Phenotypic Variation and the Behavioral Ecology of Lizards

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Abstract

Behavioral ecology is the study of how animal behavior evolves in the context of ecology, thus melding, by definition, investigations of how social, ecological, and evolutionary forces shape phenotypic variation within and across species. Framed thus, it is apparent that behavioral ecology also aims to cut across temporal scales and levels of biological organization, seeking to explain the long-term evolutionary trajectory of populations and species by understanding short-term interactions at the within-population level.

In this dissertation, I make the case that paying attention to individuals' natural history—where and how individual organisms live and whom and what they interact with, in natural conditions—can open avenues into studying the behavioral ecology of previously understudied organisms, and more importantly, recast our understanding of taxa we think we know well. In Chapters 1 and 2, I investigate the consequences of paying attention to individuals' movement patterns for understanding the mating system of *Anolis* lizards (Dactyloidae). Chapter 1 is a historical review of *Anolis* social and reproductive behavior, in which I show that because individual variation in movement and social behavior was consistently ignored or downplayed in studies of *Anolis* mating systems, the conclusion that anoles are territorial and polygynous remains poorly supported by behavioral evidence. In Chapter 2, I examine movement behavior in a population of *Anolis sagrei*, and show that individuals' movement behavior allows females to encounter and potentially mate with multiple males, which is counter to previous behavioral descriptions of *Anolis* mating systems but is consistent with growing genetic evidence for female multiple mating. The potential implications for sexual selection are discussed. In Chapter 3, I show that individual *A. sagrei* are specialized in habitat use, and that the degree of specialization among individuals in the sampled population in Gainesville, FL, is comparable to the degree of specialization across habitat specialist species in a community of Greater Antillean anoles. However, individual specialization in habitat use is not related to available habitat or to the morphological traits that explain habitat use specialization across species and populations of habitat use, suggesting that macroevolutionary patterns in this group are not simply microevolutionary patterns "writ large." Finally, in Chapter 4, I quantify variation in display behavior, morphology, and habitat in the fan-throated lizard (*Sitana* and *Sarada*; Agamidae) species complex, and find that display behavior is partially but not completely associated with ornament elaboration in this group. Moreover, though habitat structure does not play a role in the maintenance of throat-fan and display variation, sexual selection very likely shaped the dramatic variation in ornament morphology in this group.

Table of Contents

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Introduction

The goal of behavioral ecology is to "understand how behavior evolves in the natural world" (Davies et al. 2012), thus melding, by definition, investigations of how social, ecological, and evolutionary forces shape phenotypic variation within and across species. This framing gives us behavioral ecologists both conceptual and practical ways to position our work.

Conceptually, this definition offers behavioral ecology as a way to understand behavioral variation in animals across a range of spatial, temporal, and causal scales. For example, Tinbergen's (1963) four questions, which are the foundation on which much of modern animal behavior research is built, are an explicit expression of behavioral ecology's goal of transcending causal scale. Since Tinbergen's time, the span of behavioral ecology has continued to increase, with its continued integration with genetics (e.g. Weber et al. 2013) and neuroscience on one hand (e.g. Riffell et al. 2013) and the development of tools that allow us to expand sampling both spatially and temporally on the other (Kays et al. 2015).

But the definition of behavioral ecology also indicates that, fundamentally, it is centered on the *individual* as a unit of understanding—what behavioral ecologists seek to learn is why individuals behave in the ways that they do, in their natural environments. This lends perspective to the work that behavioral ecologists engage in on a practical level—it is primarily the work of a naturalist. Defined as "descriptive ecology and ethology" (Greene 2005), or, in more detail, as "direct knowledge of organisms—what they are, where they live, what they eat, why they behave the way they do, how they die" (Tewksbury et al. 2014), natural history is the bedrock on which behavioral ecology, not to mention most other subfields of organismal biology, rests. Yet the debate over whether biologists pay enough attention to organisms' natural history has persisted for decades (Greene and Losos 1988; Noss 1996; Greene 2005; Tewksbury et al. 2014). That this debate exists at all is likely perplexing to many behavioral ecologists—what would "too much" attention to natural history look like, on a planet where over 80% of species remain undescribed (Mora et al. 2011) and the basic biology of an even greater proportion of species remains unknown? Nevertheless, natural history education and research are considered to be in decline (Tewksbury et al. 2014).

In this dissertation, I make the case that paying close attention to individual animals' natural history can not only shape how we study their behavioral ecology, but also alter existing narratives about their evolution, with the potential to influence our understanding of phenotypic variation across a range of scales of biological organization, from within populations to across species.

The pertinence of natural history investigations to behavioral ecology research is completely non-controversial when applied to organisms whose biology is mostly unknown, such as the fan-throated lizard species complex (*Sitana* and *Sarada*; Agamidae; Deepak et al. 2016). Despite being common and locally abundant across much of the South Asian subcontinent, we know remarkably little about variation in the behavior, morphology, and habitat use of fan-throated lizards. I examined a suite of traits predicted to co-vary with throat-fan morphology across populations of fan-throated lizards across peninsular India, with two goals (Chapter 4). First, I examined if lizards with differently sized and colored throat fans displayed differently from one another, to begin to understand whether and how display behavior and throat-fan morphology coevolve or are constrained by one another. Second, I examined if indicators of either sexual selection or habitat structure co-varied with throat-fan size and color, to begin to understand the ecological and evolutionary forces shaping phenotypic diversification in this clade. I found that display behavior and throat-fan morphology co-varied partially, and that sexual selection likely played a role in the origin and maintenance of throat-fan diversification. From these data, I also predicted that increased throat-fan size and coloration had evolved at least twice in this clade, a prediction that is consistent with later results from Deepak et al. (2016) on the systematics of this group.

In the remainder of this dissertation, I contend that paying attention to individuals' natural history is important even for research on organisms that we think we know well. *Anolis* is a genus of diurnal insectivorous lizards distributed primarily across the Neotropics (reviewed in Losos 2009). The evolutionary and behavioral ecology of *Anolis* lizards have been studied for decades, and they are a model system for understanding the dynamics of rapid evolution and adaptive radiation. Of the 400 species in *Anolis*, the brown anole, *Anolis sagrei*, is one of the best studied. Here, I examine phenotypic variation across individuals in habitat use behavior (Chapter 3) and movement behavior (Chapter 2) in populations of *A. sagrei* lizards in Gainesville, FL.

Anolis lizards are a textbook example of convergent evolution. On each of the four islands of the Greater Antilles, species of anoles have independently converged in a suite of behavioral, ecological, and morphological traits, repeatedly evolving a community of habitat-use specialists whose morphologies are adapted to the particular habitat they occupy (reviewed in Losos 2009). Populations within a species that diverge in habitat use also rapidly evolve morphological differences that recapitulate these adaptive differences between species (e.g. Schoener 1975; Losos *et al.* 2006; Stuart *et al.* 2014). By examining individual variation in habitat use in a population of *A. sagrei*, I first asked if individuals show specialization in habitat use and second, if this specialization is associated with morphology in a manner similar to the ecomorphological associations seen across species and populations. I found that while individuals are in fact specialized in habitat use, to a degree comparable to the specialization seen across species of *Anolis* in a community, this specialization is not associated with morphological traits in the same way as it is across species or populations, suggesting that patterns of macroevolution in *Anolis* are not simply patterns of microevolution "writ large" (Mayr 1942; Eldredge 1985).

Compared to our understanding of natural selection in *Anolis*, the role of sexual selection in shaping their phenotypic variation remains more of a puzzle. Decades of behavioral research on anoles' social organization and mating systems have used the framework of territoriality to understand these lizards' reproductive interactions (e.g. Evans 1938; Rand 1967; Ruby 1984; Jenssen et al. 1995). However, in a historical review of the literature on *Anolis* social behavior (Chapter 1), I show that the earliest studies concluded that anoles are territorial with little evidence. Later studies, taking prior conclusions at face value, ended up being designed such that they were unlikely to detect or consider important evidence of individual variation in movement behavior and social interactions that is inconsistent with territoriality. Consequently, we know less about *Anolis* mating systems than we think we do.

To begin to reframe our understanding of *Anolis* mating systems such that it is independent of the constraints of a territorial framework, I measured the movement patterns of individuals in a population of *A. sagrei* and quantified the co-occurrences of males and females in space and time (Chapter 2). Movement patterns predict that many females encounter multiple males across the breeding season, and males are unlikely to maintain exclusive access to the females they encounter. Thus the movement patterns of these lizards allow for complex polygynandrous reproductive dynamics, leading to important implications for the opportunity for sexual selection in anoles.

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Chapter 1

The erratic and contingent progression of research on territoriality: a case study.

Ambika Kamath and Jonathan Losos

1.1 Summary

Our understanding of animal mating systems has changed dramatically with the advent of molecular methods to determine individuals' reproductive success. But why are older behavioral descriptions and newer genetic descriptions of mating systems often seemingly inconsistent? We argue that a potentially important reason for such inconsistencies is a research trajectory rooted in early studies that were equivocal and overreaching, followed by studies that accepted earlier conclusions at face value and assumed, rather than tested, key ideas about animal mating systems. We illustrate our argument using *Anolis* lizards, whose social behavior has been studied for nearly a century. A dominant view emerging from this behavioral research was that anoles display strict territorial polygyny, where females mate with just the one male in whose territory they reside. However, all genetic evidence suggests that females frequently mate with multiple males. We trace this mismatch to early studies that concluded that anoles are territorial based on limited data. Subsequent research assumed territoriality implicitly or explicitly, resulting in studies that were unlikely to uncover or consider important any evidence of anoles' departures from strict territorial polygyny. . Thus, descriptions of anole behavior were largely led away from predicting a pattern of female multiple mating. We end by considering the broader implications of such erratic trajectories for the study of animal mating systems, and posit that precise definitions, renewed attention to natural history, and explicitly questioning assumptions made while collecting behavioral observations will allow us to move towards a fuller understanding of animal mating systems.

1.2 Background

Variation among species in social and reproductive organization has long been of interest to naturalists and evolutionary biologists. Why are some species monogamous, others polygynous, and yet others polyandrous? Why do some species exhibit a wide variety of different reproductive and social behaviors? Understanding the selective pressures driving such variation requires quantifying the extent to which different behaviors lead to reproductive success. For decades, behavioral ecologists could not quantify reproductive success directly, and used proxies such as the number of observed mates or offspring produced (Emlen and Oring 1977; Klug 2011). Inferring reproductive success from such proxies involved making assumptions about species' biology. For example, using the number of mates as a proxy for male fitness meant assuming that females do not vary in fecundity, and using the number of eggs in the nest of a breeding pair as a proxy for the male's fitness meant assuming that the female does not engage in extra pair copulations or that occasional extra pair mates are unlikely to sire offspring.

However, in the last three decades, the advent of molecular means of assessing parentage has allowed direct and precise measurements of reproductive fitness, enabling novel insight into the complex landscapes of sexual selection acting both before and after copulation (e.g. Coltman et al. 2002; Birkhead 2010; Fisher and Hoekstra 2010). In many cases, these molecular measures have demonstrated that what we thought we knew about reproductive success was mistaken (e.g. Avise et al. 2002; Griffith et al. 2002; Uller and Olsson 2008; Boomsma et al. 2009). Specifically, biologists have discovered that the assumptions linking behavioral proxies to reproductive success were often not met. For example, females can vary in fecundity (Clutton-Brock 2009), mate outside of observed social bonds (Griffith et al. 2002), and can store sperm, allowing for post-copulatory female mate choice (reviewed in Orr and Brennan 2015). In such cases, the reason for the mismatch between behavioral and genetic descriptions of mating systems is that, despite intensive field studies, researchers were yet to observe important components of a population's mating system.

However, in this paper, we argue that mismatches between behavioral and genetic descriptions of mating systems can arise not only from undiscovered biology but also from the erratic and contingent progression of scientific research. In such a progression, poorly-supported conclusions from the earliest studies are inadvertently reified by later researchers, who, without examining the evidence for earlier conclusions, assume rather than test key ideas. Breaking away from such a progression of research is not inevitable, because it requires reinvestigating ideas believed to be true. Consequently, relatively unsupported corpora of knowledge about species' social behaviors and mating systems may remain undiagnosed.

We illustrate our argument using *Anolis* lizards, a model system for evolutionary ecology in which social behavior and mating systems have been studied for nearly a century (reviewed in Losos 2009). These decades of behavioral research yielded the near-unanimous conclusion that anoles are territorial and polygynous. In a chapter reviewing behavioral descriptions of *Anolis* mating systems, Losos (2009) concluded that "as a rule, male anoles are highly territorial." Elsewhere, some of the best studied species in this genus have been described, based on behavioral observations, as matching "the paradigm of a territorial polygynous species" (Schoener and Schoener 1982). Stan Rand, in what remains one of the best studies of anole social behavior in the wild (Rand 1967a), described their mating system thus:

> "…the lizards live together more or less permanently and the females usually mate with a single male (the male with the one or more females that have home ranges within his)."

Judy Stamps, who spent her whole career studying anole territoriality, summarized their mating system as follows (Stamps 1995):

> "During the breeding season, male anoles defend territories that enclose the home ranges of adult females, and defend these mating territories against conspecific males. Although DNA paternity studies are not yet available for anoles, males probably father most of the hatchlings produced by the females within their territory."

Tokarz (1998), describing the prevailing views from behavioral data on anole mating systems, said that it is "generally believed that in territorial species of lizards, females that reside within a given male's territory would have relatively few opportunities to mate with more than one male." Together, these quotes help to delineate the prevailing view of anole spatial and social organization based on behavioral data. Under this view, which we describe as "strict territorial polygyny" and illustrate in Figure 1.1, males have the potential to mate with one or more females within their territory, but females mate with only the one male in whose territory they are contained. If these territories are maintained for the duration of the breeding season or longer, as suggested by Rand (1967a), then all of a female's offspring are expected to be sired by a single male.

However, all the genetic evidence collected subsequently indicated that females' offspring are frequently sired by multiple males, and therefore that the prediction about strict territorial polygyny in *Anolis* lizards was not met (reviewed below; Passek 2002; Calsbeek et al. 2007; Johnson 2007; Harrison 2014). Quite to the contrary, female multiple mating is common in anoles, calling into question the behavioral descriptions predicting that female anoles will mate with just one male.

At the heart of this discrepancy between behavioral predictions and genetic data on female mating patterns is the concept of territoriality. Though territoriality is central to the behavioral descriptions of mating systems in many animals (Emlen and Oring 1977; Fitzpatrick and Wellington 1982; Lott 1984), the term itself is fraught with inconsistency and imprecision across different studies. Most often, the term "territorial" is used to describe individuals that defend an exclusive area in a fixed spatial location (Tinbergen 1957; Martins 1994; Maher and Lott 1995), indicating that the definition of territoriality incorporates two features: site fidelity (the tendency of an individual to remain in or return to a fixed spatial location) and exclusivity (the tendency of an individual to exclude other individuals, particularly conspecifics of the same sex, from the area they occupy). Under the strictest interpretation of territoriality in *Anolis* (Figure 1.1), females mate with just one male; however, more relaxed interpretations of territoriality incorporating some variation in site fidelity, exclusivity, or both, can be consistent with female multiple mating. Imprecise and changing interpretations of territoriality across studies of anole social behavior may therefore have played an important role in producing the mismatch between behavioral and genetic descriptions of their mating system.

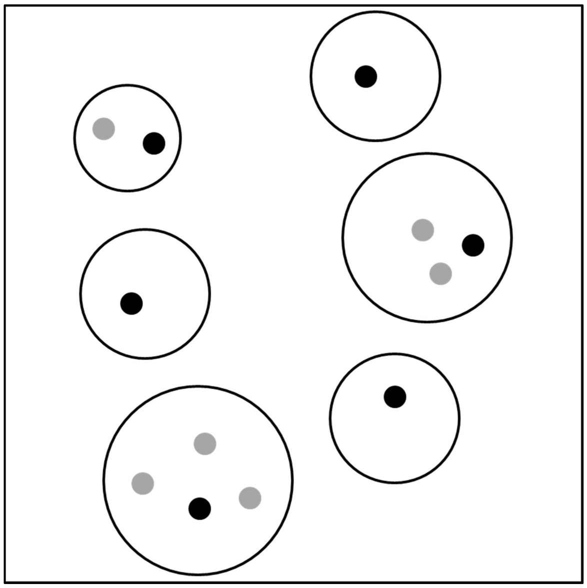

Figure 1.1 A pictorial representation of strict territorial polygyny. i.e. males (black) may mate with multiple females (grey) within their territories (black circles), but females mate with just the one male in whose territory they are contained. If this spatial organization is maintained for the duration of the breeding season, then all of a female's offspring will be sired by just one male.

In this paper, we trace the evidence for the idea that anoles are territorial, and that this idea of territoriality led to the expectation of polygynous mating patterns. To this end, we examine nearly a century of research on *Anolis* mating systems (see the Appendix 1 for a list of papers considered). Our goal is to discern *how* we came to expect that female anoles mate with just one male when in fact they frequently mate with multiple males. Specifically, we examine if this research was somehow set on a path towards reifying a particular conception of territoriality that is inconsistent with widespread female multiple mating, leading to the erroneous expectation that anoles show strict territorial polygyny (Figure 1.1). Throughout, we highlight whether the definitions and interpretations of territoriality employed by different researchers include site fidelity, exclusivity, or both, and pay attention to whether variation in site fidelity and exclusivity that could have explained female multiple mating remained undetected or was otherwise ignored.

We show that current ideas about anole social structure originated in studies whose scope and content is not commensurate with the weight they currently bear. These equivocal demonstrations of territorial behavior in early studies were seemingly taken at face value by later researchers, whose research included implicit and explicit assumptions about the existence of territoriality. Consequently, the design of later studies was often such that these studies were unable to detect variation in site fidelity and exclusivity. Moreover, even when later researchers found evidence for departures from strict territorial polygyny, this evidence was often deemphasized or ignored during data analysis and in the discussion of results. Given that mismatches between behavioral and genetic descriptions of mating systems are taxonomically widespread, our historical investigation reveals concerns that are likely not unique to *Anolis*. We conclude by considering the broader consequences of our case study for future research on animal mating systems.

1.3 The Earliest Studies of Anole Social Interactions

The first study of lizard mating systems—Noble and Bradley (1933)—combined a review of existing natural history literature with laboratory observations on a taxonomically wide variety of lizard species. Both the lizards' survival ("less than a year" for five species of *Anolis*, which typically live for at least a year even in the wild; Losos 2009) and their behavior indicated that the conditions under which these lizards were housed were likely stressful. Nearly half of all instances of copulatory behavior observed in *Anolis* by Noble and Bradley (1933) was between males. While this behavior was recognized as unusual, it was nonetheless interpreted as supporting territoriality—because lizards frequently engage in male-male copulations only in the lab, in nature these male-male copulations must be prevented by *something*.

This "something" was concluded to be the maintenance of exclusive territories, as evidenced by males' propensity for aggression toward one another. Noble and Bradley (1933) remarked that "males tend to fight, and would, no doubt, tend to mark out territories for themselves." Later, they said, about lizards in general, that "the only mechanism which is present to prevent males from copulating with other males as frequently as with females is that males when meeting each other during the breeding season tend to fight. The result is that males tend to occupy discrete territories, which are difficult to recognize in the laboratory but which have been described in the field." The field studies of *Anolis* behavior referenced by Noble and Bradley (1933) only describe male-male aggression, and not site fidelity by either males or females. Thus, the existence of territoriality in anoles was first concluded on the basis of male-male aggression.

Evans (1936 a, b, c) also concluded from laboratory experiments that male and female *Anolis* lizards maintain territories. Evans (1936 a, c) detailed a weight-based social hierarchy among male *Anolis carolinensis* based on their aggressive interactions, which were described as the "urge to hold territory." Again, conclusions were extrapolated from cages, in which animals were kept at high densities, to the field. For example, Evans (1936c) suggested, without reference to field data, that "the behavior of caged male *Anolis* is probably a modification of the behavior in the field. Under natural conditions when a strange male approached a particular territory which is in possession of another, a fight results…the beaten male retreats, leaving the victor in possession of the territory."

Evans' (1938a) subsequent field study was the first systematic research on anole territorial behavior in nature. Watching a population of *Anolis sagrei* for about a month, Evans (1938a) concluded that "*Anolis sagrei* exhibits a strong urge to select and defend a definite circumscribed territory." Though this conclusion was largely based on observations of male-male aggression, Evans (1938a) also said that "proof that the species is territorial is given by the fact that the same individual has been observed many times on consecutive days upon a particular territory." This dual approach indicates that Evans (1938a) included site fidelity as well as exclusivity in his conception of territoriality. Fortuitously, Evans (1938a) included transcriptions of all field notes taken during this study, which reveal that he concluded site fidelity based on a mean of three distinct observations per lizard. Though his systematic field-based approach was certainly path-breaking for its time, three observations made within a short period relative to the full breeding season (*A. sagrei* breed for at least six months; Tokarz et al. 1998) cannot be considered sufficient to demonstrate persistent site fidelity.

Critique from Evans (1938a, b) prompted Greenberg and Noble (1944) to modify the conditions under which observations were conducted in the lab—they housed and observed *A. carolinensis* lizards in larger cages and greenhouses, up to 5 m × 5 m. But these larger arenas may still have been too small to assess if the multiple males they contained each maintained exclusive areas and showed site fidelity. The authors mentioned that "an active adult male usually succeeded in dominating the entire cage," which implies that males in these cages did not maintain exclusive areas, potentially an artefact of a small arena size. The conditions in the cage were nonetheless described as "near-normal competitive conditions."

Oliver's (1948) methods for observing *A. sagrei* in the Bahamas were similar to Evans' (1938a)—17 lizards in an area approximately 4 × 20 m were "marked and casually observed for a period of slightly less than one month." And though Oliver (1948) "planned to present elsewhere at a later date a detailed account of the individual and social activity of this species," to the best of our knowledge, no such account was published. Oliver (1948) summarized his results as showing that "definite territories are maintained and defended by both sexes." However, the territories he described were not exclusive, because "within the area occupied by each large male there was a smaller male," and it is not clear if these smaller males were reproductively active or not. His conception of territoriality in anoles was therefore potentially consistent with female multiple mating.

Approximately contemporaneous natural history studies described anoles as territorial based on far less evidence. For example, Thompson (1954) observed a single male *A. carolinensis* displaying at a "jar containing about a dozen swifts (*Sceloporus undulatus*) that I had collected the day before," as well as at a skink, and concluded that "during the entire performance it seemed that the anolis [sic] might have been trying to hold or establish a territory." In sum, these early studies of anole social behavior all readily described these lizards as territorial, despite presenting limited data that was insufficient to demonstrate site fidelity and did not always demonstrate exclusivity.

1.4 The Firm Establishment of Territorial Polygyny

In the decades that followed these early studies, territoriality remained a frequently used description for anole space use behavior and social interactions; the next watershed moments in this research trajectory came when descriptions of *Anolis* mating systems grew to explicitly include a polygynous mating system.

In what remains one of the most detailed studies of *Anolis* territoriality, A. Stanley Rand spent almost a year observing the movement patterns and social interactions of *Anolis lineatopus* in Jamaica. This yielded a paper in which Rand (1967a) fully expressed the tension between adhering to a territorial framework on one hand, and observing variation in site fidelity and exclusivity on the other. Nonetheless, Rand (1967a, b) proposed a tight link between territoriality and polygyny based on the idea that males maintain exclusive mating access to females.

At least part of Rand's (1967a) conception of territoriality was derived from earlier research on anoles. For example, he cited Evans (1938a) in describing the pattern of "a male with a home range shared by one or several females that are his mates" in *A. sagrei*. He also suggested that *A. lineatopus* and *A. sagrei* have similar social behavior based on Oliver's (1948) description of the latter as territorial. But Rand (1967a) demonstrated the complications of fitting messy field data into this territorial framework.

These complications are best captured by Rand's (1967a) descriptions of these lizards' site fidelity. First, he stated that "an *A. lineatopus* seldom travels far and most of the area it visits is visible to it from its usual perch." But following this he describes how, in calculating the area over which an individual lizard is active, he "omitted the occasional visits that certain *A. lineatopus* made to perches well outside of the area where they were usually seen." Thus departures from site fidelity that may have been reproductively important were excluded while attempting to establish site fidelity.

A similar dissonance was also evident when Rand (1967a) first stated that "the activity range of an adult *A. lineatopus* seems relatively permanent and certainly shows no seasonal variation" but then described data that may have suggested otherwise. Documenting the locations of 16 adult males in one of his field sites, he noted that these males were seen multiple times while sampling in September and October but only seven of these—less than half—were still present in the site five months later. Rand (1967a) acknowledged that "of those nine which had not been seen in March, two were dead, but it is possible that the other seven had shifted their areas outside of the study plot." In other words, Rand (1967a) considered that almost half of the adult males in this site may have shown seasonal departures from site fidelity, but nevertheless concluded that these lizards remain in fixed locations permanently.

Rand's (1967a) thoughts on exclusivity were complex, illustrated by his statement that "individual aggression may be expressed as either of two types: dominance hierarchies and territoriality…The behavior of *A. lineatopus* can not be assigned to either of these categories because it has important aspects of each of them." He went on to explain that while "every *A. lineatopus* holds a territory, defending it against neighbors of the same size…each is a member of a straight line dominance hierarchy that consists of all those anoles of different sizes whose home ranges overlap its own home range." Because large as well as small males were observed mating, such a spatial organization appears inconsistent with the idea that males maintain exclusive mating access to the females within their territory.

Despite these dissonances and complexities, Rand (1967a) unequivocally linked territoriality to polygyny, by proposing that male territoriality is adaptive in *Anolis* because it allows males to maintain exclusive mating access to females:

> "I think the general occurrence of aggressive behavior and the spacing out it produces in all sizes of *A. lineatopus* can be explained by…ecological advantages…but the greater aggressiveness of the adult males requires additional explanation. I think the explanation lies in a function of territory discussed at length by Tinbergen (1957), which demonstrates the selective advantage that is conferred on an adult male if he can insure himself exclusive mating rights to certain females by keeping other males away from them. If he can do this for a single female, he insures that he will father at least some offspring, and the more females he can keep isolated, the more offspring he will have and the greater his contribution to the gene pool of the next generation. This being true, there must be a strong selection pressure for any mechanism that will insure a male exclusive mating rights to one or more females. The aggressive behavior of adult male *A. lineatopus* that keeps other males out of the area in which females are permanently living is just such a mechanism."

In a second paper based on these data, Rand (1967b) continued to make the case that *A. lineatopus* exemplifies territorial polygyny, with a more explicit examination of the adaptive significance of territorial behavior in lizards. He concluded that while all individuals defend territories for access to food, males also defend access to mates, thereby reinforcing the link between territoriality and polygyny in *Anolis*. This idea that males maintain exclusive mating access to females was almost certainly a sign of the times. Hinde (1956), in his introduction to an issue of *Ibis* devoted to territoriality in birds, proposed a hypothesis similar to the one espoused by Rand (1967a, b): "Any behaviour of the male which helps to prevent his mate being fertilized by another male is likely to carry a great selective advantage." This notion of the "monopolizability" of females, or of the resources to which females are attracted, became the foundation of how behavioral ecologists understand the evolution of animal mating systems (Orians 1969; Emlen and Oring, 1977). In anoles, it was quite possibly the basis of the expectation of strict territorial polygyny, which rests on the assumption that males maintain exclusive mating access to the females in their territory (Figure 1.1).

Though research on anole mating systems grew rapidly after 1967 (discussed below), the next major step towards firmly establishing the link between territoriality and polygyny came 17 years later. Ruby (1984) examined male breeding success in *A. carolinensis* in the context of space use, motivated by the assessment that "mating systems of reptiles are poorly known…and formative factors remain undetermined." Sampling for over five months for each of two consecutive years, including daily observations for three months each breeding season (though over only a 460 m^2 area), Ruby (1984) discovered ways in which these lizards' behavior did not conform to the expectations of territorial polygyny that were laid out by Rand (1967a, b). For example, he noted that "only 17 of the 68 (25%) males remained 12 weeks or longer during a single breeding season of 20 weeks," potentially indicating variation among males in site fidelity. Moreover, he found that "female [territories] overlapped more than one male in about 25% of the receptive periods [two week intervals in the breeding season]" and in calculating the number of potential mates of males, each "female was assigned to all overlapping males."

These observations and analytic choices indicate that Ruby (1984) uncovered the potential for females to mate with multiple males, and thus documented a mating system in which males do not maintain exclusive mating access to individual females. Ruby (1984) even considered the possibility that sperm storage is an adaptation for female mate choice in these lizards. Nonetheless, at the very outset of the paper, Ruby (1984) proposed that mating systems in lizards range from monogamy to polygyny and described territoriality as "one means of gaining exclusive mating access to females." Later in the paper, he stated that "because the *Anolis* breeding system appears to be resource defense polygyny (Emlen and Oring 1977), territoriality is favored as a means of restricting access to mates." It is possible that Ruby's (1984) data led him to soften his stand from expecting males to maintain "exclusive" mating access to expecting "restrict[ed]" mating access; nonetheless, Ruby (1984) was subsequently frequently cited as supporting the idea that anoles are territorial and polygynous without explicitly acknowledging this potential for female multiple mating (e.g. Qualls and Jaeger 1991; Stamps 1995; Lovern 2000; Jenssen et al. 2000, 2005).

1.5 The Consequences of Limited Sampling

Research on anole behavior blossomed between Rand (1967a, b) and Ruby (1984). However, because by this point the consensus seemed to be that anoles are territorial, this research was not often designed to explicitly test if these lizards behave territorially, i.e. to show that they exhibit site fidelity and exclusivity. . Specifically, territoriality was an almost foregone conclusion in studies with a limited spatial and temporal extent of sampling. In other words, the design of many of these studies was such that they were unlikely to uncover evidence that individual anoles vary in site fidelity or exclusivity, and therefore were unlikely to point to the possibility that females often mate with multiple males

If the sampling period of a study of social behavior is not long enough, then relatively infrequent but reproductively consequential departures from either male-male exclusivity or site fidelity may not be detected often enough that they are considered signal and not noise. For site fidelity, this includes not only occasional forays away from and returns to a fixed territory, but also shifts in territory location that may take place only a few times per breeding season—neither would be detected by studies with short durations. An extreme example of a constrained sampling period can be seen in Philibosian's (1975) study of *Anolis acutus* and *Anolis cristatellus*, in which he stated that "often an observation period of one day was sufficient to record enough positions and enough encounters involving the residents on a tree to make reasonably accurate territory descriptions." As researchers became more certain that anoles are territorial, they became comfortable making more extreme assumptions. For example, in estimating the number of neighbors of individual *A. sagrei*, Calsbeek (2009) estimated the center of a lizard's territory as simply the first location at which that lizard was observed.

Moreover, if a study of social behavior does not sample over a large enough area and a sampled individual disappears from the study site, researchers cannot know if the individual has died or simply moved. Thus, studies with limited sampling areas will be most likely to sample only those individuals who stay in the same place. For example, Trivers (1976), studying the Jamaican *Anolis garmani*, "attempted to map male territories by concentrating on a small portion of the study area." He stated that "males are sighted too infrequently to measure territory size the usual way; that is, to construct a volume fitting such sightings." These infrequent sightings could conceivably be due to the low chance of re-spotting individuals with low site fidelity. But Trivers (1976) continued by saying that “fortunately males 105 mm and larger show a strong tendency to occupy trees…Typically, during a given visit, a large male will be sighted between five and ten times in a large tree.” Thus, Trivers (1976) limited his sampling for estimating territory size to a small area known to be occupied by individuals with high site fidelity.

The combination of spatially and temporally restricted sampling can be seen in work by Jenssen and colleagues (e.g., Jenssen et al. 1995; Jenssen and Nunez 1998), who documented the behavior of a population of *A. carolinensis* along the Augusta Canal in Georgia. This population inhabited a thin strip of vegetation (three to six meters wide), which comprised clumps of trees observable from an elevated walkway, and the activity of lizards in each clump of trees was watched for only eight days, out of a months-long breeding season. Nonetheless, these data were interpreted to conclude that “males are polygynous, defend closely monitored and stable territories, and devoted large blocks of time and energy on territory maintenance” (Jenssen et al. 1995). With time, statements of territorial polygyny thought to be supported by these data became even stronger, such as this statement from Jenssen et al. (2000): “the *A. carolinensis* mating system is driven by the outcome of intermale territorial aggression. Winners achieve and maintain direct mating access to varying numbers of females…because females are relatively sedentary and clustered in small contiguous home ranges.”

1.6 Four Fates of Documented Departures from Territoriality

Evidence for variation in territorial behavior, namely the extent of site fidelity and exclusivity, was implicitly and explicitly excluded through much of the later literature on *Anolis* social behavior. This exclusion took on at least four different forms. The first and second forms correspond to what is known as the “primary simplification” of scientific research, whereby the construction of facts is influenced by scientists' decisions on how to present the data in a paper (Dewsbury 1998).

In the first form, already seen in Rand (1967a), departures from territoriality were removed at the time of analysis. For example, Trivers (1976) quantified male *A. garmani* territory sizes based on the size of trees that individuals occupied, and "a tree was assigned to a male if he was seen three or more times in it without any other adult male being seen therein." However, "if, as happened several times, a large tree was also known to be occupied by a small adult male (85 mm – 104 mm), both males were excluded from the data, since too few data were available to partition the tree between them." Thus, even though male *A. garmani* as small as 87 mm in size were observed copulating with females, their departures from male-male exclusivity were explicitly excluded when considering these lizards' territoriality. Similar choices were also made in considerations of site fidelity. For example, Schoener (1981) argued that in calculating home range areas based on location data, "the inclusion of the outermost observations…may still be undesirable" because "the utilization may resemble a more compact distribution if outliers were disregarded." As a result, the home ranges of four anole species in the Bahamas were calculated without including the "10% of points farthest from the geometric center" (Schoener and Schoener 1982). While this analytic choice is certainly justifiable for calculating the centers of individuals' activity, it compromises the ability to predict mating patterns from space use behavior, unless one is certain that individuals do not mate when at the 10% of points farthest from the geometric center.

A second fate of observed departures from territoriality, as seen in Ruby (1984), involved quantifying them but omitting them from interpretation. For instance, Schoener and Schoener (1980) describe *Anolis sagrei* as exemplifying the "paradigm of a territorial, polygynous species" even though between 3% and 28% of males in six populations remained within their study sites for less than a week, potentially indicating frequent deviations from site fidelity. An implicit justification for ignoring this often substantial proportion of males from a description of the lizards' mating system is that these "floating" males do not mate with females. Though this is a reasonable and testable hypothesis, *assuming* that non-territorial males do not reproduce simply because they are not territorial is unjustified. In another example, Fleishman (1988) categorized adult male *Anolis auratus* as either territorial or non-territorial, based on their display behavior and levels of aggression. Even though non-territorial males were observed copulating with females within the territories of territorial males, Fleishman (1988) stated that "territories of *Anolis* males are primarily for exclusive access to mates."

In a third, distinct fate, research that explicitly documented departures from territoriality stayed unpublished and was therefore relatively uninfluential. Consider two abstracts submitted to the annual meeting of the Society for Integrative and Comparative Biology. Both studies (Alworth 1986; Webster and Greenberg 1988) examined *A. carolinensis* behavior in enclosures. While Webster and Greenberg (1988) found that "the average site fidelity was 52%," Alworth (1986) concluded that "territoriality in these lizards [should] be regarded as a highly flexible behavioral tactic adaptive only in specific contexts" and that "the broad characterization of a genus or species as territorial is misleading." However, to the best of our knowledge, neither of these studies was published.

Finally, in the fourth fate, deviations from territorial polygyny in *Anolis* were documented and acknowledged fully, but the species' social behavior was described as an exception to the rule. For example, *Anolis valencienni* was described by Hicks and Trivers (1983) as displaying "many features atypical of other *Anolis*," including the lack of territorial behavior by either males or females. Consequently, "because many adults of both sexes encounter each other daily, there are unusual opportunities for female choice...over a period of six weeks, a female may copulate with five or more males." This "unusual" opportunity for female multiple mating was hypothesized to be due to *A. valencienni*'s tendency to forage more actively than other anoles. We are not suggesting that *A. valencienni* does not differ in its behavior from other anoles; in fact, its behavior *must* be different enough that even researchers working within the paradigm of territorial polygyny recognized it as exceptional. But because *A. valencienni* was positioned as exceptional, its behavior was never cause to question or re-evaluate the behavior of other anole species.

1.7 Two Exceptions

In seven decades of research on anoles, two studies explicitly described these lizards' social behavior as being consistent with female multiple mating. The first—Gordon (1956)—remained relatively uninfluential, but the second—Tokarz (1998)—began the process of reconciling behavioral observations with subsequent genetic studies that in fact detected evidence for female multiple mating.

In his dissertation, Gordon (1956) aimed "to analyze, biodemographically, two local populations" of *A. carolinensis*. The work comprised primarily of nocturnal censuses in two 20 m × 20 m plots every two weeks for over a year, with all captured individuals marked permanently. Gordon's (1956) data revealed the potential for departures from site fidelity: 73% of 1024 marked lizards were observed just once within the study site, and only 8% of all lizards, and 13% of adults, were observed three or more times. Though some of the disappearances were undoubtedly due to predation and others must have resulted from the failure to detect individuals again, the data are also consistent with many individuals in this population exhibiting low site fidelity. Gordon (1956) later questioned anoles' site fidelity when describing lengthy disappearances of individual lizards from the study site and frequent long distant movements. He also wrote the following:

> "The individual female may copulate with more than one male per season. The social group is maintained by the activity of the dominant male, and sexual bonds between

> the male and his females are loosely formed. Females tend to wander more than males and ample opportunity is present for a female to be attracted to, and take up residence in, another male's territory. In cases of territorial hierarchy, the dominant male and his subordinates may share the same group of females."

Though it certainly had the potential to do so, Gordon's (1956) thesis did not end up provoking a shift in how behavioral ecologists think about anole mating systems. For example, three influential papers on *Anolis* territorial behavior (Schoener and Schoener 1982; Ruby 1984; Jenssen et al. 1995) cite Gordon (1956) but do not refer to his conclusion that female anoles may readily mate with multiple males.

Over four decades later, behavioral observations by Tokarz (1998) demonstrated even more clearly that female *A. sagrei* have the opportunity to mate with multiple males. He explicitly questioned the idea that males maintain exclusive mating access to females in their territories, saying that "few studies have attempted to record the mating pattern of individual females in nature as a means of evaluating the potential for female mate choice and sperm competition." Tokarz's (1998) data revealed that "most females (75%) had more than one mating partner, and this was due almost entirely to females mating with new males that successfully supplanted previous males from their territories." A decade later, curiously, Tokarz (2008) minimized his own previous findings, saying that "male territories in *A. sagrei* appear to be relatively stable at least during the midsummer portion of the breeding season (Evans, 1938[a]), although instances of males being supplanted from their territories by other males have been observed (Tokarz, 1998)."

It is tempting to conclude that Tokarz's (1998) results solve the problem of the mismatch between behavioral and genetic descriptions of anoles' mating system. And to an extent, they do, but his documentation of turnover in male territory occupancy is only one of many different ways in which departures from strict territorial polygyny (Figure 1.1) could facilitate female multiple mating. Other ways, such as multiple reproductive males occupying overlapping areas, had been documented in anoles by previous researchers, but their potential relevance to female multiple mating was downplayed. Yet other ways, such as the existence of reproductive males or females who wander non-territorially, are unlikely to be detected in studies with small sampling areas or durations. This includes Tokarz (1998), who watched 16 individuals occupying a single tree that was 2 m in diameter, for just over a month. That said, even Tokarz (1998) observed "six instances in which males…entered an adjoining male's territory and courted females there."

These different possible routes to multiple female mating have different implications for anoles' reproductive dynamics and sexual selection. Multiple mating resulting from male territorial turnover may lead to serial polygyny, in which at any one time, a territorial male is the exclusive mate of females residing within his territory. Alternatively, the other routes lead to situations in which at any given time, females may be able to mate with several males, allowing for female mate choice. While the serial territorial polygyny that Tokarz (1998) observed may certainly be a male adaptation for achieving high reproductive success, we cannot know from existing behavioral data if it is the only reproductive strategy, or even the dominant reproductive strategy, adopted by male anoles.

1.8 The Age of Genetics

The use of genetic tools uncovered female multiple mating in three species of anoles—*A. carolinensis*, *A. sagrei*, and *A. cristatellus*. Each of these studies (one paper published in a peer reviewed journal, as well as three theses that, at present, are unpublished) discussed the implications of their findings for territoriality to different extents.

Passek (2002) examined the possibility for sperm choice or competition in *A. carolinensis* using a combination of behavioral and genetic approaches. She invoked variation in site fidelity and exclusivity when saying that "while males defend territories that contain multiple female home ranges (Jenssen et al. 1995), the potential exists for extra-pair paternity due to temporary invasion by “floater” males or female home ranges being overlapped by more than one male (Ruby 1984).” Though Passek’s (2002) description suggests only occasional departures from territoriality, her genetic data showed that 48% of offspring were sired by males other than the one identified as the territory owner, including 21% sired by smaller males within the same territory and 15% sired by neighboring males. The paternity of the remaining 12% of offspring could not be determined.

In her conclusion, Passek (2002) expressed skepticism that anyone had accurately measured “the frequency of territorial exchanges resulting from territory takeovers.” She also spoke strongly against laboratory studies that formed the basis of research on *Anolis* social behavior. As she put it, “we cannot remove an animal from its environment and expect to be able to correctly interpret its behavior nor should we make the mistake of failing to question theories constructed solely based on laboratory-derived observations. These mistakes have been made for many years with *A. carolinensis*.”

Johnson (2007) mapped *A. cristatellus* space use behavior over a three week period, and found that females’ “territories overlapped an average of 3.3 males.” Genetic data confirmed this potential for females to mate multiply, showing that “52% of females laid eggs sired by multiple males.” Moreover, variation in site fidelity also played a role in facilitating female multiple mating, because “26% of offspring were sired by males whose territories did not overlap that of the mother.” Johnson (2007) concluded that “these results may be explained by a combination of a male dominance hierarchy…and female mate choice,” mating strategies and interactions that are inconsistent with strict territorial polygyny (Figure 1.1).

In the only published evidence for multiple mating by female anoles, Calsbeek et al. (2007) found that “more than 80% of field-caught *A. sagrei* females that produced two or more progeny had mated with multiple males [making] *A. sagrei* one of the most promiscuous amniote vertebrates studied to date.” However, this paper did not tackle the implications of its results for territoriality.

Finally, the most direct evidence for departures from territoriality influencing anole mating systems again combined behavioral observations with genetic data (Harrison 2014). Studying *A. carolinensis*, Harrison (2014) assumed site fidelity in her behavioral sampling by mapping the home ranges of lizards after observing individual's spatial locations for 30-minute focal observations (it is not clear how many focal observations were conducted for each individual; Harrison (2014) does mention that "behavioral observations were conducted at irregular intervals, making it difficult to determine whether males shifted their territories during the study period"). However, her genetic data revealed that spatial proximity, as determined by the focal observations, did not predict mating between pairs of males and females. In fact, the mean distance between mating pairs was 33± 22 m, over five times the mean estimated territory diameter in that population. This indicates that individual lizards *must have* moved between when they mated and when they were observed. In the face of this evidence, Harrison (2014) continued to invoke a territorial paradigm to understand anole social behavior, at least initially: "males and females from opposite sides of the study site mated relatively frequently…often traversing distances over 60 m. For this to occur, either the male or female (or both) left its territory at some point, or they mated before establishing territories and used stored sperm." Later, however, she proposed a number of hypotheses for male movement behavior, including the existence of an alternative non-territorial, wandering male strategy adopted by adult males, and temporal variation in individual site fidelity within a single breeding season, that definitely break out of the mold of territoriality.

1.9 Broader Implications for Animal Mating Systems

This century-long trajectory of research on *Anolis* mating systems exemplifies several larger issues that could plague the study of animal mating systems more generally. However, it is challenging to establish that the problems we identify here are generally applicable, because discerning their applicability to a particular taxon demands a close familiarity with the full body of literature on that taxon's biology, as well as familiarity with the organism's biology itself. In this final section, we identify the main driving forces that led to the incomplete and possibly incorrect descriptions of *Anolis* social behavior, culminating in the erroneous prediction that each female's offspring will be sired by the single male in whose territory she resides. We hope this discussion will prompt researchers who are intimately familiar with other organisms' biology to consider the basis of what we "know" to be true about those organisms' social behavior.

The history of research on *Anolis* mating systems demonstrates multiple ways in which the erratic and contingent progress of research may have prevented researchers from fully describing the behaviors that facilitate female multiple mating in these lizards. The central problem was described well by Stamps (1994), although she was discussing specific aspects of territoriality not covered in this review:

> "Current ideas about the behavior of territorial animals are based on a series of assumptions…in some cases these assumptions have not been adequately tested. By virtue of repetition, untested assumptions have a tendency to solidify into "quasi-facts.""

Such repetition certainly characterized the earliest studies of *Anolis* social behavior, where studies repeatedly concluded that anoles are territorial based on often flimsy evidence. It is not clear whether the authors of these earliest studies considered the implications of these lizards' space use and movement patterns for their mating system. It is possible that territoriality was so readily assumed and concluded in these early studies *precisely because*, under the strictest interpretation, territoriality is incompatible with female multiple mating. Charles Darwin, in his seminal text on sexual selection, expressed the prevailing view at the time that females are generally "coy," "passive," and "less eager" to mate than are males (Darwin 1871). This view was eventually translated into the assumption that variance in female reproductive success is lower than variance in male reproductive success (discussed in Hrdy 1986; Dewsbury 2005; Tang-Martinez and Ryder 2005; Tang-Martinez

2016). Moreover, many biologists at the time believed that females of most species were unlikely to possess the cognitive ability to make choices about which males to mate with, and ignored evidence to the contrary (reviewed in Milam 2010). Invoking a mating system such as territorial polygyny, which under the strictest interpretation leaves females unable to choose between males and implies high variance in male reproductive success, thus may have been a sign of the times.

However, Greenberg and Noble (1944) conducted experiments explicitly to test whether females chose mates on the basis of males' dewlaps, asking if females preferred to mate with males with intact or manipulated dewlaps. They found no effect of dewlap manipulation on mating success, but by asking the question, these authors revealed that they considered female mate choice possible in anoles, and thus considered that females have the opportunity to mate with multiple males. In contrast, later researchers studying anole territorial behavior frequently maintained that female mate choice was unlikely because it is precluded by territoriality. For example, Schoener and Schoener (1980) suggested that "adult females seem quite sedentary in [*A. sagrei*], and the opportunity for female choice would seem correspondingly limited," and Stamps (1983), in a review of lizard territoriality and polygyny, said the following:

> "In most insectivores, female choice of mating partner is probably fairly limited. Since females do not leave their home ranges in order to mate, prospective male partners must have home ranges overlapping that of the female. A female with a home range on the border between 2 male home ranges might be able to choose between them, but this option is restricted in territorial species by the males' tendencies to arrange their territories to completely enclose female home ranges."

Thus, though researchers all the way from Noble and Bradley (1933) to Stamps (1983) and beyond described anoles as territorial, the predictions for mating patterns derived from that behavioral description, such as whether females have the opportunity to choose mates, could be inconsistent with one another.

That the term "territoriality" as interpreted by different researchers could be compatible with fundamentally different expectations for patterns of mating and sexual selection highlights the fact that very few studies define territoriality explicitly (Maher and Lott 1995). Different authors' conceptions of territoriality include different degrees of variation in both site fidelity and exclusivity, and therefore lead to different expectations for female multiple mating. This fuzziness in the definition of territoriality also raises the following question—at what point might we conclude that territoriality is too imprecise a term to be useful as a predictor of a species' mating patterns? Departures from male-male exclusivity have been observed in anoles (e.g. Rand 1967a; Trivers 1976; Fleishman 1988), but these examples were still considered to be within the fold of territoriality because "exclusivity" was qualified or limited to mean that males only exclude size-matched individuals. These qualifications were made even though males in smaller size categories were observed to mate with females. Similarly, a lack of clarity about the meaning of site fidelity permeates research on territorial behavior—does "site fidelity" mean staying in the same place, leaving but always returning to the same place, or attempting (but possibly failing) to stay in or return to the same place? How long does an individual have to stay in a certain place to be considered site faithful? Almost all possible answers to these questions have, at some point in the last century, been implicitly or explicitly accepted as consistent with territorial behavior, even though each answer can lead to very different expectations for mating patterns.

Once territoriality became established as a description of anoles' mating system, the design and interpretation of subsequent studies of these lizards' social behavior made it difficult to detect variation among individuals in site fidelity or exclusivity, variation that could easily be reproductively consequential. Which individuals were studied, the extent of sampling area and duration, the data that were analyzed versus excluded, and the extent to which inconsistent findings were deemphasized—each of these scientific decisions involved choices that would determine whether the study could actually test the precepts of territoriality or whether it simply assumed them. For the most part, the choices made were such that territoriality remained untested. . However, these studies were written and interpreted as if the idea that anoles are territorial had been tested, and each thus seemed to provide independent confirmation of this description of their spatial and social organization. In fact, even though these studies were conducted by different researchers on different populations and species of anoles, they were conceptually non-independent, unintentionally leading the earliest studies to "assume a stature that their original authors never intended" (Stamps 1994).

It is this problem—adhering to a conceptual paradigm while designing studies that are consequently unlikely to uncover or take seriously the evidence that would allow you to escape that paradigm—that we believe is the most important problem revealed by our review. This problem cannot be solved simply by collecting more data; reaching a solution additionally requires that we explicitly identify and question the assumptions made when designing research (Gowaty 2003). But framing the challenge thus also makes the solution clear—we should continue collecting observations of animals' behavior in a manner that is as free as possible from existing conceptual frameworks, even in taxa whose biology we think we know well. In other words, the solution calls for renewed and continued attention to organisms' natural history (Greene 2005; Tewkesbury et al. 2014). As Greene (2005), who defined natural history as "descriptive ecology and ethology," put it, "discoveries of new organisms and new facts about organisms often reset the research cycles of hypothesis testing and theory refinement that underlie good progressive science."

The call for a close relationship between natural history observations and the advance of research in animal mating systems is far from new. We conclude with a remarkably apt excerpt from a 1958 letter to the editor of *Ibis* from John T. Emlen, following an issue about territoriality in birds (Hinde 1956):

> “There is a growing tendency among ornithologists to blindly and devotedly follow what is becoming a fixed or conventional concept of territory. Instead of describing their observations directly, authors often seem to go out of their way to fit them into the “accepted” pattern through the “approved” terms and phrases.”

Emlen (1958) continued:

> “My concern in this letter is with the tyranny of words and with the dangers inherent in patterned thinking. The fascination of catch phrases and the reverence with which they come to be held are major, though subtle, obstructions to free and accurate thinking. Conventionalized phrasing, furthermore, often leads to conventionalized thinking, the very antithesis of free investigation and the arch-enemy of scientific progress. A neat, substantive definition of territory has the fascination of finality, but in a virile science dead ends must be avoided, not sought; it has the fascination of authority, but basically we recognize that the study of natural phenomena must not be subordinated to the study of intellectual creations.”

The accurate quantification by genetic means of individuals’ reproductive success in natural populations is valuable not just because such data help to render more complete descriptions of animals’ social and reproductive behaviors. These data also let us identify taxa in which the erratic and contingent progression of scientific research may have led behavioral ecologists towards erroneous conclusions about animals’ mating systems. But the genetic data alone do not shed light on the question of how we come to believe such conclusions. We contend that taxon-specific historical investigations into this question allow us to escape the confines of “conventionalized phrasing” and “conventionalized thinking,” and are an important step towards designing studies that will let us understand animal social behavior in its full complexity.

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Chapter 2

Matching movement patterns to mating patterns in the lizard *Anolis sagrei.*

Ambika Kamath and Jonathan Losos

2.1 Summary

Space-use behavior and movement patterns in animals are closely linked to mating systems and the opportunity for sexual selection. Though individuals' locations in both space and time are important for understanding potential social and reproductive interactions, in practice much of the research on animal mating systems has inferred these interactions from purely spatial characterizations of individuals' home ranges. In this study, we use an explicitly spatiotemporal approach to estimate the number of potential mates of male and female *Anolis sagrei* lizards from their movement behavior. We find that females frequently encounter, and thus have the potential to mate with, multiple males. Our results bridge a disconnect between previous behavioral research that suggested that females mate with just a single male in whose territory they reside and genetic evidence demonstrating female multiple mating. Males' body size and spatial extent are both related to the number of females they encounter. However, males rarely maintain exclusive access to females, suggesting the potential for complex polygynandrous reproductive dynamics in these lizards, including the possibility of both pre- and post-copulatory mate choice. We hypothesize that networks of dominance hierarchies may be a fruitful approach in future studies for explaining social interactions and mating systems in *Anolis* lizards, paving the way for understanding the role of sexual selection in shaping phenotypic diversification in this clade.

2.2 Introduction

In the heyday of theoretical and conceptual research on the evolution of animal mating systems (Hinde 1956; Tinbergen 1957; Orians 1969; Emlen and Oring 1977), knowing the locations of males and females in both space and time was recognized to be crucial to predicting mating patterns. The broadest framework for understanding the evolution of animals' social behavior links the distribution of resources across space and time to individuals' ability to monopolize access to potential mates (Emlen and Oring 1977; Shuster and Wade 2003). Thus, documenting the spatiotemporal movement patterns of males and females is key to understanding how animal behavior shapes and is shaped by sexual selection.

In practice, however, animal mating systems are often inferred from individuals' spatial locations alone, emphasizing the quantification of the boundaries and size of the areas—called the "home range"—within which individuals' movements are contained (reviewed in Borger et al. 2008). Using repeated observations of individuals' spatial locations to estimate their home ranges has been an enduring approach to understanding space use behavior (e.g. Hamilton 1937; Jennrich and Turner 1969; Schoener 1981; Getz et al. 2007; Fieberg and Borger 2012; Fleming et al. 2015). Estimating individuals' home ranges immediately suggests a way to predict their mating patterns—individuals mate with those members of the opposite sex whose home ranges overlap theirs (Jarman 1974; Stamps 1977; Maher and Lott 2000). But such a prediction elides the fact that, to interact with one another, individuals must not only occupy the same place, they must do so at the same time (Moorhouse and MacDonald 2005; Aureli et al. 2008; Cantor et al. 2012).

The increasing integration of temporal patterns of movement with space use has allowed for a deeper understanding of a wide range of animal behaviors, from fine-scale resource selection to long-distance migration (reviewed in Borger et al. 2008; Nathan et al. 2008; Benhamou 2014;

Fleming et al. 2016). However, the intersection of this spatiotemporal framework with descriptions of mating systems remains relatively unexplored. Explicitly incorporating a temporal component into estimations of space use also offers an immediate way to predict mating patterns—individuals can potentially mate with the members of the opposite sex with whom they co-occur in space and time (Kokko and Mappes 2012).

In this paper, we estimate co-occurrences in space and time between and among males and females in a population of *Anolis sagrei* lizards as a means of understanding what social interactions and mating patterns are possible in that population. Lizards in the genus *Anolis* have long been described as territorial, and this behavioral description has been coupled with an often implicit expectation that they mate strictly polygynously, i.e., males mate with multiple females, but females mate with just the one mate in whose territory they reside (reviewed in Chapter 1). For example, based primarily on home range estimations, Schoener and Schoener (1982) described *A. sagrei* as matching "the paradigm of a territorial polygynous species" nearly perfectly. However, all the genetic evidence collected so far suggests that females frequently mate with multiple males (Passek 2002; Calsbeek et al. 2007; Johnson 2007), with Calsbeek et al. (2007) describing *A. sagrei* as "one of the most promiscuous amniote vertebrates studied."

We ask if the apparent inconsistency between behavioral and genetic descriptions of anoles' mating systems can be resolved by using spatiotemporal location data to estimate co-occurrences between individuals, instead of predicting social interactions from purely spatial descriptions of home ranges, as has been done previously. To this end, we quantify the movement patterns of a population of *A. sagrei* in Gainesville, FL, asking if these lizards' space use behavior is consistent with the potential for females to mate with multiple males.

2.3 Methods

2.3.1. Field Sampling

Anolis sagrei lizards were marked and monitored in the University Gardens on the University of Florida campus in Gainesville, FL from March 4, 2015 to May 25, 2015 between 0900 and 1800 hours. The start date of sampling coincided approximately with the emergence of these lizards after the winter and the beginning of the breeding season; the end of the sampling period coincided approximately with the time at which female *A. sagrei* began laying eggs.

We caught almost every lizard within a 7140 m^2 area (only 4% of observations were of unmarked individuals), and marked each captured individual with a unique bead tag (Fisher and Muth 1998), which allowed us to subsequently observe and identify individuals from a distance without disturbing them. When captured, we also measured each individual's snout-vent length (SVL). At each subsequent observation of a lizard, we noted its identity as well as the time and location of the observation. Observations of the same individual were separated by at least one hour. Approximately once a month, we recaptured and re-measured males to estimate the average growth rate of males in this population.

To create a map of the locations at which lizards were observed, we measured distances between locations to triangulate their position. Locations more than 1m apart were considered distinct. We also mapped the location of all remaining trees within the site, so as to include all trees to which a lizard could have moved in our estimations of their movement patterns. A total of 318 locations were mapped.

2.3.2 Statistical analysis

All analyses were carried out in R v. 3.3.2 (R Core Team 2016). We used a discrete time Markov chain to model movements between the 318 mapped locations in the site. We divided the day time hours (0800 to 2000 hours) for the duration of the sampling period (83 days) into 996 hour-long blocks, and observations were binned accordingly. Transition probabilities between locations were fitted as exponentially declining with distance ($P(d) \alpha e^{\lambda d}$). In other words, lizards were modelled as less likely to move to distant locations than to close locations. Separate models were fit for males and females, and λ for each model was estimated using maximum likelihood (*bbmle* package; Bolker and R Development Core Team 2016). Paths of lizards were interpolated between known observations at known times using the best fit Markov chain model. To calculate the co-occurrence between pairs of lizards, we multiplied the probabilities for each individual in the pair, and used empirically derived probability cutoffs to designate co-occurrences as a binary variable ("yes/no"), based on pairs of lizards observed in the same location within an hour of one another. See Appendix 2.1 for further details. To quantify potential mating opportunities for each individual, we calculated the number of females encountered by each male and the mean number of co-occurrences per female for each male, as well as similar statistics for females.

To assess whether the observed movement patterns of male and female lizards led to more or fewer co-occurrences than expected with members of the same and opposite sex, we randomly shifted the day and time on which the first observation of individuals was made, and the time of the remaining observations for each individual were shifted accordingly, to maintain the same temporal sequence of observations.. We time-shifted either males or females, and co-occurrences were compared separately for male-male pairs, female-female pairs, and male-female pairs. Shifts were constrained to keep all data within the total sampling period. Locations at which lizards were observed were not altered in this time-shifted data set. Co-occurrences were calculated as above, and the number of pairs co-occurring in the time-shifted datasets was compared to the number of co-occurring pairs in the observed dataset. The time-shift was repeated 100 times. A greater number of co-occurring pairs in the time-shifted datasets compared to the observed dataset would indicate that individuals in this population move to avoid one another, whereas a smaller number would indicate that individuals move to seek out one another. While this randomization will not change the number of co-occurrences of hypothetical individuals spotted at the same location for the entire duration of the sampling period, pairs of such individuals co-occur either completely or not at all, and are clearly not moving to engage in or avoid encounters with other individuals, because they are not moving at all.

We quantified the spatial extent of individuals' movement in two ways. First, we calculated the mean of the distances from each observation to the centroid of all observations of the individual (mean distance from centroid). Lower mean distances to the centroid indicate smaller spatial extent. Next, for each individual observed three or more times, we calculated the area of the minimum convex polygon (MCP) around the locations at which it was observed (for repeated observation at the same location, we jittered points randomly within 0.5 m along both the X and Y axis). We compared spatial extent between males and females using Mann-Whitney U tests, and examined if variation in spatial extent was related to body size in either males or females, using Spearman rank correlation tests of SVL at first capture vs. mean distance to centroid and MCP area.

To understand if individuals in our sampled population were fundamentally different in space use behavior from previously studied populations of anoles, we asked if a purely spatial predictor— the overlap in MCPs between pairs of individuals—indicated that females encounter just one male. We also subsampled from our dataset to match either the median area (400 m^2) or the median duration of sampling (4 weeks) of previous studies, to ask if limited sampling in space or time influences the predicted male-female encounters, even when using a purely spatial description of space use behavior (limited sampling reviewed in Chapter 1; see Appendix 2 for studies and sample areas and durations included in the calculation of the medians). Finally, we assessed if the area of MCP overlap between a pair of individuals was associated with the number of times that pair encountered one another.

To examine if potential mate number varied with the spatial extent of individuals' movement, we asked if either mean distance to the centroid or MCP area is correlated with the number of females encountered or the number of co-occurrences per female for males using Spearman rank correlations. Similar correlations were performed for females.

We then asked if variation in body size among males was related to the number of potential mates they encounter. Using measurements of male SVL at initial capture as well as at subsequent recaptures, we estimated a logistic growth curve for males in the sampled population (see Appendix 3 for details). We used this model to estimate the SVL of each male on the day of each of his encounters, based on his SVL at the nearest capture. We then calculated the mean size of each male at his encounters with females, and assessed if mean estimated SVL was correlated with either the number of females he encountered or his mean number of co-occurrences per female, using Spearman rank correlation tests. We also used a Wilcoxon rank-sum test to compare initial SVL between males who did and did not encounter any females.

To assess the potential for males to maintain exclusive mating access to females, we first calculated the mean number of males encountered by the females encountered by each male. We defined the inverse of this number, which will range from a lower bound of 0 to a maximum of 1, as the "exclusivity index." For males that maintain perfectly exclusive access to females, the exclusivity index is expected to be 1, because each female encounters only that male; lower values of the exclusivity index for a particular male indicate that the females he encounters in turn encounter other males, and therefore that the focal male is less likely to maintain exclusive access to the females he encounters. We examined if the exclusivity index varies among males in relation to male spatial extent or mean SVL at encounters using Spearman rank correlations.

We examined the difference in estimated SVL between co-occurring males, and compared this to the difference in estimated SVL between randomly chosen pairs of males on the same days as the observed encounters (five random pairs per pair of males observed to co-occur; random pairs where either individual had an estimated SVL less than the minimum observed SVL were omitted).

2.4 Results

A total of 253 individuals (161 males, 92 females) were caught and marked during the sampling period. These individuals were observed a total of 5629 times, with the number of observations per individual ranging from one to 128 (the median number of observations per individual for males and females was 11 and 15 respectively). One hundred and twenty males and 75 females were observed three or more times.

Females encountered 5.1 ± 3.7 males (mean ± S.D.) and males encountered 2.9 ± 2.9 females (Figure 2.1). Restricting observations to only those individuals who encountered at least one individual of the opposite sex, we estimated that females encountered 5.4 ± 3.6 males and males encountered 3.7 ± 2.9 females. Males encountered an average of 4.5 ± 3.6 other males, whereas females encountered an average of 2.3 ± 1.3 other females.

Shifting the initial date and time of observation by a random amount for each sampled individual, we found 11% more male-male co-occurrences in the observed dataset than in the time-shifted dataset, consistent with males seeking one another out (number of pairs encountering one another estimated in observed vs. time-shifted datasets: 297 vs. 267 ± 12; $P = 0.005$). However, the number of pairs of females encountering one another estimated from the observed dataset did not differ from that estimated from the time-shifted datasets (84 vs. 84 ± 4; $P = 0.94$). For male-female encounters, shifting the start date and time for either only males or only females, we found that male movement patterns were consistent with them moving to seek females out (6% increase in observed vs. time-shifted datasets; 472 vs. 445 ± 11; $P = 0.01$) but females did not move to avoid or seek out males (3% increase in observed vs. time-shifted datasets; 472 vs. 459 ± 10; $P = 0.19$).

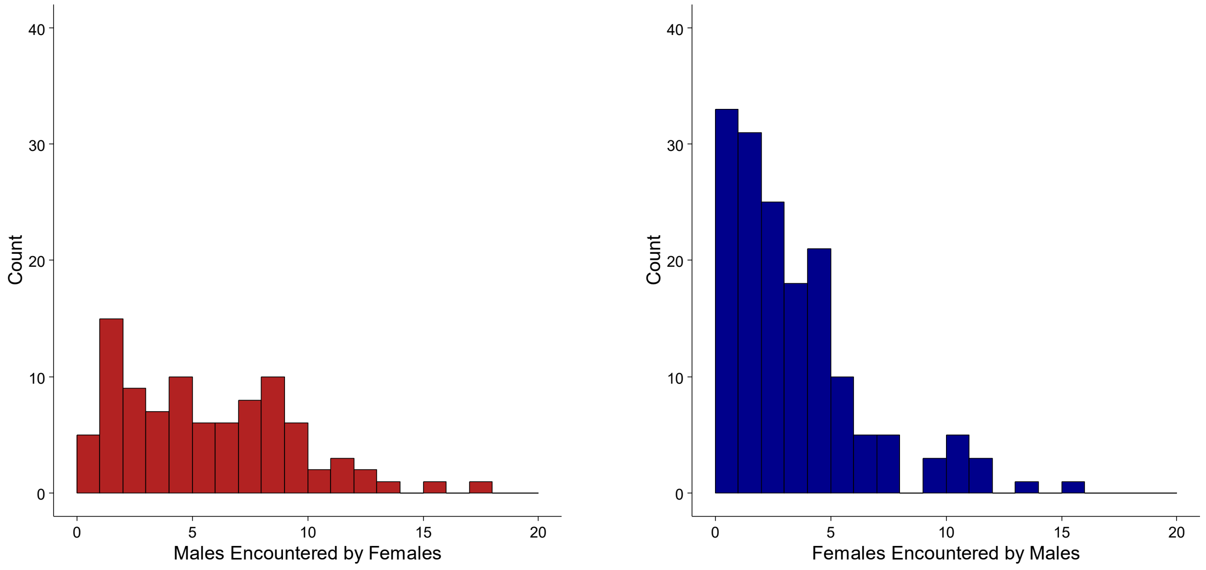

Figure 2.1 Histograms of the number of males encountered by females (left) and females encountered by males (right).

The mean distance from the centroid ranged from 0 m (i.e. the individual was observed at a single location only) to 41 m for males and 21 m for females. Minimum convex polygon area ranged from 0.18 m^2 to 875 m^2 for females, and from 0.26 m^2 to 1740 m^2 for males. Spatial extent was greater in males than females (mean distance to centroid for males vs. females: 5.8 ± 7.0 m vs. 2.2 ± 3.0 m; $W = 4612$, $P < 0.01$; MCP area for males vs. females: 226 ± 337 m^2 vs. 36 ± 109 m^2; $W = 2164$, $P < 0.01$). Neither measure of spatial extent was associated with SVL at initial capture for either males (mean distance to centroid: rho = 0.004, *P* = 0.95; MCP area: rho = 0.13, *P* = 0.17) or females (mean distance to centroid: rho = -0.16, *P* = 0.13; MCP area: rho = -0.02, *P* = 0.89).

On average, female MCPs overlap with those of 11.0 ± 8.1 males, whereas male MCPs overlap with those of 6.5 ± 4.7 females. In subsamples of a randomly selected area of 400 m^2 (repeated 479 times), we calculated that females overlapped a mean of 1.4 ± 0.6 males and males overlapped a mean of 1.1 ±0.4 females. In subsamples of a duration of 4 weeks (for each of a possible 55 start dates), we calculated that females overlapped a mean of 2.0 ± 1.7 males and males overlapped a mean of 1.5 ± 1.0 females.

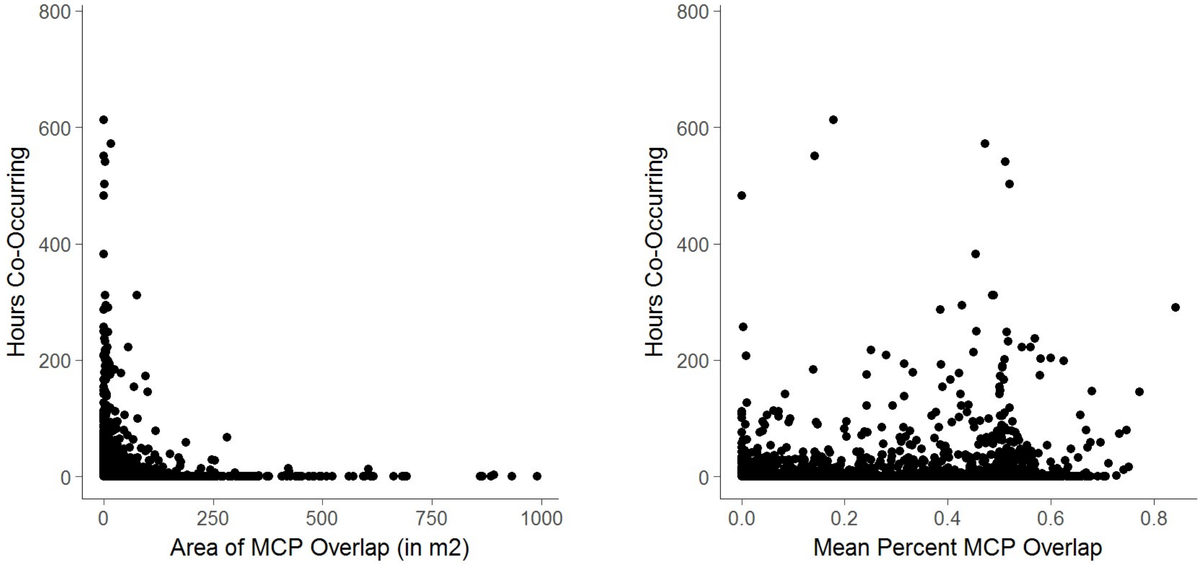

Figure 2.2 Purely spatial predictors of pairwise interactions (area of MCP overlap and mean percent area overlap of MCPs) were not closely associated with our spatiotemporal predictor of pairwise interactions (the number of hours they were estimated to co-occur), though they were correlated.

Purely spatial predictors of pairwise interactions (area of MCP overlap and mean percent area overlap of MCPs) were not closely associated with our spatiotemporal predictor of pairwise interactions (the number of hours a pair was estimated to co-occur; Figure 2.2), though they were correlated (number of hours of co-occurrence vs. area of MCP overlap: N= 18915, rho = 0.50, *P* <

0.001; removing all pairs not estimated to co-occur spatiotemporally: N= 727, rho = -0.06, *P* = 0.08; number of hours of co-occurrence vs. mean percent area overlap of MCPs: N= 18915, rho = 0.51, *P* < 0.001; removing all pairs not estimated to co-occur spatiotemporally: N= 727, rho = 0.21, *P* < 0.001).

Males with a greater spatial extent encountered more females (mean distance to centroid: rho = 0.49, *P* <0.001, Figure 2.3; MCP area: rho = 0.60, *P* <0.001), but spatial extent was not associated with the number of encounters per female (mean distance to centroid: rho = 0.14, *P* = 0.07; MCP area: rho = 0.12, *P* = 0.21). In females, the number of males encountered was unrelated to the mean distance to the centroid (rho = 0.16, *P* = 0.13) but increased with increasing MCP area (rho = 0.25, *P* = 0.03); spatial extent was unrelated to the number of encounters per male (mean distance to the centroid: rho = -0.01, *P* = 0.92; MCP area: rho = -0.04, *P* = 0.72).

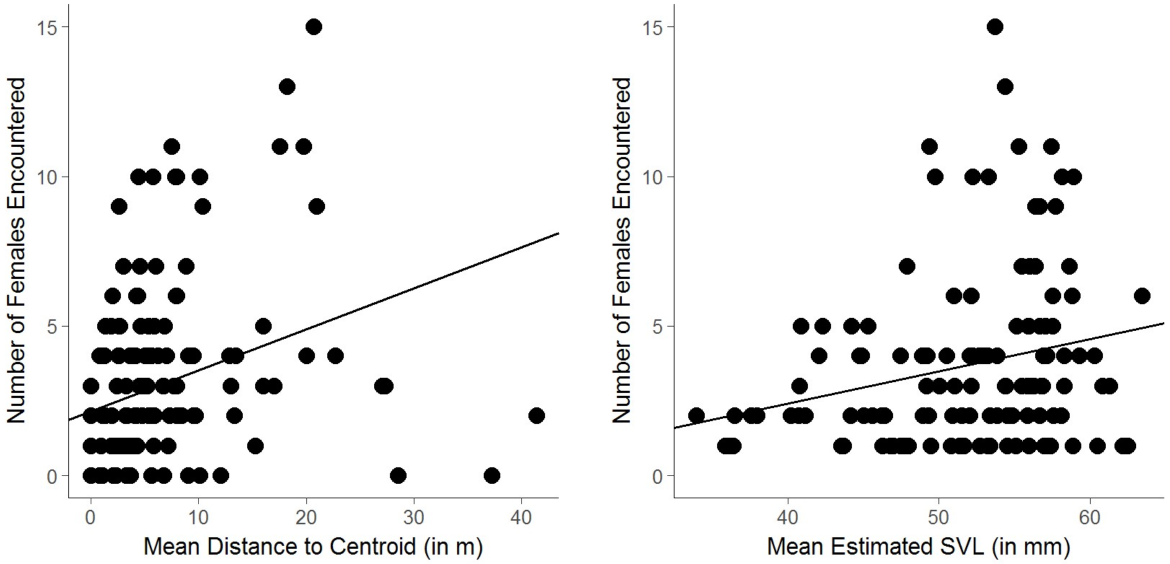

Figure 2.3 The number of females encountered by males increased with both increasing spatial extent (mean distance to centroid; left) and increasing mean snout vent length estimated at encounters with females (right).

For males that encountered at least one female, the exclusivity index decreased with spatial extent (rho =-0.18, $P = 0.045$), indicating that males with greater spatial extent had lower potential to maintain exclusive access to the females they encountered. However, the exclusivity index was unrelated to mean SVL at encounters (rho = 0.03, $P = 0.77$; Figure 2.4).

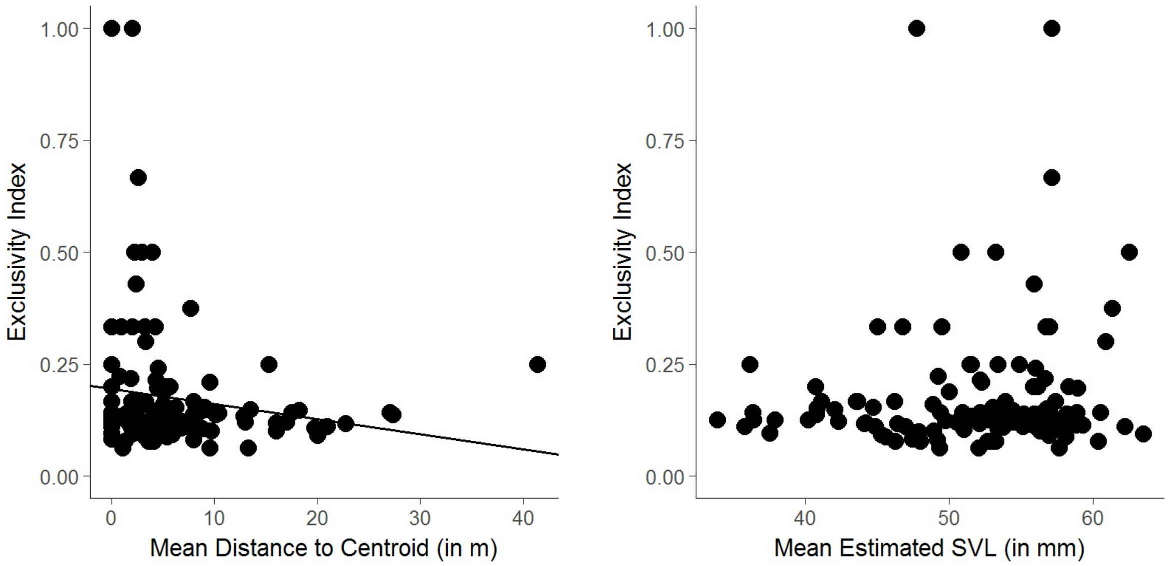

Figure 2.4 Whether a male has the potential to maintain exclusive access to the females he encounters is weakly related to his spatial extent, and unrelated to his mean estimated body size at encounters with females.

Males who were larger in size at their encounters with females encountered more females (rho = 0.24, $P = 0.006$), but the number of encounters per female was unrelated to mean SVL at encounters (rho = 0.09, $P = 0.32$). Initial SVL did not differ between males that did and did not encounter any females (mean ± SD for males that encountered and did not encounter females, respectively: 48.5 ± 7.0; 48.5 ± 7.8; $W_{33, 128} = 1880$, $P = 0.33$).

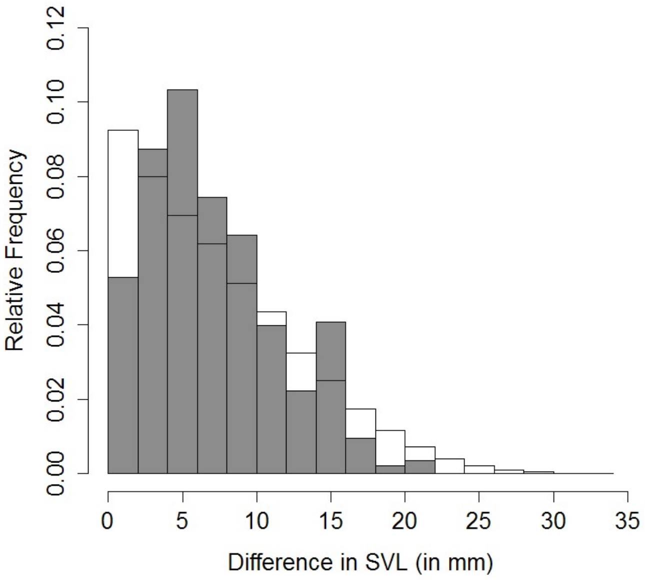

Figure 2.5 Estimated SVL differences between male pairs estimated to co-occur (grey bars), compared with pairwise SVL differences between randomly chosen pairs of males, with sizes estimated on the same days at the observed co-occurrences (white bars).

The mean difference in estimated body size between pairs of males observed to co-occur (7.1 ± 4.5 mm) was comparable to the mean difference between randomly chosen pairs of males whose size was estimated on the same days as the observed co-occurrences (7.4 ± 5.7 mm), though the observed size differences were underrepresented in the smallest (0-2 mm) and largest (>16 mm) categories compared to the random pairwise size differences (Figure 2.5). The number of co-occurrences between a pair of males was positively correlated with the mean estimated size difference at encounters between them (rho = 0.20, $P < 0.001$), and the pattern appeared to be driven by a high proportion of male-male pairs with small size differences between them who co-occurred only a few times.

2.5 Discussion

The movement patterns of individual *A. sagrei* in the sampled population were consistent with females encountering and potentially mating with multiple males over the course of the breeding season, which is inconsistent with many previous characterizations of anole mating systems (e.g. Schoener and Schoener 1982; Jenssen et al. 1995; but see Tokarz 1998). However, we found that males had a greater spatial extent than did females, which is consistent with previous estimates of sex differences in territory size (e.g. Schoener and Schoener 1982; Jenssen and Nunez 1998), and also with evidence for male-biased dispersal in anoles (Johansson et al. 2008; Calsbeek 2009). But the spatial extent for both sexes in this population is orders of magnitude higher than previous estimates of territory size in this and ecologically similar species (e.g. Schoener and Schoener [1982] found 13 m^2 and 3 m^2 territory areas for male and female *A. sagrei* and Rand [1967] reported a maximum territory area of 14 m^2 for *Anolis lineatopus*, but see Chapter 1 for methodological complications; Calsbeek and Marnocha [2006] reported territories of approximately 10 m^2 for *A. sagrei*). While this difference is potentially attributable to differences across populations and species in movement behavior, it is also at least partially due to limited sampling in previous studies.

The consequences of limited sampling also illuminate the question of why female multiple mating has rarely been considered important in past research on anole territoriality. As discussed in Chapter 1, studies with limited spatial or temporal sampling extents will be constrained in what behaviors they can detect. By subsampling from our dataset, we showed that limiting the spatial or temporal sampling extent drastically reduces the number of male-female pairs whose home ranges are estimated to overlap with one another, compared to the same metric calculated for the whole dataset. This suggests that previous studies have underestimated the complexity of *Anolis* lizards' movement patterns and social interactions.

Though having a large spatial extent is not necessarily inconsistent with territoriality, males in the sampled population did not maintain exclusive access to the females they encountered, and the females that encountered males with larger spatial extents in turn encountered more males. Together, these results suggest that individuals in this population of *A. sagrei* neither remain within a compact confined area nor interact such that males maintain exclusive access to females, raising the question of whether territoriality is in fact a useful way of understanding these lizards' mating system. In the remainder of this discussion, we explore what we can deduce about anole mating systems from our explicitly spatiotemporal approach to understanding their movement patterns, without relying on the framework of territoriality.

The pattern of females encountering multiple males in this population could be attributed to males, but not females, moving to seek out members of the opposite sex more frequently than expected at random. This is consistent with the classic theory and data, wherein males are expected to adopt a movement and mating strategy in response to the spatiotemporal distribution of receptive females, whereas females' spatiotemporal distribution is influenced by resource availability (Emlen and Oring 1977; Davies and Lundberg 1984; Shuster and Wade 2003). Empirical evidence from anoles supports this theory. For example, female densities of *Anolis humilis* increased disproportionately compared to male densities in response to the addition of food (Guyer 1988), and the simultaneous emergence of male and female *Anolis carolinensis* at the start of the breeding season may allow for males to settle in response to females' locations (Jenssen et al. 2001). Such data have usually been interpreted to mean that females choose territories on the basis of resource availability, whereas males choose territories on the basis of female locations (Rand 1967; Stamps 1977; Schoener and Schoener 1980). However, the movement patterns we observed suggest that sex differences in decision rules regarding movement behavior can be inferred even in the absence of a territorial framework.

There is no consensus on whether multiple mating by females is adaptive or not, with evidence from different taxa suggesting different effects of female multiple mating on fitness (Arnqvist and Nilsson 2000; Fox and Rauter 2003; Sarhan and Kokko 2007; Uller and Olsson 2008; Crean and Marshall 2009; Kvarnemo and Simmons 2013; Noble et al 2013a). If female *A. sagrei* benefit from mating with multiple males, we would expect them to move to seek out encounters with males, whereas if female multiple mating were costly, they may avoid moving to encounter males. Our evidence supports neither of these possibilities. Instead, movement patterns in the sampled population of *A. sagrei* are consistent with the model that female multiple mating is simply a consequence of females mating with every male they encounter, which is adaptive in situations where potential mates are encountered unpredictably (Kokko and Mappes 2012; Keogh et al. 2013). Because female anoles can store sperm (Fox 1963), post-copulatory female choice could counter some of the potential negative fitness consequences of mating indiscriminately (Orr and Brennan 2015).

We also saw evidence that males moved to encounter one another more often than at random. This was counter to expectations, because in a species long thought to be territorial, one may expect males to avoid each other. However, a simple explanation for this behavior is that it is easier for males to detect other males than it is for them to detect females, and that males therefore use the presence of other males as an indirect cue for female location (see also Stamps [1991, 1994] for evidence of conspecific cuing in juvenile anoles). Male displays include the extension of a colorful dewlap as well as conspicuous pushup and head-bob motions, and are likely visible from relatively far away. This may be especially pertinent in relatively open habitats with low lizard densities, like the habitat sampled here (as well as the habitats sampled in many studies of *Anolis* space use behavior e.g. Evans 1938; Rand 1967; Trivers 1976; Tokarz 1998). If males are adopting such a strategy to locate females, then describing social interactions subsequent to co-occurrence will be all the more important to understanding mating patterns, emphasizing that documenting spatiotemporal dynamics is definitely necessary but not sufficient for understanding reproductive dynamics.

The estimated difference in size between males that co-occur begins to shed some light on the possible social interactions following male-male co-occurrence, revealing insights more consistent with the traditional expectations of territoriality. Body size is thought to play an important role in determining the outcome of agonistic interactions in anoles (Evans 1936a, b, c; Tokarz 1985; Jenssen et al. 2005; but see Bush et al. 2016), and the maintenance of exclusive territories by males is often qualified to refer *only* to the exclusion of similarly sized individuals from a particular area (e.g. Rand 1967; Trivers 1976). Though the mean size difference between males estimated to encounter one another in the sampled population did not differ from random pairs of males, the distribution of the differences showed that pairs of males that were very similar in size (0 – 2 mm) were underrepresented in the observed dataset relative to the random dataset, suggesting that males may avoid encountering size-matched males, or that the length of the co-occurrence between size-matched males is shorter and thus such encounters are observed less often. If so, males must have a way to assess others' size from a distance, suggesting a possible function for male broadcast displays that does not depend on the maintenance of territories (broadcast displays have previously been interpreted as males' advertisement of territory ownership; e.g. Jenssen et al. 2000). Moreover, pairs of males that were similar in size that *did* encounter one another did so only a few times, possibly suggesting that these males avoid one another after determining that they are closely size-matched.

In contrast to males, females do not move to either avoid or seek out one another. This result is puzzling, because females do fight with one another (Figure 2.6; Edwards and Lailvaux 2013), presumably over access to resources such as food, basking sites, or nesting sites, and may thus be expected to avoid one another. Agonistic interactions in species described as territorial have traditionally been thought to determine which individuals retain access to particular resource-rich areas. However, Stamps (1994) argued against this interpretation of agonistic behavior, in part because she found that, subsequent to fights among juvenile *Anolis aeneus*, neither the loser nor the winner remained in the area of the fight. A similar outcome was observed in the female-female fight observed in our sampled population. This raises the question of why females or juveniles fight at all.

One possible explanation for fighting in females and juveniles, which could readily apply to males as well, is that anoles maintain dominance hierarchies for the resolution of competition over any of a number of resources. Our results show that individuals have the chance to interact with many conspecifics of both sexes over the course of the breeding season, and anoles are known to be capable of individual recognition (Orrell and Jenssen 2002; Paterson and McMann 2004; Tokarz 2008; McMann and Paterson 2012), which can help to stabilize dominance hierarchies by reducing the costs of agonistic interactions (Tibbetts and Dale 2007). Dominance hierarchies are readily recognized in anoles in high density situations, particularly in the lab (e.g. Evans 1936a, b; Bush et al. 2016), but the establishment of dominance hierarchies has previously been contrasted with the establishment of territories (Rand 1967; Stamps 1973; Bush et al. 2016). However, given the equivocal evidence for territoriality in anoles (see Chapter 1), we hypothesize that local or individual dominance hierarchies, uniting to form dominance networks, may prove a useful framework for understanding these lizards' social interactions across a range of environmental conditions (Sih et al. 2009).

Figure 2.6 Two tagged females in the sampled population fighting with one another.

Male body size was correlated with the number of females encountered, which is consistent with conventional wisdom in anoles that larger males achieve higher reproductive success than smaller males, and is more generally consistent with evidence from across animals that body size in males is an important predictor of reproductive success (Andersson 1994). However, much of the evidence in favor of this hypothesis in anoles is based on the estimation of mating patterns from home range area and overlap (e.g. Trivers 1976; Ruby 1984). More recent genetic evidence has been less definite—Johnson (2007) found a marginally significant trend towards sires of offspring being larger than males who did not sire offspring in a wild population of *Anolis cristatellus*, and Cox and Calsbeek (2010) similarly found a marginal trend towards larger *A. sagrei* males siring more offspring than small males in an experimental set up where females were presented with males of different sizes. However, Harrison (2014) found that body size did not predict reproductive success in *Anolis* *carolinensis*. Thus, we remain uncertain whether the widespread sexual dimorphism in body size in anoles is a consequence of sexual selection. That said, there are multiple aspects of reproductive dynamics that could be influenced by male body size, and our results show that the very first step—encountering potential mates—is consistent with selection for larger males.

However, being large is not the only male trait related to the number of females encountered. Males with larger spatial extents also encountered more females. Thus it appears that there are multiple ways in which males can behave so as to encounter more females. Because spatial extent was unrelated to body size, these do not appear indicative of ontogenetic shifts in movement behavior. Our results are similar to those of Noble et al. (2013b), who found evidence for independent effects of body size and home range area on reproductive success in male skinks, *Eulamprus quoyii*; it remains to be seen whether male anoles that move widely are as likely to sire offspring as males with smaller spatial extents. More generally, we do not yet know if there is strong ongoing sexual selection on movement patterns or subsequent behavior in the context of social interactions in anoles. Alternatively, males may instead make context-dependent decisions "matching" their phenotype to the social and environmental situations they find themselves in, thus maximizing individual reproductive success and leading to relatively low variation or only stochastically determined variation across individuals in reproductive success. The latter scenario is often referred to as the maintenance of "alternative mating strategies" (reviewed in Shuster 2010), though this variation need not be strictly discrete (e.g. Shine et al. 2005; Noble et al. 2013b). In species described as territorial, males are often categorized as having either "territorial" or "sneaker" mating strategies; our results do not support such a discrete categorization in this population of *A. sagrei*.

In this paper, we approach understanding the movement patterns of individuals in a population as a necessary precursor to understanding mating patterns. Our spatiotemporal method for predicting interactions between and among males and females yields results that are often inconsistent with previous purely spatial approaches; at least a few of these inconsistencies are explained by differences in the scope of sampling.

Though anoles' social organization and interactions have been studied for decades, we argued in Chapter 1 that studies of their movement patterns have been shaped by the imposition of a framework of territoriality, which limited the potential for discovering the full complexity of these lizards' space-use behavior. Future studies must tackle not only the quantification of individuals' movement patterns across space and through time in a range of environmental conditions but also integrate these with existing and new quantifications of agonistic interactions and pre- and post-copulatory mate choice behavior to finally understand how sexual selection has shaped the evolution of this widely studied group of lizards.

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Chapter 3

Does ecological specialization transcend scale? Habitat partitioning among individuals and species of *Anolis* lizards

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3.1 Summary

Ecological specialization is common across all levels of biological organization, raising the question of whether the evolution of specialization at one scale in a taxon is linked to specialization at other scales. *Anolis* lizards have diversified repeatedly along axes of habitat use, but it remains unknown if this diversification into habitat use specialists is underlain by individual specialization. From repeated observations of individuals in a population of *Anolis sagrei* in Florida, we show that the extent of habitat use specialization among individuals is comparable to the extent of specialization in the same traits among ten sympatric *Anolis* habitat specialist species in Cuba. However, the adaptive correlations between habitat use and morphology commonly seen across species of *Anolis* were not observed across individuals in the sampled population. Our results therefore suggest that while patterns of ecological specialization can transcend scale, these parallels are the consequence of distinct ecological processes acting at microevolutionary and macroevolutionary scales.

3.2 Introduction

Ecological specialization is common across a range of scales, from individual specialists to whole clades comprised of specialist species (MacArthur 1972; Cox & Ricklefs 1977; Futuyma & Moreno 1988; Losos & de Queiroz 1997; Johnson & Steiner 2000; Araujo *et al.* 2011; Siefert *et al.* 2015). Conceptual and mathematical models have long considered whether and how resource-use specialization at one scale can influence ecological interactions and evolutionary trajectories at other scales (Roughgarden 1972; Dieckmann & Doebeli 1999; Bolnick *et al.* 2003, 2011; Ravigné *et al.* 2009; Pfennig & Pfennig 2012; Violle *et al.* 2012; Gilbert *et al.* 2015; Hart *et al.* 2016). Though the specifics of these models vary, together they raise the question of whether the extent of ecological specialization is linked across scale.

At one extreme, it is possible that populations made up of individual specialists diversify into clades of specialized species (Dieckmann & Doebeli 1999; Doebeli & Dieckmann 2000; Ravigné *et al.* 2009), suggesting that interspecific interactions and macroevolutionary patterns are simply intraspecific interactions and microevolutionary patterns "writ large" (Mayr 1942; Eldredge 1985). At the other extreme, it is possible that the degree of specialization across species in a clade is not influenced by whether these species are made up of individuals that are specialists or generalists, thereby indicating that populations' evolutionary trajectories over macro-evolutionary timescales are relatively unaffected by individuals' ecological interactions and the population's microevolutionary dynamics (Gould 1981). Most clades likely lie between these two extremes, with specialization transcending scale to some extent (Brooks & McLennan 1999; Bolnick *et al.* 2003; Gilbert *et al.* 2015). However, relatively few taxa are well-suited for empirical examinations of ecological specialization across a range of scales, from clades to species to populations to individuals.

A group especially well-poised for such examinations is *Anolis* lizards. Anoles have undergone repeated evolutionary diversification in the Greater Antilles, wherein ancestral species on each island have diverged into a community of species, each of which is morphologically specialized to use a different microhabitat (Williams 1972; Losos *et al.* 1998). Two key traits involved in anole specialization are toepad dimensions and limb length: more arboreal anoles tend to have better-developed toepads for clinging to smooth surfaces high in trees, whereas variation in limb length reflects conflicting demands for rapid movement on broad surfaces and agility on narrow surfaces (reviewed in Losos 2009). These ecomorphological correlations are also seen at the scale of populations within the same species—populations of anoles in different localities that differ in perch height or diameter also differ predictably in toepad dimensions or limb length (Schoener 1975; Lister 1976a; Jenssen *et al.* 1984; Losos *et al.* 2006; Stuart *et al.* 2014).

Because these ecomorphological relationships at the species and population levels are adaptive, it is plausible that similar adaptive habitat specialization is also present across individuals within a population. Indeed, mechanisms of diversification that begin with individual specialization in habitat use have been proposed to explain the *Anolis* adaptive radiation (Doebeli & Dieckmann 2000; Shaw *et al.* 2000; Thomas *et al.* 2003). However, it remains unknown if individual anoles do actually specialize in habitat use and whether individuals' habitat use is correlated with their morphology, as it is at the among-population and among-species levels.

In this study, we quantify the extent of individual specialization in habitat use in a population of *Anolis sagrei,* from repeated observations of marked individuals over a six-week period. We compare the degree of specialization between individuals in this population to the degree of habitat use specialization among ten sympatric Greater Antillean *Anolis* species, to assess if ecological specialization is similar at different scales. We also examine if variation in habitat use across individuals in the sampled population of *A. sagrei* is a consequence of variation in habitat availability. Finally, we test if individual habitat use is associated with morphology. Specifically, we predict that correlations between habitat use and morphology across individuals within a population will be similar to the well-established adaptive ecomorphological correlations (between perch height and toepad dimensions and between perch diameter and limb length) seen across populations and species of anoles (Williams 1972; Schoener 1975; Lister 1976a; Jenssen *et al.* 1984; Losos *et al.* 1998; Losos *et al.* 2006; Stuart *et al.* 2014).

3.3 Materials and Methods

3.3.1 *Study Species*

Anolis sagrei, the brown anole, is native to Cuba and the Bahamas, but has been established in Florida for over 70 years (Collette 1961; Kolbe *et al.* 2004) and has spread northward to South Carolina and has also dispersed to Louisiana and Texas since its introduction. A member of the "trunk-ground" habitat specialist type or "ecomorph", *A. sagrei* perches at low heights and on broad surfaces, and consequently has longer limbs and smaller toepads with fewer lamellae, compared to other habitat specialist types (reviewed in Losos 2009). Throughout most of its range in the USA, *A. sagrei* co-occurs with the native trunk-crown species *Anolis carolinensis*; this was true in our sampled population as well, though densities of *A. carolinensis* were low (pers. obs.).

3.3.2 *Field Data Collection*

Anolis sagrei lizards were observed in a forested area in Possum Creek Skate Park in Gainesville, FL (29.70209°N, 82.38125°W) from 12th June to 1st August, 2014. We surveyed an area of about 1,300 m^2 between 0800 and 1700 hours almost daily, and recorded all locations at which lizards were observed. We also measured the height at which each lizard was observed, and the diameter of the perch on which it was seen. Lizards were caught at the first observation, at which time we measured their snout vent length (SVL) as an estimate of body size and tagged them with unique bead tags for individual identification (Fisher & Muth 1989). Lizards were released at their initial location within 24 hours of capture. A total of 31 males and 49 females were marked. In subsequent surveys, marked lizards were identified from a distance by their tags; their location, perch height, and perch diameter were recorded. Observations of the same individual were separated by at least 60 minutes.

At the end of the survey period, we recaptured 18 male and 20 female lizards to re-measure SVL as well as measure the total length of both forelimbs and hindlimbs, using calipers. All caliper measurements were made by one person (AK). We imaged the lizards' toepads on a flatbed digital scanner to measure toepad area and count the number of lamellae on the toepad of the longest toe on each foot using ImageJ (third toe of the forelimb, fourth toe of the hindlimb; Schneider *et al.* 2012). Toepad area and lamella number on both right and left hindlimbs were measured independently by two people (R. Moon and C. Perez) and the four values were averaged for analysis. Right and left measurements were averaged for limb length, toepad area, and lamella number on the forelimbs, as well as hindlimb length. We then took the mean of forelimb and hindlimb measurements, yielding one value per individual for limb length, toepad area, and lamella number (results were similar for forelimbs and hindlimbs considered separately, and are not shown here).

To assess the habitat available to individual lizards, we quantified perch diameters in the vicinity of 158 locations of the 38 recaptured lizards (6.1 ± 2.6 locations per lizard; multiple lizards were often seen at a single location). Specifically, we randomly picked three of the locations at which each recaptured lizard was seen during the survey period (except one individual that was seen only at two locations). We then counted the perches within a 50 cm radius of the flagged location at three heights: 25 cm, 100 cm, and 125 cm. Perches were categorized into the following five classes based on their diameters: 0-1 cm, 1-5 cm, 5-10 cm, 10-20 cm, >20 cm. Perches included all stems, branches, and trunks. We limited our counts at a single location and height to a maximum of 30 perches per diameter class; this limit was reached in only 2% of the 2370 location × height × diameter classes in which perches were counted. Additionally, we incorporated the ground as one available perch in the >20 cm category for each location. For each individual, we calculated a distribution of perch diameters available to that lizard by summing the number of perches in each diameter category across heights and locations. Availability of perch heights was not quantified as we thought it unlikely to vary across individuals, and thus unlikely to influence individual specialization in habitat use; most trees in the sampled site were much taller than 5 m, whereas the maximum observed perch height in the population was 4.55 m.

3.3.3 *Statistical Analyses: Individual and Species Specialization*

All statistical analyses were performed in R v. 3.2.2 (R Core Team 2015). First, we examined if individuals specialize in perching at particular heights. Specifically, we calculated the mean proportional similarity (mean PSi, also referred to as IS, an index of individual specialization) between individual and population distributions, to ask if distributions of perch heights used by each individual are similar to the distribution of perch heights used by all individuals (Test I in Table 3.1; Bolnick *et al.* 2002). We used the *PSicalc* function in *RInSp* package (Zaccarelli *et al.* 2013), which also calculates a P-value by randomly sampling individual distributions from the population distribution. Values of PSi closer to 1 indicate high overlap between the two distributions being considered and, in this case, demonstrate low individual specialization. In contrast, lower values of PSi indicate lower overlap between distributions and, in this case, demonstrate higher individual specialization. To calculate distributions, we classified observations of perch height into five classes (0-50 cm, 50-100 cm, 100-150 cm, 150-200 cm, >200 cm). We similarly calculated individual specialization in perch diameter (Test II in Table 3.1), with observations classified into diameter categories as above.

Table 3.1 Tests to compare the proportional similarity (PSi) of distributions of Perch Height (PH) and Perch Diameter (PD) in the sampled population of *A. sagrei*. Values of PSi closer to 1 indicate higher similarity between the distributions being compared. P-values, which indicate if the similarity between Distributions A and B is significantly different than the similarity of Distribution B to random samples drawn from Distribution B, were all < 0.001.

Test	**Distribution A**	**Distribution B**	**PSi (mean ± SD)**
I	Individual Used PH	All Used PH	0.62 ± 0.17
II	Individual Used PD	All Used PD	0.61 ± 0.16
III	Species Used PH	All Species Used PH	0.69 ± 0.21
IV	Species Used PD	All Species Used PD	0.72 ± 0.14
V	Habitat Specialist Type Used PH	All Habitat Spcialists Used PH	0.62 ± 0.22
VI	Habitat Specialist Type Used PD	All Habitat Specialists Used PD	0.68 ± 0.14
VII	Individual Available PD	All Available PD	0.94 ± 0.04
VIII	Individual Used PD	Individual Available PD	0.25 ± 0.11

Using data from Rodríguez-Schettino *et al.* (2010), we calculated the mean PSi for ten sympatric *Anolis* species from Soroa, Cuba, to ask if distributions of perch heights used by each species are similar to the distribution of perch heights used by the whole community of species (Test III in Table 3.1). Because four of the ten species belonged to the trunk-ground habitat specialist type (Table 3.2) and are expected to show similar habitat use, we repeated the mean PSi calculations after grouping perch height distributions by habitat specialist type instead of species (Test V in Table 3.1).

Specialization in perch diameter was calculated similarly for species and for habitat specialist type (Tests IV and VI in Table 3.1).

Table 3.2 Species sampled by Rodríguez-Schettino *et al.* 2010, with their habitat specialist type categorizations, used here to calculate the degree of specialization in habitat use among sympatric *Anolis*.

Species	**Habitat Specialist Type**
Anolis allogus	Trunk Ground
Anolis alutaceus	Grass Bush
Anolis angusticeps	Twig
Anolis homolechis	Trunk Ground
Anolis loysianus	Trunk
Anolis luteogularis	Crown Giant
Anolis mestrei	Trunk Ground
Anolis porcatus	Trunk Crown
Anolis sagrei	Trunk Ground
Anolis vermiculatus	Aquatic

3.3.4 *Statistical Analyses: Habitat Availability*

We divided our investigation of whether individual variation in perch diameter was a consequence of habitat availability into three parts. First, we assessed the proportional similarity between the distributions of perch diameters available in the vicinity of each individual's locations and the common distribution of available perch diameters across all individuals (Test VII in Table 4.1). Here, a mean PSi value closer to 1 would indicate that similar distributions of perch diameters are available to all individuals. Next, we calculated the proportional similarity between the distribution of perches available to an individual and the distribution of perch diameters used by that individual (Test VIII in Table 4.1). Here, a mean PSi value close to 1 would indicate that individuals tend to use perches of certain diameters in proportion to their availability. For the latter comparison, we simulated a distribution of mean PSi values under the criterion that individuals sampled from their available perches at random, to calculate a P-value for the comparison. Third, we used a chi-square test to compare the proportion of perches in each diameter category between all available and all used perches.

3.3.5 *Statistical Analyses: Ecomorphological Correlations*

To account for variation in habitat use with body size (Schoener 1968; Jenssen *et al.* 1998), we first assessed the relationship between mean perch height and SVL, and mean perch diameter and SVL using linear models, weighted by the number of observations for each individual. Because female anoles both perch lower than males and are smaller than males (Schoener 1968; Perry 1996), we also split the dataset by sex and examined the correlation for males and females separately. Regressions of habitat variables against SVL were conducted for all sampled individuals, as we measured SVL when they were first captured.

We then used linear models to assess if individual morphology was related to individual habitat use. In particular, we examined if mean perch height was positively correlated with toepad area or lamella number, and if mean perch diameter was positively correlated with limb length, in concordance with the patterns of ecomorphological variation seen across species and populations of anoles (reviewed in Losos 2009). Each linear model included SVL as a covariate to account for variation in body size, and was weighted by the number of observations for each individual. All morphological variables were log transformed.

3.4 Results

3.4.1 *Individual Specialization*

Lizards were observed between one and 46 times (mean ± SD: 12.6 ± 11.2 observations). Individuals in this population were specialized in both perch height and diameter, as indicated by the indices of specialization for both perch height (Figure 3.1a; Test I in Table 3.1) and perch diameter (Figure 3.1b; Test II in Table 3.1). This specialization implies that different individuals used perches of particular heights and diameters in different proportions. The degree of specialization in habitat use between ten species (Tests III and IV in Table 3.1) and seven types of habitat specialists (Tests V and VI in Table 3.1) of sympatric anoles from Soroa, Cuba, was comparable to the degree of specialization between individuals in the sampled population (Figure 3.2).

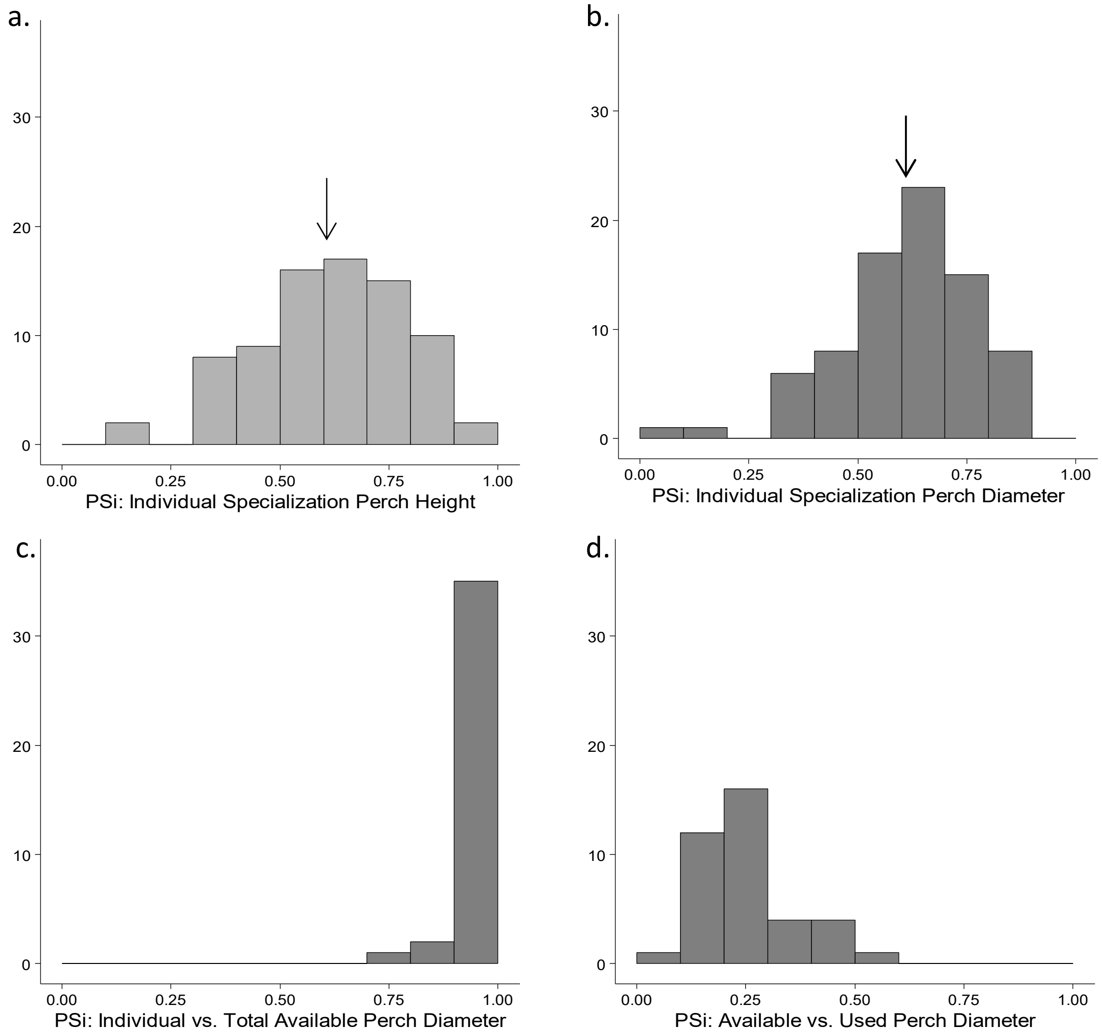

Figure 3.1 Distributions of proportional similarity (PSi) indicating (a) individual specialization in perch height and (b) perch diameter; arrows indicate the mean PSi; (c) high similarity between the distributions of perch diameters available to each individual and the total distribution of available perch diameters; and (d) low similarity between perch diameters available to and the perch diameters used by each individual.

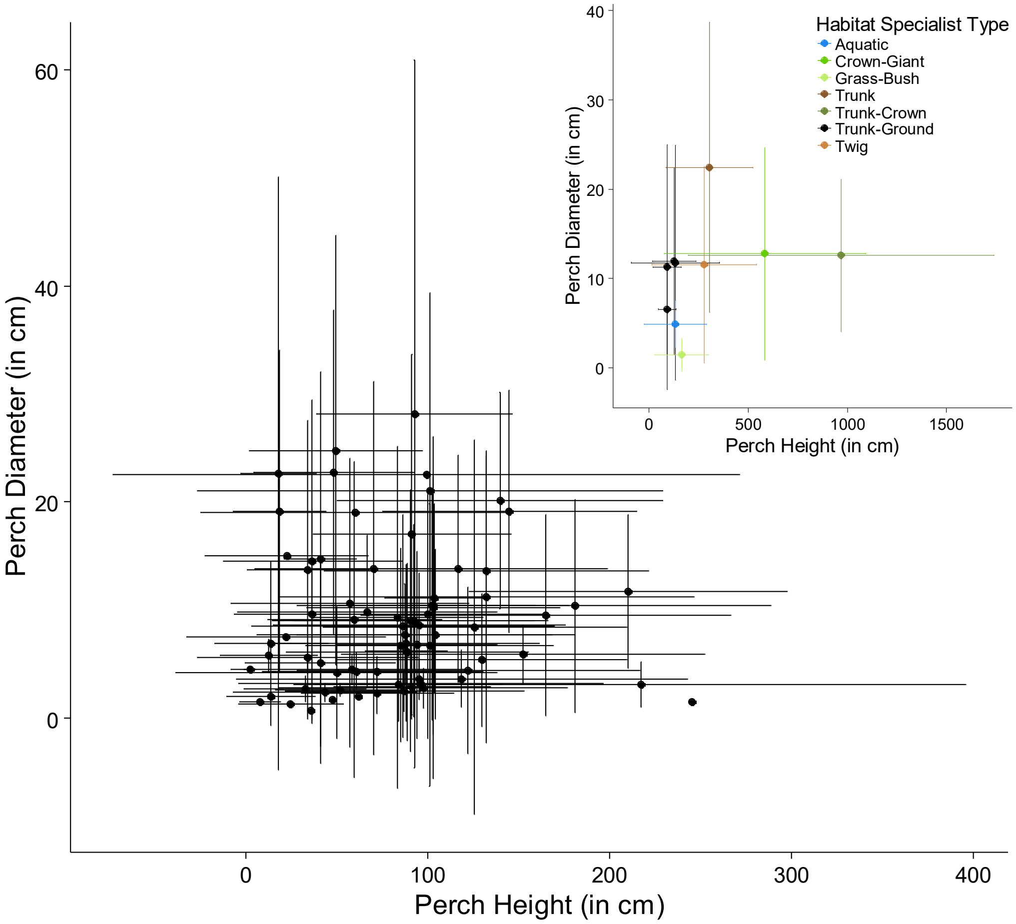

Figure 3.2 Mean ± SD of perch height and diameter for individuals of *A. sagrei* from a population in Gainesville FL, and (inset) sympatric species of Greater Antillean anoles (data from Rodríguez-Schettino *et al.* 2010). Mean PSi (±SD) for perch height and perch diameter respectively were 0.62 ± 0.17 and 0.61 ± 0.16 for individuals, and 0.69 ± 0.21 and 0.72 ± 0.14 for species (see text, Table 3.1 for details).

3.4.2 *Habitat Availability*

Individual specialization in perch diameter was not determined by available habitat, as the distributions of perch diameters available to each individual were very similar to the distribution of perch diameters available across all individuals in this population (though not identical; Figure 3.1c; Test VII in Table 3.1). Moreover, the distributions of perch diameters used by individuals was different than the distribution of perch diameters available to that individual, suggesting that, with respect to diameter, individuals do not use perches in proportion to their availability (Figure 3.1d; Test VIII in Table 3.1). The distributions of diameters of all available and all used perches were different from one another (χ^2_4 = 2667, $P < 0.001$), with lizards primarily avoiding the narrowest perches (Figure 3.3; results [not shown] were similar when excluding the narrowest perch diameter category).

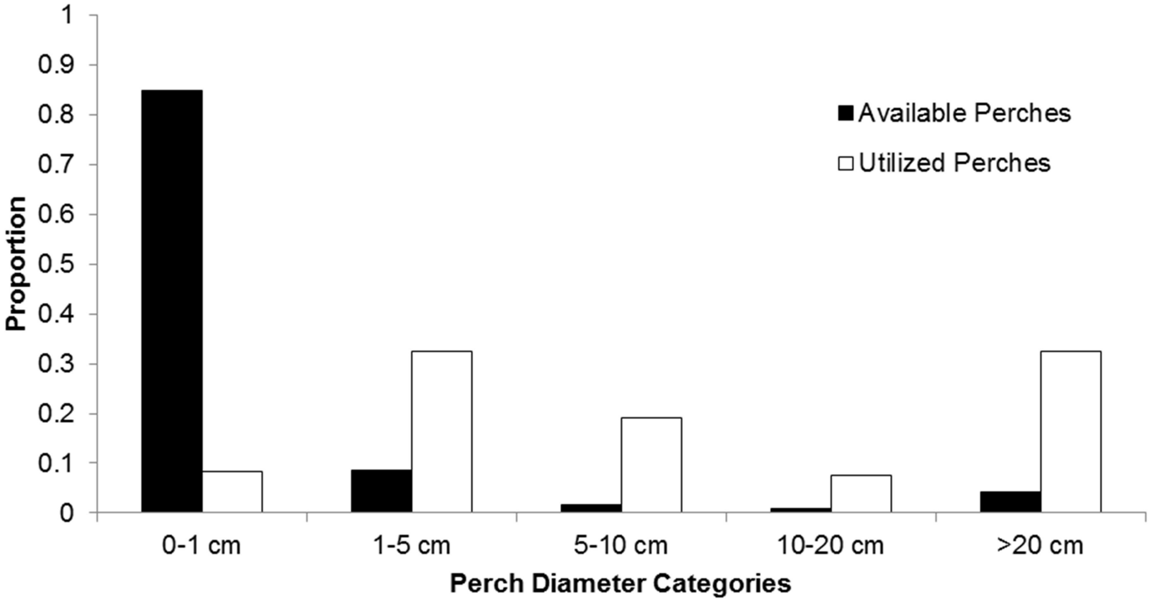

Figure 4.3 Comparison of the diameters of available and used perches in the sampled population of *A. sagrei*.

3.4.3 *Ecomorphological Correlations*

Variation in habitat use across individuals was partly related to body size: mean perch height, but not mean perch diameter, was positively correlated with SVL (perch height: β ± SE= 201 ± 31, t_{78} = 6.6, $P < 0.001$; perch diameter: β ± SE = 4 ± 4, t_{73} = 1.06, $P = 0.29$). Splitting the dataset by sex, we found that mean perch height and SVL were positively correlated for males (β ± SE= 484 ± 117, t_{29} = 4.1, $P < 0.001$), but not for females (β ± SE= 147 ± 121, t_{47} = 1.2, $P = 0.23$).

However, after accounting for body size, none of our predictions for relationships between habitat variables and morphological variables were met. Mean perch height was not positively correlated with toepad area (β ± SE = -91 ± 48, t_{35} = -1.9, $P_{\text{one-tailed}}$ = 0.97) or lamella number (β ± SE = -48 ± 109, t_{35} = -0.4, $P_{\text{one-tailed}}$ = 0.67), and mean perch diameter was not positively correlated with limb length (β ± SE = -13 ± 23, t_{35} = -0.6, $P_{\text{one-tailed}}$ = 0.72). Relationships were similar (results not shown) between the residuals from a regression of habitat variables against SVL and the residuals from a regression of morphological variables against SVL.

3.5 Discussion

Ecological specialization is widespread across taxonomic scales, from clades of specialist species to specialized individuals within populations. Parallels in ecological specialization across scales can suggest whether microevolutionary forces determine macroevolutionary patterns (Dieckmann & Doebeli 1999; Doebeli & Dieckman 2000; Ravigné *et al.* 2009; Bolnick *et al.* 2003, Gilbert *et al.* 2015). With their well-documented specialization in habitat use across species and populations, *Anolis* lizards are well-suited to test if macroevolutionary patterns of ecological specialization are paralleled at the microevolutionary scale of individuals within a population.

We found that individuals in a population of *A. sagrei* were specialized in their habitat use, specifically in both the height and the diameter of the surfaces on which they perched. The degree of specialization of individuals in this population was comparable to the degree of specialization of ten sympatric species of *Anolis*, along the same axes of habitat use. In other words, habitat use was partitioned to a similar extent by individuals in a population of *A. sagrei* as by sympatric species of *Anolis*. Thus, anoles can be equally specialized whether considering individuals within a population or species within a community—ecological specialization in *Anolis* can transcend scale.

Habitat specialist species in the *Anolis* adaptive radiation also differ consistently in morphology, presumably as a result of adaptation to using different parts of the environment (reviewed in Losos 2009). If both within- and between-species specialization in habitat use that we observed is driven by the same adaptive processes, then we would expect the morphological relationships to also be parallel across scales. Theoretical work suggests a reason to expect such a parallel. Mechanisms of ecologically mediated sympatric speciation suggest that interspecific adaptive divergence arises out of within-population processes that drive an initially homogeneous population to diverge in situ as a result of disruptive selection, eventually becoming distinct species (Dieckmann & Doebeli 1999; Ravigné *et al.* 2009; reviewed in Via 2001). Critically, these theories posit the development of an intrapopulational link between individual habitat choice and phenotype as an important stage in this process (Via 2001; Bolnick *et al.* 2003). Repeated cycles of this process of disruptive selection on habitat use followed by speciation have been proposed to explain the *Anolis* adaptive radiation (Doebeli & Dieckmann 2000; Shaw et al 2000; Thomas et al 2003).

However, the adaptive correlations between habitat use and morphology that are common across populations and species of *Anolis* lizards were not observed across individuals within the sampled population of *A. sagrei*. Our results therefore do not support the model of disruptive selection leading to sympatric speciation as a path to adaptive diversification in *Anolis*. This conclusion is in accord with biogeographical evidence that suggests that sympatric speciation is not common in anoles (Losos 2009).

If the correlations among *Anolis* species between habitat and morphology are adaptive, why do we not see similar correlations, albeit at a reduced scale, among individuals within a single population? One possibility is that the variation in morphology across individuals in the sampled population was too low to result in differences in performance that are visible to selection.

However, the variation we observed was comparable to that seen in studies documenting correlated shifts in habitat and morphology between populations of anoles (e.g., coefficient of variation for lamellae number in this study vs. Stuart *et al.* [2014]: 0.099 vs. 0.050). A second possibility is that our study was underpowered. However, our sampling appears sufficient to detect correlations comparable to those seen between habitat and morphology across populations (e.g., power analyses showed that we could detect correlations as low as $r^2 = 0.29$ with 95% power; in comparison, the correlation between mean lamellae number and perch height across populations in Stuart et al. [2014] had $r^2 = 0.37$). A third possibility is that differences among individuals in habitat use are entirely a consequence of variation in the habitat available to each individual, with little opportunity for individuals to choose preferred perches. However, we found that the distributions of available perch diameters were similar across locations inhabited by different individuals in the sampled *A. sagrei* population. Moreover, individuals did not use perches of different diameters in the proportion that they were available (see Rodriguez-Robles et al. 2005 for similar results across individuals in *Anolis gundlachi*). These results indicate that substantial inter-individual variation exists in both morphology and habitat use, but this variation is not linked: individuals do not choose to use the habitats to which they are presumably best adapted according to morphology. In contrast, at the interspecific level, habitat choice is evident among sympatric species, with different species using habitat appropriate for their morphology (Irschick and Losos 1999; Johnson et al. 2006; these studies also reveal substantial intraspecific variation in habitat use, in agreement with our study).

Why such habitat selection behavior has not evolved at the individual level is an unanswered question. It is possible that the admixed genetic background of populations in the invasive range of *A. sagrei* (Kolbe et al. 2004, 2008) may have broken up adaptive genetic correlations between habitat use behavior and morphology, and that sufficient time has not passed since the invasion of *A. sagrei* into Florida for these correlations to reform; similar studies in other populations of *A.*

sagrei as well as other anole species could examine this possibility. In the absence of adaptive habitat use behavior, however, coupled disruptive selection cannot act on habitat use and morphology within populations, and thus cannot lead to sympatric speciation and adaptive radiation.

One potential mechanism that could partially explain the observed individual specialization in habitat use is suggested by the relationship we observed between perch height and body size in male, but not female, *A. sagrei*. This result suggests that intraspecific social interactions, specifically social conflict between males, may shape daily perch use choices. Perching higher than one's competitors is known to be important to male anoles in several social contexts—male anoles display from higher perches compared to their average perch use (Andrews 1971; Kamath *et al.* 2013), and the male that perches relatively higher than its rival during an agonistic encounter is more likely to win that encounter (Tokarz 1985). Body size is also known to influence the outcome of male-male agonistic interactions—large males win fights against small males (e.g. Tokarz 1985; Jenssen *et al.* 2005). Thus, the increase in perch height with body size in male *A. sagrei* may derive from larger males winning agonistic encounters and obtaining access to higher perches from which to display, in turn preventing smaller, competitively inferior, males from occupying high perches. But smaller individuals could gain access to higher perches as they grow older and larger, thereby becoming more likely to win agonistic interactions.

Though the relationship between male body size and perch height does not necessarily preclude the existence of other adaptive ecomorphological relationships, it may be that an individual's fitness via reproductive success depends more on the former than its fitness via survival depends on the latter. Thus, adaptive social behavior may act to impede the evolution of adaptive ecomorphological relationships within populations (Huey et al. 2003). Moreover, if the association between body size and perch height in male *A. sagrei* is largely due to ontogenetic change, it will have few direct consequences for the evolution of habitat use specialization at higher taxonomic levels (Lister 1976a). Of course life history traits with a genetic basis, such as those that influence growth rates, may consequently be subject to selection.

While the degree of specialization we observed was similar between individuals and species, the total extent of habitat used is different between the population of *A. sagrei* and the community of *Anolis*. In particular, a broader range of perch heights were used by ten species (and seven habitat specialist types) of anoles than by individuals in the sampled population of *A. sagrei* (Figure 3.2). On one hand, this consideration points to the utility of metrics of specialization for facilitating comparisons across different ecological situations, including different taxa and resources (Bolnick *et al.* 2002, 2003; Araujo *et al.* 2011; Dall *et al.* 2012). On the other hand, we run the risk of losing sight of the ecological relevance of such disparate comparisons. In particular, our results do not mean that an individual in a population of *A. sagrei*, a trunk-ground anole, is likely to have similar perch use to an individual belonging to a trunk-crown species, for example. Rather, they imply that individuals in a population of *A. sagrei* can be as non-overlapping in their habitat use as sympatric *Anolis* species, even those belonging to different habitat specialist types. Similar studies conducted on multiple populations and in different species, especially across varying competition and predation regimes, will reveal the extent to which the degree of ecological specialization transcends both scale and ecological conditions. Such studies will shed light on how microevolutionary processes drive macroevolutionary patterns of diversification via ecological interactions.

In sum, our results suggest that while ecological specialization itself can be similar across scales in *Anolis* lizards, the morphological correlates, and thus the underlying causes, of this specialization, may differ between the within-population scale and the between-species scales. The transitions between microevolutionary processes and macroevolutionary patterns in *Anolis* therefore may not be seamless; understanding these transitions will require integrating an understanding of both ecological and social selective pressures on individuals within populations and forecasting the consequences of these pressures for population and species evolution.

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Chapter 4

Variation in display behavior, ornament morphology, sexual size dimorphism, and habitat structure in the Fan-Throated Lizard (***Sitana***, Agamidae)

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4.1 Summary

Fan-throated lizards (*Sitana*; Agamidae) are a widespread yet little-studied genus of lizards found in dry habitats throughout South Asia. Male lizards in this genus bear a fan-like structure under their throats that is displayed by rapid extension and retraction during the breeding season, particularly during courtship and male-male interactions. Throat-fans vary dramatically in both size and coloration across the genus, ranging from small and white to large and blue, black, and orange. In this paper, I investigated variation in throat-fan morphology and display behavior in eight populations of fan-throated lizards. These lizards' displays included partial and complete throat-fan extensions, changes in body position, rapid head turning behavior, and occasional bipedality. Part of the variation in display behavior across these lizards was associated with throat-fan elaboration, and increased throat-fan size and coloration were associated with male-biased sexual size dimorphism, but not with changes in habitat. These results suggest that sexual selection may underlie increases in both throat-fan size and coloration in the genus *Sitana*. Fan-throated lizards are thus a promising system in which to further investigate the coevolution of different display components of a striking visual signal.

4.2 Introduction

The evolution of colorful ornaments displayed by animals during courtship and agonistic interactions has long been of interest to behavioral ecologists. Indeed, the theory of sexual selection was proposed to explain the presence of conspicuous and costly ornaments that are almost certainly detrimental to survival (Darwin, 1871; Andersson, 1994). However, many factors other than sexual selection can also play a role in shaping ornament morphology, including the environmental contexts in which ornaments are displayed (Endler, 1992; Seehausen et al., 1997; Bro-Jørgensen, 2009), and physiological and biomechanical constraints that limit or direct ornament elaboration (Podos, 2001; Irschick et al., 2007; Rosenthal, 2007). Ornaments are also often deployed as part of complex multicomponent and multimodal displays, and all of the above factors can influence the relationships between different display components and modalities (Hebets and Papaj, 2005; Bradbury and Vehrencamp, 2011). This multitude of interacting forces that drive ornament evolution offers a number of starting points from which to begin investigating the origin and maintenance of ornament variation in understudied taxa. In this paper, I explore some behavioral, environmental, and morphological correlates of ornament variation in fan-throated lizards (*Sitana*, Agamidae), a widespread yet little-studied genus from South Asia.

Showy ornaments, including fans, frills, and horns, are often central to lizard displays, though many species also incorporate movement, changes in body coloration, chemical cues, and even sound (e.g. Marcellini, 1977; Duvall, 1979; Cooper and Greenberg, 1992; Fleishman, 1992). Each of the factors that drive display evolution has played an important role in shaping the evolution of lizard ornamentation. For example, sexual selection, especially male-male competition, is thought to have driven the evolution of male ornaments and colors in both agamid and lacertid lizards, such that species with more intense sexual selection show more elaborate ornamentation (Stuart-Fox and Ord, 2004; Chen et al., 2012; Perez i de Lanuza et al., 2013). Habitat structure and the visual environment affect both color and motion signals in *Anolis* lizards, as well as ultraviolet color signals in *Bradypodion* chameleons, with signals varying such that they are maximally conspicuous in the habitat in which they occur (Leal and Fleishman, 2002, 2004; Ord et al., 2007; Stuart-Fox et al., 2007; Ng et al., 2013). Conversely, conspicuousness may also be selected against in habitats where lizards suffer high rates of predation (e.g. in *Ctenophorus* lizards [Stuart-Fox et al., 2003] and *Crotaphytus* lizards [Husak et al., 2008]), leading to geographic variation in coloration that corresponds to variation in predation risk (McLean et al., 2014). Finally, anatomical and biomechanical constraints affect variation in motion signaling between closely related species of anoles (Ord et al., 2013). Variation across lizard taxa in not only the ornaments themselves but also the proximate and ultimate causes for ornament diversification makes lizards an interesting group in which to examine ornament evolution.

Fan-throated lizards, belonging to the South Asian agamid genus *Sitana*, are a promising taxon in which to investigate the patterns and processes of visual display diversification. These lizards are named for fan-like structures, also known as "dewlaps," that are borne under the throats of males. The throat-fan is displayed by rapid extension and retraction during the breeding season, particularly during courtship and male-male interactions (Kratzer, 1980; Kästle, 1998; Patankar et al., 2013). These lizards' ornamentation drew the attention of Darwin, who, in his treatise on the evolution of secondary sexual characters, described them thus: "the males alone are furnished with a large throat-pouch, which can be folded up like a fan, and is colored blue, black, and red…The female does not possess even a rudiment of this appendage" (Darwin, 1871:33). Though Darwin was correct about the sexual dimorphism of their ornamentation (Kratzer, 1980; Pal et al., 2011), he appeared unaware that male *Sitana* vary substantially in the size and coloration of their throat-fan (Figure 4.1). While males with the large blue, black, and orange throat-fans described by Darwin ("colored-fan variant") are found predominantly in western peninsular India, males in most of the remainder of the range of this genus have smaller white throat-fans with blue margins ("white-fan variant"), except for southern peninsular India and Sri Lanka, where males have intermediately colored throat-fans ("intermediate-fan variant").

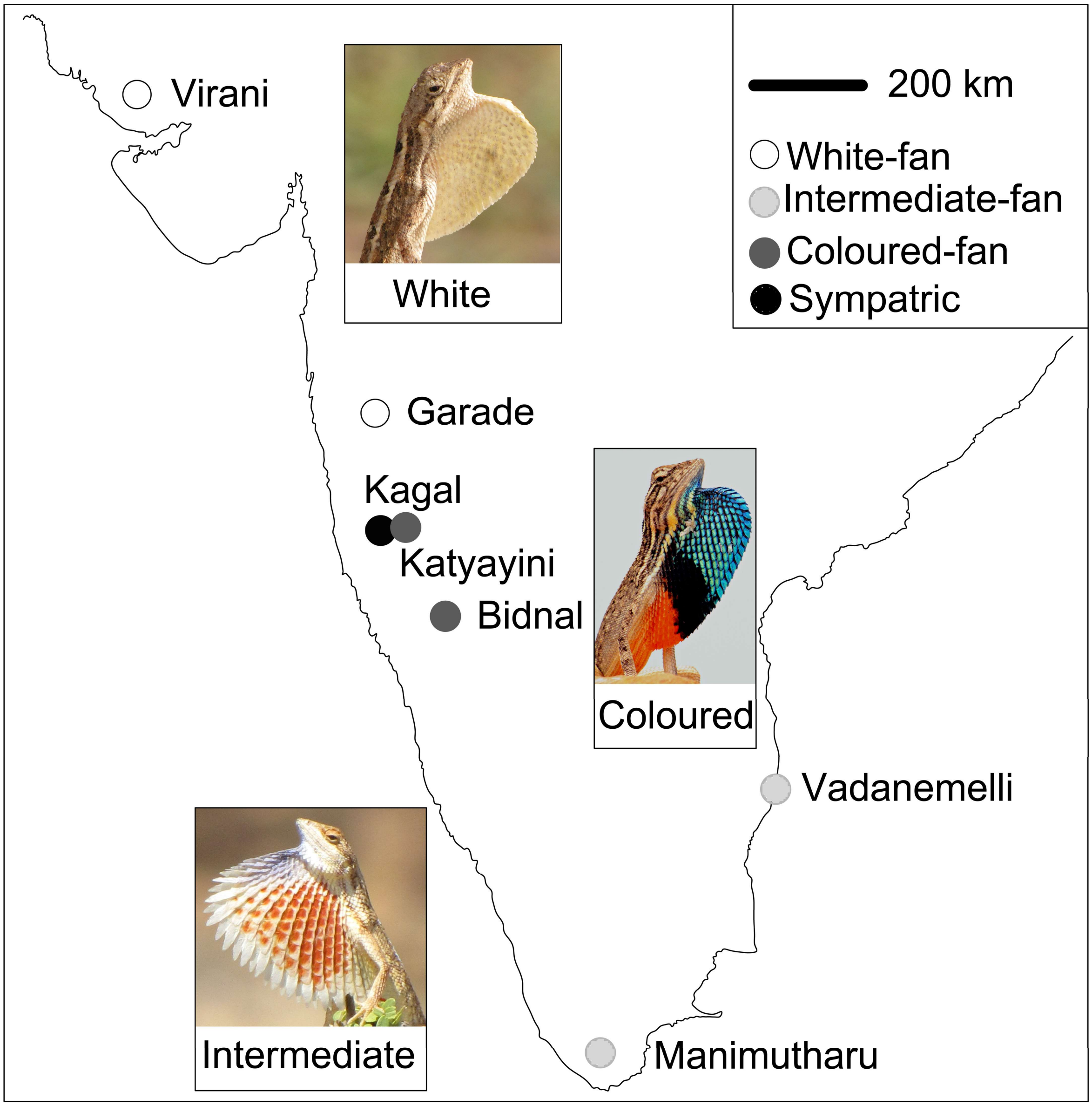

Figure 4.1 Locations of sites sampled in this study in India, with representative photographs of male throat-fans from a white-fan population (Virani), colored-fan population (Katyayini; photograph by Varad Giri), and intermediate-fan population (Manimutharu). The sympatric site included lizards of both the white-fan and the colored-fan variants.

Despite their ubiquity in dry grassland, thorn-scrub, and coastal habitats across South Asia, fan-throated lizards remain very poorly studied— species delimitations and phylogenetic relationships of species within the genus are currently being determined (Amarasinghe et al. 2015; Deepak and Karanth, pers. comm.), and very little attention has been paid to their ornamentation and display behavior (but see Kästle, 1998; Patankar et al., 2013). In this paper, I first investigate variation in ornament morphology and display behavior in fan-throated lizards, asking if lizards with morphologically different throat-fans deploy these ornaments using different display behaviors. Next, I examine variation in male body size, sexual size dimorphism (SSD), and habitat openness across populations of fan-throated lizards with morphologically different throat-fans. These comparisons provide a starting point for future investigations into the role of sexual selection and environmental context in the origin and maintenance of variation in ornament morphology in these lizards.

4.3 Materials and Methods

4.3.1 *Study Sites*

I determined localities for the three throat-fan variants by contacting ecologists and naturalists across India through the Young Ecologists Talk and Interact listserv as well as from georeferenced photographs of fan-throated lizards on the India Nature Watch website (www.indianaturewatch.net). I sampled from seven sites, two each of the white-fan, intermediate-fan, and colored-fan variants, as well as one site, Kagal, in which the white-fan and colored-fan variants were sympatric (Figure 4.1). Preliminary data on the phylogenetics of *Sitana* suggest that the throat-fan variants belong to different clades (Deepak and Karanth, pers. comm.) and do not interbreed, though species demarcations have yet to be determined. Moreover, both males and females of the white-fan and colored-fan variants can be distinguished from one another on the basis of head shape and patterning (pers. obs.; Figure S1 in Appendix 4). Therefore, the sympatric white-fan and colored-fan variants at Kagal were considered distinct populations (KagW and KagC), amounting to a total of eight sampled populations. Also, throat-fan size and coloration differed substantially between the two intermediate-fan populations (Vadanemelli [Vad] in northern Tamil Nadu, and Manimutharu [Man] in southern Tamil Nadu), despite their geographic proximity (see Figure 4.1 and Results; see also Amarasinghe et al. [2015], who documented substantially different throat-fan coloration in the intermediate-fan variant in Sri Lanka). Pairwise comparisons of these two intermediate-fan populations were therefore performed for behavioral and morphological variables. Sites were outside of protected areas, in habitats ranging from fallow agricultural fields and grazing fields to thorn scrub vegetation. I sampled sites during the lizards' breeding season in 2012 and 2013, prior to the arrival of the monsoon rains, i.e. between April and June before the south-west monsoon in white-fan and colored-fan populations in Karnataka, Maharashtra, and Gujarat, and between September and October before the north-east monsoon in the intermediate-fan populations in Tamil Nadu.

4.3.2 Display Behavior

Display behavior was recorded opportunistically in the field using a Canon Vixia HF S21HD Camcorder. I spotted individual lizards while walking slowly through the environment (Rand, 1964). Individuals were identified as males by the presence of (a) a throat-fan, (b) blue coloration on the first diamond below the head on the dorsum, or (c) blue coloration on the throat, depending on the population. Undisturbed males were observed from a distance of approximately 10 m for up to 30 min or as long as the lizard remained in sight (mean length of observation per individual ± SD: 20.8 ± 12.4 min).

Video observations of displays in the field were analyzed frame-by-frame to quantify display behavior. Each display included one or more extensions of the throat-fan; extensions separated by 10 s or more were counted as separate displays, whereas extensions separated by less than 10 s were counted as part of the same display. For each individual, I measured the proportion of time observed that the individual spent displaying, and the number of displays performed per unit time observed. For each display, the following variables were measured and averaged by individual (Table 4.1): the total duration in s of the display from the beginning of the first throat-fan extension to the end of the last throat-fan extension, the number of partial and complete throat-fan extensions, the number of linked throat-fan extensions (i.e. an extension of the throat-fan that follows an incomplete retraction of an already extended throat-fan comprises two linked extensions), the number of turns to the left or right, and the number of changes in body position i.e. up or down movements, or changes in the angle between the lizard's body and the substrate. Additionally, the presence or absence of the following display modifiers (Jenssen, 1977) was scored as a 1 or 0 for each display and scores were averaged by individual: raised nuchal crest, raised dorsal crest, bipedality, and raised tail (Figure 4.2).

4.3.3 *Morphology*

After concluding the observation, I attempted to capture the lizard using standard noosing techniques; additionally, males disturbed by my presence and all females were caught immediately after they were spotted. I was able to capture 86% of the spotted lizards. The snout-vent length (SVL) of all individuals was recorded as a measure of body-size; additionally, for males, throat-fan area was assessed by photographing the extended throat-fan. A metric scale was included in each photograph, and the outline of the throat-fan was traced in the program ImageJ (Schneider et al., 2012) to measure throat-fan area. For males from all populations except Vadanemelli, I used an Ocean Optics USB2000 spectrophotometer with a pulsed-xenon light source to measure the reflectance spectra of different color patches on the throat-fan: blue and orange patches were measured on colored-fan and intermediate-fan males, black areas were measured in colored-fan males, and white areas were measured on white-fan and intermediate-fan males. Two readings were taken per color per individual.

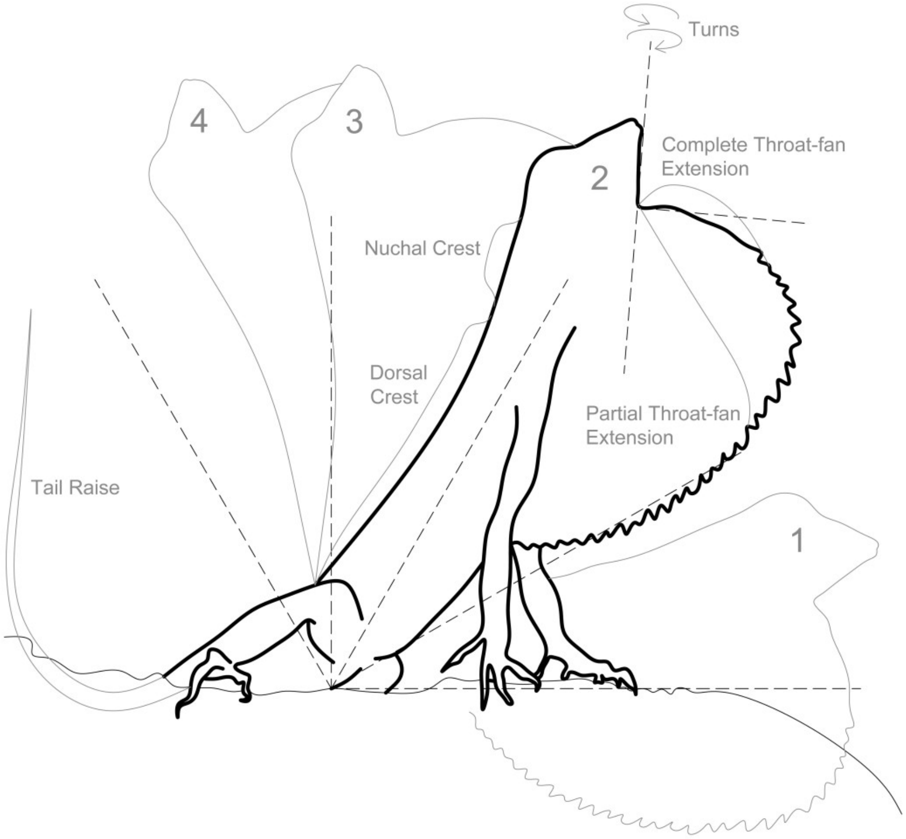

Figure 4.2 Measurements of display behavior. Throat-fan extensions were considered complete if the minimum angle between ventral surface of the head and the front margin of the throat-fan was estimated as 90° or less; for angles estimated as > 90°, throat-fan extensions were considered partial. Body position was categorized based on the estimated angle between the substrate and the ventral surface of the body: 1: 0°–30°, 2: 30°–60°, 3: 60°–90°, and 4: >90°, and the number of changes between these four body positions was counted for each display. The number of head turns as well as the presence of four display modifiers—raised nuchal crest, raised dorsal crest, raised tail, and bipedality (not depicted here)—were assessed.

Lizards were marked on the flanks and ventrally using non-toxic sharpie markers and dorsally using temporary colored cardboard queen-bee tags (Johnson, 2005) or white paint before releasing, to avoid resampling individuals.

4.3.4 Environmental Variables

For eight randomly located transects per site, I assessed the presence of vegetation and rocks on the transect every 30 cm for 15 m. Ground cover was calculated as the proportion of points at which vegetation or rocks were present on the transect. For four of the eight transects, I measured the height in cm of every plant and rock directly on the transect to calculate the average height of the ground cover at the site. These variables were chosen as simple measures of visual environment—more open environments are expected to have a lower proportion of ground cover or shorter ground cover than more closed environments. Further, I measured perch height at which lizards were first seen perching to the nearest cm, to assess if the throat-fan variants occupy distinct microhabitats, which may also contribute to differences in the visual environment in which their throat-fans are deployed.

4.3.5 Statistical Analysis

All statistical analyses were conducted in R v. 3.0.2 (R Core Team, 2013). Throat-fan area and SVL were log-transformed prior to analysis. A linear mixed effects model (*nlme* package; Pinheiro et al., 2013) with a fixed effect of throat-fan variant and a random effect of population was used to compare SVL among males of different throat-fan variants. Variance was allowed to vary with population to improve the normality and homoscedasticity of model residuals. Throat-fan area was similarly compared across throat-fan variants, both with and without SVL included as a covariate. Additionally, both SVL and throat-fan area were compared between the two intermediate-fan populations using *t*-tests, because preliminary observations revealed unexpectedly large differences in throat-fan morphology between these two populations. Finally, the direction of SSD was assessed using *t*-tests in each population, with a sequential Bonferroni correction to account for multiple comparisons. An analysis of variance (ANOVA) on SVL with main effects of population and sex, and a population × sex interaction, was used to test if the degree of SSD differed across populations.

Spectral data were smoothed and condensed to 1 nm intervals from 300 to 700 nm wavelengths using CLR v1.05 (Montgomerie, 2008) and averaged by individual. Mean and 95% confidence intervals of reflectance at one nm intervals were calculated and plotted for each color in each population.

A principal components analysis was conducted on 12 behavioral variables and the first principal component axis (PC1), which explained 31% of the variation in the behavioral variables, was used as a measure of display behavior. Subsequent PC axes each explained less than 15% of the total variation in display behavior and were not readily biologically interpretable in conjunction with PC1, and were therefore not analyzed further. Though this approach does not analyze all of the behavioral variation, which includes among-individual and among-population variation as well as differences between throat-fan variants, PC1 by definition represents the largest independent axis of variation in display behavior.

A linear mixed effects model with a fixed effect of throat-fan variant and a random effect of population was used to evaluate the difference in display behavior (PC1) between the three throat-fan variants. Variance was allowed to vary with population to improve the normality and homoscedasticity of model residuals. A *t*-test was used to investigate if the two intermediate-fan populations, which differ substantially in throat-fan morphology, had different display behavior (PC1). Additionally, we compared patterns of variation across populations in two movement components—changes in body position (up-and-down movements) and head turns (side-to-side movements), and examined the relationship between throat-fan area and body position changes across populations. However, we did not perform hypothesis-testing for these comparisons, as these specific patterns were not predicted and were instead observed a posteriori.

The proportion of ground cover was compared across throat-fan variants using a generalized linear mixed effects model (GLMM, *lme4* package; Bates et al., 2014) with a binomial distribution, with a fixed effect of variant and a random effect of site. A GLMM with a negative binomial distribution, with a fixed effect of variant and a random effect of site was used to compare the height of ground cover across throat-fan variants. The site at which the white-fan and colored-fan variants were sympatric was treated as a separate variant category for these two comparisons. A GLMM with a negative binomial distribution, a fixed effect of throat-fan variant and a random effect of population was used to compare perch height at lizards' initial positions across the eight sampled populations. For all models, overall significance of the fixed effect of throat-fan variant was assessed by comparison with a null model in which the term was dropped.

4.4 Results

4.4.1 *Morphology*

Morphology was measured from an average of 23.4 males (range: 17–26) and 20.0 females (range: 16–24) per population (see Tables S1, S2 in Appendix 4 for sample sizes and summary statistics). Fan-throated lizards are small, with a mean SVL (± SD) of 53 ± 9 mm for males and 49 ± 4 mm for females across all populations. However, both size and the degree of SSD varied substantially across populations (Figure 4.3).

Males of the colored-fan variant were larger than males of the intermediate-fan variant ($\beta = 0.24 \pm 0.05$, $t_5 = 4.56$, $P = 0.006$) and the white-fan variant ($\beta = 0.31 \pm 0.05$, $t_5 = 6.58$, $P = 0.001$), but SVL did not differ between white-fan and intermediate-fan variant males ($t_5 = 1.30$, $P = 0.25$). Comparing the two intermediate-fan populations, males were larger in the southern population (Man) than in the northern population (Vad; $t_{32.5} = 8.33$, $P < 0.001$).

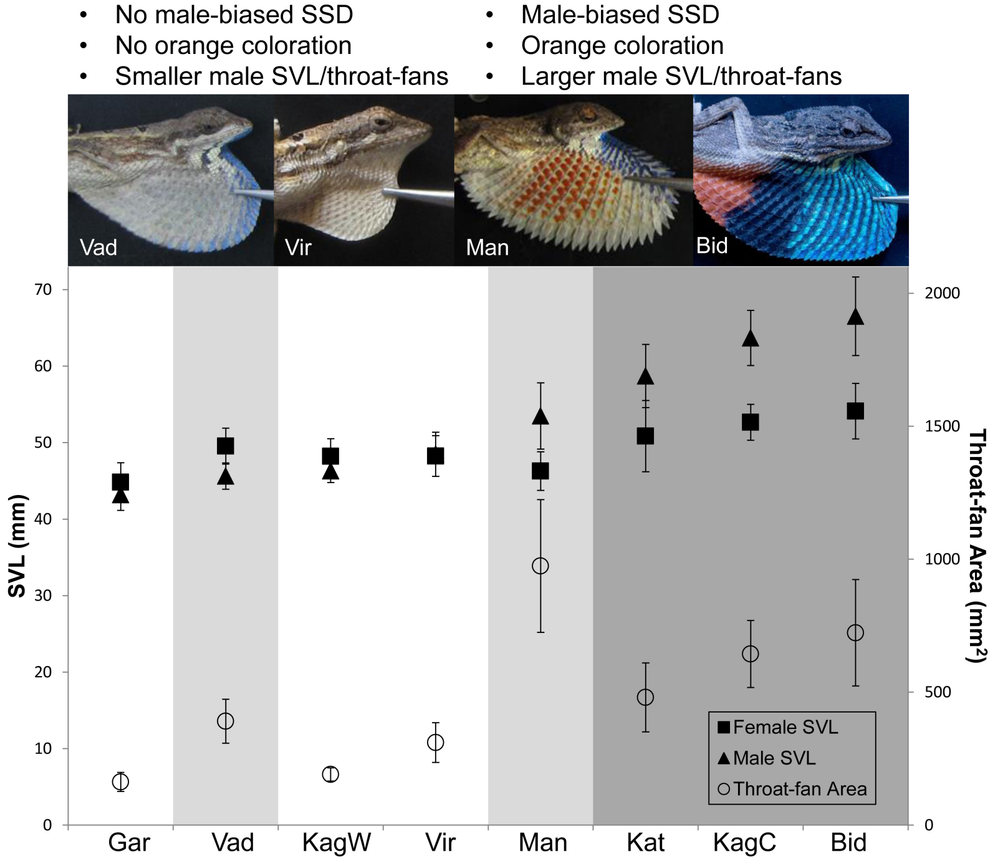

Figure 4.3 Sexual size dimorphism (SSD) in the snout-vent length (SVL) and variation in throat-fan area in sampled populations of fan-throated lizards, including photographs of representative individuals from the white-fan variant (Vir), colored-fan variant (Bid), and the northern (Vad) and southern (Man) intermediate-fan populations depicting variation in throat-fan coloration. Populations are arranged in order of increasing male SVL.

Body size differed between males and females in seven of the eight populations, ranging from males being 4% smaller to 23% larger than females (Figure 4.3). Male-biased SSD was observed in all three colored-fan populations (Bid: $\alpha = 0.007$, $t_{42.4} = -9.49$, $P < 0.001$; Kat: $\alpha = 0.006$, $t_{35.0} = -10.54$, $P < 0.001$; KagC: $\alpha = 0.008$, $t_{27.7} = -10.48$, $P < 0.001$) and the southern intermediate-fan population (Man: $\alpha = 0.01$, $t_{39.6} = -6.98$, $P < 0.001$). Sexual size dimorphism was female-biased in two white-fan populations (Gar: $\alpha = 0.025$, $t_{42.4} = 2.44$, $P = 0.019$; KagW: $\alpha = 0.017$, $t_{27.9} = 2.85$, $P = 0.008$) and the northern intermediate-fan population (Vad: $\alpha = 0.013$, $t_{24.9} = 5.79$, $P < 0.001$). Male and female body size did not differ from one another in the remaining white-fan population (Vir: $\alpha = 0.05$, $t_{48} = -0.30$, $P = 0.76$). The degree of SSD differed significantly across populations (population × sex interaction: $F_7 = 43.8$, $P < 0.001$).

Throat-fans varied substantially across populations in both size and coloration (Figure 4.3). Throat-fan area was smaller in males of the white-fan variant than in males of the colored-fan variant ($\beta = 1.04 \pm 0.24$, $t_5 = 4.26$, $P = 0.008$) and the intermediate-fan variant ($\beta = 1.05 \pm 0.27$, $t_5 = 3.81$, $P = 0.01$), though throat-fan area did not differ between the colored-fan and intermediate-fan variants ($t_5 = 0.04$, $P = 0.97$). Comparing the two intermediate-fan populations, throat-fan area was larger in males in the southern population (Man) than in the northern population (Vad; $t_{32.5} = 8.33$, $P < 0.001$). On including SVL as a covariate, I determined that, relative to white-fan populations, the increase in throat-fan area in colored-fan populations was proportionate to the increase in SVL (i.e. there was no difference in the intercepts of the linear relationship between the two variants: $\beta = 0.10 \pm 0.10$, $t_5 = 0.94$, $P = 0.39$). In contrast, the increase in throat-fan area in intermediate-fan populations was disproportionate relative to the increase in SVL ($\beta = 0.80 \pm 0.10$, $t_5 = 7.66$, $P = 0.0006$; Figure S2 in Appendix 4).

In colored-fan populations, throat-fans included blue, black, and orange sections in the front, middle, and rear of the throat-fan; these sections comprised 60 ± 5%, 28 ± 5%, and 12 ± 4%, of the throat-fan area respectively (see Table S2 in Appendix 4 for population averages). Males in white-fan populations could induce a thin margin of blue coloration along the front edge of their throat-fans, but this coloration was not always expressed (area not measured; see also Kästle, 1998;

Patankar et al., 2013). The change in color from white to blue in white-fan populations was observed to take place within seconds, often in the presence of other lizards (pers. obs.); in contrast, throat-fan colors in colored-fan populations were not observed to change. The coloration of the throat-fan differed in the two intermediate-fan populations (Fig. 3). In Vadanemelli in northern Tamil Nadu, throat-fans were white with an inducible blue patch (26 ± 6% of the throat-fan area) toward the front of the throat-fan. In Manimutharu in southern Tamil Nadu, throat-fans were large and white with an inducible blue patch at the front of the throat-fan and an orange patch toward the center and rear of the throat-fan (13 ± 3% and 44 ± 10% of the throat-fan area respectively; see Figure S3 in Appendix 4 for an example of color change on the throat-fan from this population). Lizards in Manimutharu also had enlarged lanceolate scales along the edge of the throat-fan (see also Kratzer, 1980; Kästle, 1998). Reflectance spectra of throat-fan colors were similar in all colored-fan populations (for blue, black, and orange patches) and in all white-fan populations (for white areas; Figure 4.4). However, both blue and orange reflectance spectra differed substantially between colored-fan populations and the southern intermediate-fan population (Man), and white reflectance spectra differed slightly between white-fan populations and the southern intermediate fan population, particularly in the ultraviolet region (Figure 4.4; recall that reflectance data were not collected from the northern intermediate-fan population, Vad). This is at least partially a consequence of the difference in scale margin coloration between the throat-fan variants (note the white scale margins in the Man population; Figure 4.3).

In summary, male-biased SSD, large throat-fan size, and the presence of orange coloration on the throat-fan were found in all three colored-fan populations as well as the southern intermediate-fan population (Man). However, the southern intermediate-fan population differed from the colored-fan populations in both reflectance spectra and the relationship between SVL and throat-fan area. In the remaining populations (white-fan populations and the northern intermediate-fan population), males were smaller in size and bore smaller dewlaps lacking orange coloration, and male-biased SSD was not observed.

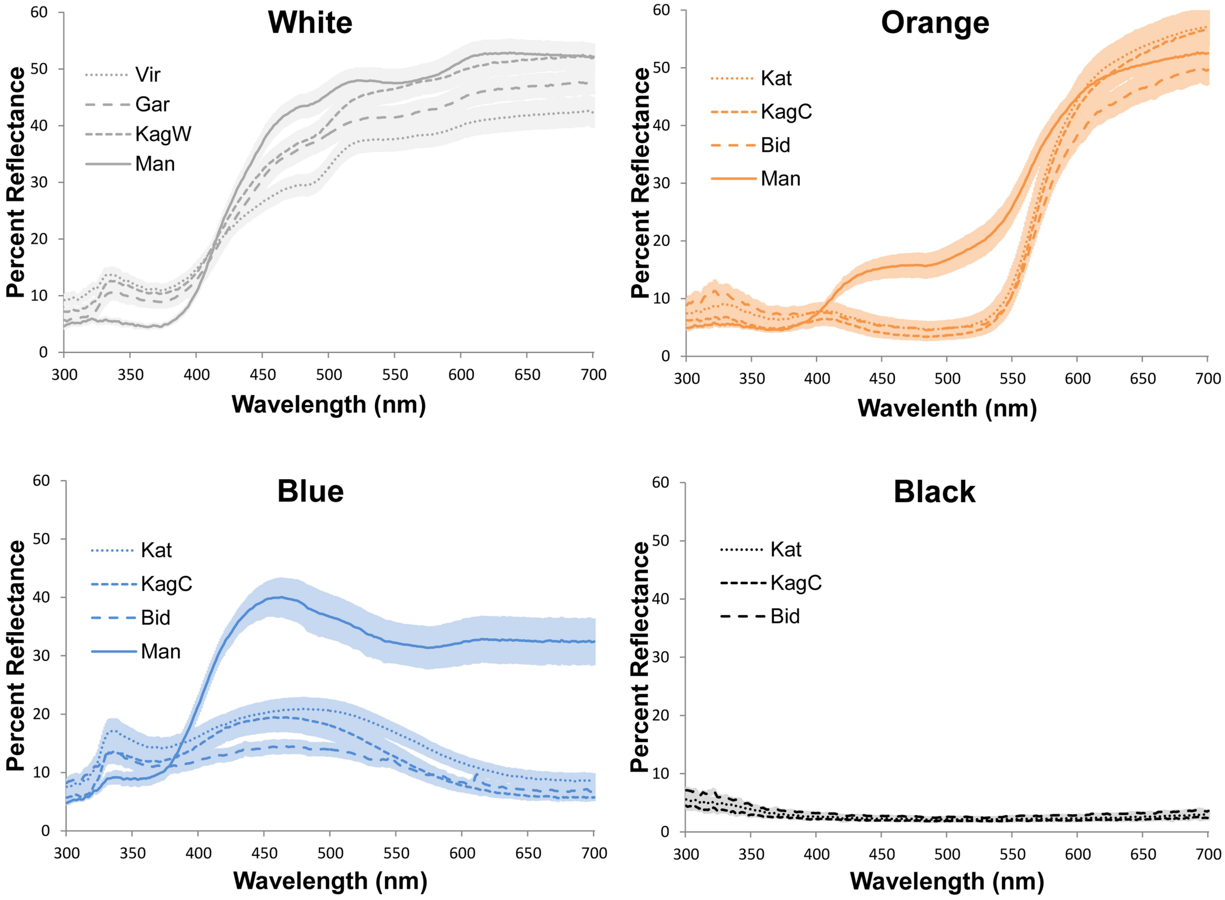

Figure 4.4 Mean and 95% confidence intervals of reflectance spectra from all populations except the northern intermediate-fan population (Vad). Solid lines indicate mean reflectance spectra from the southern intermediate-fan population (Man; for the white, blue, and orange spectra), while broken lines indicate mean reflectance spectra for the white-fan populations (for the white spectra) populations or the colored-fan populations (for the blue, black, and orange spectra).

4.4.2 Display Behavior

Display behavior was observed for an average of 20.1 males per population (range: 14–25). Displays comprised 1–112 throat-fan extensions, and ranged from 0.04 s to over 2 min in duration.

Principal component 1 had absolute values of loadings > 0.10 for most variables (Table 4.1; see Table S3 in Appendix 4for loadings of subsequent principal component axes) and differed significantly between the throat fan variants ($\chi^2_{(2)} = 25.6$, $P < 0.001$). In particular, PC1 differed between the colored-fan variant and the white-fan and intermediate-fan variants (colored-fan vs. white-fan: $\beta = 3.21 \pm 0.32$, $t_5 = 10.1$, $P < 0.001$; colored-fan vs. intermediate-fan: $\beta = 3.22 \pm 0.35$, $t_5 = 9.20$, $P < 0.001$; Figure 4.5). However, the white-fan and intermediate-fan displays did not differ from one another ($t_5 = 0.06$, $P = 0.95$). Display behavior did not differ between the two intermediate-fan populations ($t_{35.1} = 0.85$, $P = 0.40$). Loadings of the behavioral variables on PC1 indicate that displays in colored-fan populations included more partial and complete throat-fan extensions, as well as more turns and modifiers, but fewer changes in body position. Moreover, though individual displays in colored-fan populations were longer, the number of displays per unit time and the proportion of time spent displaying were lower compared with white-fan and intermediate-fan populations. Examples of displays of each throat-fan variant (including both northern and southern populations of the intermediate-fan variant) are included as supplementary material (videos S1a– d; links in Appendix 4).

Table 4.1 Loadings of 12 behavioral variables on Principal component 1.

Variable	**Variable Description**	**PC1 Loading**
Mean display duration (s)	The length in s from the beginning of the first throat-fan extension to the end of the last extension. Throat-fan extensions separated by >10s were considered to belong to separate displays.	-0.47
Proportion of time spent displaying	Sum of all display durations divided by the total time the individual was observed.	0.32

Table 4.1 Loadings of 12 behavioral variables on Principal component 1. (Continued)

Number of displays per unit time observed	Total number of displays (as defined above) divided by the total time the individual was observed	0.25
Number of partial throat-fan extensions	Partial throat-fan extensions were defined as extensions in which the angle between the top margin of the throat-fan and the bottom of the lizard's jaw was >90°. See Figure 2.	-0.37
Number of complete throat-fan extensions	Complete throat-fan extensions were defined as extensions in which the angle between the top margin of the throat-fan and the bottom of the lizard's jaw was ≤90°. See Figure 2.	-0.40
Number of linked throat-fan extensions	Throat-fan extensions in which a second extension was begun before a previous extension was completed (i.e. before the throat-fan was completely retracted) were considered linked.	0.03
Number of turns	Number of side-to-side change in the position of the head and upper body of the lizard conducted during a display.	-0.38
Changes in body position	A change in the angle between the ventral surface of the lizard's body and the substrate between the following angle intervals: 0°-30°; 30°-60°; 60°-90°; >90°. See Figure 2	0.16
Raised nuchal crest	Coded as a binary variable.	-0.19
Raised dorsal crest	Coded as a binary variable.	-0.11
Presence of bipedality	Coded as a binary variable (did the lizard's front legs not touch the substrate at any point during the display).	-0.28
Presence of tail raises	Coded as a binary variable (whether or not the tail was raised off the substrate at any point during the display).	-0.13

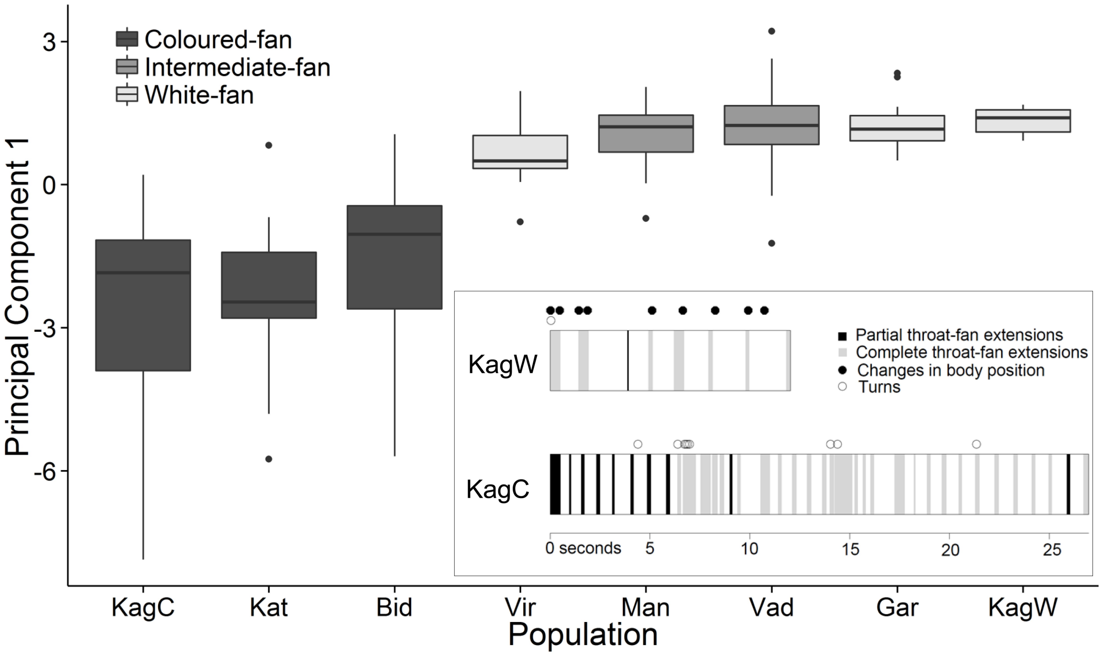

Figure 4.5 Variation in display behavior, as measured by the first axis in a principal components analysis on 12 behavioral variables (see Table 1 for loadings) among the three throat-fan variants. Inset: representative displays from the populations with the greatest difference in mean PC1. The individuals from the white-fan and colored-fan populations in Kagal whose displays are depicted here have PC1 values of 1.57 and -1.54 respectively.

Fan-throated lizards' displays include two striking movement components—changes in body position (up-and-down movements) and head turns (side-to-side movements; Figure 4.2). Populations varied in the frequency at which these two movement components are deployed (Figure 4.6), and this variation can be linked to among-population variation in dewlap size and coloration. In particular, displays by individuals in populations with larger throat-fans include fewer changes in body position than displays by individuals in populations with smaller throat-fans (estimated slope in linear regression between population means of body position changes against throat-fan area: -0.47 ± 0.23, adjusted $r^2 = 0.32$).

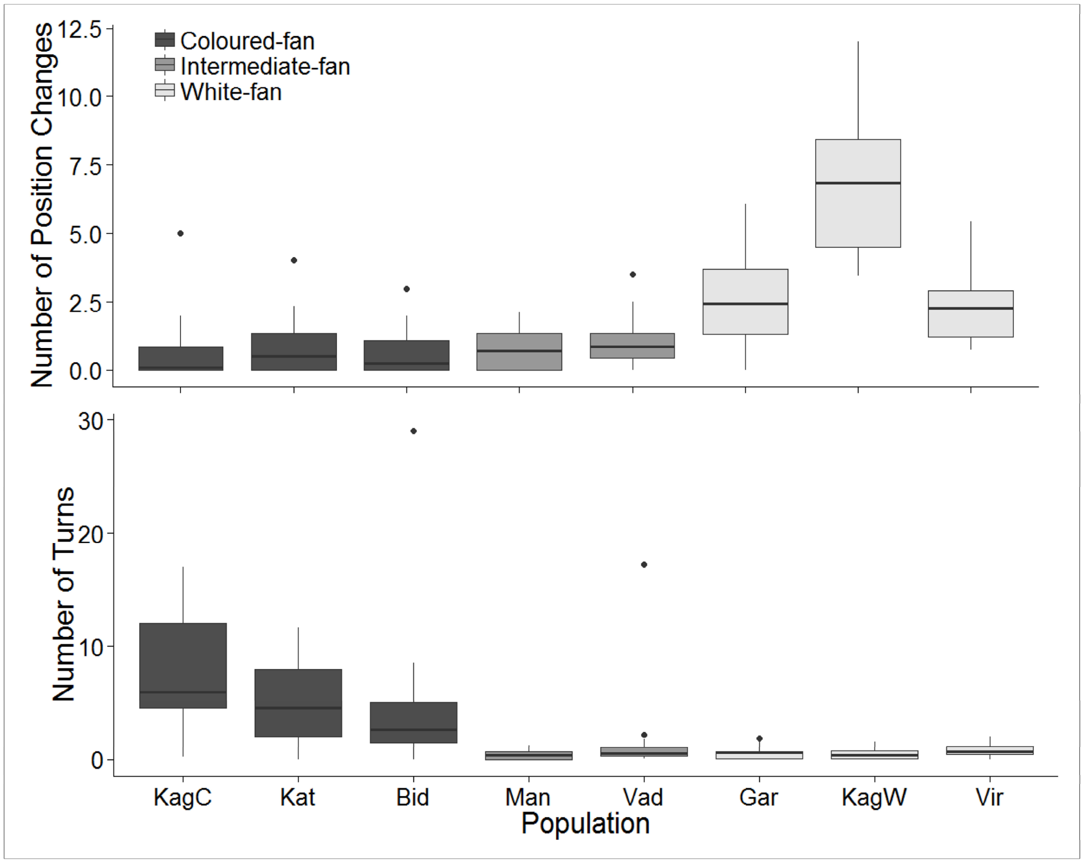

Figure 4.6 Variation among the sampled populations in the number of body position changes (up and down movements) and turns (side to side movements) observed in displays.

4.4.3 Environmental Variables

The proportion and height of ground cover did not differ among the sites in which the different throat-fan variants were found (proportion of ground cover: $\chi^2_{(3)} = 4.40$, $P = 0.22$; height of ground cover: $\chi^2_{(3)} = 3.05$, $P = 0.38$; Figure S4 in Appendix 4). Fan-throated lizards perch low (mean initial perch height across all populations = 18.9 ± 17.5 cm), usually on the ground (modal initial perch height = 0 cm) but also on rocks, vegetation, and piles of mud. Perch height did not differ among throat-fan variants ($\chi^2_{(2)} = 1.94$, $P = 0.38$).

4.5. Discussion

Fan-throated lizard displays include not only extensions and retractions of the throat-fan, but also other movements such as head turns and changes in body position, as well as modifiers such as raised nuchal and dorsal crests, raised tails, and bipedality. The display behavior of colored-fan males differs from the display behavior of white-fan and intermediate-fan males, suggesting that at least part of the variation in the display behavior of the fan-throated lizard is related to the morphological elaboration of the throat-fan. Increased throat-fan size and coloration in the colored-fan populations and one of the intermediate-fan populations is associated with male-biased SSD, but the habitats in which the different throat-fan variants are found today do not differ from each other in ground cover, vegetation height, or the lizards' perch height.

On one hand, the displays of colored-fan variants are distinct from the displays of white-fan and intermediate-fan variants. On the other hand, displays are similar in all white-fan and intermediate-fan populations despite large variation across these populations in throat-fan size and coloration. The association between ornament elaboration and variation in display behavior is therefore not straightforward. The reasons for such a complex association can include the structural constraints imposed and opportunities afforded by changes in throat-fan size and color. In particular, fan-throated lizards' displays include two striking movement components—changes in body position (up-and-down movements) and head turns (side-to-side movements), that vary in frequency among populations (Figure 4.6). This variation points to possible structural constraints that may shape display behavior. For example, the ability of a lizard with a large throat-fan to adopt a body position that is nearly horizontal (body position 1; Figure 4.2) with a fully extended throat-fan must be limited. Indeed, a pattern of displays by individuals in populations with larger throat-fans including fewer changes in body position than displays by individuals in populations with smaller throat-fans was observed. The higher prevalence of head turns in colored-fan populations is also potentially explained by throat-fan morphology, specifically iridescent coloration. Unlike white-fan and intermediate-fan populations, colored-fan variant males express what appears to be iridescent blue coloration on their throat-fans throughout the breeding season (pers. obs; see video S1a). Because the perceived coloration of iridescent surfaces depends on the angles between incident light, the surface, and the viewer (Prum, 2006; Meadows et al., 2011), rapid turning can ensure that most receivers will observe the iridescence irrespective of viewing geometry, and may increase the conspicuousness of the signal. Research on the biomechanics of displays and the visual anatomy of signal recipients (Hebets and Papaj, 2005; Rosenthal, 2007) may reveal proximate explanations for the relationship between display behavior and ornament morphology in fan-throated lizards.

Intricate interactions between multiple types of cells known as chromatophores are responsible for the diversity of colors seen in reptile ornaments and displays (reviewed in Grether et al., 2004). The presence of structural color (iridescent blue), melanin-based color (black), and pteridine- or carotenoid-based color (orange) on their throat-fans, as well as variation in throat-fan size and the size of each color-patch, suggests that many potentially honest signals of male quality may be contained within the fan-throated lizards' display (Grether et al., 2004; Hill and McGraw, 2006), each of which may convey different information to the recipient or act to amplify one another (Hebets and Papaj 2005). Moreover, in addition to rapid changes in blue coloration on the throat-fan in some populations, *Sitana* can change color on many different parts of the body, including the nuchal crest, dorsum, tail, lips, eyelids, and hind legs (see Figure S5 in Appendix 4 for examples; Kästle, 1998). In light of recent research on the complex physiologies underlying color production and change in lizards (Saenko et al., 2014; Teyssier et al., 2015) and comprehensive frameworks for the analysis of coloration in natural populations (Kemp et al., 2015), fan-throated lizards offer a veritable cornucopia to biologists interested in the physiological basis of coloration.

The association across populations of increased throat-fan size and coloration with increased male body size and male-biased SSD strongly suggests that sexual selection has played a role in shaping ornament variation in fan-throated lizards. Male-male competition is often suggested as the mechanism of sexual selection in lizards, and both increased body size and increased ornamentation are expected under stronger male-male competition (Stamps, 1977; Tokarz, 1995). Larger individuals frequently win agonistic interactions against smaller individuals (Stamps, 1977, 1983; Cox et al., 2007), and ornamentation is thought to signal fighting ability to potential competitors (Ord et al., 2001; Vanhooydonck et al., 2005; Whiting et al., 2006; Irschick et al., 2007). The co-elaboration of both male body size and ornamentation is therefore interpreted as evidence for sexual selection via male-male competition (Ord et al., 2001; Stuart-Fox and Ord, 2004; Perez i de Lanuza et al., 2013). However, explicit measurements of the correlations between reproductive success and male body size and ornamentation within populations will be necessary to confirm whether and how sexual selection acts in this system. Also, the correlation between signal components and performance metrics such as bite force (Vanhooydonck et al., 2005; Irschick et al., 2007) will need to be examined in different environmental and social conditions to understand their role in signaling during male-male competition (Bro-Jørgenson, 2009; Lailvaux and Kasumovic, 2011) and other social interactions. More fundamentally, the mating systems of these lizards remain unknown, so we cannot know the precise mechanisms by which sexual selection acts upon them. It will be fascinating to learn if mating systems vary across these different throat-fan variants, possibly as a consequence of variation in ecological factors such as densities and resource distributions (Emlen and Oring, 1977).

The importance of environmental context in driving ornament diversification in fan-throated lizards is difficult to ascertain because these lizards persist today in highly anthropogenically modified environments. Modified habitats, such as the sites sampled in this study, are likely very different from the environments in which these lizards diversified. Nevertheless, the present-day habitats of all three throat-fan variants are similar, and the colored-fan and white-fan variants co-occur in at least one site, suggesting that the throat-fan variants are not restricted to different environmental conditions. Therefore, environmental context likely does not play a role in maintaining variation in ornament morphology in fan-throated lizards, similar to other agamid lizards (e.g. Chen et al., 2012). However, this is in contrast with *Anolis* lizards, which bear a throat-fan that is functionally similar to that of *Sitana* (Ord et al., 2015). Changes in visual environment from xeric to mesic forests are correlated with variation in throat-fan coloration within *Anolis* species that is consistent with selection for maximum conspicuousness of the throat-fan in each habitat (Leal and Fleishman, 2004; Ng et al., 2013). Precise measurements of both the visual environment and throat-fan coloration across a larger sample of populations may reveal similar relationships in fan-throated lizards, but at present, there is little evidence for the importance of environmental context in ornament elaboration in this genus.

Of course, environmental factors other than light environment may also drive ornament elaboration. In particular, variation in predation pressure across populations is expected not only to influence ornament morphology (Stuart-Fox et al., 2003; Husak et al., 2008; McLean et al., 2014) but may also affect how ornaments are deployed in displays. However, it will be challenging to quantify the role of a dynamically displayed ornament in attracting the attention of predators. Also, given the extensive presence of fan-throated lizards in human-modified environments, it may prove tricky to discern how variation in predation pressure has historically influenced throat-fan evolution in *Sitana*, though contemporary effects of predation on conspicuousness and crypsis in these lizards certainly warrant attention.

Although the potential for the throat-fan to function in interspecific communication was not explicitly explored in this study, fan-throated lizards may provide an opportunity for such studies in the future. In populations where closely related taxa are sympatric, signals are often crucial for species recognition (Ryan and Rand, 1993; Panhuis et al., 2001). For example, both throat-fan morphology and patterns of headbobbing differ among sympatric *Anolis* species, likely to facilitate species recognition (Rand and Williams, 1970; Jenssen, 1977; Ord and Martins, 2006). The throat-fan variants of *Sitana*, which belong to different clades (Deepak and Karanth, pers. comm.) and are likely different species (Amarasinghe et al. 2015), are rarely sympatric. The site sampled in this study in which colored-fan and white-fan variants coexist is, to my knowledge, the only recorded occurrence of sympatry between throat-fan variants. The white-fan and colored-fan populations in this sympatric site showed a greater difference in display behavior than any two allopatric throat-fan variant populations (Figure 4.5), suggesting that displays might play a role in species recognition where different *Sitana* coexist. Species delimitations within *Sitana*, as well as fine-scale mapping of the ranges of these species and the locations at which they are sympatric, will determine the utility of this genus in understanding the co-option of a signal used in intraspecific communication for species recognition.

Understanding the systematics of *Sitana* and the phylogenetic relationships among the different throat-fan variants will also shed light on how often the throat-fan has changed in size and color across this genus, as well as its close relatives in the genus *Otocryptis*, some of which also bear throat-fans (Das, 2002; Bahir and Silva 2005). That the colored-fan and intermediate-fan variants of *Sitana* differ in not only the spectral reflectance of blue and orange patches of the throat-fan but also the allometric relationships between body size and throat-fan size suggest the intriguing possibility that ornament elaboration has evolved by different mechanisms, perhaps multiple times, in these lizards.

Very few previous studies have examined the behavioral ecology of fan-throated lizards, despite their ubiquity across drier areas in South Asia (Daniel, 2002; Das, 2002), their high local densities (Shanbhag et al., 2003, Subramanean and Reddy, 2010), and their readily observable display behavior. In this paper, I document an association between throat-fan morphology and display behavior in fan-throated lizards, and show that both sexual selection and structural constraints and opportunities may have shaped the dramatic diversity in the size and coloration of their throat-fans. These results suggest that fan-throated lizards are a promising system in which to further investigate the coevolution of different display components of a striking visual signal.

4.6 Acknowledgments

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Conclusions and Future Directions

In this dissertation, I have argued that paying close attention to individual variation in animals' natural history can influence the ways in which we study their behavioral ecology. I show that natural history is important for understanding the evolution of both poorly known organisms and highly studied organisms whose biology we think we know well. Natural history is also important for understanding variation at both within- and across-population levels of biological organization, and is pertinent to questions of both natural and sexual selection.

In Chapter 1, I showed that in nearly a century of research on *Anolis* lizards' social organization, individual variation in movement behavior was ignored in favor of fitting observations into the framework of territoriality, thus limiting our understanding of *Anolis* mating patterns. This research shows not only the substantial consequences of what Emlen (1958) called the "tyranny of words," but also demonstrates the challenges of escaping such tyranny. Though the genesis of this interrogation of territoriality in *Anolis* lay in genetic data, its resolution lay in paying attention to the individual variation in movement behavior that was either undetectable or documented but ignored in previous research. Knowing *a priori* the extent to which such tyrannical rule of ideas is widespread or consequential in behavioral ecology is almost impossibly difficult, but repeatedly traversing the feedback loop between hypothesis-free natural history research and hypothesis-driven investigations of behavioral ecology offers us a way to not only diagnose the extent of this tyranny but also discover how to overthrow it in the context of a particular biological puzzle.

In Chapter 2, I quantified and analyzed the movement patterns of male and female *A. sagrei* in a manner that is independent of territoriality, and showed that such an approach predicts that females encounter, and thus have the opportunity to mate with, multiple males; as discussed in Chapter 1, female multiple mating has been a point of some confusion and contention in previous research in *Anolis* lizards. Moreover, I find that males who move more widely, as well as larger males, encounter more females, suggesting the opportunity for sexual selection on both body size and movement behavior. Ongoing work in this system includes determining the reproductive success of males to quantify the extent to which this opportunity for sexual selection is realized, and thus inferring the role of social interactions and post-copulatory mate choice in bridging the gap between movement patterns and mating patterns. Again, a return to careful natural history observations in future studies is called for. What will our descriptions of male-male and male-female interactions look like without the terminology of territoriality to lean on? It will be imperative, in these future descriptions, to try to resist what Emlen (1958) called "the dangers inherent in patterned thinking." In particular, we will need to avoid the temptation to categorize or discretize what is often continuous variation in behavioral and morphological traits, which has proven to be a constraint in past research on mating systems (e.g. "territorial" vs. "sneaker" or "floater" males). Furthermore, needless to say, similar quantifications of movement behavior and social interactions should be carried out in a range of species and populations, occupying different habitats with different resource distributions, densities, sex ratios, and predation pressures. We still have a long way to go before we understand what sexual selection looks like in *Anolis* lizards.

In Chapter 3, I showed that individuals within a population of *A. sagrei* are specialized in their habitat use, but their morphology is not correlated with habitat use in the ways that we would predict based on across-species and across-population ecomorphological correlations in *Anolis*. Instead, male perch height was correlated with male body size, indicating a possible role for male-male agonistic social interactions in shaping the daily perch use choices of animals in this population. These results point to the importance of integrating social interactions as selective pressures into studies of natural selection. At the risk of sounding like a broken record, the relevance of such an integration is clear when documenting natural history—watching an animal go about its day, it is impossible to escape the conclusion that it behaves in ways that influence and are influenced by not only its survival but also its reproduction. Moreover, it is likely that habitat use-morphology relationships within populations vary across populations with different competition and predation regimes, and future work examining these interacting effects, ideally in an experimental context, will clarify the pathways that anoles have followed from individual interactions within populations to adaptive diversification across the whole clade.

Finally, in Chapter 4, I show that sexual selection has likely played a role in the phenotypic diversification of the fan-throated lizard species complex. The utility of basic natural history descriptions here is obvious—we cannot discover anything about the behavioral ecology of animals about which we know next to nothing. However, I hope that this work demonstrates that natural history descriptions can be integrated into broad hypothesis-testing frameworks derived from our knowledge of better-studied organisms, thus appeasing even those biologists who consider descriptive or exploratory research anathema. The downside of this approach, however, is that "knowledge" of better-studied organisms is not fixed and may not even be well-founded, as seen in Chapters 1 and 2. In any case, the research presented here on *Sitana* display behavior and ornament morphology provides a starting point for a variety of research trajectories on these little-studied animals, including investigating the evolution of ornament variation and color signaling, biomechanical co-constraints on display behavior, the potential co-option of an intraspecific signal for interspecific interactions, as well as more fine-scale questions about why and how sexual selection varies across populations of these lizards in ways that shape their diversification.

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Appendices

Appendix 1

A list of all the papers examined in our historical investigation of territorial polygyny (Chapter 1) in *Anolis* lizards, in alphabetical order. We searched for papers on Web of Science using keywords "*Anolis*" or "*Norops*" and "territor*". From the results, we selected papers that were directly relevant to *Anolis* territoriality, in that the authors studied male-male aggression or site fidelity, including mapping home ranges, or based their study or discussion of *Anolis* social or reproductive behavior on prior conclusions of territoriality. We also followed relevant citations from within the sampled papers, yielding a set of 106 papers that spanned over nine decades and included field- and lab-based studies, as well as conceptual papers and reviews.

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Appendix 2.1

Interpolating movement patterns (Chapter 2)

We interpolated the movement patterns of individual lizards between known observations based on a Markov chain model. To calculate the transition probability matrix, we applied an exponential decline function ($P(d) \propto e^{\lambda d}$) to the matrix of distances between all locations in the site at which lizards were observed plus all trees within the site (318 locations in total), with rows then normalized to sum to one. The value of λ was estimated by maximizing the likelihood of the observed data, with separate models generated for males ($\lambda = -0.78$) and females ($\lambda = -1.27$).

Though a Markov chain is memoryless, the interpolation was not—the calculated probability of observing a lizard at a particular place at a particular time depended not only on where that lizard was seen previously but also where it was seen next. However, the influence of the observed data extended only to the previous and the next observation. In other words, if a lizard was observed at a particular location, its subsequent path was not modelled to depend on how it got to that location. Let **M** be the transition matrix of the Markov chain model, and let an individual lizard have been observed at location A_m at time T_m and then at location A_n at time T_n. We calculated the probability that that individual was found at a particular location (L) at an intermediate time step ($T \in (T_m, \ldots, T_{n-1})$) as follows:

$$P(L, T | A_m, T_m, A_n, T_n) = \frac{\mathbf{M}^{T-Tm+1}[A_m, L] \times \mathbf{M}^{Tn-T+1}[L, A_n]}{\sum_{i=1}^{318} \mathbf{M}^{T-Tm+1}[A_m, A_i] \times \mathbf{M}^{Tn-T+1}[A_i, A_n]} \qquad \text{(Equation 1)}$$

For times preceding the first observation and following the last observation, lizards were assumed to as being equally likely to be anywhere in the site (i.e. the appropriate row or column of the transition matrix in equation 1 was replaced by a unit vector).

To estimate encounters between pairs of lizards, we multiplied the probability matrices for each pair of lizards, and summed probabilities across all locations for each hour. Probabilities were summed across locations to capture as encounters those time steps at which two individuals were moderately likely to co-occur at multiple locations. Observed encounters, defined as a pair of lizards observed in the same location within one hour of each other, were used to set cutoffs for the minimum total probability of co-occurrence in a particular time step. Because the probability of remaining in a particular location within an hour depends on the distance of that location to nearby locations, we set cutoffs based on the mean distance to the ten closest locations from the locations at which co-occurrences were observed. We binned minimum distances from locations of known co-occurrences into 1 m increments, and set the minimum probability of an observed co-occurrence in each bin as a cutoff for estimating encounters in the remainder of the dataset (Figure A2.1.1). For each time step, the minimum of the mean closest distances to the locations of the previous and next observations was used to set probability cutoffs for defining co-occurrences.

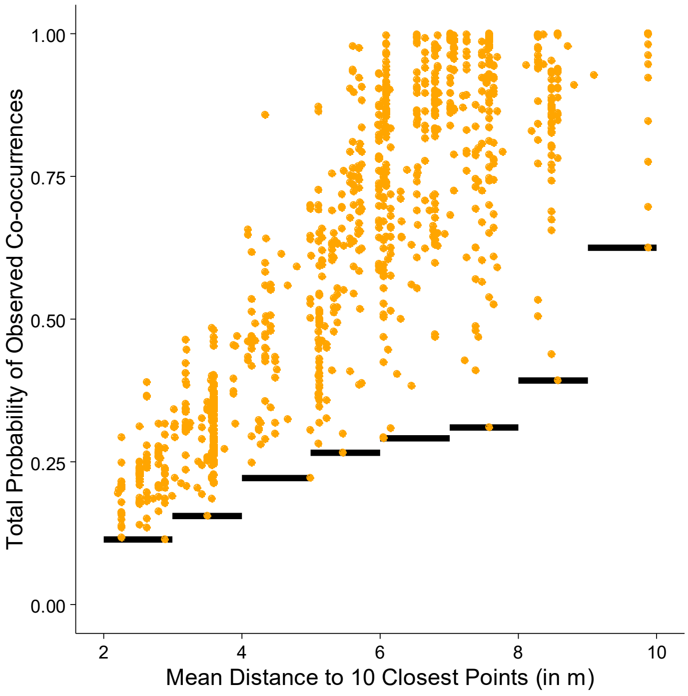

Figure A2.1.1 Cutoffs (black lines) for defining encounters, based on the mean distance from each location to the ten closest locations. Points indicate the sum of probabilities of co-occurrences across all locations, for pairs of individuals at hours where the two were observed at the same location within an hour of one another.

Appendix 2.2

Sampling area and duration of previous studies on *Anolis* home ranges (Chapter 2)

Full citations for all the studies below can be found in Appendix 1. Note that though the median duration is 3.5 weeks, a more conservative value of 4 weeks was used in the subsampling analysis in Chapter 2.

Study	**Sampling Area (in m^2)**	**Sampling Duration (in weeks)**
Evans 1938a	150000	3
Greenberg and Noble 1944	25	47
Gordon 1956	400	52
Sexton et al. 1963	200	4
Rand 1967a	425	5
Jenssen 1970	930	8
Jackson 1973	14000	1
Philibosian 1975	420	0.2
Stamps 1977	9.5	5
	34	13
	47	13
	37	15
Hicks and Trivers 1983	12000	9
Ruby 1984	441	28
Fleishman 1988	169	10
Jenssen and Nunez 1998	36	1
Tokarz 1998	137	5
Pereira et al. 2002	12	1
	70	1
Paterson 2002	400	1
McMann and Paterson 2003	400	1
Calsbeek 2009	1500	2
Johnson et al. 2010	500	3
Nicholson and Richards 2011	14000	52
Bush et al. 2016	875	3
Schoener and Schoener 1982	100	–
Fitch and Henderson 1976	–	1
Fitch and Henderson 1987	–	2
Fobes et al. 1992.	–	1.5
Median	**400**	**3.5**

Appendix 2.3

Estimating male growth rates (Chapter 2)

Sixty eight males were recaptured and their snout-vent length (SVL) re-measured a total of 94 times, with 32 ± 15 (mean ± SD) days elapsed between measurements. We estimated the growth curve of males in this population by fitting the following logistics equation to the observed data using nonlinear least squares regression (Schoener and Schoener 1978):

$$\mathrm{L2} = \frac{\mathrm{a L_1}}{\mathrm{L_1} + (\mathrm{a} - \mathrm{L_1}) e^{\mathrm{rD}}}$$

where L_1 and L_2 are the SVL of an individual measured at two successive captures, and D is the number of days between the two captures. We estimated a = 63.7 and r = -0.016. SVLs predicted by the model were highly correlated with measured SVLs ($r^2 = 0.92$; Figure A2.3.1).

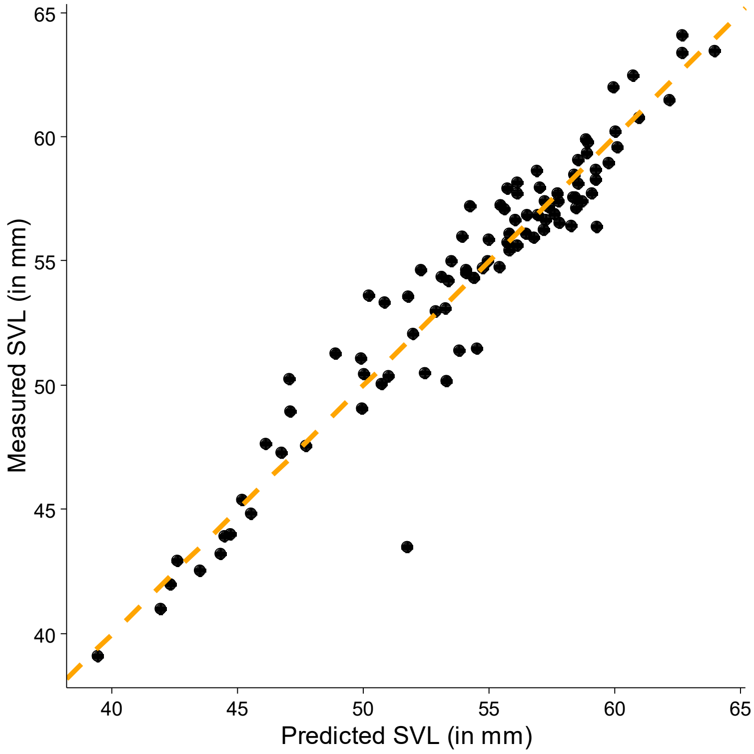

Figure A2.3.1 Snout-vent length (SVL) predicted by the logistic growth curve were highly correlated with observed measurements that were used to fit the model. The orange dashed line has an intercept of 0 and a slope of 1.

Appendix 4

<u>Supplemental information for Chapter 4</u>

(As published in the *Journal of Herpetology* 50: 394 – 403 [2016])

Supplementary Tables

Table S1. Sample sizes for the morphological datasets and mean mass and SVL for males and females from the eight populations sampled in this study.

Population	Throat-fan Variant	Sex	Sample Size	Mass (mean ±SD; in g)	SVL (mean ±SD; in mm)
Bidnal	Colored-fan	Female	20	4.7 ± 0.9	54.1 ± 3.6
		Male	25	8.3 ± 1.8	66.5 ± 5.1
KagalC	Colored-fan	Female	16	4.0 ± 0.6	52.6 ± 2.3
		Male	17	6.6 ± 1.3	63.7 ± 3.6
Katyayini	Colored-fan	Female	24	3.3 ± 0.5	49.0 ± 2.0
		Male	25	5.4 ± 1.1	58.7 ± 4.1
Garade	White-fan	Female	23	2.7 ± 0.4	44.8 ± 2.5
		Male	26	2.4 ± 0.4	43.2 ± 2.1
KagalW	White-fan	Female	17	3.6 ± 0.6	48.2 ± 2.3
		Male	17	3.1 ± 0.3	46.3 ± 1.5
Virani	White-fan	Female	24	3.2 ± 0.6	48.3 ± 2.7
		Male	26	3.2 ± 0.6	48.5 ± 2.9
Manimutharu	Intermediate-fan	Female	20	3.1 ± 0.6	46.3 ± 2.5
		Male	25	4.3 ± 0.9	53.5 ± 4.3
Vadanemelli	Intermediate-fan	Female	16	3.9 ± 0.5	49.6 ± 2.4
		Male	26	2.5 ± 0.3	45.6 ± 1.7

Table S2 Mean throat-fan area, and percentage of throat-fan area that is blue, black, or orange, by population.

Population	Throat-fan Variant	Throat-fan area (mean ± SD; in mm^2)	Percentage of Blue Area (mean ± SD)	Percentage of Black Area (mean ± SD)	Percentage of Orange Area (mean ± SD)
Bidnal	Colored-fan	723 ± 200	61% ± 4%	28% ± 5%	10% ± 3%
KagalC	Colored-fan	644 ± 126	58% ± 6%	28% ± 6%	14% ± 2%
Katyayini	Colored-fan	480 ± 130	61% ± 4%	27% ± 4%	13% ± 4%
Garade	White-fan	163 ± 36	—	—	—
KagalW	White-fan	191 ± 25	—	—	—
Virani	White-fan	311 ± 75	—	—	—
Manimutharu	Intermediate-fan	975 ± 250	13% ± 3%	—	44% ± 10%
Vadanemelli	Intermediate-fan	391 ± 83	26% ± 6%	—	—

Table S3 Loadings of principal component axes explaining >10% of variation in display behavior.

Variable	PC1 Loading	PC2 Loading	PC3 Loading
Proportion Variation explained	31%	15%	12%
Mean display duration (s)	-0.47	0.09	0.07
Proportion of time spent displaying	0.32	0.04	0.48
Number of displays per unit time observed	0.25	0.09	0.58
Number of partial throat-fan extensions	-0.37	0.24	0.32
Number of complete throat-fan extensions	-0.40	0.01	-0.09
Number of linked throat-fan extensions	0.03	0.03	-0.22
Number of turns	-0.38	0.22	0.09
Changes in body position	0.16	-005	-0.38
Presence of raised nuchal crest	-0.19	-0.63	0.12
Presence of raised dorsal crest	-0.11	-0.67	0.11
Presence of bipedality	-0.28	-0.04	0.25
Presence of tail raises	-0.13	0.11	-0.16

Supplementary Figures

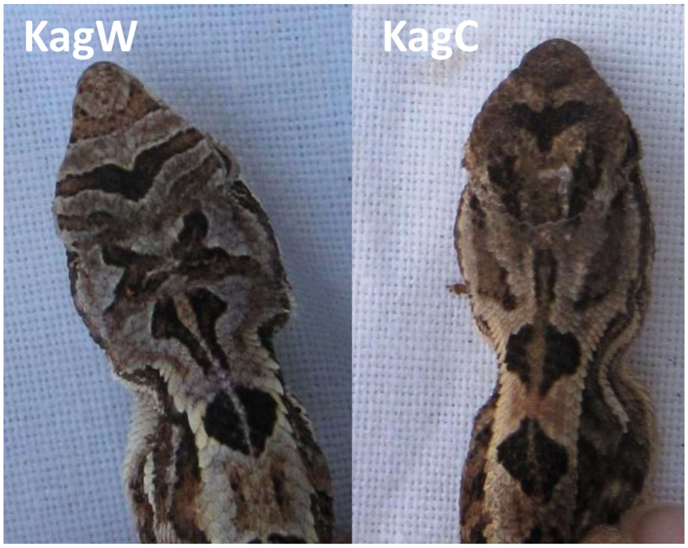

Figure S1 Examples of head pattern and shape of white-fan (KagW) and colored-fan (KagC) individuals in Kagal, where the two throat-fan variants were sympatric.

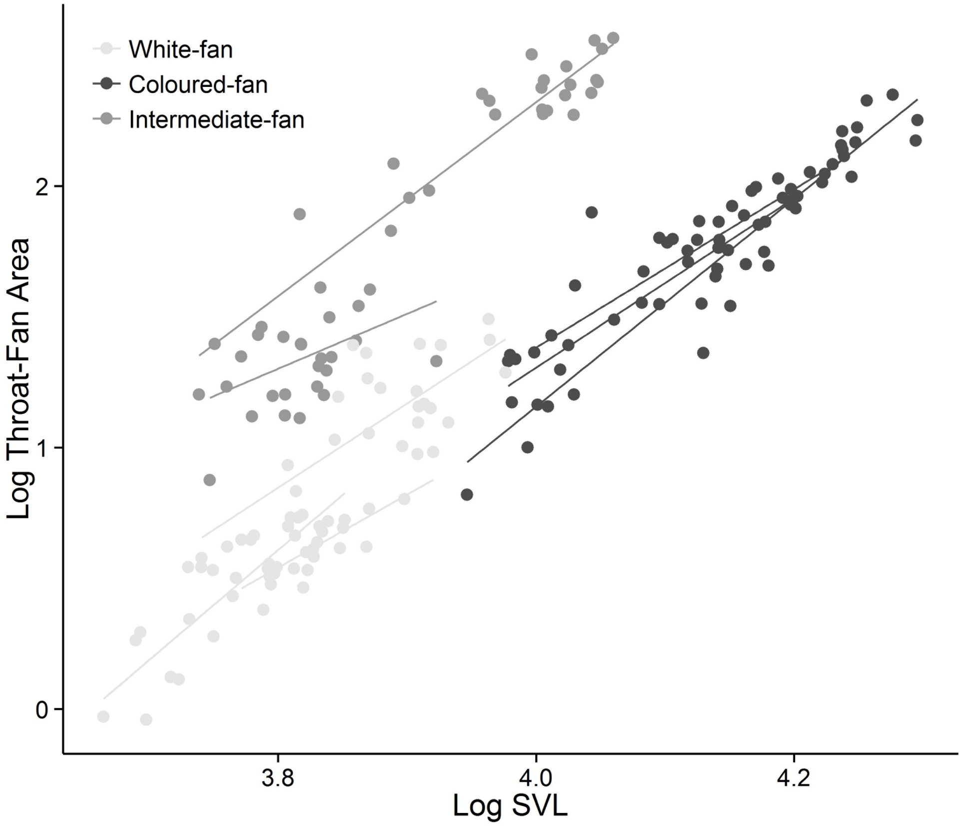

Figure S2 Linear relationships between SVL and throat-fan area in white-fan, intermediate-fan, and colored-fan populations.

0 seconds 35 seconds 520 seconds

Figure S3 An example of the changing extent of blue coloration on the throat-fan with time, in an individual in the Manimutharu population (southern population of the intermediate-fan variant).

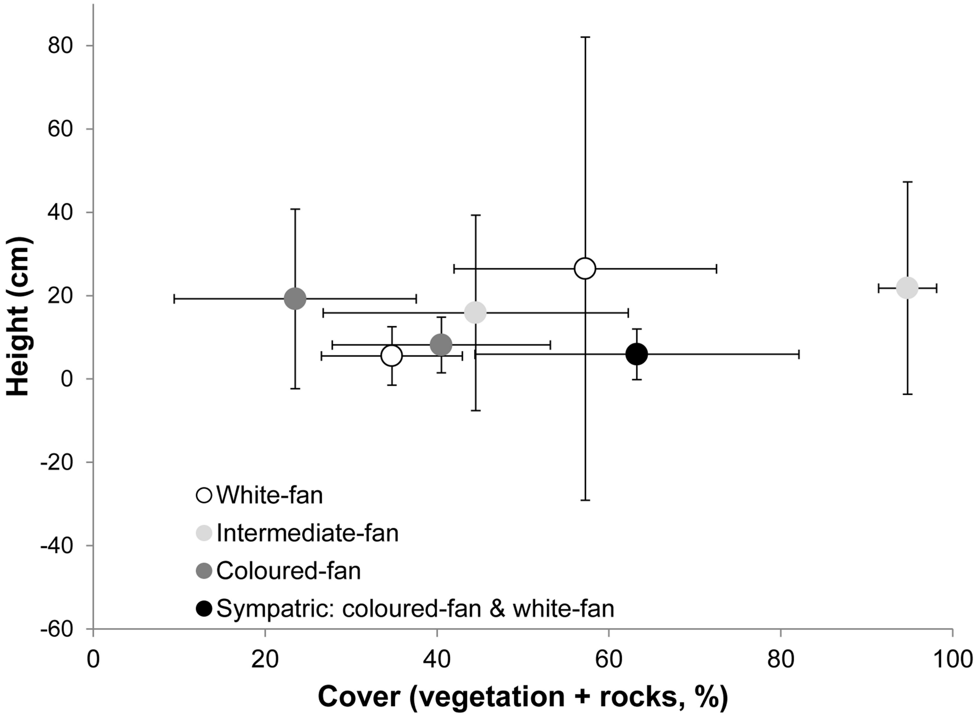

Figure S4 Mean (± standard error) proportion and height of ground cover, sampled along random transects in each site.

Figure S5 Examples of coloration induced at various different locations on male fan-throated lizards, including the lips (A, B), eyelids (B, C), dorsum and tail (D, G), and the nuchal crest (E, F). Photographed individuals are from Kagal (A, B), Manimutharu (C), Bidnal (D), and Virani (E, F, G).

Supplementary Video Links

Video S1 Examples of displays from the (a) colored-fan variant (Katyayini population); (b) white-fan variant (KagalW population); (c) intermediate-fan variation (northern Vadanemelli population) and (d) intermediate-fan variant (southern Manimutharu population). For the colored-fan variant, the video is also repeated at 0.25X speed to better discern the head-turning behavior and iridescent coloration.

Links to Supplementary Videos:

S1a: http://youtu.be/2ojPVIkrvXk

S1b: http://youtu.be/4VUzjiZwPhM

S1c: http://youtu.be/91nFxQV2_Nk

S1d: http://youtu.be/uQ7rsBBbkXQ