. 2011. Is the urban coyote a misantrhopic synanthrope? The case from Chicago. Cities and the Environment 4:3.
- Gehrt, S. D., and S. P. D. Riley. 2010. Coyotes (Canis latrans). Pages 79–96 in S. D. Gehrt, S. P. D. Riley, and B. L. Cypher, editors. Urban Carnivores: Ecology, Conflict, and Conservation. The Johns Hopkins University Press, Baltimore, Maryland, USA.
- Gelman, A., and J. Hill. 2007. Data analysis using regression and multilevel/hierarchical models. Cambridge University Press, New York, New York.
- Goad, E. H., L. Pejchar, S. E. Reed, and R. L. Knight. 2014. Habitat use by mammals varies along an exurban development gradient in northern Colorado. Biological Conservation 176:172–182.
- Gompper, M. E. 2002. Top carnivores in the suburbs? Ecological and conservation issues raised by colonization of Northeastern North America by coyotes. BioScience 52:185.
- Gosselink, T. E., T. R. Van Deelen, R. E. Warner, and M. G. Joselyn. 2003. Temporal habitat partitioning and spatial use of coyotes and red foxes in east-central Illinois. The Journal of Wildlife Management 67:90–103.
- Gosselink, T. E., T. R. Van Deelen, R. E. Warner, P. C. Mankin, T. E. Gosselink, I. Natural, H. Survey, and E. P. Drive. 2007. Survival and cause-specific mortality of red foxes in agricultural and urban areas of Illinois. Journal of Wildlife Management 71:1862–1873.
- Greene, W. 2008. Functional forms for the negative binomial model for count data. Economics Letters 99:585–590.
- Harrison, D. J., J. A. Bissonette, and J. A. Sherburne. 1989. Spatial relationships between

coyotes and red foxes in Eastern Maine. Journal of Wildlife Management 53:181–185.

- Hartigan, J. A., and M. A. Wong. 1979. Algorithm AS 136: A K-Means Clustering Algorithm. Journal of the Royal Statistical Society C 28:100–108.
- Hooten, M. B., and A. N. T. Hobbs. 2015. A guide to Bayesian model selection for ecologists. Ecological Monographs 85:3–28.
- Hovardas, T., editor. 2018. Large carnivore conservation and management: Human dimensions. 1st Editio. Routledge, New York, New York, USA.
- Karanth, K. U., A. Srivathsa, D. Vasudev, M. Puri, R. Parameshwaran, and N. S. Kumar. 2017. Spatio-temporal interactions facilitate large carnivore sympatry across a resource gradient. Proceedings of the Royal Society B: Biological Sciences 284:20161860.
- Kays, R., A. W. Parsons, M. C. Baker, E. L. Kalies, T. Forrester, R. Costello, C. T. Rota, J. J. Millspaugh, and W. J. Mcshea. 2016. Does hunting or hiking affect wildlife communities in protected areas? Journal of Applied Ecology 54:242–252.
- Kays, R. W., M. E. Gompper, and J. C. Ray. 2008. Landscape ecology of eastern coyotes based on large-scale estimates of abundance. Ecological Applications 18:1014–1027.
- Kéry, M., and J. A. Royle. 2015. Applied hierarchical modeling in ecology: Analysis of distribution, abundance and species richness in R and BUGS / Volume 1, Prelude and static models. Elsevier, San Diego, California.
- Kuijper, D. P. J., J. W. Bubnicki, M. Churski, B. Mols, and P. Van Hooft. 2015. Context dependence of risk effects: Wolves and tree logs create patches of fear in an old-growth forest. Behavioral Ecology 26:1558–1568.
- Kuijper, D. P. J., E. Sahlén, B. Elmhagen, S. Chamaillé-Jammes, H. Sand, K. Lone, and J. P. G. M. Cromsigt. 2016. Paws without claws? Ecological effects of large carnivores in anthropogenic landscapes. Proceedings of the Royal Society B: Biological Sciences 283:20161625.
- Lashley, M. A., M. V Cove, M. C. Chitwood, G. Penido, B. Gardner, C. S. Deperno, and C. E. Moorman. 2018. Estimating wildlife activity curves: comparison of methods and sample size. Scientific Reports:1–11.
- Lesmeister, D. B., C. K. Nielsen, E. M. Schauber, and E. C. Hellgren. 2015. Spatial and temporal structure of a mesocarnivore guild in Midwestern North America. Wildlife Monographs 191:1–61.
- Levi, T., and C. Wilmers. 2012. Wolves coyotes foxes : a cascade among carnivores. Ecology 93:921–929.

- Levin, S. A. 1992. The problem of pattern and scale in ecology: the Robert H. MacArthur Award lecture. Ecology 73:1943–1967.
- Lima, S. L. 2002. Putting predators back into behavioral predator prey interactions. Trends in Ecology and Evolution 17:70–75.
- Loveridge, A. J., M. Valeix, N. B. Elliot, and D. W. Macdonald. 2017. The landscape of anthropogenic mortality: how African lions respond to spatial variation in risk. Journal of Applied Ecology 54:815–825.
- MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248–2255.
- Magle, S. B., V. M. Hunt, M. Vernon, and K. R. Crooks. 2012. Urban wildlife research: Past, present, and future. Biological Conservation 155:23–32.
- Mao, J. S., M. S. Boyce, D. W. Smith, F. J. Singer, D. J. Vales, J. M. Vore, and E. H. Merrill. 2005. Habitat selection by elk before and after wolf reintroduction in Yellowstone National Park. Journal of Wildlife Management 69:1691–1707.
- Marks, C. A., and T. E. Bloomfield. 2006. Home-range size and selection of natal den and diurnal shelter sites by urban red foxes (Vulpes vulpes) in Melbourne. Wildlife Research 33:339–347.
- McKinney, M. L. 2006. Urbanization as a major cause of biotic homogenization. Biological Conservation 127:247–260.
- Meredith, M., and M. Ridout. 2014. overlap: Estimates of coefficient of overlapping for animal activity patterns.
- Mielke, P. W., K. J. Berry, and E. S. Johnson. 1976. Multi-response permutation procedures for a priori classifications. Communications in Statistics Theory and Methods 5:1409–1424.
- Mitchell, N., M. W. Strohbach, R. Pratt, W. C. Finn, and E. G. Strauss. 2015. Space use by resident and transient coyotes in an urban-rural landscape mosaic. Wildlife Research 42:461–469.
- Moll, R. J., K. Kilshaw, R. A. Montgomery, L. Abade, R. D. Campbell, L. A. Harrington, J. J. Millspaugh, J. D. S. Birks, and D. W. Macdonald. 2016a. Clarifying habitat niche width using broad-scale, hierarchical occupancy models: A case study with a recovering mesocarnivore. Journal of Zoology 300:177–185.
- Moll, R. J., K. M. Redilla, T. Mudumba, A. B. Muneza, S. M. Gray, L. Abade, M. W. Hayward, J. J. Millspaugh, and R. A. Montgomery. 2017. The many faces of fear: A synthesis of methodological variation in characterizing predation risk. Journal of Animal Ecology

86:749-765.

- Moll, R. J., D. Steel, and R. A. Montgomery. 2016b. AIC and the challenge of complexity: A case study from ecology. Studies in History and Philosophy of Biological and Biomedical Sciences 60:35–43.
- Monterroso, P., P. C. Alves, and P. Ferreras. 2013. Catch me if you can: Diel activity patterns of mammalian prey and predators. Ethology 119:1044–1056.
- Morey, P. S., E. M. Gense, and S. D. Gehrt. 2007. Spatial and temporal variation in the diet of coyotes in the Chicago metropolitan area. The American Midland Naturalist 158:147–161.
- Mueller, M. A., D. Drake, and M. L. Allen. 2018. Coexistence of coyotes (Canis latrans) and red foxes (Vulpes vulpes) in an urban landscape:1–19.
- Newey, S., P. Davidson, S. Nazir, G. Fairhurst, F. Verdicchio, R. J. Irvine, and R. van der Wal. 2015. Limitations of recreational camera traps for wildlife management and conservation research: A practitioner's perspective. Ambio 44:624–635.
- Niedballa, J., R. Sollmann, A. Courtiol, and A. Wilting. 2016. camtrapR: An R package for efficient camera trap data management. Methods in Ecology and Evolution 7:1457–1462.
- Nouvellet, P., G. S. A. Rasmussen, D. W. MacDonald, and F. Courchamp. 2012. Noisy clocks and silent sunrises: Measurement methods of daily activity pattern. Journal of Zoology 286:179–184.
- Ordeñana, M. A., K. R. Crooks, E. E. Boydston, R. N. Fisher, L. M. Lyren, S. Siudyla, C. D. Haas, S. Harris, S. a Hathaway, G. M. Turschak, A. Keith, and D. H. Van Vuren. 2010. Effects of urbanization on carnivore species distribution and richness. Journal of Mammalogy 91:1322–1331.
- Oriol-Cotterill, A., M. Valeix, L. G. Frank, C. Riginos, and D. W. Macdonald. 2015. Landscapes of Coexistence for terrestrial carnivores: The ecological consequences of being downgraded from ultimate to penultimate predator by humans. Oikos 124:1263–1273.
- Plummer, M. 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. Page 124:1-8 Proceedings of the 3rd International Workshop on Distributed Statistical Computing.
- Poessel, S. A., S. Breck, T. L. Teel, S. Shwif, and K. R. Crooks. 2012. Patterns of human coyote conflicts in the Denver Metropolitan Area. The Journal of Wildlife Management 77:297–305.
- Polis, G. A., and R. D. Holt. 1992. Intraguild predation: The dynamics of complex trophic interactions.

Ramalho, C. E., and R. J. Hobbs. 2012. Time for a change: Dynamic urban ecology. Trends in

Ecology and Evolution 27:179–188.

- Randa, L. A., and J. A. Yunger. 2006. Carnivore occurrence along an urban-rural gradient: A landscape-level analysis. Journal of Mammalogy 87:1154–1164.
- Ridout, M. S., and M. Linkie. 2009. Estimating overlap of daily activity patterns from camera trap data. Journal of Agricultural, Biological, and Environmental Statistics 14:322–337.
- Ripple, W. J., J. A. Estes, R. L. Beschta, C. C. Wilmers, E. G. Ritchie, M. Hebblewhite, J. Berger, B. Elmhagen, M. Letnic, M. P. Nelson, O. J. Schmitz, D. W. Smith, A. D. Wallach, and A. J. Wirsing. 2014. Status and ecological effects of the world's largest carnivores. Science 343:1241484.
- Royle, J. A., and R. M. Dorazio. 2008. Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations and communities. Elsevier Academic Press, Oxford, UK.
- Šálek, M., L. Drahníková, and E. Tkadlec. 2015. Changes in home range sizes and population densities of carnivore species along the natural to urban habitat gradient. Mammal Review 45:1–15.
- Sargeant, A. B., and S. H. Allen. 1989. Observed interactions between coyotes and red foxes. Journal of Mammalogy 70:631–633.
- Sargeant, A. B., S. H. Allen, and J. O. Hastings. 1987. Spatial relations between sympatric coyotes and red foxes in North Dakota. Journal of Wildlife Management 51:285–293.
- Schmitz, O. J., J. R. B. Miller, A. M. Trainor, and B. Abrahms. 2017. Toward a community ecology of landscapes: predicting multiple predator-prey interactions across geographic space. Ecology 98:2281–2292.
- Schoener, T. W. 1974. Resource partitioning in ecological communities. Science 185:27–39.
- Smith, J. A., J. P. Suraci, M. Clinchy, A. Crawford, D. Roberts, L. Y. Zanette, and C. C. Wilmers. 2017. Fear of the human 'super predator' reduces feeding time in large carnivores. Proceedings of the Royal Society B: Biological Sciences 284:20170433.
- Stevens, D. L., and A. R. Olsen. 2003. Variance estimation for spatially balanced samples of environmental resources. Environmetrics 14:593–610.
- Su, Y. S., and M. Yajima. 2012. R2jags: a package for running jags from R. R Foundation for Statistical Computing.
- Theberge, J. B., and C. H. R. Wedeles. 1989. Prey selection and habitat partitioning in sympatric coyote and red fox populations, southwest Yukon. Canadian Journal of Zoology 67:1285–1290.

- Treves, A., and K. U. Karanth. 2003. Human-Carnivore Conflict and Perspectives on Carnivore Management Worldwide. Conservation Biology 17:1491–1499.
- Vanak, A. T., D. Fortin, M. Thaker, M. Ogden, C. Owen, S. Greatwood, and R. Slotow. 2013. Moving to stay in place: Behavioral mechanisms for coexistence of African large carnivores. Ecology 94:2619–2631.
- Wang, Y., M. L. Allen, and C. C. Wilmers. 2015. Mesopredator spatial and temporal responses to large predators and human development in the Santa Cruz Mountains of California. Biological Conservation 190:23–33.
- Wapenaar, W., F. de Bie, D. Johnston, R. M. O'Handley, and H. W. Barkema. 2012. Population structure of harvested red foxes (Vulpes vulpes) and coyotes (Canis latrans) on Prince Edward Island, Canada. The Canadian Field-Naturalist 126:288–294.
- Weins, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3:385–397.
- Werner, E. E., and S. D. Peacor. 2003. A review of trait-mediated indirect interactions in ecological communities. Ecology 84:1083–1100.
- Wilmers, C. C., Y. Wang, B. Nickel, P. Houghtaling, Y. Shakeri, M. L. Allen, J. Kermish-Wells, V. Yovovich, and T. Williams. 2013. Scale dependent behavioral responses to human development by a large predator, the puma. PLoS ONE 8:e60590.
- Woodroffe, R. 2000. Predators and people : using human densities to interpret declines of large carnivores. Animal Conservation 3:165–173.
- Zuur, A. F., E. N. Ieno, and C. S. Elphick. 2010. A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1:3–14.