NOMADIC ANIMAL MOVEMENT AND INFECTIOUS DISEASE IN CHANGING LANDSCAPES

by

CLAIRE STEWART TEITELBAUM

(Under the Direction of Sonia Altizer and Richard J. Hall)

ABSTRACT

Animal movements are important for individual fitness and population dynamics, and also affect species interactions, community composition, and ecosystem functioning. Long-distance animal movements, such as migration and nomadism, are particularly important for community and ecosystem processes, including the dispersal and transmission of infectious diseases. Spatio-temporal variability in resources (e.g., food, water, habitat) is a key driver of these long-distance movements. Human activities such as urbanization, agricultural development, and climate change alter the quantity and stability of resources available to wildlife, which can in turn alter the distance and frequency of animal movements. Understanding the interactions between landscape change, animal movement, and infectious disease transmission is crucial for informing wildlife conservation and public health in changing landscapes. In this dissertation, I focus on nomadic animal movements, which are irregular long-distance movements with little seasonal signature. First, I review the literature on nomadic movements and describe their prevalence across space and taxa; their patterns and drivers; and their potential impacts on communities and ecosystems. I then perform a comparative analysis to understand the relationship between movement behavior (resident, nomadic, or migratory) and parasite diversity across ungulate species. Next, I build a mathematical model of nomadic animal movements in both naturally-varying and human-stabilized landscapes. I use this model to explore the mechanisms underlying nomadic movements, as well as how animals moving according to different mechanisms perform under environmental change that stabilizes resources. I then analyze GPS tracking data from American white ibis (*Eudocimus albus*) in South Florida, USA, to understand how individual movement patterns in an urban area scale up to affect habitat connectivity between urban and non-urban patches. Finally, I extend my mechanistic model of nomadic movements to explore how altered movement patterns and reduced connectivity in urban landscapes affect infectious disease transmission. Collectively, this research demonstrates that nomadic animal movement is a crucial link between landscape change and infectious disease transmission in wildlife; however, these effects are complex and their direction depends on the drivers and cues of movement. This work also provides multiple frameworks and avenues for further understanding the ecological effects of wildlife responses to human development.

INDEX WORDS: Animal movement, Disease ecology, Foraging, Network analysis, Nomadism, Population dynamics, Resource dynamics, Urbanization, Wildlife

NOMADIC ANIMAL MOVEMENT AND INFECTIOUS DISEASE IN CHANGING LANDSCAPES

by

CLAIRE STEWART TEITELBAUM

B.A., Pomona College, 2014

A Dissertation Submitted to the Graduate Faculty of The University of Georgia in Partial Fulfillment of the Requirements for the Degree

DOCTOR OF PHILOSOPHY

ATHENS, GEORGIA

2021

NOMADIC ANIMAL MOVEMENT AND INFECTIOUS DISEASE IN CHANGING LANDSCAPES

by

CLAIRE STEWART TEITELBAUM

Major Professors:	Sonia Altizer Richard J. Hall
Committee:	Vanessa O. Ezenwa Jeffrey Hepinstall-Cymerman Ricardo M. Holdo

Electronic Version Approved:

Ron Walcott
Vice Provost for Graduate Education and Dean of the Graduate School
The University of Georgia
May 2021

ACKNOWLEDGEMENTS

This work would not have been possible without the professional, personal, intellectual, and institutional support of countless people and organizations. First, I am grateful to my advisors, Richard Hall and Sonia Altizer, for their guidance and support. Richard, thank you for always thinking through problems with me, reading drafts over and over, and keeping track of the details of every model. Sonia, thank you for always seeing the big picture and for your writing comments, which have made each subsequent paper better and a little easier to write. Both of you are incredible scientists and mentors. I am also grateful to my committee members, Vanessa Ezenwa, Jeff Hepinstall-Cymerman, and Rico Holdo, for their helpful feedback on my proposed project ideas and being willing and available to talk through analyses and ideas.

This research was collaborative and relied on many people beyond the author list of each publication. I am always grateful to Thomas Mueller for helping me enter ecology research and being a constant source of encouragement and knowledge. The research in Chapter 5 also relied on a team who collected data on ibis, including Marueen Murray, Sonia Hernandez, Taylor Ellison, Henry Adams, Catie Welch, Anjelika Kidd, and Ethan Cooper. Thank you for your physical effort and skill, without which my analysis would have been impossible. Thanks to Anje Kidd in particular for insights into ibis movement behavior – your thesis research was a crucial piece of the ibis puzzle.

The Odum graduate student community made my PhD experience more fun, interesting, and productive, and was a highlight of my years at UGA. I am thankful to the

members of the Hall and Altizer labs, especially Cecilia Sánchez, Cali Wilson, Isabella Ragonese, Ania Majewska, Paola Barriga, Megan Tomamichel, and Anna Willoughby, for their feedback on my work and for their collegial support. I was also lucky to be a member of a graduate student writing group; I thank Rachel Smith for organizing it, and Michelle Evans, Paige Miller, Ania Majewska, and Amy Briggs for feedback on my manuscripts and for help improving my writing practices. I am grateful for having a group of friends to each lunch with most days, and that #lunchmunchbunch continued even virtually. Thanks to Robbie Richards, Joy Vaz, Kate Sabey, Cecilia Sánchez, Michelle Evans, Annakate Schatz, Cali Wilson, and many others for being part of such a pleasant break in the day (and even discussing research sometimes).

The work of the staff in Odum enabled me to complete my PhD. I am grateful to the building services staff, including Dewayne Green, Jennifer Yearby, and Josh Harris, for their work making the Ecology building a clean and pleasant place to be. Thanks to the front office staff for their behind-the-scenes work to keep the school running smoothly. And thank you to Julie Gunby and Katherine Adams for making sure every form was submitted correctly, and for being sources of support and positivity.

This work was funded by a Graduate Research Fellowship from the National Science Foundation and by the UGA Graduate School, with additional support from the NSF Macroecology of Infectious Diseases Research Coordination Network. I am grateful for these funds, which allowed me to focus on this research with few other responsibilities. Thanks also to the Odum and UGA Graduate School staff, particularly Caitlin McDonald and Tiffany Drayton, for help administering these funds.

Athens was a wonderful place to spend these years, and I am grateful to the many artists, musicians, activists, and community members who make Athens a lively and fun place to be. The University of Georgia is located on the ancestral lands of the Muscogee (Creek) and Cherokee peoples, and I acknowledge their stewardship of the land and important contributions to the region.

Finally, the support of my family and friends has been crucial for my well-being during my PhD. I would not be here without their love, humor, and encouragement.

TABLE OF CONTENTS

CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Movement is ubiquitous across the animal kingdom; few animals are born and die in the exact same location. Moving can increase individual fitness by promoting access to resources such as food, mates or shelter; enabling dispersal and colonization of new environments; and allowing individuals to escape adverse environmental conditions [1]. However, moving animals also incur energetic and fitness costs [2], making animal movement an important driver of population dynamics and crucial for species conservation [3]. Across taxa, animal movements are often a response to resource dynamics, where animals move to track changes in resource availability across space and time [4–6]. This resource tracking behavior can produce spectacular long-distance movements, including seasonal migration, nomadism, and natal dispersal.

Beyond their importance for individual fitness and population dynamics, animals' movements affect the communities and ecosystems through which they move. These ecological effects include trophic interactions (e.g., predation, foraging) and transport effects (e.g., propagule dispersal, nutrient deposition, parasite transmission) [7]. The effects of animal movements on communities and ecosystems can be particularly significant if animals move long distances; for example, animals disperse seeds farther than would be likely using only wind or water [8,9]. For infectious diseases, animal movements can transport diverse parasites among local environments, conspecifics, and heterospecifics [7,10]. On the other hand, movement can reduce infection risk for mobile hosts by promoting gene flow that spreads resistance genes; reducing infection rates by culling infected animals; and allowing animals to escape from contaminated environments [10]. The costs of infection can also feed back to affect behavior and movement patterns on both ecological and evolutionary time scales [11,12].

Human activities are altering landscapes worldwide through activities including urbanization, agricultural development, and anthropogenic climate change. These developments often change the amount and stability of resources available for wildlife, which in turn can alter their movement patterns. Often, animals move less frequently or shorter distances in developed landscapes, as has been observed in migratory butterflies [13], birds [14], and mammals [15]. Within a single population, individuals may also differ in their movement patterns and responses to landscape change, with some individuals tolerating human-dominated areas, and others avoiding them [16,17]. These changes in movement behavior and within-population variation in urban and agricultural landscapes can affect population dynamics [17,18]. Moreover, because of the importance of long-distance movements for species interactions and ecosystem functioning, anthropogenic changes to landscapes could alter communities and ecosystems via changes in the movement patterns of highly mobile animals [10,19,20].

To date, studies of long-distance animal movements have largely focused on seasonal migrations, which are predictable, round-trip, directed movements between distinct areas [21]. In contrast to these regular migrations, many highly mobile animals move in irregular patterns with little seasonal signature, a movement behavior known as nomadism [4,22]. Nomads can expend just as much energy on movement and often travel even farther than migrants annually [23,24]. However, how nomadic movements impact populations, communities, and ecosystems remains largely unexplored. In particular, studies of the effects of nomadism on infectious diseases are limited to a few investigations of avian influenza [25,26] and case studies involving pathogen transmission between livestock and nomadic animals [27]. Nomadic animals' movements are very flexible in response to changes in environmental cues [22,28], so their movement patterns could change substantially in human-altered environments. Given that many nomadic species are of conservation concern [29], and that the pathogens they carry could impact both wildlife and human health, it is important to understand how nomadic movements affect population persistence and disease transmission within nomadic populations, as well as how future human development could alter these relationships.

My dissertation research combines literature review, mechanistic models, and statistical analysis of empirical data to explore the ecology of nomadic movements, focusing on how nomadic animals respond to changing resource dynamics, and how their movements affect infectious disease transmission. In Chapter 2, I review the current literature on nomadic animal movements, including their distributions, drivers, and ecological effects. I find that nomadic movements are widespread geographically and taxonomically, and are usually associated with environments where resources vary unpredictably. Nomadic movements have the potential to impact species interactions, communities, and ecosystems, but these effects are generally not well described.

Next, in Chapter 3, I explore relationships between movement behavior and parasitism at a broad spatial and taxonomic scale. Using a database of host-parasite associations and information about species' movement patterns, I ask whether parasite diversity differs across nomadic, migratory, and resident ungulate species. I find that migrants tend to have higher parasite diversity than nomads or residents, possibly because migrants track a single niche and thus experience more stable environmental conditions year-round.

Next, in Chapter 4, I use a mathematical model to explore the rules that might govern nomadic animal movement, and to assess the performance of these different rules under environmental change. I build a model in which nomadic animals move among patches that vary in their resource availability, then test simple rules based on resources, density, and memory to ask which of these rules perform best in landscapes with different patterns of resource availability. I find that animals using nomadic movement rules based on resource availability and density perform better than non-nomadic animals or those using only density cues in variable environments, and that the additional complexity of memory provides little benefit. This result indicates that even simple rules can help us understand animals' responses to their environments. However, I also find that nomadic animals move less and perform no better than residents in environments with stable resource availability. These results suggest that urbanization and other human development that stabilizes resources could benefit residents but not nomads, and/or could promote residency in formerly nomadic animals.

Next, I use empirical data to explore how the theory developed in Chapter 4 applies in a real-world system. In Chapter 5, I use GPS-tracking data of American white ibis *(Eudocimus albus*) in South Florida to examine the movements and habitat use of this seasonally nomadic species in a heterogeneous urban landscape. Using a network approach, I find that the connectivity of the ibis movement network is low relative to a null model designed to simulate nomadic movement, suggesting that ibis display some site fidelity. In addition, individual ibis specialize in different habitat types, such that some individuals use urban habitats and others use wetland habitats, but few individuals use both habitat types. This specialization produces a network of patches that are relatively weakly connected, potentially limiting the spread of pathogens or contaminants between sites with different land cover.

Finally, in Chapter 6, I explore the consequences of habitat specialization in urban landscapes for population and infection dynamics. As an extension of the framework from Chapter 4, I model nomadic movements and the spread of infection on a network of urban and non-urban patches, where some individuals specialize in urban or non-urban habitat types. I find that, in the absence of specialization, urbanization that stabilizes resource availability has nonlinear effects on pathogen prevalence and survival, such that survival is lowest in partially urban landscapes and infection prevalence is highest in natural or partially urban landscapes. However, habitat specialization increases survival and reduces infection prevalence by reducing densities at urban sites and limiting the spread of infection across the network. These results indicate that habitat specialization can benefit populations in heterogeneous landscapes by reducing the potential for source-sink dynamics and infection spread, but could also limit the provision of beneficial functions of animal movement such as seed dispersal.

My dissertation research uses a range of methods (i.e., statistical and mathematical modeling; literature review; analysis of field- and literature-based data) and considers multiple vertebrate taxa to provide a broad understanding of the ecology of animal nomadism. Collectively, this work shows that nomadic animals have the potential to have strong effects on communities and ecosystems, and that human modifications to resource dynamics have complex effects on both movement patterns and infectious disease dynamics in nomadic wildlife.

CHAPTER 2

BEYOND MIGRATION: CAUSES AND CONSEQUENCES OF NOMADIC ANIMAL MOVEMENTS[1]

---

[1] Teitelbaum CS, Mueller T. Beyond Migration: Causes and Consequences of Nomadic Animal Movements. Trends Ecol Evol. 2019;34(6):569-581. Reprinted here with permission of the publisher.

ABSTRACT

Recent advances in animal tracking reveal that many species display irregular movements that do not fall into classical categories of movement patterns such as range residency or migration. Here, we develop a unifying framework that distinguishes these nomadic movements based on their patterns, drivers, and mechanisms. Though they occur in diverse taxa and geographic regions, nomadic movements are united by both their underlying environmental drivers, mainly environmental stochasticity, and the resulting irregular, far-ranging movement patterns. The framework further classifies types of nomadic movements, including full, seasonal, phase, irruptive and partial nomadism. Nomadic movements can have unique effects on populations, communities, and ecosystems, most notably providing intermittent disturbances and novel introductions of propagules.

NOMADIC MOVEMENTS: A COMMON, IRREGULAR PHENOMENON

Movement is a primary way that animals respond to environmental variability. Depending on the environmental context [30], the function of movement [1], and an animal's navigation and movement capacities [31], different movement types emerge, including the well-described classes of home ranging, seasonal **migration** (see Glossary), and natal **dispersal** [21,32]. To date, studies of long-distance animal movement have focused on animals' responses to environments that fluctuate seasonally (e.g., [33]). Less research has considered environments that are highly variable in both space and time; in these environments, many animals are **nomadic**, moving between distinct locations in a seemingly unpredictable manner [22,30]. Data from recent developments in animal tracking technology (e.g., longer-lasting and lighter GPS devices) [34] show that species previously considered migrants or **range residents** can show irregular, often long-distance, movement patterns [35–37], suggesting that nomadic movements are more common than assumed. However, while nomadism has been defined multiple times previously [4,38,39] and the term “nomadic” appears widely in the literature (Figure 2.1), few studies have systematically described the drivers and patterns that unite nomadic movements across taxa and make it a distinct movement type on par with classic patterns such as range residency and migration (but see [4]).

Similar to other movement types such as seasonal migration [33,40] nomadic movements share a set of common drivers, which produce its distinctive population-level patterns via multiple behavioral mechanisms. Nomadism is driven by environmental variability and unpredictability, which lead to its distinctive wide-ranging and irregular patterns [22]. These movement patterns can be described and quantified at the levels of individuals, populations and species (Box 2.1). In addition, we argue that the irregularity of nomadic movements could impact communities and ecosystems in unique ways that differ substantially from other movement types [41]. Nonetheless, despite the potentially significant ecological role of nomadic movements in structuring communities and ecosystems, nomadism is not well understood [4], possibly because nomadic animals are difficult to locate and track due to their large ranging areas and irregular movements [42]. At the same time, nomadic species could be particularly threatened by anthropogenic landscape changes [39], so understanding these movements is important for conserving both nomadic species and the ecosystem processes they influence.

Here, we review the patterns and processes associated with nomadic movements, with four main goals: (1) describe the patterns of nomadic movements across taxa; (2) classify types of nomadic movement; (3) identify the main drivers of nomadism and the behavioral mechanisms that link these drivers to movement patterns; and (4) describe the effects of nomadic movements on populations, communities, and ecosystems, including their conservation implications.

Patterns of nomadic animal movements

In contrast to traditional definitions of nomadism as an alternate form of migration or dispersal [43], recent analyses of newly available tracking data have used characteristics of movement paths to classify nomadism as a movement type of its own [38,44–46], distinct from migration or range residency [30,46]. Building on these analyses, we here define nomadism as a movement behavior where individuals or populations respond to non-seasonal environmental variability with movements that are highly variable in their timing and direction, both within and between years (Figure 2.2; Figure 2.3A). Because this definition stretches across years, distinguishing nomadism from other movement types requires observing patterns over long time scales. Nomadic movement patterns can generally be distinguished from other types of movement because range sizes of nomads (e.g., measured by net squared displacement [38]) expand over long time periods, whereas the homing tendencies of residents and migrants produce range sizes that reach an asymptote relatively quickly (e.g., within one year for long-lived animals [4,38,47]) (Box 2.1). For instance, nomadic bald eagles *(Haliaeetus leucocephalus*) used areas more than twice as large as those used by residents over 3.5

years, even though they moved only 10% farther at a daily timescale [36]. While not required in the definition of nomadism, this larger area use of nomads compared to residents usually emerges as a property of the unbounded nature of nomadic movements.

Large area use and infrequent revisitations

On the individual level, nomadic animals move between distinct sites rather than remaining in a static home range [48]. While home range sizes of residents are limited by energetic constraints on their ability to cross their range regularly [49–51], nomads often use areas that are much larger than expected based on energetics alone (e.g., ~45,000 km^2 range of nomadic Mongolian gazelle (*Procapra gutturosa*) [52] vs. 382 km^2 annual range of larger resident woodland caribou (*Rangifer tarandus*) [53]). Migratory animals can have equally large ranges, but unlike migrants, most nomadic animals visit new and unfamiliar areas on both short [54] and long [55] timescales. Some nomads revisit sites (Box 2.2), but these revisitations occur irregularly and often at a lower frequency than in migrants [56].

Irregular timing and direction of movements

Nomadic movements generally lack spatial and/or temporal regularity in their timing and direction (Figure 2.2C). While seasonal migration patterns can vary between years (e.g. low site fidelity [14]), migrations remain predictable in the direction and seasonal associations of movement (e.g., northward movements in spring and southward movements in autumn in the Northern Hemisphere). In contrast, the timing and direction of nomadic movements are irregular (e.g., southward or northward movements in different years [57]). Similarly, nomadic movements show high variability in their velocity across time [28].

Frequent and recurring movements

Nomadic movements are often considered a type of dispersive behavior [58–61], and indeed nomadism may be indistinguishable from dispersal at short time scales. However, these two movement types produce different long-term patterns at both the individual and population levels [38] (Figure 2.2A,C). Nomadic movements usually occur multiple times within an individual's lifetime, whereas natal and breeding dispersal usually occur only once (e.g., immediately following sexual maturity) (Figure 2.3B) [32]. These two movement types also differ in their ultimate effects on distribution; natal dispersal is primarily a means of establishing new territories or reproduction sites [1,62], whereas nomads sometimes cover long distances only to breed at or near their natal site [56] or move to new sites each year [63]. Depending on the type of nomadic movement (see below, "Types of nomadic movement"), long-distance displacements of nomads can occur more or less frequently than migratory movements (Figure 2.3B).

TYPES OF NOMADIC MOVEMENTS

Nomadic movements occur in a taxonomically diverse group of organisms, including birds [42], grazing mammals [64], insects [65], crustaceans [66], and marine animals [67]. Nomads also represent multiple locomotion strategies [30,68,69] and occur worldwide, from Australia and southern Africa to the arid landscapes of Central Asia (Figure 2.1). Though both marine and terrestrial systems contain nomadic species, less is known about aquatic and marine movements because aquatic species were difficult to track until recently [67,70]. Nomadism is best described in birds and mammals, which likely reflects limitations on collecting movement data for smaller taxa [65] and the taxonomic biases of ecology research [71]. Though these biases also apply to this review, our descriptions are meant to apply across taxa, and we give examples from groups other than birds and mammals when possible. There is also substantial variation in movement patterns within the group of nomadic animals, as has been described for migrants (e.g., partial vs. full migration [72]) and residents (e.g., territoriality vs. central place foraging [46]). While some species move nomadically throughout their entire lives (e.g., Mongolian gazelles [30,57]), others are nomadic only at certain times and places. In addition to full nomadism, we identify four additional types of nomadic movements: phase nomadism, seasonal nomadism, irruptive nomadism, and partial nomadism.

Phase nomadism

In some nomadic species or populations, individuals' movement patterns differ according to their life history stage (Figure 2.2D), a type of nomadism we classify as *phase nomadism.* For instance, spiny lobsters (*Panulirus argus*) are nomadic as adults but show strong site fidelity as juveniles [73]; the reverse pattern is present in Australian freshwater crocodiles (*Crocodylus johnstoni*) and common ravens (*Corvus corax*) [59,74]. These changes in movement behavior across life stages can be driven by trade-offs between resource acquisition and the risks associated with movement [45,73] or by a need to maintain territories or breeding sites as adults [75]. Nomadic movements in the juvenile phase may appear similar to natal dispersal; however, dispersal is defined by settlement at a distance from the natal site [62], whereas nomadic movements do not necessarily impact reproductive site selection at adulthood [74].

Seasonal nomadism

Beyond these differences in movement behavior between life stages, some individuals change their movement behavior over the course of a year (Figure 2.2E). These *seasonal nomads* include trumpeter hornbills (*Bycanistes bucinator*), which move nomadically during the nonbreeding season but maintain small home ranges during the breeding season [76] and grey-headed flying-foxes (*Pteropus poliocephalus*), which can be nomadic either year-round or seasonally, depending on local resource availability [77]. Although there is a predictable element to the occurrence of these seasonal nomadic movements, their direction, frequency, and intra-season timing are variable between years.

Irruptive nomadism

Some nomadic animals punctuate periods of residency with unpredictable, long-distance movements that are neither seasonal nor dependent on life-stage. These movements have traditionally been called irruptive migration [78], but in many cases both their timing and direction are erratic, aligning them more closely with nomadism than with migration (Figure 2.2F) [79,80] (but see [81], an example of an irruptive migrant). *Irruptive nomads* include species such as the banded stilt (*Cladorhynchus leucocephalus*), which depart *en masse* from saltwater ponds following rainfall events and move individually to new foraging areas [82]. In other cases, such as the well-known desert locust (*Schistocerca gregaria*), irruptive nomadic periods vary drastically in their duration, potentially encompassing multiple generations [83].

Partial nomadism

Partial nomadism, where only a portion of a population is nomadic, exists in multiple taxa and environments [67] (Figure 2.2G). As in partial migration, this within-population variation can stem from differences in life history within a population (e.g., if adult males are territorial [75]), but are sometimes more complex (e.g., movements of moose (*Alces alces*) in Scandinavia depend on interactions between age, snow depth, and human presence [45]).

DRIVERS OF NOMADIC BEHAVIOR

Unpredictable, limiting resources

Nomadism is most often considered a response to landscapes that are unpredictable ("unpredictable resources hypothesis") and resource-poor ("resource limitation hypothesis") [4]. Theory and models predict that patchy, dynamic landscapes should produce nomadic behavior as animals track resources that vary non-seasonally [4], and a previous review of the niches occupied by nomads supports the role of highly variable environments in driving nomadic movements [22] (Figure 2.3A). Unpredictable environments can also drive nomadic behavior by reducing the benefits of restricted movements (e.g., homing behavior of migrants and residents), since familiarity with an area is less beneficial where conditions vary widely in space and time [84]. Environmental variability can be quantified using measurements of variation in time (e.g., standard deviation across time [30]), space (e.g., spatial autocorrelation [22]), or both (e.g., wavelet analysis [22]).

The geographic distribution of terrestrial nomads supports the resource limitation hypothesis, with large numbers of nomadic birds in the arid landscapes of Australia and southern Africa [26,68] and nomadic ungulates in drylands (e.g., Arabian oryx (*Oryx leucoryx*) in Oman [85]; saiga antelope (*Saiga tatarica*) and Mongolian gazelle in the Gobi steppe ecosystem [30,57]). Nomads also live in landscapes that may not appear resource-limited (e.g., temperate, non-arid environments), but resource identity varies from species to species, from prey [56,86] to vegetation [64], and can include non-food habitat requirements [87]. In contrast to seasonal migration [45], temperature is rarely considered a driver of nomadism, possibly because temperature usually changes in a predictable, seasonal pattern (but see “escape from natural disasters” below).

Despite the role of resource limitation in driving nomadism, the energetic costs of movement can limit when and where these movements occur. When resources are extremely scarce, animals might lack the energy to undertake long-distance movements, as has been shown for dispersal [88]. Further, limiting resources are probably more important drivers of full-time [57] and seasonal nomadism [63] than phase and partial nomadism, where local residents obtain sufficient resources year-round. Irruptive nomadic movements can also be resource-driven if rapid changes in abiotic conditions quickly transform previously-unsuitable areas into high-quality foraging sites (e.g., rainfall for banded stilts and grey teal (*Anas gracilis*) [24,82]). The overwhelming evidence indicates that unpredictable resources drive nomadic movements, much as seasonal resources drive migration [22], highlighting resource dynamics as a key driver of multiple forms of animal movement.

Escape from natural disasters

Nomadism sometimes manifests as an escape from abnormally poor conditions, rather than as constant movement as resources slowly change. For instance, dune larks (*Calendulauda erythrochlamys*) moved away from their vegetated islands in the Sahara during drought [89] and Asiatic wild asses (*Equus hemionus*) moved to novel locations during a severe winter storm [90]. If these poor conditions occur infrequently enough, then populations would be irruptively nomadic [22], but if severe weather is common, movements will occur more frequently. The relative importance of resource tracking ("pull") versus escape ("push") in determining nomadic movements depends on the population and environment (Box 2.2), but flexibility in movement behavior is known to increase survival in areas where severe weather is common [90].

Escape from parasites and predators

Nomadic behavior can also provide escape from natural enemies. Livestock-rearing practices have demonstrated that occasional movements of herds between pastures reduces infection by environmentally-transmitted pathogens [91]. Similarly, nomadism could reduce the intensity or prevalence of infection in wild animals if nomads move away from areas of high parasite exposure, particularly if contamination occurs at large spatiotemporal scales (e.g., for environmentally persistent pathogens). This process has also been documented in seasonal migrants [10] and may drive nomadism in army ants (*Eciton burchellii*), which move their nests continuously if they experience persistent infection [92]. However, studies of pathogens in nomads are rare and have largely focused on spread of zoonotic pathogens [26], rather than on how infection drives or maintains nomadic movements.

Similarly, nomadism could provide an escape from predation if predators are less mobile than their nomadic prey [93]. Wood warblers (*Phylloscopus sibilatrix*) take advantage of their relatively high mobility to move their nest sites annually, avoiding nesting in areas where their predators are locally abundant [94]. Predator avoidance is widely considered a potential driver of seasonal migration [33], and nomadism could provide an even more effective escape if predators are unable to adjust their behavior for the unpredictable arrival of their nomadic prey.

BEHAVIORAL MECHANISMS OF NOMADIC MOVEMENT

Behavioral mechanisms provide the link between environmental drivers and movement patterns [95]. Diverse mechanisms produce nomadic movements; for instance, the striking variation in nomadic movement patterns among individuals and across time [96,97] may stem from relatively weak endogenous control of movement in nomads [22]. Another common characteristic shared across nomadic populations is their use of social behaviors and cues, which can help nomads identify suitable areas in variable environments (e.g., through conspecific attraction) [98,99], even if they are not social year-round [98]. Alongside these social cues, multiple mechanisms can mediate the link between nomadism's unique drivers and patterns (Box 2.2). This diversity of mechanisms also exists for other movement types (e.g., both gradient-following [100] and memory [40] are important for migration), and multiple behavioral mechanisms even can act simultaneously [40,101]. In fact, movement types are probably linked more closely by their drivers and patterns than by their mechanisms [95].

ECOLOGICAL EFFECTS AND CONSERVATION IMPLICATIONS OF NOMADIC MOVEMENTS

Population-level processes

Nomadic movements can affect demographic processes including birth and mortality rates, ultimately affecting population stability. Long-distance movements generally increase population viability by reducing the likelihood that animals will overexploit local resources [102]. Nomadic movements could produce particularly large population sizes if low interannual site fidelity allows nomads to move to wherever resources are abundant in a given year [22,103] (Figure 2.4A). Migratory species with high seasonal site fidelity can experience rapid population declines following habitat disturbance [104], suggesting that nomadism, which is characterized by low site fidelity, should buffer populations from changing conditions. However, it is important to note that severe weather events can still have strong negative effects on nomadic populations [105].

Nomadic movements can also affect population genetic structure (Figure 2.4B). Given that dispersive (as opposed to coordinated) movements generally increase gene flow [60,106], we would predict high gene flow in nomadic species. However, gene flow requires that populations mix as movement occurs [60], and nomadic populations often (though not always) move as a group [4]. Accordingly, animals that are nomadic only in the nonbreeding season may maintain genetic differentiation between populations, whereas full or partial nomads should have higher gene flow (e.g., [107]).

Community- and ecosystem-level processes

Much like migratory movements, which provide both transport effects (e.g., moving propagules) and trophic effects (e.g., subsidizing predators) [7], nomadism can connect and alter communities of less mobile organisms [7,8,25,108]. Even if propagule dispersal occurs infrequently, it can have important ecosystem-level effects [109], particularly when there are few other mechanisms of dispersal [8]. Additionally, because they frequently visit new sites, nomads could be more likely than migrants to disperse propagules to novel habitats [110] (Figure 2.4C).

Animals also carry pathogens with them as they move, which can introduce infections to novel habitats and novel species. The probability of pathogen spread depends on a host's movement rate relative to the shedding period [25], and thus differs among hosts, pathogens, and environments. For this reason, predicting disease outbreaks can be difficult when individuals are nomadic because nomadic movements can introduce connectivity between distant locations [111]. Seasonal migration is known to affect infection spread [10], but studies of pathogen dispersal by nomadic species are mostly restricted to avian influenza [25,26], meaning that we do not know whether hypotheses derived for migration apply to nomadic movements (but see [112]).

Nomadic animals also participate in trophic interactions that affect community and ecosystem structure [7] (Figure 2.4D). For instance, nomadic predators can synchronize regional prey dynamics [113]; nomadic herbivores can alter plant community composition and nutrient flow by preferentially eating certain plant species and sporadically depositing large quantities of nutrients [64,114] (Figure 2.4E). These trophic interactions usually stabilize ecosystems [102] but can also be destabilizing (e.g., disturbances from the irregular inter-annual habitat use of locusts [83]).

Issues in the conservation of nomadic animals

Traditional conservation methods such as protected areas are often ineffective for highly mobile species [104,115]. For migratory species with high site fidelity, protecting seasonal sites can be effective [116], but nomadic species will usually remain outside protected zones for a substantial period of time [30,67]. Conservation measures for nomads should prioritize areas that are critical for survival, which requires understanding cues for nomadic movement (e.g., vegetation, water [117]) as well as how animals move between these key areas. For instance, barriers to movement are particularly damaging for walking nomads [118], so maintaining connectivity and landscape permeability across large spatial scales is important. In some cases, these actions might require protecting many small sites, rather than large swaths of land [118]. Dynamic conservation measures (e.g., “mobile” protected areas whose locations change over time [119]) are a particularly promising strategy for conserving highly mobile species, especially as real-time tracking data make identifying crucial areas more feasible [120].

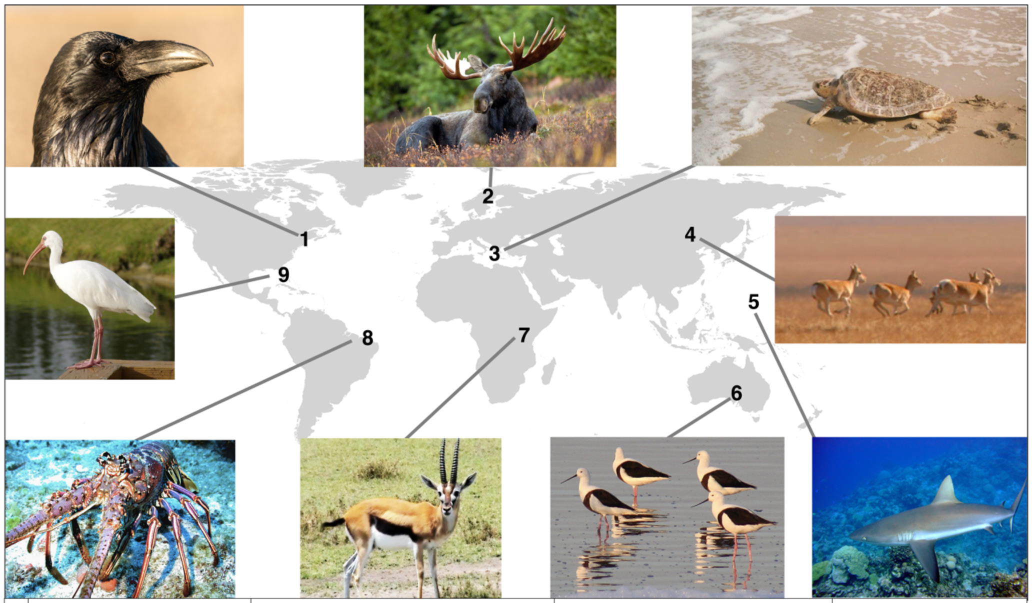
The success of conservation measures depends on monitoring the status of nomadic populations [39,104], but population sizes of nomads are easily overestimated [77] or underestimated [105] because of their large range sizes and irregular movements. Species distribution models for nomadic species are easily compromised by seasonal changes in habitat requirements or use of ephemeral resources [121]. Nevertheless, behavioral flexibility allows animals to respond to changing environmental conditions (e.g., via flexible breeding site selection), suggesting that nomads may be more adaptable than species with fixed movement patterns [90,122]. Evidence from migrants shows that species with more diverse movement strategies are less threatened than those with only one [123], pointing to the importance of behavioral flexibility for long-term survival in a changing world.

CONCLUDING REMARKS AND FUTURE DIRECTIONS

The drivers of nomadic movements are the best-studied aspect of nomadism, trending towards consensus that nomadism is driven by limiting and unpredictable resources. However, the exact determinants of specific movements are not well established (i.e., the cues that trigger a population or individual to move), and contributions of nomadic animals to ecosystem structure and function require more investigation (See Outstanding Questions). Advances in animal tracking and remote sensing have increased the amount of data available to answer these questions [34,124]; however, mechanistic models are needed to link these data to hypotheses and concepts [125]. In particular, simulation studies of potential movement mechanisms and use of artificial intelligence and machine learning could be crucial steps towards understanding the cognitive and behavioral mechanisms of nomadic movements. In addition, future studies should focus on developing conservation concepts for nomadic species, in particular the challenges of managing species whose habitat occupancy is unpredictable. These studies, combined with descriptions of population-level movement patterns, are necessary to determine exactly how nomads affect the structure and functions of their environments, as well as how best to conserve this unique movement behavior.

ACKNOWLEDGEMENTS

We thank A.A. Briggs, A.A. Majewska, P.B. Miller, R. Smith, and members of the Altizer and Hall lab groups at UGA for comments on earlier versions of the manuscript. We thank B.Z. Taylor for help producing the Figure360. CST was supported by a UGA Presidential Fellowship and an NSF Graduate Research Fellowship; TM was supported by the Robert Bosch Foundation and the German Federal Ministry of Education and Research (BMBF, 01LC1710A & FKZ 01LC1820A). Images of raven and Mongolian gazelle in Figure 2.1 are by T. Mueller; all other images are in the public domain.



	Species	Presumed driver of movement	Approximate movement distance or range area	Type of nomadism
1	**Common raven (*Corvus corax*)**	Food availability and territoriality: movement between discrete carcasses defended by adults	Annual ranging of at least 1800 sq. km	Phase: only juveniles are nomadic
2	**Moose (*Alces alces*)**	Food availability; snow cover; less harsh conditions than where migration occurs	Annual net displacement of ~10 km	Partial: 8-10% of individuals are nomadic
3	**Loggerhead turtle (*Caretta caretta*)**	Habitat quality, measured as barometric pressure	10-100 km over a 15-day period	Partial: only females are nomadic
4	**Mongolian gazelle (*Procapra gutturosa*)**	Food quality and availability	Gazelles ranged over an area of 45,000 sq. km in one year	Full-time
5	**Grey reef shark (*Carcharhinus amblyrhynchos*)**	Behavioral and ecosystem effects of fishing pressure	Highly variable between individuals; up to 135 km in 48 hours	Partial: larger individuals are more likely to be nomadic
6	**Banded stilt (*Cladorhynchus leucocephalus*)**	Habitat availability	Displacements of 680-2000 km in a 6-day period	Full-time or irruptive
7	**Thomson's gazelle (*Eudorcas thomsonii*)**	High variability in food availability	Annual range of up to 25,000 sq. km	Full-time
8	**Spiny lobster (*Panulirus argus*)**	Food availability; shelter availability	Up to hundreds of kilometers	Phase: juveniles are nomadic
9	**White ibis (*Eudocimus albus*)**	Weather; breeding site quality	Annual movement distances of up to 1,300 km	Seasonal

Figure 2.1: Examples of nomadic movements from around the world. These examples represent nine nomadic populations from diverse taxa and geographic locations. The main findings of each study with regards to the drivers, movement distances, and type of nomadic behavior are described for each species, where known. References for each species in numerical order are: (1) [126]; (2) [38,45]; (3) [127]; (4) [52]; (5) [69]; (6) [82]; (7) [122]; (8) [128]; (9) [63].

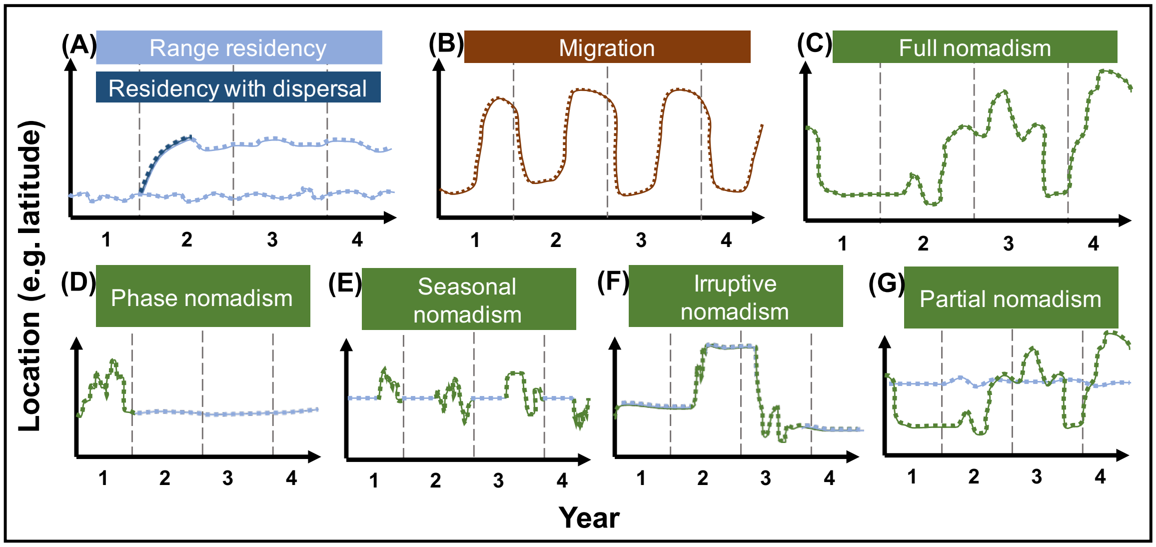


Figure 2.2: One-dimensional depiction of hypothetical patterns representing different movement types. (A, B) show non-nomadic movement types of range residency and migration. (C) shows full-time nomadism. (D-G) show other types of nomadic movements, where nomadism occurs at different temporal scales (D-F) or differs between individuals in a population (G). Light blue sections in each panel indicate periods of residency. Tracks illustrate key differences between movement types and do not represent real movement tracks.

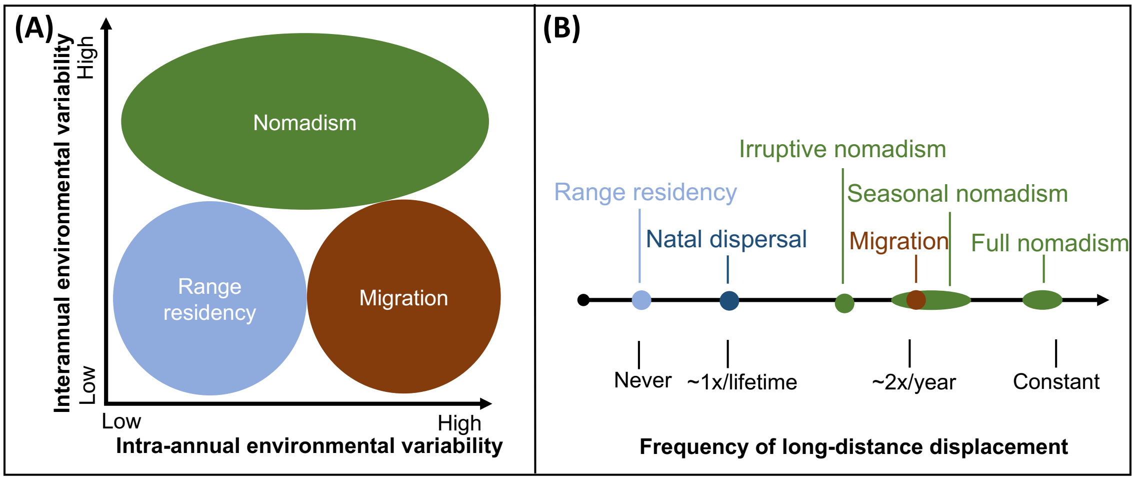


Figure 2.3: Drivers and patterns of different movement types. (A) Nomadism, migration, and range residency result from differences in the amount of within-year and between-year environmental variability. Nomadism tends to occur in areas with high interannual environmental variability, where conditions at a point in one year are a poor predictor of conditions at the same point in other years. In contrast, range residency is characterized by low intra- and interannual environmental variability; migration has high within-year but low between-year variability, leading animals to revisit spatially separated areas seasonally. (B) This environmental variability produces movement types that occur along a spectrum of frequency. Nomadic movements are frequent, occurring more than once in a lifetime and sometimes constantly. Migratory movements occur twice annually. Natal dispersal occurs once in an animal's lifetime.

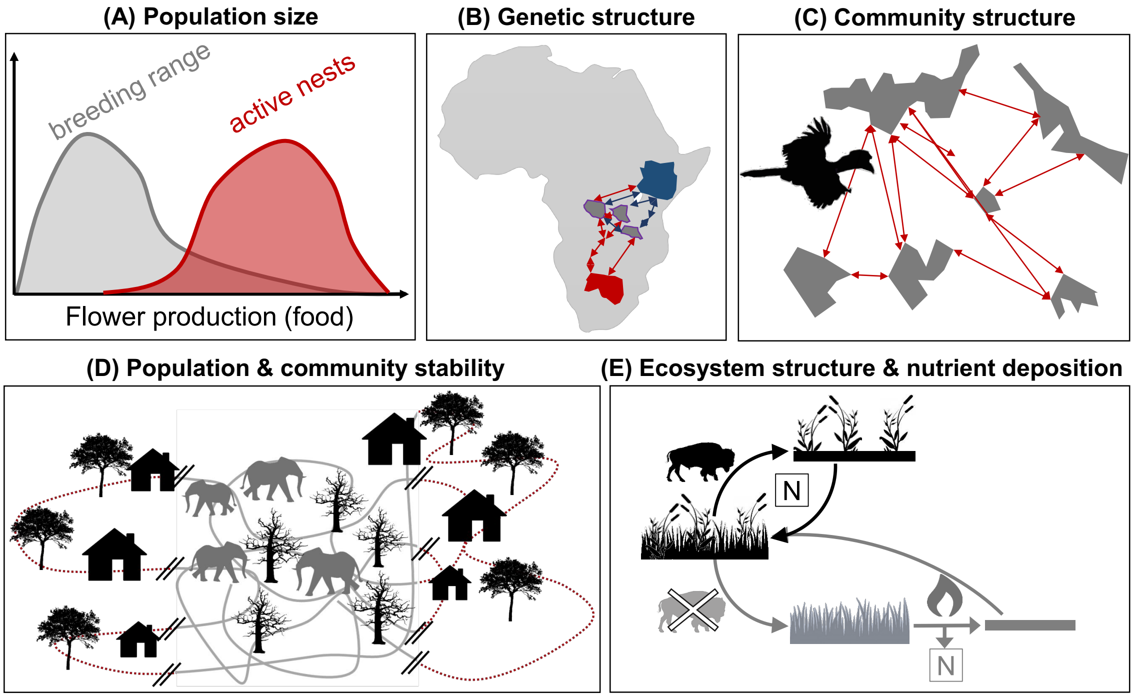


Figure 2.4: Effects of nomadic movements on populations, communities and ecosystems. (A) Swift parrots (*Lathamus discolor*) nested in different areas each year, but always at sites that were locally productive, increasing their reproductive output [103]. (B) Small but continuous gene flow occurs between lesser flamingo (*Phoeniconaias minor*) populations via nomadic movements to shared wetlands [129]. (C) Between-patch seed dispersal by trumpeter hornbills occurs twice as frequently during the nomadic season [8]. (D) Elephant (*Loxodonta africana*) populations declined and trees were over-browsed during a drought, possibly because nomadic movements were restricted by nearby human development [102]; grey lines indicate elephant movements and dotted red lines suggest potential movement paths eliminated by human development. (E) Bison (*Bison bison*) suppress fire by grazing preferentially on grass, which reduces nitrogen loss from the system; their nomadic movements allow communities to recover between periods of grazing [114].

Glossary

Dispersal (natal dispersal, breeding dispersal): a directed movement away from a previously-used area and into a new area that occurs irregularly (usually once during an individual's lifetime), where both the source and destination areas are usually used for an extended period

Migration: a long-distance movement type where individuals or populations of animals move seasonally between discrete locations, producing within- but not between-year variability in location and movement patterns

Nomadism: a movement type where individuals or populations of animals move frequently between locations with irregular timing and/or direction, producing both within-year and between-year variability in location and movement patterns. Nomadic movements often produce large range sizes, especially when compared to conspecific range residents

> ***Irruptive nomadism***: a form of nomadic movement where long-distance movement events are unpredictable in their timing and direction, but may be interspersed by relatively long periods of residency
>
> ***Partial nomadism***: a form of nomadic movement where some individuals in a population are nomadic and others are range residents or migratory
>
> ***Phase nomadism***: a form of nomadic movement where animals are nomadic during one portion of the life cycle. Phase nomadism is distinct from dispersal in that displacement events occur multiple times and/or do not result in establishment of new territory or range

Seasonal nomadism: a form of nomadic movement where animals are nomadic during only a part of the year

Range residency: a form of movement where individuals or populations of animals have substantial overlap in area use both within and between years

Box 2.1: Quantifying nomadic animal movements

The past decade has seen substantial growth in the statistical methods to quantify movement patterns; the majority of these methods are concerned with developing sophisticated ways to quantify range residency and estimate home ranges [130], but some also explicitly quantify migratory patterns (i.e., estimating seasonal ranges and movement distances) [131]. Attempts to quantify nomadism and disentangle it from other movement types, however, are relatively rare. Bunnefeld *et al.* [38] propose a straightforward approach to categorize trajectories of individual animals using net squared displacement (NSD), which is the distance between a trajectory's starting point and any point on that trajectory. In general, NSD for nomadic animals increases over time in a more or less linear pattern; in contrast, NSD for migrants follows a sinusoidal pattern, and for residents quickly reaches an asymptote [38,44]. Another approach uses statistical signatures of movement tracks to differentiate movement types. Abrahms *et al.* [46] distinguish nomads from migrants and residents based on distance-independent metrics, including relatively low correlation in turning angles, intermediate volume of intersection between monthly ranges, and short residence time of nomadic movement paths. Importantly, recently-developed home range estimators using continuous-time approaches can be helpful in detecting whether an animal is nomadic by quantifying whether or not an individual has a range limit and estimating its range-crossing time [132].

Movement types also produce distinct patterns at the population level, but few methods quantify patterns above the individual level. One population-level approach delineates movement types using a set of indices that compare relocation patterns between individual animals [30]. For example, *population dispersion* measures whether relocations among individuals are clustered (characteristic of migrants), dispersed (characteristic of residents), or independent (characteristic of nomads); *realized mobilit*y quantifies an individual's annual range as a proportion of the population range, which is higher for both nomads and migrants than for residents. Finally, the correlation among individuals' locations can indicate whether animals move together to and from common targets (as is common in migration) or independently from one other (as is common in nomadism [133]).

Last, different movement types can be simulated using random walks. For nomadic animals, random walks are often assumed to be uncorrelated [38]. However, recent simulations of nomadic movements have incorporated nonrandom steps, such as attraction to resources [134], conspecifics [98], or switching between foraging and long-distance search behavior [46], as part of a recognition that nomadic movements are not random with respect to their drivers.

Box 2.2: Mechanisms of search and navigation

As animals move long distances, they rely on a combination of search behavior (i.e., exploration of new, unfamiliar sites) and navigation (i.e., movement to a known destination) [95]. Seasonal migration usually requires navigation between known locations [40,47]; in contrast, the unpredictable environments in which nomads live mean that they often lack information about potential targets, increasing the importance of search behavior [4] or prospecting and revisitation [24]. Nomadic movements may occur via three main mechanisms requiring different combinations of search and navigation: First, they may be "push" movements out of inhospitable areas (e.g., due to a lack of food or high predation pressure), with no defined target [90]. Alternatively, they may be "pull" movements where animals search for or navigate to unpredictable high-quality resources (e.g. for species with specific breeding habitat requirements) [63]. And last, nomadic movements may be irregular in time but require navigation between known locations (e.g. via prospecting and revisitation, where conditions at distant sites are unpredictable but their locations are known) [56]. Animals can also use combinations of these mechanisms simultaneously [4,63].

Unlike navigation, which relies on orientation and spatial memory [4], little is known about long-distance search behaviors. For instance, large group sizes are considered adaptive for migrants because they facilitate collective navigation [135], but nomadic animals can also display impressive aggregations [63,136], suggesting that groups may also be beneficial for search behavior. However, nomads can also be solitary [98], indicating that sociality is not a prerequisite for nomadism, and aggregations may occur because resources are locally concentrated [98]. In the context of migration, these groups facilitate knowledge transmission, where juveniles may learn from more experienced individuals [14]. The role of this cultural learning for nomadic movement has not been investigated, but would provide information about the mechanisms by which nomads find new suitable patches (See Outstanding Questions).

Outstanding Questions

- What characterizes nomadic movements of taxa other than birds and mammals (e.g., marine and aquatic species, short-lived species)? How do these movements differ from those that have been well described?
- What cues trigger nomads to move between distant sites? What search and navigation mechanisms allow them to find new patches?
- What life-history and behavioral traits are shared across nomadic species?
- How do nomadic movements affect population stability of nomads?
- What is the role of nomadic animals in the spread of propagules and infectious diseases across large spatial scales?
- What conservation strategies are necessary to protect nomadic populations?

Highlights

- Many animals move over large areas in an irregular manner, and thus do not fit into the conventional categories of either seasonal migration or range residency.
- These nomadic movements can be distinguished from other forms of movement both qualitatively and quantitatively.
- Nomadism usually occurs in highly variable, resource-limited environments. It can also provide escape from natural disasters, predators and parasites.
- Nomadic movements have unique impacts on animal populations, community ecology, and ecosystems.

- These impacts include increasing population sizes, promoting dispersal of propagules to novel environments, and stabilizing ecosystems.

CHAPTER 3

MIGRATORY BEHAVIOR PREDICTS GREATER PARASITE DIVERSITY IN UNGULATES[2]

---

[2] Teitelbaum CS, Huang S, Hall RJ, Altizer S. Migratory behaviour predicts greater parasite diversity in ungulates. Proc R Soc B Biol Sci. 2018;285(1875):1–8. https://royalsocietypublishing.org/doi/10.1098/rspb.2018.0089. Reprinted here with permission of the publisher.

ABSTRACT

Long-distance animal movements can increase exposure to diverse parasites, but can also reduce infection risk through escape from contaminated habitats or culling of infected individuals. These mechanisms have been demonstrated within and between populations in single-host/single-parasite interactions, but how long-distance movement behaviors shape parasite diversity and prevalence across host taxa is largely unknown. Using a comparative approach, we analyze the parasite communities of 93 migratory, nomadic, and resident ungulate species. We find that migrants have higher parasite species richness than residents or nomads, even after considering other factors known to influence parasite diversity, such as body size and host geographic range area. Further analyses support a novel "environmental tracking" hypothesis, whereby migration allows parasites to experience environments favorable to transmission year-round. In addition, the social aggregation and large group sizes that facilitate migration might increase infection risk for migrants. In contrast, we find little support for previously-proposed hypotheses, including migratory escape and culling, in explaining the relationship between host movement and parasitism in mammals at this cross-species scale. Our findings, which support mechanistic links between long-distance movement and increased parasite richness at the species level, could help predict the effects of future environmental change on parasitism in migratory animals.

Keywords: animal movement, comparative analysis, disease ecology, habitat diversity, nomadism, range residency

INTRODUCTION

Long-distance movements, most notably seasonal migration, are widespread across animal taxa [21]. These movements can have profound consequences for many ecological processes [7], including host-pathogen interactions [10,137]. In fact, escape from harmful parasites may be one of the evolutionary drivers of seasonal migration [33], but these interactions are complex, and studies from various scales have shown that migrants can have both higher [138–140] and lower [19,141] levels of parasitism than residents. Established relationships between movement behavior and infection patterns are largely based on studies of the prevalence (i.e. the proportion of a population that is infected by a given parasite) of one or a few parasite species in a single host species [141,142]. In contrast, few studies have examined how movement behavior affects the diversity of parasites across large numbers of host species, with some notable exceptions focused on birds [138–140,143]. This is an important gap, especially given that mobility is a key predictor of infection risk at the population level [142] and that highly mobile animal taxa are important sources for parasites of domestic animals and humans [144]. Further, many highly mobile animals are nomadic, moving in a less predictable manner than seasonal migrants (in regards to timing, direction, or both) [4], but hypotheses about nomadic movements and parasitism are less developed. Comparing parasite diversity and prevalence across migratory, nomadic and resident taxa can help identify the ecological and evolutionary mechanisms that underlie relationships between long-distance movement and infection risk.

Migration can increase infection risk through at least two different mechanisms: environmental sampling and environmental tracking (Figure 3.1). As migrants move annually between distant breeding and wintering grounds, they can acquire diverse parasites through exposure to parasite environmental stages, interactions with diverse heterospecifics, and/or contact with other populations of conspecifics [7,140,143,145]. Similarly, nomadic animals may encounter diverse parasite species because of their large ranging area [26] (Figure 3.1a). This process of environmental sampling is frequently proposed to explain positive relationships between migration and parasitism [145]. Migration could also increase parasite diversity because migrants experience less environmental variability than residents in seasonal environments. As they move between distant habitats, many migrants track environmental conditions favorable to resource availability ("surfing the green wave" [146]) and avoid exposure to climate extremes [147,148]. Environmental tracking could promote year-round parasite transmission by increasing host exposure to infectious environmental stages or pathogen vectors that survive better in mild climates [149], which might increase both parasite diversity and infection prevalence in migrants (Figure 3.1b). In contrast, nomads tend to live in environments that are variable or resource-limited year-round [4,22], which could limit parasite survival and transmission (Figure 3.1b). Latitudinal trends in parasite diversity in primates [150] and humans [151] are consistent with harsher environments supporting lower parasitism. Previous studies have shown that mild climates promote parasite survival [152,153], most prominently in the broad context of how climate change alters disease dynamics. Here, we propose that favorable environmental conditions could be a mechanism underlying a positive relationship between migration and parasitism.

Migration has also been suggested to decrease parasite survival and transmission if migrants (and their parasites) experience harsh environmental conditions or physiological stress during migratory journeys [20,154]. Migration can remove infected individuals during strenuous journeys (‘migratory culling’) [20,154] and/or kill parasites as migrants move across strong environmental gradients (‘migratory recovery’) [155]. The harsh environments inhabited by nomads could replicate these effects, especially because long-distance movements are particularly costly under low-resource conditions [104] (Figure 3.1c). In addition, migration can allow animals to escape habitats where parasite infectious stages have accumulated and/or move to areas where parasite diversity is low due to harsh environmental conditions at other times of the year (‘migratory escape’) [10,20,156,157]. Similarly, the irregularity of nomadic movements might reduce the frequency of resampling the same environments, further diminishing parasite diversity in nomads (Figure 3.1d).

Here, we present the first large-scale comparative study of the relationship between parasitism and movement strategy in mammals, using the ungulates (orders Artiodactyla and Perissodactyla) as a model group that includes many migratory land animals [158]. Ungulates are globally distributed with a variety of movement strategies, including seasonal migration, nomadism, and range residency. Long-distance movements in ungulates are primarily driven by changes in food availability and energetic costs due to temperature, precipitation, and/or snow cover [33,159], but can also be linked to predation [33]. Partial migration is also common in ungulates [45,160], which could further modify the mechanisms proposed for fully migratory populations. The parasites of wild ungulates have been intensively studied [142,161], in part because of the importance of these animals as a resource for humans, and also because they can alter infectious disease dynamics in closely-related domestic livestock [144]. Highly mobile ungulates are threatened by human activities [96,162], as evidenced by recent declines in both their population sizes and the scope of their long-distance movements [96,162]. Understanding the link between host movement and parasite diversity is important for anticipating changes in overall biodiversity in face of changing environments.

Our analysis examined the degree to which host movement strategy predicts variation in the diversity and prevalence of both micro- and macroparasites in ungulates (see Methods). Our predictions, summarized in Figure 3.1, are as follows: (1) If *environmental sampling* increases parasite exposure in highly mobile hosts, then both migratory and nomadic species will have higher parasite species richness (the number of parasite species infecting a single host species) than resident species, but average infection prevalence will be similar among groups, since sampling is unlikely to affect parasite survival. Migratory and nomadic species will also have more diverse habitats represented within their geographic ranges than residents. (2) If *environmental tracking* increases parasite transmission, then migratory hosts will have greater parasite diversity and infection prevalence than either residents or nomads, but species with different movement modes will not necessarily differ in the diversity of habitats within their geographic ranges. (3) Alternatively, if *migratory escape and culling* reduce parasite transmission and the survival of infected hosts, then parasite diversity and prevalence will be lower in migratory and nomadic hosts than in residents. To determine whether movement behavior acts separately from other mechanisms known to influence parasitism across host species, we considered additional predictors of parasite diversity, including host geographic range area, body size, and social grouping [163–167]; we also calculated a metric of habitat diversity in each species' range to differentiate between the processes of environmental sampling and environmental tracking.

METHODS

Host-parasite infection data

We used the Global Mammal Parasite Database 2.0 (GMPD), which contains host-parasite association records reported from literature for free-ranging populations of Artiodactyla and Perissodactyla [161]. For each ungulate host species, we counted the observed parasite species richness in the GMPD [164,167,168]. To account for uneven sampling effort across host species (Appendix A Figure S3.1), we calculated the estimated parasite species richness in each host species using the Chao2 estimator [169] (following Huang *et al.* [168]). We also controlled for sampling effort using an alternative method, following additional previously-published approaches [164,166–168]. Because results were similar across the different methods, we report only results using Chao2 estimator in the main text; we provide further details on parasite richness estimates in Appendix A and on sensitivity tests of the Chao2 estimator below.

Host movement data

We gathered data on the movement strategy of each ungulate species from published definitions and descriptions (Appendix A). We used descriptions of species' movement patterns from the journal *Mammalian Species*, other published literature, and the online databases *Animal Diversity Web* and *Ultimate Ungulate*. Using these data, we categorized population movement patterns as migratory, nomadic, or resident, based on definitions in Mueller *et al.* [4]. Additional details on movement data compilation are reported in Appendix A.

Because many ungulate species have intraspecific variation in movement behavior (e.g. [45,160,170]), we assigned a species-level movement strategy hierarchically. Species with any migratory populations were considered migratory; species that were nomadic but not migratory were considered nomadic; and species were considered resident only if there was no evidence for migration or nomadism. To examine the sensitivity of our results to this hierarchical scheme, we also used two alternative categorizations: one where we excluded 12 species that were both migratory and nomadic, and one where we included "migratory/nomadic" as a fourth movement category. We focus our discussion on the results based on the original hierarchical categorization, but these alternative schemes produced similar results (Appendix A Table S3.1; Appendix A Table S3.2).

Additional variables

We considered other host traits that could drive parasite species richness [142,163,166,168] (Appendix A). These traits were: host adult body mass and population group size, derived from the PanTHERIA database [171]; geographic range area (in km^2) and the mid-range latitude calculated from IUCN species distribution maps [172]; and the number of WWF ecoregions [173] that overlapped with the species' geographic range (from IUCN range maps) as a measure of habitat diversity. Additional details on life-history and geographic range data are available in Appendix A.

Data analysis

We used a suite of linear models to analyze predictors of estimated parasite species richness. The candidate explanatory variables were: movement strategy, body mass (log); geographic range area (log), number of ecoregions within the species' geographic range (log), and absolute mid-range latitude. Population group size was not included in these analyses because data were available for only a small number of host species (n=24 of 93 ungulate hosts), but a preliminary analysis of these data are presented in the Discussion. Models predicted estimated parasite species richness (log) from all combinations of these variables (with no interactions), excluding models that included both geographic range area and number of ecoregions because they were highly collinear (following [174]). We selected the models with the lowest AICc (ΔAICc < 2) as the set of models best predicting parasite species richness [175], and used Akaike weights within this set to produce the average best model [175,176]. Separately, we examined whether species with different movement strategies differ in their geographic range area, habitat diversity, body mass, and population group size.

To evaluate the effectiveness of the Chao2 estimator in controlling for sampling effort, we first tested for a signal of sampling effort in the residuals of our averaged model, using the number of hits for a species' Latin binomial on Web of Science (WOS) (collected on 2 November 2016) as a measure of sampling effort (following [164,166–168]). Based on the results of this analysis, we used a set of models that explicitly considered sampling effort by including sampling effort (log) as an additional explanatory variable and a weighting scheme based on the number of individuals sampled per species in the GMPD. These models predicted raw (rather than estimated) parasite species richness; the model selection process was identical to that described above.

Closely-related species often have similar traits, so we tested for a phylogenetic signal in the residuals of the averaged model by calculating Pagel's λ [177] using phylogeny from the mammalian supertree [178]. We found no evidence for phylogenetic structure in the residuals of our model ($\lambda=6.75*10^{-5}$; ΔAIC=0.005 when comparing this value to a model where $\lambda=0$), so we did not repeat the analyses using a phylogenetically informed method.

We also investigated whether movement behavior predicts estimated species richness of subsets of parasites (macroparasites vs. microparasites and contact-transmitted vs. environmentally-transmitted parasites). For each parasite group, we constructed a set of linear models predicting estimated species richness of that group used the same model averaging process as for the full dataset. These models included movement strategy, number of ecoregions, and body mass as explanatory variables.

Some GMPD records also include infection prevalence data, which were recorded for 89% of entries included in this analysis. We used these data to compare the prevalence of individual parasite species that infect both migratory and resident hosts; nomadic hosts had too few prevalence records to be included in this analysis. For each parasite species, we found the difference in average prevalence between migratory and resident host species and then analyzed this difference in prevalence using an intercept-only linear model.

We conducted all analyses in R version 3.4.1 [179], with packages 'rgdal' [180] and 'raster' [181] for processing and analyzing spatial data; package 'MuMIn' for AICc calculation and model averaging [182]; modified functions from the package 'phylosignal' for calculating Pagel's λ [183]; and the 'multcomp' package [184] for multiple comparisons. Additional details on all analyses are available in the electronic supplementary material.

RESULTS

Our final dataset included 93 ungulate species hosting 765 unique parasite species. The sampled parasite species richness of a single host species ranged from 1 to 118 parasite species. Using the Chao2 estimator, estimated parasite species richness was up to 142 parasite species per host. Of the 93 host species, 35 showed evidence for migratory behavior, 10 were nomadic but not migratory, and 48 were resident only.

Four models best explained parasite diversity (i.e., $\Delta AIC_c<2$, Appendix A Table S3.3). In the average model produced from these four models, movement strategy and habitat diversity were the strongest predictors of parasite species richness (Table 3.1). Migratory species had a richer parasite community than resident or nomadic species (Figure 3.2a; Table 3.1); of the species present in the database, the averaged model predicted that the average migratory host would harbor 2.4 and 3.7 times as many unique parasite species as resident and nomadic hosts, respectively. The parasite species richness of nomadic and resident hosts was not significantly different (Figure 3.2). When considered separately, species with both migratory and nomadic populations (n=12) had parasite species richness similar to migrants (Appendix A Table S3.2).

In addition to movement strategy, we detected a robust signal of habitat diversity, where species with more ecoregions within their geographic ranges had richer parasite communities. However, despite the strong relationship between habitat diversity and geographic range area (r=0.90), geographic range area was not included in any of the four top models. In addition, there was no systematic difference in geographic range area or habitat diversity between species with different movement strategies (Appendix A Figure S3.2). Host body mass and latitude were included in some of the top models, but were not strong predictors of parasite diversity (Table 3.1). Migratory species had, on average, slightly larger body mass than resident species (Appendix A Figure S3.3).

Even after using the Chao2 estimator to control for sampling effort, the residuals of the averaged model contained a weak albeit significant signal of sampling effort ($R^2 = 0.047$, $p = 0.036$). In an alternative set of models that explicitly considered sampling effort (thus diminishing the signal of sampling effort in the residuals: $R^2 < 0.001$, $p=0.955$), the effects of movement strategy, habitat diversity, and other variables were qualitatively similar to those from the model of estimated parasite species richness (Appendix A Table S3.4).

The pattern of higher parasite diversity in migratory species was consistent for microparasites but not for macroparasites (Table 3.1; Figure 3.2b,c). Additionally, migrants had higher species richness of contact-transmitted parasites than resident and nomadic species, but this pattern was not present for environmentally-transmitted parasites (Appendix A Table S3.5); the majority of contact-transmitted parasites were microparasites (65%, SE: 4.0%), whereas the majority of environmentally-transmitted parasites were macroparasites (80%, SE: 2.0%).

In our analysis of parasite prevalence in relation to migratory behavior, we found that 86 parasite species had sufficient prevalence data; these were sampled from 61 ungulate hosts and included 31 species of helminths, 23 viruses, 14 arthropods, 12 bacteria, and 6 protozoa. Per-parasite infection prevalence tended to be higher in migratory than in resident species (Figure 3.3), but this difference was small and not significant (3.5%, CI: [0.00, 0.69]).

DISCUSSION

Our analysis of parasitism and movement strategies in wild ungulates showed greater parasite diversity in species with at least some populations that migrate than in those that have no migratory populations, similar to patterns previously shown for waterfowl [139]. This result, in combination with the strong positive association between habitat diversity and parasite diversity, supports both the environmental sampling and environmental tracking hypotheses.

The most widely-suggested mechanism driving increased parasite diversity in migrants is environmental sampling, where migrants are exposed to more diverse parasites as they cross large geographic distances, move through different habitat types, and contact more con- and heterospecifics [10,138,143]. In support of this process, we found that habitat diversity, measured as the number of ecoregions in a species' geographic range, predicted higher parasite diversity in ungulates. In fact, habitat diversity was a better predictor of parasite diversity than was geographic range area, suggesting that environmental sampling is a key mechanism driving established positive relationships between geographic range area and parasite diversity across taxa [163,166,168]. However, movement strategy did not predict the diversity of habitats in a species' geographic range (see also [185]), and our final model included effects of both habitat diversity and migratory behavior, indicating that migration itself is associated with higher parasite diversity independent of any increase in the diversity of sampled habitats. Thus, while environmental sampling might increase parasite diversity, separate mechanisms are necessary to explain the positive relationship between migration and parasitism in ungulates.

By tracking favorable environments throughout the year [146–148], migratory species might increase both their own fitness and that of their parasites. Parasites infecting resource-tracking hosts could benefit from reduced seasonality and conditions favorable for survival (e.g. relatively high moisture), in a similar way as stably high productivity promotes higher diversity of free-living organisms [186]. Although nomadic ungulates also move to follow resource availability [187], these animals often live in regions where conditions are harsh and highly variable [22], which should reduce infected host survival, parasite survival, and parasite transmission [27]. Indeed, the lower parasite diversity we observed in nomads as compared to migrants could be related to the difference in the average environmental harshness experienced by these two groups [22], providing support for environmental tracking as a key mechanism that increases parasite diversity in migrants.

In addition to environmental factors, migratory species may share life-history traits that promote exposure to, and persistence of, a diversity of parasites. In particular, highly mobile ungulates tend to be social [188], likely because aggregation and social contact provide protection from predation [188] and facilitate the collective knowledge that aids in navigation [135]. Accordingly, the migratory ungulates in our dataset had, on average, larger population group sizes than residents. Large group sizes often increase infection risk [142,189,190] and should affect contact transmission more strongly than environmental transmission [189,191]. Consistent with this expectation, we saw that migratory behavior was positively associated with species richness of microparasites and contact-transmitted parasites, but less so with species richness of macroparasites and environmentally-transmitted parasites. However, we did not see the same pattern of parasite diversity in nomads, which are also often social and can display impressive aggregations [22,27,136], and had intermediate group sizes in our dataset. Whether this difference could again be due to differences in environments inhabited by migrants and nomads requires further investigation. Overall, our results suggest that social behavior could promote associations between migration and parasitism, and call for further development of mechanistic models of the interactions between these three traits.

Consistent with our findings on parasite diversity, we found a small but positive effect of migratory behavior on parasite prevalence. This result was in the opposite direction of predictions from prior work on migratory escape and culling, which show lower infection prevalence in migratory hosts [10,19,20,155]. This discrepancy in prevalence patterns may stem from characteristics particular to ungulates. Specifically, parasite sharing with domestic livestock [192] and high plasticity in movement behavior, including partial migration [160], could weaken the effects of migratory escape by allowing year-round parasite transmission. In addition, though the stresses of migration can suppress immune function to some extent [193], it may be less physiologically demanding for energy-minimizing ungulate migrants that feed as they move [100,146] than for time-minimizing flying migrants [194,195], thus reducing the effects of migratory culling. Interactions with other ecological processes may also mask relationships between parasitism and migration. For example, predation can reduce parasite prevalence in prey populations when predators cull infected hosts [196], but if migration allows escape from predation [33], it could result in higher parasite prevalence in migratory prey. Finally, evidence for lower infection prevalence in migrants comes from within- and between-population comparisons of single host species, whereas in this study we examined parasitism at the multi-species level. Comparisons across scales are rarely straightforward in ecology, and unexpected patterns at higher levels can emerge from interactions of mechanisms at lower levels [197]. Further studies of the processes that link these hierarchical levels and that operate at the intermediate scale (i.e. differences among populations of the same species) are needed to better understand drivers of parasite diversity and prevalence across scales.

In interpreting our results it is important to note that high parasite diversity on the species level does not necessarily indicate that all individuals or populations of a host species harbor diverse parasite communities, nor does it imply that hosts are suffering from high costs of disease [163]. For example, in partially migratory species, resident and migratory populations might show differences in parasite diversity, with some populations having lower disease risk. In addition, high parasite diversity does not necessarily predict reduced host fitness, and can even reflect low parasite virulence or high host tolerance of infection [198]. Host investment in immune defense can also lead to variation in disease risk across individuals. In birds, immune function can be downregulated prior to migration as animals allocate energy towards preparation for flight [193], but comparative analyses have shown that migratory birds may have more immunity-related genes than resident species [199] and generally invest more in development of immune defense [200,201]. The relative importance of these processes and how they influence broad-scale patterns of parasite diversity in hosts with different movement behaviors is still unclear. Comparative studies of immune function in relation to movement behavior would help identify whether differential resistance and tolerance to infection drive patterns of parasite diversity in migratory hosts.

Human alterations to natural systems have diminished or even eliminated the annual journeys of many migratory populations [96,162]. It is not yet clear how these changes will affect parasite biodiversity, which is a crucial regulator host population sizes, community dynamics [202], and evolutionary diversification [168]. If migration increases parasite transmission and persistence independent of other host traits, and if migratory hosts harbor specialist pathogens not found on other hosts, then the loss of migratory behavior could lead to parasite extinction even without host extinction. Moreover, parasites have been implicated in the decline of many threatened species, including the high-profile example of the migratory and nomadic saiga antelope [203]. Our results show that migrants have greater parasite diversity; however, it remains unknown whether migrants might be more susceptible to unexpected disease-related declines, which could increase the number of threats facing these already-vulnerable animals. Given the importance of wild ungulates for human use [144], as well as their potential to transmit pathogens to domestic livestock [192], understanding how migratory ungulates are affected by their high parasite diversity is a question of both conservation and economic importance.

DATA ACCESSIBILITY

All data and code are available on Dryad Digital Repository (https://doi.org/10.5061/dryad.j7401).

ACKNOWLEDGEMENTS

We thank the members of the Macroecology of Infectious Disease Research Coordination Network (including P. Stephens and P. Pappalardo), the Altizer research group at UGA and the Böhning-Gaese & Mueller research groups at BiK-F for helpful discussion and development of ideas and methods; and R. Holdo, V. Ezenwa, M. Boots, and two anonymous referees for their comments on the manuscript and analyses.

FUNDING

This work was supported by NSF/NIH/USDA grant DEB 1316223 to SA, including a student travel grant awarded to CST, and by NSF grant DEB 1518611 to SA and RJH. CST was supported by a University of Georgia Presidential Fellowship. SH was supported by the Alexander von Humboldt Foundation through a postdoctoral fellowship.

COMPETING INTERESTS

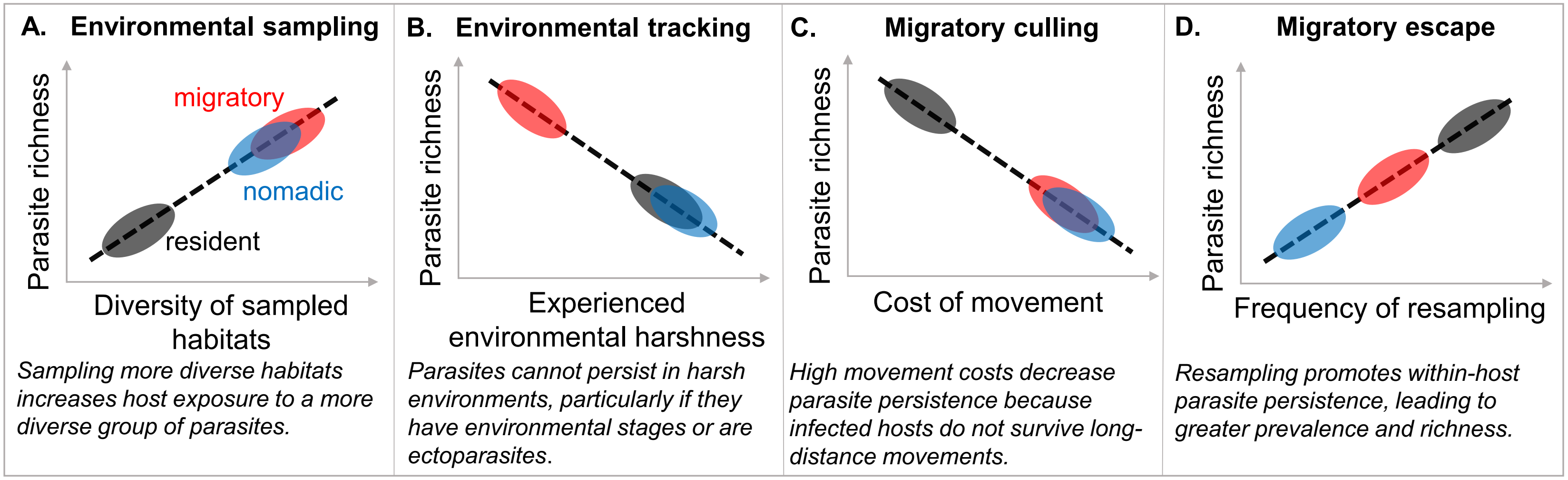
We have no competing interests

AUTHORS' CONTRIBUTIONS

CST conceived of the study, collected movement data and performed analyses. RJH and SA contributed to development of ideas and refining analyses. SH provided expertise on analytical techniques and GMPD data and helped interpret results. CST wrote the first draft of the manuscript and all authors contributed substantially to revisions.

Table 3.1: Model results from the averaged models predicting estimated parasite species richness (log). "Lower" and "upper" represent the bounds of a 95% confidence interval for each parameter. Candidate predictor variables in the suite of models for total parasite species richness were: movement strategy, habitat diversity (log), body mass (log), absolute mid-range latitude, and geographic range area (log); geographic range area was not present in any of the four best models. Candidate predictor variables for models of estimated macroparasite and microparasite species richness were: movement strategy, habitat diversity (log), and body mass (log).

	Total			**Macroparasites**			**Microparasites**		
	Estimate	**Lower**	**Upper**	**Estimate**	**Lower**	**Upper**	**Estimate**	**Lower**	**Upper**
Intercept	1.780	0.388	3.173	2.025	0.512	3.537	0.599	-0.885	2.083
nomadic	-1.326	-2.211	-0.44	-0.642	-2.000	0.716	-1.169	-2.125	-0.212
resident	-0.788	-1.377	-0.199	-0.392	-1.214	0.429	-0.903	-1.463	-0.343
Habitat diversity	0.362	0.094	0.629	0.097	-0.224	0.418	0.341	0.076	0.607
Body mass	0.083	-0.125	0.291	0.072	-0.156	0.301	0.14	-0.125	0.405
Mid-range latitude	0.004	-0.01	0.018	-	-	-	-	-	-



Sampling more diverse habitats increases host exposure to a more diverse group of parasites.

Parasites cannot persist in harsh environments, particularly if they have environmental stages or are ectoparasites.

High movement costs decrease parasite persistence because infected hosts do not survive long-distance movements.

Resampling promotes within-host parasite persistence, leading to greater prevalence and richness.

Figure 3.1: Conceptual illustration of hypothesized relationships between movement strategies and parasite richness in resident, migratory, and nomadic animals. In each case, black shaded regions represent resident species, red regions represent migrants, and blue regions represent nomads; overlap of shaded regions represents variability or uncertainty in the relative placement of each movement strategy.

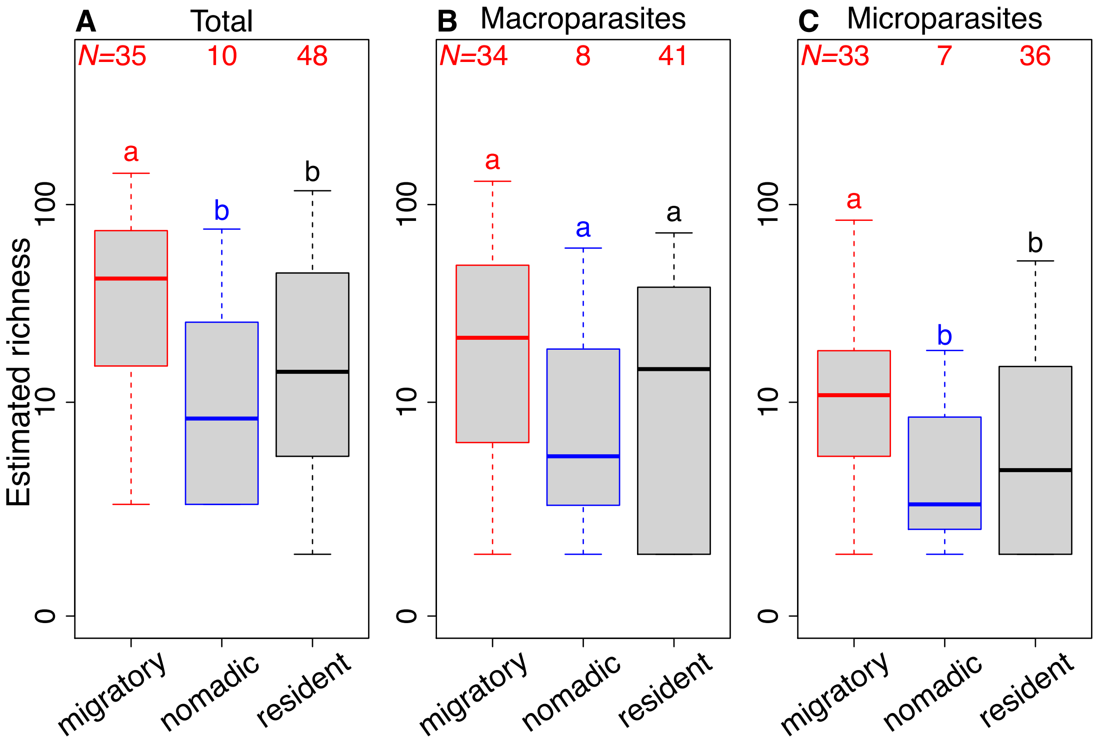


Figure 3.2: Estimated parasite species richness for ungulate hosts with different movement strategies. Boxplots show the median, interquartile range, and range for (A) estimated total parasite species richness, (B) estimated macroparasite species richness, and (C) estimated microparasite species richness. Different letters above the boxes represent significantly different predictions (Tukey test, α=0.05) from an averaged model using movement mode, habitat diversity, body mass, and mid-range latitude to predict parasite species richness (Table 3.1).

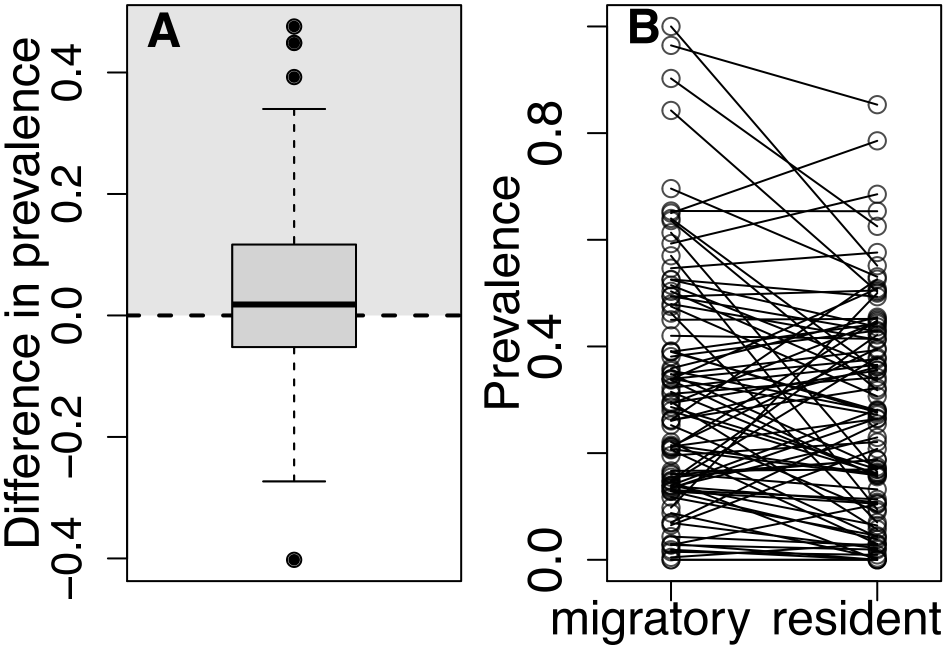


Figure 3.3: Difference in prevalence between migratory and resident species for each of 41 parasite species by host movement strategy. In (A), values above zero indicate that migratory species had higher prevalence and values below zero indicate that resident species had higher prevalence. Whiskers extend to 1.5 times the interquartile range. On average, migrants had 3.5% higher prevalence than resident species (modeled difference: 0.035; 95% CI: [0.000, 0.069]). (B) Prevalence values for individual parasite species in migratory and resident hosts; lines connect values for the same parasite.

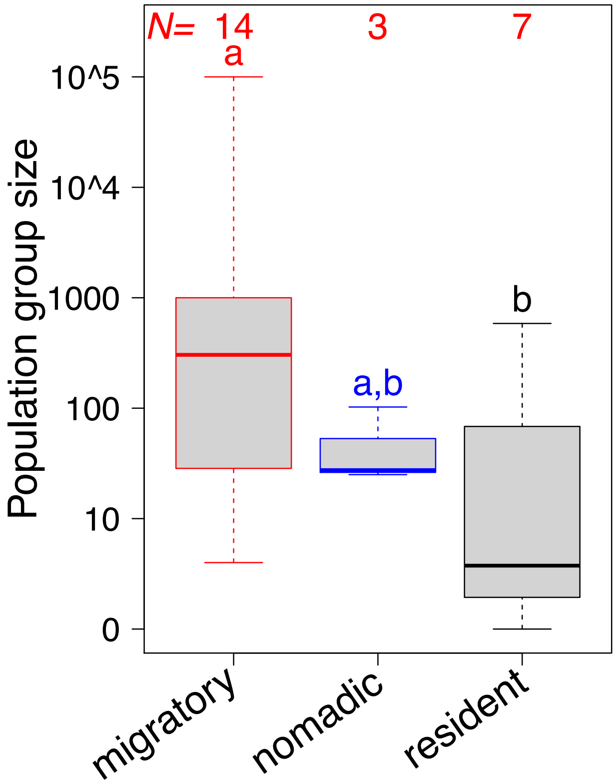


Figure 3.4: Population group sizes for ungulate host species with different movement strategies. Population group size is the number of individuals that spend the majority of their time in a day together and is roughly equivalent to herd size for ungulates. Boxplots show the median, interquartile range, and range for each group. Migratory species had significantly larger group sizes than resident species, and nomadic species were not distinguishable from either resident or migratory species (Tukey test, α=0.05).

CHAPTER 4

MOVEMENT RULES DETERMINE NOMADIC SPECIES' RESPONSES TO RESOURCE SUPPLEMENTATION AND DEGRADATION[3]

---

[3] Teitelbaum CS, Altizer S, Hall RJ. Movement rules determine nomadic species' responses to resource supplementation and degradation. J Anim Ecol. 2020;89:2644–56. Reprinted here with permission of the publisher.

ABSTRACT

1. In environments that vary unpredictably, many animals are nomadic, moving in an irregular pattern that differs from year to year. Exploring the mechanisms of nomadic movement is needed to understand how animals survive in highly variable environments, and to predict behavioral and population responses to environmental change.
2. We developed a network model to identify plausible mechanisms of nomadic animal movement by comparing the performance of multiple movement rules along a continuum from nomadism to residency. Using simulations and analytical results, we explored how different types of habitat modifications (that augment or decrease resource availability) might affect the abundance and movement rates of animals following each of these rules.
3. Movement rules for which departure from patches depended on resource availability and/or competition performed almost equally well and better than residency or uninformed movement under most conditions, even though animals using each rule moved at substantially different rates. Habitat modifications that stabilized resources, either by resource supplementation or degradation, eroded the benefits of informed nomadic movements, particularly for movements based on resource availability alone.
4. These results suggest that simple movement rules can explain nomadic animal movements and determine species' responses to environmental change. In particular, landscape stabilization and supplementation might be useful strategies for promoting populations of resident animals, but would be less beneficial for

managing highly mobile species, many of which are threatened by habitat disruption and changes in climate.

INTRODUCTION

Long-distance animal movements influence population dynamics and species interactions, and can transport energy and nutrients between distant sites [7,109]. Resource distributions are a key driver of animal movement patterns, with animals moving to track abundant resources and avoid resource-scarce environments. Seasonally migratory species often make repeated, round-trip journeys to track changes in resources over predictable, annual cycles [5,158,204]. In other environments, different movement patterns can emerge, such as range residency (including territoriality) and nomadism [30,205]; these patterns depend on the underlying landscape, resource variability, and species' movement and navigation capacities [95,206,207].

Nomadism, characterized by irregular movements in both time and space, occurs in landscapes that vary unpredictably on large spatial scales [4,22,208]. Nomadic species are geographically widespread and taxonomically diverse, and include species such as banded stilts (*Cladorhynchus leucocephalus*), which move between saltwater ponds in Australia [82], and Thompson's gazelle (*Eudorcas thomsonii*) in the Serengeti, whose movements track grass availability [122]. Although nomadic movements can appear to be random or complex [48,209], simple environmental and social conditions probably cue departure events and movement patterns (e.g., [28,209]). Nomadism can be characterized by search behavior (i.e., exploration of unfamiliar sites), navigation (i.e., movement to a known destination), and revisitation of previously-occupied patches [208]. Because many nomadic species are declining [39], identifying mechanisms that underlie nomadic animal movements, and their responses to environmental change, are needed to better predict and conserve this widespread movement behavior.

Models of animal movements in response to resources (i.e., foraging theory) have historically assumed that animals have complete information about their environments (e.g., the ideal free distribution: Charnov, 1976; Fretwell & Lucas, 1969; McNamara, 1982) [101]. This assumption is often unrealistic, so more recent models of foraging and migration have incorporated memory and perception to understand more realistic movement patterns (e.g., [40,101,213–215]). For nomadic species inhabiting unpredictable environments, however, memory might not help in navigating to profitable patches [54]. Furthermore, resource patches can be far apart in nomadic systems [28], which means that nomads' movements can depend more strongly on decisions to depart a patch [216] than on using perception to move up a continuous resource gradient [101]. As a result, predicting nomadic movements requires understanding the cues that animals use when deciding when to leave their current patch.

Humans are currently altering resource dynamics across the globe [217]. Many anthropogenic habitat modifications decrease resource variability [218], either by providing supplemental resources for wildlife, or by degrading habitats leading to the loss of resources [219]. Such habitat modifications can have dramatic effects on animal population sizes and movement patterns [220–222]. Some species that are highly mobile in their natural habitats have recently adopted resident behaviors in urban, suburban, and agricultural areas that offer consistent year-round access to resources (e.g., at bird feeders, garbage dumps, and gardens). Examples include decreased migration propensity and smaller foraging ranges in Spanish white storks using landfills and establishment of resident populations of nomadic grey-headed flying foxes in urban areas in Australia [223–225]. However, these studies have largely focused on changes in resource quantity, rather than changes in variability [226]; because nomadic movements tend to occur in environments that are highly variable in both space and time [208], decreased spatiotemporal variability in resource availability due to human development could reduce the benefits of this unique movement behavior.

Here, we propose simple departure rules for nomadic animal movements, explore the dynamical outcomes of these departure rules in variable landscapes, and investigate how departure rules determine nomadic animals' responses to habitat modification. We develop a network model of nomadic animal movements across discrete patches that vary in resource availability over space and time. To identify movement mechanisms that best promote survival, we compare the population sizes of nomadic animals using departure rules based on resource availability and/or conspecific density to randomly-moving nomadic animals. We also explore different movement propensities within each of these rules, based on the observation that movement types exist along a spectrum of movement frequency [208]. When movement propensities are extremely low, animals become range residents, which we analyze as another movement rule. Because nomadic animals tend to live in unpredictable environments with high variability [22,30], we predict that nomadic departure rules will perform better than residency in variable environments. Given that human habitat modifications can decrease resource variability, we also explore the effects of resource supplementation, stabilization, and degradation on populations of animals moving according to different rules. This experiment can help predict how nomadic species’ abundances and movement patterns will respond to human-mediated landscape change, and whether conservation strategies established for range residents can also benefit nomadic species.

MATERIALS AND METHODS

Model development

We model animal movement on a network of interconnected patches similar to a migratory network, which consists of nodes of habitat patches connected by edges that represent migration routes [227]. Unlike a migratory network, our nomadic network is fully connected, similar to a classic metapopulation model [228,229]. In other words, movement can occur between any pair of patches, consistent with the multidirectional movements of nomadic animals [46,208]. Because of the long-distance nature of nomadic movements, we assume that patches in the nomadic network are large and far apart. We explicitly model only long-distance interpatch movements; shorter-distance movements are implicitly possible but occur within patches. Movement between patches depends on departure rules (described below), and departing animals redistribute equally to all other habitat patches. We thus model navigation as an asocial process, which is consistent with expectations for nomadic movements in environments where multiple patches can be resource-rich simultaneously [4]. We consider movements over the nomad’s nonbreeding season, so that survival depends on current resource availability at the patch and movement costs during inter-patch movements, and no reproduction occurs.

Landscape structure

Resource availability varies across both space and time in P patches. Resource availability in patch i and time t, $A_i(t)$, is a quantity scaled between 0 (no resources) and 1 (maximum resource availability). There is no spatial autocorrelation in resource availability, based on the observation that there is little autocorrelation in the environments usually inhabited by nomadic animals [22] and our assumption that patches are far apart. Landscape-level variability (V) controls the minimum and maximum values of resource availability at all patches in the landscape, where higher values of V correspond to more variable landscapes (Figure 4.1A, B). At each patch, resource availability is drawn from the uniform distribution $U\left(\frac{1-V}{2}, \frac{1+V}{2}\right)$. We also simulate landscapes with different levels of temporal stability, where resources remain stable for E timesteps (Figure 4.1C, D). Changing resource variability (V) does not affect temporal autocorrelation; changing E affects temporal autocorrelation but not spatial variance or mean resource availability (Appendix B Figure S4.1). Each simulation consists of 52 timesteps, designed to represent weeks in a year. We simulate 100 landscapes of for each of five values of V between 0.2 and 1, two values of E (1 and 3), and three values of P (3, 10, and 15).

Animal movement

We investigate departure rules based on current or past conditions at the occupied patch, and assume that departing animals distribute equally to all other patches. Though some nomadic animals move to known destinations (e.g., [209]), assuming that destinations are random is realistic for animals that use non-oriented movement or where patches are far enough apart that sensory mechanisms cannot inform a destination [4]. Using a fully-connected network allows us to investigate the importance of the departure mechanism alone for nomadic populations, independent of the roles of spatial structure or destination mechanisms.

We consider three fundamental informed nomadic departure rules (Figure 4.2; Appendix B Table S4.1): a resource-based rule, a density-based rule, and a competition-based rule. In the resource-based rule, animals only depart a patch if the current resource availability $A_i(t)$ falls below a threshold, W (see McNamara, 1982) (Figure 4.2A). Below this threshold, the number of animals departing patch i, $M_i(t)$, is a linear function of the resource availability at that patch, with all animals departing if resource availability drops to zero, i.e.

if $A_i(t) < W$:

$$M_i(t) = N_i(t)\frac{W - A_i(t)}{W}$$

if $A_i(t) \geq W$: $M_i(t) = 0$

where $N_i(t)$ is the number of individuals at patch i at time t.

We also explore a variant of this rule that incorporates short-term memory over a single time step to explore whether memory could be useful for nomadic movements. In this case, departure is cued by predicted resource availability in the next timestep, based on a linear extrapolation from the previous and current timesteps (Figure 4.2D):

$$A_{forecast}(t) = A_i(t) + (A_i(t) - A_i(t-1))$$

if $A_{forecast}(t) < W$:

$$M_i(t) = N_i(t)\frac{W - A_{forecast}(t)}{W}$$

if $A_{forecast}(t) \geq W$: $M_i(t) = 0$

We also consider a rule where departure is based on conspecific density, in which animals depart when density exceeds a threshold T (Figure 4.2B):

if $N_i(t) > T$:

$$M_i(t) = N_i(t) - T$$

if $N_i(t) \leq T$: $M_i(t) = 0$

We explore a separate informed departure rule based on competition (a combination of resources and conspecific density), following concepts of density-dependent movement and the ideal free distribution [210,230]. In this case, departure depends on the difference between the number of individuals at a patch and that patch's carrying capacity, $\alpha A_i(t)$ (Figure 4.2C); in essence, this rule assumes that individuals can sense patch carrying capacity, either directly or if competition reduces patch suitability by reducing intake rates [210,231]. The parameter α represents the number of individuals supported by one unit of resource availability:

if $N_i(t) > \alpha A_i(t)$:

$$M_i(t) = N_i(t) - \alpha A_i(t)$$

if $N_i(t) \leq \alpha A_i(t)$: $M_i(t) = 0$

We also consider the equivalent departure rule that incorporates memory (Figure 4.2E).

We compared the performance of informed movement rules to null rules, where movement is unrelated to environmental cues. The first is uninformed (random) nomadic movement, in which a fixed proportion of animals ($0 \leq p \leq 1$) moves in each timestep (Figure 4.2F), independent of resources:

$$M_i(t) = pN_i(t).$$

The second is residency, where no movement occurs (Figure 4.2G). Residency can occur as an extreme case of the uninformed rule, when p=0, or an extreme case of the resource rule, where W=0. It can also be formulated simply as $M_i(t) = 0$.

Demographics

Each simulation begins with each patch at its carrying capacity, $N_i(0) = \alpha A_i(0)$. Mortality occurs twice during each timestep: during movement and at a patch. During movement, the number of animals departing patch *i* that survive movement is $(1 - c)M_i(t)$, where c is the cost of movement ($0 \leq c \leq 1$), assumed to be equal between any two patches (Table 4.1). The number of individuals at patch *i* following departure and immigration is therefore

$$L_i(t) = N_i(t) - M_i(t) + \frac{1-c}{P-1} \sum_{j \neq i} M_j(t)$$

where P is the total number of patches.

Mortality at the destination patch can occur after movement. Site mortality has both density-independent and density-dependent components based on resource availability and conspecific density. The parameters μ_0 and μ_1 control the per capita density-independent and density-dependent components respectively, where higher values of μ indicate higher mortality ($0 \leq \mu \leq 1$). Density-independent mortality is a linear function of resource availability (Appendix B Figure S4.2), such that survival is 100% in patches where $A_i(t) = 1$ and μ_0 in patches where $A_i(t) = 0$. Density-dependent mortality only occurs when the number of animals exceeds carrying capacity (Appendix B Figure S4.2).

If $L_i(t) > \mathrm{a}A_i(t)$:

$$N_i(t+1) = L_i(t) - \mu_0 L_i(t)\big(1 - A_i(t)\big) - \mu_1\left(L_i(t) - \alpha A_i(t)\right)$$

otherwise:

$$N_i(t+1) = L_i(t) - \mu_0 L_i(t)\big(1 - A_i(t)\big),$$

where $L_i(t)$ is the number of individuals at patch *i* after movement and α is as described above.

Parameters and outputs

We used parameters that represent realistic movement and mortality rates for a long-lived vertebrate species (Table 4.1), and assume that animals update their movement decisions on a weekly basis (e.g., as has been modeled previously in ungulates [204,232] and steelhead [233]). The mortality rates selected correspond to ~50% annual survival in the lowest-quality habitat and 100% survival in the highest-quality habitat at or below carrying capacity, based on studies of ungulates during harsh conditions (Appendix B) [234–237].

We examined two variables at the end of the simulation as a metric of the performance of each rule in a given landscape: (1) population size at the end of the simulation and (2) annual survival; this second variable standardizes population sizes to account for differences in initial population size across landscapes simulated with the same parameters. We examined the sensitivity of these outputs to our different parameter sets. We also calculated these output metrics halfway through the simulation period to test whether results were sensitive to the duration of the nonbreeding season. When comparing between rules, we used the threshold resource level (*W*) or density value (*T*) that produced the largest population size for each combination of other parameters (Appendix B).

Resource supplementation, stabilization and degradation

We modeled anthropogenic habitat modification by changing the per-patch resource availability to a constant value, rather than one that changes over time. We explored three potential scenarios of habitat modification relative to average resource availability of 0.5 in the unmodified landscape: resource supplementation (resource availability at modified patches = 0.7), stabilization with no change in the mean (modified patches = 0.5), and resource degradation (modified patches = 0.3) (Appendix B Figure S4.3). For each value, we considered the effect of 0-100% of the patches in the network being modified. At its extreme, this modification produces stable resource availability at all patches and time points (i.e., V=0). Because portions of our model become analytically tractable under this condition, we solved equations for the quantity $\frac{L_i(t)}{N_i(t)}$ for each movement rule, which can be interpreted as the realized cost of movement (Appendix B). Based on these solutions, we expected that resource supplementation would favor informed movement over uninformed movement and residency, but that informed movement would no longer provide any benefit or would even be detrimental in degraded landscapes.

All simulations for habitat modification were based on a single parameterization of the nomadic network model for both landscape and movement parameters (Table 4.1, baseline value column). These parameters represent a highly variable landscape (i.e., one likely to be inhabited by nomads), a low cost of movement, and moderate density dependence. We used the same process as above to simulate movement and population dynamics, and the parameters in each departure rule (e.g., *W*) remained unchanged regardless of the number of modified patches.

All simulations and analyses were implemented in R Version 3.5.1 [179].

RESULTS

Performance of departure rules in variable environments

Animals using informed nomadic departure rules (resource-based and competition-based) performed better than residents, animals using a density-only rule, or uninformed nomadic animals in variable environments (Figure 4.3A, Appendix B Figure S4.4). Population sizes and survival rates almost always declined with increasing landscape variability; however, this decline was less dramatic for nomadic than resident animals (Figure 4.3A, Appendix B Figure S4.5). Specifically, population sizes of residents were 21% smaller in highly variable landscapes as compared to less variable landscapes. In comparison, this decrease in population size was 18% for animals using the density-only rule, 17% for animals using uninformed movement, 14% for animals using resource-based movement, and 12% for animals using competition-based movement. When density-independent mortality rates were high, population sizes of animals using resource- and competition-based movement rules were unaffected or even increased with increasing landscape variability, but residents or populations using uninformed movement declined (Appendix B Figure S4.6). Higher landscape variability generally favored higher movement propensities for animals using resource-based and uninformed movement (Appendix B Figure S4.7, Appendix B Figure S4.8). For example, the optimal value of the departure threshold W was 0.01 (the lowest value tested) when V=0.2 and W=0.5 when V=1 (Table 4.1, Appendix B Figure S4.7).

The relative performance of the different movement rules was qualitatively insensitive to the duration of the simulation (Appendix B Figure S4.10), the number of patches in the system, or mortality rates.

Departure rules that incorporated short-term memory generally performed slightly worse than simpler rules that did not incorporate memory when there was no temporal autocorrelation in the landscape, but performed slightly better in landscapes with some temporal autocorrelation (Appendix B Figure S4.11). However, the benefits of memory were small relative to the benefits of informed movement over residency. For example, movement rules based on competition conferred a 20% benefit to population size relative to residency, but memory conferred only an 2% additional benefit relative to competition alone (when V=1 and E=3).

Higher costs of movement negatively affected all mobile animals, with the strongest negative effect on animals moving according to resource-based rules. For animals using resource-based movement, those with higher movement propensities (i.e., a higher movement threshold, W) performed better only when movement costs were low, density-dependent mortality was strong, and landscape variability was high (Appendix B Figure S4.7, Appendix B Figure S4.12). When the cost of movement between patches was low, resource-based and competition-based departure rules performed similarly in variable environments (Figure 4.3A, B). However, as the cost of movement increased, residency began to outperform informed movement rules (Figure 4.3B; Appendix B Figure S4.12), owing to higher movement rates for animals using the informed departure rules (Figure 4.3C). The relative performance of the competition-based and resource-based rules also depended on density-dependent and density-independent mortality rates; when density-independent mortality rates were high, resource-based movement performed better, and when density-dependent mortality rates were high, competition-based movement performed better (Appendix B Figure S4.6).

Habitat modification

All three types of habitat modification reduced or eliminated the benefits of informed movement strategies (Figure 4.4). Resource supplementation increased survival rates for all departure rules (Figure 4.4A), with the largest increase for residents. Rules that incorporated memory performed no better than those that did not, and even performed worse when the proportion of modified habitat was low (Appendix B Figure S4.13).

Similarly, habitat modification that stabilized resources (without changing the landscape-level mean) increased survival rates, with the strongest positive effects for residents (Figure 4.4B). However, for animals using competition-based movement, these benefits appeared only when at least 30% of habitat was stabilized, whereas residents and animals using uninformed movement benefitted from any level of modification (Figure 4.4B). Survival rates of animals using resource-based movement declined steeply when the proportion of patches modified was low, possibly because the movement threshold *W* was 0.5, equal to resource availability in the stabilized patches, meaning that animals never departed these patches even when densities were high.

When resources were degraded, residents and animals using uninformed movement still benefitted from increased stability (Figure 4.4C). In contrast, population sizes of animals using resource-based movement declined, and those of animals using competition-based movement remained unchanged or declined slightly, as we expected from our analytical solutions (Appendix B). For all types and levels of modification, the competition-based rule performed at least as well as any other rule, even though its benefit (especially relative to residency) declined to zero with increasing modification. Though resource-based movement performed well in highly variable environments, it was the worst-performing rule when a large proportion of habitat was degraded.

Differences in the performance of each departure rule under habitat degradation resulted partially from differences in movement rates of animals using each rule. For the competition-based rule, movement rates decreased with increasing resource stability, and movement eventually ceased in 100% modified landscapes (Appendix B Figure S4.14). In contrast, animals using the resource-based rule increased their movement rates in degraded landscapes, even at high levels of modification.

DISCUSSION

Our network-based model showed that simple informed nomadic rules (for which departure was based on resources and/or competition cues) outperformed both residency and uninformed movement in variable environments. Animals using resource-based movement usually moved more than animals using competition-based movement, and the relative performance of competition-based and resource-based movement strategies depended on the mortality costs of movement, resource availability, and competition. Not surprisingly, the benefits of informed movement rules declined in more stable environments, and movement responses to human-altered resources depended on a population's movement strategy. Residents derived the greatest benefit from habitat modification that stabilized resources. In contrast, populations using resource-based rules declined the most under resource degradation. This result suggests that animals using resources as departure cues could be particularly vulnerable to declines under habitat degradation, as a result of moving more than is optimal in homogenized landscapes.

Mechanisms of nomadic movement in highly variable landscapes

Our model results confirmed the adaptive value of nomadic movements in variable and unpredictable environments [22]. More variable landscapes also favored higher movement propensities for resource-based movement, further supporting that, along a spectrum from residency to nomadism, increasing landscape variability favors more nomadic movements. In contrast, uninformed movement and density-only movement rules performed poorly in all environments, suggesting that nomadism is unlikely to be random wandering or purely social, but rather must be based on environmental cues [209]. That both resource-based and competition-based departure rules performed well also suggests that both are plausible mechanisms for nomadic movement; the existence of multiple mechanisms is consistent with observations of nomadic animals (Appendix B Table S4.1). For instance, resource-based movements have been observed in loggerhead turtles, [127], grey-headed flying foxes [238], and some desert birds [68]. Competition-based movements are well described in locusts [239] and birds [68] as well as in planthoppers, where the highly mobile state is more common in animals living in more variable habitats and at high densities [240]. Our modeling results confirm that both of these mechanisms could be adaptive in variable landscapes.

Incorporating memory into movement decisions improved performance only in landscapes with some temporal autocorrelation. In other words, while informed nomadic movement outperforms uninformed movement, the identity of this information is also important [241,242]. In environments with no spatial or temporal autocorrelation, memory is unlikely to be useful because the past is a poor predictor of the future [4]. In environments with low or moderate autocorrelation, memory could become useful for making navigation decisions, but the scale of memory must match the scale of autocorrelation [206]. For example, autocorrelation could occur because the mechanisms driving resource dynamics create temporal autocorrelation (e.g., vegetation green-up or drying) or from spatial patterns in abiotic drivers such as rainfall, each of which can occur at a different spatiotemporal scale in different environments. Future studies could investigate the interactions between the type and scale of autocorrelation and the types of memory that are beneficial for making nomadic movement decisions [243].

Lower movement costs favored higher movement propensities (i.e., more nomadic behavior) in animals using resource-based movement (see also [212]). This result suggests that resource-based nomadic movements might be less likely to occur in species or landscapes where movement is costly. Because the energetic cost of locomotion is lowest for animals that swim [244], resource-based movements could be more common in swimming than in walking or flying animals (particularly walking animals: [245]). Among non-aquatic species, turtles, flying foxes, and birds all use relatively low-cost locomotion strategies and have been hypothesized to follow resource-based rules (see above), whereas walking ungulates have been hypothesized to move based on conspecific density [246]. Similarly, resource-based movement performed better when density-dependent mortality was lower than density-independent mortality, suggesting that these mechanisms could be more common in systems where intraspecific competition is weak. For example, if food availability is controlled by environmental stochasticity, not by depletion by consumers [78,247], or the nomadic species is a less successful competitor than local heterospecifics [248], density-independent mortality could dominate.

Effects of resource supplementation, stabilization, and removal on nomadic animals

Humans are modifying resources for countless mobile species. In many cases, these changes stabilize resources, whether through subsidy or degradation, by making habitat patches more uniform over time [218,226]. When we examined the effects of habitat modification on nomadic animals, we found that competition-based movement was more resilient than resource-based movement and that residents benefitted most from habitat modification. Animals using competition-based movement were resilient because they moved less as more patches became degraded, eventually becoming resident at high levels of modification. In contrast, animals using resource-based and uninformed rules continued moving as habitat degradation continued, thus incurring a cost even when movement was no longer beneficial. It is important to note that such movements could have benefits we do not consider here, such as identification of new, suitable patches [56], or maintaining genetic connectivity [249]. Our modeling results suggest that departure rules that incorporate information on both resources and density perform slightly better both in variable environments and under environmental change, compared to departure rules that are based on resources alone.

Consistent with these modeling results, empirical studies show that movement rates can change following habitat modification. Food supplementation can reduce movements, for example in spiders [250], goshawks [251], and even humans in hunter-gatherer societies [252]. In nomadic white ibis (*Eudocimus albus*) inhabiting urban areas, a higher proportion of provisioned food is associated with higher site fidelity (Maureen Murray, pers. comm), and nomadic grey-headed flying foxes have established permanent camps in urban areas, where food is more stable [224,253]. At the same time, some species may continue moving even in altered landscapes where movement is no longer as adaptive. Increases in winter temperatures are predicted to promote residency in partially migratory populations, but the proportion of blue tits migrating has remained steady as temperatures have increased, probably because they respond to non-temperature cues [254]. Our results highlight the importance of considering not just changes in mean resource availability, but also changes in resource dynamics, when studying how habitat modifications impact animal populations.

Different movement modes are likely to respond differently to various forms of landscape change (e.g., fragmentation vs. loss, Fahrig 2007). Although we lack empirical evidence that discriminates the effects of habitat modification on animals moving according to different rules, our model showed that each departure rule responded differently to landscape stabilization. In addition, even without a change in the departure rule in our model, movement rates changed alongside habitat modification; this behavioral adaptation suggests that management that preserves or restores dynamic landscapes could also restore natural movement patterns quickly, even in the absence of natural selection.

Implications and future directions

Modeling is a powerful way to explore multiple scenarios in cases where field studies may be too time- or extent-limited to draw useful conclusions. Here, we build the first mechanistic model of departure rules underlying nomadic movements in variable and modified landscapes; we show that the responses of nomadic animals to habitat modification are linked to their movement mechanisms, and that residents benefit more from habitat modification than do mobile animals. These results and this modeling framework provide an opportunity for future investigations of nomadic species in changing landscapes. For instance, future models could explore whether more complex movement mechanisms (e.g., destination rules or exploratory movements, Bennetts & Kitchens, 2000) allow nomadic animals to better respond to environmental change, particularly in regions where climate models predict increased environmental variability [255]. In addition, if mortality rates increase with habitat modification (e.g., due to movement costs of roads and other barriers [256] or novel species interactions [257]), then mobile animals might suffer, even under landscape changes that increase resource availability. A spatially-explicit version of this model could help elucidate whether variation in movement costs across the landscape affects the benefits of nomadic movements and populations' responses to interacting environmental changes.

Future empirical studies should focus on evidence for differential effects of habitat modification on species using different movement strategies. These studies could come in the form of comparative analyses of the relative abundance of more and less mobile species living in the same areas ("species pairs"), as has been done for regionally co-occurring migratory and resident species [158]. Alternatively, investigating intraspecific variation in movement strategies would reveal whether population abundances and growth rates are related to their movement strategy and/or characteristics of the landscapes in which they live. Future models could incorporate additional aspects of landscape change (e.g., climate extremes) and social behavior, since some nomadic species move in groups rather than making independent movement decisions [208]. In addition, our simple model considers only a single species, but in reality, animals exist in communities. Future studies should explore how nomadic movements affect species interactions (e.g., with competitors or parasites) and how changes in movement patterns could alter these interactions.

We saw that the effect of habitat modification differed depending on both the type of modification (e.g., resource degradation vs. supplementation) and a population's movement strategy, where residents benefitted most from these changes. In migratory species, phenological mismatches can cause population declines when migrants do not track environmental change [95]. These declines may be less dramatic in nomads because their movement patterns are more flexible. In this model, animals using a competition-based rule adapted to modified landscapes by changing their movement patterns (i.e., decreasing their movement rates). Though this reduction in movement increased their performance in modified landscapes, it could also reduce the ecosystem-level benefits of nomadism (e.g., seed dispersal in fragmented landscapes or trophic effects: Bauer & Hoye, 2014; Mueller, Lenz, Caprano, Fiedler, & Böhning-Gaese, 2014; Teitelbaum & Mueller, 2019). Thus, management goals for mobile animals should consider not only population sizes, but also maintaining historical movement patterns.

Our study provides insight into movement mechanisms that promote the survival of nomadic species in highly variable landscapes. There are probably multiple mechanisms operating simultaneously, each of which will respond differently to habitat modification. We urge researchers and managers to consider the cues for movement when considering study design and conservation actions, since these behavioral mechanisms ultimately mediate the responses of species to their environments.

ACKNOWLEDGEMENTS

We thank T. Mueller, R.M. Holdo, V.O. Ezenwa, J. Hepinstall-Cymerman, and the Hall and Altizer laboratory groups at UGA for helpful discussion. We thank M.V. Evans, R.S. Smith, and C.A. Sanchez for comments on an earlier version of the manuscript and K. Sabey for assistance with the graphical abstract. This research was supported by a UGA Presidential Fellowship and an NSF Graduate Research Fellowship to CST and NSF grants DEB-1518611 and DEB-1754392 to SA and RJH.

AUTHOR CONTRIBUTIONS

CST conceived the study. All authors participated in designing project goals. CST and RJH developed the model and derived analytical solutions. CST implemented simulations and designed figures and tables. CST wrote the first draft of the manuscript and all authors contributed to subsequent revisions.

DATA AVAILABILITY

Data are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.dbrv15dzg.

Table 4.1: Parameters used in the network model. We performed sensitivity analyses over a range of values for each parameter (“Range”). For habitat modification experiments, we used a single parameter set (“Baseline value”) representing a variable environment (V=1) with no temporal stability (E=1). For the resource and density rules, we selected the threshold (W=0.5 and T=0.5) that produced the largest population size for the parameterization in the “Baseline value” column (Appendix B). Density-dependent and density-independent mortality are present and of moderate strength (μ_1=0.5, μ_0=0.0132) and there is a low cost of movement (c=0.01).

Parameter	**Description**	**Range**	**Baseline value**
Landscape parameters			
V	Controls minimum and maximum value of resource availability	0.2-1	1
E	Number of timesteps where resource availability remains constant	1, 3	1
P	Number of patches	3, 10, 15	10
Movement parameters			
W	Resource threshold (value of resource availability below which movement starts to occur)	0.1-1	0.5
T	Density threshold (population size above which movement occurs)	0.1-1	0.5
p	Movement rate for uninformed movement (individuals/timestep)	0.3	0.05
Species parameters			
μ_1	Strength of density-dependent mortality	0.0433, 0.0229, 0.0132	0.0229
μ_0	Strength of density-independent mortality; weekly *per capita* mortality rate when *A*=0	0.0433, 0.0229, 0.0132	0.0229
c	Cost of movement; proportion dying during one movement event	0-0.05	0.01
α	Scaling parameter; number of individuals supported by one unit of resources at carrying capacity	1	1

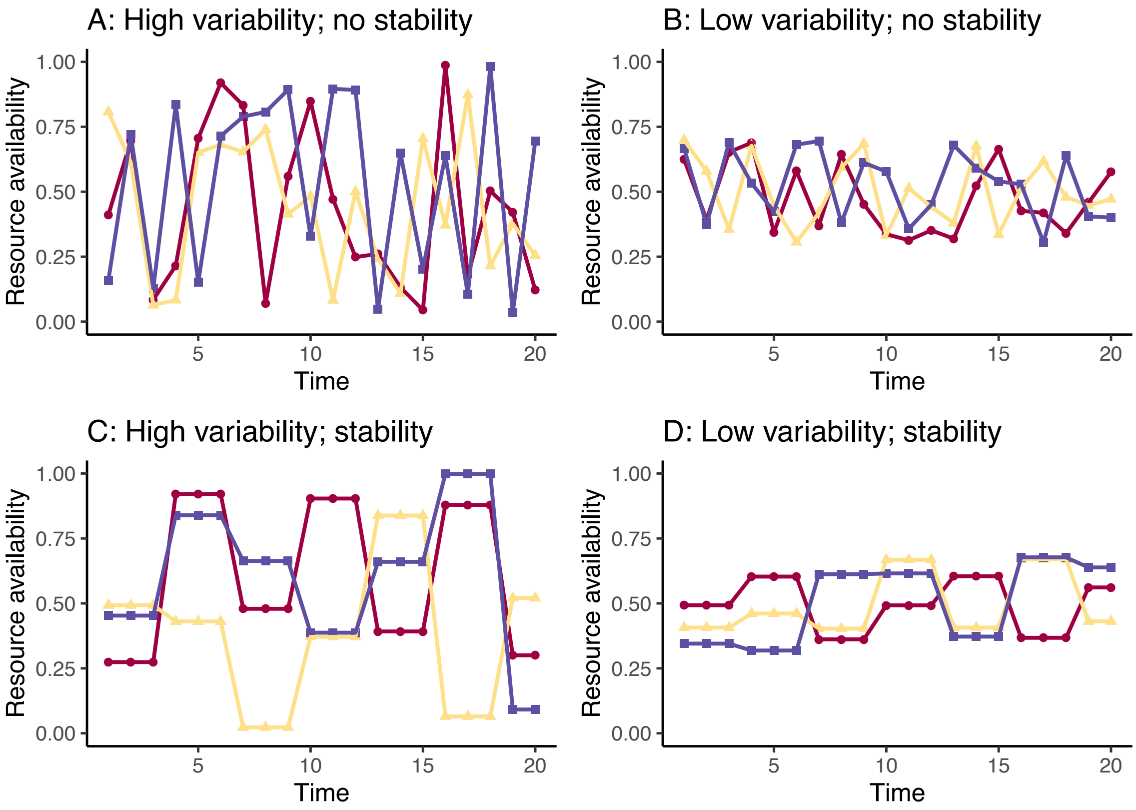


Figure 4.1: Examples of landscapes that differ in their variability (V) and temporal stability (E). Lines of different colors and points of different shapes represent individual patches; only three patches are shown for visualization purposes, but the full network contained up to 15 patches. (A, C) Highly variable environments (V=1). (B, D) Less variable environments (V=0.4). (A, B) No temporal stability (E=1). (C, D) Some temporal stability (E=3). 20 timesteps are shown for visualization only; full simulations were 52 timesteps.

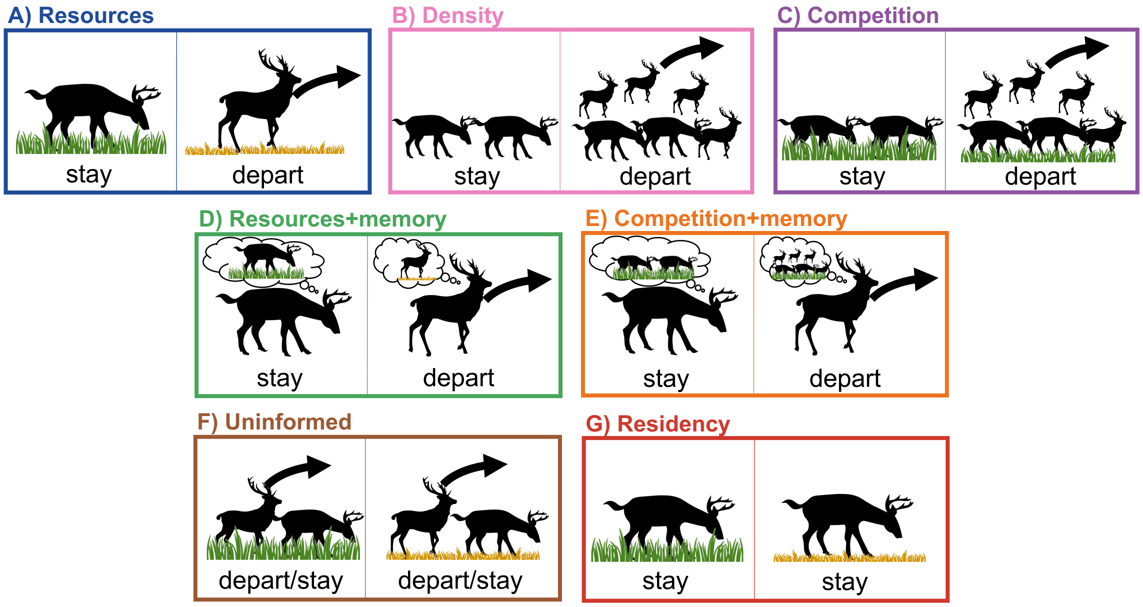


Figure 4.2: Conceptual illustration of departure rules used in this study. (A) Resources: animals move when current resource availability falls below a threshold. (B) Density: animals move when current density exceeds a threshold. (C) Competition: animals move when conspecific density exceeds carrying capacity. (D) Resources+memory: animals leave when resource availability is expected to drop below a threshold in the next time step, based on the previous and current time steps. The image in the bubble represents an individual's forecast of future conditions. (E) Competition+memory: animals leave when conspecific density is expected to exceed carrying capacity, based on the previous and current time steps. (F) Uninformed: movement occurs at a constant rate, irrespective of conditions at a patch. (G) Residency: no movement between patches. Residency is an extreme case of uninformed or resource rules. Movement rules are further summarized in Appendix B Table S4.1, along with examples of systems in which they occur.

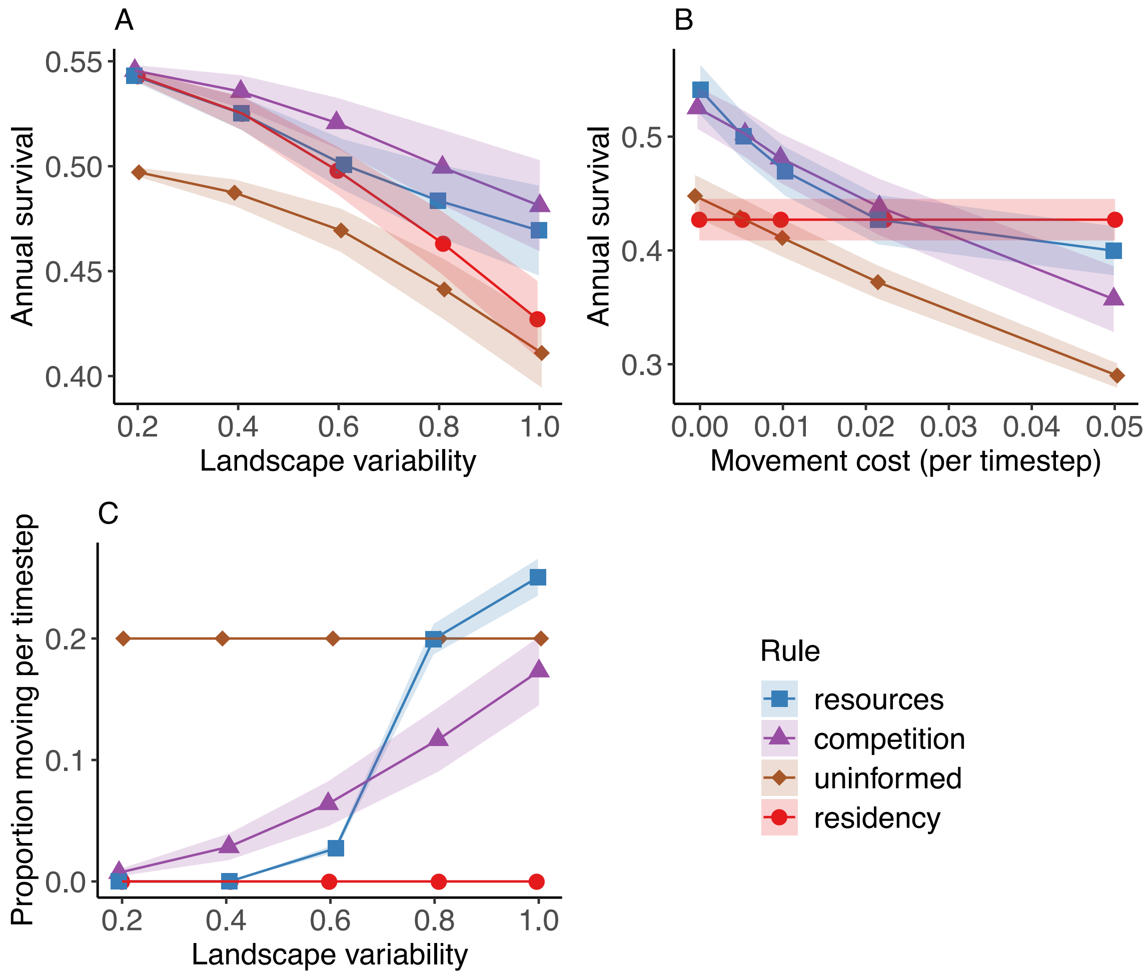


Figure 4.3: Effects of departure rules on survival in variable environments. Shaded areas show the standard deviation across 100 simulations. Points are jittered along the x-axis for visualization only. (A) Survival rates for each departure rule at the end of the simulation (one nonbreeding season). Population sizes are standardized to account for differences in initial population size across simulated landscapes; see Appendix B Figure S4.5 for other metrics of performance. At this low movement cost (0.01; Table 4.1), informed nomadic departure rules perform better than residency except in low-variability environments and uninformed movement always performs worst. (B) As the cost of movement increases, the benefits of informed movement disappear. Results are from a

highly variable environment with no autocorrelation (V=1, E=1). (C) This difference in performance between competition-based and resource-based departure in the most variable environments stems from higher movement rates of animals moving based on resources only.

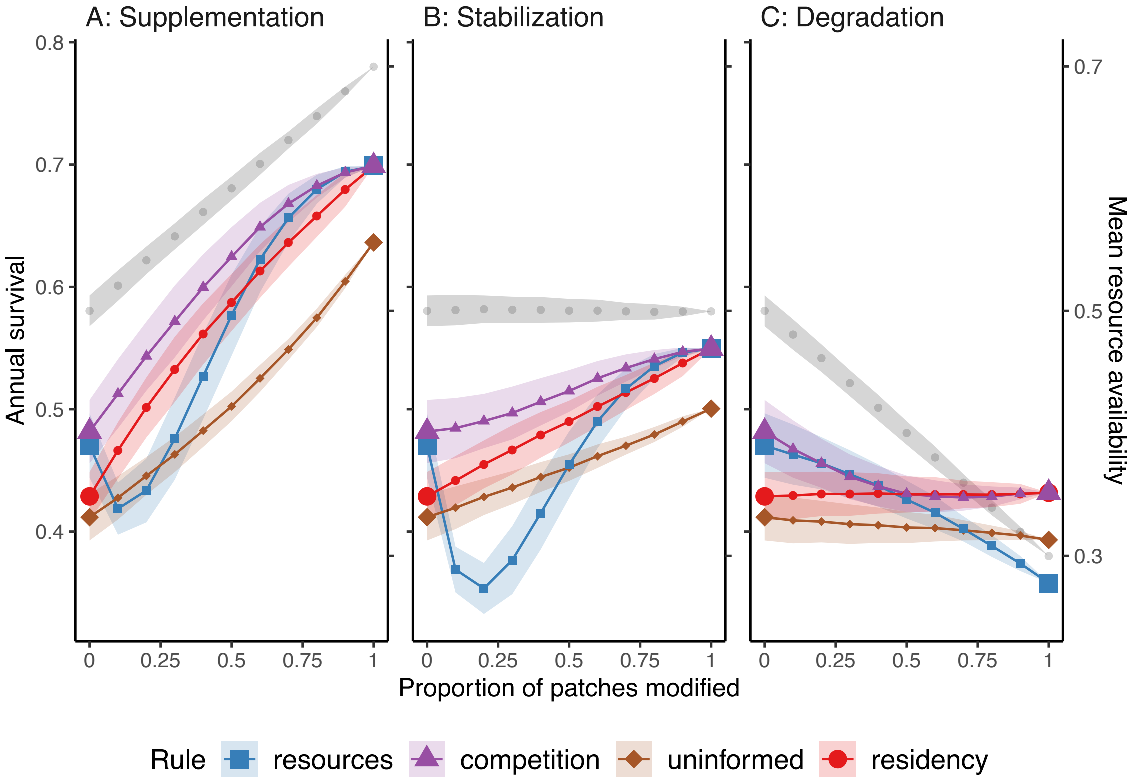


Figure 4.4: Effects of habitat modification on the survival of populations using different departure rules. Panels show different values of modified patches (A: 0.7; B: 0.5; C: 0.3), corresponding to a 40% increase, no change, or a 40% decrease in mean resource availability at modified patches. All simulations use the same parameter set (Table 4.1) that corresponds to the set of points at V=1 in Figure 4.3A. Gray points and shaded areas show the mean resource availability and standard deviation across the landscape (right-hand axis). (A) Increasing mean resource availability and stability benefits all

populations, except at low rates of modification for animals using the resource-based rule. (B) When modification does not change mean resource availability, stability has positive effects when modification is widespread, but for informed nomadic departure rules stabilization is initially negative or neutral. (C) Decreasing mean resource availability but increasing stability has small effects on populations of residents and animals moving with uninformed movement, but is negative for populations using informed departure rules.

CHAPTER 5

URBAN SPECIALIZATION REDUCES HABITAT CONNECTIVITY BY A HIGHLY MOBILE WADING BIRD[4]

---

[4] Teitelbaum CS, Hepinstall-Cymerman J, Kidd-Weaver A, Hernandez SM, Altizer S, Hall RJ. Habitat specialization reduces connectivity by a highly mobile waterbird. Mov Ecol. 2020. https://movementecologyjournal.biomedcentral.com/articles/10.1186/s40462-020-00233-7. Reprinted here under Creative Commons Attribution License 4.0.

ABSTRACT

Background: Mobile animals transport nutrients and propagules across habitats, and are crucial for the functioning of food webs and for ecosystem services. Human activities such as urbanization can alter animal movement behavior, including site fidelity and resource use. Because many urban areas are adjacent to natural sites, mobile animals might connect natural and urban habitats. More generally, understanding animal movement patterns in urban areas can help predict how urban expansion will affect the roles of highly mobile animals in ecological processes.

Methods: Here, we examined movements by a seasonally nomadic wading bird, the American white ibis (*Eudocimus albus*), in South Florida, USA. White ibis are colonial wading birds that forage on aquatic prey; in recent years, some ibis have shifted their behavior to forage in urban parks, where they are fed by people. We used a spatial network approach to investigate how individual movement patterns influence connectivity between urban and non-urban sites. We built a network of habitat connectivity using GPS tracking data from ibis during their non-breeding season and compared this network to simulated networks that assumed individuals moved indiscriminately with respect to habitat type.

Results: We found that the observed network was less connected than the simulated networks, that urban-urban and natural-natural connections were strong, and that individuals using urban sites had the least-variable habitat use. Importantly, the few ibis that used both urban and natural habitats contributed the most to connectivity.

Conclusions: Habitat specialization in urban-acclimated wildlife could reduce the exchange of propagules and nutrients between urban and natural areas, which has

consequences both for beneficial effects of connectivity such as gene flow and for detrimental effects such as the spread of contaminants or pathogens.

BACKGROUND

Habitat connectivity, defined as the movement of organisms and materials among patches on landscapes [258], is important for ecological processes and their outcomes, including population viability, genetic structure, infection dynamics, and ecosystem services [225,259–263]. By definition, animal movements are a key component of habitat connectivity [9,41]. Animal movements across ecosystem boundaries can facilitate the transfer of nutrients, seeds, and beneficial microbes between environments that differ in their productivity or community composition [41,264]. For example, seabirds that move from pelagic to coastal systems in the Pacific Ocean transport nutrients and increase soil nitrogen levels on islands, with further downstream effects that increase nutrient loads in runoff, zooplankton biomass, and manta ray abundance [265]. This functional connectivity of heterogeneous landscapes depends on animals' movement abilities, distances between patches, patch sizes, resistance or barriers to movement, and other landscape properties [266].

Human activities can alter both the physical properties of landscapes and animal behavior, producing changes in functional connectivity [266]. In the Pacific, seabirds tend to avoid coastlines dominated by human-associated coconut palms, making these areas less connected to pelagic systems and resulting in lower abundances of zooplankton and manta rays [265]. Urbanization is another human activity that alters animal movement by fragmenting landscapes, and also by providing novel resources for species that can adapt or acclimate to urban environments [267]. Although some animals can move easily in urban landscapes, urbanization generally reduces connectivity by increasing the distance between patches and introducing barriers to movement [266,268]. Species that are habitat generalists and have high movement capacity might be less limited by barriers or fragmentation than habitat specialists [269,270], but even species that are highly mobile in natural environments often move less in urban areas (e.g., have smaller home ranges, show higher site fidelity, are less likely to migrate seasonally) [271–273]. This reduced movement stems in part from the presence of reliable resources in urban landscapes [218]; for instance, migratory white storks that feed on landfills have recently established resident populations [223] and brown bears revisit known feeding sites in winter when resources are otherwise scarce [274]. These less-frequent or shorter-distance movements can limit connectivity to the extent of creating apparent landscape fragmentation, even when it is not present structurally (i.e., habitat-independent fragmentation: [275]). Highly mobile species can be particularly important for connectivity because they transport propagules over long distances [8], so understanding their movement responses to urbanization is important for understanding both population and ecosystem processes.

Functional connectivity, defined as the connectivity of a landscape from the perspective of a focal organism [276], is often modeled by combining information on patch locations, non-habitat matrix, and average species movements [266,276,277]. Many models assume that interpatch distances are the primary determinant of connectivity, using random walks [278] or dispersal kernels [279]. In many cases, movement is assumed to be optimal and equivalent across all individuals [280] (but see [281]).

However, individuals often differ in their movement patterns [282,283], which can complicate estimates of functional connectivity. For example, individuals can specialize in their use of habitat types (e.g., “urban” and “nonurban” individuals) [16,284], especially in circumstances where urban habitats favor specific behavioral types [267]. This specialization could reduce the frequency of movements across ecosystem boundaries. Conversely, individuals might gain complementary resources from urban and natural areas, which would increase movement rates between habitat types [258]. Incorporating individual variation into habitat selection models substantially improved the accuracy of connectivity estimates for elephants [285]; overall, if habitat selection varies between individuals or if movements are based on habitat type, connectivity could be lower (or higher) than that predicted based on distances alone.

Here, we analyze movements of American white ibis (*Eudocimus albus*) in the southeastern United States to investigate connectivity across a patchy landscape of urban and natural sites. The term “natural” has many definitions [286]; in this paper, we use “natural” to refer to non-urban habitats that maintain the historical structure and function of local ecosystems, even if these habitats are managed or constructed by people (e.g., managed wetlands). White ibis are colonial wading birds that inhabit wetlands, where they feed on fish and aquatic invertebrates [287]. Ibis in these natural areas are nomadic, moving to new foraging and roosting sites in the region when conditions change [288]. Their high mobility means that they could be important for connecting distant patches (ibis can move 30-60 km daily between roosting and foraging sites, [289,290]). At the same time, urbanization in South Florida is associated with shifts in ibis foraging and movement behavior. Many ibis now forage in city parks, where they feed on human-provided resources (including bread) and show higher site fidelity, returning to the same parks over weeks or months [291,292]. Past work in this system showed that ibis can be infected by generalist enteric pathogens such as *Salmonella,* for which infection prevalence is highest in urban flocks [293,294]. Ibis might contribute to *Salmonella* transmission, or their exposure could reflect transmission from other reservoir species or environmental sources [295].

Here, we use a spatial network approach to study ibis movements during the nonbreeding season. Our goals are to better understand animal movement responses to urbanization, and to predict the consequences of these movements for the dispersal of ecosystem services, pathogens and contaminants across urban and natural sites. Specifically, we: (i) build an empirically-derived network representing ibis movements among frequently visited patches over a 3-year period; (ii) compare this observed network to networks based on simulated movements to determine whether ibis movements increase or decrease habitat connectivity; and (iii) examine how individual birds differ in their habitat use and connectivity roles.

We predict that site fidelity and habitat specialization will reduce network connectivity, as measured by edge density, assortativity, and modularity (Table 5.1). If individuals show minimal site fidelity or habitat specialization, then these three properties would be the same in the observed and simulated networks. In contrast, if individuals show high site fidelity, then edge density will be lower and modularity will be higher in the observed network than in the simulated networks. Further, if individuals specialize in their use of habitat types, then assortativity of land cover will be higher in the observed network than in the simulated networks and modules (defined as groups of nodes that are closely connected: Table 5.1) will differ in their land cover.

We further predict that ibis that more spend time in urban habitats will be site-faithful and show greater habitat specialization, based on observations of ibis and other species in urban areas [261,292,296]. Individuals might differ in their roles for connecting the network [97,297]; in particular, we predict that the least specialized individuals (i.e., those that frequently use both urban and natural sites) will contribute disproportionately to network connectivity.

METHODS

Field methods

Ibis were captured and fitted with GPS transmitters at 20 sites in South Florida, USA (Figure 5.1) [292]. Ibis in this region are common in urban settings, including public parks, lawns, golf courses, and residential areas. At urban locations, ibis can forage on human-provided food such as picnic scraps and bread thrown intentionally to feed ibis and other wildlife [291]. Ibis also inhabit natural habitats in South Florida, including restored wetlands, wetlands for wastewater management, and coastal areas (Figure 5.1b). At night, they roost communally in trees at sites that differ from foraging locations [298]. Ibis in this population often disperse away from coastal areas in the breeding season, but some remain in coastal South Florida [292], and some have begun breeding at urban sites with large water bodies in the last five years (S. Hernandez, *pers. obs.*).

Ibis were captured in multiple seasons at sites designed to represent a gradient of urban land use [291]. At urban sites, individuals were captured with nylon slip-knot leg lassos and modified manually operated flip traps [299]. At natural sites, ibis were captured using mist nets with decoys. A subset of captured ibis were fitted with EcoTone Kite GPS-GSM trackers (http://www.ecotone-telemetry.com; North Star Science and Technology, Oakton, VA, USA) (Figure 5.1a, b). Ibis were only fit with transmitters if the attachment was <3% of the bird's body mass. Tags collected GPS locations every two hours during daylight hours and collected one location after sunset or before sunrise, because ibis usually roost in place at night [292].

Tracking data

All analyses are based on GPS tracking data of 34 ibis between 15 October 2015 and 24 March 2018, using coordinates restricted to South Florida (Figure 5.1a, b). For each of the GPS-tagged ibis, we subsetted data to include only the nonbreeding season, which is the time when most individuals in the population move within the study area. We defined the nonbreeding season based on a previous analysis of characteristic locations and movement patterns that define behavioral seasons [292], rather than from dates alone. The nonbreeding season usually began between September and November and ended in March, though there were some exceptions (Figure 5.1c).

We separated data by bird-year for subsequent analyses, resulting in 61 tracks that included all the relocations of an individual bird in a single nonbreeding season. Many individuals (13) were tracked in only one nonbreeding season, 21 were tracked over two nonbreeding seasons and two were tracked over three (Figure 5.1c). For each track, we normalized the fix rate to two hours with a tolerance of 20 minutes and filtered out location errors by removing any points whose locations would produce an apparent speed of greater than 43 km/h (12 m/s, [300]) between subsequent relocations.

We used R Version 4.0.1 for all analyses [179] and the package *amt* for normalizing fix rates [301].

Identifying habitat nodes

To distinguish unique sites that would be defined as habitat nodes in the spatial network, we identified clusters of GPS points. We calculated pairwise distances between all GPS fixes using an equidistant conic projection (parallels at 33˚N and 45˚N), then used a 650-m buffer to group points in close proximity. This 650-m buffer represents the expected foraging radius of ibis in this population [291]. After calculating the distance matrix, we assigned clusters starting with the point with the most neighbors (i.e., the point with the largest number of other points within 650 m). Any location within 650 m of this point was assigned to the first cluster. From the set of remaining points (i.e., those not in the first cluster), we then identified the point with the most neighbors, and assigned that point and its neighbors to the second cluster. We continued this process until only points with no neighbors remained; each of these was then assigned to its own cluster.

Some clusters were adjacent to one another, which could occur if foraging areas were large (e.g., part of a large wetland complex) or very close together (e.g., an urban park proximate to a golf course). Therefore, we joined clusters if their points were within 325 m of each other. We did so by buffering all points in each cluster by 325 m; if any points from other clusters fell within this buffer, the two clusters were joined. A node was defined as the polygon made up of all 325-m buffered points from that node. We selected this shorter distance for forming nodes because preliminary analysis indicated that larger clustering distances of 650 m would yield unrealistically large nodes (some >15 km^2). Nodes ranged in geographic area from 0.33 to 8.79 km^2.

Land cover and node characteristics

We extracted land cover data within each node. Land cover data was sourced from the 2016 Cooperative Land Cover (CLC Version 3.2) map for the state of Florida [302]. This dataset includes 279 land cover classes in the region, but we reclassified it to 12 classes that represent relevant differences in habitat for ibis: artificial impoundments/reservoirs, coastal, cropland, estuarine, forest, freshwater forested wetlands, freshwater non-forested wetlands, lakes, parks/zoos, scrub, urban, and urban open land. Using this reclassified map, we calculated the percent cover of each land cover type within each node.

We further simplified these 12 land cover classes using non-metric multidimensional scaling (NMDS) in three dimensions. The input variables in the NMDS analysis were the proportion of each node that consisted of each land cover variable, where each node was a data point. In this analysis, we saw gradient of human development along the first NMDS axis, with wetlands and scrub habitats having negative values and urban and other human-dominated habitats having the most positive values (Appendix C Figure S5.1). Thus, in future analysis we used a node's NMDS1 value as a proxy for urbanization.

We used R packages *raster*, *rgdal*, and *rgeos* for spatial analyses [180,181,303].

Building networks

We built a network of habitat nodes using observed relocations of GPS-tracked individuals (Figure 5.1a). We considered a pair of nodes to be connected if an individual ibis moved between those nodes in one time step (i.e., the 2-hour fix interval with 20-minute tolerance). This two-hour interval is roughly the gut-passage time of an ibis (fed pelletized food, [304]), and thus is relevant to the inter-site transport of microbes, nutrients and contaminants acquired during foraging. We built a weighted, directed network from these connections. Edge weights were calculated as the number of observed relocations between a pair of nodes across all bird-years. Node sizes were the total number of visits to each node. Note that this definition of node size differs from the total number of fixes at each node because consecutive fixes at the same node count as one visit; we selected this metric of node size because we were more interested in movements between nodes than in time spent at each node. For each node and edge, we also recorded the number of unique bird-years using that node or path. We clipped the network to include only nodes within the extent of -80.52° to -80° longitude and 26.25° to 27.5° latitude, to exclude 146 nodes. We also removed additional sites (n=107) with no observed connections to other sites within the study area. This cropping also removed five bird-years from analysis (i.e., individuals who never entered the study area). The final network included 377 nodes over 56 bird-years. We used the *igraph* package for building networks and network analysis [305].

Simulating null networks

To test how ibis movements determine network-level properties, and to account for spatial structure in our network, we created null models to compare with our observed data (Figure 5.2a). To create these networks, we simulated random walks between nodes on the observed network (i.e., movements were not free on the landscape, but were constrained by node locations in the observed network). Each random walk was paired with an observed track (the full observed trajectory of an individual over a nonbreeding season); random walks began at the same starting point as the corresponding ibis track and were the same number of time steps as the observed track. In each time step, simulated ibis movements were based on two parameters derived from the tracking data: the probability of moving to a new node, and, if the individual moved, the probability of moving to each other node in the network. We used two different distributions for each of these parameters: one that pooled data across all individuals and one where parameters were based only on the specific track being simulated. These two distributions were designed to test the possibility that individuals are equal in their movement capacities and habitat preferences (pooled data) or that individuals differ in their movement patterns but still move independently of habitat type. In either case, the probability of moving to a new node was equal to the average proportion of 2-hour intervals where (an) individual(s) moved among nodes. If an individual moved, the probability of moving between any pair of nodes was proportional to edge-length distribution (i.e., weighted interpatch distances) in the tracking data. Simulated networks thus accounted for the spatial arrangement of nodes on the landscape and ibis movement propensities, but not for site fidelity or habitat selection.

We repeated this process 50 times to create 50 sets of tracks that corresponded to the observed tracking dataset. We used these sets of simulated tracks to build 50 weighted, directed networks to compare to the observed network (Figure 5.2a).

Network properties and statistical analyses

We calculated network-level and node-level properties of both the observed and simulated networks (Table 5.1). At the node level, we analyzed degree centrality, betweenness centrality, and node size, each of which represented one aspect a node's connectivity role (Table 5.1). Because our network was directed, we calculated degree centrality as out-degree, which is defined as the number of nodes that were visited by individuals departing from (not arriving at) a given node. We examined whether node land cover or spatial position predicted degree, betweenness, or node size using generalized linear models, where the predictor variables in each model were a node's urbanization score (i.e., NMDS1), latitude, longitude, and quadratic terms for latitude and longitude (to model node geographic centrality). We centered and scaled all predictor variables to have a mean of 0 and a standard deviation of 1 to allow us to directly compare across parameter estimates. For degree and node size, we used a Poisson model with a log link because these measurements are counts; for betweenness, used a Gaussian distribution and log-transformed the response variable.

At the network level, we calculated three metrics of network-scale connectivity (edge density, assortativity, and modularity; Table 5.1) for both observed and simulated networks. *Edge density* is the proportion of potential connections that are realized and represents network-scale connectivity [306]. We also calculated *assortativity*, the tendency of nodes with similar properties to be connected to one another [307]; we calculated assortativity for each land cover class separately, as well as for urbanization score (NMDS1, described above). We also identified modules, which are groups of nodes where a high proportion of edges exist within groups rather than between groups [307]. We tested three methods of module estimation: edge-betweenness [308], modularity optimization [309], and simulated annealing [308,310], all calculated using the *igraph* package in R [305]. We compared the module membership of each node across the three methods; though each produced different numbers of modules, the module membership was qualitatively similar (Appendix C Figure S5.2), so we used the method that produced the smallest number of modules (modularity optimization) in future analyses. We calculated the *modularity* coefficient (*Q*) of the networks, which measures the strength of modularity and ranges from 0 to 1.

To test whether edge density, assortativity, or modularity differed between observed and simulated networks, we used linear models predicting density, assortativity, or modularity from network type (observed/simulated). For assortativity of each land cover class, we used a multivariate linear model predicting assortativity from network type, land cover class, and their interaction. To determine whether modules differed in their land cover, used an analysis-of-variance (ANOVA) to identify whether module was a significant predictor of NMDS1.

Variation in movement and habitat use across individuals

We used linear models to examine whether ibis differed in their use of nodes with different land covers. For this analysis, we compiled a dataset of all the nodes used by each individual and their NMDS1 scores. We used an ANOVA to identify whether individual was a significant predictor of NMDS1. For each individual, we also measured average urban habitat use by calculating a weighted average and weighted standard deviation of NMDS1 scores (i.e. NMDS1 score of each node, weighted by the number of times the individual was observed using that node) using the *Hmisc* package [311]. We examined whether urban habitat use was related to variation in habitat use (i.e., whether individuals using more urban habitats had more or less variation in their use of different land cover classes); to do so, we used a linear model with an individual's weighted NMDS1 score as the response variable and the weighted standard deviation in NMDS1 score and its quadratic term as predictor variables.

To identify whether individuals differed in their importance for network connectivity, we removed each individual from the network one at a time. We calculated the differences in edge density and assortativity between the full and sparse network (i.e., a network with an individual removed). We used these differences to quantify the "connectivity role" of each individual in the network. We asked whether urban habitat use predicted an individual's connectivity role using linear models, where the change in edge density or assortativity was the response variable and the individual's weighted NMDS1 score and weighted standard deviation in NMDS1 score were predictor variables.

We repeated all of these analyses both at the level of the track (i.e., bird-year) and at the level of the individual to account for consistency and/or differences in individual node use across years.

RESULTS

Network attributes

Ibis visited a network of 377 nodes across 56 bird-years within our study area (Figure 5.2a). In our NMDS analysis, nodes separated along an urban-natural gradient; negative values in the first NMDS axis were associated with land cover classes that are less developed (i.e., freshwater non-forested wetlands, freshwater forested wetlands, and scrub) as well as croplands. Positive NMDS1 values were associated with land cover classes with higher anthropogenic influence, such as urban areas, parks/zoos, and urban open land (Appendix C Figure S5.1). The stress value of the NMDS was 0.11, indicating a moderately good fit [312,313]. We used the first NMDS axis as an urbanization score in future analyses.

The edge density of the observed network was less than half of the mean edge density in the simulated networks (Figure 5.2b). In other words, a significantly lower proportion of potential connections were realized than if birds were moving between nodes based on distance alone. Edge density was low in both observed and simulated networks (0.008 for observed and 0.020-0.023 for simulated networks), probably because we identified a large number of nodes but had movement data for only a small proportion of the local ibis population; thus, the relative values of edge density between the observed and simulated networks are more informative than raw values.

Assortativity was positive in both the observed and simulated networks and was higher in the observed than in the simulated networks, both for urbanization score and for each land cover class (Figure 5.2c, Appendix C Figure S5.3). Positive assortativity means that connections between nodes with similar urbanization scores or land cover classes were stronger than connections between nodes with different scores land cover classes, indicating clustering of nodes with of similar types. This pattern was stronger in the observed than in the simulated networks, suggesting that spatial proximity alone did not explain assortativity. Assortativity was highest for urban and wetland land cover classes in both the observed and simulated networks (Appendix C Figure S5.3).

We identified 19 modules in the observed network, with a modularity coefficient (Q) of 0.811. Within the nodes that made up each module, there was variation in urbanization score, but there was also distinct clustering along an urban/natural gradient (Appendix C Figure S5.4). Module was significantly related to urbanization score ($F=23.09$, $p<0.001$), meaning that modules differed systematically in their level of urbanization. The observed network was significantly more modular than the simulated networks, measured using both Q (0.661 ± 0.021 SD in simulated networks) and the number of modules (range: 4-7 modules in simulated networks) (Figure 5.2d, Appendix C Figure S5.5).

These patterns, where connectivity was lower and assortativity was higher in the observed network, could arise either from individual specialization in habitat selection or from individual differences in movement propensities. However, even when we incorporated individual-specific movement parameters into null models, simulated networks were less assortative and more connected than the observed network, indicating that observed connectivity cannot be explained solely by variation in movement distances among individuals; rather, individuals differ in their use of habitat types.

Node attributes

Each node was visited 33 times on average (SD: 109.7), but this distribution was right-skewed; the median number of visits was two, and 206 nodes (54%) were visited fewer than three times (Figure 5.1d). In the simulated networks, the average number of visits per node was 14 (SD: 8.15) and this distribution was less skewed (median: 12.8). At the node level, degree was negatively associated with node urbanization score (Appendix C Table S5.1). All measurements of centrality (i.e., degree, betweenness, and node size) tended to increase at the latitudinal center of the study area (i.e., negative association with latitude^2). Neither node size nor betweenness was significantly related to node urbanization score. Geographic area was explained only by the number of visits to a node, and not by land cover or spatial position (Appendix C Table S5.2), probably because node geographic area was determined by the method of identifying nodes from GPS data (i.e., nodes were created by aggregating and buffering ibis locations).

Individual variation in movement patterns

Ibis differed in the number and types of nodes they used (mean: 13 nodes per track, range: 1 to 77). Many birds were consistent in their use of specific land cover classes, particularly those that used primarily urban nodes (Figure 5.3a). Individual (i.e., track or bird-year) was a significant predictor of node urbanization score ($F=18.2$, $p<0.001$). There was a hump-shaped relationship between the mean and variation in an individual's habitat use, such that individuals with intermediate urbanization scores tended to have the highest variation in their urbanization score. Individuals using the most urban habitats had the lowest variation in their urbanization score (Figure 5.3b).

When we removed individuals from the observed network, edge density decreased between 0 and 9.97% after the removal of a single track (Figure 5.3c). This decrease was greatest at intermediate levels of urban habitat use, meaning that birds using primarily urban or wetland habitats had a smaller effect on edge density than did birds using both (i.e., negative effect of standard deviation in NMDS1, Appendix C Table S5.3). Assortativity changed in both directions – either increasing or decreasing – upon removal of a single individual. Increases in assortativity tended to occur when individuals with intermediate urbanization scores and high variation in urbanization scores were removed (Figure 5.3d, Appendix C Table S5.3). These results were consistent, though slightly weaker, when analyzing individual birds (movement paths over multiple years) rather than tracks (path of an individual bird in a single year) (Appendix C Figure S5.6).

DISCUSSION

Highly mobile animals can facilitate connectivity across space and between habitat types, but changes to movement in urban landscapes can alter connectivity. Our results suggest that connectivity in an urban-natural landscape mosaic depends on both the tendencies of individual birds and the characteristics of the sites they use. In particular, habitat specialization and site fidelity by individual ibis produced fewer connections and higher assortativity in the observed network. Ibis were less likely to make connections between nodes of different land cover classes than between nodes of the same class, and this pattern was stronger in our observed network than if ibis moved based on distance alone. Further, in the observed network, sets of nodes that were strongly interconnected (i.e., modules) tended to have similar land cover. The small number of birds that used both natural and urban sites contributed disproportionately to connectivity, and individuals that used the most urban sites were the most specialized in their habitat use, suggesting that continued urbanization could further reduce connectivity provided by this historically mobile species.

Individual specialization in habitat use, and in urban habitats in particular, contributed to low connectivity in our network analysis. Habitat specialization by individuals could arise if it provides fitness benefits [284,314]. For example, urban environments can increase fitness in individuals with reduced antipredator responses [315] or favorable behavioral traits like boldness [267]. In this system and others, individuals captured in urban areas show isotopic signatures of anthropogenic food in their diet [291,316], suggesting that urban specialization could increase food intake rates [317] (though it can have mixed effects on health outcomes: [291,296]). In addition to these benefits, specialization could be maintained genetically if it reduces gene flow between urban and natural sub-populations; we focused on the nonbreeding season in this study, but individuals that use urban areas in the nonbreeding season can also be less likely to migrate long distances to breed (e.g., in wood storks: [318]) and ibis have recently begun nesting in urban areas in Palm Beach County (S. Hernandez, *pers. obs*). Our results show that, in addition to its potential benefits for individuals [284], habitat specialization has broader ecological effects by reducing overall connectivity.

The presence of habitat specialization in this population also calls into question the description of ibis as nomadic [288], at least in urban areas. The observed network differed from networks simulated by random walks for every metric we analyzed, which suggests that nomadic movements cannot be represented with random walks, and/or that urban ibis are not nomadic. For snail kites, a nomadic bird, distance alone does not explain movements [310], highlighting that random walks probably oversimplify nomadic movements. In addition, snail kite connectivity networks were not modular in the nonbreeding season, when they are nomadic in response to highly variable food resources [310]. In contrast, the observed ibis network was modular, suggesting that nomadism may not be an accurate description of ibis movements in this system at the scale of the nonbreeding season. The presence of stable resources in urban areas might reduce the benefits of nomadism [218,317,319]; comparing ibis movements in urban Palm Beach County with nearby populations in non-urban areas (e.g., in the Everglades) could clarify the role of urbanization in driving this non-nomadic movement.

Many individuals used primarily urban or natural sites, but a small number of habitat generalists connected urban and natural nodes. Ibis that used the most urban habitats had the smallest variance in their habitat use and were generally the least important for connectivity; the few individuals that visited the largest number of nodes had the greatest variation in their habitat use and played the largest role in connecting urban and natural nodes. These results indicate that individuals can be classified as natural specialists, urban specialists, or generalists (as in coyotes: [316]). Given their importance for maintaining connectivity, it is important to understand the abundance and characteristics of generalists in the population. Variation in movement and habitat use among individuals can stem from differences in phenotype, condition (e.g., body condition, reproductive state), and/or from environmental drivers [320–322]. If declines in natural site quality or the advantages of exploiting novel urban resources [322] were to make generalist individuals less common in the future, then connectivity could further decline. The outsize effect of generalists on connectivity is analogous to that of keystone individuals, which have a disproportionate impact on group dynamics [323], and whose removal affects reproductive success, social stability, and other population processes [323]. Understanding the ecology of generalist individuals can help predict whether their movement patterns will remain consistent as the environment changes, and therefore how other ecological processes will be affected.

The low connectivity that we identified between urban and natural areas could affect species interactions and community composition by limiting the dispersal of pathogens or propagules between sites of different types. For example, red squirrels are more likely to acquire paramyxovirus infections in conifer than in broadleaf forests [324], in which case low connectivity between conifer and broadleaf forests could reduce the risk of viral spread. At the same time, increases in site fidelity and decreases in movement can increase the size of epidemics in urban areas, particularly if urban sites accumulate high numbers of susceptible hosts [225]. Ibis sampled at urban sites have significantly higher prevalence of enteric *Salmonella* [293] and differences in their bacterial microbiome compared to ibis at natural sites [294], indicating that species interactions and pathogen transmission differ between urban and natural sites (see also [295]).The presence of generalist individuals in the population could maintain pathogen dispersal [325,326], but the importance of highly mobile individuals for infection dynamics depends on both their abundance and the relative rates of movement and recovery [327], so the impact of generalists could be limited if they are much less common than habitat specialists.

Mobile animals are also important for nutrient transfer between habitats, so reduced connectivity in urban areas could affect ecosystem functioning. For example, in one study, approximately 86% of nutrients deposited by sharks at an atoll were derived from nearshore systems [328]; if these movements were to change in their frequency or location, this atoll could lose a substantial proportion of its nutrient inputs. In the ibis system, urban and natural diets differ in their nutrient composition [291] and phosphorous inputs from roosting birds can drive vegetation growth (e.g., tree islands in the Everglades [329]), so changes in diet and movement patterns in urban landscapes could have knock-on effects on landscape structure and ecosystem functioning.

The nonrandom nature of ibis movements we identified in this study highlights the importance of understanding drivers of movement for predicting connectivity. While it is well accepted that most movements are nonrandom, particularly at large spatial scales [330], connectivity studies often rely on random walks because other information is not available [331–333]. By incorporating movement data, we are able to more accurately illustrate how sites are connected by a focal species. We show that distance between sites is not the only component that needs to be considered for connectivity; if attempting to promote connectivity, managers should consider the characteristics that attract individuals to each site, and whether those characteristics vary across individuals. Our results showed no consistent relationship between node land cover and network centrality, suggesting that spatial position and/or other characteristics (e.g., disturbance, food availability) are more important in determining a site's role in connecting the network. Efforts for maintaining connectivity are often based on establishing habitat corridors and removing barriers [333,334], but for species whose movements are less limited by barriers it is necessary to develop other strategies that realistically incorporate the drivers and constraints on movement.

Understanding connectivity at the landscape scale is important for decisions about conservation and habitat management. To better inform these strategies, future studies could explore the characteristics of "stepping stone" patches that connect urban and natural areas, with the goal of managing these patches to increase or limit movements. Similarly, it is important to understand how landscape-scale connectivity and the strength of individual specialization impact gene flow, species interactions, and nutrient transfer. Last, future studies could examine how these patterns apply to larger spatial and temporal scales, such as whether habitat preferences are heritable and how they connect to longer-distance movements such as breeding dispersal.

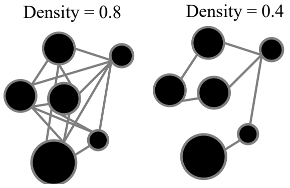
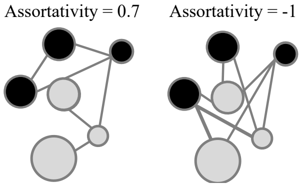
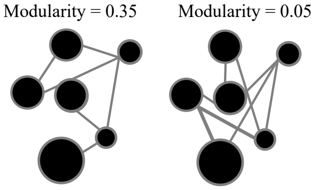
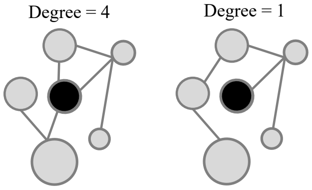
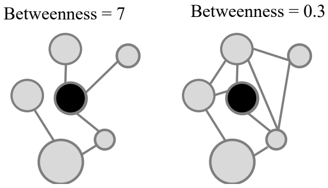
CONCLUSIONS

Urbanization and individual movement patterns can reduce connectivity, especially between urban and natural land cover classes. This reduction is true even for a highly mobile species whose movements are only minimally limited by habitat fragmentation. Instead, differences in habitat use between individuals reduce connectivity in a heterogeneous landscape, where individuals that use urban sites have the smallest role in connectivity because they rarely use non-urban sites. Lower connectivity could reduce the potential spread of pathogens or contaminants from urban to natural areas and the import of ecosystem services and beneficial nutrients or microbes from natural to urban areas [331].

DECLARATIONS

- Ethics approval: Animal capture and handling procedures were reviewed by the University of Georgia's Institutional Animal Care and Use Committee (IACUC # A2016 11-019-Y2-A0). Capture and handling were conducted under Florida Wildlife Conservation Commission permit LSSC-11- 00119F and United States Fish and Wildlife Agency permit MB779238-0.
- Consent for publication: not applicable
- Availability of data and materials: The datasets analyzed in this study and the code to generate results will be made available at Dryad.
- Competing interests: The authors declare that they have no competing interests.
- Funding: Funding was provided by a National Science Foundation Graduate Research Fellowship to CST and by National Science Foundation EEID grant DEB-1518611.
- Authors' contributions: CST, JHC, SMH, SA, and RJH conceived the study and developed ideas for analysis. CST implemented analyses described in this manuscript. AKW and JHC produced and provided data used as input into analyses (behavioral seasons and landcover classification). CST wrote the first draft of the manuscript and all authors contributed to revisions. All authors approve this submission.
- Acknowledgements: We thank Henry Adams, Shannon Curry, Taylor Ellison, Maureen Murray, and Catharine Welch for field data collection. We thank members of the Hall and Altizer labs for constructive comments on an earlier version of the manuscript.

Table 5.1: Network metrics used in this study. In each example diagram, nodes of different colors represent different habitat types or land cover classes.

Name	**Definition**	**Ecological interpretation**	**Range of values**	**Example**
Network-level metrics				
Edge density	The proportion of potential connections in the network that are realized	Landscape connectedness	(0,1]	
Assortativity	The tendency of nodes with similar properties to be connected to one another	Connectivity among habitats of the same vs. of different types	[-1,1]	
Modularity	The ability of a network to be divided into communities, where there are few edges between communities	Aggregation of groups of patches, "functional spatial structure" [310]	[0,1]	
Node-level metrics				
Degree centrality	The number of links of a focal node. In a directed network, can be *in-degree* (the number of incoming links) or *out-degree* (the number of outgoing links)	The potential number of other patches that a contaminant, nutrient, etc. could directly spread to (out-degree) or come from (in-degree)	(0,N] (N=# of nodes in net-work)	
Betweenness centrality	The fraction of shortest paths between nodes that pass through the focal node	Role of a patch as a "stepping stone" that connects otherwise-separated groups of patches	[0,1]	
Node size	Sum of all edge weights entering and leaving a node	Number of visits to a patch	[1,Infinity)	

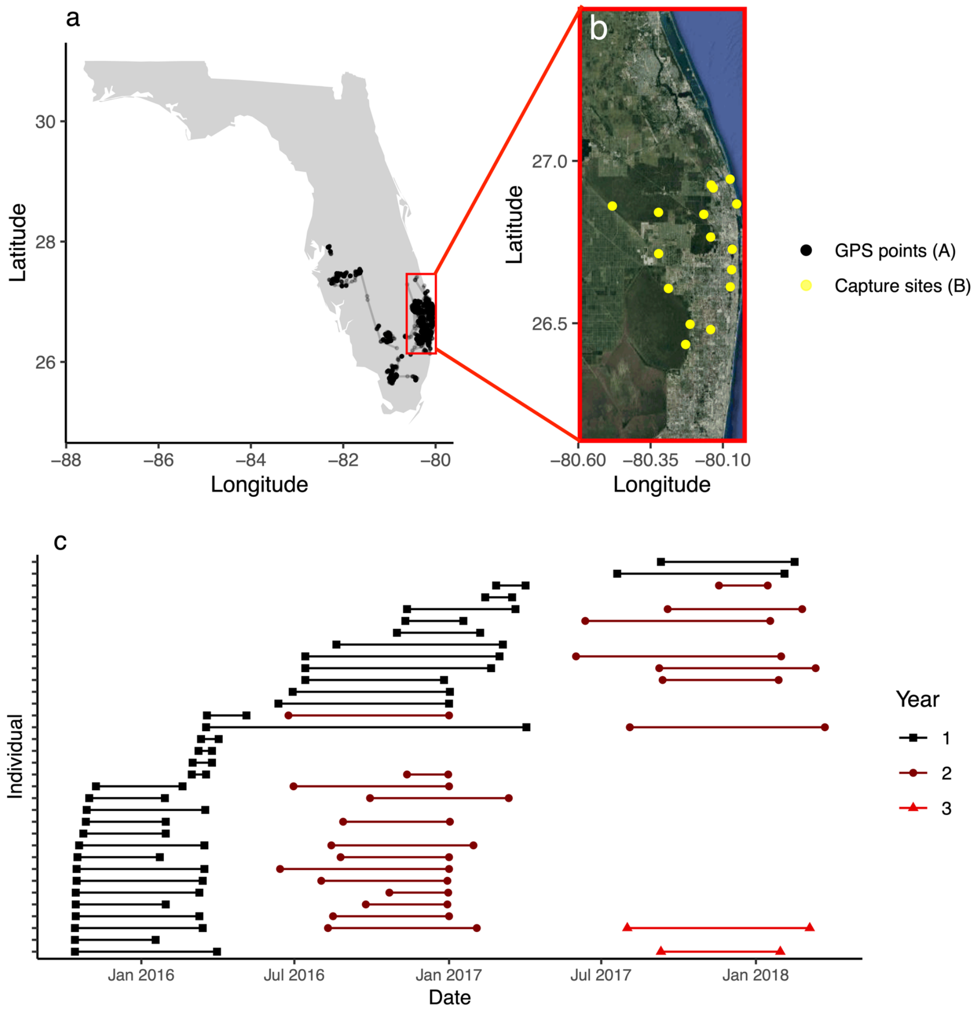


Figure 5.1: Study area and tracking data used in analyses. (a) All GPS tracking data (n=46,111 points) for the nonbreeding season on a map of Florida, USA. The red outline shows the study area used in analyses. Tracks that fell entirely outside the study area (n=5) were excluded because they were not connected to the core study area during an entire nonbreeding season. (b) Satellite imagery and capture site locations within the study area. (c) Nonbreeding season timing for each individual included in analyses across the study period. Each horizontal bar shows the timing (start and end) and duration of the nonbreeding season and each row is a unique individual. For individuals monitored for

>1 year, colored bars show the second year (circles) and third year (triangles) of monitoring.

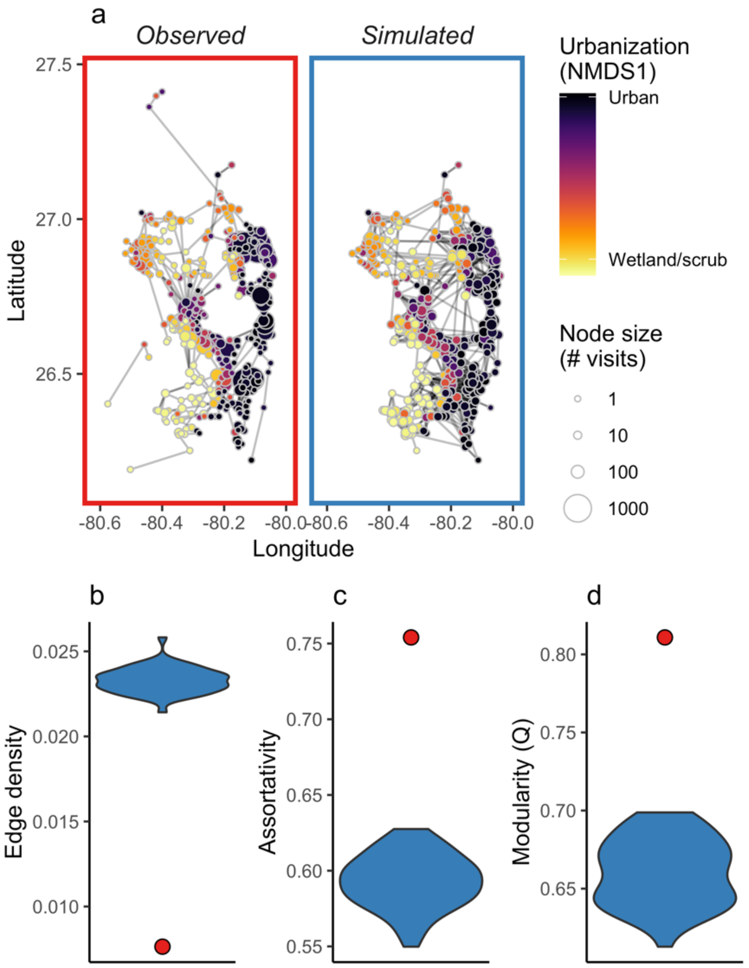


Figure 5.2: Networks and network properties. (a) Networks (visualized in geographic space) from observed tracking data and a representative simulated network. Points are colored by their urbanization score, measured as the first axis from the NMDS analysis of land cover proportions. Node size indicates total number of visits. (b-d) Properties of observed and simulated networks. Blue violin plots show the distribution of values for the random walk networks and red dots show the value for the observed network. (b) Edge

density, the proportion of potential edges that are realized. Higher edge density indicates a more connected network. (c) Assortativity by site urbanization score (NMDS1). Higher assortativity indicates that nodes with similar properties are more connected with one another. (d) Modularity (Q) in the observed and simulated networks. Higher modularity indicates that the network can be divided more clearly into separate communities.

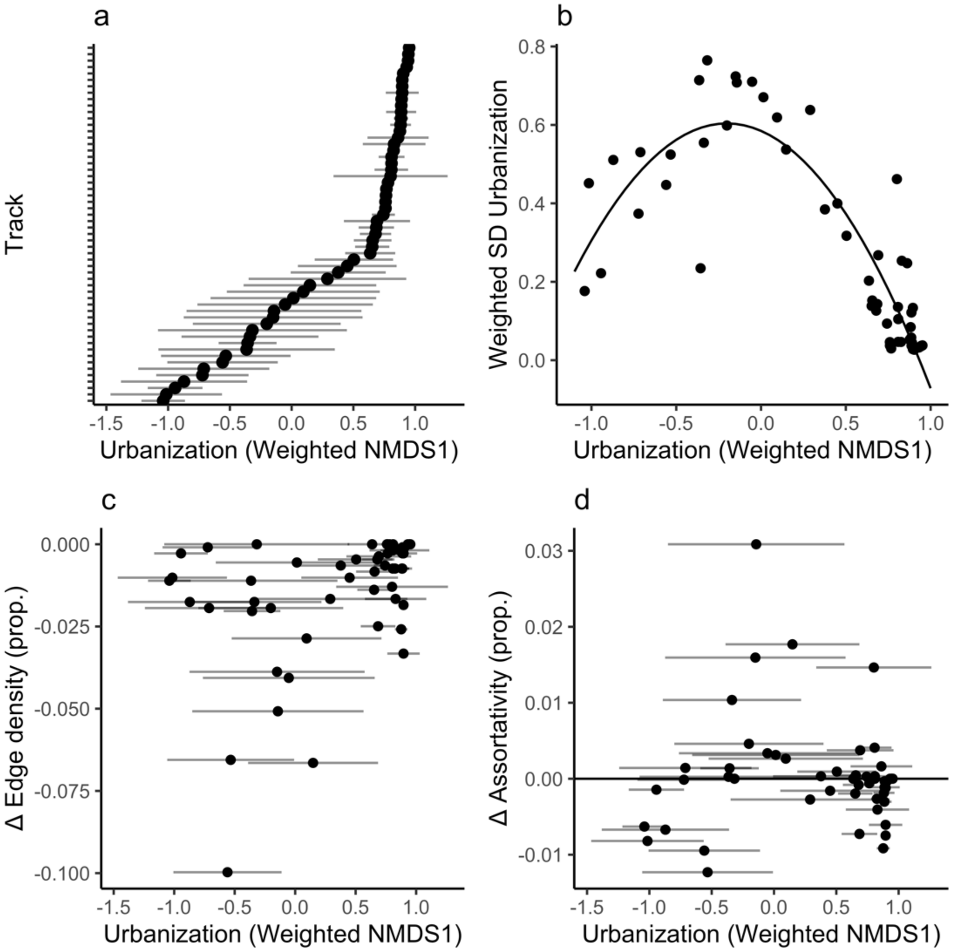


Figure 5.3: Individuals differ in their habitat use and their roles in network connectivity. (a) Weighted mean and weighted standard deviation of urbanization score (NMDS1) of all sites used by each individual bird-year. Individuals are sorted by their mean

urbanization score. (b) Relationship between mean and standard deviation in weighted urbanization score. The curve shows the results from a linear model relating the two variables. (c) Relationship between an individual's urbanization score and the change in edge density when they are removed from the network. Density can only decrease upon removal of an individual, so larger negative values indicate a larger influence of an individual on connectivity. (d) Relationship between an individual's urbanization score and the change in assortativity when they are removed from the network. The horizontal line at y=0 represents no change in assortativity.

CHAPTER 6

HABITAT SPECIALIZATION BY WILDLIFE REDUCES PATHOGEN SPREAD IN URBANIZING LANDSCAPES[5]

---

[5] Teitelbaum CS, Altizer S, Hall RJ. Habitat specialization by wildlife reduces pathogen spread in urbanizing landscapes. In review at The American Naturalist.

ABSTRACT

Urban areas are expanding globally, with far-reaching ecological consequences, including for wildlife-pathogen interactions. Wildlife show tremendous variation in their responses to urbanization; for example, even within a single population, some individuals can specialize on urban or non-urban habitat types. This specialization could impact landscape-level pathogen dispersal and pathogen impacts on host populations via changes to wildlife movement and aggregation. Here, we build a mechanistic model to explore how habitat specialization in urban landscapes affects wildlife-pathogen interactions in mobile hosts. We model movement on a network of resource-stable urban sites and resource-fluctuating natural sites, where hosts are either urban specialists, non-urban specialists, or habitat generalists that use both patch types. We find that, for generalists, partially urban landscapes produce the highest infection prevalence and mortality, driven by the combination of high densities at urban sites and high movement rates at non-urban sites. However, habitat specialization protects hosts from these negative effects of partially urban landscapes by limiting movement between patch types. These findings suggest that habitat specialization can benefit populations by reducing infectious disease transmission, but could also carry the cost of reducing other movement-related ecosystem functions such as seed dispersal and pollination by reducing movement between habitat types.

INTRODUCTION

As urbanization intensifies and urban areas expand worldwide, wildlife are increasingly using urban environments. Although urbanization extirpates some species

[335], many animal species survive and even thrive in cities [336]. For species that are able to adapt to urban environments, living in cities can alter behavior, diet, and local abundance [267], which in turn can affect ecological processes at the community and ecosystem scales [226,337]. One important ecological consequence of urbanization involves changes to animal-parasite interactions [338], including pathogen transmission between wildlife and humans [339].

Urbanization can amplify the transmission of some pathogens and limit the spread of others, depending on the details of host and pathogen biology [338]. For example, food resources are often patchily distributed in urban areas, which promotes host aggregation and increases contact rates, thus increasing the rate of pathogen transmission [263,340]. Urban environments can also expose animals to novel pathogens or high densities of pathogen infectious stages, as is the case for woodchucks, which are exposed to *Toxoplasma gondii* when they come into contact with fecal contamination from domestic cats in urban areas [341]. In addition, changes in diet in urban areas can increase host immunity owing to abundant food resources (e.g., bird feeders, dumpsters), but can also decrease host immunity via exposure to contaminants [342]. These mechanisms often operate simultaneously to alter the intensity, timing, and severity of pathogen outbreaks in urban wildlife.

Urbanization also affects wildlife-pathogen dynamics through changes to animal movement. In cities, many animals move less, exhibiting higher site fidelity, smaller home ranges, and/or lower migratory propensity [273,343,344]. These changes are often associated with stable and abundant resources in urban areas [218,226], and can subsequently affect transmission patterns and infection outcomes [263]. For example, naturally nomadic flying foxes have become more sedentary in urban gardens that provide year-round flowering resources, producing larger but less frequent outbreaks of Hendra virus [225]. Similarly, raccoons in urban areas have more stable home ranges than those in suburban and exurban areas, which can limit the spatial spread of rabies by reducing long-distance movements of infectious individuals [271,345].

Another way that urbanization influences animal movement – and potentially infection dynamics – is through habitat specialization, where some individuals specialize in urban or non-urban habitats [346–348]. For example, herring gulls specialize in different habitat types, and spatial overlap between individuals is highest in human-dominated habitats such as fishing ports [346]. Infection risk for three different zoonotic bacteria is also high at fishing ports in this species [349], suggesting that individual habitat specialization could amplify within- and cross-species transmission. Habitat specialization is favored in heterogeneous environments with high resource diversity [322,350], conditions often created by human development [322]. Because of the complex interactions between urbanization, specialization, and infection, and the importance of urban wildlife pathogens for animal and human health, a general theory that predicts how specialization should impact infection dynamics in urban wildlife is needed.

Here, we investigate the effects of urbanization and habitat specialization on population dynamics and infectious disease dynamics in a wildlife metapopulation. Our general model is motivated by recent work that found that an American white ibis (*Eudocimus albus*) population in South Florida, USA consists of a mixture of urban habitat specialists, non-urban habitat specialists, and generalists, which reduces connectivity across a network of sites [348]. Urban-foraging ibis can also maintain transmission of *Salmonella spp.* [295] and individuals sampled in urban areas differ significantly in their gut microbial composition compared to those from non-urban areas [294], suggesting that habitat specialization could be related to shifts in symbiont transmission patterns.

We build a model where animals move among natural patches, which vary in their resource availability over space and time, and urban patches, which provide stable resources year-round. We then introduce a pathogen and measure its prevalence, rate of spread, and population-wide host survival. Last, we explore how habitat specialization, where some hosts use only urban areas and others use only natural areas, affects survival and infection outcomes. We hypothesize that (1) population-level survival will be higher in landscapes with more urban patches because of greater resource stability; (2) pathogen prevalence will be higher in urban patches and landscapes with more urban patches due to higher contact rates and/or densities; (3) pathogens will spread more slowly across landscapes with more urban patches because of decreased movement, and (4) habitat specialization will reduce the rate at which pathogens spread across the landscape by reducing mixing among hosts. These results can inform expectations for how urbanization affects wildlife-pathogen dynamics, and ultimately species conservation in urban landscapes.

METHODS

Model framework

Landscape structure

We model landscapes as fully-connected networks, such that movement is possible between any pair of patches [319] (Figure 6.1a). Resource availability in each patch can vary over time between 0 (no resources) and 1 (maximum possible resource availability). Patches in the network can be either urban (u) or natural (w). Resource availability at a natural patch i at time t ($A_i(t)$) is drawn from a uniform distribution: $A_i(t) = U(0,1)$. We use a weekly timestep, so A_i changes weekly at natural patches, but remains constant ($A_i(t) = A_u$) at urban patches. When $A_u = 0.5$, resource availability at urban patches is equal to average resource availability at natural patches. A landscape consists of P patches, and we model movement and infection (see below) across landscapes that vary in the proportion of their patches that are urban.

Movement

We consider movement and infection over a single annual cycle outside of hosts' breeding season. Inter-patch movement occurs at the same weekly time step that resource availability changes. Movement is a function of two elements: a departure decision and a selection of destination (Figure 6.1b, c). Departure from a focal patch follows a density-dependent departure rule [319], where the proportion of individuals departing a patch decreases with resource availability ($A_i(t)$) and increases with host density ($N_i(t)$). The number of hosts of type q departing patch i at time t is denoted as $M_i^q(t)$.

$$M_i^q(t) = \begin{cases} N_i^q\left(1 - \dfrac{A_i(t)}{N_i(t)}\right), & \text{if } N_i(t) > A_i(t) \\ 0, & \text{if } N_i(t) \leq A(t) \end{cases}$$

Next, hosts that depart must select a destination. This destination depends on the host type and the destination patch type. Hosts are defined according to their habitat specialization (q): natural (w), urban (u), and generalist (i.e. no preference, r). Generalist hosts ($q = r$), distribute equally among all other patches, under the assumption that departing individuals have no knowledge of conditions at other patches. Specialized hosts move only to destination patches of their own type. Hosts do not return to the patch from which they departed, unless they are specialized and there is only one patch of that type. Thus, $M_{ij}^q(t)$, the number of hosts of type q moving from patch i to patch j, is:

$$M_{ij}^q(t) = \begin{cases} M_i^q(t)\dfrac{1}{P-1}, & \text{if } q = r \\ M_i^q(t)\dfrac{1}{P_p - 1}, & \text{if } q = u, w \text{ and } P_q > 1 \\ M_i^q(t), & \text{if } q = u, w \text{ and } P_q = 1 \end{cases}$$

where P_q is the number of patches of type q. In all cases, the initial conditions are such that the number of habitat specialists of each type is proportional to the frequency of the corresponding patch type on the landscape; for example, if the landscape is 30% urban (i.e., $P = 10$, $P_u = 3$), then 30% of specialized hosts will be urban specialists and 70% of specialized hosts will be non-urban specialists.

We assume that movement is instantaneous, has no mortality cost, and is independent of host infection status. Thus, accounting for patch departures and patch immigration, the number of hosts at a patch at the end of a time step is:

$$N_i^q(t+1) = N_i^q(t) - M_i^q(t) + \sum_{j \neq i} M_{ji}^q(t)$$

Population and infection dynamics

We model demography and infection dynamics on a faster timescale than movement or changes in resource availability, so that transmission and mortality occur in continuous time between weekly bouts of movement. Thus, for infection and population dynamics within each week-long period of residency, we use τ in [0,7] to represent time.

Natural mortality has both density-dependent and density-independent components. We assume no adaptive benefit of specialization (i.e., survival does not depend on host type, patch type, or their interaction). A patch's carrying capacity is equal to its resource availability, and additional density-dependent mortality occurs only when the population exceeds carrying capacity (i.e., when $N_i(t) > A_i(t)$). Because we model dynamics for the non-breeding season, the within-patch dynamics excludes a term for host births.

$$\mu_i(t) = \begin{cases} \mu_0 + \mu_1 \left(\dfrac{N_i(t)}{A_i(t)}\right), & \text{if } N_i > A_i \text{ and } A_i > 0 \\ \mu_0, & \text{otherwise} \end{cases}$$

We model the dynamics of an infection where individuals transition between susceptible (S) and infectious (I) classes, and recovered hosts have no immunity and can be re-infected (i.e. an S-I-S compartmental model of infection; Figure 6.1d). We assume that all transmission occurs within patches, rather than during inter-patch movement. Transmission occurs at the density-dependent contact rate β between susceptible and infectious individuals. Infectious individuals recover and become susceptible at rate γ.

Infected individuals experience an additional infection-induced mortality rate v, which scales linearly with resource availability such that infection-induced mortality is 0 when $A_i = 1$ and attains a maximum of v when $A_i = 0$.

$$\frac{dS_i^q}{d\tau} = -S_i^q\mu_i(\mathrm{t}) - \beta S_i^q I_i + \gamma I_i^q$$

$$\frac{dI_i^q}{d\tau} = -I_i^q\mu_i(\mathrm{t}) + \beta S_i^q I_i - \gamma I_i^q - I_i^q v(1 - A_i)$$

Model implementation

We ran four sets of models to understand how the proportion of urban patches and specialized hosts affect population dynamics and infection outcomes. To explore the effect of urbanization alone on host population dynamics, we ran models with no infection or specialization (i.e., $\beta = 0$, $\lambda = 0$, $\nu = 0$, *proportion specialized* = 0). Next, we included infection to analyze relationships among urbanization, infection, and population dynamics (i.e., $\beta > 0$). We then explored how specialization interacts with urbanization by running models that included specialization but no infection (i.e. *proportion specialized* > 0). Last, we included urbanization, specialization, and infection. For each model set, we examined the sensitivity of our results to several parameters (Table 6.1).

For each parameter combination (Table 6.1), we ran 20 replicate simulations of the model, each with a different simulated time series of resource availability at natural patches. Each simulation started with each patch at its average carrying capacity (i.e., 0.5 for natural patches and A_u for urban patches); these numbers do not represent whole individuals, but are scaled relative to the hypothetical maximum population size if all patches in the system were at their maximum resource availability. For models that included infection ($\beta > 0$), we seeded infection by initializing each simulation with 10% of hosts at one patch infected. When the landscape contained both urban and natural patches, we performed half of the simulations (N=10) with infection seeded an urban patch and half with infection seeded at a natural patch. For each time step, we solved the mortality and infection equations numerically using the *deSolve* package in R Version 4.0.1 [179,351] for $\tau_{max}=7$, then applied the movement equations. We repeated this process for 40 weekly time steps.

For each simulation, we calculated demographic, infection, and movement outcomes. First, we calculated the proportion of individuals surviving the entire non-breeding season for each simulation (end population size/starting population size). Next, we quantified the cumulative number of movements that occurred across all patches for the entire simulation. For simulations that included infection, we quantified host infection prevalence as the proportion of hosts infected at the end of the simulation. As a metric of transient dynamics, we also calculated the maximum infection prevalence over the course of the simulation ($prev_{max}$), the time to reach maximum prevalence (t_{prev}, in weeks), and the rate of infection spread ($\frac{prev_{max}-prev_0}{t_{prev}}$). To measure spatial spread, we calculated the spatial variation in end prevalence as the coefficient of variation in end-of-season infection prevalence across patches. Last, in simulations that included specialization, we measured the difference in end prevalence between urban and natural hosts.

For each parameter set, we calculated the mean and standard deviation of each outcome across the eight simulations. We examined how the proportion of urban habitat and the proportion of specialists affected each of these outcomes and performed sensitivity analyses for contact rates (β), recover rates (γ), mortality rates (μ_0, μ_1), and infection-induced mortality (ν).

RESULTS

Urbanization, movement, and survival

In the absence of infection or specialization, urbanization had a relatively small effect on population-level survival. Across the urbanization gradient, between 67.5% and 75.6% of hosts survived a full non-breeding season (Figure 6.2a). There was a U-shaped relationship between urbanization and survival, such that survival (i.e., the proportion of animals surviving a full season) was lowest in partially urban landscapes and highest in 100% urban landscapes. The U-shaped relationship was magnified at higher rates of density-dependent mortality (μ_1, Appendix D Figure S6.1) and was driven by high mortality rates at urban patches in partially urban landscapes. When both urban and natural patches were present, urban patches persisted at or above carrying capacity (Figure 6.2b-c), which produced high mortality rates (Appendix D Figure S6.2). In addition, movement rates declined as urbanization increased (Appendix D Figure S6.3) because movement depended on resource availability. While resource availability at natural sites frequently dropped below 0.5, urban sites never dropped below 0.5, meaning that departure from urban sites was less frequent than departure from natural sites.

Urbanization and infection

Introducing a pathogen magnified the depth of the U-shaped relationship between urbanization and population-level host survival. It also altered the shape of this relationship, reducing survival in 100% natural landscapes but only minimally in 100% urban landscapes (Figure 6.1a). Infection prevalence was highest in landscapes that were 0-60% urban and close to zero in 100% urban landscapes. These patterns were magnified when contact rates were higher and when pathogen virulence was intermediate (Appendix D Figure S6.4). End-of-season infection prevalence was correlated with other metrics of infection outcomes (Appendix D Table S6.1), meaning that infection spread more slowly and reached lower peak prevalence in the presence of specialization (Appendix D Figure S6.5).

These nonlinear relationships between urbanization, infection, and population survival were produced by changes in host movement and density. In predominantly urban landscapes, low movement rates reduced pathogen spread between patches, resulting in minimal transmission. In mostly-natural landscapes, high movement rates promoted pathogen spread. In partially urban landscapes, host movement from natural patches allowed the pathogen to spread, and high densities at urban patches allowed the pathogen to transmit efficiently. In support of this mechanism, in partially urban landscapes, host density and infection prevalence were higher at urban patches than at natural patches (Figure 6.1e-f, Appendix D Figure S6.6).

Habitat specialization and survival

Habitat specialization, where some or all hosts moved preferentially to urban or natural habitats, increased survival across all levels of urbanization, and especially when the proportion of urban patches was between 10-60% (Figure 6.3a). When all hosts were specialized, urbanization had only a minimal effect on survival, and the relationship between urbanization and survival was positive and linear (Figure 6.3a). These patterns occurred because specialization prevented urban patches from accumulating individuals above their carrying capacity, which increased survival for both urban and natural hosts. When all hosts were specialized, survival was higher for urban specialists than for natural specialists. Otherwise, when not all hosts were specialized, survival was higher for natural specialists, because the movements of generalist individuals increased densities and reduced survival at urban sites. Specialization had relatively small effects on movement rates at the metapopulation scale, but slightly increased movement rates in 50-90% urban landscapes (Appendix D Figure S6.3) because larger population sizes in the presence of specialization meant a higher number of cumulative movements.

Habitat specialization and infection

Host habitat specialization decreased infection prevalence relative to a generalist host population. When all hosts were specialized, infection prevalence declined monotonically with urbanization (Figure 6.3c). The negative effect of specialization on infection prevalence was due to lower effective population sizes (i.e., in a 100% specialized population, a 10-node network is subdivided into two separate networks) and especially lower densities at urban patches in the presence of specialization. Moreover, prevalence was more variable across patches when hosts were specialized (Figure 6.3d), because there was limited movement between urban and natural patches.

DISCUSSION

Relationships between urbanization and wildlife population or infection dynamics have been observed across a number of previous studies, but often in contrasting directions [338,352]. For example, wildlife in urban areas can have higher [353] or lower [354] infection prevalence than in natural areas. By linking resource dynamics, infection, and movement in a single framework, our model clarifies that changes in host movement patterns in urban areas can link landscape-level resource variability to pathogen transmission and host population dynamics. Further, these results highlight that the effects of urbanization on infection dynamics depend not only on how urban landscapes affect transmission within patches, but also on how individual hosts vary in their movement responses to urbanization. Some degree of habitat specialization has been reported across taxa, from insects to birds to mammals [350]. Our results show that host habitat affinity in heterogeneous landscapes can have clear downstream effects on population-level survival and infection prevalence.

In our model, urbanization had nonlinear effects on survival and infection prevalence in an urban-adapted host population, such that survival was lowest and infection prevalence peaked in partially urban landscapes. In these partially urban landscapes, urban and natural patches played different roles in driving population and infection dynamics. Urban patches persisted at high densities, which produced population sinks and high mortality rates. High host densities at urban sites also increased pathogen prevalence by promoting transmission, even though our model did not assume that contact rates would be inherently higher at urban patches (which is common due to aggregation in fragmented habitats or around human-provided food sources [338,353]). These results are consistent with field studies that report higher *Salmonella* infection prevalence in urban flocks of American white ibis (Murray et al., unpublished manuscript) and higher risk of disease-induced mortality in urban raccoons [355]. At the same time, our models showed the highest survival and lowest infection prevalence in 100% urban landscapes. In these fully urban landscapes, the lack of interpatch movement created low effective population sizes and limited pathogen spread. It is important to note, however, that this scenario – where resources are completely stable and uniform across space and time – is unlikely to occur frequently in the real world, since most cities include some natural areas (e.g., large parks or undeveloped sections) and would be best represented by a partially urban landscape in our model.

These general relationships between infection prevalence with urbanization align with results from other models of infection, movement, and resources. For example, mechanistic models have confirmed the importance of movement characteristics for infection dynamics, for example by showing that the effect of long-distance nomadic movements on outbreaks depends on movement frequency [327], and that outbreaks are more intense when hosts can detect suitable habitat over longer distances [356]. Similar to our result that urban sites promoted transmission in partially urban landscapes, one metapopulation model that incorporated the effects of urbanization on movement showed that that food provisioning tends to decrease infection prevalence when it promotes site fidelity [357]. Another individual-based model found that between-patch disease transmission was fastest at intermediate levels of landscape permeability [358]. In contrast, in another metapopulation model, toxicant-contaminated urban patches reduced landscape-level infection transmission by decreasing survival [359]. These contrasting results indicate that the effect of urbanization on infection prevalence depends on whether a species is urban-adapted or not (i.e., whether urban patches increase or decrease survival and movement). Together, these patterns suggest that urban patches drive pathogen transmission and natural patches drive pathogen spread in heterogeneous landscapes, but that the directions of these effects depend on a focal species' movement and survival responses to urbanization.

In our model, habitat specialization increased population-level survival, and this effect was particularly strong in partially urban landscapes. Host densities at urban patches were lower in the presence of specialization, which reduced density-dependent mortality rates. This pattern emerged despite the fact that parameters for individual-level traits (e.g., mortality rates μ_0 and μ_1) were equal across host types, which suggests that habitat specialization could increase host success even if it provides no *a priori* fitness benefit. Previous work has shown that niche specialization should affect fitness [284] and could potentially increase the range of habitats or geographic space over which a species can persist [360]; our results show that it can have further benefits by preventing source-sink dynamics in heterogeneous landscapes.

Habitat specialization also reduced infection prevalence by reducing host densities at urban patches and limiting movement between urban and nonurban patches. This reduced movement effectively created a spatially structured population; in structured populations, pathogens must be more transmissible in order to spread, since they must persist within a group long enough for movement to occur between groups [361]. These findings coincide with those from studies of bumblebees, in which strong individual specialization in flower use can affect foraging network structure [362], with potential effects on pathogen prevalence [363]. However, it is important to note that the relative timescales of contact and the transmissibility of a pathogen are important for the relationships between interpatch movements and the spread of infection. For example, feline immunodeficiency virus shows less genetic isolation than do its mountain lion hosts, possibly because the threshold for virus transmission is lower than that for gene flow among mountain lions [364]. These patterns suggest that habitat specialization could eventually drive the evolution of pathogen traits, such as recovery rates and virulence, that would allow them to persist in a spatially structured population [365,366].

Movement rates declined substantially as urbanization increased, with interpatch movements ultimately ceasing in fully urban landscapes. Though this pattern was important for limiting pathogen spread, it also indicates that provision of beneficial ecosystem services and functions by mobile wildlife could be at risk in urban landscapes. For example, nomadic movements of trumpeter hornbills more than double the probability of long-distance seed dispersal in a fragmented forested landscape [8], and reductions in movement would erode this transport service. Counterintuitively, specialization actually increased movement rates in many cases, both because it increased population sizes (and thus the potential number of individuals moving) and because it prevented hosts from getting “stuck” in urban patches. These effects were relatively small, but they indicate that specialization could provide some rescue from the negative effects of urbanization on movement. At the same time, specialization limited movements between habitat types, which could decrease dispersal of nutrients or seeds across ecosystem boundaries [41,260]. On the other hand, since urban habitats can be sources of pollutants and invasive species [367,368], specialization could prevent the export of these potentially harmful materials from urban sites [369].

Beyond their importance for understanding host-pathogen dynamics, our results imply that effectively managing infections in urban wildlife requires understanding how individuals respond to urbanization. For example, individual American white ibis vary in their use of urban and wetland habitats [348], and ibis in urban areas have high prevalence of *Salmonella* infection [293]. Similarly, transmission of *Mycoplasma gallisepticum* in house finches centers around domestic bird feeders [370]. If only some individuals specialize on or dominate use of feeders (e.g. as in house sparrows, [371]), population-wide infection spread will be limited. In each of these examples, using human-dominated landscapes (i.e., urban parks or bird feeders) to monitor population health would provide a biased sample in which infection prevalence is higher than in the population as a whole. In addition, our results reveal a potential tradeoff in the outcomes of habitat restoration. Restoration is beneficial because it can increase population sizes [222], especially for non-urban-adapted species. It can also reduce also the potential for spillover of zoonotic pathogens such as *Salmonella* and Hendra virus by drawing wildlife away from urban areas, where contact between humans and wildlife is more likely [372]. However, in our model, partially urban landscapes had the highest prevalence of infection, so restoration could have unintended consequences for wildlife health, especially if individuals move frequently between urban and restored habitats. Thus, monitoring and managing wildlife infectious diseases in urban areas will be more effective with a better understanding of how individuals differ in their responses to landscape heterogeneity.

These results motivate future investigations of the interactions between urbanization, wildlife movement, and health. Our model provides predictions for how urbanization should affect infection; integrating these predictions with observational data on resources, movement, survival, and infection in a real-world system would help understand the generality and condition-dependence of the model results. In addition, this flexible framework provides several opportunities for exploring additional interactions between movement and infection. First, infection can change movement patterns and habitat use; for example, coyotes are more likely to forage in urban areas when infected because human resources are easier to access [296]. Incorporating feedbacks between infection and movement could reveal different dynamics and applications to more systems. In addition, we used a simple susceptible-infected framework to model transmission, which can apply to bacteria, arthropods, or other pathogens in which immunity is minimal or nonexistent. Future models could incorporate different assumptions about immunity and transmission modes, for example seeking to model the Hendra virus-flying fox system [225], in which immunity is important, or the white ibis-*Salmonella* system, where bacteria can be transmitted via the environment [295]. Finally, specialization can have fitness consequences on its own [284], and future models could help understand the how pathogen transmission could affect the evolution of specialization, as well as how specialization could affect pathogen evolution.

ACKNOWLEDGEMENTS

This work was supported by a National Science Foundation (NSF) Graduate Research Fellowship to CST, NSF DEB-1754392 and NSF EEID grant DEB-1518611to SA and RJH, and NSF EEID grant DEB-1911925 to RJH. We thank the Hall and Altizer labs for helpful feedback on early versions of this model.

Table 6.1: Parameter descriptions and values

Parameter	Description	Units	Tested values
Movement parameters			
Proportion generalist	Proportion of hosts in the population with no habitat preference (r)	none	0, 0.5, 0.9, 1
Infection parameters			
β	Contact/transmission rate	/infected-day	0, 0.03, 0.06, 0.09, 0.15
γ	Recovery rate	/day	0, 0.03, 0.06, 0.09
ν	Maximum disease-induced mortality (when A=0)	/unit resource availability-day	0, 0.01, 0.1
Demography parameters			
μ_0	Density-independent mortality: natural mortality independent of resources or infection	/day	0.000, 0.001, 0.002
μ_1	Density-dependent mortality: depends on resource availability and patch density	unit resource availability/ individual-day	0.000, 0.002, 0.004
Other model parameters			
t_{max}	Simulation duration	weeks	40
τ_{max}	Timescale on which resources are updated and movement occurs	days	7
P	Number of patches in the system		10
Proportion urban	Proportion of patches that are urban		0, 0.1, 0.2, …, 1
A_u	Resource availability at urban patches		0.5

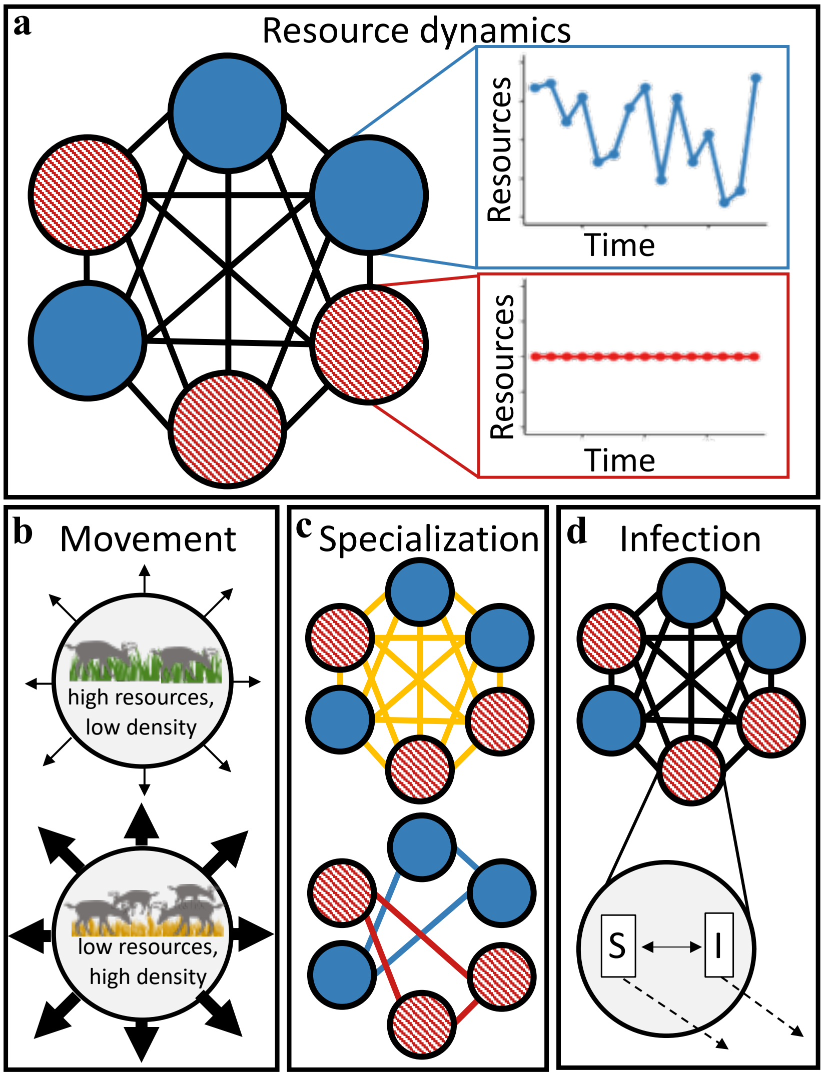


Figure 6.1: Model framework for inter-patch movement and infection dynamics. (a) The landscape is structured as a fully-connected network of patches. Natural sites (blue) have resources that vary over time, and urban sites (red, striped) have stable resources. (b) Departure from patches is a function of resource availability and host density. (c) Selection of a destination patch depends on habitat specialization. Generalists (orange, top) move indiscriminately with respect to habitat type; urban or natural specialists (bottom) move only to patches of their own type. (d) Infection and mortality occur within each patch according to an S-I-S framework.

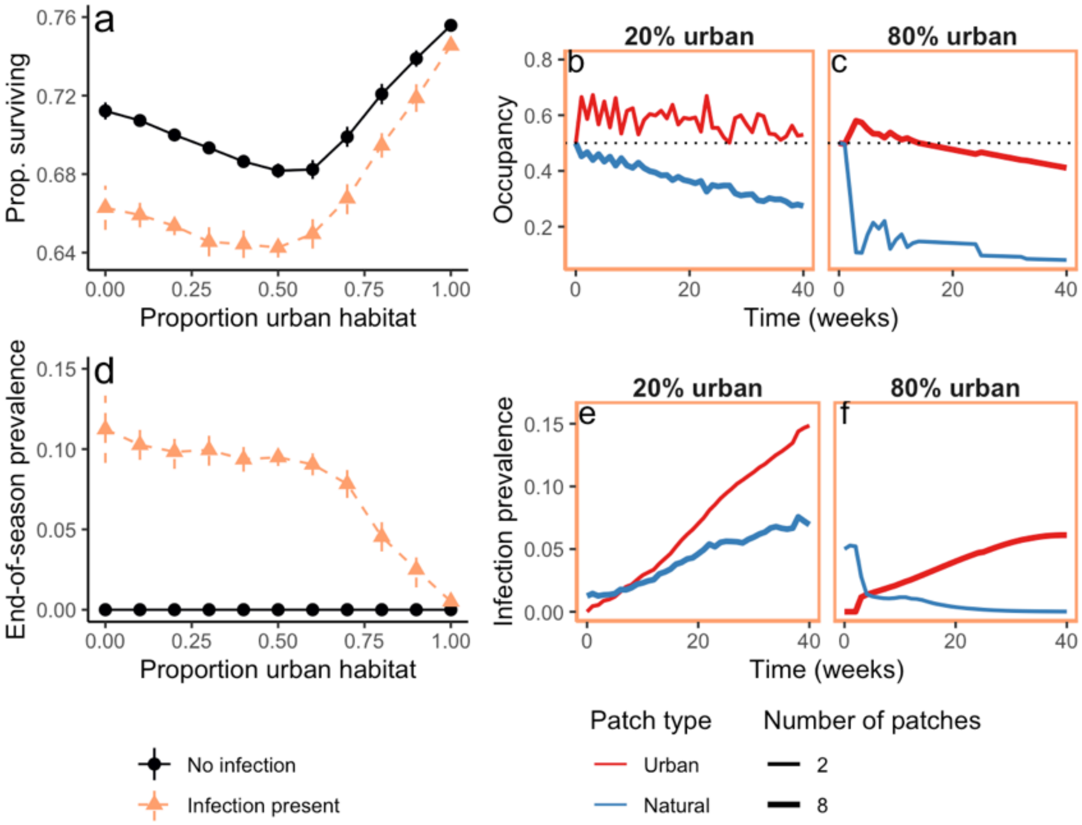


Figure 6.2: Effects of urbanization and infection on (a-c) the proportion of individuals surviving across the networks of patches and (d-f) mean infection prevalence, when there is no habitat specialization. (a) The fewest individuals survive in partially urban landscapes, both in the absence (black circles, solid line) and presence (orange triangles, dashed line) of infection. (b, c) Occupancy at urban patches is always higher than at natural patches. Occupancy is the mean population size at a patch of each type. The horizontal line at 0.5 is the carrying capacity of an urban site. In 20% urban landscapes, urban patches persist above carrying capacity because of immigration from natural patches. (d) End-of-season infection prevalence (proportion of the population that is infected at t=40 weeks) is highest in 0-60% urban landscapes. (e, f) Prevalence is always

higher at urban than at natural patches. Prevalence displayed is the mean prevalence at a site of a given type. Parameter values used for these simulations are shown in Table 6.1. Error bars in (a, d) show the standard deviation of the mean across eight simulations.

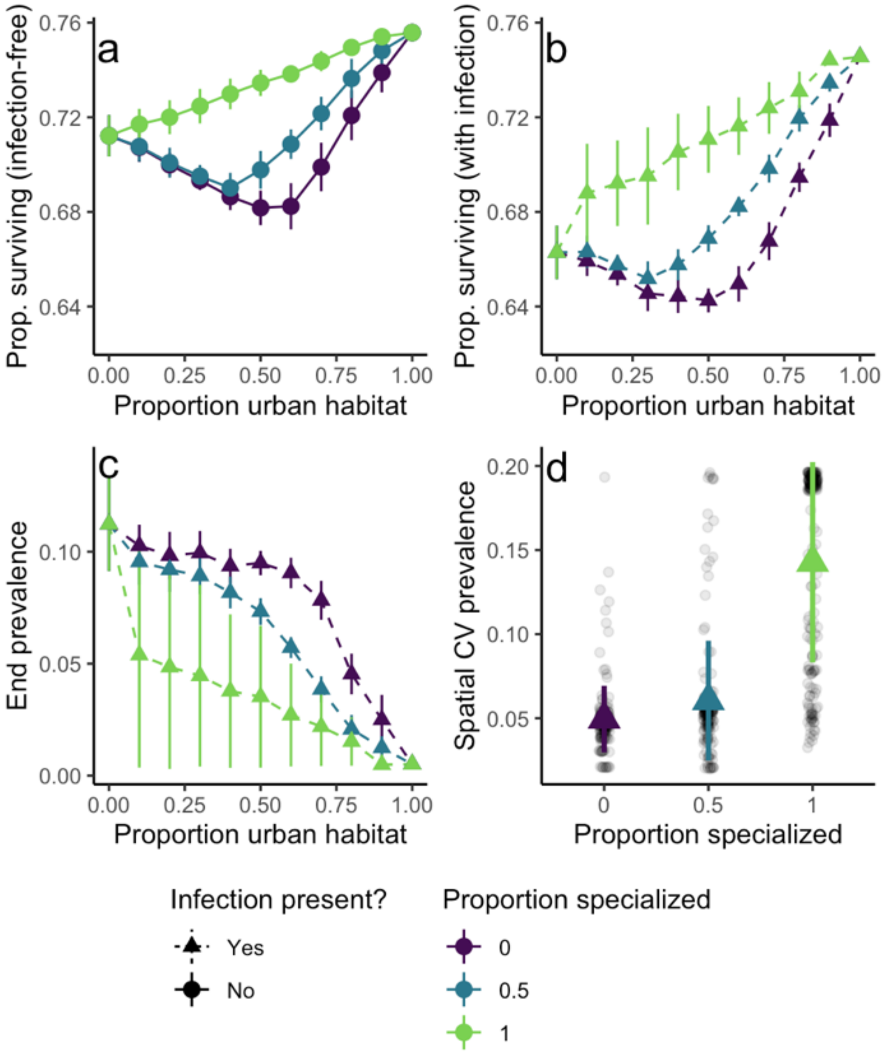


Figure 6.3: Effects of host habitat specialization on (a, b) population-level survival and (c, d) infection prevalence. (a) Specialization (blue and green lines) increases survival relative to full generalism. (b) In the presence of infection, specialization further increases population-level survival. (c) Specialization reduces infection prevalence, especially in partially urban landscapes. In (a-c), error bars show the standard deviation

of the mean across eight simulations. (d) Specialization increases spatial variation in infection prevalence, measured as the coefficient of variation in infection prevalence across patches ($\mathrm{CV} = \frac{\sigma}{\mu}$). Each bar shows the mean and standard deviation of the CV of prevalence across all partially urban landscapes (i.e., 0 < proportion urban < 1). Partially transparent points are data from individual simulations.

CHAPTER 7

CONCLUSIONS

The overarching goal of this dissertation was to examine relationships between resource dynamics, animal movement patterns, and infectious disease transmission in wildlife, particularly in human-dominated landscapes. I focused on nomadic animal movements, an unpredictable long-distance movement pattern that is widespread but poorly understood relative to seasonal migration. I first conducted a literature review on nomadic animal movements to synthesize current information and identify research gaps (Chapter 2). In the subsequent chapters, I further explored three outstanding questions identified in Chapter 2: (1) what mechanisms do nomadic animals use when moving?; (2) what effects do nomadic movements have on species interactions, communities, and ecosystems, in particular infectious disease dynamics?; and (3) what is the ecology of partially nomadic and seasonally nomadic species?

In Chapter 2, I found that multiple mechanisms could potentially underlie nomadic movements, especially given that nomadism is prevalent across diverse taxa. Based on this finding, in Chapter 4 I explored the cues that nomadic animals might use when deciding when to depart one location and move to another. I found that animals using decision rules that incorporated resources and conspecific density outperformed residents in the variable landscapes in which nomadic animals live. However, the benefits of these nomadic movement rules declined in more stable landscapes. I also found that nomadic animals that moved using density and resource cues moved less in landscapes with stable resources, which could allow them to adapt to urban environments. Accordingly, when I used GPS tracking data to investigate nomadic movements of American white ibis in Chapter 5, I found that ibis that used urban areas had the least variation in their habitat use. This habitat specialization by ibis produced a network of sites that was sparsely connected. Together, these two studies suggest that nomadic animal movements perform better in variable than in stable landscapes, which is consistent with the geographic distribution of nomadic animals [22]. At the same time, both studies show that the mechanisms of nomadic movements could allow nomadic animals to modify their behavior when resource dynamics change. As such, although nomadic animals are threatened by human development [256], many nomadic species might be able to adapt to continuing human development by reducing their movement rates and becoming more resident. Future studies of longitudinal changes in nomadic animal movement patterns could test this hypothesis and identify what factors limit ability of nomadic animals to adapt to changing landscapes.

These changes in movement patterns in human-modified landscapes could affect nomads' roles in dispersing propagules, including pathogens, across space. In Chapter 2, I found that nomadic movements could affect community composition and ecosystem functioning through transport and trophic effects, but that these interactions are not well described. In Chapter 6, I explored one potential effect of nomadic movements by modeling infectious disease transmission across a network of urban and natural sites, where hosts were either habitat generalists (i.e., nomads) or specialized on urban or natural habitats. I found that movement patterns that were more nomadic tended to increase pathogen prevalence compared to a population containing habitat specialists, especially in natural and partially urban landscapes. This result stemmed from the importance of both movement and density for pathogen transmission; in undeveloped landscapes, movement rates were high, but density was low, which limited pathogen transmission. In other words, nomadic movements tended to increase pathogen spread, but mainly when they were coupled with high-density locales (i.e., urban sites). However, this pattern stands in contrast to that from Chapter 3, where I compared parasite species richness across ungulate species with different movement strategies. In this study, nomads had lower parasite species richness than migrants, and equivalent parasite species richness to residents. Further, group size was unrelated to parasite diversity. The discrepancy between these results could stem from the different measurements used in each study (i.e., parasite prevalence vs. parasite diversity) [11]. Future studies that explore how movement affects different metrics of parasitism could tease apart these complex relationships. However, despite their differences, both studies show that the exact patterns of nomadic movements drive their effects on parasitism. The unique characteristics of nomadic movements (e.g., the tight relationship between nomadic movements and resources; their high spatio-temporal flexibility) mean that nomadism, migration, and site fidelity can affect species interactions in divergent ways (see [19,373]).

Although nomadism is classically construed as a population-level and year-round trait, it can also be partial or seasonal, where some of the population is nomadic or nomadism occurs during only part of the year. Characterizing the axes of this diversity was one key outcome of Chapter 2. I further explored the consequences of this variation in nomadic behavior in Chapters 5 and 6. In Chapter 5, I focused on American white ibis, which migrate to breed and are nomadic during the nonbreeding season (i.e., seasonal nomadism). The results from this study show that ibis can also be classified as partially nomadic, since some individuals showed signs of site fidelity during the nonbreeding season. Partial nomadism was linked to urban areas, which highlights the context-dependence of the different types of nomadic behavior. In Chapter 6, I examined the consequences of this variation in nomadic movement, where some individuals in a population were specialized while others were fully nomadic. Specialization tended to increase survival and decrease pathogen prevalence, even when only a portion of the population was specialized. Individual variation in movement patterns exists across taxa and can be driven by multiple interacting forces at different scales [17,282]. The results from Chapters 5 and 6 highlight that this variation among individuals within a population might be particularly common in heterogeneous urban areas, and that it can have direct effects on population- and community-level outcomes. Future studies that link variation in movement behavior to patterns of infectious disease prevalence in empirical systems would help clarify when and where infectious disease dynamics respond most strongly to individual variation in movement. Understanding the scale and characteristics of this variation will important for making management and conservation decisions, especially for wildlife in urban areas [17].

This dissertation provides insight into several fundamental aspects of nomadic movement behavior. At its core, nomadism is a response to spatiotemporal variation in resource availability, as discussed in Chapter 2. The conservation of highly mobile animals has usually focused on resource quantity or barriers to movement [256,374]; by studying nomadic movements in resource-variable and resource-stable environments, my results highlight that resource variability, not just resource quantity or connectivity, is important for preserving nomadic animal movements. Further, this dissertation shows that these movements are important for processes at the community and ecosystem levels. Chapter 5 reveals low connectivity in the ibis movement network in an urban area, which suggests that changes to nomadic movement patterns could reduce the transport of nutrients and microbes across space. Chapter 6 supports this hypothesis for a hypothetical infectious disease, and Chapter 3 illustrates that parasitism differs between nomadic ungulates and seasonal migrants at a broad spatial and taxonomic scale. Together, these chapters show that resource variability is a key driver of movement patterns and their linked species interactions across taxa.

The importance of resource variability has implications for conservation and management. Specifically, if conservation projects aim to protect nomadic animal movements and the services they provide, they must promote resource variability in preserved or restored landscapes. Human development tends to stabilize resource availability over space and time through actions like irrigation and planting of non-native plant species [226], and it can be tempting to provide year-round resources for wildlife, especially those of conservation concern. However, this work emphasizes that times and places of low resource availability might actually be crucial for maintaining species movement. For example, this dissertation and other empirical studies (e.g. [10]) show that periods of resource scarcity are important for the mechanisms that link movement and infection dynamics. Nomadic movements probably play a similar role in the dispersal of seeds and nutrients [8]. Strategies to maintain this resource variability could include: focusing on native plant species that have natural periods of dormancy [375]; maintaining seasonal or irregular cycles of water availability in irrigated landscapes [376]; and managing livestock or other competing species in areas shared with wildlife [377]. Implementing any of these or similar strategies could help support nomadic populations, as long as the landscape provides sufficient resource availability and connectivity between habitat patches.

Highly mobile wildlife, including nomads, are widespread and serve an essential function in their ecosystems. Therefore, conserving these animals is essential for biodiversity and ecosystem functioning. As human development continues, diverse conservation strategies are needed, including both preserving natural habitats for species that are unable to adapt to urban life and promoting wildlife adaptation to developed landscapes. This dissertation provides a better understanding of several key elements of these management decisions – cues for movement, variation among individuals, and effects of movement on infectious diseases – and provides implications of these findings for the conservation of nomadic animal populations.

REFERENCES

1 Cote, J. *et al.* (2016) Behavioural synchronization of large-scale animal movements - disperse alone, but migrate together? *Biol. Rev.* 92, 1275–1296

2 Hedenström, A. (2008) Adaptations to migration in birds: behavioural strategies, morphology and scaling effects. *Philos. Trans. R. Soc. London B Biol. Sci.* 363, 287–99

3 Morales, J.M. *et al.* (2010) Building the bridge between animal movement and population dynamics. *Philos. Trans. R. Soc. B Biol. Sci.* 365, 2289–2301

4 Mueller, T. and Fagan, W. (2008) Search and navigation in dynamic environments–from individual behaviors to population distributions. *Oikos* 117, 654–664

5 Levey, D.J. and Stiles, F.G. (1992) Evolutionary precursors of long-distance migration: Resource availability and movement patterns in neotropical landbirds. *Am. Nat.* 140, 447–476

6 Abrahms, B. *et al.* (2020) Emerging Perspectives on Resource Tracking and Animal Movement Ecology. *Trends Ecol. Evol.* In Press, 1–13

7 Bauer, S. and Hoye, B.J. (2014) Migratory animals couple biodiversity and ecosystem functioning worldwide. *Science* 344, 1242552

8 Mueller, T. *et al.* (2014) Large frugivorous birds facilitate functional connectivity of fragmented landscapes. *J. Appl. Ecol.* 51, 684–692

9 Nathan, R. *et al.* (2008) Mechanisms of long-distance seed dispersal. *Trends Ecol.*

Evol. 23, 638–647

10 Altizer, S. *et al.* (2011) Animal migration and infectious disease risk. *Science* 331, 296–302

11 Shaw, A.K. *et al.* (2018) Metrics matter: The effect of parasite richness, intensity and prevalence on the evolution of host migration. *Proc. R. Soc. B Biol. Sci.* 285,

12 Ezenwa, V.O. *et al.* (2016) Host behaviour – parasite feedback: an essential link between animal behaviour and disease ecology. *Proc. R. Soc. B* 283, 20153078

13 Batalden, R. V and Oberhauser, K.S. (2015) Potential changes in eastern North American monarch migration in response to an introduced milkweed, *Asclepias curassavica*. In *Monarchs in a changing world: Biology and conservation of an iconic butterfly* pp. 215–224, Cornell University Press Ithaca, NY

14 Teitelbaum, C.S. *et al.* (2016) Experience drives innovation of new migration patterns of whooping cranes in response to global change. *Nat. Commun.* 7, 12793

15 Jones, J.D. *et al.* (2014) Supplemental feeding alters migration of a temperate ungulate. *Ecol. Appl.* 24, 1769–1779

16 Spiegel, O. *et al.* (2017) What's your move? Movement as a link between personality and spatial dynamics in animal populations. *Ecol. Lett.* 20, 3–18

17 Merrick, M.J. and Koprowski, J.L. (2017) Should we consider individual behavior differences in applied wildlife conservation studies? *Biol. Conserv.* 209, 34–44

18 Orams, M.B. (2002) Feeding wildlife as a tourism attraction: A review of issues and impacts. *Tour. Manag.* 23, 281–293

19 Satterfield, D.A. *et al.* (2015) Loss of migratory behaviour increases infection risk for a butterfly host. *Proc. R. Soc. B Biol. Sci.* 282, 20141734–20141734

20 Hall, R.J. *et al.* (2014) Greater migratory propensity in hosts lowers pathogen transmission and impacts. *J. Anim. Ecol.* 83, 1068–1077

21 Dingle, H. (2014) *Migration: the Biology of Life on the Move*, Oxford University Press, USA.

22 Jonzén, N. *et al.* (2011) Uncertainty and predictability: the niches of migrants and nomads. In *Animal Migration: A Synthesis* (Milner-Gulland, E. J. et al., eds), pp. 91–109, Oxford University Press

23 Olson, K.A. *et al.* (2010) Annual movements of Mongolian gazelles: Nomads in the Eastern Steppe. *J. Arid Environ.* 74, 1435–1442

24 Roshier, D. *et al.* (2008) What drives long-distance movements in the nomadic Grey Teal *Anas gracilis* in Australia? *Ibis* 150, 474–484

25 Gaidet, N. *et al.* (2010) Potential spread of highly pathogenic avian influenza H5N1 by wildfowl: Dispersal ranges and rates determined from large-scale satellite telemetry. *J. Appl. Ecol.* 47, 1147–1157

26 Tracey, J.P. *et al.* (2004) The role of wild birds in the transmission of avian influenza for Australia: An ecological perspective. *Emu* 104, 109–124

27 Morgan, E.R. *et al.* (2006) Assessing risks of disease transmission between wildlife and livestock: The Saiga antelope as a case study. *Biol. Conserv.* 131, 244–254

28 McEvoy, J.F. *et al.* (2015) Proximate cues to phases of movement in a highly dispersive waterfowl, *Anas superciliosa*. *Mov. Ecol.* 3, 1–13

29 Cottee-Jones, H.E.W. *et al.* (2015) The movement shortfall in bird conservation: Accounting for nomadic, dispersive and irruptive species. *Anim. Conserv.* 19, 227–

234

30 Mueller, T. *et al.* (2011) How landscape dynamics link individual- to population-level movement patterns: a multispecies comparison of ungulate relocation data. *Glob. Ecol. Biogeogr.* 20, 683–694

31 Nathan, R. *et al.* (2008) A movement ecology paradigm movement research for unifying organismal movement research. *Proc. Natl. Acad. Sci. U. S. A.* 105, 19052–19059

32 Cote, J. *et al.* (2017) Behavioural synchronization of large-scale animal movements – disperse alone, but migrate together? *Biol. Rev.* 92, 1275–1296

33 Avgar, T. *et al.* (2014) On the adaptive benefits of mammal migration. *Can. J. Zool.* 92, 481–490

34 Kays, R. *et al.* (2015) Terrestrial animal tracking as an eye on life and planet. *Science* 348, 1222–1232

35 Rodríguez, J.P. *et al.* (2017) Big data analyses reveal patterns and drivers of the movements of southern elephant seals. *Sci. Rep.* 7, 1–10

36 Wheat, R.E. *et al.* (2017) To migrate, stay put, or wander? Varied movement strategies in bald eagles (*Haliaeetus leucocephalus*). *Mov. Ecol.* 5, 1–10

37 Hays, G. *et al.* (2006) Flexible foraging movements of leatherback turtles across the north atlantic ocean. *Ecology* 87, 2647–2656

38 Bunnefeld, N. *et al.* (2011) A model-driven approach to quantify migration patterns: individual, regional and yearly differences. *J. Anim. Ecol.* 80, 466–76

39 Runge, C.A. *et al.* (2014) Conserving mobile species. *Front. Ecol. Environ.* 12, 395–402

40 Bracis, C. and Mueller, T. (2017) Memory, not just perception, plays an important role in terrestrial mammalian migration. *Proc. R. Soc. B Biol. Sci.* 284, 20170449

41 Earl, J.E. and Zollner, P.A. (2017) Advancing research on animal-transported subsidies by integrating animal movement and ecosystem modelling. *J. Anim. Ecol.* 86, 987–997

42 Runge, C.A. *et al.* (2015) Geographic range size and extinction risk assessment in nomadic species. *Conserv. Biol.* 29, 865–876

43 Heape, W. (1931) *Emigration, Migration and Nomadism*, W. Heffer & Sons.

44 Bastille-Rousseau, G. *et al.* (2016) Flexible characterization of animal movement pattern using net squared displacement and a latent state model. *Mov. Ecol.* 4, 1–12

45 Singh, N.J. *et al.* (2012) From migration to nomadism: movement variability in a northern ungulate across its latitudinal range. *Ecol. Appl.* 22, 2007–2020

46 Abrahms, B. *et al.* (2017) Suite of simple metrics reveals common movement syndromes across vertebrate taxa. *Mov. Ecol.* 5, 1–11

47 Alerstam, T. (2006) Conflicting evidence about long-distance animal navigation. *Science* 313, 791–794

48 Roshier, D.A. and Reid, J.R.W. (2003) On animal distributions in dynamic landscapes. *Ecography* 26, 539–544

49 Ofstad, E.G. *et al.* (2016) Home ranges, habitat and body mass: simple correlates of home range size in ungulates. *Proc. R. Soc. B Biol. Sci.* 283, 1–8

50 Tucker, M.A. *et al.* (2014) Evolutionary predictors of mammalian home range size: Body mass, diet and the environment. *Glob. Ecol. Biogeogr.* 23, 1105–1114

51 McNab, B.K. (1963) Bioenergetics and the determination of home range size. *Am. Nat.* 97, 133–140

52 Mueller, T. *et al.* (2008) In search of forage: predicting dynamic habitats of Mongolian gazelles using satellite-based estimates of vegetation productivity. *J. Appl. Ecol.* 45, 649–658

53 Tracz, B. V *et al.* (2007) Annual and monthly range fidelity of female boreal woodland caribou in response to petroleum development. *Landsc. Manag.* 30, 31–44

54 Berbert, J.M. and Fagan, W.F. (2012) How the interplay between individual spatial memory and landscape persistence can generate population distribution patterns. *Ecol. Complex.* 12, 1–12

55 Loarie, S.R. *et al.* (2009) Fences and artificial water affect African savannah elephant movement patterns. *Biol. Conserv.* 142, 3086–3098

56 Bennetts, R.E. and Kitchens, W.M. (2000) Factors influencing movement probabilities of a nomadic food specialist: proximate foraging benefits or ultimate gains from exploration? *Oikos* 91, 459–467

57 Ito, T.Y. *et al.* (2013) Effects of interannual variations in environmental conditions on seasonal range selection by Mongolian gazelles. *J. Arid Environ.* 91, 61–68

58 Morrison, J.L. and Wood, P.B. (2009) Broadening our approaches to studying dispersal in raptors. *J. Raptor Res.* 43, 81–89

59 Tucker, A.D. *et al.* (1997) Movements and home ranges of *Crocodylus johnstoni* in the Lynd River, Queensland. *Wildl. Res.* 24, 379–396

60 Greenwood, P.J. and Harvey, P.H. (1982) The natal and breeding dispersal of

birds. *Annu. Rev. Ecol. Syst.* 13, 1–21

61 Acosta, C.A. (2002) Spatially explicit dispersal dynamics and equilibrium population sizes in marine harvest refuges. *ICES J. Mar. Sci.* 59, 458–468

62 Howard, W.E. (1960) Innate and environmental dispersal of individual vertebrates. *Am. Midl. Nat.* 63, 152–161

63 Frederick, P.C. *et al.* (1996) Conservation of large, nomadic populations of White Ibises (*Eudocimus albus*) in the United States. *Conserv. Biol.* 10, 203–216

64 McNaughton, S.J. (1985) Ecology of a grazing ecosystem: the Serengeti. *Ecol. Monogr.* 55, 259–294

65 Chapman, J.W. *et al.* (2015) Long-range seasonal migration in insects: Mechanisms, evolutionary drivers and ecological consequences. *Ecol. Lett.* 18, 287–302

66 Quinn, T.P. and Brodeur, R.D. (1991) Intra-Specific Variations in the Movement Patterns of Marine Animals. *Am. Zool.* 31, 231–241

67 Grüss, A. *et al.* (2011) Consequences of adult and juvenile movement for marine protected areas. *Biol. Conserv.* 144, 692–702

68 Dean, W.R.J. (2004) *Nomadic Desert Birds*, Springer-Verlag.

69 Heupel, M.R. *et al.* (2010) Large-scale movement and reef fidelity of grey reef sharks. *PLoS One* 5, e9650

70 Hussey, N.E. *et al.* (2015) Aquatic animal telemetry: A panoramic window into the underwater world. *Science* 348, 1255642–1255642

71 Clark, J.A. and May, R.M. (2002) Taxonomic bias in conservation research. *Science* 297, 191–192

72 Chapman, B.B. *et al.* (2011) The ecology and evolution of partial migration. *Oikos* 120, 1764–1775

73 Butler IV, M.J. (1995) Cascading disturbances in Florida Bay, USA: cyanobacteria blooms, sponge mortality, and implications for juvenile spiny lobsters *Panulirus argus*. *Mar. Ecol. Prog. Ser.* 129, 119–125

74 Marzluff, J.M. and Heinrich, B. (1991) Foraging by common ravens in the presence and absence of territory holders: an experimental analysis of social foraging. *Anim. Behav.* 42, 755–770

75 Hipkiss, T. *et al.* (2002) Sex ratio and age structure of nomadic Tengmalm's owls: a molecular approach. *J. Avian Biol.* 33, 107–110

76 Lenz, J. *et al.* (2015) Nomadism and seasonal range expansion in a large frugivorous bird. *Ecography* 38, 54–62

77 Eby, P. *et al.* (1999) The distribution, abundance and vulnerability to population reduction of a nomadic nectarivore, the Grey-headed Flying-fox *Pteropus poliocephalus* in New South Wales, during a period of resource concentration. *Aust. Zool.* 31, 240–253

78 Newton, I. (2006) Advances in the study of irruptive migration. *Ardea* 94, 433–460

79 Hollyer, J.N. (1970) The invasion of nutcrackers in autumn 1968. *Br. Birds* 63, 353–373

80 Svärdson, G. (1957) The "invasion" type of bird migration. *Br. Birds* 50, 314–343

81 Hochachka, W.M. *et al.* (1999) Irruptive migration of common redpolls. *Condor* 101, 195–204

82 Pedler, R.D. *et al.* (2014) Extreme nomadism in desert waterbirds: flights of the banded stilt. *Biol. Lett.* 10, 1–5

83 Pedgley, D.E. (1981) *Desert Locust Forecasting Manual*, Centre for Overseas Pest Research.

84 Mettke-Hofmann, C. *et al.* (2012) Residency and a broad feeding spectrum are related to extensive spatial exploration in parrots. *Behav. Ecol.* 23, 1365–1371

85 Tear, T.H. *et al.* (1997) Landscape-scale foraging decisions by reintroduced Arabian Oryx. *J. Wildl. Manage.* 61, 1142–1154

86 Andersson, M. and Erlinge, S. (1977) Influence of predation on rodent populations. *Oikos* 29, 591–597

87 Wesołowski, T. *et al.* (2009) Wood Warbler *Phylloscopus sibilatrix*: a nomadic insectivore in search of safe breeding grounds? *Bird Study* 56, 26–33

88 Bonte, D. *et al.* (2012) Costs of dispersal. *Biol. Rev.* 87, 290–312

89 Dean, W.R.J. *et al.* (2009) When to stay, when to go: trade-offs for southern African arid-zone birds in times of drought. *S. Afr. J. Sci.* 105, 24–28

90 Kaczensky, P. *et al.* (2011) The danger of having all your eggs in one basket-winter crash of the re-introduced Przewalski's Horses in the Mongolian Gobi. *PLoS One* 6, 1–8

91 Stear, M.J. *et al.* (2007) Alternatives to anthelmintics for the control of nematodes in livestock. *Parasitology* 134, 139–151

92 McGlynn, T.P. (2012) The ecology of nest movement in social Insects. *Annu. Rev. Entomol.* 57, 291–308

93 Skogland, T. (1991) What are the effects of predators on large ungulate

populations? *Oikos* 61, 401–411

94 Szymkowiak, J. and Kuczyński, L. (2015) Avoiding predators in a fluctuating environment: responses of the wood warbler to pulsed resources. *Behav. Ecol.* 26, 601–608

95 Winkler, D.W. *et al.* (2014) Cues, strategies, and outcomes: how migrating vertebrates track environmental change. *Mov. Ecol.* 2, 10

96 Harris, G. *et al.* (2009) Global decline in aggregated migrations of large terrestrial mammals. *Endanger. Species Res.* 7, 55–76

97 Roshier, D.A. *et al.* (2008) Animal movement in dynamic landscapes: Interaction between behavioural strategies and resource distributions. *Oecologia* 156, 465–477

98 Hancock, P.A. *et al.* (2006) Modelling the many-wrongs principle: The navigational advantages of aggregation in nomadic foragers. *J. Theor. Biol.* 240, 302–310

99 Mariette, M.M. and Griffith, S.C. (2012) Conspecific attraction and nest site selection in a nomadic species, the zebra finch. *Oikos* 121, 823–834

100 Bischof, R. *et al.* (2012) A migratory northern ungulate in the pursuit of spring: Jumping or surfing the green wave? *Am. Nat.* 180, 407–424

101 Fagan, W.F. *et al.* (2017) Perceptual ranges, information gathering, and foraging success in dynamic landscapes. *Am. Nat.* 189, 474–489

102 Coughenour, M.B. (1991) Spatial components of plant-herbivore interactions in pastoral, ranching, and native ungulate ecosystems. *J. Rangel. Manag.* 44, 530–542

103 Stojanovic, D. *et al.* (2015) Exploiting the richest patch has a fitness pay-off for

the migratory swift parrot. *J. Anim. Ecol.* 84, 1194–1201

104 Bolger, D.T. *et al.* (2007) The need for integrative approaches to understand and conserve migratory ungulates. *Ecol. Lett.* 11, 63–77

105 Milner-Gulland, E.J. and Lhagvasuren, B. (1998) Population dynamics of the Mongolian gazelle *Procapra gutturosa*: An historical analysis. *J. Appl. Ecol.* 35, 240–251

106 Slatkin, M. (1987) Gene flow and the geographic structure of natural populations. *Science* 236, 787–792

107 Soare, T.W. *et al.* (2014) Genetic evidence for landscape effects on dispersal in the army ant *Eciton burchellii*. *Mol. Ecol.* 23, 96–109

108 Green, A.J. *et al.* (2008) The potential role of waterbirds in dispersing invertebrates and plants in arid Australia. *Freshw. Biol.* 53, 380–392

109 Lundberg, J. and Moberg, F. (2003) Mobile link organisms and ecosystem functioning: Implications for ecosystem resilience and management. *Ecosystems* 6, 87–98

110 Couvreur, M. *et al.* (2004) Large herbivores as mobile links between isolated nature reserves through adhesive seed dispersal. *Appl. Veg. Sci.* 7, 229–236

111 Craft, M.E. *et al.* (2009) Distinguishing epidemic waves from disease spillover in a wildlife population. *Proc. R. Soc. B Biol. Sci.* 276, 1777–1785

112 Teitelbaum, C.S. *et al.* (2018) Migratory behaviour predicts greater parasite diversity in ungulates. *Proc. R. Soc. B Biol. Sci.* 285, 1–8

113 Sundell, J. (2006) Experimental tests of the role of predation in the population dynamics of voles and lemmings. *Mamm. Rev.* 36, 107–141

114 Knapp, A.K. *et al.* (1999) The keystone role of bison in American tallgrass prairie. *Bioscience* 49, 39–50

115 Robinson, R.A. *et al.* (2009) Travelling through a warming world: climate change and migratory species. *Endanger. Species Res.* 7, 87–99

116 Martin, T.G. *et al.* (2007) Optimal conservation of migratory species. *PLoS One* 2, 3–7

117 Roshier, D.. *et al.* (2002) Responses of waterbirds to flooding in an arid region of Australia and implications for conservation. *Biol. Conserv.* 106, 399–411

118 Nandintsetseg, D. *et al.* (2016) Spatiotemporal habitat dynamics of ungulates in unpredictable environments: The khulan (*Equus hemionus*) in the Mongolian Gobi desert as a case study. *Biol. Conserv.* 204, 313–321

119 Bull, J.W. *et al.* (2013) Conservation when nothing stands still: Moving targets and biodiversity offsets. *Front. Ecol. Environ.* 11, 203–210

120 Reynolds, M.D. *et al.* (2017) Dynamic conservation for migratory species. *Sci. Adv.* 3, e1700707

121 McPherson, J.M. and Jetz, W. (2007) Effects of species' ecology on the accuracy of distribution models. *Ecography* 30, 135–151

122 Fryxell, J.M. *et al.* (2004) Predictive models of movement by Serengeti grazers. *Ecology* 85, 2429–2435

123 Gilroy, J.J. *et al.* (2016) Migratory diversity predicts population declines in birds. *Ecol. Lett.* 19, 308–317

124 Neumann, W. *et al.* (2015) Opportunities for the application of advanced remotely-sensed data in ecological studies of terrestrial animal movement. *Mov. Ecol.* 3, 8

125 Torney, C.J. *et al.* (2018) From single steps to mass migration : the problem of scale in the movement ecology of the Serengeti wildebeest. *Philos. Trans. R. Soc. B Biol. Sci.* 373, 20170012

126 Heinrich, B. (1988) Winter foraging at carcasses by three sympatric corvids, with emphasis on recruitment by the raven, *Corvus corax*. *Behav. Ecol. Sociobiol.* 23, 141–156

127 Schofield, G. *et al.* (2010) Inter-annual variability in the home range of breeding turtles: Implications for current and future conservation management. *Biol. Conserv.* 143, 722–730

128 Herrnkind, W.F. (1980) Spiny lobsters: patterns of movement. In *Biology and Management of Lobsters: Physiology and Behavior* pp. 349–407

129 Zaccara, S. *et al.* (2011) Lesser Flamingo *Phoeniconaias minor* as a nomadic species in African shallow alkaline lakes and pans: Genetic structure and future perspectives. *Ostrich* 82, 95–100

130 Noonan, M.J. *et al.* (2018) A comprehensive analysis of autocorrelation and bias in home range estimation. *Ecol. Monogr.* 89, e01344

131 Gurarie, E. *et al.* (2017) A framework for modelling range shifts and migrations: asking when, whither, whether and will it return. *J. Anim. Ecol.* 86, 943–959

132 Fleming, C.H. *et al.* (2014) From fine-scale foraging to home ranges: a semivariance approach to identifying movement modes across spatiotemporal scales. *Am. Nat.* 183, E154–E167

133 Calabrese, J.M. *et al.* (2018) Disentangling social interactions and environmental drivers in multi-individual wildlife tracking data. *Philos. Trans. R. Soc. B Biol. Sci.*

373, 20170007

134 Hancock, P.A. and Milner-Gulland, E.J. (2006) Optimal movement strategies for social foragers in unpredictable environments. *Ecology* 87, 2094–2102

135 Guttal, V. and Couzin, I.D. (2010) Social interactions, information use, and the evolution of collective migration. *Proc. Natl. Acad. Sci. U. S. A.* 107, 16172–16177

136 Olson, K.A. *et al.* (2009) A mega-herd of more than 200,000 Mongolian gazelles *Procapra gutturosa*: a consequence of habitat quality. *Oryx* 43, 149–153

137 Buehler, D.M. *et al.* (2010) How do migratory species stay healthy over the annual cycle? A conceptual model for immune function and for resistance to disease. *Integr. Comp. Biol.* 50, 346–357

138 Figuerola, J. and Green, A.J. (2000) Haematozoan parasites and migratory behaviour in waterfowl. *Evol. Ecol.* 14, 143–153

139 Koprivnikar, J. and Leung, T.L.F. (2015) Flying with diverse passengers: Greater richness of parasitic nematodes in migratory birds. *Oikos* 124, 399–405

140 Leung, T.L.F. and Koprivnikar, J. (2016) Nematode parasite diversity in birds: the role of host ecology, life history, and migration. *J. Anim. Ecol.* 85, 1471–1480

141 Altizer, S. *et al.* (2015) Do healthy monarchs migrate farther? Tracking natal origins of parasitized vs. uninfected monarch butterflies overwintering in Mexico. *PLoS One* 10, e0141371

142 Ezenwa, V.O. (2004) Host social behavior and parasitic infection: A multifactorial approach. *Behav. Ecol.* 15, 446–454

143 Gutierrez, J.S. *et al.* (2017) Migration and parasitism: habitat use, not migration

distance, influences helminth species richness in Charadriiform birds. *J. Biogeogr.* 44, 1137–1147

144 Apollonio, M. *et al.* (2010) *European ungulates and their management in the 21st century*, Cambridge University Press.

145 Fritzsche McKay, A. and Hoye, B.J. (2016) Are migratory animals superspreaders of infection? *Integr. Comp. Biol.* 56, 260–267

146 Aikens, E.O. *et al.* (2017) The greenscape shapes surfing of resource waves in a large migratory herbivore. *Ecol. Lett.* 20, 741–750

147 Somveille, M. *et al.* (2015) Why do birds migrate? A macroecological perspective. *Glob. Ecol. Biogeogr.* 24, 664–674

148 Gómez, C. *et al.* (2016) Niche-tracking migrants and niche-switching residents: evolution of climatic niches in New World warblers (Parulidae). *Proc. R. Soc. B Biol. Sci.* 283, 20152458

149 Altizer, S. *et al.* (2006) Seasonality and the dynamics of infectious diseases. *Ecol. Lett.* 9, 467–484

150 Nunn, C.L. *et al.* (2005) Latitudinal gradients of parasite species richness in primates. *Divers. Distrib.* 11, 249–256

151 Guernier, V. *et al.* (2004) Ecology drives the worldwide distribution of human diseases. *PLoS Biol.* 2, e141

152 Epstein, P. (2010) The ecology of climate change and infectious disease. *Ecology* 3, 925–928

153 Møller, A.P. *et al.* (2013) Assessing the effects of climate on host-parasite interactions: A comparative study of european birds and their parasites. *PLoS One*

8, e82886

154 Bartel, R. *et al.* (2011) Monarch butterfly migration and parasite transmission in eastern North America. *Ecology* 92, 342–351

155 Shaw, A.K. and Binning, S.A. (2016) Migratory recovery from infection as a selective pressure for the evolution of migration. *Am. Nat.* 187, 491–501

156 Folstad, I. *et al.* (1991) Parasite avoidance: the cause of post-calving migrations in Rangifer? *Can. J. Zool.* 69, 2423–2429

157 Johns, S. and Shaw, A.K. (2016) Theoretical insight into three disease-related benefits of migration. *Popul. Ecol.* 58, 213–221

158 Fryxell, J.M. *et al.* (1988) Why are migratory ungulates so abundant? *Am. Nat.* 131, 781–798

159 Teitelbaum, C.S. *et al.* (2015) How far to go? Determinants of migration distance in land mammals. *Ecol. Lett.* 18, 545–552

160 Cagnacci, F. *et al.* (2011) Partial migration in roe deer: Migratory and resident tactics are end points of a behavioural gradient determined by ecological factors. *Oikos* 120, 1790–1802

161 Stephens, P.R. *et al.* (2017) Global Mammal Parasite Database version 2.0. *Ecology* 98, 1476

162 Wilcove, D.S. and Wikelski, M. (2008) Going, going, gone: Is animal migration disappearing? *PLoS Biol.* 6, e188

163 Kamiya, T. *et al.* (2014) What determines species richness of parasitic organisms? A meta-analysis across animal, plant and fungal hosts. *Biol. Rev.* 89, 123–134

164 Ezenwa, V.O. *et al.* (2006) Host traits and parasite species richness in even and

odd-toed hoofed mammals, Artiodactyla and Perissodactyla. *Oikos* 115, 526–536

165 Stephens, P.R. *et al.* (2016) The macroecology of infectious diseases: a new perspective on global-scale drivers of pathogen distributions and impacts. *Ecol. Lett.* 19, 1159–1171

166 Nunn, C.L. *et al.* (2003) Comparative tests of parasite species richness in primates. *Am. Nat.* 162, 597–614

167 Lindenfors, P. *et al.* (2007) Parasite species richness in carnivores: Effects of host body mass, latitude, geographical range and population density. *Glob. Ecol. Biogeogr.* 16, 496–509

168 Huang, S. *et al.* (2015) Parasite diversity declines with host evolutionary distinctiveness: A global analysis of carnivores. *Evolution (N. Y).* 69, 621–630

169 Walther, B.A. and Moore, J.L. (2005) The concepts of bias, precision and accuracy, and their use in testing the performance of species richness estimators, with a literature review of estimator performance. *Ecography* 28, 815–829

170 Eggeman, S.L. *et al.* (2016) Behavioural flexibility in migratory behaviour in a long-lived large herbivore. *J. Anim. Ecol.* 85, 785–797

171 Jones, K.E. *et al.* (2009) PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology* 90, 2648

172 IUCN The IUCN Red List of Threatened Species. Version 2016-1. (2016)

173 Olson, D.M. *et al.* (2001) Terrestrial ecoregions of the world: a new map of life on Earth. *Bioscience* 51, 933–938

174 Bellwood, D.R. *et al.* (2005) Environmental and geometric constraints on Indo-Pacific coral reef biodiversity. *Ecol. Lett.* 8, 643–651

175 Grueber, C.E. *et al.* (2011) Multimodel inference in ecology and evolution: Challenges and solutions. *J. Evol. Biol.* 24, 699–711

176 Burnham, K.P. and Anderson, D.R. (2004) Multimodel Inference. *Sociol. Methods Res.* 33, 261–304

177 Revell, L.J. (2010) Phylogenetic signal and linear regression on species data. *Methods Ecol. Evol.* 1, 319–329

178 Fritz, S.A. *et al.* (2009) Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics. *Ecol. Lett.* 12, 538–549

179 R Development Core Team R: A Language and Environment for Statistical Computing. Version 4.0.1. R Foundation for Statistical Computing, Vienna Austria. (2020)

180 Bivand, R. *et al.* rgdal: Bindings for the Geospatial Data Abstraction Library. R package version 1.5-10. (2020)

181 Hijmans, R.J. raster: Geographic Data Analysis and Modeling. R package version 3.1-5. (2020)

182 Barton, K. MuMIn: Multi-model inference. R package version 1.15.6. (2015)

183 Keck, F. *et al.* (2016) Phylosignal: An R package to measure, test, and explore the phylogenetic signal. *Ecol. Evol.* 6, 2774–2780

184 Hothorn, T. *et al.* (2008) Multcomp: simultaneous inference for general linear hypotheses. *Biometrical J.* 50, 346–363

185 Lester, S. *et al.* (2007) The relationships between dispersal ability and geographic range size. *Ecol. Lett.* 10, 745–758

186 Valentine, J.W. and Jablonski, D. (2015) A twofold role for global energy

gradients in marine biodiversity trends. *J. Biogeogr.* 42, 997–1005

187 Ito, T.Y. *et al.* (2006) Satellite tracking of Mongolian gazelles (*Procapra gutturosa*) and habitat shifts in their seasonal ranges. *J. Zool.* 269, 291–298

188 Fryxell, J.M. (1995) Aggregation and migration by grazing ungulates in relation to resources and predators. In *Serengeti II: dynamics, management, and conservation of an ecosystem* (Sinclair, A. R. E. and Arcese, P., eds), pp. 257–273, University of Chicago Press

189 Rifkin, J.L. *et al.* (2012) Do animals living in larger groups experience greater parasitism? A meta-analysis. *Am. Nat.* 180, 70–82

190 Altizer, S. *et al.* (2003) Social organization and parasite risk in mammals: Integrating theory and empirical studies. *Annu. Rev. Ecol. Evol. Syst.* 34, 517–547

191 Han, B.A. *et al.* (2015) Infectious disease transmission and behavioural allometry in wild mammals. *J. Anim. Ecol.* 84, 637–646

192 Gortázar, C. *et al.* (2007) Diseases shared between wildlife and livestock: a European perspective. *Eur. J. Wildl. Res.* 53, 241–256

193 Owen, J.C. and Moore, F.R. (2008) Swainson’s thrushes in migratory disposition exhibit reduced immune function. *J. Ethol.* 26, 383–388

194 Hedenström, A. (2003) Optimal migration strategies in animals that run: a range equation and its consequences. *Anim. Behav.* 66, 631–636

195 Alexander, R.M. (1998) When is migration worthwhile for animals that walk, swim or fly? *J. Avian Biol.* 29, 387–394

196 Packer, C. *et al.* (2003) Keeping the herds healthy and alert: implications of predator control for infectious disease. *Ecol. Lett.* 6, 797–802

197 Jablonski, D. (2007) Scale and hierarchy in macroevolution. *Palaeontology* 50, 87–109

198 Miller, M.R. *et al.* (2006) The evolution of parasites in response to tolerance in their hosts: the good, the bad, and apparent commensalism. *Evolution (N. Y).* 60, 945–956

199 Westerdahl, H. *et al.* (2014) Pathogens and hosts on the move. In *Animal Movement Across Scales* (1st edn) pp. 126–148, Oxford University Press

200 Møller, A.P. and Erritzøe, J. (1998) Host immune defence and migration in birds. *Evol. Ecol.* 12, 945–953

201 Møller, A.P. and Szép, T. (2010) The role of parasites in ecology and evolution of migration and migratory connectivity. *J. Ornithol.* 152, 1–10

202 Johnson, P.T.J. *et al.* (2013) Host and parasite diversity jointly control disease risk in complex communities. *Proc. Natl. Acad. Sci. U. S. A.* 110, 16916–21

203 Milner-Gulland, E.J. (2015) Catastrophe and hope for the saiga. *Oryx* 49, 577–578

204 Holdo, R.M. *et al.* (2009) Opposing rainfall and plant nutritional gradients best explain the wldebeest migration in the Serengeti. *Am. Nat.* 173, 431–445

205 Johnson, A.R. *et al.* (1992) Animal movements and population dynamics in heterogeneous landscapes. *Landsc. Ecol.* 7, 63–75

206 Mettke-Hofmann, C. (2014) Cognitive ecology: ecological factors, life-styles, and cognition. *Wiley Interdiscip. Rev. Cogn. Sci.* 5, 345–360

207 Gautestad, A.O. (2011) Memory matters: Influence from a cognitive map on animal space use. *J. Theor. Biol.* 287, 26–36

208 Teitelbaum, C.S. and Mueller, T. (2019) Beyond migration: causes and

consequences of nomadic animal movements. *Trends Ecol. Evol.* 34, 569–581

209 Roshier, D.A. *et al.* (2006) Movements of a nomadic waterfowl, Grey Teal *Anas gracilis*, across inland Australia – results from satellite telemetry spanning fifteen months. *Ardea* 94, 461–475

210 Fretwell, S.D. and Lucas, H.L. (1969) On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheor.* 19, 16–36

211 Charnov, E.L. (1976) Optimal Foraging, the Marginal Value Theorem. *Theor. Popul. Biol.* 9, 129–136

212 McNamara, J. (1982) Optimal patch use in a stochastic environment. *Theor. Popul. Biol.* 21, 269–288

213 Avgar, T. *et al.* (2013) An empirically parameterized individual based model of animal movement, perception, and memory. *Ecol. Modell.* 251, 158–172

214 Bateman, A.W. *et al.* (2015) Territoriality and home-range dynamics in meerkats, Suricata suricatta: A mechanistic modelling approach. *J. Anim. Ecol.* 84, 260–271

215 Tao, Y. *et al.* (2016) Dynamic range size analysis of territorial animals: An optimality approach. *Am. Nat.* 188, 460–474

216 Van Moorter, B. *et al.* (2016) Movement is the glue connecting home ranges and habitat selection. *J. Anim. Ecol.* 85, 21–31

217 Rowe, R.J. *et al.* (2011) Environmental change and declining resource availability for small-mammal communities in the Great Basin. *Ecology* 92, 1366–1375

218 Oro, D. *et al.* (2013) Ecological and evolutionary implications of food subsidies from humans. *Ecol. Lett.* 16, 1501–1514

219 Fensholt, R. and Proud, S.R. (2012) Evaluation of earth observation based global long term vegetation trends—Comparing GIMMS and MODIS global NDVI time series. *Remote Sens. Environ.* 119, 131–147

220 Rode, K.D. *et al.* (2014) Variation in the response of an Arctic top predator experiencing habitat loss: Feeding and reproductive ecology of two polar bear populations. *Glob. Chang. Biol.* 20, 76–88

221 Iwamura, T. *et al.* (2013) Migratory connectivity magnifies the consequences of habitat loss from sea-level rise for shorebird populations. *Proc. R. Soc. B Biol. Sci.* 280, 1–8

222 Wiegand, T. *et al.* (2005) Effects of habitat loss and fragmentation on population dynamics. *Conserv. Biol.* 19, 108–121

223 Gilbert, N.I. *et al.* (2015) Are white storks addicted to junk food? Impacts of landfill use on the movement and behaviour of resident white storks (*Ciconia ciconia*) from a partially migratory population. *Mov. Ecol.* 4, 1–13

224 van der Ree, R. *et al.* (2006) The establishment and dynamics of a recently established urban camp of flying foxes (*Pteropus poliocephalus*) outside their geographic range. *J. Zool.* 268, 177–185

225 Plowright, R.K. *et al.* (2011) Urban habituation, ecological connectivity and epidemic dampening: The emergence of hendra virus from flying foxes (*Pteropus spp.*). *Proc. R. Soc. B Biol. Sci.* 278, 3703–3712

226 Shochat, E. *et al.* (2006) From patterns to emerging processes in mechanistic urban ecology. *Trends Ecol. Evol.* 21, 186–191

227 Taylor, C.M. and Norris, D.R. (2010) Population dynamics in migratory networks.

Theor. Ecol. 3, 65–73

228 Hanski, I. and Ovaskainen, O. (2000) The metapopulation capacity of a fragmented landscape. *Nature* 404, 755–758

229 Levins, R. (1969) Some Demographic and Genetic Consequences of Environmental Heterogeneity for Biological Control. *Bull. Entomol. Soc. Am.* 15, 237–240

230 Matsumura, S. *et al.* (2010) Foraging on spatially distributed resources with sub-optimal movement, imperfect information, and travelling costs: Departures from the ideal free distribution. *Oikos* 119, 1469–1483

231 Hopcraft, J.G.C. *et al.* (2014) Competition, predation, and migration: Individual choice patterns of Serengeti migrants captured by hierarchical models. *Ecol. Monogr.* 84, 355–372

232 López-Alfaro, C. *et al.* (2012) Individual-based modeling as a decision tool for the conservation of the endangered huemul deer (*Hippocamelus bisulcus*) in southern Chile. *Ecol. Modell.* 244, 104–116

233 Satterthwaite, W.H. *et al.* (2012) State-dependent migration timing and use of multiple habitat types in anadromous salmonids. *Trans. Am. Fish. Soc.* 141, 781–794

234 Clutton-Brock, T.H. and Coulson, T. (2002) Comparative ungulate dynamics: the devil is in the detail. *Philos. Trans. R. Soc. B Biol. Sci.* 357, 1285–1298

235 Owen-Smith, N. *et al.* (2005) Correlates of survival rates for 10 African ungulate populations: Density, rainfall and predation. *J. Anim. Ecol.* 74, 774–788

236 Milner-Gulland, E.J. (1997) A stochastic dynamic programming model for the

management of the saiga antelope. *Ecol. Appl.* 7, 130–142

237 Coulson, T. *et al.* (2000) The relative roles of density and climatic variation on population dynamics and fecundity rates in three contrasting ungulate species. *Proc. R. Soc. B Biol. Sci.* 267, 1771–1779

238 Parry-Jones, K.A. and Augee, M.L. (1992) Movements of grey-headed flying foxes (*Pteropus poliocephalus*) to and from a colony site on the central coast of New South Wales. *Wildl. Res.* 19, 331–340

239 Bazazi, S. *et al.* (2011) Nutritional state and collective motion: from individuals to mass migration. *Proc. R. Soc. B Biol. Sci.* 278, 356–363

240 Denno, R.F. *et al.* (2011) Density-related migration in planthoppers (Homoptera : Delphacidae): the role of habitat persistence. *Am. Nat.* 138, 1513–1541

241 Stephens, D.W. (1989) Variance and the value of information. *Am. Nat.* 134, 128–140

242 Krebs, J.R. and Inman, A.J. (2006) Learning and foraging: individuals , groups, and populations. *Am. Nat.* 140, S63–S84

243 Fagan, W.F. *et al.* (2013) Spatial memory and animal movement. *Ecol. Lett.* 16, 1316–1329

244 Schmidt-Nielsen, K. (1972) Locomotion: energy cost of swimming, flying, and running. *Science* 177, 222–228

245 Hein, A.M. *et al.* (2012) Energetic and biomechanical constraints on animal migration distance. *Ecol. Lett.* 15, 104–10

246 Morelle, K. *et al.* (2015) Towards understanding wild boar Sus scrofa movement: A synthetic movement ecology approach. *Mamm. Rev.* 45, 15–29

247 Fahrig, L. (2007) Non-optimal animal movement in human-altered landscapes. *Funct. Ecol.* 21, 1003–1015

248 Dahbi, A. *et al.* (2008) Nest-moving by the polydomous ant Cataglyphis iberica. *J. Ethol.* 26, 119–126

249 Fischer, J. and Lindenmayer, D.B. (2007) Landscape modification and habitat fragmentation: a synthesis. *Glob. Ecol. Biogeogr.* 16, 265–280

250 Kreiter, N.A. and Wise, D.H. (2001) Prey availability limits fecundity and influences the movement pattern of female fishing spiders. *Oecologia* 127, 417–424

251 Kennedy, P.L. and Ward, J.M. (2003) Effects of experimental food supplementation on movements of juvenile northern goshawks (*Accipiter gentilis atricapillus*). *Oecologia* 134, 284–291

252 Testart, A. *et al.* (1982) The significance of food storage among hunter-gatherers: residence patterns, population densities, and social inequalities. *Curr. Anthropol.* 23, 523–537

253 Williams, N.S.G. *et al.* (2006) Range expansion due to urbanization: Increased food resources attract Grey-headed Flying-foxes (*Pteropus poliocephalus*) to Melbourne. *Austral Ecol.* 31, 190–198

254 Nilsson, A.L. *et al.* (2006) The effect of climate change on partial migration – the blue tit paradox. *Glob. Chang. Biol.* 12, 2014–2022

255 Meehl, G.A. and Tebaldi, C. (2004) More intense, more frequent, and longer lasting heat waves in the 21st century. *Science* 305, 994–7

256 Nandintsetseg, D. *et al.* (2019) Challenges in the conservation of wide-ranging

nomadic species. *J. Appl. Ecol.* 56, 1916–1926

257 Stojanovic, D. *et al.* (2014) Discovery of a novel predator reveals extreme but highly variable mortality for an endangered migratory bird. *Divers. Distrib.* 20, 1200–1207

258 Taylor, P.D. *et al.* (1993) Connectivity is a vital element of landscape structure. *Oikos* 68, 571–573

259 Mitchell, M.G.E. *et al.* (2013) Linking Landscape Connectivity and Ecosystem Service Provision: Current Knowledge and Research Gaps. *Ecosystems* 16, 894–908

260 Loreau, M. *et al.* (2003) Meta-ecosystems: a theoretical framework for a spatial ecosystem ecology. *Ecol. Lett.* 6, 673–679

261 Stillfried, M. *et al.* (2017) Do cities represent sources, sinks or isolated islands for urban wild boar population structure? *J. Appl. Ecol.* 54, 272–281

262 Krosby, M. *et al.* (2010) Ecological Connectivity for a Changing Climate. *Conserv. Biol.* 24, 1686–1689

263 McCallum, H. and Dobson, A. (2006) Disease and connectivity. In *Connectivity Conservation* (Crooks, K. R. and Sanjayan, M., eds), pp. 479–501

264 Polis, G.A. *et al.* (1997) Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annu. Rev. Ecol. Syst.* 28, 289–316

265 McCauley, D.J. *et al.* (2012) From wing to wing: The persistence of long ecological interaction chains in less-disturbed ecosystems. *Sci. Rep.* 2,

266 LaPoint, S. *et al.* (2015) Ecological connectivity research in urban areas. *Funct.*

Ecol. 29, 868–878

267 Lowry, H. *et al.* (2013) Behavioural responses of wildlife to urban environments. *Biol. Rev.* 88, 537–549

268 Braaker, S. *et al.* (2014) Assessing habitat connectivity for ground-dwelling animals in an urban environment. *Ecol. Appl.* 24, 1583–1595

269 Ibarra-Macias, A. *et al.* (2011) Experimental evaluation of bird movements in a fragmented Neotropical landscape. *Biol. Conserv.* 144, 703–712

270 Ricketts, T.H. (2001) The matrix matters: Effective isolation in fragmented landscapes. *Am. Nat.* 158, 87–99

271 Prange, S. *et al.* (2006) Influences of anthropogenic resources on raccoon (*Procyon lotor*) movements and spatial distribution. *J. Mammal.* 85, 483–490

272 Plummer, K.E. *et al.* (2015) Is supplementary feeding in gardens a driver of evolutionary change in a migratory bird species? *Glob. Chang. Biol.* 21, 4353–4363

273 Tucker, M.A. *et al.* (2018) Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *Science* 359, 466–469

274 Selva, N. *et al.* (2017) Supplementary ungulate feeding affects movement behavior of brown bears. *Basic Appl. Ecol.* 24, 68–76

275 Berger-Tal, O. and Saltz, D. (2019) Invisible barriers: Anthropogenic impacts on inter- And intra-specific interactions as drivers of landscape-independent fragmentation. *Philos. Trans. R. Soc. B Biol. Sci.* 374, 20180049

276 Pe'er, G. *et al.* (2011) Breaking Functional Connectivity into Components: A Novel Approach Using an Individual-Based Model, and First Outcomes. *PLoS*

One 6, e22355

277 Poli, C. *et al.* (2020) Validating network connectivity with observed movement in experimental landscapes undergoing habitat destruction. *J. Appl. Ecol.* 57, 1426–1437

278 Fletcher, R.J.J. *et al.* (2019) Toward a unified framework for connectivity that disentangles movement and mortality in space and time. *Ecol. Lett.* 22, 1680–1689

279 Bierwagen, B.G. (2007) Connectivity in urbanizing landscapes: The importance of habitat configuration, urban area size, and dispersal. *Urban Ecosyst.* 10, 29–42

280 McClure, M.L. *et al.* (2016) Connecting models to movements: testing connectivity model predictions against empirical migration and dispersal data. *Landsc. Ecol.* 31, 1419–1432

281 Coulon, A. *et al.* (2015) A stochastic movement simulator improves estimates of landscape connectivity. *Ecology* 96, 2203–2213

282 Shaw, A. (2020) Causes and consequences of individual variation in animal movement. *Mov. Ecol.* 8, 1–12

283 Shaw, A.K. *et al.* (2014) Population-level consequences of risky dispersal. *Oikos* 123, 1003–1013

284 Bolnick, D.I. *et al.* (2003) The ecology of individuals: Incidence and implications of individual specialization. *Am. Nat.* 161, 1–28

285 Osipova, L. *et al.* (2019) Using step-selection functions to model landscape connectivity for African elephants: accounting for variability across individuals and seasons. *Anim. Conserv.* 22, 35–48

286 Uggla, Y. (2010) What is this thing called “natural”? The nature-culture divide in

climate change and biodiversity policy. *J. Polit. Ecol.* 17, 79

287 Kushlan, J.A. (1979) Feeding ecology and prey selection in the white ibis. *Condor* 81, 376–389

288 Melvin, S.L. *et al.* (1999) Long-Term Movement Patterns for Seven Species of Wading Birds. *Int. J. Waterbird Biol.* 22, 411–416

289 Frederick, P. *et al.* (2009) The White Ibis and Wood Stork as indicators for restoration of the everglades ecosystem. *Ecol. Indic.* 9, S83–S95

290 Kushlan, J.A. (1986) Responses of Wading Birds to Seasonally Fluctuating Water Levels: Strategies and Their Limits. *Colon. Waterbirds* 9, 155

291 Murray, M.H. *et al.* (2018) From wetland specialist to hand-fed generalist: shifts in diet and condition with provisioning for a recently urbanized wading bird. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 373, 20170100

292 Kidd-Weaver, A. *et al.* (2020) The movements of a recently urbanized wading bird reveal changes in season timing and length related to resource use. *PLoS One* 15, e0230158

293 Hernandez, S.M. *et al.* (2016) Urbanized White Ibises (*Eudocimus albus*) as carriers of Salmonella enterica of significance to public health and wildlife. *PLoS One* 11, e0164402

294 Murray, M.H. *et al.* (2020) Gut microbiome shifts with urbanization and potentially facilitates a zoonotic pathogen in a wading bird. *PLoS One* 15, 1–16

295 Becker, D.J. *et al.* (2018) Assessing the contributions of intraspecific and environmental sources of infection in urban wildlife: Salmonella enterica and white ibis as a case study. *J. R. Soc. Interface* 15, 20180654

296 Murray, M. *et al.* (2015) Poor health is associated with use of anthropogenic resources in an urban carnivore. *Proc. R. Soc. B Biol. Sci.* 282, 20150009

297 Bélisle, M. (2005) Measuring landscape connectivity: the challenge of behavioral landscape ecology. *Ecology* 86, 1988–1995

298 Deng, J. and Frederick, P. (2001) Nocturnal Flight Behavior of Waterbirds in Close Proximity to a Transmission Powerline in the Florida Everglades. *Waterbirds* 24, 419–424

299 Adams, H. *et al.* (2019) Capturing American White Ibises in urban South Florida using two novel techniques. *J. F. Ornithol.* 90, 373–381

300 Pennycuick, C.J. (1989) Flight Speeds and Energy Requirements for White Ibises on Foraging Flights. *Auk* 106, 141–144

301 Signer, J. *et al.* (2019) Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. *Ecol. Evol.* 9, 880–890

302 Florida Fish and Wildlife Conservation Commission and Florida Natural Areas Inventory Florida Cooperative Land Cover Map, Version 3.2. (2016)

303 Bivand, R. and Rundel, C. rgeos: Interface to Geometry Engine - Open Source ('GEOS’). R package version 0.5-3. (2020)

304 Adams, E.M. *et al.* (2009) Sublethal effects of methylmercury on fecal metabolites of testosterone, estradiol, and corticosterone in captive juvenile White Ibises (*Eudocimus albus*). *Environ. Toxicol. Chem.* 28, 982–989

305 Csardi, G. and Nepusz, T. (2006) The igraph software package for complex network research. *InterJournal* Complex Sy, 1695

306 Fletcher, R.J. *et al.* (2011) Social network models predict movement and

connectivity in ecological landscapes. *Proc. Natl. Acad. Sci.* 108, 19282–19287

307 Farine, D.R. and Whitehead, H. (2015) Constructing, conducting and interpreting animal social network analysis. *J. Anim. Ecol.* 84, 1144–1163

308 Newman, M.E.J. and Girvan, M. (2004) Finding and evaluating community structure in networks. *Phys. Rev. E* 69, 026113

309 Clauset, A. *et al.* (2004) Finding community structure in very large networks. *Phys. Rev. E* 70, 066111

310 Reichert, B.E. *et al.* (2016) Consistent scaling of population structure across landscapes despite intraspecific variation in movement and connectivity. *J. Anim. Ecol.* 85, 1563–1573

311 Harrell Jr, F.E. Hmisc: Harrell Miscellaneous. R package version 4.4-0. (2020)

312 Clarke, K.R. (1993) Non-parametric multivariate analyses of changes in community structure. *Austral Ecol.* 18, 117–143

313 Cao, Y. and Hawkins, C.P. (2005) Simulating biological impairment to evaluate the accuracy of ecological indicators. *J. Appl. Ecol.* 42, 954–965

314 Camacho, C. *et al.* (2020) Experimental evidence that matching habitat choice drives local adaptation in a wild population. *Proc. R. Soc. B Biol. Sci.* 287, 20200721.

315 Carrete, M. and Tella, J.L. (2017) Behavioral correlations associated with fear of humans differ between rural and urban burrowing owls. *Front. Ecol. Evol.* 5, 1–9

316 Newsome, S.D. *et al.* (2015) Individual variation in anthropogenic resource use in an urban carnivore. *Oecologia* 178, 115–128

317 Páez, D.J. *et al.* (2018) Optimal foraging in seasonal environments : implications

for residency of Australian flying foxes in food-subsidized urban landscapes. *Philos. Trans. R. Soc. B* 373, 20170097

318 Picardi, S. *et al.* (2020) Partial migration in a subtropical wading bird in the southeastern United States. *Ecosphere* 11, e03054

319 Teitelbaum, C.S. *et al.* (2020) Movement rules determine nomadic species' responses to resource supplementation and degradation. *J. Anim. Ecol.* 89, 2644–2656

320 Clobert, J. *et al.* Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. , *Ecology Letters*, 12. (2009) , 197–209

321 Robertson, A. *et al.* (2015) Resource availability affects individual niche variation and its consequences in group-living European badgers Meles meles. *Oecologia* 178, 31–43

322 Layman, C.A. *et al.* (2015) Individual-level niche specialization within populations: emerging areas of study. *Oecologia* 178, 1–4

323 Modlmeier, A.P. *et al.* (2014) The keystone individual concept: An ecological and evolutionary overview. *Anim. Behav.* 89, 53–62

324 Rushton, S.P. *et al.* (2000) Modelling the spatial dynamics of parapoxvirus disease in red and grey squirrels: a possible cause of the decline in the red squirrel in the UK? *J. Appl. Ecol.* 37, 997–1012

325 Boulinier, T. *et al.* (2016) Migration, Prospecting, Dispersal? What Host Movement Matters for Infectious Agent Circulation? *Integr. Comp. Biol.* 56, 330–342

326 Daversa, D.R. *et al.* (2017) Infections on the move: how transient phases of host movement influence disease spread. *Proc. R. Soc. B Biol. Sci.* 284, 20171807

327 Craft, M.E. *et al.* (2011) Disease transmission in territorial populations: the small-world network of Serengeti lions. *J. R. Soc. Interface* 8, 776–786

328 Williams, J.J. *et al.* (2018) Mobile marine predators : an understudied source of nutrients to coral reefs in an unfished atoll. *Proc. R. Soc. B* 285, 20172456

329 Irick, D.L. *et al.* (2015) Wading bird guano enrichment of soil nutrients in tree islands of the Florida Everglades. *Sci. Total Environ.* 532, 40–47

330 Schick, R.S. *et al.* (2008) Understanding movement data and movement processes: Current and emerging directions. *Ecol. Lett.* 11, 1338–1350

331 Uden, D.R. *et al.* (2014) The role of reserves and anthropogenic habitats for functional connectivity and resilience of ephemeral wetlands. *Ecol. Appl.* 24, 1569–1582

332 Börger, L. *et al.* (2008) Are there general mechanisms of animal home range behaviour? A review and prospects for future research. *Ecol. Lett.* 11, 637–650

333 Dickson, B.G. *et al.* (2019) Circuit-theory applications to connectivity science and conservation. *Conserv. Biol.* 33, 239–249

334 McRae, B.H. *et al.* (2012) Where to Restore Ecological Connectivity? Detecting Barriers and Quantifying Restoration Benefits. *PLoS One* 7, e52604

335 Mcdonald, R.I. *et al.* (2008) The implications of current and future urbanization for global protected areas and biodiversity conservation. *Biol. Conserv.* 141, 1695–1703

336 McKinney, M.L. (2006) Urbanization as a major cause of biotic homogenization.

Biol. Conserv. 127, 247–260

337 Jokimäki, J. *et al.* (2011) Merging wildlife community ecology with animal behavioral ecology for a better urban landscape planning. *Landsc. Urban Plan.* 100, 383–385

338 Bradley, C.A. and Altizer, S. (2007) Urbanization and the ecology of wildlife diseases. *Trends Ecol. Evol.* 22, 95–102

339 Hassell, J.M. *et al.* (2017) Urbanization and Disease Emergence: Dynamics at the Wildlife–Livestock–Human Interface. *Trends Ecol. Evol.* 32, 55–67

340 Farnsworth, M.L. *et al.* (2005) Human land use influences chronic wasting disease prevalence in mule deer. *Ecol. Appl.* 15, 119–126

341 Lehrer, E.W. *et al.* (2010) Prevalence of antibodies to Toxoplasma gondii in woodchucks across an urban-rural gradient. *J. Wildl. Dis.* 46, 977–980

342 Becker, D.J. *et al.* (2015) Linking anthropogenic resources to wildlife-pathogen dynamics: A review and meta-analysis. *Ecol. Lett.* 18, 483–495

343 Fuirst, M. *et al.* (2018) Effects of urbanization on the foraging ecology and microbiota of the generalist seabird Larus argentatus. *PLoS One* 13, 1–22

344 Partecke, J. and Gwinner, E. (2007) Increased sedentariness in European blackbirds following urbanization: A consequence of local adaptation? *Ecology* 88, 882–890

345 McClure, K.M. *et al.* (2020) Variation in host home range size decreases rabies vaccination effectiveness by increasing the spatial spread of rabies virus. *J. Anim. Ecol.* 89, 1375–1386

346 Navarro, J. *et al.* (2017) Shifting individual habitat specialization of a successful

predator living in anthrop ogeniclandscapes. *Mar. Ecol. Prog. Ser.* 578, 243–251

347 Cryan, P.M. *et al.* (2012) Evidence of cryptic individual specialization in an opportunistic insectivorous bat. *J. Mammal.* 93, 381–389

348 Teitelbaum, C.S. *et al.* (2020) Urban specialization reduces habitat connectivity by a highly mobile wading bird. *Mov. Ecol.* 8, 1–13

349 Navarro, J. *et al.* (2019) Pathogen transmission risk by opportunistic gulls moving across human landscapes. *Sci. Rep.* 9, 1–5

350 Araújo, M.S. *et al.* (2011) The ecological causes of individual specialisation. *Ecol. Lett.* 14, 948–958

351 Soetaert, K.E.R. *et al.* (2010) Solving differential equations in R: package deSolve. *J. Stat. Softw.* 33,

352 Brearley, G. *et al.* (2013) Wildlife disease prevalence in human-modified landscapes. *Biol. Rev.* 88, 427–442

353 Murray, M.H. *et al.* (2016) Wildlife health and supplemental feeding: A review and management recommendations. *Biol. Conserv.* 204, 163–174

354 Fischer, C. *et al.* (2005) Echinococcus multilocularis infections of rural, residential and urban foxes (*Vulpes vulpes*) in the canton of Geneva, Switzerland. *Parasite* 12, 339–346

355 Prange, S. *et al.* (2003) Demographic Factors Contributing to High Raccoon Densities in Urban Landscapes. *J. Wildl. Manage.* 67, 324–333

356 White, L.A. *et al.* (2018) Disease outbreak thresholds emerge from interactions between movement behavior, landscape structure, and epidemiology. *Proc. Natl. Acad. Sci. U. S. A.* 115, 7374–7379

357 Becker, D.J. *et al.* (2018) Host dispersal responses to resource supplementation determine pathogen spread in wildlife metapopulations. *Am. Nat.* 192, 503–517

358 Tracey, J.A. *et al.* (2014) An agent-based movement model to assess the impact of landscape fragmentation on disease transmission. *Ecosphere* 5, 1–24

359 Sánchez, C.A. *et al.* (2020) Landscape-level toxicant exposure mediates infection impacts on wildlife populations. *Biol. Lett.* 6, 20200559

360 Holt, R.D. (1985) Population dynamics in two-patch environments: Some anomalous consequences of an optimal habitat distribution. *Theor. Popul. Biol.* 28, 181–208

361 Cross, P.C. *et al.* (2007) Utility of R_0 as a predictor of disease invasion in structured populations. *J. R. Soc. Interface* 4, 315–324

362 Tur, C. *et al.* (2014) Downscaling pollen-transport networks to the level of individuals. *J. Anim. Ecol.* 83, 306–317

363 Ellner, S.P. *et al.* (2020) Individual Specialization and Multihost Epidemics: Disease Spread in Plant-Pollinator Networks. *Am. Nat.* 195, E118–E131

364 Lee, J.S. *et al.* (2012) Gene flow and pathogen transmission among bobcats (*Lynx rufus*) in a fragmented urban landscape. *Mol. Ecol.* 21, 1617–1631

365 Boots, M. *et al.* (2004) Large Shifts in Pathogen Virulence Relate to Host Population Structure. *Science* 303, 842–844

366 Haraguchi, Y. and Sasaki, A. (2000) The evolution of parasite virulence transmission rate in a spatially structured population. *J. Theor. Biol.* 203, 85–96

367 Von Der Lippe, M. and Kowarik, I. (2008) Do cities export biodiversity? Traffic as dispersal vector across urban-rural gradients. *Divers. Distrib.* 14, 18–25

368 Blitzer, E.J. *et al.* (2012) Spillover of functionally important organisms between managed and natural habitats. *Agric. Ecosyst. Environ.* 146, 34–43

369 Blais, J.M. *et al.* (2007) Biologically mediated transport of contaminants to aquatic systems. *Environ. Sci. Technol.* 41, 1075–1084

370 Adelman, J.S. *et al.* (2015) Feeder use predicts both acquisition and transmission of a contagious pathogen in a North American songbird. *Proc. R. Soc. B* 282, 20151429

371 Galbraith, J.A. *et al.* (2017) Urban bird feeders dominated by a few species and individuals. *Front. Ecol. Evol.* 5, 81

372 Plowright, R.K. *et al.* (2014) Ecological dynamics of emerging bat virus spillover. *Proc. R. Soc. B Biol. Sci.* 282, 20142124

373 Brown, L.M. and Hall, R.J. (2018) Consequences of resource supplementation for disease risk in a partially migratory population. *Philos. Trans. R. Soc. B Biol. Sci.* 373, 20170095

374 Abrahms, B. *et al.* (2017) Does wildlife resource selection accurately inform corridor conservation? *J. Appl. Ecol.* 54, 412–422

375 Satterfield, D.A. *et al.* (2016) Migratory monarchs wintering in California experience low infection risk compared to monarchs breeding year-round on non-native milkweed. *Integr. Comp. Biol.* 56, 343–352

376 Barbaree, B.A. *et al.* (2018) Dynamic surface water distributions influence wetland connectivity within a highly modified interior landscape. *Landsc. Ecol.* 33, 829–844

377 Tyrrell, P. *et al.* (2017) Seasonal movements of wildlife and livestock in a

heterogenous pastoral landscape: Implications for coexistence and community based conservation. *Glob. Ecol. Conserv.* 12, 59–72

378 Farrell, M.J. *et al.* (2015) The path to host extinction can lead to loss of generalist parasites. *J. Anim. Ecol.* 84, 978–984

379 Wilson, D.E. and Reeder, D.M., eds. (2005) *Mammal species of the world: a taxonomic and geographic reference*, JHU Press.

380 Alroy, J. (2017) Effects of habitat disturbance on tropical forest biodiversity. *Proc. Natl. Acad. Sci. U. S. A.* 114, 6056–6061

381 Dove, A.D.M. and Cribb, T.H. (2006) Species accumulation curves and their applications in parasite ecology. *Trends Parasitol.* 22, 568–574

382 Freckleton, R.P. (2011) Dealing with collinearity in behavioural and ecological data: Model averaging and the problems of measurement error. *Behav. Ecol. Sociobiol.* 65, 91–101

383 Altizer, S. *et al.* (2007) Do threatened hosts have fewer parasites? A comparative study in primates. *J. Anim. Ecol.* 76, 304–314

384 Young, H. *et al.* (2013) Does habitat disturbance increase infectious disease risk for primates? *Ecol. Lett.* 16, 656–663

385 Kadmon, R. and Shmida, A. (1992) Departure rules used by bees foraging for nectar: A field test. *Evol. Ecol.* 6, 142–151

386 Gibson, A.J.F. *et al.* (2008) Are wild populations ideally distributed? Variations in density-dependent habitat use by age class in juvenile Atlantic salmon (*Salmo salar*). *Can. J. Fish. Aquat. Sci.* 65, 1667–1680

APPENDIX A

CHAPTER 3 SUPPLEMENTARY INFORMATION

SUPPLEMENTARY METHODS

Details of the GMPD

The Global Mammal Parasite Database 2.0 (GMPD) [161] contains host-parasite association records reported from literature for free-ranging populations from the mammalian orders Artiodactyla, Perissodactyla, Carnivora, and Primates. The database includes both positive and negative records (i.e., cases where a parasite was sampled for but not found in a given host). In this study, we limited our data analysis to ungulate species and excluded primarily domestic species (e.g., camels). We also included only populations sampled in their native ranges (following [164] and [378]). The GMPD uses the taxonomy of Wilson & Reeder [379], but to harmonize these data with the PanTHERIA database used in some analyses [171], we collapsed two pairs of species together where taxonomies disagreed (*Alces americanus* was included within *Alces alces* and *Alcelaphus liechtensteinii* was included within *Alcelaphus buselaphus*).

Calculations of parasite species richness

We used the parasite taxonomy provided in the GMPD to identify unique parasite operational taxonomic units (OTUs); we refer to these unique parasite OTUs as “species” throughout the manuscript, even though some parasite types (e.g. viruses) are not identified as species. We defined parasite species richness as the number of parasite species detected in all native, free-ranging populations of a host species [164,167,168]. For parasites that were identified only to the genus level, we included these in the richness measure only if no other species from that genus was also present in a given host species (e.g. *Strongyloides sp.* was counted as a unique parasite only if no other species of *Strongyloides* had been detected in that host). We excluded any records that were identified to the family level or above.

We used the Chao2 estimator to account for uneven sampling effort. The Chao2 estimator is based on the ratio of singletons to doubletons in the dataset; we selected it for this study because it has been shown to accurately predict species richness when data is in the form of presence-absence records and sample sizes for some sites or species are low [169,380,381]; it also performs better than other diversity estimators on the GMPD data [168].

Prevalence data were recorded for 89% of entries included in this analysis. These prevalence data are based either on direct detection of pathogens (by visible stages or using genetic markers) or detection of host antibodies (e.g., seroprevalence), and thus can represent either active infection or previous exposure to a given parasite.

Movement data compilation

To gather data on the movement strategy of each ungulate host species, we first searched for species reports in the journal Mammalian Species, which provides descriptions of species' ecology. If no Mammalian Species report was available for a given ungulate host or the movement strategy was not clear from the report, we searched Google Scholar for the species' binomial name along with "movement OR seasonal OR migration OR 'home range' OR nomadic OR nomadism OR sedentary OR resident", using synonyms from all known taxonomies (e.g. [172,379]). If there was no movement description in either Mammalian Species or in these articles, we searched the online databases Animal Diversity Web and Ultimate Ungulate for description of movement patterns.

To categorize populations' movement patterns, we used the following definitions, based on those by Mueller *et al.* [4,30]: a population was considered *migratory* if it showed seasonal and typically long-distance differences in location but little inter-annual variability in seasonal range use. *Nomadic* populations were those whose location was described as differing across the year but in an irregular and/or resource-driven manner. Most often, these descriptions included phrases such as "may travel long distances in search of food," "migrates to [location] in some years and elsewhere in others," and "has unpredictable movements." Last, *resident* populations were characterized by limited seasonal differences in location or home range. Most often, these assessments came from descriptions of high home range overlap between seasons or year-round territorial maintenance. In addition, any species where no migration are nomadism was described in any available source were considered resident. Under our hierarchical classifications of movement behavior, we did not consider partial migration or partial nomadism explicitly because of the difficulty in accurately defining these behaviors [38], and because our questions revolve around overall effects of migration on the species level, meaning that we consider any degree of migratory behavior as having a potential effect on infection.

Life-history and geographic range data

In PanTHERIA, adult body mass is the average mass of non-pregnant adult specimens of either sex from captive, wild, or provisioned populations. Population group size is the average number of individuals in a non-captive population that spends the majority of their time in a day together and is roughly equivalent to herd size for ungulates [171]. PanTHERIA also provides other measures of group size, but we considered population group size the most relevant to parasite transmission.

We gathered geographic data from species distribution maps downloaded from the IUCN Red List [172], from which we calculated the range area (in km^2) and the mid-range latitude of each ungulate species. We also quantified the diversity of habitats used by each species using WWF's definitions of ecoregions, which are geographic areas defined by characteristic biotic assemblages and abiotic conditions [173]. For each species, we counted the number of unique ecoregions that overlapped with the species' geographic range (from IUCN range maps) as a measure of habitat diversity.

Data analysis

During our model selection process, we excluded any models that included both geographic range area and number of ecoregions to increase the accuracy of our parameter estimates (following [174]). Model averaging performs well when predictor variables are moderately collinear, but still results in biased parameter estimates when predictor variables are highly collinear, as is the case here (r=0.90 after log transformation) [382].

In our models that explicitly accounted for sampling effort, we used the number of hits for a species' Latin binomial on Web of Science as our measure of sampling effort, following other studies using similar datasets [164,166–168]. WOS citation count reflects the overall effort spent on studying the biology of a species. In this model set, we used log-transformed observed parasite species richness as the response variable;

included log-transformed sampling effort as an additional explanatory variable; and a weighting scheme based on the number of individuals sampled per species in the GMPD (weight = 1/(log(number of individuals) + 1).

In our models that examined different parasite groups separately, we first estimated parasite richness of each parasite group in each host species using the Chao2 estimator. Because of the smaller sample sizes for these subsetted data, we included only variables with importance >0.5 in the full model set as candidate explanatory variables, which were movement strategy, number of ecoregions, and body mass.

In our analysis of prevalence data, for each positive host-parasite interaction where at least five host individuals were sampled, we estimated the average prevalence of each parasite in each host species, (following [383] and [384]). Then, for each parasite species, we calculated the average prevalence in migratory and resident hosts separately, and found the difference between these values. A positive value indicates that the average migratory species has higher prevalence than the average resident species for a given parasite.

SUPPLEMENTARY TABLES AND FIGURES

Table S3.1: Model results from the averaged model of the four best models predicting parasite species richness using an alternative classification of movement, where we excluded species categorized as both migratory and nomadic (N=12 species excluded). Results are quantitatively and qualitatively similar to the hierarchical classification method (Table 3.1). As in the main model, geographic range area was included as a possible predictor but was not present in any of the top models.

	Estimate	**Lower**	**Upper**
Intercept	1.780	0.388	3.173
nomadic	-1.326	-2.211	-0.44
resident	-0.788	-1.377	-0.199
Habitat diversity	0.362	0.094	0.629
Body mass	0.083	-0.125	0.291
Mid-range latitude	0.004	-0.01	0.018

Table S3.2: Model results from the averaged model of the four best models predicting parasite species richness using an alternative classification of movement, where we included “migratory/nomadic” as a fourth movement category. Results are quantitatively and qualitatively similar to the hierarchical classification method (Table 3.1). As in the main model, geographic range area was included as a possible predictor but was not present in any of the top models.

	Estimate	**Lower**	**Upper**
Intercept	1.878	0.449	3.307
migratory and nomadic	-0.152	-1.016	0.712
nomadic	-1.387	-2.328	-0.446
resident	-0.847	-1.516	-0.178
Habitat diversity	0.324	-0.008	0.657
Body mass	0.088	-0.124	0.3
Mid-range latitude	0.004	-0.01	0.017
Geographic range area	0.015	-0.083	0.113

Table S3.3: AICc values for all candidate models predicting total parasite species richness. ΔAICc is the difference in AICc between a given model and the top model; models where ΔAICc<2 (in bold) are considered competitive.

Model	**AICc**	**ΔAICc**	**weight**
movementMode + log(nEcoregions) + log(bodyMass)	**305.953**	**0**	**0.221**
movementMode + log(nEcoregions) + log(bodyMass) + abs(midLat)	**306.215**	**0.262**	**0.194**
movementMode + log(nEcoregions)	**306.555**	**0.602**	**0.163**
movementMode + log(nEcoregions) + abs(midLat)	**306.877**	**0.924**	**0.139**
movementMode + log(geoAreaIUCN) + log(bodyMass)	308.044	2.091	0.078
movementMode + log(geoAreaIUCN) + log(bodyMass) + abs(midLat)	308.945	2.992	0.049
movementMode + log(geoAreaIUCN)	309.427	3.474	0.039
movementMode + log(bodyMass)	310.168	4.215	0.027
movementMode + log(geoAreaIUCN) + abs(midLat)	310.43	4.477	0.024
log(nEcoregions) + log(bodyMass) + abs(midLat)	311.167	5.214	0.016
movementMode	311.607	5.654	0.013
movementMode + log(bodyMass) + abs(midLat)	311.885	5.932	0.011
movementMode + abs(midLat)	312.649	6.696	0.008
log(nEcoregions) + abs(midLat)	313.413	7.46	0.005
log(nEcoregions) + log(bodyMass)	314.374	8.421	0.003
log(geoAreaIUCN) + log(bodyMass) + abs(midLat)	314.913	8.96	0.003
log(bodyMass) + abs(midLat)	315.285	9.332	0.002
log(bodyMass)	316.658	10.705	0.001
log(geoAreaIUCN) + log(bodyMass)	316.707	10.754	0.001
log(nEcoregions)	316.745	10.792	0.001
log(geoAreaIUCN) + abs(midLat)	316.92	10.967	0.001
log(geoAreaIUCN)	318.161	12.208	0
abs(midLat)	319.39	13.437	0

Table S3.4: Model results from the best average model of parasite species richness explicitly considering sampling effort. The model predicted raw parasite species richness (log); candidate independent variables were WOS citations (log), movement strategy, habitat diversity (log), body mass (log), absolute mid-range latitude, and geographic range area (log).

	Estimate	Lower	Upper
Intercept	0.878	-0.147	1.904
nomadic	-1.74	-2.408	-1.071
resident	-0.724	-1.271	-0.176
Habitat diversity	0.131	-0.156	0.419
Sampling effort	0.33	0.141	0.519
Mid-range latitude	-0.002	-0.012	0.008
Body mass	0.012	-0.074	0.098

Table S3.5: Model results from models predicting estimated species richness of parasites transmitted by close contact and environmentally separately, using the same predictors as the top-ranked model for total parasite species richness. Transmission modes were based on assignments in the GMPD; environmental transmission is assigned as “nonclose” in the GMPD.

	Environmental			Contact		
	Estimate	**Lower**	**Upper**	**Estimate**	**Lower**	**Upper**
(Intercept)	1.906	0.781	3.031	0.013	-1.274	1.3
nomadic	-1.832	-2.697	-0.968	-0.848	-1.672	-0.025
resident	-0.402	-0.93	0.127	-0.573	-1.069	-0.078
Habitat diversity	0.183	-0.144	0.509	0.293	0.044	0.542
Body mass	-	-	-	0.132	-0.094	0.358

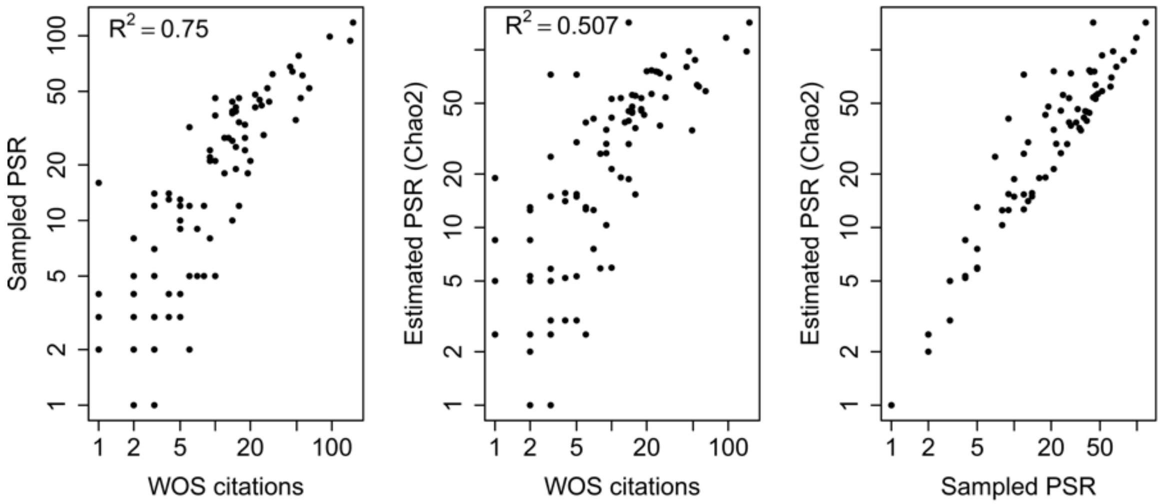


Figure S3.1: Effects of sampling effort on sampled and estimated parasite species richness (PSR) in the Global Mammal Parasite Database (GMPD). Sampled PSR is closely related to sampling effort, measured as the number of studies of a given host species in the GMPD (R^2=0.750, A). The bias-corrected Chao2 estimator reduces the strength of this relationship (R^2=0.507, B). Estimated PSR is always equal to or greater than sampled PSR (C).

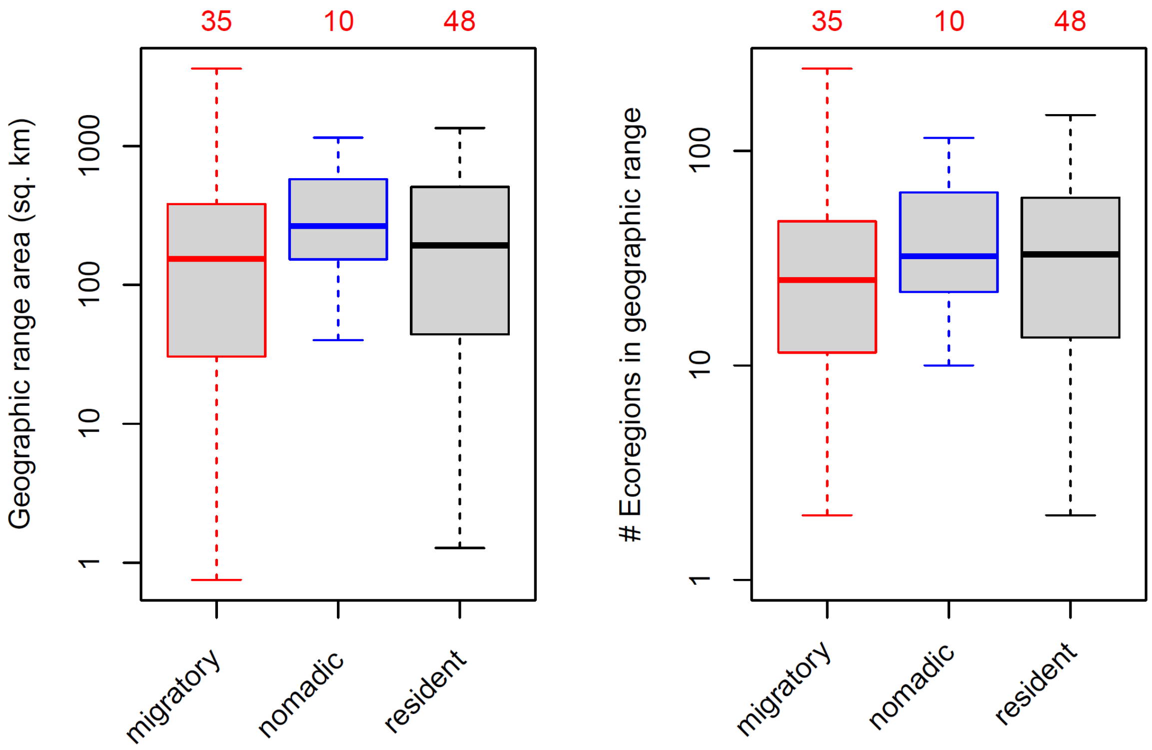


Figure S3.2: Geographic range size and habitat diversity of ungulate species with different movement strategies. No differences between groups were statistically significant (Tukey test, α=0.05).

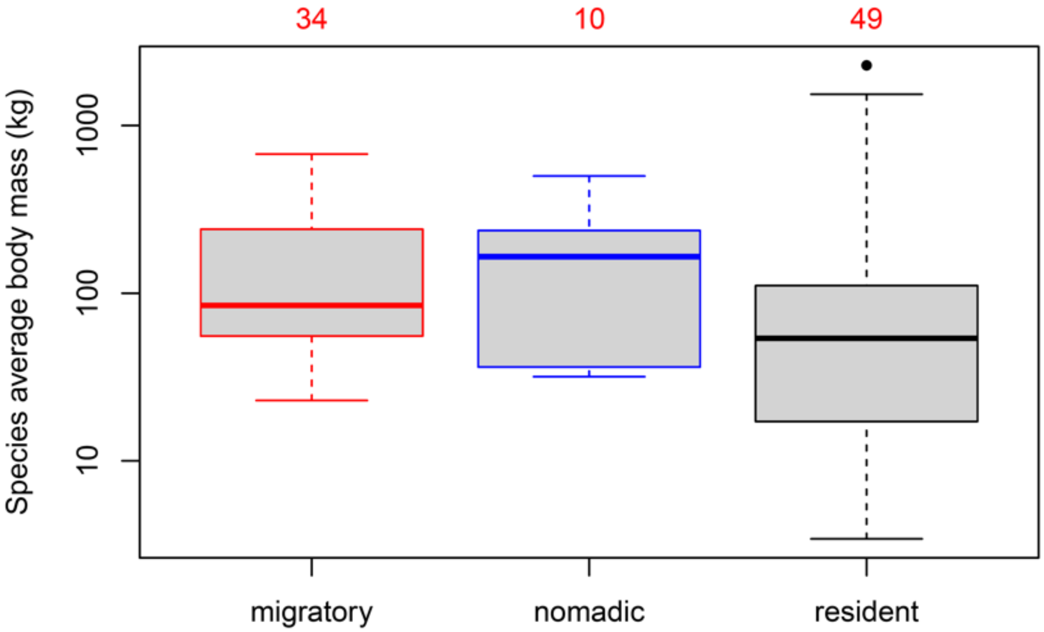


Figure S3.3: Average body mass of species with different movement modes. Resident species had, on average, marginally lower body mass than migratory species (Tukey test, p=0.050); nomadic species were not statistically distinguishable from either other group.

APPENDIX B

CHAPTER 4 SUPPLEMENTARY INFORMATION

Table S4.1: Departure rules used in the nomadic network model. In each case, $M_i(t)$ is the number of individuals leaving patch i, $N_i(t)$ is the number of individuals at the patch at the beginning of the timestep, $A_i(t)$ is the resource availability at patch *i* in that timestep. For some rules: *p* is the fixed departure proportion and W is the threshold value of *A* at which animals begin to depart.

Rule name	**Departure based on…**	**Mathematical formulation**	**Example**
resources	current patch suitability/attractiveness	if $A_i(t) < W$: $M_i(t) = N_i(t)\frac{W - A_i(t)}{W}$ if $A_i(t) \geq W$: $M_i(t) = 0$	grazing ungulates move between patches when resource availability is low [122]
resources + memory	predicted suitability in the next timestep based on linear extrapolation from the change in patch suitability over the last timestep	$A_{i,forecast}(t) = A_i(t) + (A_i(t) - A_i(t-1))$ if $A_{i,forecast}(t) < W$: $M_i(t) = N_i(t)\frac{W - A_{i,forecast}(t)}{W}$ if $A_{i,forecast}(t) > W$: $M_i(t) = 0$	bumblebees' departure from flowers depends on the amount of reward gained at previously-visited flowers [385]
density	Current patch density	if $N_i(t) > V$: $M_i(t) = N_i(t) - V$ if $N_i(t) \leq V$: $M_i(t) = 0$	fish and lobsters disperse from protected areas when densities increase [67]

competition	patch suitability and conspecific density	if $N > \alpha A_i(t)$: $M_i(t) = N_i(t) - \alpha A_i(t)$ if $N \leq \alpha A_i(t)$: $M_i(t) = 0$	the densities of juvenile salmon in sections of a river change according to habitat quality and conspecific density [386]
competition + memory	memory rule applied to patch suitability and conspecific density	if $N_i(t) > \alpha A_{i,forecast}(t)$: $M_i(t) = N_i(t) - \alpha A_{i,forecast}(t)$ if $N_i(t) \leq \alpha A_{i,forecast}(t)$: $M_i(t) = 0$	
residency	no movement	$M_i(t) = 0$	
uninformed	fixed departure proportion (null)	$M_i(t) = pN_i(t)$	

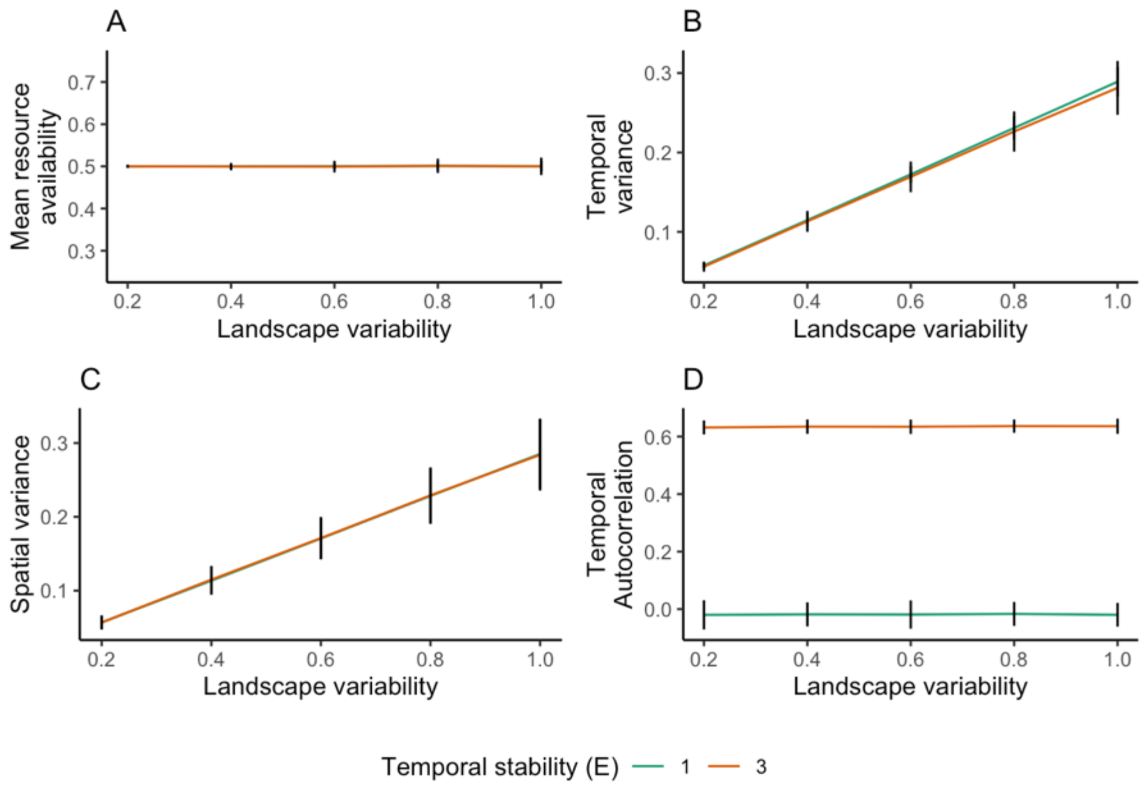


Figure S4.1: Effects of landscape variability and temporal autocorrelation on multiple metrics of landscape structure. Error bars show standard deviations of the mean across 100 simulated landscapes. (A) Mean values remain unchanged when landscape variability changes. (B, C) Variance in across both time (i.e., a single patch over time) and space (i.e., between patches at each time point) increase with increased variability in attractiveness but are unaffected by temporal autocorrelation. (D) Autocorrelation at one timestep is unaffected by changing landscape variability but is larger in landscapes with temporal stability (*E*>1).

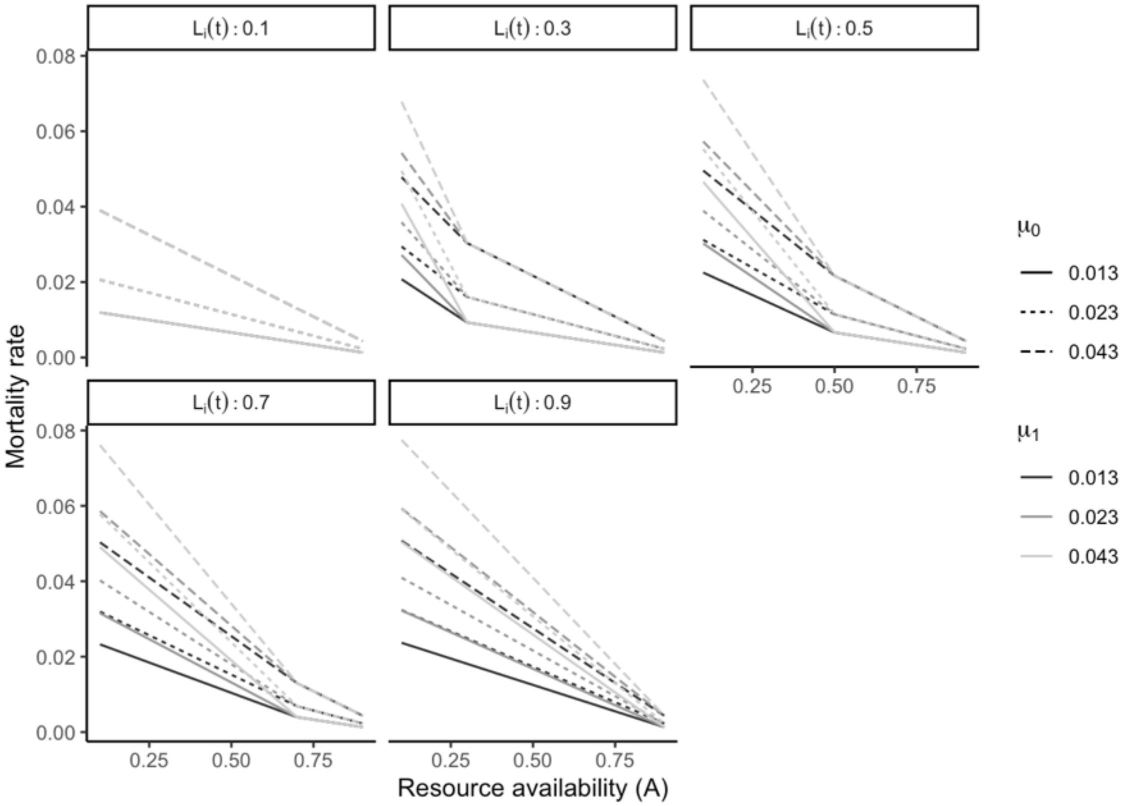


Figure S4.2: Illustration of mortality rates. Each panel shows the relationship between resource availability (A) and weekly *per capita* mortality rate as a function of a different value of $L_i(t)$. Lines of different shades show different values of μ_1 (density-dependent mortality); solid, dashed and dotted lines show different values of μ_0 (density-independent mortality). Mortality rates increase with higher *L* and lower *A*.

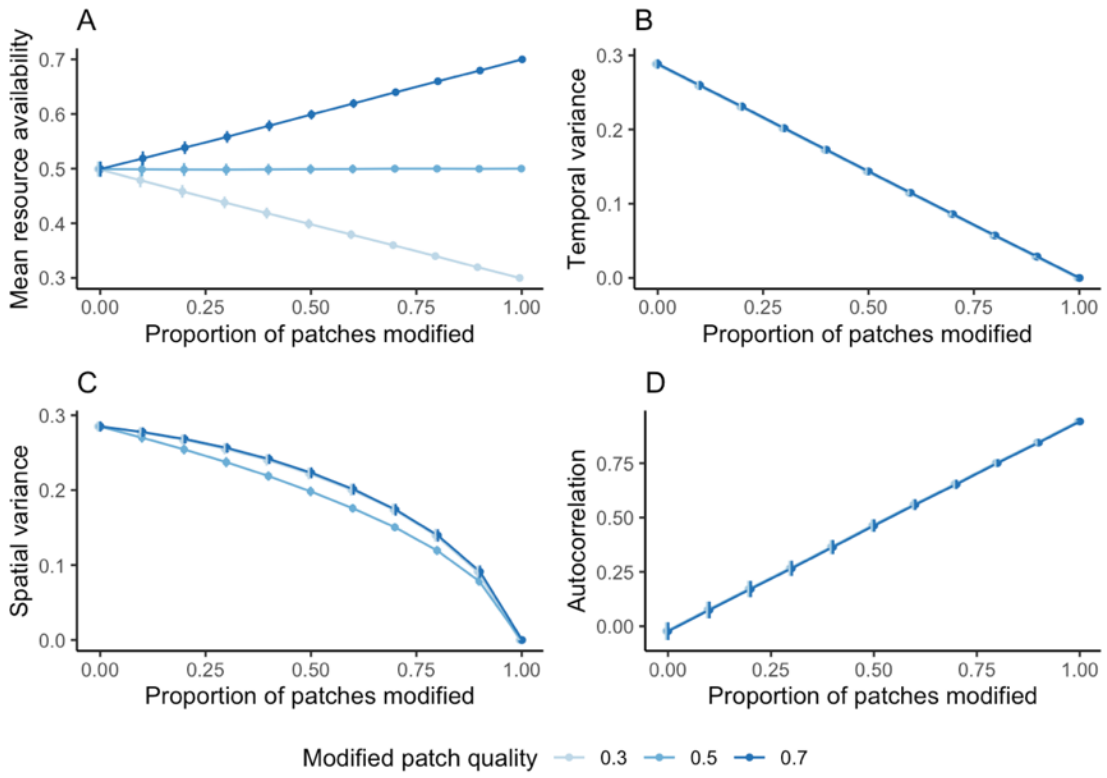


Figure S4.3: Effect of habitat modification on multiple metrics of landscape structure. Error bars show standard deviations of the mean across 100 simulations. X-axis jitter is for visualization only. Colors show different values of modified habitat. Mean resource availability increases or decreases depending on the value of stabilization (A). As the proportion of patches stabilized increases, the temporal variance (B) declines. (C) Spatial variance eventually declines with increased proportion of patches modified, but initially increases for very high or very low values of modification (i.e. 0 or 0.7). Landscape-level autocorrelation increases with proportion modified (D).

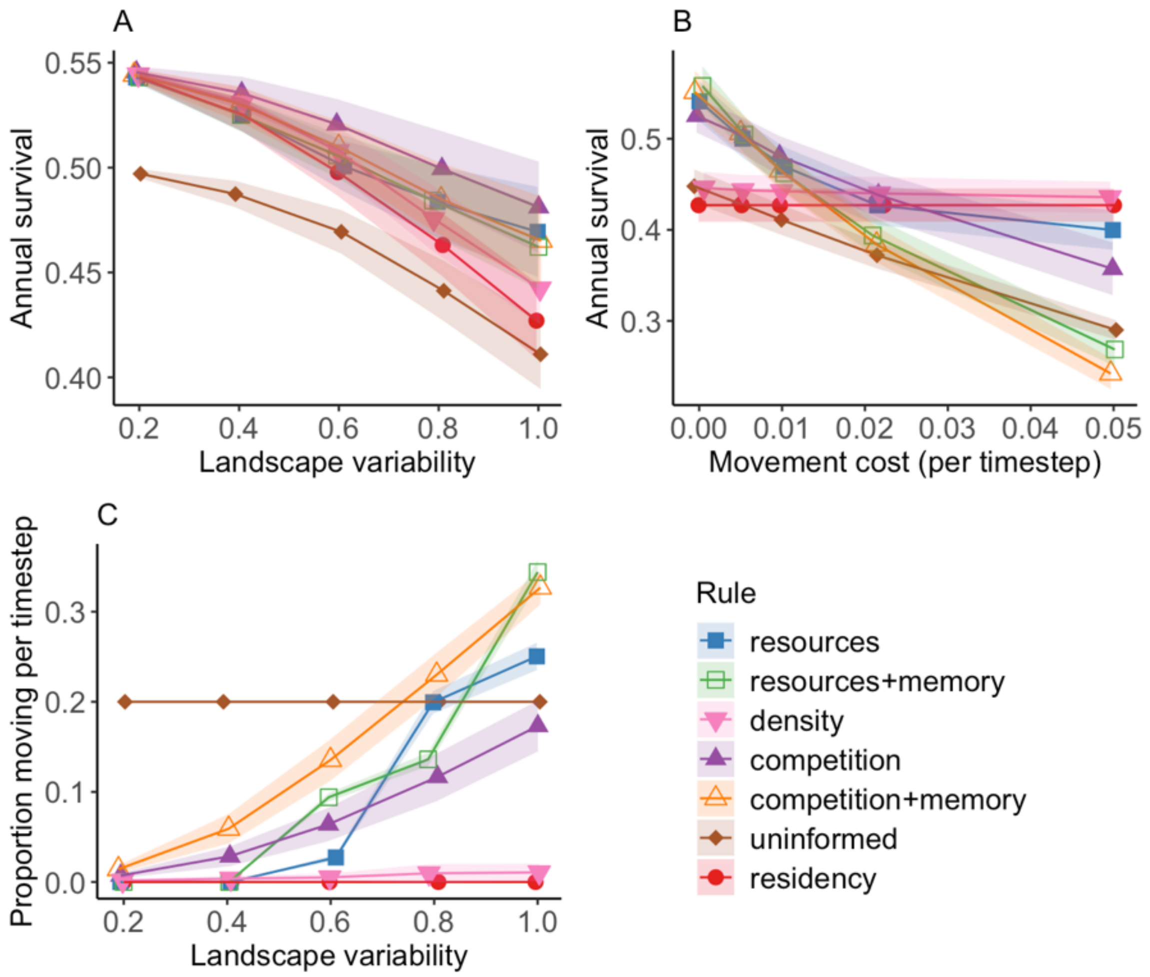


Figure S4.4: Relative performance and movement rates of all movement rules, including the density-only rule and rules that incorporate memory. Parameters are the same as those used in Figure 4.3 in the main text.

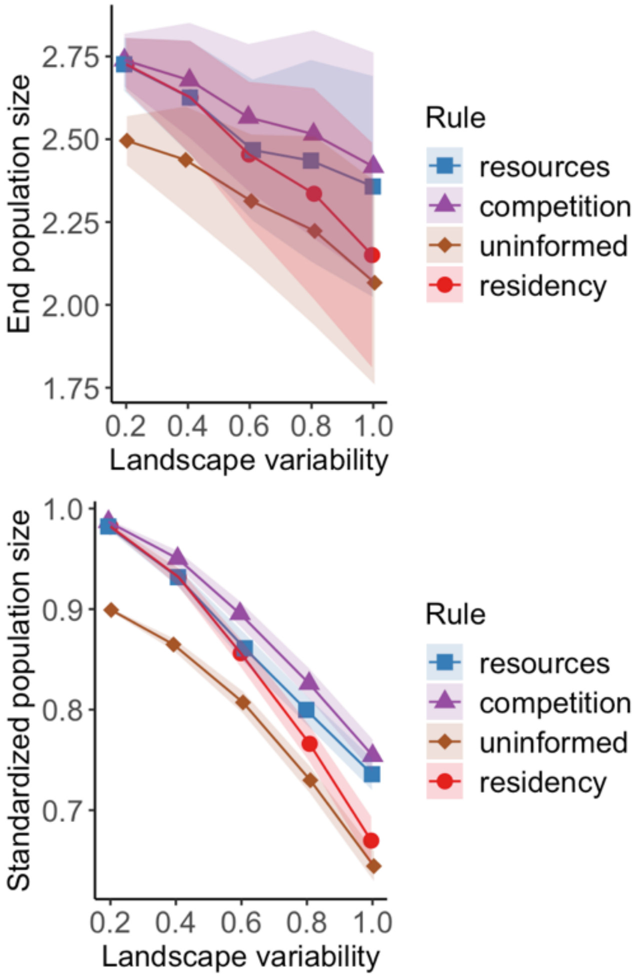


Figure S4.5: Alternative metrics of population performance show similar trends as annual survival. Raw population size at the end of the simulation (top) is more variable than survival (Figure 3 in main text) because of differences in resource dynamics across simulations, but average trends are consistent with the results in Figure 4.3. Standardized population size (bottom) is the end population size of a population relative to the population size that would be achieved in that landscape by animals redistributing according to the ideal free distribution with no movement cost; this standardization takes into account differences in resource dynamics and initial population sizes across simulations.

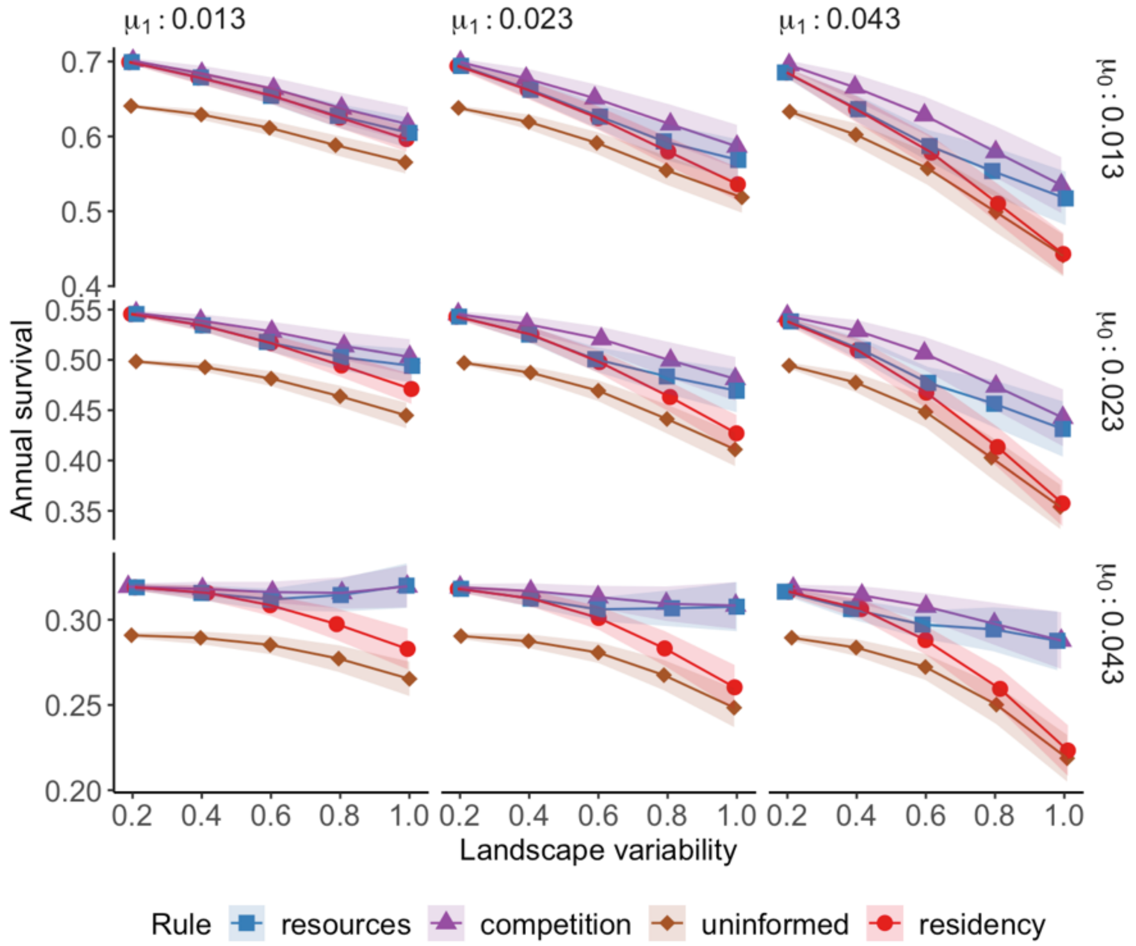


Figure S4.6: Effects of mortality rates on the relative performance of different departure rules. Rows show different values of density-independent mortality and columns show density-dependent mortality. Error bars show the standard deviation of the mean across 100 simulations. Points are jittered along the x-axis for visualization only. Note the different scales of the y-axes across rows. Competition-based movement tends to perform better than resource-based movement when density-independent mortality is low.

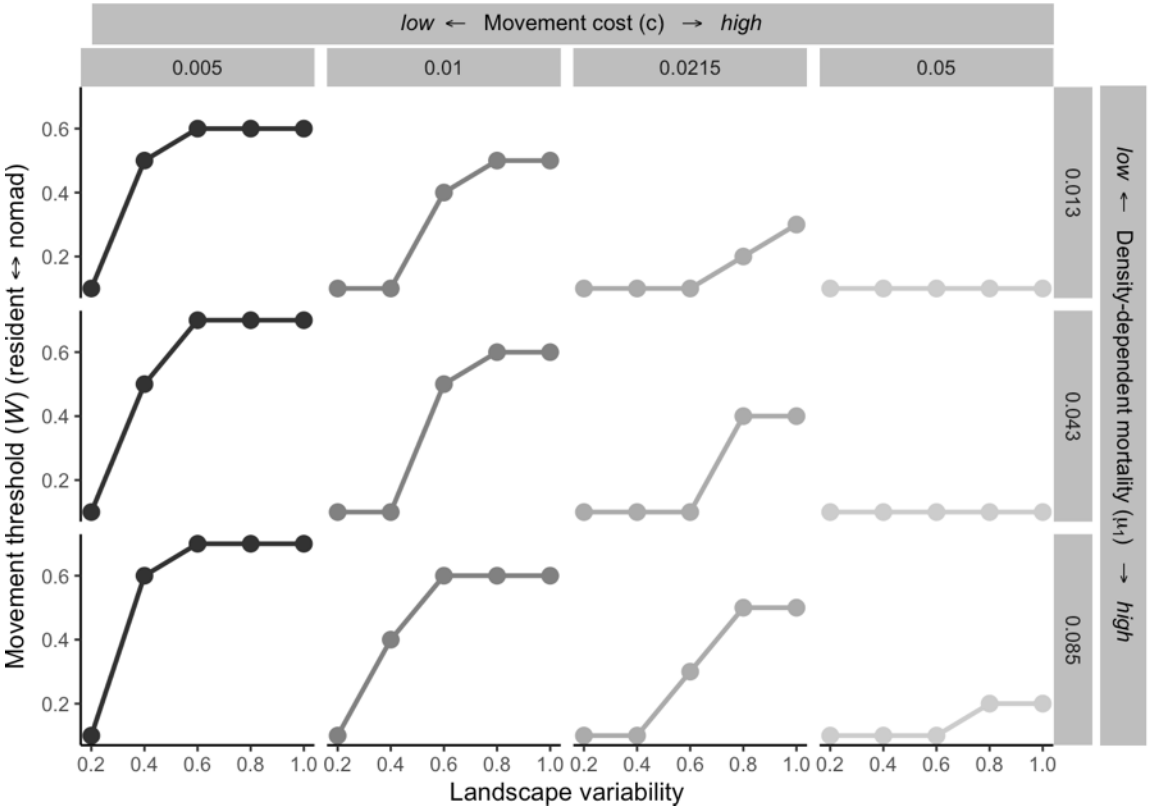


Figure S4.7: A population's optimal movement propensity (i.e., the movement threshold *W*) tends to increase with landscape variability, the strength of density-dependent mortality, and a decreasing cost of movement. The optimal movement threshold is the value of *W* that produces the largest population size for each parameter set. Columns are different movement costs (*c*) and rows are different strengths of density-dependent mortality (μ_1).

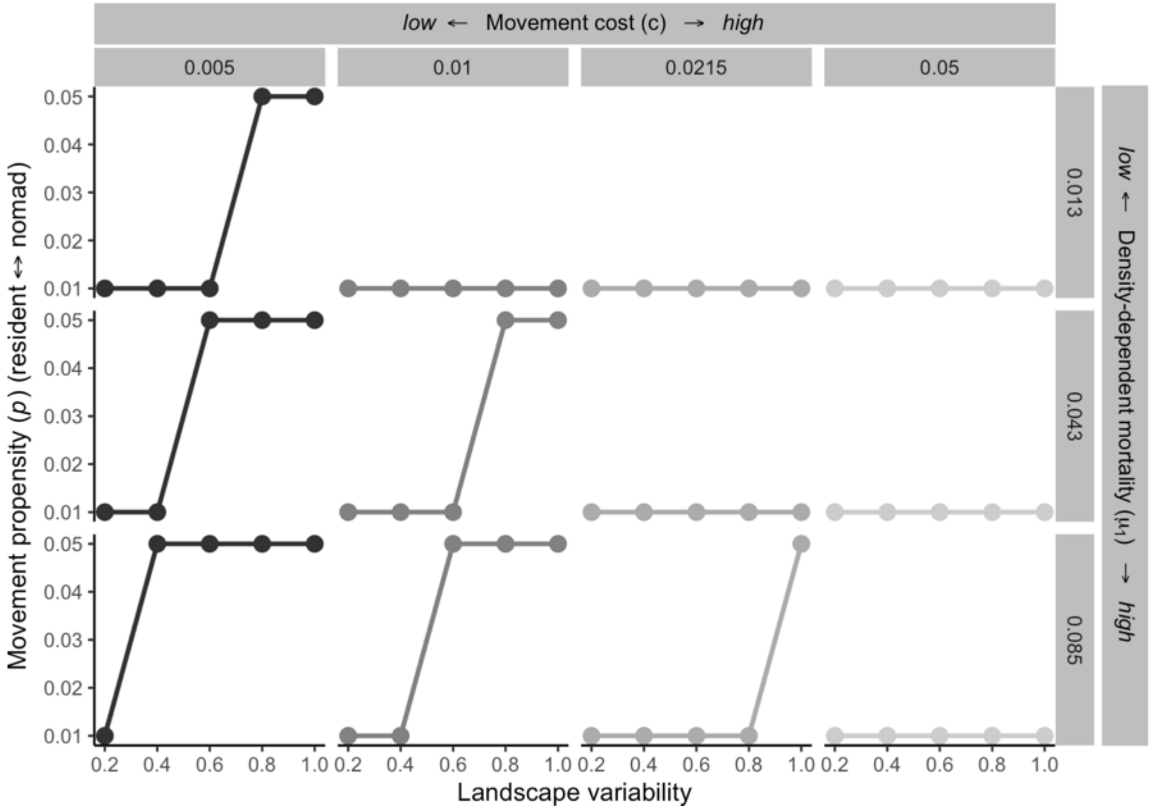


Figure S4.8: An uninformed population's optimal movement propensity (i.e., the parameter *p*) tends to increase with a decreasing cost of movement and slightly with increasing density-dependent mortality and landscape variability. The optimal movement propensity is the value of *p* that produces the largest population size for each parameter set (i.e., each combination of *V*, μ_I and *c*). Columns are different movement costs (*c*) and rows are different strengths of density-dependent mortality (μ_I).

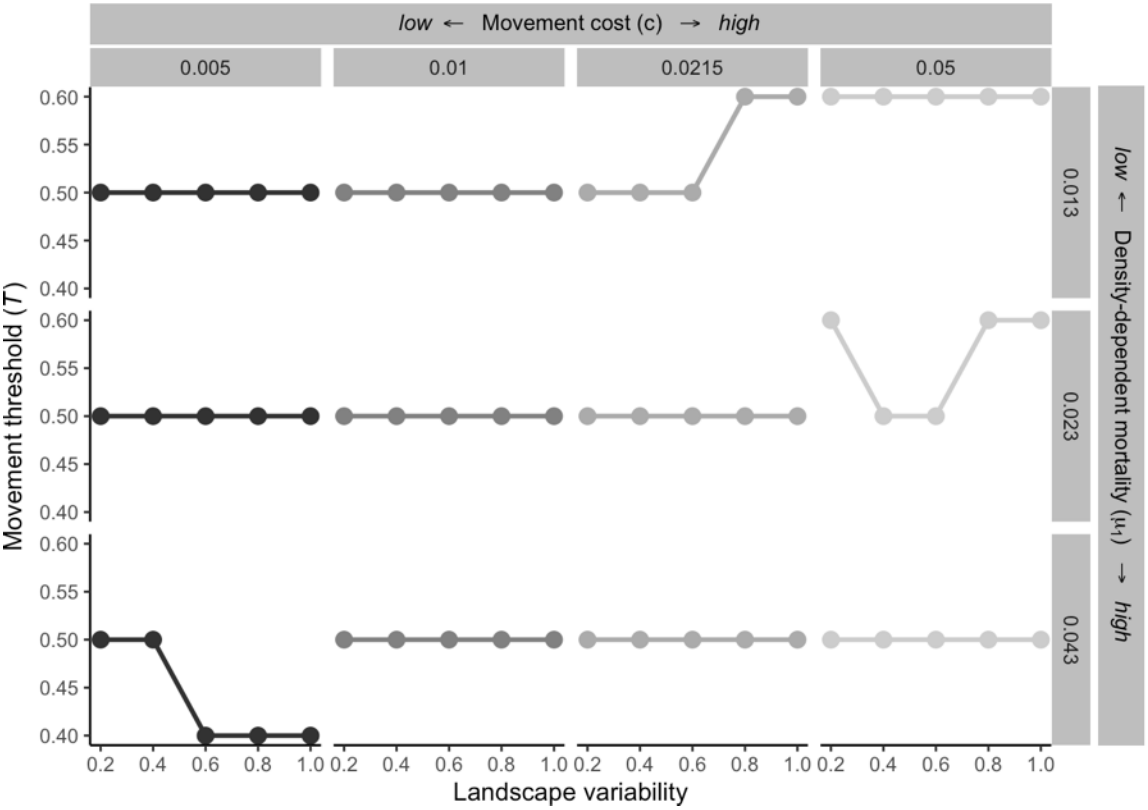


Figure S4.9: The optimal movement threshold *V* for a population using density-only cues varies little depending on the cost of movement or mortality rates. The optimal movement threshold is the value of *V* that produces the largest population size for each parameter set. Columns are different movement costs (*c*) and rows are different strengths of density-dependent mortality (μ_1).

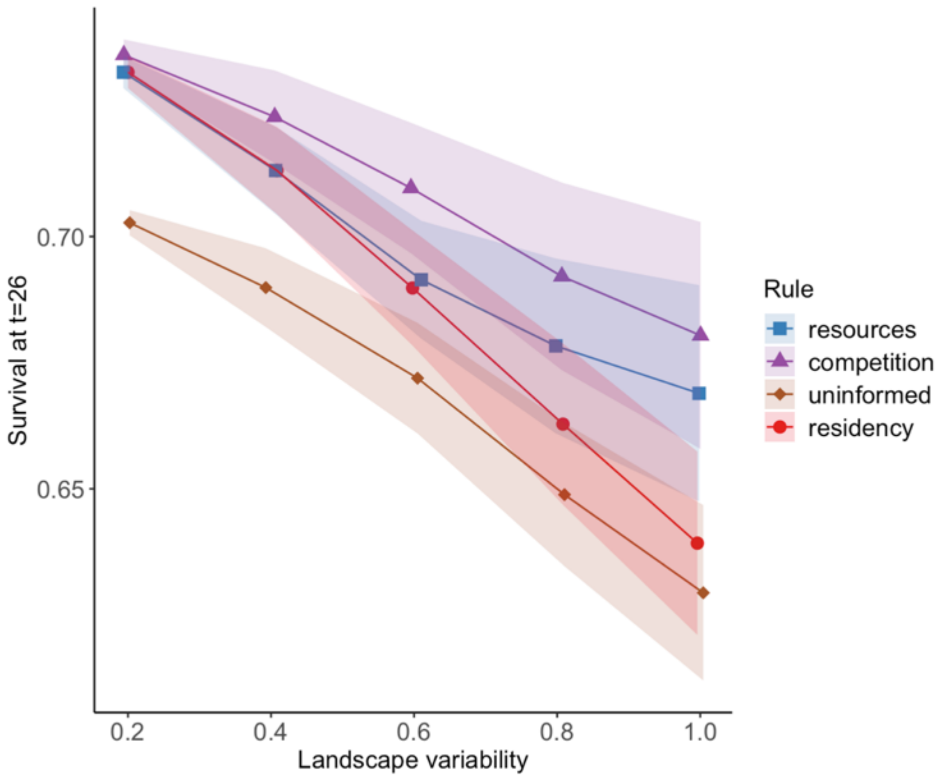


Figure S4.10: Effects of nomadic departure rules on survival at six months (*t*=26, half of the timescale shown in Figure 4.3). Error bars show the standard deviation of the mean across 100 simulations. Points are jittered along the x-axis for visualization only.

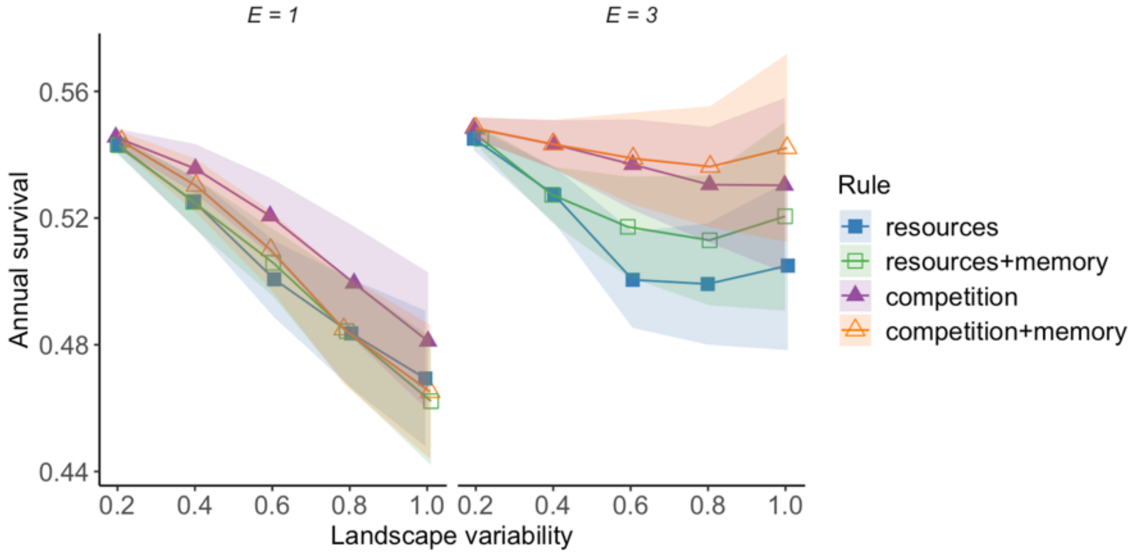


Figure S4.11: Effects of landscape variability and temporal autocorrelation on the survivals moving according to different rules. The parameter *E* controls temporal stability; landscapes where *E*=1 (left) have no autocorrelation and landscapes where *E*=3 have stability over one timestep (Figure 4.1 in main text). Rules that incorporate memory (open symbols) perform no better than those that do not (filled symbols) in landscapes without autocorrelation (left) but marginally better in those that have some autocorrelation (right). These differences are important only when landscape variability is relatively high (e.g., $V > 0.5$).

APPENDIX C

CHAPTER 5 SUPPLEMENTARY INFORMATION

Table S5.1: Results from generalized linear models predicting metrics of node centrality and node size from spatial variables and urbanization score. All predictor variables were scaled to be centered at 0 with a standard deviation of 1, so larger parameter estimates indicate a stronger effect of a predictor variable. P-values below 0.05 are shown in bold.

Degree centrality

Variable	**Estimate**	**SE**	**z**	**p**
(Intercept)	1.01	0.062	16.232	**<0.001**
NMDS1	-0.124	0.051	-2.463	**0.014**
lat	0.074	0.042	1.768	0.077
long	0.212	0.051	4.146	**<0.001**
lat^2	-0.261	0.044	-5.911	**<0.001**
$long^2$	0.021	0.039	0.549	0.583

Betweenness centrality

Variable	**Estimate**	**SE**	**z**	**p**
(Intercept)	5.313	0.306	17.389	**<0.001**
NMDS1	-0.266	0.251	-1.062	0.289
lat	0.621	0.183	3.39	**0.001**
long	0.013	0.267	0.05	0.96
lat^2	-0.406	0.153	-2.65	**0.008**
$long^2$	-0.271	0.195	-1.391	0.165

Node size

Variable	**Estimate**	**SE**	**z**	**p**
(Intercept)	1.536	0.153	10.073	**<0.001**

NMDS1	-0.055	0.125	-0.438	0.661
lat	0.054	0.091	0.586	0.558
long	0.431	0.133	3.234	**0.001**
lat^2	-0.24	0.076	-3.139	**0.002**
long^2	0.137	0.097	1.409	0.16

Table S5.2: Results from a linear model predicting node geographic area (log-transformed area in km^2) as a function of urbanization score (NMDS1), latitude, longitude, and number of visits to the node. P-values below 0.05 are shown in bold.

Variable	**Estimate**	**SE**	**z**	**p**
(Intercept)	146.433	25583.505	0.006	0.995
NMDS1	0.067	0.097	0.691	0.49
lat	94.325	50.477	1.869	0.062
long	34.939	636.684	0.055	0.956
lat^2	-1.767	0.946	-1.869	0.062
long^2	0.217	3.965	0.055	0.956
# visits	0.008	0.001	14.316	**<0.001**

Table S5.3: Results from generalized linear models predicting change in network properties following the removal of a single individuals. Both models used the proportional change in each network property (edge density or assortativity of NMDS1) as the response variable and the mean urbanization score (NMDS1) of all nodes used by an individual and the standard deviation of NMDS1 of all nodes used by an individual as predictor variables.

Edge density

Variable	Estimate	SE	z	p
(Intercept)	0.002	0.002	0.956	0.344
Mean NMDS1	-0.001	0.001	-0.837	0.406
SD NMDS1	0.007	0.003	2.1	0.041

Assortativity

Variable	Estimate	SE	z	p
(Intercept)	-0.007	0.002	-3.15	0.003
Mean NMDS1	0.003	0.002	1.903	0.063
SD NMDS1	0.015	0.004	3.882	<0.001

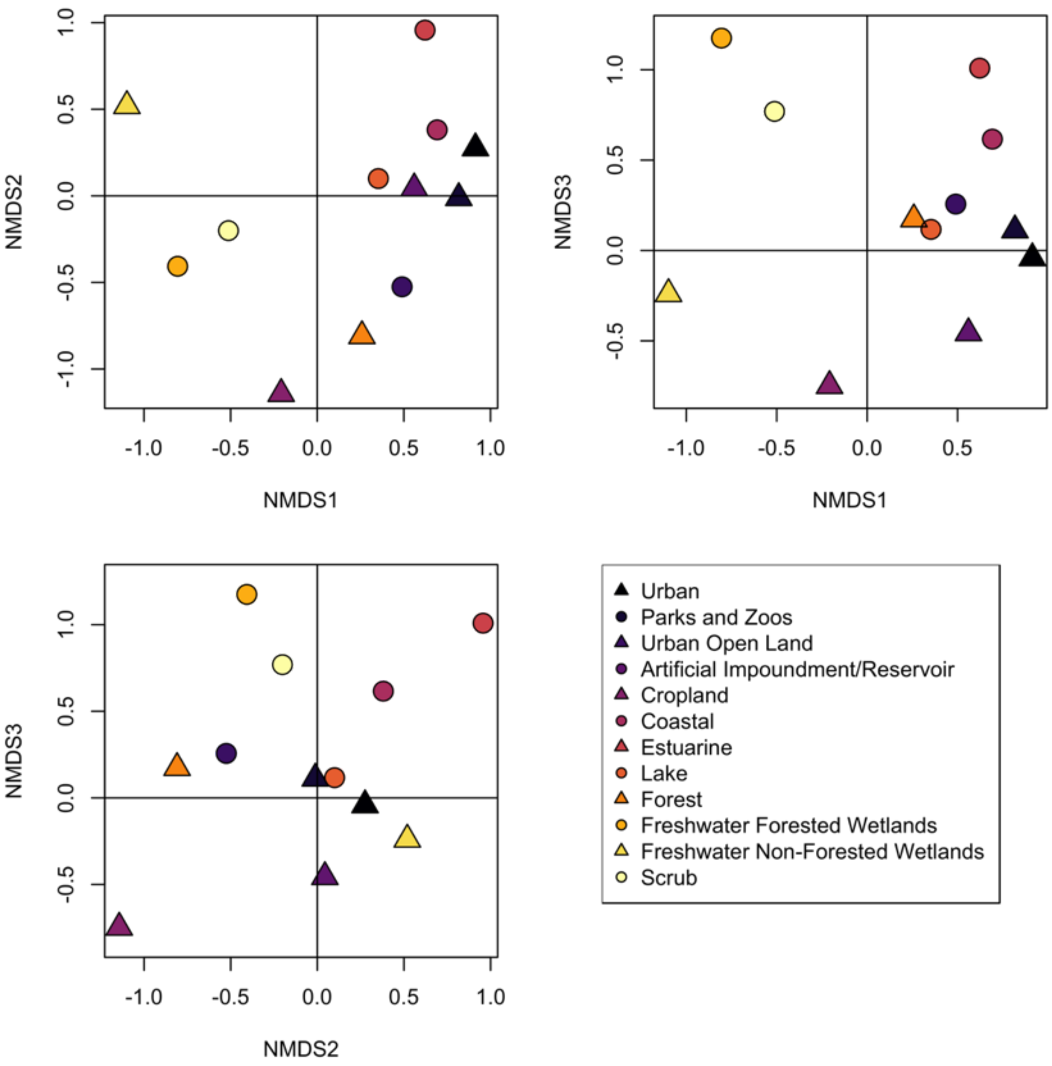


Figure S5.1: NMDS loadings for each of the 12 land cover categories. Colors are sorted by *a priori* categorizations of degree of human development; lighter colors show less developed habitats. Different shapes are included only to assist in identifying land cover classes but are not otherwise meaningful. Along the first NMDS axis, nodes separate out along a natural-urban gradient.

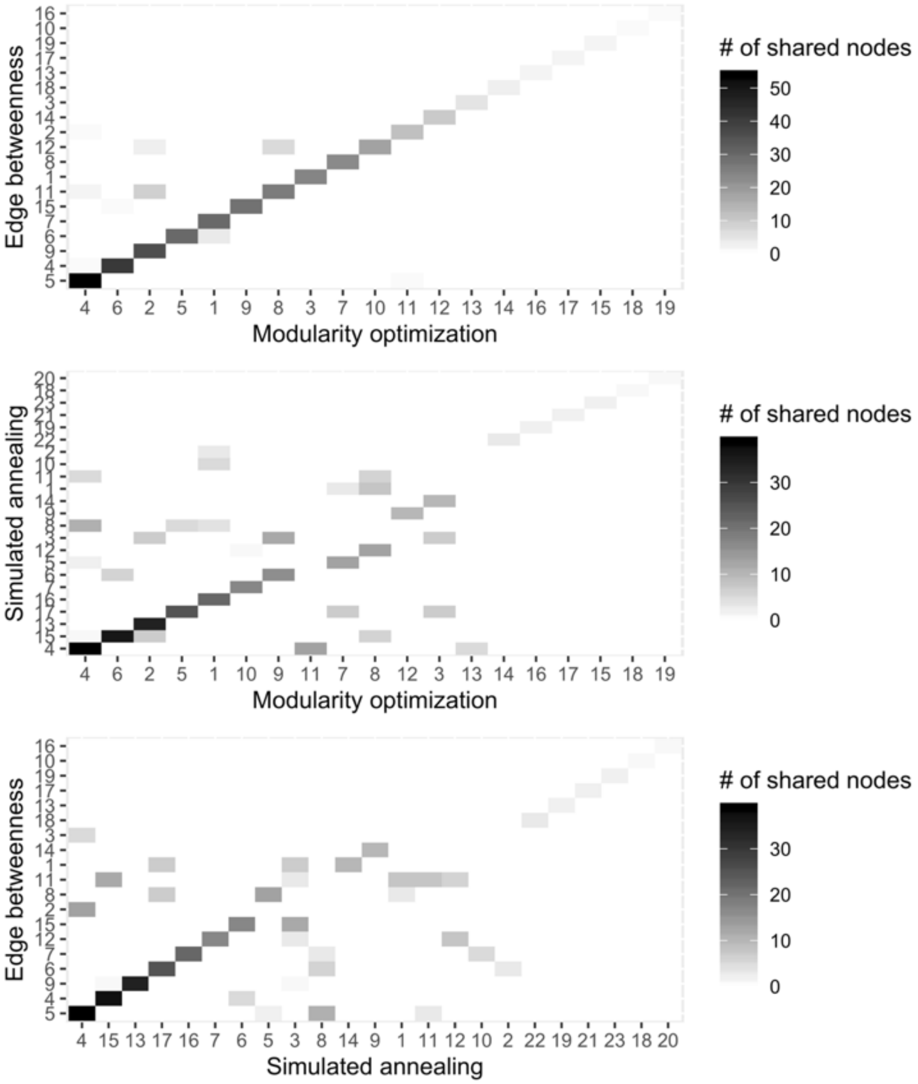


Figure S5.2: Module membership across methods. Each matrix shows the number of nodes shared between modules in each method. Modules are sorted by their number of shared nodes on each axis. (A) Modularity optimization vs. edge-betweenness. (B) Modularity optimization vs. simulated annealing. (C) Simulated annealing vs. edge-betweenness.

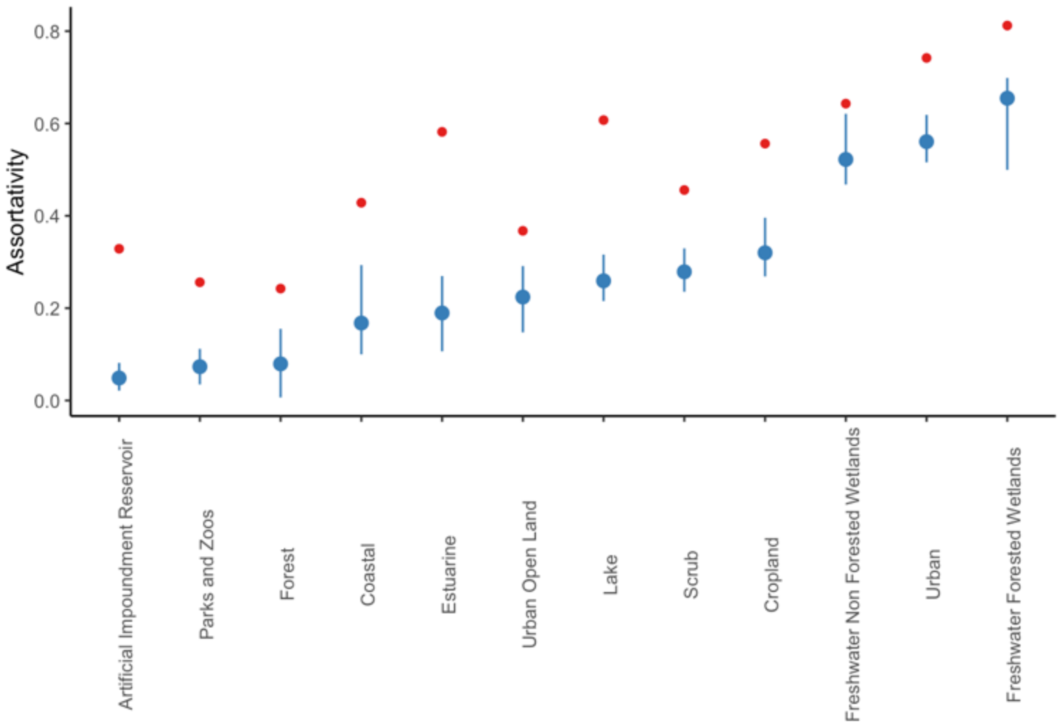


Figure S5.3: Assortativity for each land cover class. Red points show values for the observed network and blue points show the mean across 50 simulated networks. Blue lines show the range of values across the 50 simulated networks.

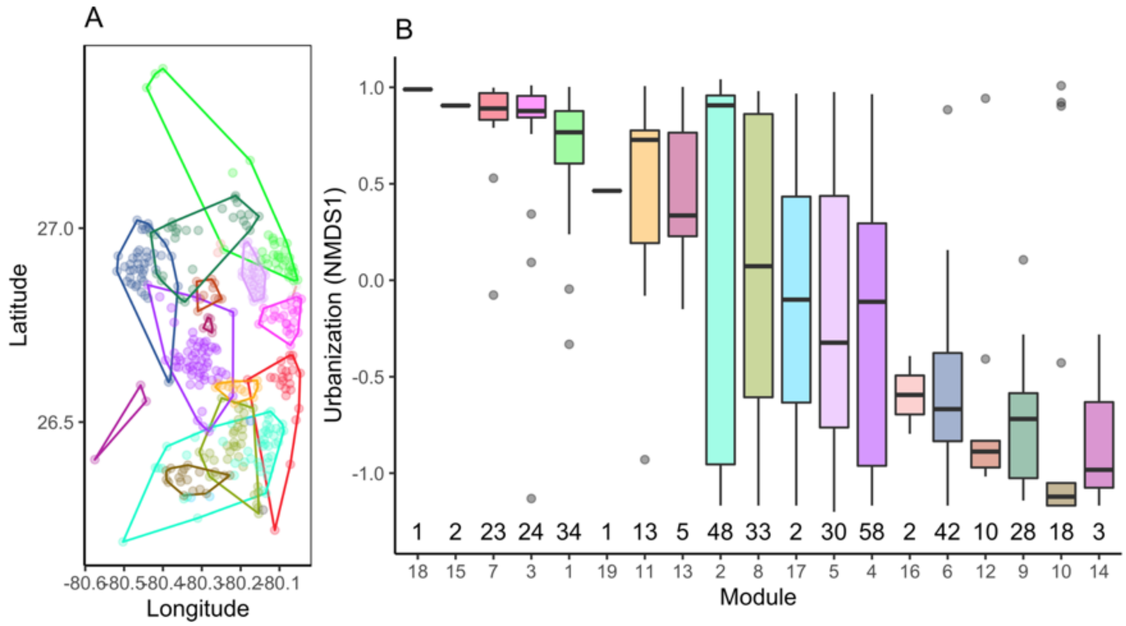


Figure S5.4: Module locations and characteristics. (A) Locations of all nodes in each module. Points show each node and polygons show convex hulls containing all nodes in a module. Modules with fewer than three points do not have a polygon drawn. (B) Urbanization score of the nodes in each module. Boxplots show the median and interquartile range of the data; whiskers extend out to 1.5* the interquartile range and outliers are shown as points. The numbers below each boxplot indicate sample size, i.e. the number of nodes in that module. The colors in the two panels correspond to the same module.

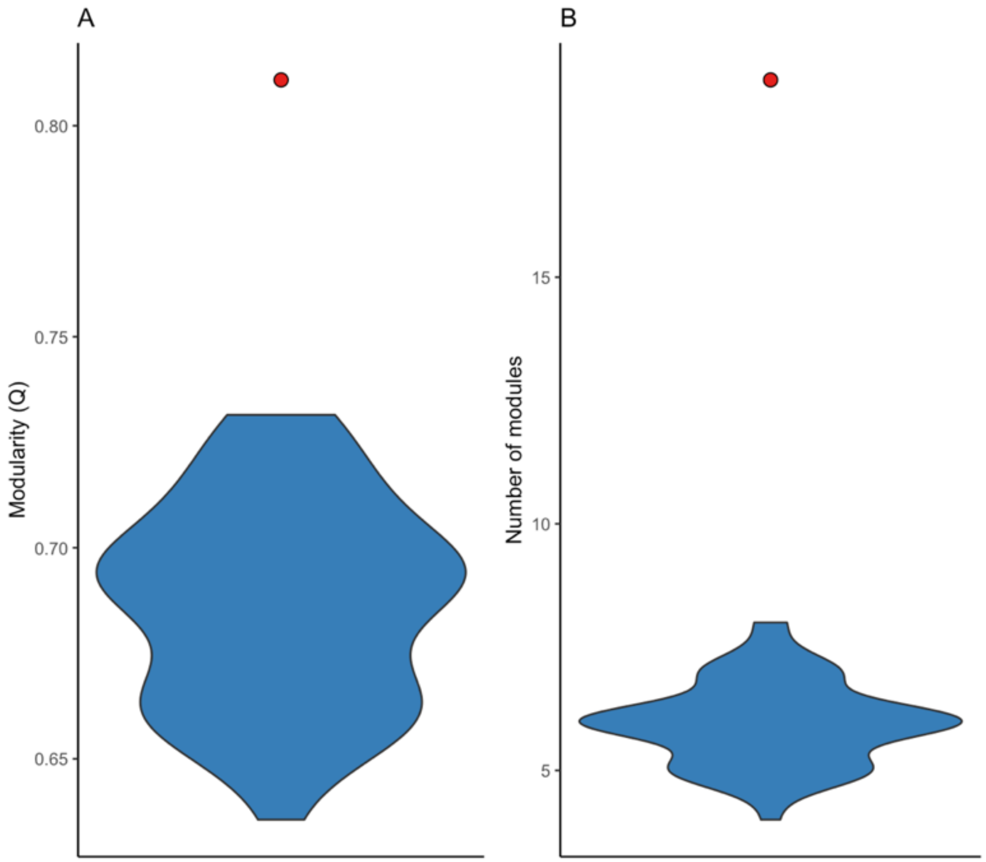


Figure S5.5: Modularity scores (A) and number of modules (B) in simulated and observed networks. Observed networks are the red points; violin plots show density distributions of values from 50 simulated networks.

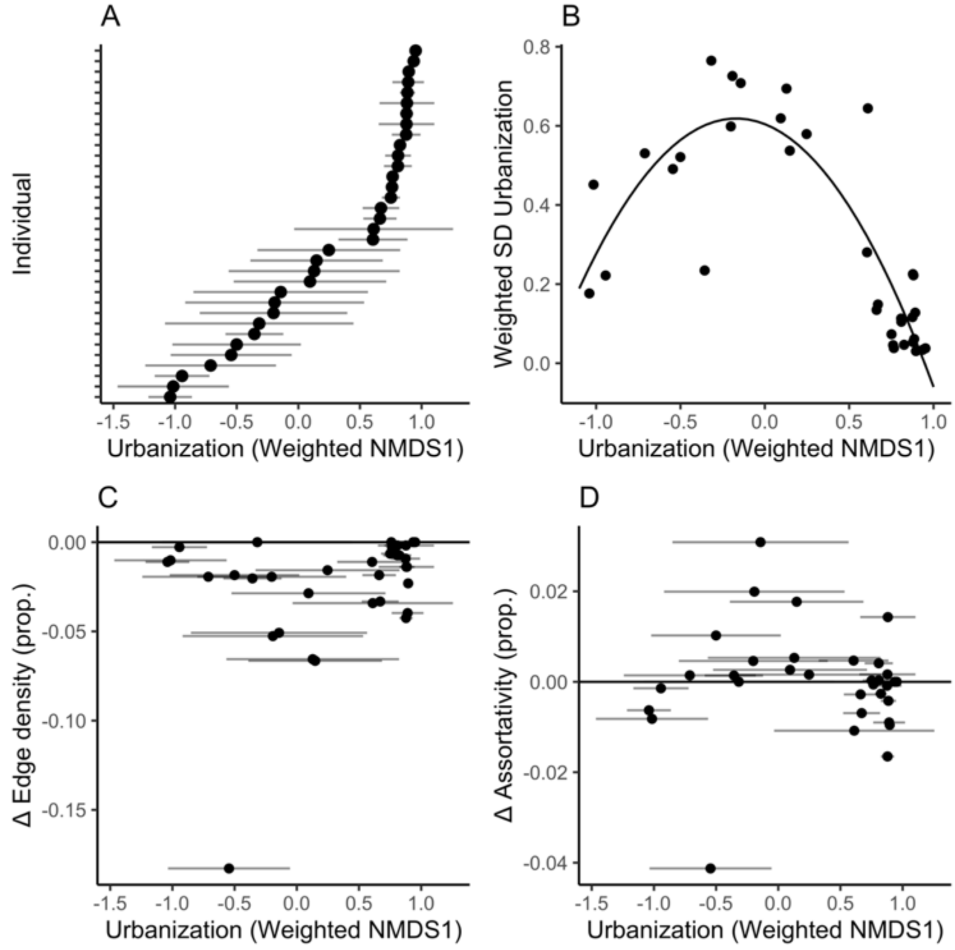


Figure S5.6: Individual habitat use and connectivity role for individual birds rather than tracks (i.e. bird-years). (A) Weighted mean and weighted standard deviation of urbanization score (NMDS1) of all sites used by each individual. (B) Relationship between mean and standard deviation in weighted NMDS1 score. The curve shows the results from a linear model relating the two variables. (C) Relationship between an individual's urbanization score and the change in edge density when they are removed from the network. Density can only decrease upon removal of an individual, so larger negative values indicate a larger influence of an individual on connectivity. (D) Relationship between an individual's urbanization score and the change in assortativity when they are removed from the network. The horizontal line at y=0 represents no change in assortativity.

APPENDIX D

CHAPTER 6 SUPPLEMENTARY INFORMATION

Table S6.1: Correlations between infection metrics. Each entry is the Pearson correlation coefficient (r) between two variables across all simulations that included infection (β>0).

	End prevalence	**Spread rate**	**Peak prevalence**	**Time to peak prevalence**	**CV site prevalence**
End prevalence	1	0.962	0.994	0.897	-0.753
Spread rate		1	0.982	0.829	-0.641
Peak prevalence			1	0.893	-0.716
Time to peak prevalence				1	-0.929
CV site prevalence					1

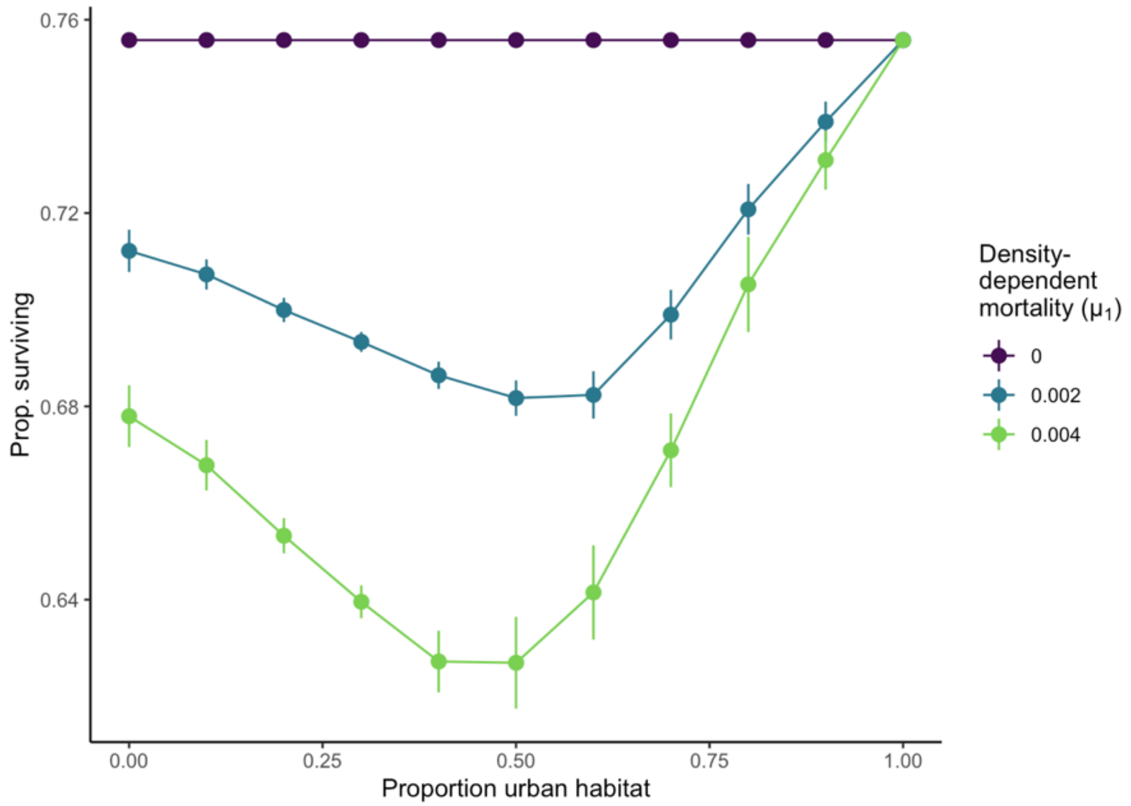


Figure S6.1: The relationship between urbanization and population-level survival depends on density-dependent mortality rates. In the presence of density-dependent mortality ($\mu_1 > 0$), survival is lowest in partially urban environments. Error bars show the standard deviation of the mean across eight simulations. Parameter values for these simulations are shown in Table 6.1.

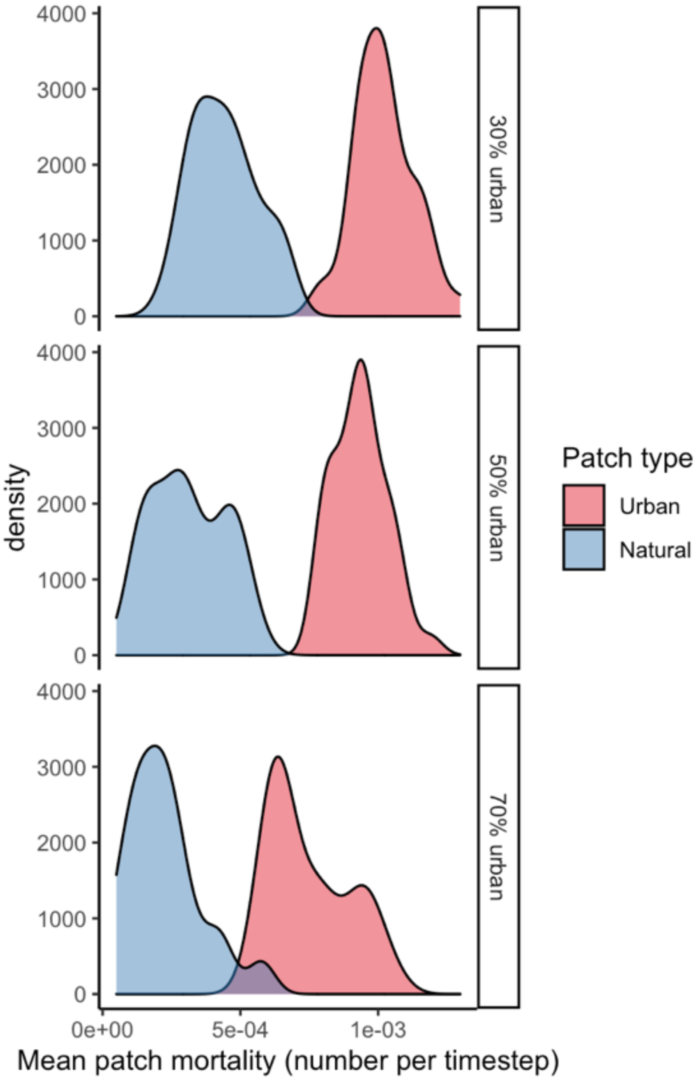


Figure S6.2: Distribution of mortality events at urban or natural patches. Mortality rates are the mean number of individuals that die at a given site type in one timestep; the mean is used rather than the total to account for different numbers of patches of each type in the three different panels (30%, 50%, or 70% urban). Mortality rates are consistently higher at urban than at natural patches, and the difference is largest in 30% urban landscapes.

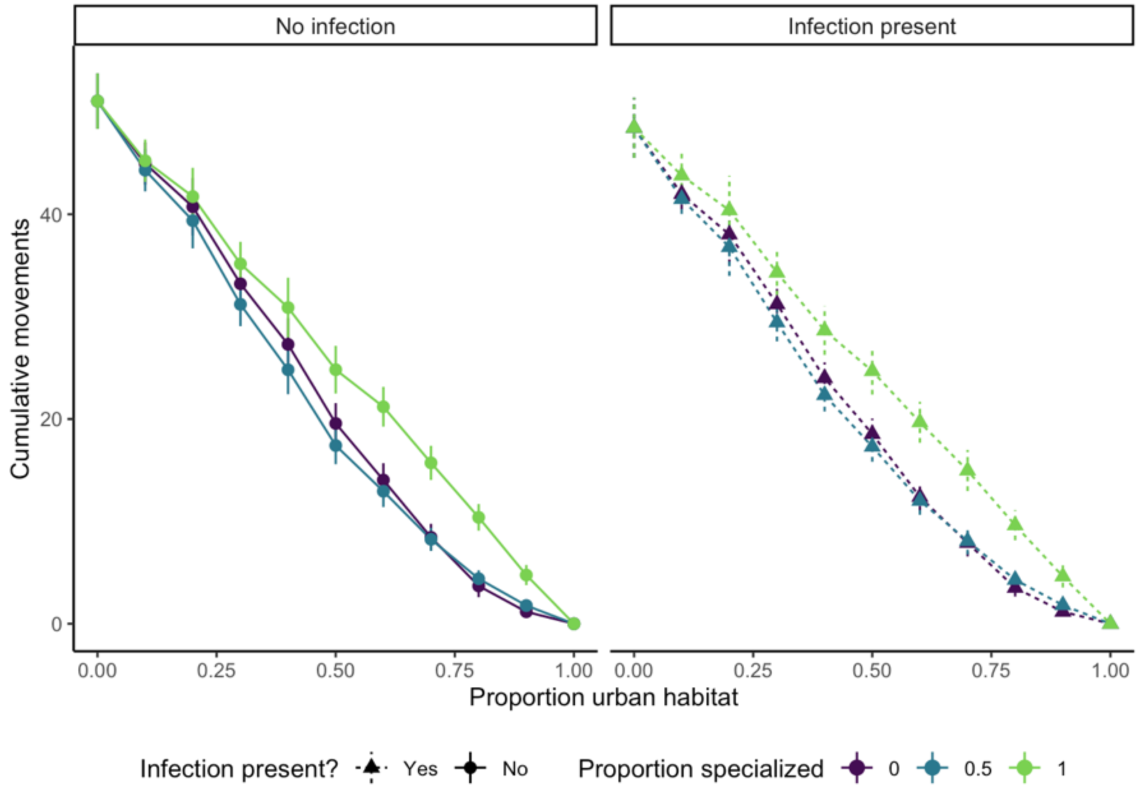


Figure S6.3: Movement rates decline with urbanization, but are relatively unaffected by the presence of infection or specialization. Movement rates are measured as the total number of movements over the 40-week simulation. Error bars show the standard deviation of the mean across eight simulations. Parameters for these simulations are shown in Table 6.1.

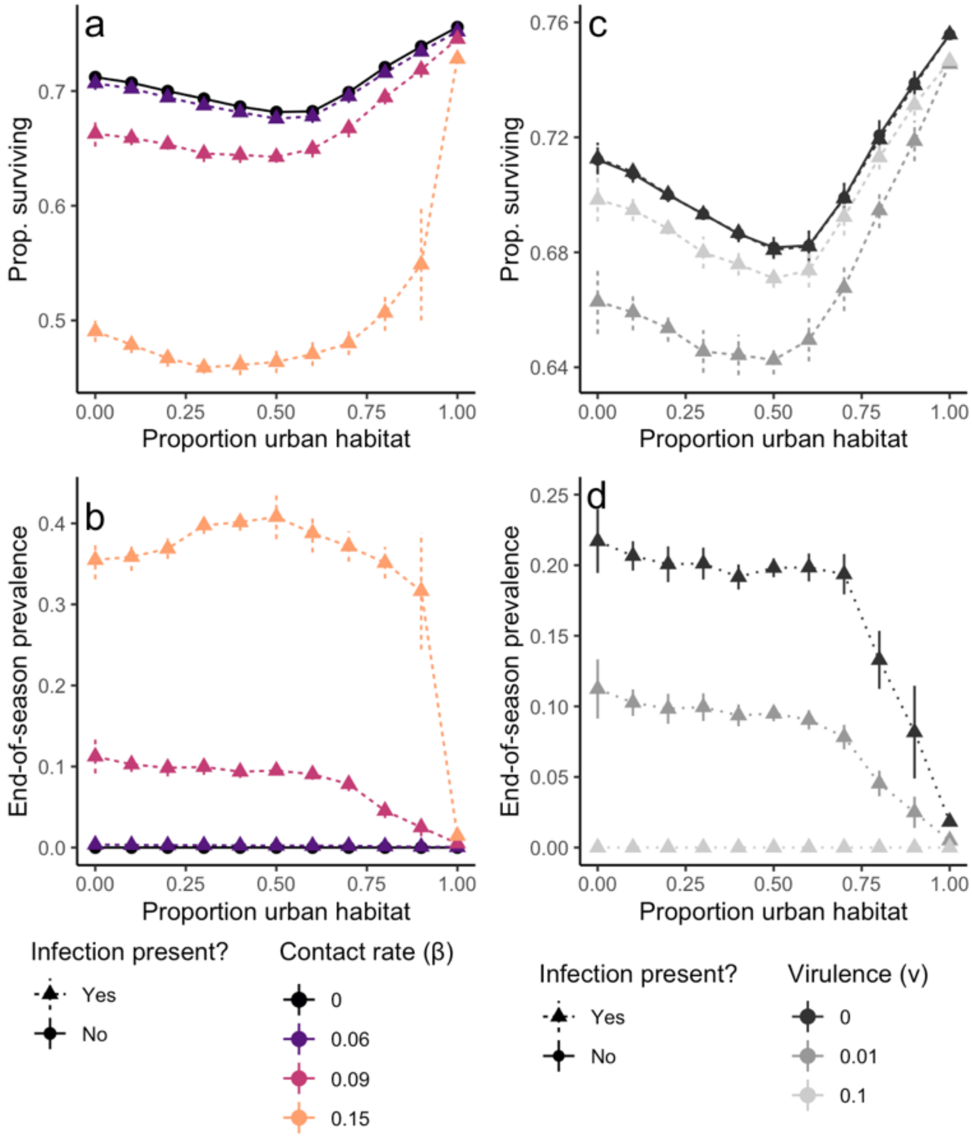


Figure S6.4: Effects of infection on (a, c) population-level survival and (b, d) infection prevalence depend on contact rates and pathogen virulence. Error bars show the standard deviation of the mean across eight simulations. (a, b) Higher contact rates reduce survival and increase prevalence for an intermediately-virulent pathogen (v=0.01). (c) The largest effect of infection on survival occurs at intermediate virulence for a pathogen with an intermediate contact rate (β=0.09). (d) Higher virulence decreases end-of-season prevalence. Other parameters used for these simulations are shown in Table 6.1.

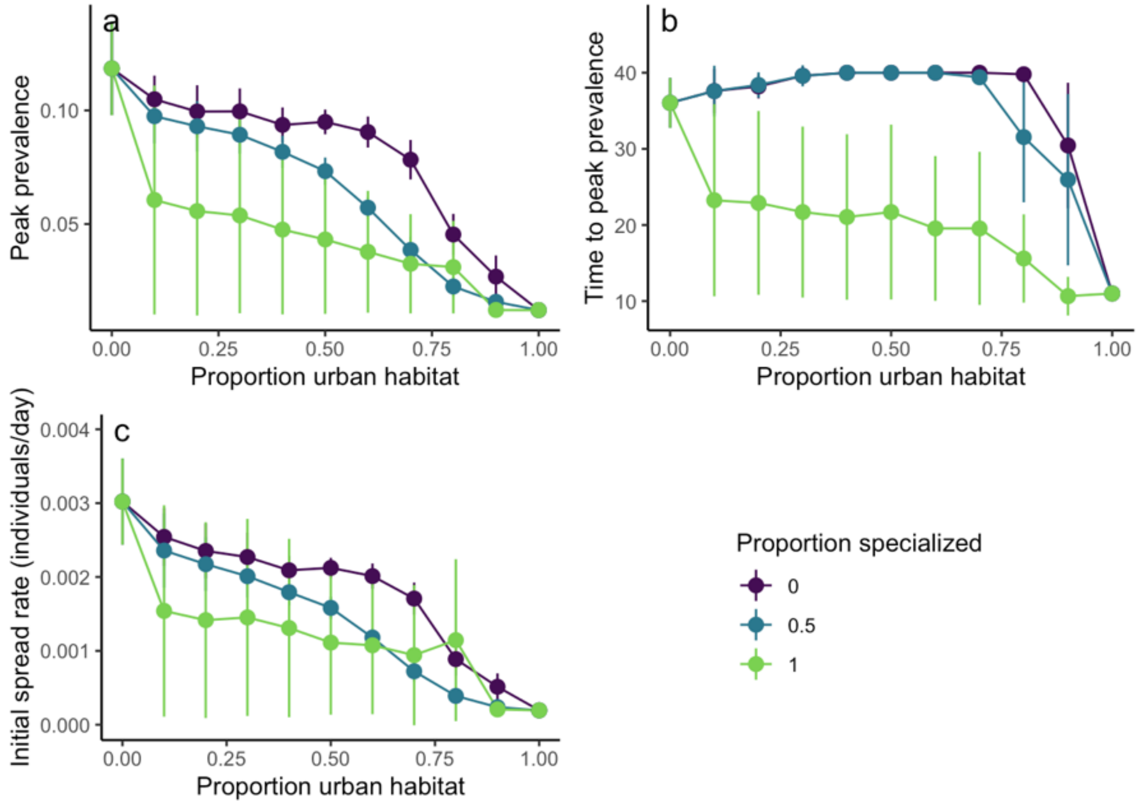


Figure S6.5: Effects of urbanization and specialization on the temporal and spatial patterns of pathogen spread. In all plots, error bars show the standard deviation of the mean across eight simulations. (a) Peak prevalence (the maximum prevalence over the entire simulation) generally declines with urbanization and specialization. (b) Peak prevalence is achieved more quickly when hosts are specialized. (c) The spread rate (the number of individuals infected per day up until peak prevalence is reached) declines with urbanization and specialization. (d) The coefficient of variation in end prevalence across patches increases with specialization.

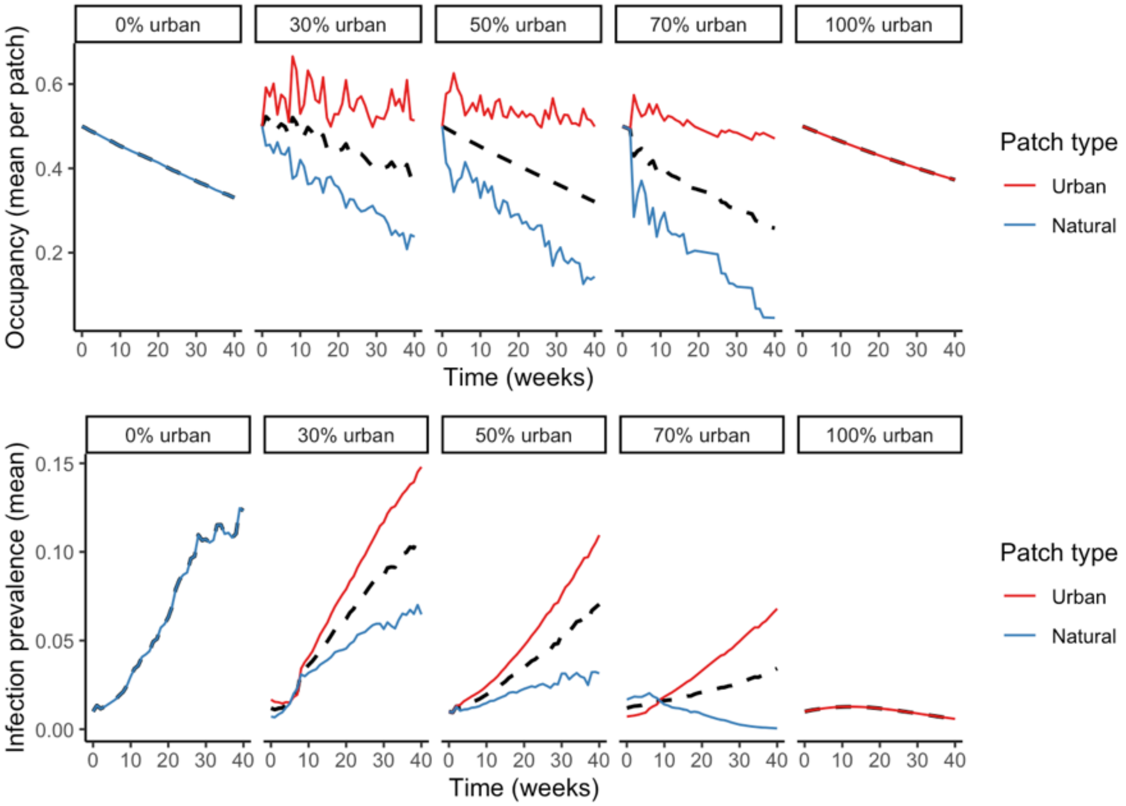


Figure S6.6: An example time series showing occupancy (top) and infection prevalence (bottom) for urban patches (red), natural patches (blue), and the mean across the landscape (black, dashed) over the course of a simulation. This simulation included no host specialization. Panels show different levels of urbanization; note that the number of patches of each type varies across the panels. All other parameters are those shown in Table 6.1.