Connecting the social and spatial behaviors of a territorial species (*Anolis carolinensis*)

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To Alfredo, Freddie, and Sophie, who fill my life with joy

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ABSTRACT

Why animals live where they do is a key question in ecology and evolution. An individual's home range determines the resources they have access to, conspecifics they encounter, and predators and pitfalls they must avoid. Home range behaviors also have an inherently social component; where animals live affects the rivals they compete with and the mates they have access to. This is especially true in territorial species, as defensive displays make up a large portion of their social behaviors. In this dissertation, I sought to understand how territorial behaviors affect the social lives of the green anole lizard (*Anolis carolinensis*). I first explored the effects of translating home range estimation methods into three dimensions, a necessary advance to fully understand the spatial behaviors of arboreal anoles. I found that home range estimators had more variable accuracy in 3D than they did in 2D, particularly for kernel density estimators, and that minimum convex polygon estimators were the most accurate metrics for patrolling species like anoles. Next, I showed that male green anoles can be unambiguously categorized into three territorial phenotypes, territory owners, sneakers, and floaters, and that these phenotypes differ in how often they interact and how much their home ranges overlap with one another. Sneaker males also showed similar behaviors to females, further supporting their hypothesized female-mimicry role. Finally, I investigated how the social and spatial behaviors of green anoles change when their populations are invaded by an invasive congener, the Cuban brown anole (*A. sagrei*). I found that while green and brown anoles did behaviorally interact, there was no evidence that brown anoles socially dominated green anoles. Altogether, this work indicates that the underlying spatial behaviors of a species can have dramatic effects on its social landscape.

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CHAPTER ONE
INTRODUCTION

Since the birth of ethology (the study of animal behavior), scientists have attempted to understand the myriad ways in which animals interact with one another. Early attempts to catalogue social systems quickly became unwieldy as biologists continued to discover new animal social interactions (e.g., Scott, 1956). Researchers instead have turned to theoretical frameworks to organize and understand animal social behaviors. E. O. Wilson (2000) conceptualizes social structures as the summation of ten continuous variables, including group size, social cohesion, and time spent on social behavior. In contrast, Hinde (1976) views social systems as emergent properties of relationships between individuals that develop over time. These frameworks have created foundations through which to understand the many complex ways in which animals form groups, divide resources, find mates, and care for their young.

Territoriality is an aspect of social organization that is observed across the animal kingdom in species as phylogenetically distinct as ants (e.g., Heinze, Foitzik, Hippert, & Hölldobler, 1996), lions (e.g., Packer et al., 2005), and tropical fish (e.g., Righton, Miller, & Ormond, 1998). *Territoriality* can be broadly defined as defending a space from potential rivals to secure exclusive or priority access to resources (Brown & Orians, 1970; Kaufmann, 1983; Maher & Lott, 1995). Some authors view territoriality as privatization of resources akin to property ownership (Sherratt & Mesterton-Gibbons, 2015; Strassmann & Queller, 2014). This is analogous to the view of territoriality as a system of spatially explicit dominance maintained through submissive individuals' willingness to cede resources to established territory owners (Kaufmann, 1983). Under these definitions, a *territory* is distinct from an undefended *home range* (R. A. Powell, 2000); while a home range encompasses the entire area in which an animal forages, mates, and cares for its young (Burt, 1943), a

territory is an area in which individuals specifically maintain exclusive access through exclusionary behaviors. An individual's territory can encompass its entire home range or constitute only a small portion of it (R. A. Powell, 2000).

Territoriality is inherently both a spatial and a social construction, tied to both the area being defended and the social relationships surrounding ownership (Kaufmann, 1983). Multiple conceptual frameworks exist for understanding how individuals establish and maintain territorial boundaries (reviewed in Adams, 2001; Hinsch & Komdeur, 2017). Adams (2001) identifies three major categories of territorial models. (1) *Focal resident models* view territoriality as an individual decision based on the relative costs of defense and benefits of resource access (e.g., Schoener, 1983). In these models, individual animals choose a territory size that optimizes some criterion, usually time or energy. (2) *Models of interactions between neighbors* predict boundary locations between neighboring territories either using geometric models (e.g., Dirichlet tessellations; Halls, Bulling, White, Garland, & Harris, 2001) or through local rules of movement and competition, such as game theory (Maynard Smith & Parker, 1976). Multiple evolutionarily stable strategies have been proposed for territorial game theory contests, such as variations of the Hawk and Dove game, where populations contain mixtures of aggressive and submissive individuals, and the Bourgeois Principle, where territory owners always fight and intruders always flee (Maynard Smith & Parker, 1976). (3) S*ettlement models* describe interactions between established territory owners and new settlers. These models predict how many individuals can establish territories in a given area by considering the effects of settlement order and dynamics between established territory owners and intruders (e.g., Stamps & Krishnan, 1990).

Much variation exists in territorial systems observed in the animal kingdom. Animals can defend many different resources, such as food, mates, or refuges, using a variety of defensive behaviors, such as visual displays, scent markings, songs, and ritualistic fights (Maher & Lott, 2000). Territoriality can be integrated into other levels of Wilson's categories of social organization, leading to variation in size of

defending groups, dominant/submissive status within a territory, and time spent on territorial behavior. Even within traditionally "territorial" species, not all individuals necessarily establish and defend territories in the same way. Sometimes individuals are unsuccessful at establishing their own territories and become "floaters" (J. N. M. Smith & Arcese, 1989). Forgoing reproduction to live as a floater for a period of time can be a viable fitness strategy in some species, as it allows floaters (often juveniles) to become familiar with an area to gain advantages in future contests (Stutchbury & Zack, 1992) and to take over territories vacated by previous owners (S. M. Smith, 1984). Some species also have behavioral or morphological polymorphisms leading to alternative spatial strategies, such as the "rock, paper, scissors" game described by Sinervo and Lively (1996). Individuals can also switch between defending and not defending resources depending on resource availability and conspecific density (Lott, 1991).

Much research in the last century has been devoted to describing territorial behaviors and understanding their fitness costs/benefits. Modern territorial research seeks to dive deeper into the nuance and complexity of territorial systems. Hinsch and Komdeur (2017) point out that territoriality is just one of many different types of animal conflicts. They emphasize the importance of considering the stakes of territorial defense: are intruders attempting to eject the owner from the territory altogether, or are they seeking to shift established boundaries, or are they intruding on the territory to steal resources? They further draw attention to the characteristics of the resources being protected, for example the rarity or renewability of food supplies (e.g., Houston, McCleery, & Davies, 1985) or the behaviors and interests of the mates being guarded (e.g., Davies, 1989).

One challenge to territorial research in the modern era is integrating new technology into study of animal spacing patterns. For many years, animals' home ranges and territories were measured by direct observation or through use of spatially limited radio-tracking collars. In recent years, advancements in radio-tracking and GPS technology have greatly increased the amount of location data

researchers can collect, improving estimates of home range size and spatial use (White & Garrott, 1990). Increased computational power and more widespread use of statistical software have also led to more sophisticated models for quantifying and visualizing home range boundaries (Joo et al., 2020; Walter, Onorato, & Fischer, 2015), for example models that incorporate animal movement patterns or environmental boundaries (e.g., Benhamou, 2011). There has also been increasing interest in moving home range and territory analyses into three dimensions for species that use a vertical habitat component (e.g., Tracey, Sheppard, Zhu, Wei, et al., 2014). Researchers have measured 3D home ranges in aquatic (Simpfendorfer, Olsen, Heupel, & Moland, 2012; Vivancos, Closs, & Tentelier, 2016), avian (Cooper, Sherry, & Marra, 2014), arboreal (Jenssen & Nunez, 1998), and subterranean (Ousterhout & Burkhart, 2017) systems. Although three-dimensional models can produce more ecologically relevant estimates than their two-dimensional counterparts, there has been little discussion of how accurate these models are under different conditions. **In Chapter 2, I explore the accuracy of three-dimensional home range estimation methods under different sampling regimes and for species with different underlying behavioral patterns.**

Another challenge for modern researchers of territoriality is understanding the full nuance in established territorial systems. Take for example the green anole lizard (*Anolis carolinensis*), a model organism in behavioral ecology and evolutionary biology (Losos, 2009). Some of the earliest studies on green anoles described them as "territorial" (e.g., Evans, 1938), setting off a century-long research trajectory that has focused largely on the behaviors of large territorial males. As a result, much is known about the mechanisms behind territory establishment, contest behaviors, and dominant-submissive dynamics in anole populations (reviewed in Losos, 2009; Stamps, 1994). Yet while territoriality is an important aspect of anole population dynamics (Bush & Simberloff, 2018), other behavioral phenotypes observed in anole populations remain poorly understood, including non-territorial floaters and "sneaker" males hypothesized to behave as

female mimics (Irschick & Lailvaux, 2006; Orrell & Jenssen, 2003). **In Chapter 3, I explore the behavioral differences between territory owners, floaters, and sneaker males in green anole lizards**.

A final challenge facing territoriality researchers today is understanding how anthropogenic change affects the behaviors, distributions, and fitness of territorial species. Factors such as climate change, urbanization, and species invasions have led to wide-scale environmental changes to wild spaces across the globe. Territorial species can be particularly affected, for example when habitat fragmentation disrupts territory establishment (e.g., Matthysen & Currie, 1996) or when invasive species outcompete native species for space and resources (e.g., Rowles & O'Dowd, 2007). Species invasions can also introduce novel competitors or predators that naïve native species do not know how to combat (Carthey & Banks, 2014). For example, after being the only anole species in the continental United States for millennia, the green anole lizard (*A. carolinensis*) is now joined in Florida by over ten species of anoles introduced from the Caribbean Islands (Krysko et al., 2016). As a result of these introductions, green anoles have shrunk their microhabitat use (Kamath, Stuart, & Campbell, 2013) and evolved different feet morphology (Stuart et al., 2014), although it is unclear how much these changes were mediated by direct competition from their territorial congeners. **In Chapter 4, I explore how an invasion by a closely related competitor (*Anolis sagrei*) affects the spatial and social behaviors of a native territorial species (*A. carolinensis*).**

CHAPTER TWO
ACCURACY OF THREE-DIMENSIONAL HOME RANGE ESTIMATES DEPENDS ON ANIMAL MOVEMENT PATTERNS

2.1 Summary

Many home range estimation tools exist, each of which can generate different estimates for the same data set. While many studies have compared these methods in two dimensions, there have been few discussions of the performance of three-dimensional home range techniques. Furthermore, discussions of home range accuracy rarely discuss the study animals' spatial behaviors, which can influence location point patterns and home range shapes. In this study, we tested how animal movement, model parameter choices, and sampling regime affect the accuracy of three-dimensional home range estimates. We used an agent-based model to generate movement data simulating five home range behaviors: random movement, random movement within a home range boundary, patrolling, movement centered around one resource, and movement centered around two resources. We then estimated the home range sizes of individuals from these points and compared the estimates to the actual space used. We compared four home range estimation methods: minimum convex polygon (MCP), fixed kernel density estimates with least-squared cross-validated bandwidths (KDE-LSCV), fixed kernel density estimates with "solve the equation" plug-in bandwidths (KDE-PB), and movement-based kernel density estimates (MKDE). Patterns in home range accuracy in two dimensions did not necessarily translate into three dimensions. In particular, MKDE methods were highly accurate in two dimensions, especially for high sample sizes, but consistently generated large overestimates in three dimensions. We also found that temporal autocorrelation within the data had larger impacts on estimator accuracy in three-dimensional space. Furthermore, our results showed that

movement behaviors affected estimator accuracy in both two and three dimensions, with MCP estimates performing the best in Patrolling simulations, KDE-LSCV performing poorly for One Resource and Two Resource simulations, and KDE-PB performing well across all simulations. Overall, we encourage researchers to apply three-dimensional home range estimation methods to species with vertical movement patterns and to consider animal movement patterns when choosing an appropriate home range estimation technique.

2.1 Introduction

Conservation biologists and wildlife ecologists frequently use home range measurements when researching natural populations and making management decisions, for example when studying seasonal changes in spatial behavior (Mysterud, 1999) or analyzing resource use (Sekercioglu, Loarie, Oviedo Brenes, Ehrlich, & Daily, 2007). Accurately estimating home range is thus vital for many aspects of ecology and conservation biology. Conceptually, a home range is commonly defined as, "that area traversed by the individual in its normal activities of food gathering, mating, and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered part of the home range" (Burt, 1943, p. 351). In practice, many researchers further turn to the operational definition given by White and Garrott (1990), which describes a "home range" as the smallest area in which an individual spends 95% of its time.

There has been increasing interest in expanding home range estimation methods into three dimensions (e.g., Tracey, Sheppard, Zhu, Wei, et al., 2014; Vivancos et al., 2016). Recent studies have calculated home range volumes in aquatic (Simpfendorfer et al., 2012; Vivancos et al., 2016), avian (Cooper et al., 2014), arboreal (Jenssen & Nunez, 1998), and subterranean (Ousterhout & Burkhart, 2017) systems. When two- and three-dimensional home range estimates are compared for species that use space in three dimensions, 3D estimates can

produce shapes that more accurately reflect the organism's actual space use (Simpfendorfer et al., 2012) and are more ecologically relevant (Vivancos et al., 2016) than 2D estimates.

A number of tools are available to estimate home range size in both two and three dimensions (e.g., Joo et al., 2020; R. A. Powell, 2000). Home range estimation methods can be loosely divided into three categories: first generation methods, such as minimum convex polygon (Mohr, 1947) and fixed kernel density estimation (Silverman, 1986); second generation methods that expand upon these original methods, such as plug-in bandwidth kernel density estimates (Jones, Marron, & Sheather, 1996); and third generation methods that incorporate time into model estimates, such as Brownian bridge (Horne, Garton, Krone, & Lewis, 2007) and movement-based kernel estimates (Benhamou, 2011; Tracey, Sheppard, Zhu, Wei, et al., 2014). Each method has different underlying assumptions, and the methods can generate different home range estimates for the same data set (Figure 2.1; e.g., Boyle, Lourenço, da Silva, & Smith, 2009; Walter et al., 2015).

Many studies have compared the accuracy of home range estimation methods under different circumstances in two dimensions. These studies discuss model parameter choices (e.g., kernel bandwidth selection; Gitzen, Millspaugh, & Kernohan, 2006; Seaman & Powell, 1996; Worton, 1995), sampling regime (e.g., Börger et al., 2006; Boyle et al., 2009), data collection techniques (e.g., GPS telemetry; Kie et al., 2010; Stark, Vaughan, Saldivar, Nathan, & Goossens, 2017), and performance against empirical data (e.g., Barg, Jones, & Robertson, 2005; Pebsworth, Morgan, & Huffman, 2012; Walter et al., 2015). Other researchers have considered the effects of point patterns (Downs et al., 2012; Downs & Horner, 2008) and data collection methods used for specific taxa (Boyle et al., 2009; Row & Blouin-Demers, 2006) on home range accuracy. Yet there has been little, if any, exploration of how home range estimation methods compare in three dimensions. Furthermore,

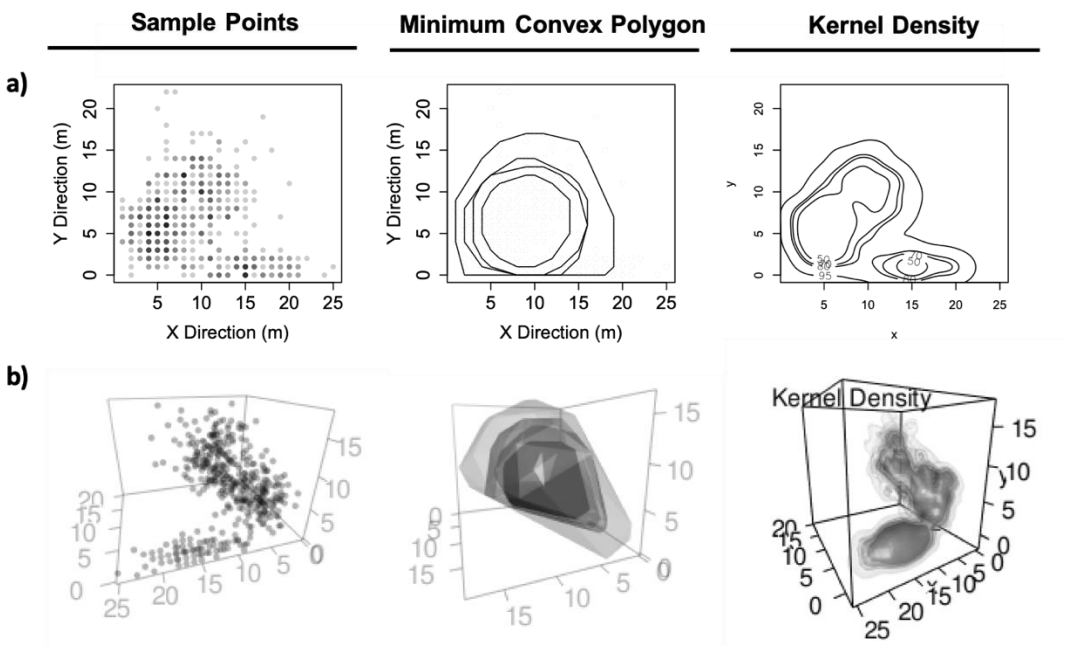

Figure 2.1 Examples of minimum convex polygon (MCP) and kernel density (KDE) home range estimates in two- and three-dimensions (a and b, respectively). Sample points were generated by combining random points from Poisson distributions with lambda = 1, 5, 10, 15. MCP estimates are shown for 50%, 70%, 80%, and 95%. KDE estimates show the 50, 70, 80, and 95 isoclines.

there have been few discussions of how animal home range behaviors affect two- and three-dimensional home range estimates. Indeed, many studies that compare different estimation techniques make recommendations using data from only a single species without considering the specific movement behaviors of that species (e.g., Stark et al., 2017; Walter et al., 2015). Animals can have a variety of spatial use patterns within their home range (Börger, Dalziel, & Fryxell, 2008; Fagan et al., 2013; Ims, 1995) that can lead to different distributions of potential location points and different home range shapes (Ims, 1995). As a result, some species may not fit the underlying assumptions of specific home range models.

In this study, we tested how animal movement patterns affect the accuracy of different home range estimators in 2D and 3D space. In particular, we were interested in whether model performance in two dimensions is comparable to performance in three dimensions.

To do this, we used an agent-based model to generate movement data simulating different home range behaviors. For each simulation, we selected a sample of "location points" to estimate the home range size using multiple estimators. We then compared these estimates to the actual space used by the agent during the simulation to determine the accuracy of the methods. We compared the performance of four home range estimators: minimum convex polygon (MCP; Mohr, 1947), fixed kernel density estimates (KDE) with least-squares cross validated bandwidth (KDE-LSCV; Stone, 1984), fixed kernel density estimates with plug-in bandwidth (KDE-PB; Jones et al., 1996), and movement-based kernel density estimates (MKDE; Benhamou, 2011; Tracey, Sheppard, Zhu, Wei, et al., 2014). We limited our analysis to variations of MCP and kernel density estimators because these are the two most common home range estimation techniques used in ecology (Laver & Kelly, 2008). Within these criteria, we chose a selection of first, second, and third generation estimates to incorporate recent advances in the field.

We also tested whether model parameters affected the accuracy of the home range estimates. We tested different values of sample size, estimator percentile (MCP) and isopleth (kernel methods), and the amount of autocorrelation in the sampled data. We predict that the sampling regime and estimator parameters will affect the accuracy of the home range methods, such that all four methods will generate the most accurate estimates under conditions of large sample sizes, high estimator percentile, and low temporal autocorrelation.

2.3 Materials and Methods

We used an agent-based model to generate movement data points for five types of movement algorithms. Each run contained one individual who moves through a uniform, discrete habitat matrix in discrete time steps. We considered habitat matrices in two and three dimensions. Runs in two dimensions consisted of 10,000 time steps on a 200 x 200 grid. Runs in three dimensions had 250,000 time steps on

a 100 x 100 x 100 grid. We increased the number of time steps in three dimensions so that individuals on both grids could move over the same percentage of available space over the course of the simulation. Edges of the grid were treated like walls, such that individuals cannot move in a direction that would take them outside the grid.

In each time step, the individual decides to move or stay where it is based on a set probability (p.move). If it moves, it can move in any of the four (or six, in three dimensions) cardinal directions. Its probability of moving in each direction is determined by the specific movement rules, discussed in the following section. Individuals start in the center of the grid.

Movement Algorithm Rules

We investigated five types of movement behaviors. As a null model, we tested individuals who move around the grid randomly without internal limitations (*Random*; Figure 2.2). The other four types of home range movement behaviors are depicted in Figure 2.2: 1) *Home Range*, where the individual moves around randomly within the bounds of a set home range, 2) *Patrolling*, where the individual spends time patrolling the edges of its home range, 3) *One Resource*, where the individual centers its movement around a fixed location (such as a nest site), and 4) *Two Resources*, where the individual divides its time between two resources with fixed locations (such as a nest site and a foraging site).

Random The individual moves around the grid in a random walk. In each time step, the individual has an equal chance of moving in any direction (except directions that would take the individual outside the grid, as described above).

Home Range The individual moves around at random within the bounds of a set home range. A home range consists of a circle (or sphere, in three dimensions) centered around the middle of the grid. While inside the home range, the individual has an equal probability of moving in any direction, as in the random algorithm. If the individual leaves the home range, there is a strong probability (0.9) that it will

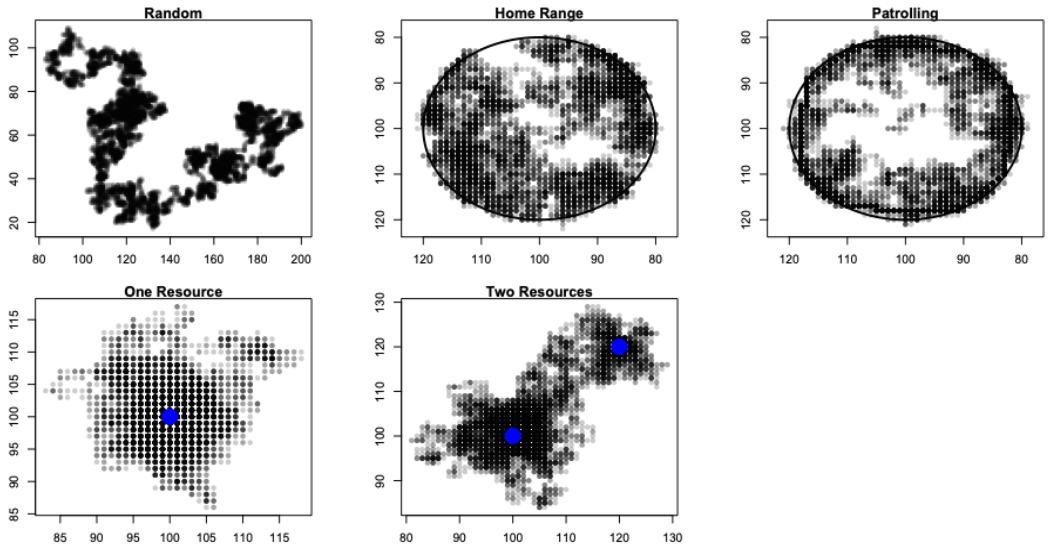

Figure 2.2 Examples of simulations in two dimensions generated with five movement pattern algorithms (1) Random, where the agent moves in any direction with equal probability, (2) Home Range, where the agent moves around randomly within the bounds of a set home range, (3) Patrolling, where the agent divides its time between randomly moving within a set home range and patrolling the boarders of the home range, (4) One Resource, where the agent centers its movement around a single resource (blue dot), and (5) Two Resources, where the agent divides its time between moving around two resources (blue dots).

move in the direction that will take it back into the home range in its next move. This parameter was held constant across all simulations.

Patrolling The individual alternates between moving within its home range at random and patrolling the edges of the home range. The agent begins the model not patrolling. In a given move, the agent decides if it is patrolling or not based on a given probability (p.patrol). If the individual is not patrolling, it moves according to the "Home Range" rules given above. When the agent switches to patrolling, a number of time steps to patrol is chosen from a random Poisson distribution (lambda = 5). While the agent is patrolling, it moves toward the closest edge of the home range. Once the individual enters "patrolling distance" from the edge (i.e., within 10% of the home range radius from the closest edge), it moves along the edge in a directed manner. In two dimensions, the individual moves counterclockwise along the home range circumference. In three dimensions, the individual moves

counter-clockwise around the edge of the sphere while maintaining a constant z-value.

One Resource The individual moves in a biased random walk attracted to a resource with a single fixed location, such as a nest site or a watering hole. The resource is placed in the middle of the grid. In a given move, the individual chooses to move towards the resource with a set probability (p.resource). If the individual is on the resource or decides not to move towards the resource, it can move in any direction with equal probability.

Two Resources The individual divides its time between two resources with fixed locations, for example a nest site and a foraging site. One resource is positioned on the center of the grid, while the other is a set distance away (resource.distance). The simulation starts with the individual moving around the first resource following the procedure described in the "One Resource" rules above. For each move, there is a probability that the agent will switch to focus on the other resource. This probability starts at zero and increases by a small, set amount each time step (switch.p.increment). The probability resets to zero each time the individual switches resources. The individual moves toward each resource with set probabilities (p.resource). In this analysis, we set the resource affinities of both resources equal to each other.

Home Range Estimators

We calculated home range estimates for each simulation using four home range estimation techniques: minimum convex polygon (MCP), fixed kernel density estimates with least-squares cross validated bandwidth (KDE-LSCV), fixed kernel density estimates with plug-in bandwidth (KDE-PB), and movement-based kernel density estimates (MKDE).

Minimum convex polygon methods, first described by Mohr (1947), involve drawing a convex shape around as many location points as possible, excluding points considered outliers. This method is easy to calculate, but it can overestimate home range size if large unoccupied areas exist within the range, and it is highly

sensitive to sample size (Worton, 1987). The method has been further criticized because it draws home range boundaries based on data points that lie along the periphery of the largest cluster, "[emphasizing] the unstable, boundary properties of a home range and [ignoring] the internal structures of home ranges and central tendencies" (R. A. Powell, 2000, p. 74).

The kernel density method, described by Silverman (1986), is a non-parametric statistical tool that builds a utility distribution atop location points. This gives an estimate for where the individual spends time, with the probability density estimate at each point corresponding to the amount of time the individual spent there (Seaman & Powell, 1996). The output of KDE methods is a series of isoclines where the individual spends a given percentage of its time. KDE estimates can be disjoint and can identify multiple centers of activity, thus avoiding incorporating unused space that MCP methods can include. However, this feature can create disjointed home range estimates composed of islands without indication of how the animal moves between areas (R. A. Powell, 2000). Furthermore, kernel density estimates are highly sensitive to smoothing parameter choice (Silverman, 1986).

In this analysis, we used two methods to choose a smoothing parameter. The first is a first-generation method that uses an iterative process to choose a bandwidth that minimizes least squares cross-validation (KDE-LSCV; Stone, 1984). This method is common among ecological studies (Laver & Kelly, 2008), in part as a result of the endorsements of Seaman and Powell (1996). However, it is sensitive to large amounts of repeated values (Hemson et al., 2005) and large sample sizes (Kie et al., 2010). We also used "solve the equation" plug-in bandwidth (KDE-PB) selection, a second-generation approach that is generally more reliable than first-generation approaches (Jones et al., 1996) and performs well with dependent data (Hall, Lahiri, & Truong, 1995). We used only fixed kernel density estimators, as adaptive estimators have been shown to be less accurate than fixed estimators for ecological data (Seaman & Powell, 1996).

Movement-based kernel density estimators use a biased random bridge method to incorporate movement between location points into kernel density estimators (Benhamou, 2011). This method uses temporal autocorrelation between samples as a source of information (rather than a violation of assumed point independence), and can incorporate species-specific movement behaviors and habitat information into home range estimates. Tracey, Sheppard, Zhu, Wei, et al. (2014) further expanded movement-based kernel estimation methods into three dimensions. Walter et al. (2015) found that movement-based third-generation methods, including MKDE, were more reliable than first and second generation methods at estimating panther home ranges. However, MKDE are computationally expensive (Tracey, Sheppard, Lockwood, et al., 2014), require large sample sizes (Benhamou & Cornélis, 2010), and are constrained by serially correlated data (e.g., Walter et al., 2015).

Estimating Home Range Sizes

For each movement run, we compared the actual amount of space the individual used to the size of the home range estimates calculated with each of the four home range estimation techniques. We calculated actual space use in two ways. For movement patterns with a set home range boundary (Home Range, Patrolling), we set the actual value equal to the home range area or volume. For movement patterns without set boundaries (Random, One Resource, Two Resources), we defined actual space use as the number of grid squares the individual occupied during the run.

To calculate the home range estimates, we first subsampled the movement points to get a set of "location points." We chose location point sample sizes within the bounds of typical ecological studies (i.e., between 20 and 500). We calculated minimum convex polygon home range estimates in 2D using the 'mcp' function from the adehabitatHR package in R (Calenge, 2006). To calculate 3D MCP estimates, we modified the 'mcp' function to include the multidimensional convex hull function 'convhulln' from the geometry package (Barber et al., 2012). We calculated KDE-

LSCV and KDE-PB estimates in both two and three dimensions using the 'ks' package in R (Duong, 2019) and used the 'mkde' package (Tracey, Sheppard, Zhu, Sinkovts, et al., 2014) to calculate 2D and 3D MKDE estimates.

Testing Parameter Choices

We ran the simulations using various parameter values to understand how variation in movement behavior, sampling effort, and model parameters affect the efficacy of home range estimates (Table 2.1). We tested number of samples used to calculate home range estimates (20, 50, 100, and 200 in 2D; 20, 50, 200, and 500 in 3D), estimator percentile/isopleth (70, 80, and 95), and amount of temporal autocorrelation in the subsampled data. To create temporal autocorrelation, we chose a set number of "sampling periods" evenly spaced across the total number of time steps and selected samples from the 200 time points (2D) or 1000 time points (3D) after the start of each period. We tested 5, 10, and 20 sampling locations and sampling time points. We scaled the number of points gathered around each location or time point based on the total number of sampling bouts and the total number of samples. For example, if we had 5 sampling bouts, we would collect 40 data points from each one for a total of 200 data points. Because of constraints with MKDE methods with autocorrelated data, we did not calculate MKDE estimates for these trials.

Evaluating Accuracy of Estimation Methods

To evaluate the effectiveness of each home range method, we compared the home range estimates to the actual values as follows:

$$Efficacy = \frac{Actual - Estimate}{Actual}$$

This formula allows us to compare the similarity between the two values while scaling to account for differences in home range size. Positive values indicate that

Table 2.1 Parameter values used in agent-based model simulations. Default values shown in bold.

Model	Parameter	2D Model	3D Model
General Simulation (held constant)	Grid size	**200 x 200**	**100 x 100 x 100**
	Number of time steps	**10,000**	**250,000**
Home Range Estimation	Number of Samples	20, 50, **100**, 200	20, 50, **200**, 500
	Estimator Percentile/Isopleth	70, 80, **95**	70, 80, **95**
	Temporal Autocorrelation (# sampling bouts)	**No autocorrelation**; 5, 10, 20	**No autocorrelation**; 5, 10, 20

the model underestimated home range size, while negative values indicate overestimates.

We performed 1000 runs for each parameter choice. For each set of runs, we calculated the 95% confidence interval of the efficacy values calculated using the four (or three, for autocorrelation trials) estimation techniques. We say that a method is "accurate" if more than half the 95% confidence interval around mean Efficacy lies within $\pm$ 0.5.

2.4 Results

Effect of Sample Size

MKDE estimates were highly variable across sample sizes, particularly for samples under 50 and in three dimensions (Figure 2.3). For high sample sizes, MKDE estimates were among the most accurate of all the estimator methods for Home Range, One Resource, and Two Resource movement patterns in two dimensions. This pattern was not observed in three dimensions, where MKDE

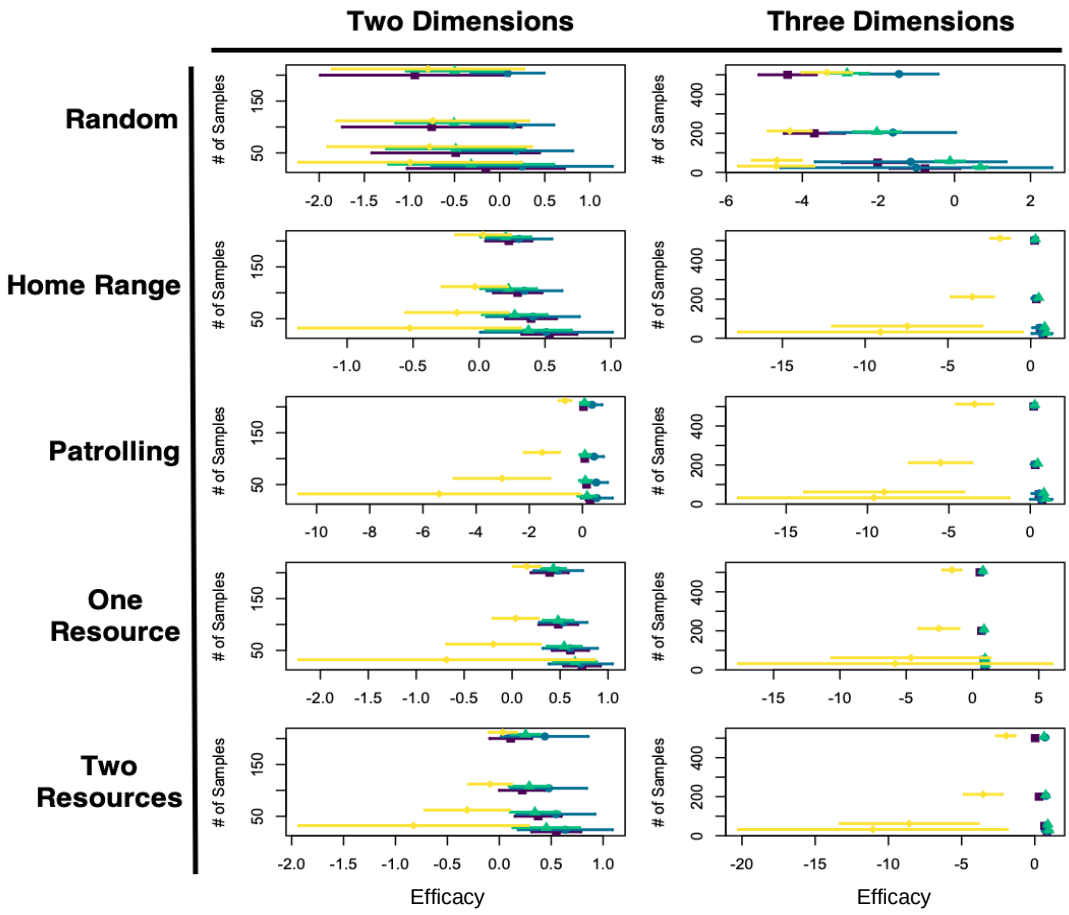

Figure 2.3 Efficacy of minimum convex polygon and kernel density estimators calculated using different sample sizes for five movement algorithms. Efficacy is reported as (Actual – Estimate)/Actual, such that positive numbers show underestimates, negative numbers show overestimates, and zero indicates a home range estimate equal to the actual space used by the individual. Points show mean values of 1000 agent-based model simulations and bars represent 95% confidence intervals. Plots on the left represent two-dimensional models and plots on the right represent three-dimensional models. MCP estimates are shown in purple, KDE-LSCV in blue, KDE-PB in green, and MKDE in yellow. Confidence intervals for each estimation method are staggered along the y-axis to increase readability.

overestimated home range sizes for all sample sizes tested. MCP and KDE-PB estimates increased in efficacy with sample size (Figure 2.3), with large sample sizes yielding accurate MCP estimates in both 2D and 3D for Home Range, Patrolling, and Two Resource patterns and accurate KDE-PB estimates for Home Range (2D and 3D), Patrolling (2D and 3D), One Resource (only 2D), and Two Resources (only 2D). KDE-LSCV methods were generally variable and were accurate only for three-dimensional Patrolling and Home Range methods with large sample sizes.

Effect of Estimator Percentile/Isopleth

All four home range methods generated larger estimates as percentile/isopleth increased, as would be expected (Fig. 2.4). In cases where the 95% estimate was an overestimate (such as Home Range and Two Resources for 3D MKDE measures), using a smaller percentile/isopleth generated estimates closer to the actual value (Fig. 2.4). MCP, KDE-LSCV, and KDE-PB were all most accurate at 95% for all movement patterns except random in both 2D and 3D (Fig. 2.4).

Effect of Autocorrelation

Temporal autocorrelation did not have a qualitative effect on the accuracy of MCP, KDE-LSCV, or KDE-PB estimates in two dimensions (Fig. 2.5). In contrast, high levels of autocorrelation reduced the accuracy of 3D home range estimates for all three home range estimators, particularly kernel density estimators of home range movement algorithms with set boundaries (Home Range, Patrolling; Figure 2.5).

2.5 Discussion

In this study, we investigated how the accuracy of four home range estimation methods compare in two and three dimensions and how these patterns can further vary depending on underlying spatial behaviors of the organisms. We found that the methods performed differently in two dimensions than they did in

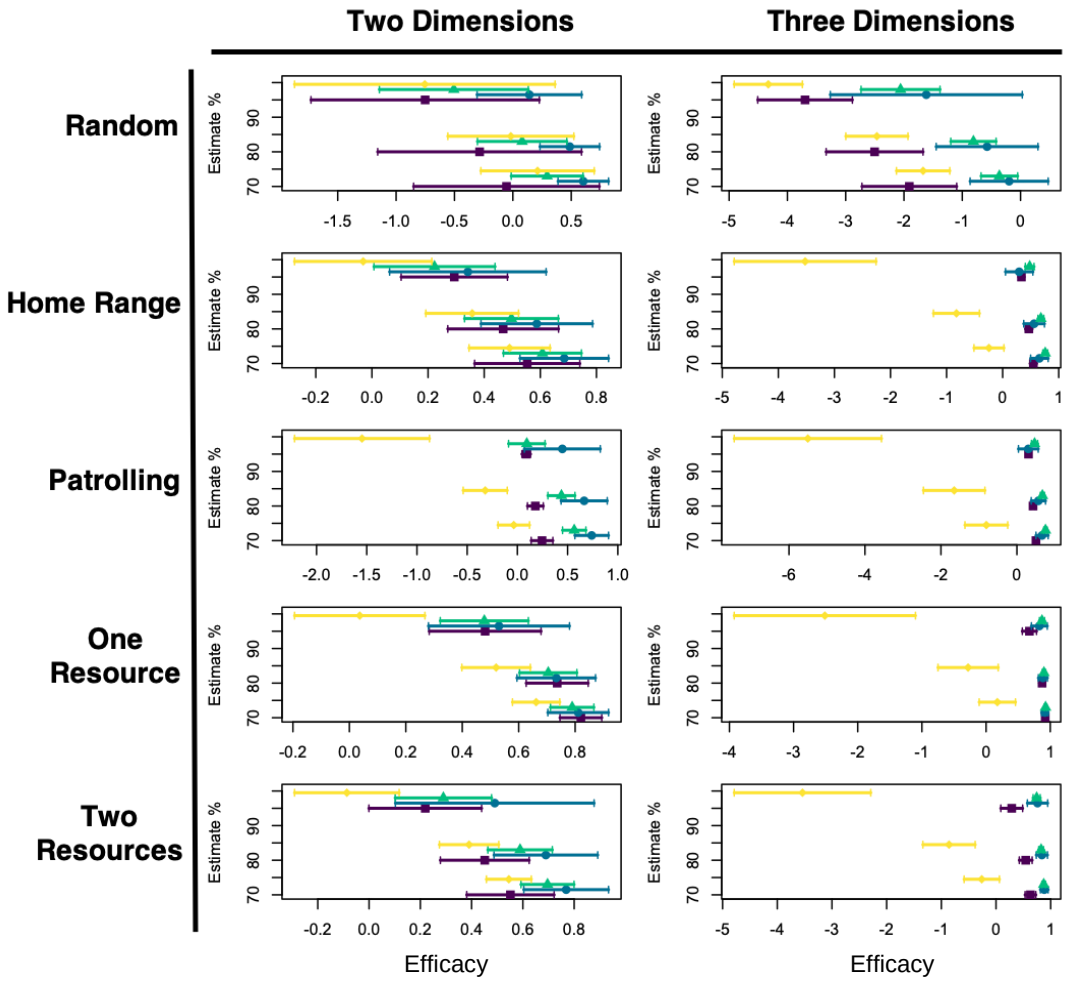

Figure 2.4 Efficacy of minimum convex polygon and kernel density estimators calculated using three estimator percentiles (70, 80, and 95) for five movement algorithms. Efficacy is reported as (Actual – Estimate)/Actual, such that positive numbers show underestimates, negative numbers show overestimates, and zero indicates a home range estimate equal to the actual space used by the individual. Points show mean values of 1000 agent-based model simulations and bars represent 95% confidence intervals. Plots on the left represent two-dimensional models and plots on the right represent three-dimensional models. MCP estimates are shown in purple, KDE-LSCV in blue, KDE-PB in green, and MKDE in yellow. Confidence intervals for each estimation method are staggered along the y-axis to increase readability.

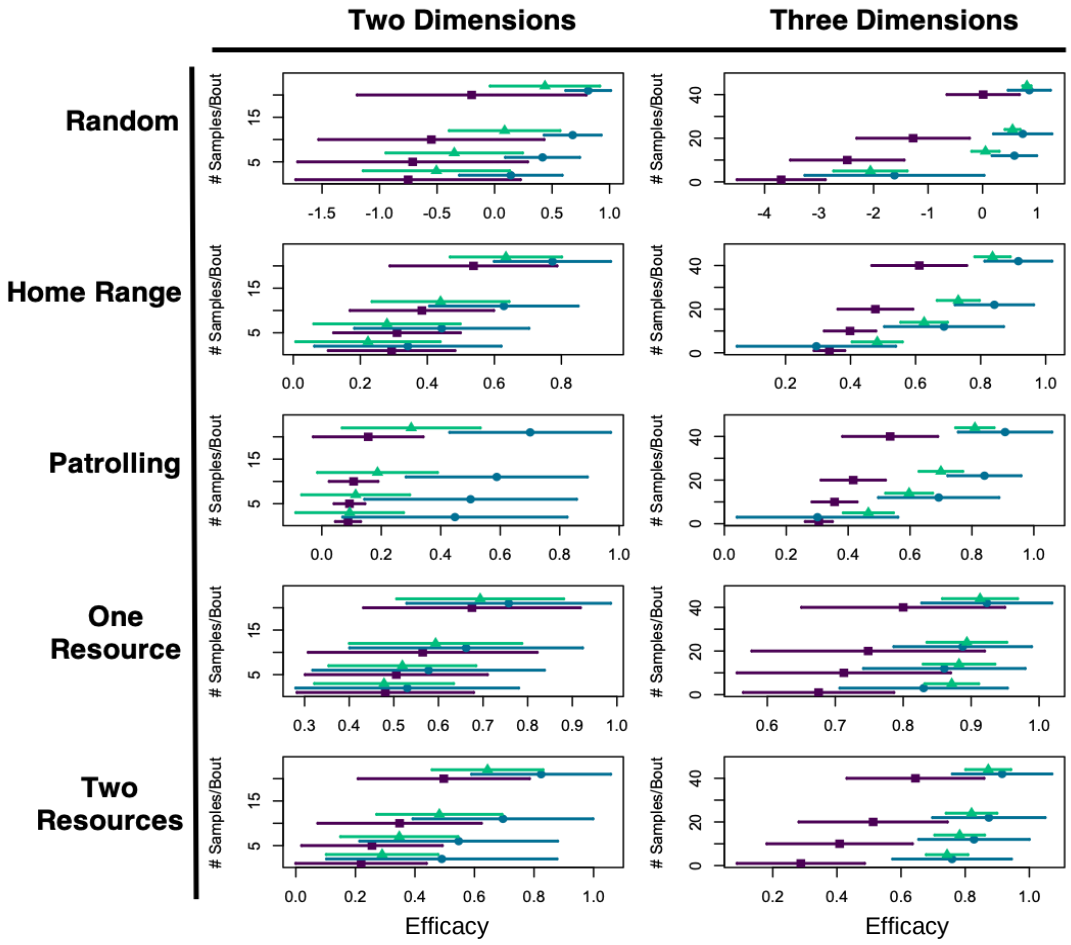

Figure 2.5 Efficacy of minimum convex polygon and kernel density estimators calculated from samples collected under different levels of temporal autocorrelation. Efficacy is reported as (Actual – Estimate)/Actual, such that positive numbers show underestimates, negative numbers show overestimates, and zero indicates a home range estimate equal to the actual space used by the individual. Points show mean values of 1000 agent-based model simulations and bars represent 95% confidence intervals. The left plot represents two-dimensional models and the right plot represents three-dimensional models. MCP estimates are shown in purple, KDE-LSCV in blue, and KDE-PB in green. Confidence intervals for each estimation method are staggered along the y-axis to increase readability. Autocorrelation is reported as the number of samples chosen at each randomly selected time/location, with 1 (all samples randomly selected) indicating no autocorrelation and 40 (40 samples selected from 5 locations, total of 200 points) being the highest amount of autocorrelation.

three dimensions, with 3D models generally overestimating home range size more than 2D models. This was especially true for movement-based kernel density estimates, which calculated some of the most accurate home range estimates in two dimensions but consistently produced estimates many times larger than the actual home ranges in three dimensions. Furthermore, we found that these home range methods performed differently for different behavioral patterns.

Accurately estimating three-dimensional home range size has the potential to greatly benefit the study of organisms that use a vertical dimension, for example by allowing better estimates of realized niche use (Belant, Millspaugh, Martin, & Gitzen, 2012) or by better describing spatial overlap with conspecifics (Simpfendorfer et al., 2012). This study is among the first to evaluate the accuracy of three-dimensional home range estimates under different conditions. Our model found that conditions under which estimates were accurate or inaccurate in two dimensions did not always hold in three dimensions. While we would expect 3D estimates to be more inaccurate than 2D estimates because of the increased dimensionality, we saw variation across our four home range patterns in how much inaccuracy the z-dimension introduced. In particular, MKDE methods were highly accurate for two-dimensional simulations, particularly at high sample sizes, but almost always overestimated 3D home range size more than other methods. We also found that autocorrelation and sample size had greater effects on three-dimensional simulations than they did in two dimensions.

Estimator accuracy varied based on underlying home range movement patterns. For example, MCP and KDE-PB methods produced consistently accurate home range estimates for Patrolling movement patterns across sampling regimes in both two and three dimensions. In contrast, KDE-LSCV and MKDE methods produced variable estimates for patrolling movement simulations, ranging from relative accuracy under some conditions to being up to twenty times too large in other conditions. When calculating territory size, it is common for authors to treat the data points as if they were quantifying an undefended home range, without

considering the underlying behavioral differences between the two types of spatial use (Anich, Benson, & Bednarz, 2009). Yet many territorial species patrol the borders of their home ranges as a means of establishing and maintaining territorial boundaries (Graf, Mayer, Zedrosser, Hackländer, & Rosell, 2016; Righton et al., 1998; Sillero-Zubiri & Macdonald, 1998). Our results indicate that territorial defense can change the accuracy of home range estimates, further emphasizing the importance of distinguishing between defended and undefended home ranges.

Mean KDE-LSCV estimates were generally comparable to MCP and KDE-PB estimates but had higher overall variance. This follows the simulation results of Jones et al. (1996), who found that least-squares cross-validated bandwidths were "centered correctly" but were "unacceptably spread out." This was especially true in our simulations for the One Resource and Two Resource data sets in both two and three dimensions, likely because of the large number of repeated values surrounding the designated resources generated in these movement algorithms. Least-squares cross validation can be disrupted by highly clustered data (Silverman, 1986), sometimes leading to failure to converge on an optimal smoothing parameter. Hemson et al. (2005) further found that LSCV had a high failure rate with sample sizes over 100 when applied to lions, a species with high site fidelity.

No method accurately estimated home ranges under the "Random" movement pattern under any parameter condition, especially in 3D. Indeed, we included this movement pattern as a null model rather than as an example of a common behavior observed in the wild. Other authors have stressed the importance of collecting data using an appropriate spatiotemporal scale to accurately reflect the animal's total space use (e.g., Hansteen, Andreassen, & Ims, 1997). Our results further demonstrate the importance of collecting sufficient data to identify the boundaries of the home range so as to avoid a seemingly "random" point distribution.

Model parameters surrounding sampling and estimate calculation affected the accuracy of home range estimates. High temporal autocorrelation decreased the

accuracy of home range estimates in three dimensions, particularly for "Home Range" and "Patrolling" behaviors. Other authors have reported similar problems with autocorrelated data in 2D (Kernohan, Gitzen, & Millspaugh, 2001). Common approaches to resolving problems caused by autocorrelation include subsampling relocation points (Worton, 1987) or using modified estimation tools designed specifically to account for high levels of autocorrelation (Katajisto & Moilanen, 2006). However, De Solla et al. (1999) found that removing autocorrelation can in turn remove biological signal from home range estimates, raising questions about how autocorrelation should be handled in three-dimensional settings. We did not find that autocorrelation decreased the accuracy of home range estimates in two dimensions.

Using different percentiles/isopleths also significantly affected estimate accuracy. We saw that home range estimates got smaller with smaller percentages (as one would expect), meaning that one could, in theory, correct a method's tendency to overestimate home range size by using a lower percentile/isopleth. For example, 95% MKDE estimates for Home Range, One Resource, and Two Resource movement algorithms were overestimates across sampling regimes in three dimensions; however, 70% MKDE efficacy values had confidence intervals that overlapped zero and exhibited low variation for these movement algorithms. Therefore, we suggest that researchers can increase home range accuracy by using lower percentages/isopleths, as recommended by Börger et al. (2006).

Previous studies have found that sample size plays a significant role in estimate accuracy, with most home range methods showing low accuracy with small sample sizes (e.g., Kernohan et al., 2001; Seaman et al., 1999). Our results mirror these findings, particularly for samples under 50 points. Also like these previous studies, we found only marginal increases in accuracy beyond a certain threshold of points for most home range methods (in 2D, 50; in 3D, 200). Although we did not run the analyses needed to recommend a minimum sample size in 3D home range studies, our results indicate that 3D estimates may require more data points than

2D estimates do to be accurate. This is likely especially true for the MKDE method, which has a higher minimum sample size than other kernel density methods (Benhamou & Cornélis, 2010). Further research could also explore the high sample sizes typical of GPS data sets, which require different considerations in choices of smoothing parameters (Kie et al., 2010).

In this manuscript, we limited our analysis to minimum convex polygon and variations of kernel density techniques, in part because these algorithms were easy to implement in three dimensions or they had been implemented in 3D previously. More work is needed to expand additional home range methods into three dimensions. Like MCP and first- and second-generation kernel-density methods, some methods logically extend into higher dimensions. For example, single-linkage clusters build home ranges by clustering location points by Euclidean distance (Kenward, Clarke, Hodder, & Walls, 2001), a process that is equivalent for two- and three-dimensional data. In contrast, other methods may require additional modifications to be used on data with vertical components. Consider local hull home range estimation, in which a triangle mesh placed over the location points is used to build a home range polygon (Downs & Horner, 2009). While it is always possible to construct a triangle mesh over a set of points in two dimensions, the logical three-dimensional equivalent, the alpha-shape, does not always converge. We recommend further research into applying additional home range techniques to three-dimensional data.

2.6 Conclusions

Three-dimensional home range estimation methods offer considerable benefits for analyzing the spatial use of species that use a vertical dimension (Simpfendorfer et al., 2012; Tracey, Sheppard, Zhu, Wei, et al., 2014). In this paper we demonstrate that the accuracy of two- dimensional estimators does not necessarily translate into three dimensions, with three-dimensional movement-

based kernel density estimates in particular tending to overestimate 3D home range size more than other methods. Furthermore, this study highlights the importance of considering the underlying spatial behavior of a species when one chooses a home range estimator. We encourage all researchers to consider the behavior of the animal when estimating home range size, rather than relying only on statistical or logistical considerations (Fieberg & Börger, 2012).

CHAPTER THREE
TERRITORY OWNERS, FLOATERS, AND SNEAKERS USE DIFFERENT BEHAVIORAL STRATEGIES IN GREEN ANOLE LIZARDS (*ANOLIS CAROLINENSIS*)

3.1 Summary

Since they were first described as "territorial" almost one hundred years ago, a great deal of research effort has gone into understanding the mechanisms behind territory establishment, contest behaviors, and dominant-submissive dynamics in *Anolis* lizard populations**.** Much of this work has focused on the behaviors of large territorial males. Yet several behavioral phenotypes are observed in male anoles, including non-territorial floaters and small "sneaker" males. In this study, we explored the behavioral differences between males exhibiting different territorial behaviors (territory owners, floaters, and sneaker males), particularly focusing on their interactions with each other and with females. To do this, we recorded the spatial and social behaviors of 12 captive populations of green anole lizards (*Anolis carolinensis*) with 12 individuals each (6 males, 6 females) housed in semi-natural enclosures. We divided the males in our populations into our three behavioral categories using criteria of site fidelity and defensive behaviors and compared interactions within and between each category using linear mixed effects models. We found that half of the males in our populations displayed non-territorial phenotypes. Although this proportion was likely inflated as a result of the spatial limitations of our enclosures, this finding demonstrates that these phenotypes likely make up an important component of anoles' social landscape in the wild.

Furthermore, we found each category was characterized by different behaviors, with territory owners engaging in the most behavioral interactions, floaters overlapping others' home ranges the most, and sneakers generally behaving more similarly to females than to other males. Females also differentiated between territorial and non-territorial males, directing more displays at territory owners despite high home range overlap with floaters and sneakers. This study supports the female mimicry hypothesis for sneaker males in anoles and indicates the importance of considering the diversity of territorial strategies employed by green anole lizards in studies of their spatial and social behaviors.

3.2 Introduction

Territoriality is a common system of social organization in which individuals defend an area against rivals in order to establish exclusive or priority access to resources such as food, habitats, and mates (Brown & Orians, 1970; Kaufmann, 1983; Maher & Lott, 1995). Although operational definitions differ, most conceptual definitions of territoriality contain some combination of three components: defensive behaviors, exclusive use, and site fidelity (Brown & Orians, 1970; Maher & Lott, 1995). Territorial behavior can vary widely across species; for example, defensive behaviors can occur at the level of the individual (e.g., Green & Patek, 2018), breeding pair (e.g., Sturmbauer et al., 2008), and group (e.g., Farabaugh, Brown, & Hughes, 1992; Rayor, 1988). Similarly, territorial behavior within a species can vary depending on phenotype (e.g., Sinervo & Lively, 1996), age (e.g., Stutchbury & Zack, 1992), or resource availability (e.g., Broom & Ruxton, 2003).

Anole lizards are a model system in behavioral ecology and evolutionary biology with a broad literature on their characteristic aggressive displays and the dominant-submissive relationships between males (Losos, 2009). Yet it remains unclear how territorial behavior affects resource distribution and mate selection in anole populations (Kamath & Losos, 2017), largely because researchers have focused almost entirely on the behaviors of large territorial males.

Anoles are thought to employ resource defense polygyny (sensu Emlen & Oring, 1977). Under this paradigm, males defend attractive areas from rivals while allowing females to establish smaller territories within their space, thus limiting access to these females by other males (Nunez & Jenssen, 1998; Ruby, 1984). Within this system it is common for small males to live within the territories of large males (e.g., Rand, 1967; Weber, 2016), which Orrell and Jenssen (2003) attribute to an alternative "sneaker male" mating strategy. It is unclear how male territorial behaviors affect anole females' mating decisions; most copulations observed in the field are between females and the large territory owner they live with (Ruby, 1984; Tokarz, 1998; Trivers, 1976), yet genetic studies show that female anoles can be highly promiscuous (Calsbeek, Bonneaud, Prabhu, Manoukis, & Smith, 2007). Sperm storage by females (Conner & Crews, 1980) and potentially rapid turnover in male territory ownership (Ruby, 1984; Tokarz, 1998) further muddy the issue. Paternity studies have shown that territory owners, sneaker males, and males without set home range boundaries ("floaters") all father offspring in the wild (Passek, 2002), suggesting that the three different behaviors are all viable fitness strategies.

In this study, we sought to understand if social interactions and home range boundaries reflect territorial relationships in the green anole lizard (*Anolis carolinensis*). To test this, we recorded the social and spatial behaviors of captive populations of green anoles housed in large aviary-like outdoor structures. We categorized males in our populations as territory owners, sneakers, or floaters based on observations of site fidelity and defensive behaviors. We predicted that each type of male would interact differently in three meaningful ways: how much their home ranges overlap, how often they interact with one another, and how symmetrical their interactions are (Table 3.1). Furthermore, we predicted that sneaker males would behave functionally similarly to females and that territory owners would treat sneaker males and females similarly.

Table 3.1 Hypothesized interactions between three behavioral phenotypes of green anole (Anolis carolinensis) males: territory owner, floater, and sneaker. We define a "territory owner" as a male who exhibits both site fidelity and defensive behaviors, a "sneaker" as a male who exhibits site fidelity but no defensive behaviors, and a "floater" as a male who does not exhibit site fidelity. We define "number of interactions" as the number of times an individual displays at, approaches, or physically encounters males of each type; "symmetry of interactions" as the proportion of interactions the focal individual initiated; and "percent home range overlap" as the proportion of the focal individual's home range occupied by other individuals.

	Signaler	**Receiver**		
		Territory Owner	**Sneaker**	**Floater**
Number of Interactions	Territory Owner	Many	Many	Many
	Sneaker	Many	Few	Few
	Floater	Many	Few	Few
Symmetry of Interactions	Territory Owner	Symmetrical	Symmetrical	Symmetrical
	Sneaker	Asymmetrical	Symmetrical	Symmetrical
	Floater	Asymmetrical	Symmetrical	Symmetrical
% Home Range Overlap	Territory Owner	Low	High	High
	Sneaker	High	Low	High
	Floater	High	High	High

3.3 Materials and Methods

Study animals and husbandry

We purchased pet-quality adult green anole lizards (*Anolis carolinensis*) from a commercial reptile distributor (LLLReptile and Supply Company, Inc., Oceanside, CA). All animals were wild caught within a few weeks of purchase. We defined individuals as "adults" if they had a snout-vent length greater than 55 mm (males) or 45 mm (females) (Lovern, Holmes, & Wade, 2004),

We housed lizards in the Walters Life Sciences animal care facility on the University of Tennessee Knoxville campus for two weeks after delivery to allow individuals to acclimate to captivity. As in the anole housing procedures of Sanger, Hime, Johnson, Diani, and Losos (2008), lizards were housed individually or in male-

female pairs in 5-gallon and 10-gallon glass tanks (10" x 10" x 10" and 20” x 10” x 12”, respectively). Each tank contained cage carpet, a wooden stick to act as a perch, and a spider plant (*Chlorophytum comosum*) to provide greenery. Cages were lit with ultraviolet (Zoo Med ReptiSun Desert Compact Fluorescent UVB Lamp, Zoo Med, San Luis Obispo, CA, U.S.A) and heat bulbs (Fluker Reptile Incandescent Daylight Bulb, Fluker Farms, Port Allem, LA, U.S.A.) on a 14:10 h light-dark cycle. We fed lizards two to four crickets every other day and misted the cages *ad libitum*. Crickets were dusted with calcium powder to provide additional nutrients.

Before being moved to the outdoor study enclosures, we marked each lizard with a unique bead tag following the methods of Fisher and Muth (1989).

Enclosure design and behavioral observations

We constructed two outdoor study enclosures at the University of Tennessee Forest Resources AgResearch and Education Center property at the University of Tennessee Arboretum in Oak Ridge, Tennessee (Figure 3.1). Enclosures were approximately 5 m x 5 m x 5m. Each enclosure had a wooden frame surrounded by two layers of mesh: interior screen door mesh to contain the study lizards protected by exterior 1-inch hardware cloth. Enclosures contained a mixture of live trees (primarily sugar maple, *Acer saccharum*, and hickory, *Carya* sp.), dead trees, and potted plants (primarily majesty palm, *Ravenea rivularis*). We covered the floor of the enclosures with gardener’s fabric to prevent study animals from laying eggs in the soil. We painted markings on the interior beams of the four walls at 6-in intervals to aid in estimating perch height. While lizards were housed inside the enclosure, they were fed crickets dusted with calcium powder *ad libitum*. We sprayed the walls and plants inside the enclosures with water between one and three times daily to provide animals with drinking water.

We performed this experiment between May and August in 2017-2019. In each round of the experiment, we introduced 12 lizards (6 males, 6 females) to each enclosure and observed their behaviors and spatial locations for ten days or until each individual had at least 60 minutes of behavioral observations (mean=143 mins,

Figure 3.1 Photographs of one of two study enclosures used in the experiment. Enclosures (5 m x 5 m x 5m) were constructed from wooden beams, screen door mesh (interior), and 1 inch hardware cloth (exterior). Enclosures contained live trees, dead trees, and potted plants to act as habitat for the lizards and metal ladders to allow researchers to access and observe the highest sections of the interior. Enclosures are located in a forested region of the University of Tennessee Forest Resources AgResearch and Education Center property in the UT Arboretum in Oak Ridge, Tennessee.

range = 60-212 mins). We allowed individuals to acclimate to the enclosures for 24 hours before beginning behavioral observations. Each focal observation lasted 30 minutes, during which we recorded the number of times the focal individual crawled, jumped, changed perches, headbobbed, or extended its dewlap. We performed focal observations between 1000 and 1800 hours, with peak activity occurring between 1300 and 1500. We did not perform focal observations if it was raining, as even highly active lizards showed marked declines in activity in the rain.

We also recorded all behavioral interactions we observed inside the enclosure (not just those occurring during a focal observation). We defined a "behavioral interaction" as a display, approach, or physical encounter that was clearly directed at another individual (i.e., there was observed eye contact between

the individuals or an observed response from the potential receiver). Male-male interactions included directed headbob and dewlap displays, chases, and lock-jawed fights, while male-female interactions included directed headbob and dewlap displays, mating attempts, and copulations.

We documented the spatial locations of individuals within the enclosure by recording lizards' locations throughout the day on to-scale maps of the enclosures (average number of locations per individual = 17, range = 5-39). We estimated the individual's perch height at each location using the painted reference markings on the enclosure walls to aid accuracy.

We performed eight rounds of this experiment for a total of 12 populations (six in each enclosure; n = 144). All lizards were euthanized after removal from the enclosures at the end of the experiment. Individuals who died or did not have enough observations were excluded from further analyses.

Identifying Territory Owners, Floaters, and Sneaker Males

In this study, we classify males as territorial, floaters, or sneakers based on whether they exhibited site fidelity or display behaviors (Brown & Orians, 1970). We exclude exclusive use as a criterion of territoriality in this system because of the high population density of our enclosures. We classify an individual as a "territory owner" if it exhibits both site fidelity and defensive behaviors, as a "sneaker male" if it exhibits site fidelity but not defensive behaviors, and as a "floater" if it did not exhibit site fidelity.

We say that an animal performed defensive behaviors if individuals performed greater than or equal to one display for every 2 minutes of observation time (0.5 displays/minute). This threshold created a bimodal distribution of display behaviors within each population for 11 out of 12 populations. For the twelfth population, a threshold of 0.53 displays/min was used instead.

We modified the method of Spencer, Cameron, and Swihart (1990) to test for site fidelity. This method entails constructing a path between an individual's sequential relocation points, calculating the mean squared distance (MSD) from the

center of activity to this path, and comparing this value to the MSDs of paths randomly constructed from the same lengths. Spencer et al. (1990) constructed random paths by sequentially choosing a random angle and a random path length from the individual's movement pattern. Because we recorded location points in three dimensions, simply selecting angles and path lengths in this manner resulted in simulated paths occurring in places where actual lizards could not go, such as in the empty space between trees. To account for this fact, we created three-dimensional polyhedrons estimating the "usable" space in the enclosure (i.e., spaces containing perches the animals could use rather than empty space) and restricted potential paths to those occurring within the polyhedrons. For each individual, we then compared the mean squared distance from the center of activity for its actual path to the MSDs of 1000 random paths. We scored an individual as exhibiting site fidelity if it had an MSD value less than the lower bound of the 95% confidence interval of the MSD values of the random paths.

Calculating home range overlap

We estimated the three-dimensional home range of each individual using minimum convex polygon estimation (Rose, 1982). We converted the handwritten location points on the maps to xy-coordinates using Fiji in ImageJ. The lower left corner of the enclosure served as the origin and perch heights became z-coordinates. We excluded location points collected in the first three days the individual was in the enclosure to allow time for home range establishment. We calculated three-dimensional MCP home range polyhedrons in the statistical software R (R Core Team, 2013) using the "convhulln" function from the geometry package (Barber et al., 2012) to modify the "mcp" function in the adehabitat package (Calenge, 2006)

We then used original code in R to calculate the volume of intersection between three-dimensional home range polyhedrons of all pairs of individuals within each population. This code used the ptinpoly (Maisog, Wang, Luta, & Liu, 2014) and geometry (Barber et al., 2012) packages in R to calculate the volumes and

the rgl package (Adler, Murdococh, & others, 2019) to visualize the three-dimensional shapes.

Comparing behavioral interactions between males

We used a series of mixed-effects models to test if male behavioral interactions were influenced by territorial identity. To do this, we created a list of all directed male-male dyads within each population and assigned these pairs to one of nine "types of interactions" based on the territorial behavior of each individual (i.e., "Territory Owner – Territory Owner," "Floater – Sneaker," etc.). We used this information to partition our data into three groups: dyads initiated by territory owners ("Territory Owners"), dyads initiated by sneakers ("Sneakers"), and dyads initiated by floaters ("Floaters"). We then calculated the value of our three response variables for each dyad. For a given dyad A – B, "number of interactions" signifies the number of times we observed A interacting with B, "symmetry of interactions" signifies the number of times A initiated an interaction with B as a proportion the number of total interactions between the two, and "home range overlap" signifies the percentage of A's home range intersected by B's home range.

For each analysis, we analyzed our three data sets (Territory Owners, Sneakers, and Floaters) separately to avoid artificially inflating our degrees of freedom within the statistical models.

We tested if males interacted more or less with individuals of specific types using generalized linear mixed effects models with a zero-inflated Poisson distribution. For each data set, we used number of interactions as a response variable, type of interaction as a fixed effect, and population as a random effect. We used the glmmTMB package in R (Brooks et al., 2017) to build the mixed effects models and tested hypotheses with the "Anova" function in the car package (Fox & Weisberg, 2018). When models demonstrated significance, we computed contrasts using the lsmeans package (Lenth, 2016) to compute least squared means.

We used linear mixed effects models to explore the effects of interaction type on symmetry of interactions and percent home range overlap. As above, we used

interaction symmetry or home range overlap as response variables, type of interaction as a fixed effect, and population as a random effect for each of our three data sets. Following the recommendation of Warton and Hui (2011) for proportional data, we used a logit transformation to normalize both response variables. We then used the "lmer" function in the lme4 package (Bates, Mächler, Bolker, & Walker, 2014) to fit the models, the "Anova" function in the car package to test our hypotheses, and the multcomp package to perform Tukey HSD tests when models demonstrated significance (Hothorn, Bretz, & Westfall, 2008). We controlled for multiple comparisons across all nine models by the Benjamini-Hochberg procedure ($q < 0.05$) (Benjamini & Hochberg, 1995).

Comparing behavioral interactions between males and females

We repeated the above analysis using interaction data for all individuals within each population, this time including females. For these analyses, we explored four data sets (Territory Owner, Floater, Sneaker, and Females) for each of the three response variables. We similarly used the Benjamini-Hochberg procedure to compare for multiple comparisons across these twelve models.

Ethical Note

This project was conducted under the approval of the University of Tennessee Institutional Animal Care and Use Committee Protocol 2429.

3.4 Results

Male categorization

Using the above criteria of site fidelity and defensive behaviors, we identified 32 territory owners, 19 sneakers, and 14 floater males in our populations.

Table 3.2 Summary of mixed effects models for each response variable when only males are considered. We calculated false-discovery rates across all nine models using the Benjamini-Hochberg procedure with q threshold of 0.05.

	Chi Squared	Df	P value	q
Number of Interactions				
Territory Owners	**17.343**	**2**	**< 0.001**	**0.001**
Sneakers	5.309	2	0.070	0.121
Floaters	2.206	2	0.331	0.332
Interaction Symmetry				
Territory Owners	**16.480**	**2**	**< 0.001**	**0.001**
Sneakers	**17.986**	**2**	**< 0.001**	**0.001**
Floaters	2.510	2	0.284	0.332
% Home Range Overlap				
Territory Owners	**10.124**	**2**	**0.006**	**0.014**
Sneakers	2.410	2	0.300	0.332
Floaters	5.0402	2	0.080	0.121

Male only models

Territory owners interacted differentially with males of different territorial identities across all three response variables (Figure 3.2, Table 3.2). In addition to initiating the most interactions of the three types of males, they interacted significantly more with sneaker males than they did with other territory owners or floaters (Figure 3.2a, Table 3.2). In contrast, sneaker and floater males interacted rarely with other males and did not interact more with any specific type of male (Figure 3.2b,c, Table 3.2).

Males exhibited high interaction symmetry across the board, with males often responding to other males' displays. While floaters responded ubiquitously to all three types of males (Figure 3.2f, Table 3.2), both sneakers and territory owners were significantly less likely to respond to displays performed by territory owners then they were to other males (Figure 3.2d,e, Table 3.2).

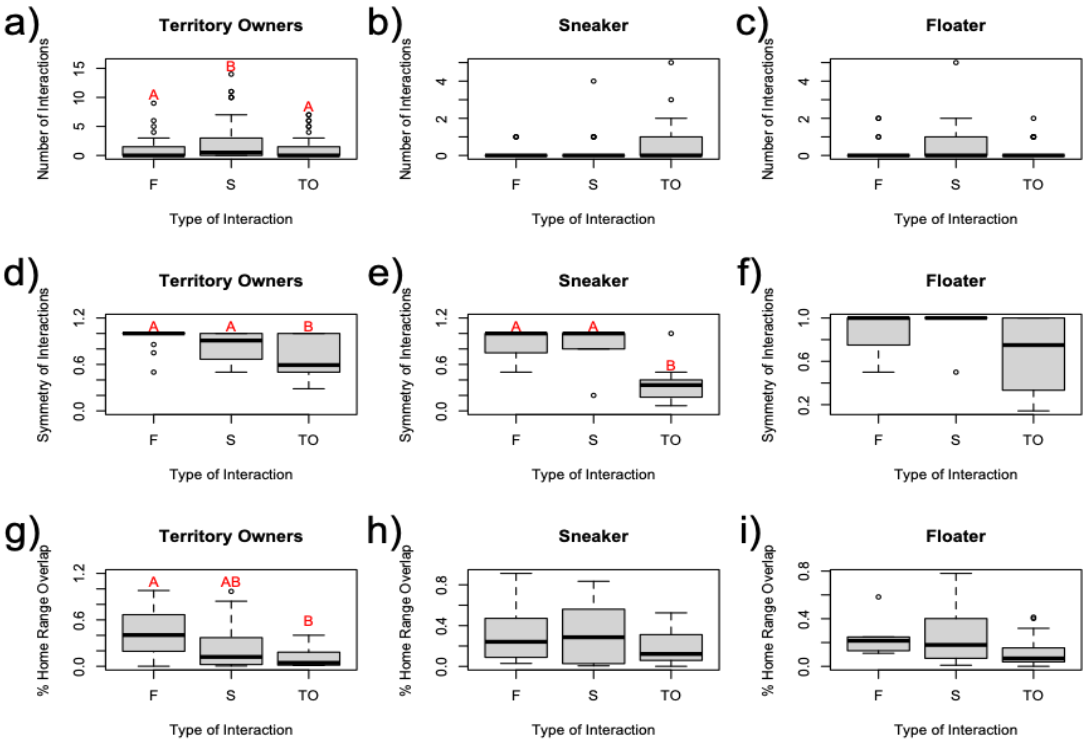

Figure 3.2 Social and spatial behaviors of territory owner (TO), sneaker (S), and floater (F) male green anole lizards (Anolis carolinensis) housed in captive populations (6 males, 6 females) in semi-natural enclosures. Plots depict interactions between focal individuals (Territory owners: a, d, and g; Sneakers: b, e, and h; and Floaters: c, f, and i) and other males within each population. Number of interactions (a, b, and c) signifies the number of times the two individuals were observed interacting. Symmetry of interactions signifies the proportion of interactions the focal individual initiated (d, e, and f). Percent home range overlap (g, h, and i) signifies the percentage of the focal individual's three-dimensional home range (estimated using minimum convex polygon estimation) overlapped by other males. Red letters indicate significant differences between categories.

Territory owners exhibited a wide range in home range overlap, displaying low overlap with other territory owners but high overlap with both floaters and sneakers (Figure 3.2g, Table 3.2). Both sneakers and floaters were equally likely to overlap with all three types of males (Figure 3.2h,i, Table 3.2). Home range overlap between territory owners and floaters was asymmetric – while floaters occupied as much as 98% of the home range of some territory owners, only as much as 40% of a floater's home range was occupied by a single territory owner.

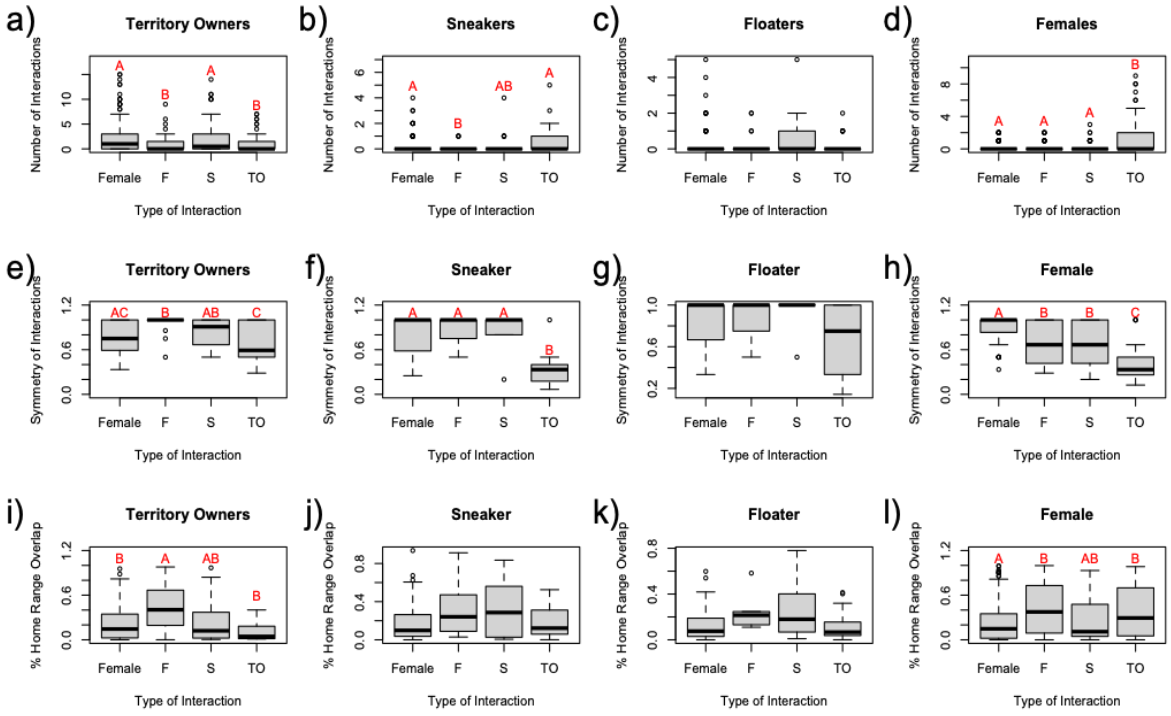

Figure 3.3 Social and spatial behaviors of territory owner (TO), sneaker (S), floater (F), and female (female) green anole lizards (Anolis carolinensis) housed in captive populations (6 males, 6 females) in semi-natural enclosures. Plots depict interactions between focal individuals (Territory owners: a, e, and i; Sneakers: b, f, and j; Floaters: c, g, and k; and Females: d, h, and l) and other individuals within each population. Number of interactions (a-d) signifies the number of times the two individuals were observed interacting. Symmetry of interactions signifies the proportion of interactions the focal individual initiated (e-h). Percent home range overlap (i-l) signifies the percentage of the focal individual's three-dimensional home range (represented by minimum convex polygon estimation) overlapped by other males. Red letters indicate significant differences between categories.

Male and female models

Females had high home range overlap with all four categories of lizards, although they overlapped with males more than with other females. Although both sneaker and floater males directed displays at females (Figure 3.3b,c), females had significantly more interactions with territory owners than they did with other types of males (Figure 3.3d, Table 3.3).

Table 3.3 Summary of mixed effects models for each response variable when males and females are considered. We calculated false-discovery rates across all twelve models using the Benjamini-Hochberg procedure with q threshold of 0.05.

	Chi Squared	Df	P value	q
Number of Interactions				
Territory Owners	**25.525**	**3**	**< 0.001**	**< 0.001**
Sneakers	**8.843**	**3**	**0.031**	**0.047**
Floaters	5.496	3	0.139	0.151
Females	**41.800**	**3**	**<0.001**	**< 0.001**
Interaction Symmetry				
Territory Owners	**16.215**	**3**	**0.001**	**0.002**
Sneakers	**28.676**	**3**	**< 0.001**	**< 0.001**
Floaters	3.332	3	0.343	0.343
Females	**102.599**	**3**	**< 0.001**	**< 0.001**
% Home Range Overlap				
Territory Owners	**10.548**	**3**	**0.0144**	**0.025**
Sneakers	5.656	3	0.130	0.151
Floaters	5.785	3	0.123	0.151
Females	**13.247**	**3**	**0.004**	**0.008**

Multiple similarities existed between the behaviors of sneaker males and females and the way that other males treated them. Territory owners engaged in similar number of interactions with females as they did with sneaker males (Figure 3.3a, Table 3.3). Both sneaker males and females also exhibited high asymmetry in interactions with territory owners (Figure 3.3f,h, Table 3.3), a pattern not found in either Territory Owners or Floaters (figure 3.3e,g).

3.5 Discussion

In this study, we sought to understand if male green anoles (*Anolis carolinensis*) with different territorial behaviors differed in how they interact with one another and with females. To do this, we used criteria of site fidelity and defensive behaviors to

assign males to territory owner, sneaker, or floater categories. We found behavioral differences between males in each category, with territory owners generally engaging in the most behavioral interactions and floaters having the highest home range overlap. We further found that females directed fewer displays at sneaker and floater males than they did at territory owners despite having high home range overlap with both non-territorial groups. Finally, we found that territory owners treated females and sneaker males similarly across all three behavioral metrics. This study indicates the importance of considering the diversity of territorial strategies employed by green anole lizards in studies of their spatial and social behaviors.

Territory owners had different patterns of behavioral interactions and home range overlap with each of the three types of males. Territory owners had lower home range overlap with each other than they did with any other group. This is in line with previous studies of anole populations in nature, which generally show low overlap between large (presumably territorial) males (e.g., Nunez & Jenssen, 1998; Rand, 1967). Territory owners were also less likely to respond to displays by other territory owners than they were to other types of males. This could indicate potential "dear enemy" relationships between our territorial males, in which territory owners show decreased aggression towards neighbors (Temeles, 1994). Both laboratory and field studies have shown support for the "dear enemy" hypothesis in anole lizards (Paterson & McMann, 2004; Qualls & Jaeger, 1991).

We further observed distinct asymmetry in the home range overlap of floater males and territory owners. Floaters in our populations had large home ranges that overlapped with many individuals but never occupied the majority of a single territory owner's home range. Floaters in most territorial species are animals that have been unable to establish their own territories, either because they were recently ejected from their previous territory (e.g., Arcese, 1989) or because they have not successfully carved out their own space (e.g., Stutchbury, 1991). In this study, we likely saw artificially elevated levels of floater overlap because our closed system did not allow displaced lizards a means of escape.

We also observed differential female responses to males, with females differentiating between territory owners and non-territory owners. Although females had high levels of home range overlap with both sneakers and floaters and both types of males directed displays at them, females initiated few interactions with either type of non-territorial male. This may be a consequence of increased territory owner interest in females, or it could be an indication of potential female preferences for territory owners. Female choice has been historically contentious in anoles (Tokarz, 1995); although there is strong evidence that female anoles prefer males giving species-specific displays (Jenssen, 1970), studies have found no or ambiguous preferences when seeking preferences within a species (e.g., Andrews, 1985; Crews, 1975a; Lailvaux & Irschick, 2006).

Territory owners treated females and sneaker males functionally equivalently across every metric measured. They directed the highest number of behavioral interactions towards these groups and showed similar levels of symmetry and home range overlap with both categories. Similarly, sneakers and females both had asymmetrical responses to territory owner's displays and responded with similar suites of three to four headbob displays without corresponding dewlap extensions (JBM, personal observation). These results support the hypothesis that the "sneaker" behavioral phenotypes could constitute a female-mimicry strategy (Orrell & Jenssen, 2003). Small males and adult females share similar morphologies and similar "nodding" display behaviors (Crews, 1975b). Small males are also frequently observed living on the home ranges of larger males in the wild (e.g., Rand, 1967; Weber, 2016). Trivers (1976) even observed larger males trying to copulate with small males living on their territories, presumably due to misidentification by the initiating male.

Female mimicry can give males competitive benefits (Saetre & Slagsvold, 1996). Lailvaux, Herrel, VanHooydonck, Meyers, and Irschick (2004) observed that male body size in anole populations is bimodally distributed and that small and large males have different morphologies (i.e., head shape), performance abilities,

and fighting tactics. Irschick and Lailvaux (2006) claim that these differences represent an age-specific forced polymorphism in green anoles, in which the largest (i.e., oldest) males are best able to establish and defend territories while small (i.e., young) males use an alternative female-mimicry strategy. This would be a version of the songbird system of Stutchbury and Zack (1992), in which juveniles with low resource-holding potential use non-territorial strategies to familiarize themselves with an area and thus gain advantages in future territory acquisition.

The semi-natural enclosure structure of our experiment offered distinct advantages over natural field studies, including allowing us to control the population sizes and to maintain the same habitat matrix across different populations. However, the short duration of this experiment prevented us from determining if copulation or paternity rates differed between the different types of male. Passek (2002) found that on average, 50% of a female's offspring were fathered by large territorial males, 25% were fathered by small males living within the larger male's territory, and 25% were from neighboring or floater males. This distribution indicates that sneaker males likely use a viable reproductive strategy that should be explored further. Furthermore, we did not distinguish between different types of display behaviors, for example the A, B, and C types of headbob displays described by Decourcy and Jenssen (1994). We recommend that further research explores if territory owner-sneaker displays are more similar to typical male-male display patterns or male-female ones.

CHAPTER FOUR
EFFECTS OF AN INVASIVE SPECIES (*ANOLIS SAGREI*) ON THE SOCIAL AND TERRITORIAL BEHAVIOUR OF A NATIVE CONGENER (*A. CAROLINENSIS*)

4.1 Summary

Interspecific aggression has important fitness consequences across the animal kingdom and can be especially important during species invasions, where asymmetric interactions between native and invasive species can lead to native species declines. We investigated the immediate behavioral consequences of interspecific interactions for a native species, the green anole lizard (*Anolis carolinensis),* after an invasion by a closely related invasive species, the Cuban brown anole (*A. sagrei*). We housed captive populations of green anoles (6 males, 6 females) in large outdoor enclosures and recorded their display behaviors (displays per minute), activity levels (movements per minute), and habitat use (2D and 3D home range size, perch height) for ten days. We then introduced brown anoles and recorded the green anoles' behaviors for another ten days, seeking differences between pre- and post-invasion behaviors. We recorded behavioral interactions between individuals (i.e., headbob and dewlap displays, chases, mating attempts, fights, and copulations) throughout the study. To serve as a density control, we duplicated the experiment in a second enclosure using green anoles as "invaders." We performed the experiment eight times with two densities of invaders: high (4 males, 4 females) and low (2 males, 2 females). We found that green anoles have smaller two-dimensional and three-dimensional home ranges and higher average perch heights after invasions but that these changes resulted from increased population densities rather than aggression from brown anole invaders.

Furthermore, we found that although green and brown anoles did display to each other, both species preferentially interacted with conspecifics and escalated aggressive behaviors between the two species (e.g., lock-jawed fights) rarely occurred. Taken together, these findings indicate that high brown anole population densities, rather than direct interference competition, could be driving green anole displacement across the brown anole's invasive range.

4.2 Introduction

Animal social interactions have important fitness consequences, affecting reproductive success (i.e., courtship behaviors, Emlen & Oring, 1977), access to resources (i.e., territory establishment and maintenance, Kaufmann, 1983), predation risk (i.e., schooling behaviors, Pavlov & Kasumyan, 2000), and health (i.e., grooming, Sparks, 1967).

Although an extensive literature treats the causes and consequences of social behaviors within species, comparatively less attention has been devoted to the behavioral mechanisms of interspecific communication (Westrip & Bell, 2015). Communication between individuals of different species, particularly aggression and territorial behavior, is relatively common across the animal kingdom (Grether et al., 2013; Peiman & Robinson, 2010). Many species enforce territorial boundaries across species lines or act aggressively towards heterospecifics over food, resources, or space (Grether et al., 2013; Grether, Losin, Anderson, & Okamoto, 2009; Murray Jr, 1971). For example, some reef fish will alter the intensity of territorial aggression based on intruder species identity by having a lower threshold of encroachment for more closely related species (Myrberg Jr & Thresher, 1974). This interspecific aggression can significantly affect fitness. For example, aggressive interference competition between large African predators results in lions often limiting population sizes of cheetahs and wild dogs (Creel & Creel, 1996). Time and energy spent interacting with heterospecifics necessarily lessens investment in conspecific

relationships, further underscoring the evolutionary significance of interspecific interactions (Peiman & Robinson, 2010).

Understanding the consequences of interspecific aggressive interactions has been particularly important in invasion biology. Invasive species often interact with native competitors in their new range, frequently resulting in native species declines (e.g., Bertolino, Di Montezemolo, Preatoni, Wauters, & Martinoli, 2014; Paini, 2004; Rowles & O'Dowd, 2007). For example, North American grey squirrels directly compete with native red squirrels for food resources, as well as transmitting squirrel pox virus, and have caused local elimination of native squirrels across Europe (Bertolino et al., 2014). Similarly, native solitary bees in Hawaii have declined in recent years in part as a result of competition and aggression from mainland social wasps (E. Wilson & Holway, 2010)

Anolis lizards are an excellent system in which to investigate interspecific communication, particularly in an invasion context. Through an evolutionary history of numerous independent instances of microhabitat specialization on islands across the Caribbean, anoles are a highly diverse genus that can live in species-rich communities (Losos, 2009). For example, as many as 15 anole species are found on large islands in the Greater Antilles (Losos, 2009). Furthermore, anoles are becoming an increasingly important taxon in invasion biology, where introductions of over 10 anole species across the United States (Krysko et al., 2016), the Pacific (e.g., Huang, Norval, Wei, & Tso, 2008; McKeown, 1996; Toda, Takahashi, Nakagawa, & Sukigara, 2010), and South America (Amador, Ayala-Varela, Nárvaez, Cruz, & Torres-Carvajal, 2017) have created novel communities in which to explore a variety of invasion mechanisms and consequences (e.g., Losos, Marks, & Schoener, 1993)

There has been great research interest in how anole species interact with one another in both native and invasive contexts. In both lab and field studies, male and female anoles show aggression towards members of other species through targeted dewlap and headbob displays and escalated ritualized fights (Ortiz and Jenssen,

1982; Edwards and Lailvaux, 2012; Tokarz, 1989; Culbertson and Herrmann, 2019, Losin, 2012). Aggressive interactions between anole species are often asymmetric, with one species dominating the other by limiting access to preferred resources (Losin, 2012; Salzburg, 1984) or by being less likely to back down from aggressive interactions (Dufour, Herrel, & Losos, 2018). Researchers have recorded aggression both within and across specialized ecomorphs (Leal, Rodríguez-Robles, & Losos, 1998; Ortiz & Jenssen, 1982), with the highest levels of aggression between species adapted to the same microhabitat (Ortiz & Jenssen, 1982).

Interspecific interactions likely have fitness consequences in anole communities, as many species exhibit lower growth rates and lower population densities in sympatric populations (Leal et al., 1998; Pacala & Roughgarden, 1982). Researchers have also observed differences in display behaviors and habitat usage between allopatric and sympatric populations. Green anoles (*Anolis carolinensis*) in Florida shift from being habitat generalists to occupying higher microhabitats in the presence of the trunk-ground ecomorph *A. sagrei* (Edwards & Lailvaux, 2012; Kamath et al., 2013; Stuart et al., 2014). Similarly, Dufour et al. (2018) observed perch height divergence after habitats occupied by native *Anolis oculatus* were invaded by *Anolis cristatellus* on the Caribbean island Dominica, while Salzburg (1984) saw *A. sagrei* alter their habitat use after sympatric *A. cristatellus* were removed. In an experimental enclosure study, Pacala and Roughgarden (1982) found that the presence of *A. wattsi* changed the perch heights and growth rates of a fellow trunk-ground anole (*A. gingivinus*) but did not impact a congener of a different ecomorph (*A. bimaculatus*). Yet changes in fitness and behavior are not generally attributed to competition over food; anoles are not usually considered food-limited (Carpenter, 1967), and enclosure studies have found no evidence of resource competition between species (Turnbough, 2016).

One species pair that has received considerable attention is the Carolina green anole (*Anolis carolinensis*) and the Cuban brown anole (*A. sagrei*). Because the green anole is the only anole species native to the continental United States (R.

Powell, Conant, & Collins, 2016), its current contact with the invasive brown anole in the southeastern US has created a "natural laboratory" in which to test for aggression and competition between closely related, previously allopatric species.

Since it began dispersing through Florida in the 1940s (Oliver, 1950), the brown anole has largely replaced native green anoles across the state (Campbell, 2000; Echternacht, 1999). Several studies have shown that green anoles limit their habitat usage to higher perch sites in brown anole-invaded areas (Edwards & Lailvaux, 2012; Kamath et al., 2013; Stuart et al., 2014), a change that has stimulated the evolution of additional toe pads (Stuart et al., 2014). Green and brown anoles also exhibit aggression towards one another in staged trials in both the lab and the field (Culbertson & Herrmann, 2019; Edwards & Lailvaux, 2013; Tokarz & Beck, 1987), although both species are more aggressive towards conspecifics than towards heterospecifics (Tokarz & Beck, 1987). Furthermore, adult brown anole disproportionately prey on juvenile green anoles, potentially affecting green anole recruitment in invaded areas (Gerber & Echternacht, 2000).

Much of the previous work on green and brown anoles has focused on the consequences of interactions between the two species over long time spans (years or decades). For example, Stuart et al. (2014) measured behavioral and morphological shifts in green anole populations six months to three years after invasion, while Edwards and Lailvaux (2012) and Kamath et al. (2013) compared long-invaded populations with uninvaded populations. Yet little is known about the proximate behavioral consequences of brown anole invasions or how the dominance relationships observed in staged trials translate into real-life competition.

In this study, we investigated the immediate behavioral consequences of interspecific interactions on green anole populations after a brown anole invasion. In particular, we sought to understand the frequency and characteristics of green and brown anole interactions under semi-natural conditions and to determine if shifts occurred in prominent green anole behaviors (activity levels, display rates,

home range size, and perch heights) after a brown anole invasion. We created captive populations of green anoles in large aviary-like outdoor structures, "invaded" these structures with brown anoles, and looked for changes in behaviors and spatial use by the original green anoles. To control for potential density effects, we also ran parallel experiments in which we added green anole "invaders" instead of brown anoles.

While our lizards were in the enclosures, we recorded behavioral interactions between individuals in our populations to create social networks of the populations post-invasion. We then calculated an assortativity value for each of these networks. Assortativity is a network metric that looks for assortative mixing within the graph, where nodes have a tendency to be connected to other nodes that share a defining characteristic. Assortativity measures are commonly used in ecological data sets, for example to see if males interact more with females than they do with other males (negative assortativity by sex; e.g., Perkins, Ferrari, & Hudson, 2008) or to look for social groupings based on physical traits such as body size . In our networks, we looked for preferential interactions by "origin," that is between the "original" green anoles added at the beginning of each experimental round and the "added" green or brown anoles introduced mid-experiment.

We hypothesized that brown and green anoles would engage in aggressive interactions with each other, but that green anoles would interact more frequently and would engage in more frequent escalated behaviors (e.g., lock-jawed fights) with each other than they would with added brown anoles. Furthermore, we predicted that social networks in brown anole-invaded populations would show more positive assortativity by origin (added versus original) than networks in green anole-invaded populations, such that both species will preferentially interact with conspecifics. We also predicted that green anoles would exhibit decreased activity levels, lower display rates, smaller home ranges, and higher perch heights after brown anole invasions as a result of perceived brown anole dominance.

4.3 Materials and Methods

Animal care facility and specimens

Green (*Anolis carolinensis*) and brown (*A. sagrei*) anole lizards were purchased from one of three commercial reptile distributors (LLLReptile and Supply Company, Inc., Oceanside, CA, U.S.A.; Underground Reptiles, Deerfield Beach, FL, U.S.A.; Backwater Reptiles, www.backwaterreptiles.com), depending on when the animals were in stock. All lizards were wild-caught in the American South, most often in Florida, and were pet-quality adults, defined as having snout-vent length (SVL) above 55 mm and 45 mm for *A. carolinensis* males and females, respectively (Lovern et al., 2004), and 44 mm and 38 mm for *A. sagrei* males and females, respectively (Licht & Gorman, 1970).

We housed lizards in the animal care facility at the University of Tennessee, Knoxville for one to two weeks after delivery to allow individuals to acclimate to captivity prior to experimental manipulation. Housing conditions followed anole care procedures outlined in Sanger et al. (2008). Lizards were sexed and placed either individually or in male-female pairs in standard 10 gallon and 5-gallon glass aquarium tanks (20" x 10" x 12" and 10” x 10” x 10”, respectively). Individuals housed in pairs were placed in different experimental enclosures whenever possible. Each tank contained a wooden branch to serve as a perch, a spider plant (*Chlorophytum comosum*) for vegetation, and cage carpet. Ultraviolet (Zoo Med ReptiSun Desert Compact Fluorescent UVB Lamp, Zoo Med, San Luis Obispo, CA, U.S.A) and heat bulbs (Fluker Reptile Incandescent Daylight Bulb, Fluker Farms, Port Allem, LA, U.S.A.) were positioned above each cage on a 14:10 h light-dark cycle. We misted each cage daily to provide lizards with drinking water and fed each lizard 2-4 crickets dusted in calcium powder on alternating days. Cages were separated by wooden dividers to prevent lizards from visually interacting. Before moving the animals into the study enclosures, we individually marked each lizard by attaching a

unique bead tag to the muscle at the base of the tail following the procedures of Fisher and Muth (1989).

Enclosure construction and experimental animal care

The study was conducted at the University of Tennessee Forest Resources AgResearch and Education Center property in the University of Tennessee Arboretum located in Oak Ridge, Tennessee between the months of May and August from 2017 to 2019. Eastern Tennessee is the northernmost edge of the green anole geographic range (R. Powell et al., 2016).

At the Arboretum, we constructed two 5m x 5m x 5m wooden framed enclosures (Figure 3.1). Each enclosure was covered with two layers of mesh: an inner layer of screen door mesh to keep the lizards from escaping and an outer layer of 1-inch hardware cloth to protect the inner mesh from damage from weather and wildlife. The ground was lined with plastic gardeners' fabric topped by a layer of hardware cloth to protect against damage from potential predators and to prevent female anoles from laying eggs in the soil. The enclosures contained live trees (primarily sugar maple*, Acer saccharum*, and hickory*, Carya* sp.), dead trees, and potted plants (primarily majesty palm, *Ravenea rivularis*) to serve as habitat for the lizards. Enclosures also included metal ladders to allow researchers to observe animals perched in the canopy. We inspected the enclosures at the beginning and end of each experimental round to look for tears in the interior mesh or gardeners' fabric, which we repaired using caulk and glue (mesh) or gorilla tape (gardeners' fabric).

We misted the enclosures daily with an industrial water-sprayer and released crickets dusted with calcium powder *ad libitum* every other day.

Experimental design

For each experimental round, we first released 12 green anole lizards (6 males, 6 females) into each enclosure. This population density (12 individuals in a 125 m^2 area) is comparable to high-density green anole populations observed in the

wild (King, 1996). We waited 24 hours before performing observations on the animals to allow them to acclimate to captive conditions. Starting the day after release, we performed 30-minute focal observations on individual lizards in which we recorded the individual's display behaviors (pushup and dewlap displays), locomotion (crawls, jumps, and perch changes), and behavioral interactions with other lizards. We define an "interaction" as a behavioral display (dewlap/pushup display, aggressive chase, mating attempt, lock-jawed fight, or copulation) by one individual directed towards another individual, as indicated by observed eye contact between the individuals or a behavioral response from the receiver. We observed each lizard a maximum of twice per day, with at least two hours between observations of the same individual. Observations occurred between 1000 and 1800 hours, with peak activity between 1300 and 1500.

We also recorded spatial locations of individuals by marking the location and perch height of the individual on a to-scale map of the enclosure, both of which were estimated visually by the observer. To increase accuracy of perch height estimates, we painted markings at six-inch intervals on the center beams of all four walls in both enclosures (Figure 3.1). We recorded up to three location points per focal observation. We also recorded individuals' positions throughout the day.

We measured the behaviors of these initial populations for ten days or until we had observed each lizard for at least 60 mins (pre-invasion: mean=143 mins, range=60-212; post-invasion: mean=135 mins, range=60-210). Delays in data collection were most often caused by rain. We did not perform observations while it was raining, as both species markedly decreased activity during rain (JMB, personal observation).

After we measured the initial populations, we "invaded" these populations by adding additional green anoles to one enclosure and brown anoles to the other. We varied which enclosure had each species so that both species were placed in each enclosure the same number of times. We then spent an additional ten days performing focal observations and recording spatial locations for the original twelve

green anole individuals, as above. We did not perform 30-minute focal observations on the new individuals, although we did record their spatial locations and behavioral interactions. We repeated this experiment eight times using two "invader" densities: low (2 males, 2 females) and high (4 males, 4 females).

Home Range Estimation

We estimated the home range size of each individual using two- and three-dimensional 95% minimum convex polygon (MCP) estimation (Figure 4.1; Rose, 1982). We excluded data points recorded in the first three days of each 10-day round to allow individuals to establish their home ranges after the populations were created or disturbed. To calculate minimum convex polygons, we used ImageJ (Rueden et al., 2017) and Fiji (Schindelin et al., 2012) to convert location points on the printed maps to x-y coordinates, with the origin set as the front left corner of the enclosure. The z coordinate for each point was the height recorded for that point. Each lizard had at least 5 location points, the minimum needed for MCP analysis (pre-invasion: mean=17, range=5-39; post-invasion: mean=16, range=5-36). We calculated two-dimensional MCP estimates using the "mcp" function in the adehabitatHR package (Calenge, 2006) in R (Figure 4.1a; R Core Team, 2013). We calculated three-dimensional MCP estimates by modifying the "mcp" function for three dimensions using the multidimensional convex hull function "convhulln" in the geometry package (Barber et al., 2012).

Social network construction and analysis

We constructed post-invasion social networks for each population (Figure 4.2). In these networks, we defined an "interaction" as a behavioral display given by one individual clearly directed at another individual. Edges in all social networks were directed, moving from signaler to receiver. In cases where both individuals participated in the interaction (e.g., lock-jawed fights and copulations), we

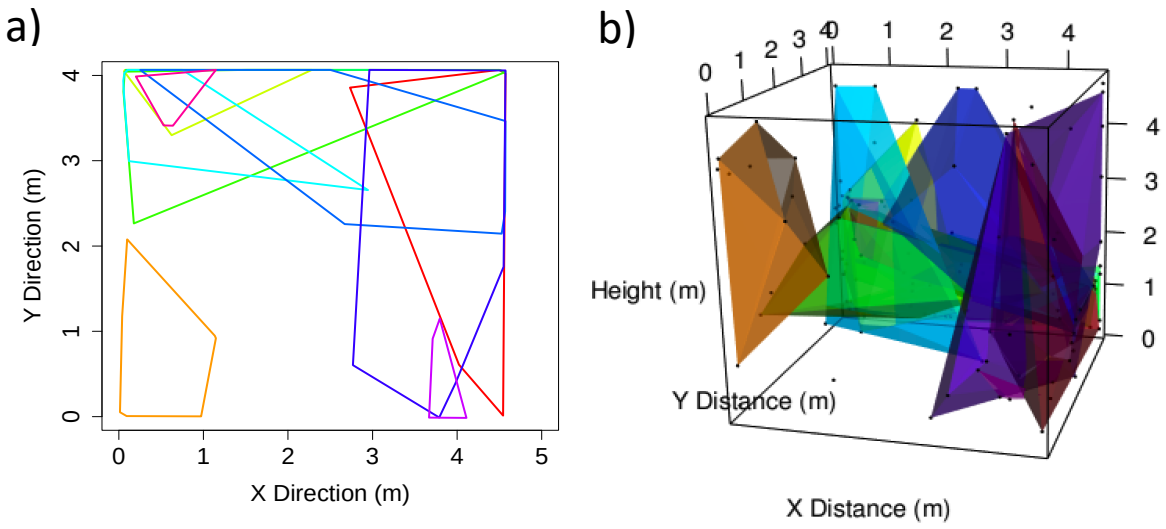

Figure 4.1 Two-dimensional (a) and three-dimensional (b) minimum convex polygon home range estimates for a population of green anole lizards (6 males, 6 females) housed in experimental enclosures. Colors represent unique individuals.

generated edges in both directions. Networks contained multiple edges to show how frequently individuals interacted, such that they contained an edge *for every* interaction between two individuals. We calculated network assortativity by origin ("original," green anoles introduced at the beginning of each round, versus "added," green or brown anoles introduced mid-round) using the "assortativity_nominal" function in the igraph package (Csardi & Nepusz, 2006). For each population, assortativity values closer to 1 indicate stronger positive assortativity by origin (i.e., added/original individuals are more likely to interact with each other), while values closer to -1 indicate negative assortativity by origin (i.e., individuals are more likely to interact with members of the opposite group) and 0 represents no assortativity.

Statistical analyses

We used a series of linear mixed effects models to assess changes in behavior (average display frequency, average activity level, two-dimensional home range

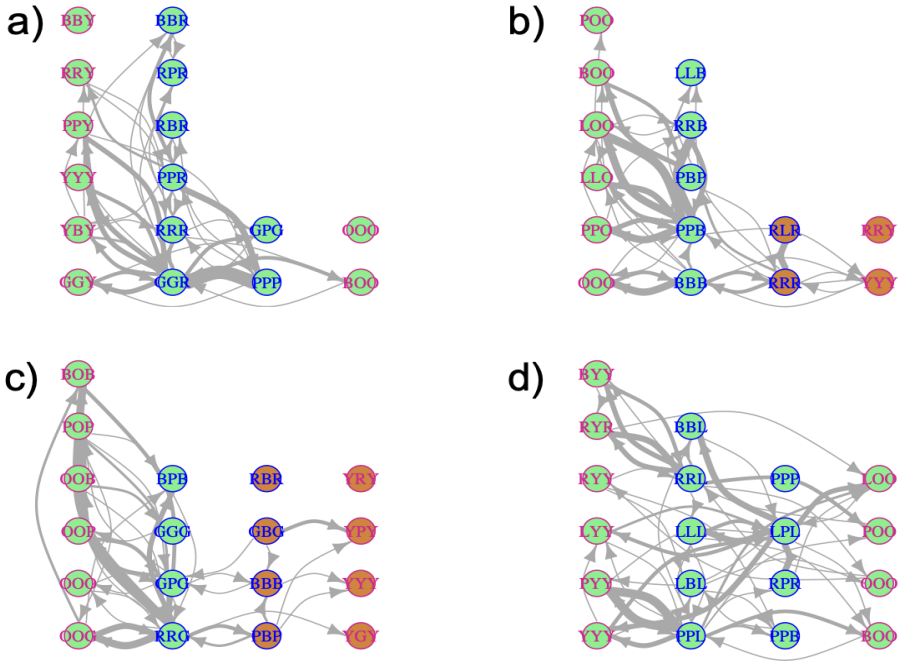

Figure 4.2 Examples of post-invasion social networks for green anole (*Anolis carolinensis*) populations experimentally invaded by low (a,b) and high (c,d) densities of green and brown anoles (*A. sagrei*). Each node represents an individual lizard in the population, with the original green anole populations aligned in the two leftmost columns and the added individuals in the two rightmost columns. Node fill color represents the individual's species, where green nodes indicate green anoles and brown nodes indicate brown anoles. Node outline color represents the individual's sex, with blue outlines indicating males and pink representing females. Edges represent social interactions between two individuals (dewlap/pushup display, aggressive chase, mating attempt, lock-jawed fight, or copulation) and are directed from signalers to receivers. For visualization purposes, edge weight represents the number of interactions between each pair, such that thicker edges indicate more frequent interactions between two individuals.

size, three-dimensional home range size, and average perch height) after invasion. For each model, we used the difference between pre- and post-invasion measurements as the dependent variable, invader species (green or brown) and density (low or high) as independent variables, and experimental round (1-8) as a

random effect. We used model selection following a backwards stepwise procedure. We constrained the models to include at least one independent variable. We defined the best model for each metric using the BIC information criterion. If the two best models had BIC values within two units of each other, we selected the model with the lowest p value from the ANOVA. We performed these analyses in R using the "lmer" function in the lmerTest package (Kuznetsova, Brockhoff, & Christensen, 2017) and tested hypotheses with the "Anova" function in the "car" package (Fox & Weisberg, 2018).

We used a similar model selection process to determine if experimental treatment affected network assortativity by origin. We used a Fisher's r-z transformation to normalize the assortativity values. We then followed the linear mixed effects model analysis described above using the transformed assortativity coefficients as the dependent variable, invader species (green or brown) and density (low or high) as independent variables, and experimental round (1-8) as a random effect.

We controlled for multiple comparisons across all six models by the Benjamini-Hochberg procedure ($q < 0.05$) (Benjamini & Hochberg, 1995). We removed from all analyses individuals who did not have enough observations or died.

Ethical Note

All experimental procedures were done in compliance with the University of Tennessee Institutional Care and Use Committee (Protocol 2429). All animals were euthanized following the experiment.

4.4 Results

Social interactions between green and brown anoles

While green and brown anoles engaged in regular social interactions in our study enclosures, green anoles interacted more with conspecifics – both members of their established population and newly added green anoles – than they did with introduced brown anoles (Table 4.1). Most interspecific interactions occurred between males and were likely aggressive in nature, although escalated aggressive interactions were uncommon (e.g., one chase and one fight; Table 4.1). Male-female interactions occurred across the two species (Table 4.1), but it was unclear if these were aggressive or sexual in nature. We did not observe mating attempts or copulations between the two species.

Original green anoles interacted more before the invasion than they did after

Table 4.1 Number of behavioral interactions observed in populations of anole lizards in experimental enclosures after populations were "invaded" by additional green (*Anolis carolinensis*) or brown (*A. sagrei*) anoles. We define an "interaction" as a behavioral display (dewlap/pushup display, aggressive chase, mating attempt, lock-jawed fight, or copulation) by one individual directed at another individual, as indicated by observed eye contact between the individuals or a behavioral response from the receiver. Display participants are divided into "Original" green anoles introduced to the enclosures at the beginning of each experimental round, and the "Green" or "Brown" anoles added during the invasion.

Display Type		**Interaction Participants**					
		Pre-Invasion	**Post-Invasion**				
		Original-Original	**Original-Original**	**Original-Green**	**Original-Brown**	**Green-Green**	**Brown-Brown**
Within Sex Interactions	Display	196	80	17	34	4	13
	Chase	106	51	2	1	2	16
	Fight	12	1	4	1	0	2
Between Sex Interactions	Display	525	304	23	13	7	19
	Mating Attempt	106	31	3	0	0	20
	Mating	12	4	1	0	0	8

the invasion across all interaction types, in particular showing markedly fewer copulations and fights in the later stage of the experiment (Table 4.1). Added brown anoles engaged in more social interactions among themselves than added green anoles did and engaged in proportionally more copulations.

Brown anole-invaded populations exhibited higher network assortativity than green anole-invaded populations in both density treatments (Table 4.2, Figure 4.3), indicating that individuals preferentially interacted with conspecifics.

Changes in behavior post-invasion

Overall, we observed several significant changes in green anole behaviors after our simulated invasions. These were most commonly associated with invader population densities rather than invader species (Table 4.2, Figure 4.4). The best mixed model for average activity levels included invader species (Table 4.2), likely reflecting the increased variability in activity level shifts exhibited in populations invaded by brown anoles (Figure 4.4b). The models we examined for the other

Table 4.2 Summary of best linear mixed effects models for each response variable, chosen based on lowest BIC value. False discovery rate (q) was calculated across all six models using the Benjamini-Hochberg procedure. We considered a q threshold of 0.05.

Response Variable	Factor	Chi Squared	Df	P value	q
Social Network Measure					
Assortativity by Origin	**Species**	**7.25**	**1**	**0.007**	**0.014**
Daily Behaviors					
Average Display Rate (display/min)	Species	0.81	1	0.368	0.368
Average Activity Level (movement/min)	**Species**	**6.102**	**1**	**0.014**	**0.021**
Spatial Behaviors					
2D Home Range Area (m^2)	**Density**	**8.827**	**1**	**0.003**	**0.009**
3D Home Range Volume (m^3)	**Density**	**4.655**	**1**	**0.031**	**0.037**
Average Perch Height (m)	**Density**	**11.821**	**1**	**0.001**	**0.006**

four behaviors failed to detect an effect of invader species. None of the models considered showed evidence of a change in display rate (Figure 4.4a; Table 4.2).

Original green anole populations exhibited smaller home range sizes in both two (Figure 4.4c) and three dimensions (Figure 4.4d), with the best linear mixed models including only invader density (Table 4.2). Similarly, invader density best explained a significant shift in green anole perch height (Table 4.2), with individuals in high-density populations perching higher than those in low-density treatments (Figure 4.4e), independently of whether the increased density comprised green or brown anoles.

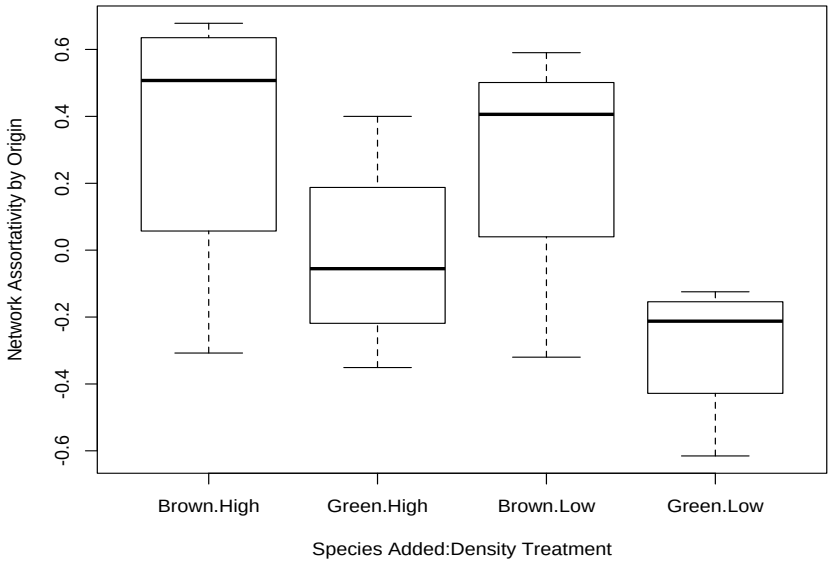

Figure 4.3 Difference in network assortativity in post-invasion, directed, multiedge social networks of adult green anoles (*Anolis carolinensis*). Each initial population of green anoles was "invaded" by a high-density (4 males, 4 females) or low-density (2 males, 2 females) group of green or brown (*A. sagrei*) anoles. Social networks consist of nodes representing individual lizards in each post-invasion population and edges representing behavioral interactions between individuals, including headbob/dewlap displays, chases, lock-jawed fights, attempted matings, and copulations. Each node in the social network was labeled as "original" (i.e., green anoles introduced at the beginning of the experimental round) or "added" (i.e., green or brown anoles added mid-experiment during the "invasion"). Assortativity was calculated using original and added labels.

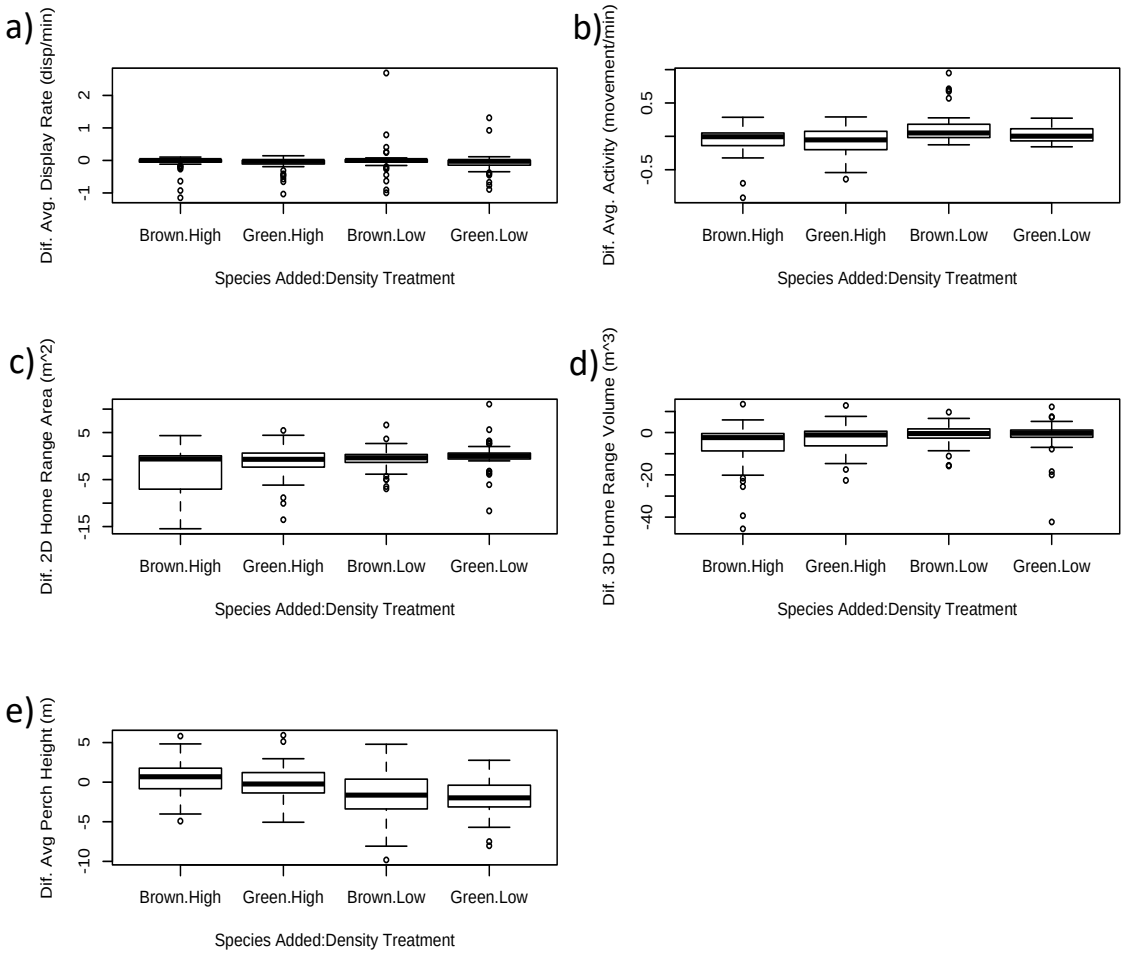

Figure 4.4 Difference in behaviors of green anoles (*Anolis carolinensis*) after being "invaded" by additional green or brown (*A. sagrei*) anoles in high-density (8 new individuals) or low-density (4 new individuals) treatments. Y axes show the difference between the behaviors recorded in the 10 days before the invasion and the 10 days after the invasion. The behaviors investigated include average display rate (a; average number of dewlap or pushup displays per minute), average activity level (b, average number of crawls, jumps, or perch changes per minute), 2D (c) and 3D (d) home range size measured using minimum convex polygon estimation, and average perch height (e).

4.5 Discussion

In this study, we sought to identify the immediate behavioral consequences of a brown anole invasion on native green anole populations. We found that green anoles invaded by high-density groups of anoles had smaller home ranges and higher average perch heights after being invaded, regardless of whether added individuals were conspecifics or heterospecifics. This finding likely indicates that green anoles are sensitive to changes in population density. We also found that social interactions between green and brown anoles were relatively common, but that both species preferentially interacted with members of their own species. Furthermore, brown anoles did not exhibit obvious social dominance in our enclosures. Overall, these results indicate that brown anoles likely do not behaviorally interfere with individual green anoles, but that the increased population densities caused by their invasions can result in disruptions to green anole communities.

Our findings indicate that green anole displacement in the southeastern US is likely not caused by direct interference competition with invasive brown anoles. Although many studies have observed changes in green anole communities post-brown anole invasions (e.g., Edwards & Lailvaux, 2012; Kamath et al., 2013; Stuart et al., 2014), there has been little evidence of resource competition between the two species. Turnbough (2016) found that green and brown anoles have similar per-capita effects on prey communities, indicating that neither species boasts superior foraging abilities. Competition over other resources, such as mates, is also considered unlikely, as observations of green-brown copulations are rare (Hammer, 1984) and no hybrid offspring have been reported.

We saw no evidence of realized brown anole social dominance over green anoles, further decreasing support for direct interference competition between the two species. Culbertson and Herrmann (2019) found that green anole males were more likely to retreat and less likely to display in staged conspecific intrusions than were brown anole males, indicating that brown anoles may have a competitive

advantage in escalated aggressive encounters between the two species. However, there is little evidence that green and brown anoles engage in large numbers of aggressive interactions in the wild. Culbertson and Herrmann (2019), Edwards and Lailvaux (2013), and Tokarz and Beck (1987) found that males in staged aggressive encounters between green and brown anoles displayed escalated aggressive behaviors (e.g., developing an eyespot, erecting a crest, attempting to bite) much less frequently than in intraspecific bouts. In our study, we observed only one lock-jawed fight between green and brown anole males, which eventually ended in a draw. In our enclosures, individuals of both species preferentially interacted with members of their own species over heterospecifics and interspecific interactions that did occur were not characterized by disproportionate aggression from one species or the other.

A common observation across the last few decades has been the exceptionally high population densities of brown anole communities. In invaded areas in Florida, brown anole populations have been recorded as high as 12,000 lizards/ha (Campbell & Echternacht, 2003). Schoener and Schoener (1980) found that brown anoles on their native islands exhibit some of the highest population densities among anole species. In a follow-up study, they further determined that brown anoles have smaller average home range sizes than other species, which likely contributes to their ability to live in dense populations (Schoener & Schoener, 1982). Brown anole populations can also experience rapid growth (Stuart et al., 2014) and exhibit accelerated reproductive rates in their invasive range (Fetters & McGlothlin, 2017).

Thus, green anoles in invaded areas likely experience higher total population densities than they would in their natural single-species communities. Green anoles in our study exhibited the most dramatic shifts in home range size and perch height in high-density invasion treatments, revealing a tendency to move when faced with high densities. Many studies have shown that animals will alter their habitat use in the face of high population densities in both single-species (e.g., Borkowski, 2000;

Bult, Riley, Haedrich, Gibson, & Heggenes, 1999) and mixed-species (e.g., Robertson, 1996) populations. Furthermore, high population densities can cause species to increase their use of lower-quality habitats (Borkowski, 2000), leading to potential fitness consequences and fulfilling a condition of migration (Taylor & Norris, 2007). As a result, green anoles living in high-density invaded populations may have access to fewer high-quality resources or be driven to migrate to new locations.

One potential limitation in our study is the semi-natural enclosure project design. Individuals in the enclosures experienced artificial habitats, such as mesh enclosure walls, and populations that were likely denser than they would experience in the wild (particularly after invasions), which could have affected behavioral patterns. We were also unable to determine the capture location of the green anoles we purchased in this study. Green anoles exhibit variation in behavior (Michaud & Echternacht, 1995), morphology (Macedonia, Echternacht, & Walguarnery, 2003), and life history traits (Lovern, Jenssen, Orrell, & Tuchak, 1999) across their native range. Green anoles from different regions will also have different experiences with brown anole invasions; individuals from northern Georgia may never have seen a brown anole, while lizards from southern Miami have been in contact with brown anoles for several decades. In future studies, it would be interesting to compare the reactions of naïve and experienced green anoles to brown anole invasions.

4.6 Conclusions

In this enclosure study, we found that green anole lizards manifested behavioral changes as a result of increased population densities, rather than because of aggression from brown anole invaders. These findings indicate that high brown anole population densities in Florida, rather than direct interference competition, could be driving green anole displacement across the state. Overall,

this project benefited from an enclosure project design, which allowed us to parse potentially conflating aspects of natural species invasions.

CHAPTER FIVE

CONCLUSIONS AND RECOMMENDATIONS

5.1 Summary

Territoriality is a complex concept, full of nuance and variation. In this dissertation, I explored various aspects of territoriality using mathematical models and semi-natural field experiments. Much of this work focused on the behaviors of a model territorial organism, the green anole lizard (*Anolis carolinensis*). In this final chapter, I summarize my main findings, discuss future research directions for each project, and end with the major conclusions of the dissertation.

5.2 Major Results

Accurately quantifying animal home ranges and territories is important for many aspects of ecological studies. Incorporating a third dimension into spatial use projections for species that use vertical habitat, such as arboreal, avian, marine, or subterranean species, results in more accurate estimates of resource use and conspecific overlap (Tracey, Sheppard, Zhu, Wei, et al., 2014; Vivancos et al., 2016). In Chapter 2, I analyzed the accuracy of three-dimensional home range estimation methods for organisms with different spatial behaviors using an agent-based model. I found that the most accurate methods in 2D were not necessarily the best methods in 3D, with the movement-based kernel method in particular generating highly accurate 2D estimates but overestimating home range size more than other methods in 3D. Furthermore, the underlying behavior of the organisms under study affected the accuracy of the methods. Specifically, I recommend researchers use

minimum convex polygon or plug-in bandwidth fixed kernel estimates for territorial species that patrol their home range borders. This study emphasizes that there is not necessarily one "best" home range estimation method and that instead researchers need to consider the species under study and the experimental design when choosing a home range metric. In the future, I encourage researchers to apply additional home range estimation methods to three-dimensional data. I also encourage researchers to further explore the role of movement behaviors on home range accuracy using real ecological data sets.

There can be hidden idiosyncrasies within well-studied behavioral systems. Since the first description of green anole territorial behavior almost one hundred years ago, much research effort has been devoted to understanding the behaviors of large territorial males. As a result, little is known about non-territorial males in anole communities or how they interact with females. In Chapter 3, I described the behaviors of male green anoles with three behavioral phenotypes (territory owners, sneakers, and floaters) in captive populations. I found that half of the males in our populations displayed non-territorial phenotypes, demonstrating that these phenotypes make up an important component of anoles' social landscape. Furthermore, I found that males of each type were characterized by different behaviors, with territory owners engaging in the most behavioral interactions, floaters overlapping others' home ranges the most, and sneakers generally behaving more similarly to females than to other males. These results support the female-mimicry hypothesis for sneakers advanced by Orrell and Jenssen (2002). Females also differentiated between territorial and non-territorial males, engaging in few behavioral interactions with sneakers and floaters despite high home range overlap. Genetic studies have found that all three types of males father offspring in the wild (e.g., Passek, 2002), indicating that non-territorial and sneaker males are employing viable fitness strategies. Future research could explore the differences between the three types of males in a natural setting, specifically looking for differences in

morphology and behavior. Researchers could also explore how plastic the different strategies are and under what circumstances an individual engages in each one.

Territorial species can be particularly sensitive to anthropogenic change, as humans can alter the distribution of resources, amount of habitat, and density of conspecifics and heterospecifics these animals encounter. This can be especially true during species invasions, which can introduce new species to compete with native organisms over space and resources. In Chapter 4, I explored the behavioral interactions between a native territorial species, the green anole, *A. carolinensis*, and an invasive congener, the Cuban brown anole, *A. sagrei*, in captive populations housed in semi-natural enclosures. I found that green and brown anoles behaviorally interacted with one another, but that both species preferentially displayed to conspecifics over heterospecifics. Furthermore, I found that green anoles exhibited smaller home ranges and higher perch heights in conditions of high invader density in both experimental (brown anole-invaded) and control (green anole-invaded) treatments. Together, these results indicate that brown anoles are likely not competitively dominant over green anoles, as is commonly postulated (e.g., Stuart et al., 2014). Instead, green anoles are likely sensitive to the increased population densities that come with invasion of the highly dense, highly fecund brown anole. Future research could further explore interactions between green and brown anoles in the wild and seek connections between green and brown anole population dynamics in invaded areas over time.

Final Thoughts

At the end of this research, several major takeaways emerge. The first is the importance of considering an organism's underlying behaviors when studying its spatial use. Fully accounting for individual behaviors can increase the accuracy of spatial use estimates and fitness consequences, particularly for species in which social behaviors are tightly tied to resource access and home range boundaries. The second takeaway is that network statistics, which are still relatively new tools for

behavioral ecologists, have the potential to greatly increase our understanding of the social lives of animals without "obvious" social relationships, like anoles. Although anoles do not form social groups or mated pairs, social interactions within anole populations are still important drivers of resource use and mating patterns. Social network models can allow researchers to understand these relationships more fully. Next, this dissertation shows that some questions can be addressed better by performing controlled experiments than by field studies. Although multiple researchers have explored green and brown anole interactions in nature, these studies were not able to control for population densities, which generated a key result in our study, or time since invasion. By designing a simple enclosure study, I was able to parse apart the effects of density and species as confounding factors, revealing the important effect of crowding on green anole behaviors. Finally, this study adds a new impact of an invasive species to the ever-expanding list. Our results indicate that brown anoles do not competitively displace green anoles, or really bother them at all. In fact, it is the brown anole's specific population dynamics that pushes green anoles into new habitats through over-crowding. This emphasizes that invasive species can have subtle but still important effects on native ecosystems.

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VITA

Jordan Bush grew up in Colorado Springs, Colorado. She graduated from Trinity University in San Antonio, Texas in 2014 with a Bachelor of Science degree in Biology and a Bachelor of Arts degree in Mathematics. She joined the Ecology and Evolutionary Biology department at the University of Tennessee Knoxville (UTK) in 2014. While at the University of Tennessee, Jordan published six papers in academic journals, was vice president of the department's graduate student organization, represented the EEB department on the graduate student senate, and was a founding member of the graduate student outreach organization Engaging Knoxville in Ecology and Evolution (EKEE). Jordan was funded for two years by the Program for Excellence and Equity in Research (PEER) at UTK and was awarded a National Science Foundation Graduate Research Fellowship in 2015. She also won the EEB department's Tom Hallam award in 2020 for excellence in math ecology.

During her time at UTK, Jordan also became interested in science journalism. She has since been featured on the Story Collider podcast and had her work published on the Society for Integrative and Comparative Biology website. She was awarded the J. P. Blakely Award of Excellence in Science Writing, Graduate Division, by the East Tennessee Chapter of the Society for Technical Communication in 2017 and she came in second place in the Tennessee Associated Press Collegiate Journalism Awards in the "Online Specialized/Topical Reporting" category in 2020. She completed a concurrent master's degree in Journalism and Electronic Media at the University of Tennessee in 2020.