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Jackson College of Graduate Studies

**EFFECTS OF HABITAT COMPLEXITY ON MALE SOCIO-SPATIAL
BEHAVIOR AND MATING SYSTEM DYNAMICS IN COLLARED LIZARDS**

A THESIS

SUBMITTED TO THE GRADUATE FACULTY

In partial fulfillment of the requirements

For the degree of

MASTER OF SCIENCE IN BIOLOGY

By

Cody A. Braun

Edmond, Oklahoma

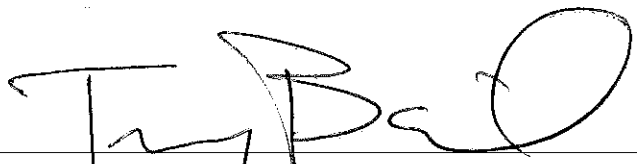
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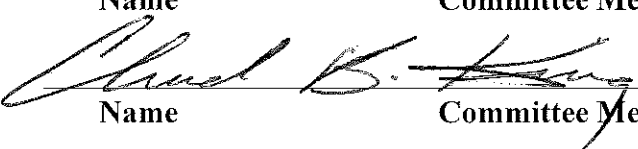
A THESIS

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ABSTRACT OF THESIS

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TITLE OF THESIS: Effects of Habitat Complexity on Male Socio-Spatial Behavior and Mating System Dynamics in Collared Lizards

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ABSTRACT: Territory defense typically involves costly behavioral tactics that may detract from mating opportunities and other fitness enhancing activities. Selection on males therefore is expected to result in their establishing territories and adopting behavior patterns that maximize mating opportunities while simultaneously minimizing costs of spatial defense, which may vary among microhabitat patches that differ in physical parameters such as size, shape, and structural complexity. Using field behavioral studies, I first tested the influence of microhabitat patch structure (simple versus complex) on social and spatial behavior in territorial and non-territorial male eastern collared lizards (*Crotaphytus collaris*). As a result of markedly different structural conditions in the two microhabitat types, I proposed two alternative sexual selection models to explain factors that may govern male behavior and fitness. Despite the relatively small size and narrow dimensions of simple microhabitats, lizards colonized both simple patches, resulting in high local densities. Nevertheless, some males still defended territories on simple patches, and they did so without initiating contests with rivals or giving broadcast

displays more frequently than territorial individuals on complex patches. By contrast, territorial males on simple patches moved throughout their territories more, and also courted a greater number of females more frequently than territorial males on complex patches. Non-territorial males in the two microhabitat types did not differ in any of the social variables measured. Increased visibility owing to the relatively flat and unobstructed surface topography of simple patches appears to promote increased courtship opportunities, while at the same time allowing males to deter same-sex competitors without significantly increasing costly defensive behaviors. Moreover, prioritization of courtship in highly competitive neighborhoods suggests that male behavior is shaped more by opportunities to interact with females than by competition for intrasexual dominant social status, perhaps because proximity to females coupled with simple habitat structure promotes monopolization of female mates.

Although sexual selection theory predicts that socially dominant males will sire more offspring than males adopting subordinate social tactics, increased structural complexity of microhabitats may compromise the ability of territory owners to detect non-territorial rivals and prevent them from mating with female residents. To test the hypothesis that the ability of males to monopolize matings with females is negatively related to the structural complexity of microhabitats, I used molecular genetic techniques to quantify reproductive success for territorial and non-territorial males in each microhabitat type. Consistent with this prediction, males defending territories on simple patches sired a greater proportion of the offspring produced by individual mates compared to territorial males on complex patches. Contrary to the expectation that increased mate monopolization by territorial males would decrease mating opportunities

for non-territorial males, neither the total number of offspring sired, nor the number of female mates differed as a function of male social status on simple patches, most likely as a result of high local female densities. By contrast, territorial males on complex patches sired more offspring total than their non-territorial rivals, and also tended to mate with more females (but not statistically so). The observation that territorial males on simple microhabitats sired a larger proportion of the offspring produced by their female mates compared to territorial males on complex patches suggests that mate monopolization may be more feasible in microhabitats that are less structurally complex because they afford territory owners high visibility while also limiting undetected movement by non-territorial males. Higher levels of mate monopolization without increased defense costs suggests that territory defense may be more economical in structurally simple microhabitats. Because the simple human-constructed microhabitats at this study site mimic some features of the natural rock outcrops and washes on which the socio-spatial behavior of collared lizards evolved, these results are more similar to what might be expected in populations in natural habitats.

THESIS INTRODUCTION

Male and female animals differ greatly in the amount of energy that they invest per gamete (Trivers 1972). Because their initial investment per sperm is small, males are capable of producing large numbers relatively quickly and inexpensively, whereas females make significantly fewer eggs because each requires a much larger investment of resources. Male reproductive potential, therefore, usually is not limited by their ability to produce sperm, but instead by the availability of fertile females (Bateman 1948; Arnold & Duvall 1994; Collet et al. 2014). By contrast, female reproductive success generally is not limited by the availability of sperm, but by the anatomical and physiological constraints of egg production. The energetic and temporal disparity in the parental investment patterns of the sexes is even greater in amniotes because females must allocate additional time and energy while carrying developing eggs after they have been fertilized. As a result, female amniotes are temporarily removed from the mating pool following fertilization, whereas males are able to return almost immediately to seek additional mates because sperm can be readily replenished (Clutton-Brock & Parker 1992). Differences in the amount of time invested per offspring, therefore, can create a marked male-biased asymmetry in the ratio of reproductively active males to receptive females within local populations (operational sex ratio; Emlen & Oring 1977). As a consequence of marked differences in pre- and post-fertilization investment by the sexes in individual offspring, females usually are the limiting sex and may become a resource for which males compete (Trivers 1972).

Because they are usually the limited sex, males sometimes engage in direct competition with one another in order to increase the number of females with which they

can mate. Intrasexual competition can range from intense physical contests to advertisement using stereotypical display patterns (Marden & Waage 1990; Baird et al. 2012). Advertisement displays may involve signals that are transmitted visually (e.g. total body size, enlarged structures/particular body dimensions, color; Baird 2013a; Blank et al. 2015), acoustically (e.g. vocalizations, drumming; Randall 1989; Bee et al. 2000), or chemically (Martín et al. 2007; Carazo et al. 2008), and are expected to evolve only if they are honest indicators of resource holding power (RHP; Parker 1974) to same-sex competitors (reviewed by Andersson 1994). Sexual selection theory predicts that variation among males will result in some individuals having high RHP achieving disproportionately higher reproductive success than males having lower RHP (Emlen & Oring 1977; Andersson & Iwasa 1996). Opportunities for high RHP males to monopolize access to multiple females are expected to increase when females or the resources that they require for survival and reproduction are more spatially clumped, and the temporal schedule of female receptivity is moderately asynchronous (Emlen & Oring 1977). Therefore, mating systems involving some form of spatial defense are likely to evolve when the potential for dominant males to monopolize several females is high (Davies 1991; McCoy et al. 2003; Shuster & Wade 2003).

Males also may strive to increase their reproductive success through interactions with females. Intersexual interactions may involve male advertisement of one or more phenotypic attributes that females find attractive (Baird et al. 2007; Alonso et al. 2010), which can result in elaborate courtship rituals (Masonjones & Lewis 1996; Fusani et al. 2007). Phenotypic traits that females use to assess the quality of males often involve many of the same visual, acoustic, or chemical signals that males advertise during

intrasexual displays (Baird 2013b). Adaptive mate choices by females, therefore, may be promoted by opportunities to observe and evaluate several males. By mating with certain males over others, females may gain direct material benefits, such as access to food, high quality nesting sites, or paternal care that increase their own fitness (Forsgren et al. 1996; Clutton-Brock & McAuliffe 2009). Alternatively, females may select certain male mates on the basis of their genetic qualities, which when inherited, enhance the fitness of offspring produced by those females (Head et al. 2005; Puurtinen et al. 2009).

One way that males may acquire matings through intrasexual competition, intersexual advertisement, or both, is by controlling particular spatial areas (i.e. reproductive territories). Reproductive territories in vertebrates vary substantially in both the resources that they contain and how long males defend them. At one extreme exemplified by lekking systems, males establish territories containing nothing more than a place in which to display to potential mates (Jiguet et al. 2000; Isvaran 2005; Vitousek et al. 2007). Receptive females compare displaying males and choose one or more mates, copulate, and then leave the lek. At the other end of this continuum, males having high RHP establish territories that contain one or more resources that are critical to females. Because the reproductive season may continue long enough for females to produce more than one batch of eggs/offspring, defense of resource-based territories is more protracted. Resource-based reproductive territories are defended using advertisement displays, patrol, and by contesting and chasing away intruders. In such systems, territory owners are predicted to garner exclusive mating access to females residing within their territories (i.e. mate monopolization) which compensate for the costs of advertisement and defense,

whereas males that are unable to acquire territories are expected to obtain few, if any matings, but also not to incur high costs (Baird 1988; Baird et al. 1996; Low 2006).

Historically, observations of territory defense date at least to Pliny (c. 50 CE) and Aristotle (c. 350 BCE). Even so, the evolutionary basis of territorial defense was poorly understood as recently as the 1950's because researchers emphasized and focused exclusively on the benefits that males were assumed to acquire through defense, especially access to female mates, without considering the potential costs incurred by defending space. This overly simplistic approach changed when Brown (1964) pioneered theoretical modeling to address the evolution of territory defense based upon the benefits that territory owners acquire relative to the costs that they incur defending space (i.e. territory economics). Several authors subsequently expanded on Brown's (1964) basic model (e.g. Hixon 1980; Schoener 1983; Davies & Houston 1984), and this approach continues to provide a valuable framework both for more sophisticated theory (Adams 2001; Stamps & Krishnan 2001; Switzer et al. 2001) and empirical tests of hypotheses about the adaptive significance of territory defense (Young & Gerber 2008; Amsler 2010; York et al. 2014). Defense costs usually are estimated by quantifying the behavior patterns that males use to exclude competitors from defended areas, including frequencies with which males initiate aggressive contests with rivals, and rates of patrol and advertisement display (Stamps 1994; Schwartz et al. 2007). Until the advent of modern molecular-genetic techniques, benefits of spatial defense were estimated by measuring behavioral and spatial variables that were hypothesized to be strong correlates of mating success, such as frequencies of intersexual interactions (Baird et al. 1996), the number of

females with which males interact (Coltman et al. 1999), and/or the number of females whose home ranges are overlapped by male territories (Lappin & Husak 2005).

Studies of the adaptive significance to individuals living within territorial-based mating systems currently are in the midst of a revolution because genetic parentage assignments provide a more rigorous estimate of variation in relative fitness among individuals within populations than studies based upon behavioral estimates alone (Jones et al. 2010; Pizzari & Wedell 2013). Combining extensive data on behavioral and morphological attributes of males with genetic measures of their parentage and reproductive success, however, allows testing of the strength and targets of intra- and intersexual selection, and addressing questions pertinent to the evolution of social and mating systems (Husak et al. 2006; York & Baird 2015) with greater insight and power than ever before.

Many combined parentage-behavioral studies of resource-based territorial systems have focused on the effects of variation in the density and ratio of male competitors and female mates on mating system dynamics (Fitze & Galliard 2008; Head et al. 2008; Dreiss et al. 2010), because these parameters may have a strong influence on the intensity of competition among males and opportunities for females to exercise mate choice (Emlen & Oring 1977; Clutton-Brock & Parker 1992; Kokko & Rankin 2006). Although conspecific density undoubtedly is important in shaping the evolution of mating systems involving defense of resource-based territories, the temporal and spatial distribution of critical resources also may be strong determinants of whether or not it is economically feasible and adaptive for some individuals to attempt mate monopolization by defending space (Grant 1993; Grand & Grant 1994). Indeed, the influence of large

variation in the distribution and abundance of food resources can be so strong that different mating systems result within populations (Davies & Lundberg 1984).

In species that are restricted to patches of specialized microhabitat, these patches themselves also may be the resource that is limiting. If suitable patches of microhabitat are limiting, then variation in the attributes among suitable available patches, such as their structural complexity and size, may have profound consequences for the animals that settle there. For example, variation in the complexity of microhabitats has been shown to influence levels of aggression and the ability of individuals to monopolize food resources in fish (Basquill & Grant 1998; Hamilton & Dill 2003), birds (Rousseu et al. 2014), and mammals (Jensen et al. 2005). Despite the potential importance of variation among available microhabitat patches for philopatric species, there appears to be few if any studies that test the effects of variation in the structural complexity among patchy microhabitats on the fitness of male vertebrates that display resource-based territory defense. Because technological advances allow more rigorous estimates of mating relationships and fitness by sampling DNA from free-ranging animals in the field than ever before, the time is opportune to combine genetic-based parentage analyses with extensive records of the behavior of these same individuals to test the possible influence of microhabitat structural complexity on the adaptive mating tactics of individuals. This thesis is such a study on the eastern collared lizard (*Crotaphytus collaris*).

I used physical variation in the human-constructed habitats occupied by collared lizards at my study site as a comparative tool to test the influence of microhabitat structural complexity and territory defense economics (benefits relative to costs) on male behavior and annual male reproductive success. In Chapter 1, I address the influence of

microhabitat complexity on male behavior. Specifically, I test the extent to which microhabitat complexity influences the costs of advertising and defending territories from rival males, and/or influences opportunities to court females, by comparing the behavior of males in two types (simple versus complex) of microhabitat. The relatively small size of simple microhabitats crowded lizard inhabitants, yet behavioral data revealed that the primary influence of a simpler habitat structure was to increase courtship opportunities without increasing costs of advertisement and defense. Therefore, in Chapter 2 I tested the reproductive consequences of male behaviors by using genetic parentage analyses to measure male reproductive success and the extent to which males monopolize the reproductive efforts of female mates in the two microhabitats.

CHAPTER 1

HABITAT COMPLEXITY INFLUENCES BEHAVIOR PATTERNS IN TERRITORIAL, BUT NOT NON-TERRITORIAL MALE COLLARED LIZARDS

ABSTRACT

Theory predicts that costs and benefits of territory defense should be influenced by variation in the spatial distribution of competitors and critical resources. Economic defensibility models, however, generally do not account for the fact that variation in the structural complexity of local habitats may have important consequences on the accessibility and defensibility of potential mates, and therefore the behavioral patterns adopted by territorial individuals and their rivals. I tested the influence of microhabitat patch complexity on the spatial and social behavior of free-ranging territorial and non-territorial male collared lizards by quantifying lizard behavior in two types of rock patches that varied significantly in their dimensions and topography. Additionally, marked differences in local social conditions in the two microhabitat types allowed me to test two alternative sexual selection models to explain factors that may influence male behavior and fitness. Complex patches were wider, more highly sloped, and consisted of boulders providing a more highly variable topography on the surface as well as an interconnected network of crawlspaces beneath the surface of these boulders. By contrast, simple patches were extremely narrow, consisting of fractured concrete that formed a much less variable and flatter surface devoid of crawlspaces beneath. The narrow dimensions of simple patches combined with the low vagility of collared lizards resulted in high local densities. Despite extreme crowding of competitors, some males

still defended territories on simple patches, but they reduced the size of their territories in a pattern opposite to increasing conspecific densities each season. Surprisingly, the rate at which these males performed broadcast displays and contested same-sex rivals was similar to that of territorial individuals on complex patches. Instead, males defending territories on simple patches moved about their territories at higher rates and courted more different females more frequently. By contrast, non-territorial males in the two types of microhabitat did not differ in any of the social variables measured. These results suggest that a simpler microhabitat structure promotes increased courtship opportunities, while at the same time allowing males to deter rivals without significantly increasing costly defensive behaviors. These results also suggest that less structurally complex microhabitats may allow territorial males to monopolize the reproductive efforts of females more effectively.

INTRODUCTION

Territory defense economic theory predicts that spatial defense is adaptive when the benefits of maintaining exclusive access to areas containing one or more resources essential for survival and reproduction exceed the costs of excluding competitors (Brown 1964; Schoener 1983; Davies & Houston 1984). For males, exclusive mating access to one or more females (i.e. mate monopolization) is one likely benefit of spatial defense, because male reproductive success often is limited by access to females (Trivers 1972; Clutton-Brock & Parker 1992; White & Rundle 2015). Territory ownership also potentially imposes numerous costs, however, including the time and energy necessary to

advertise ownership and repel same-sex competitors (Marler et al. 1995; Rovero et al. 2000; von Kuerthy et al. 2015). Conspicuous behavior associated with territoriality (i.e. advertisement displays, patrol, physical contests) also may render individuals more vulnerable to predation (Toivanen et al. 2009; Bateman & Fleming 2011), reduce the amount of time available for foraging opportunities, which may lead to decreased growth and/or survival (Marler & Moore 1988, 1989; Höjesjö et al. 2004), and detract from opportunities for males to court females (Warner & Hoffman 1980; Baird et al. 2001; Spence & Smith 2005). Selection on males, therefore, is expected to result in their establishing territories and adopting behavior patterns that maximize mating opportunities while simultaneously minimizing the costs of advertising to and repelling competitors (Grant 1993; Both & Visser 2003). The evolution of status signaling ‘badges’ (Pryke et al. 2002; Whiting et al. 2003; Baird et al. 2013) and utilization of advertisement displays rather than physical aggression (Husak 2004; Blank et al. 2015) both provide strong evidence for selection acting to minimize the chronic costs of territory defense.

Cumulative defense costs and the time available for mating activities both are likely influenced by several factors that alter the ability of males to exclude same-sex rivals from areas where females settle (Emlen & Oring 1977; Vehrencamp & Bradbury 1984). Defense costs typically are hypothesized to increase with the number (Jirotkul 1999; Grant et al. 2000; Weir et al. 2011) and density (Eshel 1979; Shuster & Wade 2003; Kokko & Rankin 2006) of male competitors relative to available female residents, and the amount of area that males attempt to defend (Schoener 1987; Adams 2001). If costs among interacting same-sex competitors become excessive, the ability of males to

court females may be compromised to the extent that males abandon territory defense altogether (Gaskin et al. 2002; Mills & Reynolds 2003), and instead adopt alternative mating tactics that do not involve spatial defense (Shine et al. 2003; Weir et al. 2010).

To date, most theoretical models of territory economics have been based on the necessity for individuals to return to and utilize/maintain centrally-placed sites (i.e. perches, burrows, nests; Brown 1964; Dill 1978; Hixon 1980). Such models likely do not provide a good framework for many species in which territory boundaries span at least one entire dimension of habitat patches, and important sites and resources are distributed throughout these patches instead of being centrally located. Central-place economic models also sometimes fall short because they assume that all rivals for the limited resource are owners of neighboring territories, or are non-territorial ‘floaters’ that reside outside of territory boundaries (Brown 1969; Tanemura & Hasegawa 1980), such that challenges with same-sex competitors occur primarily along established territory boundaries. Lastly, theoretical models often assume that the structural features of habitat patches allow territory owners to readily detect intrusions because they only occur along borders (but see Eason 1992), and that competitors can be readily chased or escorted completely outside of the territorial boundaries (Grant & Noakes 1987; Hixon 1987; Stamps 1994). All of these assumptions are realistic only when the structural features of microhabitats promote high visibility across the greatest dimensions of territories, and intruders cannot evade the attacks of territory owners without being repelled outside of these boundaries. In territorial systems that do not satisfy these assumptions, variation in factors such as the size, shape, and structural complexity of local microhabitats may alter

the accessibility and defensibility of critical resources to the extent that individuals occupying different patches adopt alternative behavior patterns.

Eastern collared lizards (*Crotaphytus collaris*) in my central Oklahoma study population provided an opportunity to test the influence of microhabitat structural complexity on the spatial and social behavior of free-ranging territorial and non-territorial males. Lizards occupied two types of human-constructed microhabitat patches that varied significantly in complexity, especially in their dimensions and topography. Simple patches were extremely narrow throughout, whereas complex patches were 3–6 times wider. Complex patches also were more highly sloped and consisted of large boulders, making the surface of the substrate more irregular. Layers of piled boulders also resulted in an extensive network of interconnected crawlspaces beneath the surface of complex patches. By contrast, simple patches were composed of a single layer of fractured concrete slab that formed a much more uniform, flatter surface. Although small crevices were numerous on simple microhabitats, they did not form a continuous network of crawlspaces beneath the surface (York & Baird 2015).

Previous studies showed that territorial males on complex patches patrolled at high rates over relatively large areas, probably to maximize advertisement to females that were dispersed throughout these microhabitats (Baird et al. 2003; Baird 2013b). Nevertheless, the extensive network of interconnected subsurface crawlspaces on complex patches made it difficult and costly for territorial males to prevent incursions by non-territorial males because there was more area to patrol, non-territorial males readily hid to evade attacks without leaving these patches, and non-territorial males traveled

significant distances throughout the subsurface crevice network without being detected by territory owners (York & Baird 2015).

By contrast, the different physical conditions on simple patches likely imposed different selection pressures on males that influenced the economics of territory defense, and perhaps the behavioral tactics adopted by non-territorial males. One possibility is that the narrower width of simple patches crowded individuals to the extent that it increased competition for opportunities to stalk and strike insect prey effectively, causing lizards to disperse to other patches. This alternative seemed unlikely, however, because collared lizards display only limited ability to disperse among patches (Hranitz & Baird 2000), instead maintaining strong philopatry to local neighborhoods throughout their lives (Schwartz et al. 2007; Baird unpublished). As a consequence of limited inter-patch dispersal, it seemed more likely that simple patches would concentrate both potential female mates and non-territorial rival males, because lizards can only space themselves apart by moving along the longitudinal axis of these elongate patches. Indeed, lizards did not disperse from simple microhabitats, and densities of both same-sex competitors and females were markedly higher than on complex patches, which provided an important variable (higher conspecific densities) for my comparative test.

High local densities on simple patches provided an opportunity to test two alternative sexual selection models to explain factors that may govern male behavior and fitness. If male behavior is influenced primarily by intrasexual competition, crowding of numerous competitors should increase energy expenditure required to engage rivals aggressively, which should lower the net benefits garnered through courtship and mating opportunities relative to that gained by males on complex patches (Figure 1A).

Alternatively, if male behavior is influenced most strongly by opportunities to interact with females (intersexual selection), and simple patches allow males to control territories effectively without significantly increasing costly competitive behaviors, increased density of females should disproportionately increase courtship and mating opportunities relative to males on complex patches, resulting in higher net benefits for these males (Figure 1B).

Here, I tested the influence of habitat structural complexity on male space use and intra- and intersexual social behavior by recording the behavior of territorial and non-territorial males occupying microhabitat patches having simple and complex structural features. Specifically, for both territorial and non-territorial individual males residing on each of these microhabitat patch types, I determined the amount of space used, the number and density of same-sex competitors as well as females, frequencies of interactions that males initiated with other males and individual females (separately), the number of females with which males interacted, the rate at which males moved about, and the frequency of broadcast displays given.

METHODS

General Ecology of Collared Lizards

The eastern collared lizard is a medium-sized iguanian that exhibits male-biased sexual dimorphism in snout-to-vent length and head dimensions (McCoy et al. 1997; Lappin & Husak 2005). Similar to many iguania, collared lizards are active only during

the day (diurnal) when the sun is shining enough that air and substrate temperatures are warm (30–38°C). Collared lizards are microhabitat specialists that are restricted to exposed rock substrata (Fitch 1956). The natural ancestral microhabitat of collared lizards consists of relatively small, discontinuous rock outcroppings or washes. In some parts of the range, however, collared lizards have colonized human-constructed rock microhabitats such as flood-control channels and spillways associated with dams (Baird 2013a). At my study site, these flood-control structures were constructed by laying fields of boulders that opportunistically provide all of the features necessary for *C. collaris* to meet its ecological requirements. Piles of irregularly shaped boulders provide abundant crevices that lizards use to seek refuge from excessive heat and potential predators (raptors, roadrunners, snakes, coyotes), and in which non-territorial males evade attacks by male territory owners (Baird 2013a). Boulders also provide elevated sites used for thermoregulation and scanning for insect prey (Curtis & Baird 2008). Like most other iguanids, collared lizards have highly developed vision that promotes their sit-and-wait predatory tactic (Baird 2013a). Once prey (primarily arthropod; Best & Pfaffenberger 1987; Husak & McCoy 2000) are located and move within striking distance (1–4 m), lizards stalk them deliberately before striking abruptly. Acute vision and visually transmitted signals also play an integral role in conspecific communication in collared lizards (Baird et al. 2003; Baird 2004).

Study Population and Subjects

This study was conducted from 20 March to 15 July 2010–2013 at the Arcadia Lake (AL) Dam flood-control spillways located 9.6 km east of Edmond, Oklahoma Co.,

OK (Baird et al. 2003). Collared lizards at AL occupied two types of human-constructed rock microhabitat patches that differed markedly in their dimensions, shape, and structural complexity (Figure 2, Table 1). One microhabitat type consisted of three topographically complex boulder fields that were highly variable in size and shape. Boulders (1–2 m diameter) were layered to form the sloped (30–40°) linings of flood-control channels. The largest of the complex patches was an elongate (423 and 464 m on the two sides) continuous expanse of boulders (19,583 m² total) that was at least 45 m wide. This patch consisted of two inclined sides that interfaced grass where arthropod prey thrived on the top side. Although significantly smaller in total area (1,230 and 1,505 m²), the other two complex boulder patches also were relatively wide throughout (20–50 m), but were surrounded by grass on all sides, and varied in shape from rectangular to polygonal. Because all of the complex patches consisted of boulders of varying size and shape, they had a highly irregular surface topography with numerous crevices leading into and out of a continuous network of crawlspaces beneath the surface of this substrate (Figure 3; York & Baird 2015). From 1990–2008, AL collared lizards were restricted to these three structurally complex microhabitat patches.

During the winter of 2008, the U.S. Army Corps of Engineers broke apart two narrow solid concrete drainage ditches that were not previously occupied by collared lizards, and left the pieces of variable size (0.1–0.5 m) and shape in place (Figure 2). The angled pieces of concrete slab provided abundant perches that were well suited for basking and scanning for prey, and provided numerous crevices for refuge. In the spring of 2009, a small number of adult collared lizards began to utilize these two new (simple) microhabitat patches, and the females laid eggs there. Adults recruited to one of these

simple patches from the complex patch that was only 10–15 m away (Figure 2). A small number of adults living on the front of the AL dam apparently moved 30–40 m to colonize the other simple patch. Offspring produced by the adults that first colonized the two simple microhabitat patches in 2009 remained and reproduced in 2010, founding new populations on each patch. Lizards remained on these relatively small patches and continued to thrive each year of the present study, resulting in markedly higher lizard densities on simple patches.

Both simple microhabitat patches were elongate (330 and 740 m) but extremely narrow (3.5 m) throughout. They were surrounded by vegetation, resulting in long, straight interfaces with arthropod-rich grass that was mowed periodically on two sides. The fractured pieces of concrete on these patches were only a single layer thick. The surface topography of the pieces of concrete was not strongly inclined and relatively flat. Although small crevices were numerous, they did not form an interconnected network of crawlspaces beneath the surface like that present below the layered boulders on complex patches (Figure 3, Table 1).

Both types of microhabitat patches were well-suited for recording use of space and behavioral interactions among known lizards. Because human access to this entire site is restricted, lizards are undisturbed and prolonged observation of individuals is unobstructed. All microhabitat patches were mapped to scale using GIS measurements (accurate to ± 1.0 m) of markers arranged in 10 m grids (Baird & Timanus 1998; Baird et al. 2003). Lizards used in this study were noosed as hatchlings, the terminal phalanges of three digits were clipped in unique combinations for permanent identification, and unique combinations of non-toxic acrylic paint spots were applied to the dorsum for

identification of individuals from a distance. Mark-recapture procedures were conducted with approval of the Institutional Animal Care and Use Committee (IACUC) at the University of Central Oklahoma (permit number 13009). I knew the ages of all study subjects because they were periodically recaptured for remarking and measurement since their first capture as hatchlings (Baird 2013a).

The Social and Spatial Behavior of Collared Lizards at Arcadia Lake

Adult lizards emerge from hibernacula in late March to early April. Intra- and intersexual social and reproductive activity begins in late April and extends to mid-July (Baird et al. 2001). The reproductive season is marked by female production of up to four successive clutches of eggs (Telemeco & Baird 2011; McGill et al. in preparation), and advertisement/defense of space by males that control territories. Following oviposition of the last clutches during the second week of July, territory defense wanes marking the end of the reproductive season. Activity by adults gradually diminishes until they become inactive and enter hibernacula by mid-September, which is the end of the adult activity season.

To date, all previous studies on collared lizards at AL have been conducted on the structurally complex microhabitat patches, because collared lizards were restricted to these patches until 2009. These studies showed that females maintained strong philopatry to relatively small, non-defended home ranges, and spent a large amount of time perched along rock-grass interfaces where prey were most abundant (Baird et al. 1996). Females dispersed themselves throughout these patches, probably to reduce

disturbance of approaching prey items by the movements of conspecifics and/or competition for the same prey items (Baird & Sloan 2003).

Throughout past studies on the AL population, males exhibited two alternative social tactics that typically were related to age, territorial versus non-territorial. Most males established breeding territories during their second season that they continued to defend throughout their lives (Schwartz et al. 2007) against neighboring territory owners as well as non-territorial, first-year males. Males sometimes acquired territories during their first seasons when established territory owners died during the breeding season, or when older males died during previous winters (Baird & Curtis 2010). Independent of male age, territorial males defended areas that spanned the width of patches using high rates of patrol and advertisement behavior (Baird 2013a) that was most likely mandated by the dispersion of females throughout these wide, structurally complex patches.

All previous studies have shown that male social behavior is initiated in two distinct contexts. The most common social behavior involved displays broadcast when males were stationary on elevated perches at least 5 m from conspecifics (Baird & Curtis 2010; Baird 2013a). Most broadcast displays consisted of males extending all four legs to elevate the torso which was compressed laterally while the dewlap was extended (= full-show; see photographs in Baird 2013a, c). While holding this full-show posture, males almost always flexed their legs to raise and lower the head and torso 1–12 times (= pushups) in succession. Much less frequently (2%), males displayed by walking in repetitive circular or figure-eight patterns while remaining on a single perch (Baird & Curtis 2010; Baird 2013a, c).

Occasionally, territory owners initiated proximal aggressive contests with rival males (Baird 2013c). In contrast with broadcast displays, male-male contests involved territorial males running directly toward an opponent to within 1 m, which always resulted in a behavioral response by that rival. Most contests were initiated toward non-territorial males, which always fled and hid. Contests between neighboring territory owners were rarer. These usually were settled by an exchange of displays (full-shows, pushups) while the two males remained in close proximity (1 m), reciprocal chases (up to 40 m) back-and-forth, and occasionally, attacks involving wrestling and biting (Baird 2013a, c).

Male territories partially overlapped the home ranges of up to eight females (Baird 2013a) that they courted frequently for prolonged periods (up to 30 min) throughout the 2.5-month reproductive season (Baird 2013b). Courtship encounters involved the same displays that males broadcast from a distance, but instead were given when one male and female were within one body length of one another, and when both lizards made frequent and prolonged physical contact (Baird 2004; York & Baird 2015). Physical contact included one lizard mounting and sitting on the dorsal surface of their partner, superimposition of the legs and/or tails, nudging their partner with the snout (Baird 2013a), or simply perching adjacent to the other lizard while touching (Baird & Sloan 2003; Baird 2004). Occasionally, males grasped the dorsal skin of the female's neck and attempted to juxtapose the vent with that of the female, presumably to attempt copulation.

Although males attain sexual maturity during their first spring, most first-year males are prevented from obtaining breeding territories and engaging in conspicuous

courtship interactions by the presence of socially dominant territorial males (Baird & Timanus 1998). Non-territorial males remained within territorial neighborhoods by adopting inconspicuous subordinate social tactics characterized by low travel and display rates (York et al. 2014). To support the energetic demands of high growth rates (Baird 2008), non-territorial first-year males spent most of their time foraging along rock-grass interfaces dispersed throughout relatively large home ranges that partially overlapped as many as 10 females (Baird 2013a). By fleeing territory owners and hiding in the network of crawlspaces beneath surface boulders, non-territorial males were able to avoid attacks without being driven away from areas where females settled (York & Baird 2015). Genetic measures of parentage showed that first-year non-territorial males mated successfully, probably because the interconnected subsurface crawlspaces allowed them to avoid attacks by territorial males and sneak copulations with females (York et al. 2014; York & Baird 2015; Chapter 2).

Recording Spatial and Social Data

To document the spatial and social behavior of lizards, I used mapped census sightings and focal individual observations that were recorded throughout the 2010–2013 reproductive seasons (1 May – 15 July) as part of on-going longitudinal studies conducted by the Baird laboratory. Data were recorded on scale-drawn maps when the substrate temperature was 30–38°C, a range over which collared lizard activity is independent of substrate temperature (Baird et al. 2001).

A minimum of 18 (range = 18–26) censuses were recorded during both May and June of each study season. Censuses involved walking the entire study site and recording the point locations and identities of all emergent lizards on scale drawn maps. For males, census sightings were combined with the beginning and ending points of focal traces to construct maps of territories and home ranges (non-territorial males; Figure 4) by enclosing the outer-most sighting points with a polygon having no convex surfaces (minimum convex polygon technique; Turner 1971). For female home ranges, I constructed maps using census sightings alone. The number of points used to construct maps of male territories/home ranges ($N = 60–65$) and female home ranges ($N = 30–40$) equaled or exceeded the number necessary to achieve an asymptotic relationship when home range/territory area was graphed against the number of sightings (Stone & Baird 2002; Baird & Sloan 2003), following the methods of Rose (1982). I used a digital planimeter (Planix 2000) to measure the area (m^2) and perimeter (m) of the space used by subject males, and calculated the ratio of the area to the perimeter of each male's territory/home range. Because simple and complex microhabitat patches differed markedly in width, and males utilized the entire width of both types of patches, the average area-to-perimeter ratio of territories/home ranges used by males on complex patches ($\bar{x} \pm 1.0 \text{ SE} = 9.0 \pm 0.59$) was five times (GLM: $t_{2, 88} = 15.41$; Cohen's $d = 2.16$, 95% CI = 1.63–2.70) that of males on simple patches ($\bar{x} \pm 1.0 \text{ SE} = 1.71 \pm 0.02$).

Individual focal observations (*sensu* Altmann 1974) were recorded to quantify the rate of travel and the frequency of social behavior patterns initiated by known males. Focal observations involved tracing the path of travel and recording all of the social acts initiated by subject males on scale-drawn maps for 20 min, including the identities of the

recipients of these social acts (Baird 2013a). Travel was recorded by tracing the path along which lizards moved by triangulating among mapping markers laid out in 10 m grids. Focal observations were recorded from 0900–1300 h and focal subjects were selected at random to control for possible temporal bias in the frequency of male behavior patterns (Baird et al. 2001). A maximum of 15 focal observations (range 5–15) were recorded on separate days for all mature males that were present during the reproductive season (complex microhabitats: territorial males, $N = 24$; non-territorial males, $N = 11$; simple microhabitats: territorial males, $N = 38$; non-territorial males, $N = 17$). The number of focal observations per male varied because some individuals died before the reproductive season ended. A minimum of five focal observations distributed over a period of two weeks is necessary to make an accurate estimate of male behavior patterns (Baird & Hews 2007; Baird & Curtis 2010). Therefore, I did not include subject males that died before five focal observations were recorded in behavioral data analyses.

I tested the influence of microhabitat patch complexity on the densities of rival males and females by determining the number of mature males and females (separately) whose territories/home ranges abutted or partially overlapped each male study subject on composite maps, divided by the territory or home range area (m^2) of those subject males. I used the cumulative data recorded during focal observations on each male to calculate hourly frequencies of broadcast displays, contests initiated with rival males, and courtship encounters initiated with females (separately), by dividing the total number of these acts/events by the total focal observation time on each subject male (Baird et al. 2007; Baird & Curtis 2010). I also determined the number of different females that males courted on the two types of microhabitat. To quantify rates of travel (m/h) for

males occupying both types of microhabitat, I used a digital planimeter (Planix 2000) to measure mapped focal traces and divided the total length of travel paths by the cumulative observation time on each male (Baird et al. 2007; Baird 2013a). Travel rates therefore are a measure of the amount of substrate males traversed per unit time, not the speed with which they moved about their territories/home ranges as the units (m/h) might suggest.

Statistical Analyses

All analyses were performed in the program R version 3.1.2 (R Core Team 2014). Because the majority of spatial and social dependent variables were found to have non-normal distributions for both territorial and non-territorial males within each microhabitat type, generalized linear models (GLM) were selected as the most appropriate analysis method because they can accommodate violations of assumptions of traditional (parametric) linear models. Additionally, GLM's provide more reliable evaluation of statistical significance because they allow the user to specify the error structure based upon the type of data being analyzed (e.g. binomial, discrete, continuous). Using GLM's, I compared the following variables in territorial and non-territorial males on simple and complex microhabitat patches: territory/home range area (m^2), the number of females overlapped, densities of same-sex competitors and females (separately; lizards/ $m^2 \times 100$), hourly frequencies of broadcast display, hourly frequencies of contests initiated with rival males and courtship encounters initiated with females (separately), the number of different females courted, and hourly rate of travel (m/h). There were no statistically significant effects of year on any of the social variables that I measured in either type of

microhabitat (95% CI of predictor variables overlapped zero); therefore, I pooled all years for statistical analyses of social variables. On simple microhabitats, year did have an effect on competitor and female densities, as well as territory area. Therefore, I examined among year variation for each of these variables on simple microhabitats separately using a post hoc Tukey HSD test, but also pooled all years for each variable for between microhabitat comparisons. Because the number of females overlapped and courted were discrete variables, I used a GLM with Poisson error structure and log link function in these analyses. The response variables for all other GLM's were continuous, so I used a Gaussian error structure and identity link function in analyses of these variables. I used linear models (LM) to test for significant correlations between predictor (independent) and response (dependent) variables, and between response variables for males within each microhabitat type where appropriate. I used the package 'compute.es' to calculate standardized (mean = 0, standard deviation = 1) effect sizes (Cohen's *d*) and associated 95% confidence intervals (CI) for all models.

For all analyses, I evaluated statistical significance by determining whether or not the 95% CI of predictor variables overlapped zero. If they did not, predictor (independent) variables were deemed to have a significant effect on the dependent variable being examined. In most cases I do not report traditional *P*-values (post hoc Tukey HSD tests being the exception), because they are subject to sample size variation and do not reveal the biological significance or statistical uncertainty of the variables of interest (Colegrave & Ruxton 2003; Nakagawa & Cuthill 2007). Instead, I use standardized effect sizes with CI because they provide both biologically and statistically meaningful inference at a specified degree of certainty (Colegrave & Ruxton 2003). I

also report t and z values, GLM test statistics derived by R for analyses involving continuous and discrete data, respectively. They are derived differently from traditional t and z test statistics, and so should not be confused with them.

RESULTS

Influence of Microhabitat Complexity on Lizard Density and Male Behavior

For all years pooled, local competitor densities on simple patches were 8.1 times higher (GLM: $t_{2,59} = 6.70$; Cohen's $d = 1.76$, 95% CI = 1.14–2.37) for territorial males and 6.7 times higher (GLM: $t_{2,25} = 4.11$; Cohen's $d = 1.67$, 95% CI = 0.71–2.63) for non-territorial males relative to their counterparts on complex patches (Table 2).

Similarly, local female densities on simple patches were 9.5 times higher (GLM: $t_{2,59} = 7.12$; Cohen's $d = 1.87$, 95% CI = 1.24–2.49) for territorial males and 10.5 times higher (GLM: $t_{2,25} = 4.84$; Cohen's $d = 1.97$, 95% CI = 0.96–2.98) for non-territorial males for all years pooled relative to complex patches (Table 2).

There was no significant effect of year on either competitor (GLM: $t_{3,22} = -0.59$; Cohen's $d = 0.25$, 95% CI = -0.64 to 1.15) or female (GLM: $t_{3,22} = 0.54$; Cohen's $d = 0.23$, 95% CI = -0.66 to 1.12) density on complex microhabitat patches for territorial males. In marked contrast, because simple patches were first colonized in 2009, the number of lizards present in 2010 was limited to those few adult 2009 colonists that survived, plus their surviving offspring. Lizard dispersal away from these patches was rare. Therefore, for territorial males, the local density of both competitors (GLM: $t_{3,36} =$

5.08; Cohen's $d = 1.71$, 95% CI = 0.92–2.50) and females (GLM: $t_{3,36} = 5.90$; Cohen's $d = 1.99$, 95% CI = 1.16–2.82) increased steadily throughout the study (Figure 5). Density of competitors was statistically higher in 2013 relative to all other years (Figure 5; 2012, $z = 3.16$, $p < 0.01$; 2011, $z = 3.45$, $p < 0.01$; 2010, $z = 4.33$, $p < 0.001$). Local density of females also was highest in 2013 relative to all other years (Figure 5; 2012, $z = 2.74$, $p = 0.03$; 2011, $z = 4.30$, $p < 0.001$; 2010, $z = 4.86$, $p < 0.001$).

Despite the higher density of same-sex competitors, the basic social structure among males on simple patches remained unchanged. All males that were two-years and older defended territories, as did a subset of first-year males. Similar to complex patches, territorial males on simple patches exhibited rates of travel (GLM: $t_{2,52} = 5.86$; Cohen's $d = 1.64$, 95% CI = 0.99–2.28), frequencies of broadcast display (GLM: $t_{2,52} = 6.23$; Cohen's $d = 1.74$, 95% CI = 1.08–2.39), and frequencies of intrasexual contests initiated (GLM: $t_{2,52} = 3.10$; Cohen's $d = 0.86$, 95% CI = 0.28–1.44) that were significantly higher than non-territorial males (Table 3). Non-territorial males used home ranges that were larger (GLM: $t_{2,52} = -2.91$; Cohen's $d = 0.81$, 95% CI = 0.23–1.39) than the areas defended by territorial males (Table 3) and, hence, moved throughout several territories over the course of the reproductive season.

Males defending territories on simple microhabitat patches also travelled at higher rates (GLM: $t_{2,59} = 2.28$; Cohen's $d = 0.59$, 95% CI = 0.06–1.13) than their counterparts living on complex patches, but both the frequency of broadcast displays (GLM: $t_{2,59} = 0.29$; Cohen's $d = 0.07$, 95% CI = -0.45 to 0.60) and contests initiated with rivals (GLM: $t_{2,59} = 1.15$; Cohen's $d = 0.30$, 95% CI = -0.23 to 0.82) were similar on the two types of microhabitat (Table 3). On average, territories on simple patches were 5.6 times smaller

(GLM: $t_{2,59} = -7.68$; Cohen's $d = 2.01$, 95% CI = 1.37–2.65) than those on complex patches (Table 3). Within each microhabitat type, the amount of space that territorial males defended decreased as local competitor density increased (Figure 6A, complex microhabitats: LM: $t_{1,22} = -3.76$; $r = -0.625$, 95% CI = -0.82 to -0.30; Figure 6B, simple microhabitats: LM: $t_{1,36} = -6.52$; $r = -0.736$, 95% CI = -0.85 to -0.54). In contrast with territorial males, rates of travel (GLM: $t_{2,25} = 0.33$; Cohen's $d = 0.13$, 95% CI = -0.70 to 0.96), frequencies of broadcast display (GLM: $t_{2,25} = 1.57$; Cohen's $d = 0.63$, 95% CI = -0.22 to 1.48), and frequencies of contests with rivals (GLM: $t_{2,25} = 1.54$; Cohen's $d = 0.62$, 95% CI = -0.23 to 1.46) did not differ in non-territorial males as a function of the type of microhabitat patch (Table 3).

Independent of microhabitat complexity, females occupied non-defended home ranges that were distributed throughout the available substrate. As a consequence of markedly higher female densities on simple patches (Table 2), both male territories (GLM: $z_{2,59} = 5.13$; Cohen's $d = 1.51$, 95% CI = 0.92–2.10) and home ranges occupied by non-territorial males (GLM: $z_{2,25} = 6.16$; Cohen's $d = 4.01$, 95% CI = 2.57–5.44) on simple patches overlapped the home ranges of more females than those on complex patches, even though the male areas were smaller (Table 3). In both types of microhabitat, male territory area was inversely correlated with female density (Figure 7A, complex microhabitats: LM: $t_{1,22} = -3.26$; $r = -0.571$, 95% CI = -0.79 to -0.22; Figure 7B, simple microhabitats: LM: $t_{1,36} = -6.61$; $r = -0.741$, 95% CI = -0.86 to -0.55).

The frequency of courtship encounters initiated by territorial males was two times higher (GLM: $t_{2,59} = 4.04$; Cohen's $d = 1.06$, 95% CI = 0.50–1.61) on simple patches, and these males courted nearly twice as many different females (GLM: $z_{2,59} = 3.85$;

Cohen's $d = 1.08$, 95% CI = 0.52–1.64) than males controlling territories on complex patches (Table 3). Travel by territorial males on simple patches was positively correlated with courtship frequency (Figure 8A, LM: $t_{1,36} = 4.79$; $r = 0.624$, 95% CI = 0.38–0.79), the number of different females courted (Figure 8B, LM: $t_{1,36} = 3.99$; $r = 0.554$, 95% CI = 0.28–0.74), and the frequency of broadcast displays (Figure 8C, LM: $t_{1,36} = 5.59$; $r = 0.682$, 95% CI = 0.46–0.82), but not with contests initiated with rival males (Figure 8D, LM: $t_{1,36} = 1.94$; $r = 0.307$, 95% CI = –0.01 to 0.57). The presence of socially dominant males generally inhibited courtship by non-territorial males in both microhabitats, and the frequency of courtship did not differ for non-territorial males in simple and complex patches (GLM: $t_{2,25} = 1.21$; Cohen's $d = 0.48$, 95% CI = –0.36 to 1.32; Table 3). Nevertheless, non-territorial males on simple patches tended to interact with more females than their counterparts on complex patches, although the difference was not statistically significant (GLM: $z_{2,25} = 2.00$; Cohen's $d = 0.84$, 95% CI = –0.02 to 1.71; Table 3).

Influence of Competitor and Female Density on Male Territory Area

On complex microhabitat patches, the size of male territories did not vary annually (GLM: $t_{3,22} = 1.51$; Cohen's $d = 0.65$, 95% CI = –0.27 to 1.56). By contrast, on simple patches, territory areas decreased (GLM: $t_{3,36} = -5.69$; Cohen's $d = 1.92$, 95% CI = 1.10–2.73) over the course of the study in a pattern strikingly opposite to the increase in competitor and female densities (Figure 5). When lizards were least dense in 2010 because this was the first full season following colonization, territories were larger than in all other years (2011, $z = -2.56$, $p = 0.04$; 2012, $z = -3.75$, $p < 0.001$; 2013, $z = -5.64$,

$p < 0.001$). Territory area then decreased significantly in 2011 ($z = -2.56$, $p = 0.04$), and declined again when lizard densities increased in both 2012 and 2013, but not significantly so (2011 to 2012, $z = -0.79$, $p = 0.85$; 2012 to 2013, $z = -2.03$, $p = 0.17$; Figure 5).

DISCUSSION

My results support the hypothesis that the structural complexity of local microhabitats exerts an influence on the adaptive value of behavior patterns associated with territory defense in male collared lizards. The extremely small area of simple microhabitat patches combined with the low vagility of lizards inhabiting these patches resulted in local densities of male competitors and potential female mates that were nearly an order of magnitude greater than those on complex patches. Despite the high density of competitors, some males still opted to defend territories, but they did so without initiating contests with rival males or giving broadcast displays more frequently. Furthermore, territory owners prevented non-territorial competitors from interacting with females just as efficiently as they did on complex patches. After the first year following initial colonization of the simple patches, male territories decreased in size relative to those on complex patches. Intrasexual male aggression has been shown to increase with local population density in many vertebrates (Clutton-Brock et al. 1997; Byrne & Robers 2004; Spence & Smith 2005), whereas in other species, territory defense breaks down entirely when intruder pressure increases the costs of repelling competitors to the point that defense of space is not economically feasible (Mills & Reynolds 2003; Reichard et

al. 2004; Hinsch & Komdeur 2010). Neither of these occurred on the two simple microhabitat patches at the AL site, despite substantial crowding of the collared lizard inhabitants.

Several physical features of the microhabitat on the simple patches at AL likely promoted more cost-effective defense of territories even though the density of male competitors was much higher. The narrow shape and relatively flat surface topography of the substrate almost certainly enhanced the ability of territory owners to visually detect and deter competitors, which was especially important because of the numerous non-territorial males that thrived within the boundaries of these territories. Moreover, it was difficult if not impossible for non-territorial males to travel inconspicuously within simple patches, because the subsurface network of interconnected crawlspaces that characterized complex microhabitats (York & Baird 2015) was absent. As a consequence, when confronted by territory owners, non-territorial males quickly took refuge in crevices that were abundant, but not connected to an extensive subsurface network of crawlspaces. Therefore, these males could not move very far from their refuges without emerging to the surface, because doing so would again reveal their presence to territory owners. Alternatively, non-territorial males also sometimes evaded aggression by fleeing into the surrounding grass which was always less than 2 m away because of the extremely narrow width of these patches. Instead of travelling through the grass to re-enter the hard substrate distant to where they were chased off, these males almost always remained motionless until territory owners directed their attention elsewhere, and then returned to the hard substrate near to (< 10 m) where they left. It

seems likely that movement over long distances in the grass would increase exposure to both snake and avian predators, selecting against such behavior.

Although some males continued to defend territories on simple patches, the amount of space that they were able to defend showed a steady annual decrease as the number of same-sex competitors increased. The reciprocal relationship between territory area and competitor density suggests that territory area decreased as a consequence of increasing defense costs. This possibility is difficult to disentangle from an alternative explanation that males defended less area in response to annually increasing female densities (Figure 4). The prolonged courtship interactions that are typical between territorial males and the female residents of their territories (Baird 2013b) appear to suggest that mating relationships between individual males and females require time to develop. Female receptivity for fertilization is asynchronous throughout the 2.5-month reproductive season because as many as four successive egg clutches are produced by individual females each season, and the schedule of egg production is staggered depending upon female age and when individuals begin to ripen their first egg clutches (Baird 2004; Telemeco & Baird 2011; McGill et al. in preparation). Territory area, therefore, may have decreased in part, because the number of available females within smaller areas on simple patches met or exceeded the number of females with which males could develop mating relationships while still defending the integrity of their territories from rivals.

Consistent with the intersexual interaction hypothesis (Figure 1), instead of giving broadcast displays or initiating contests with rivals more frequently, territorial males on simple microhabitat patches courted more females more frequently than their

counterparts on complex patches. Territorial males on simple patches also travelled throughout their territories at higher rates, even though the amount of space they defended was much smaller. Moreover, both courtship frequency and the number of females courted were positively correlated with the rate of travel, whereas the frequency of contests with rivals was not. Together these results suggest that territorial males on smaller, less structurally complex microhabitat patches moved throughout their territories more to increase social interactions with females, rather than to engage same-sex competitors more often.

One possible explanation of the adaptive significance of increased interaction with females is that it allows males to advertise heritable genetic qualities that promote the fitness of offspring (Candolin 2003; Kokko et al. 2003; Andersson & Simmons 2006). The hypothesis that courtship functions to advertise male genetic quality is not supported, however, by results showing that survival of offspring sired by males defending territories on complex patches increased with the frequency of broadcast displays instead of with courtship frequency (York & Baird in review). An alternative explanation is that proximity to females may promote higher courtship frequency and diminish the potential for non-territorial males to mate surreptitiously, enhancing the efficiency with which territorial males can monopolize the reproductive efforts of females. Previous parentage studies on collared lizards occupying complex microhabitat patches at AL revealed that males were not able to monopolize matings with female residents of their territories, apparently because the extensive network of subsurface crawlspaces that characterized these patches promoted successful matings by non-territorial males employing stealthy tactics (York et al. 2014; York & Baird 2015). Evaluation of this hypothesis requires

comparison of the extent to which territorial males on the two microhabitats monopolize matings with the females that reside on their territories. In Chapter 2, I test the fitness consequences of habitat complexity on male reproductive success by using parentage analyses to determine the number of female mates, the number of offspring sired, and especially the efficiency of mate monopolization in males occupying the two types of microhabitat.

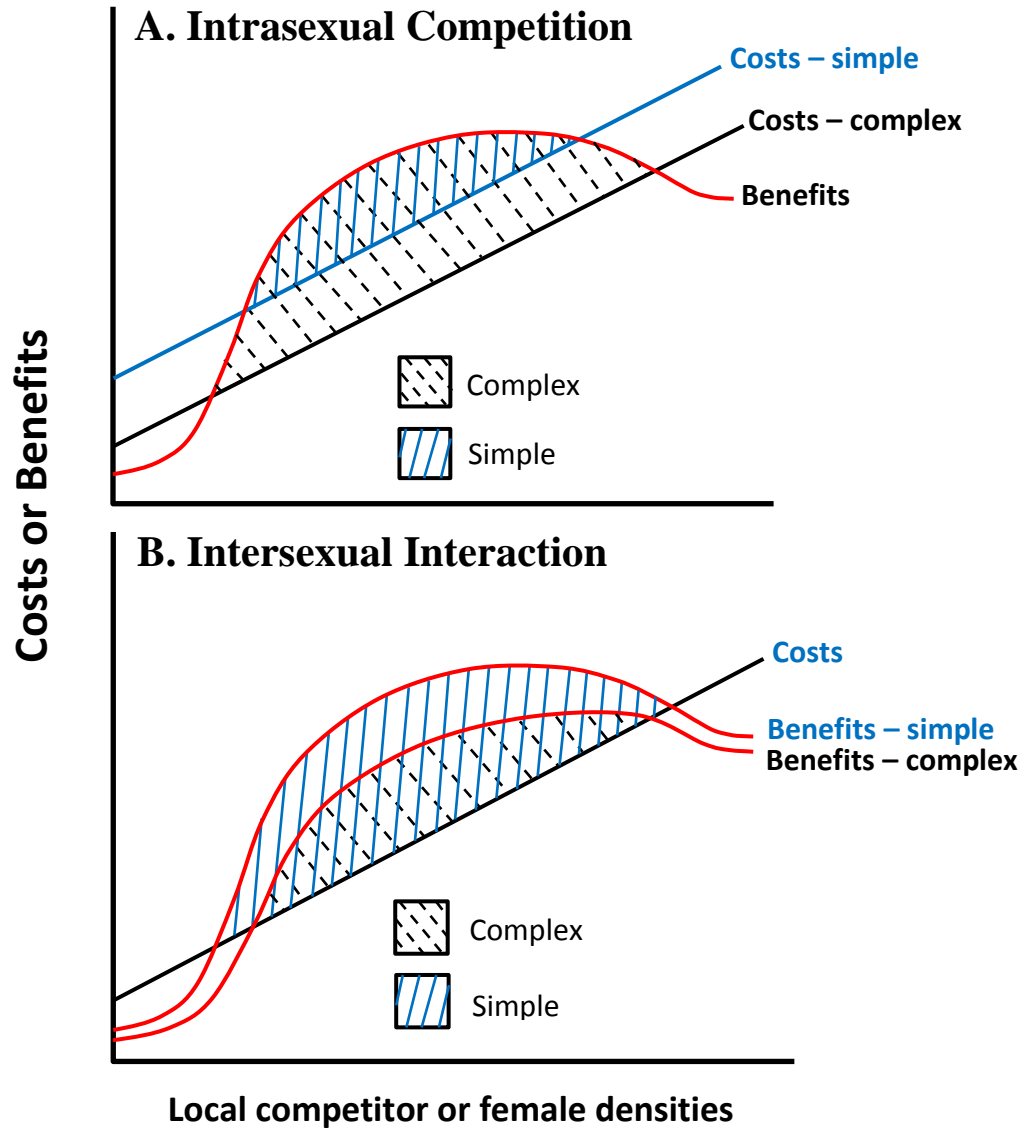


Figure 1. Predicted net benefits (areas indicated by different hatching patterns) derived through male territory defense as a function of conspecific densities and selection pressures on males in different microhabitats. *A. Intrasexual competition model.* Higher density of competitors increases costs of defense on simple patches, resulting in lower net benefits relative to that on complex patches. *B. Intersexual interaction model.* Costs of defense are independent of competitor density, but increased proximity to females disproportionately increases mating opportunities on simple patches, resulting in higher net benefits relative to that on complex patches.

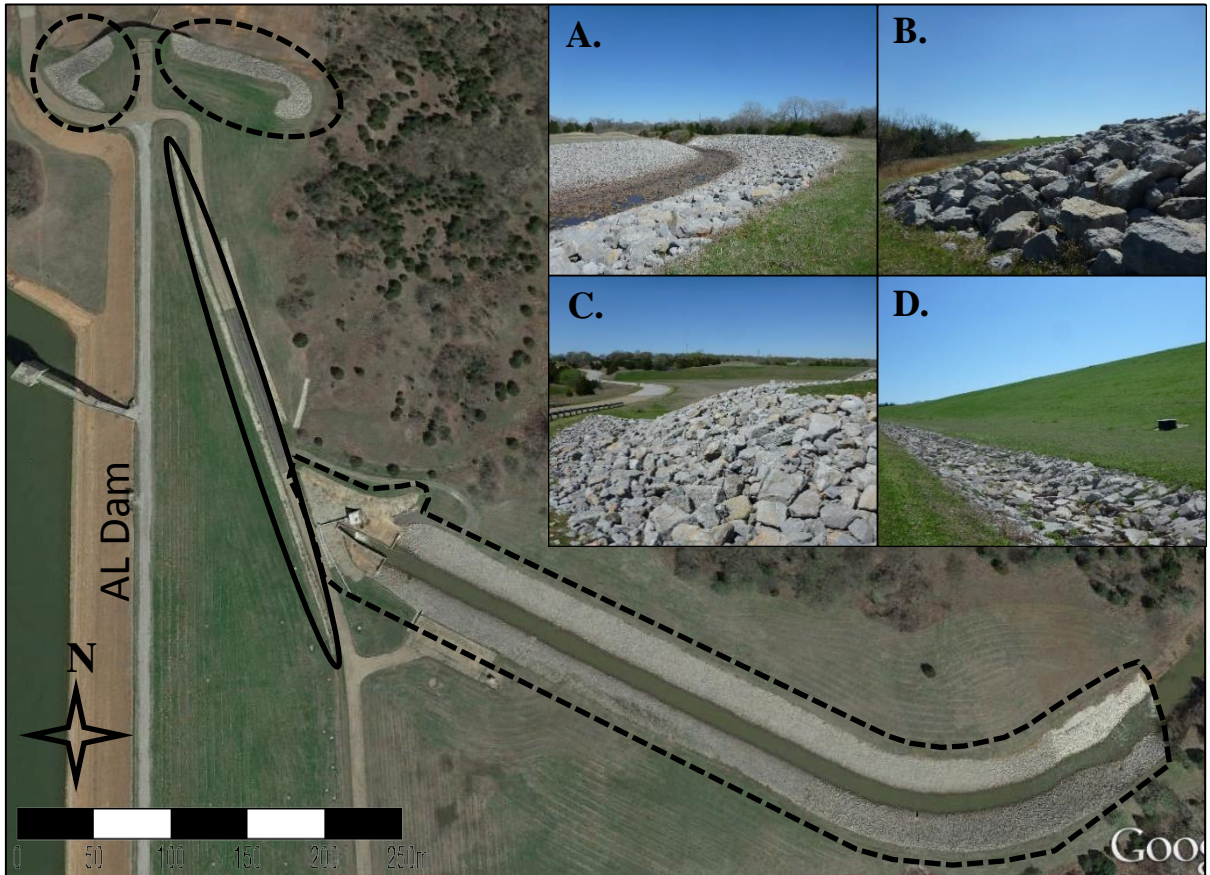


Figure 2. Aerial and ground-level photographs (inset) of the Arcadia Lake Dam spillway study site showing the two markedly different types of human-constructed microhabitat patches occupied by collared lizards. Structurally complex patches (encircled by dotted lines) consisted of wide (> 20 m) boulder fields that were sloped (Insets A, B, and C). Simple patches (encircled by a solid oval) consisted of narrow (3.5 m) strips of fractured concrete that were not inclined and flatter on the surface (Inset D). A second (740 m long) simple microhabitat patch is out of view, 285 m to the south of the southern edge of the simple patch seen above.

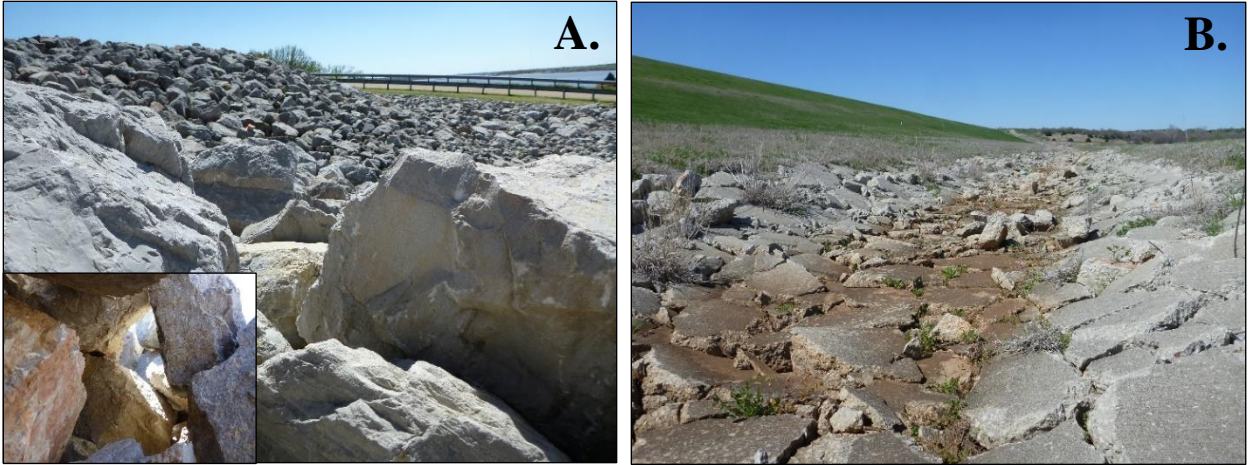


Figure 3. Markedly different surface topographies of structurally complex (A) and simple (B) microhabitat patches at the Arcadia Lake spillway site. Structurally complex patches were characterized by a network of crawlspaces beneath surface boulders (inset), whereas such a network of continuous crawlspaces was lacking on simple patches.

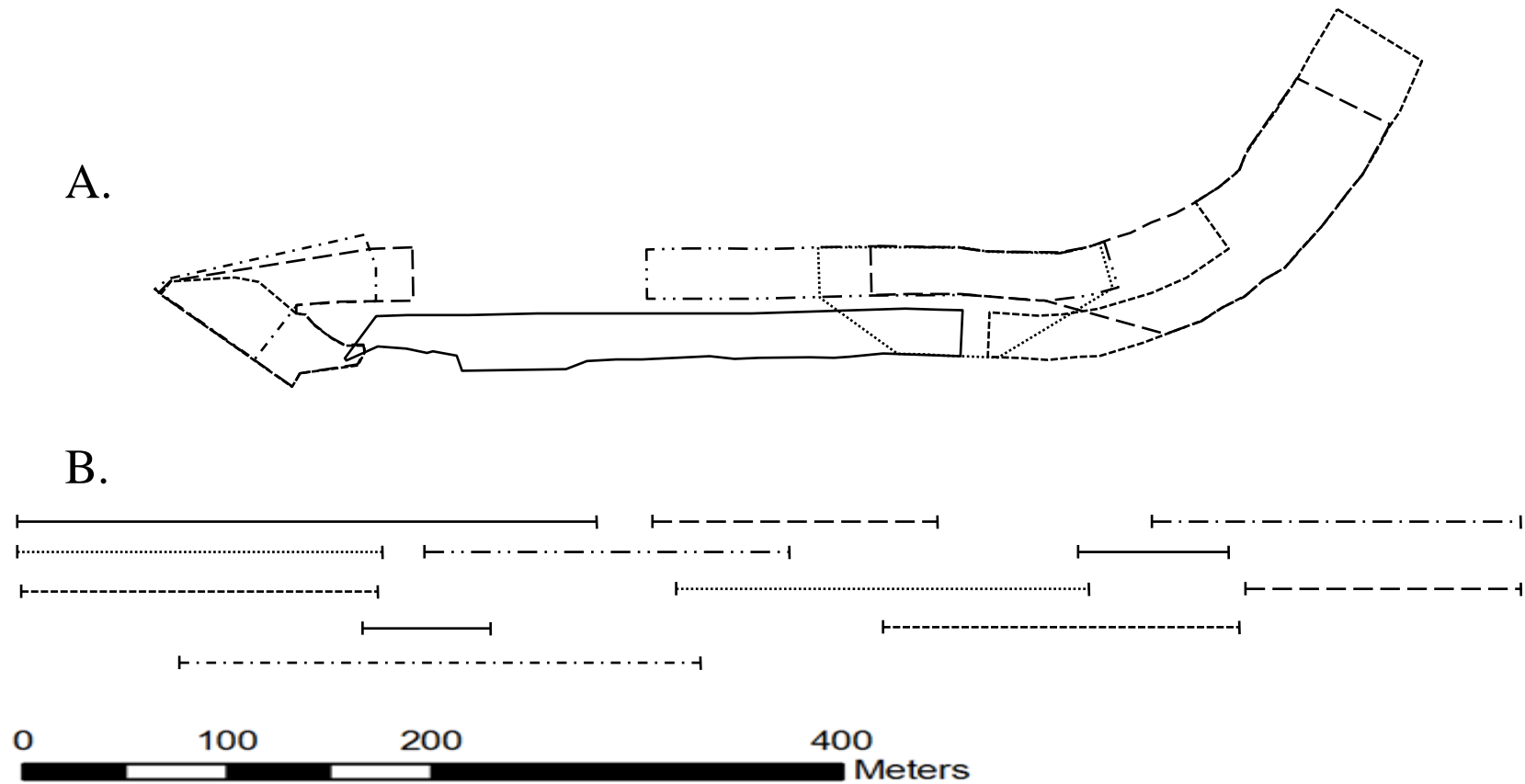


Figure 4. Example composite maps of male territories and home ranges on complex (A) and simple (B) microhabitat patches at the Arcadia Lake spillway site. Individual territories/home ranges are indicated by lines having different patterns. All territories and home ranges on simple microhabitats spanned the entire width of their respective patch because both patches were only 3.5 m wide throughout. Therefore, the length of each territory/home range is indicated by a single enclosed line (B).

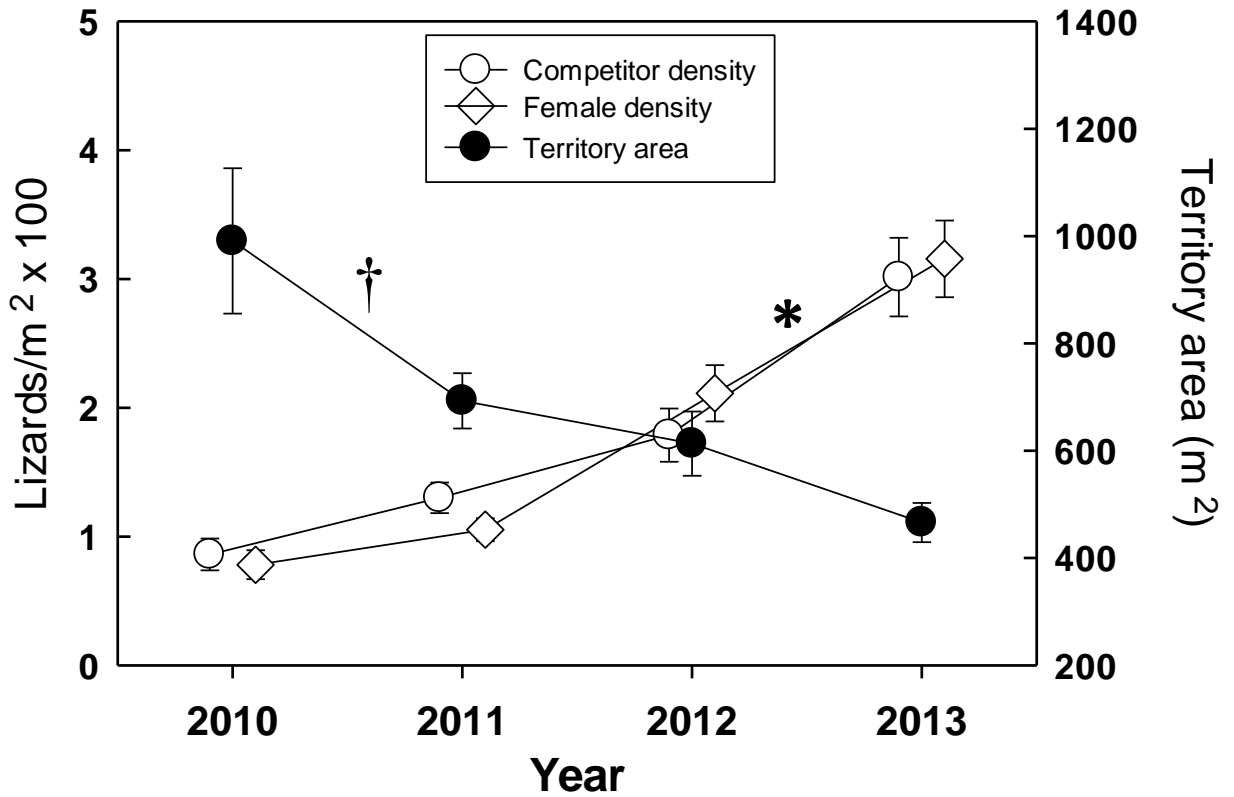


Figure 5. Local competitor density, female density, and amount of area defended by territorial male collared lizards on simple microhabitat patches in 2010–2013. Data are means \pm 1.0 SEs. The asterisk indicates a statistically significant increase in the densities of both competitors and females in 2013 relative to all other years. The dagger indicates a statistically significant decrease in territory area between 2010 and 2011.

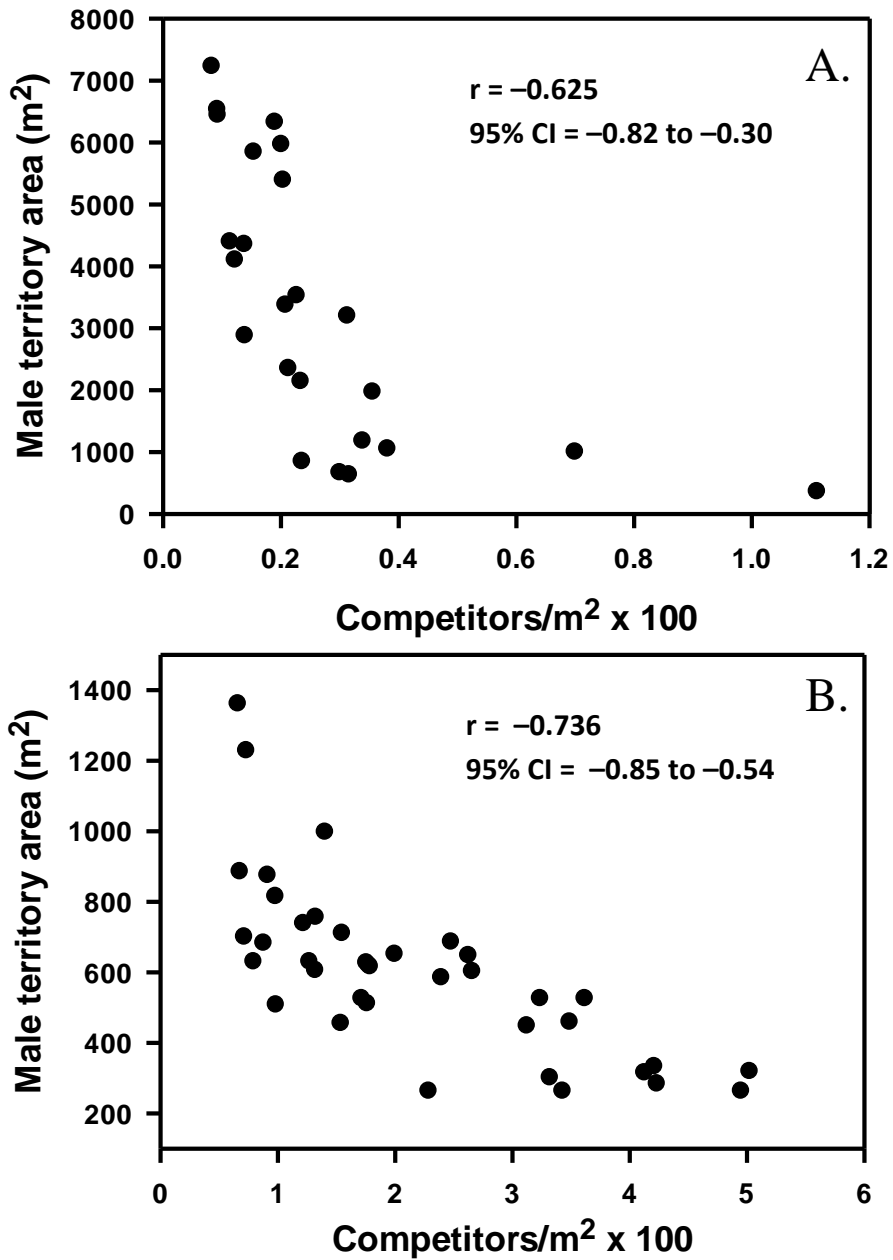


Figure 6. Correlation between competitor density and male territory area in structurally complex (A) and simple (B) microhabitat patches.

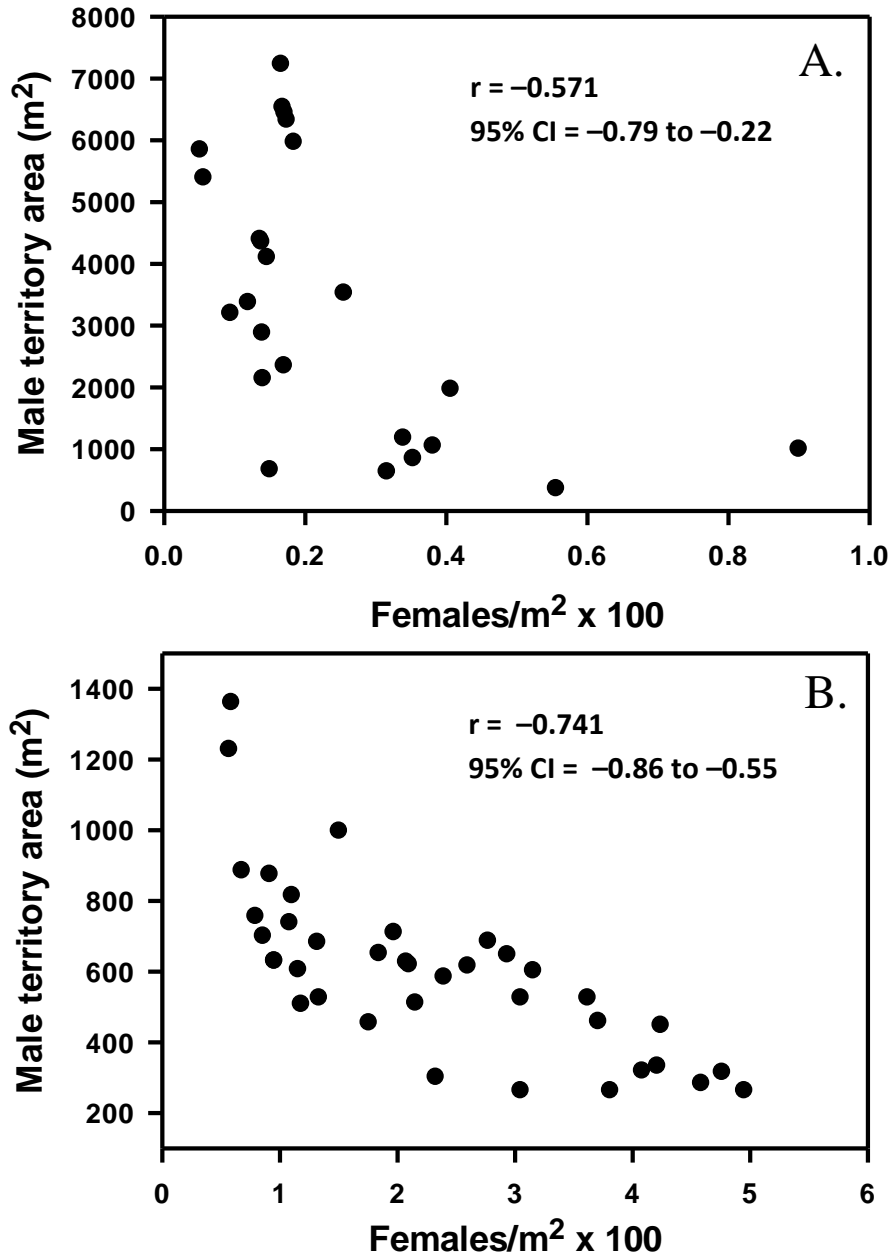


Figure 7. Correlation between female density and male territory area in structurally complex (A) and simple (B) microhabitat patches.

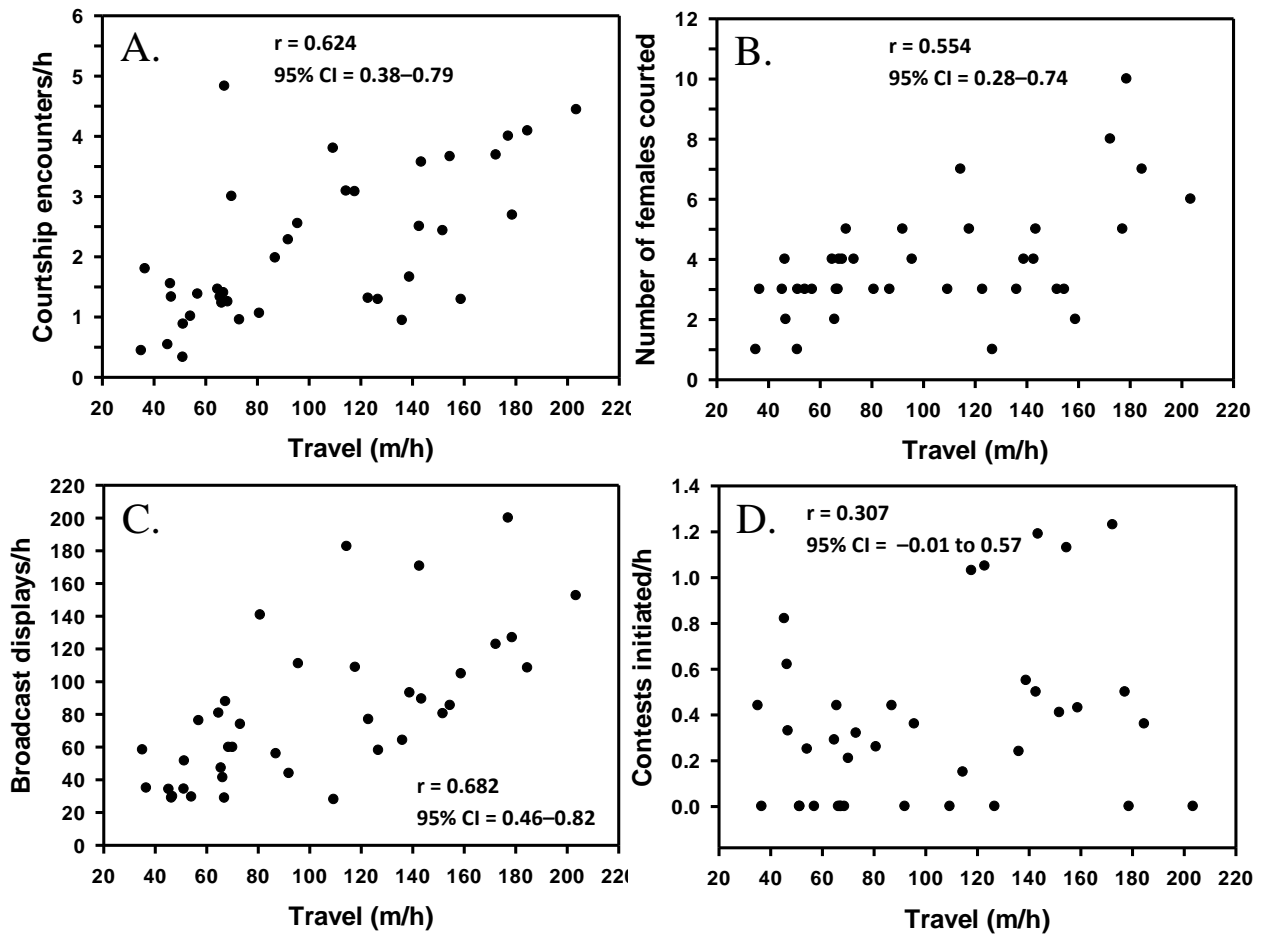


Figure 8. Correlation between travel by territorial males in simple microhabitat patches and courtship frequency (A), the number of different females courted (B), the frequency of broadcast displays (C), and contest frequency (D).

Table 1. Summary of physical parameters that differed between structurally complex and simple microhabitat patches at the Arcadia Lake Dam spillway.

Parameter	Microhabitat Type	
	Complex	Simple
Patch shape/width	Rectangular-polygonal, wider	Rectangular, narrower
Surface topography	Large boulders in inclined fields	Small broken concrete, flat
Transmission of lizard visual cues	Lower	Higher
Sub-surface network of interconnected crevices	Extensive	Limited

Table 2. Local densities of same-sex competitors and females (lizards/m² x 100) as a function of male social status and microhabitat type. Data are means \pm 1.0 SE in parentheses. Asterisks indicate statistically significant differences (95% CI did not include zero) between lizards occupying the two different microhabitat types.

Male Social Status	Microhabitat Type	
	Complex	Simple
Territorial		
Competitors	0.27 (0.05)	* 2.18 (0.21)
Females	0.24 (0.04)	* 2.29 (0.21)
Non-territorial		
Competitors	0.30 (0.06)	* 2.00 (0.36)
Females	0.20 (0.04)	* 2.11 (0.38)

Table 3. Summary of GLM analyses comparing social and spatial variables as a function of male social status and microhabitat type. Data are means \pm 1.0 SE in parentheses. Asterisks indicate statistically significant differences (95% CI did not include zero) between males occupying the two microhabitat types. Daggers indicate statistically different values for territorial males relative to non-territorial males occupying the same type of microhabitat.

Male Social Status	Microhabitat Type	
	Complex	Simple
Territorial		
<i>Advertisement</i>		
Rate of travel (m/h)	76.4 (6.7) [†]	* 101.5 (7.9) [†]
Broadcast displays/h	79.6 (9.8) [†]	80.5 (7.4) [†]
<i>Intrasexual Competition</i>		
Contests initiated/h	0.25 (0.07) [†]	0.36 (0.06) [†]
Territory area (m ²)	3408 (453)	* 604 (40) [†]
<i>Intersexual Courtship</i>		
Number of females overlapped	5.8 (0.7)	* 11.5 (0.7) [†]
Courtship encounters/h	1.03 (0.15) [†]	* 2.11 (0.20) [†]
Number of females courted	2.0 (0.3) [†]	* 3.8 (0.3) [†]

Male Social Status	Complex		Simple
Non-territorial			
<i>Advertisement</i>			
Rate of travel (m/h)	32.8 (6.1)		31.5 (4.3)
Broadcast displays/h	6.6 (2.2)		10.8 (2.3)
<i>Intrasexual Competition</i>			
Contests initiated/h	0.00 (0.00)		0.05 (0.03)
Home range area (m ²)	3261 (759)	*	999 (161)
<i>Intersexual Courtship</i>			
Number of females overlapped	4.4 (0.9)	*	13.2 (1.4)
Courtship encounters/h	0.20 (0.08)		0.37 (0.11)
Number of females courted	0.5 (0.2)		1.2 (0.3)

CHAPTER 2

HABITAT COMPLEXITY INFLUENCES MATE MONOPOLIZATION IN TERRITORIAL MALE COLLARED LIZARDS

ABSTRACT

Variation in habitat complexity is hypothesized to influence the defensibility of critical resources in animals restricted to microhabitats having patchy distributions, but empirical data on possible fitness consequences in free-ranging animals is scarce. Collared lizards inhabit discrete patches of rocky substrate, and at my study site occupied two types of semi-natural microhabitat patches that varied in several physical parameters that influenced their structural complexity. Previous studies on the behavior of males occupying simple and complex patches showed that males on structurally simple patches interacted with more females more frequently, and continued to limit non-territorial male interactions with females without significantly increasing display and contest rates. These observations suggest that territory defense may be more cost effective for males in less structurally complex microhabitats. Here, I used genetic determination of parentage over four reproductive seasons to test the fitness consequences of habitat complexity for males. Specifically, I compared the total number of offspring sired, the number of female mates, and the proportion of offspring produced by individual females that were sired by territorial males (i.e. mate monopolization) in the two microhabitat types. I also compared the number of offspring sired and the number of female mates for territorial and non-territorial males within each microhabitat type. Although males defending territories on complex patches mated with more females and sired more offspring total

than their counterparts on simple patches, territorial males on simple patches sired a greater proportion of the offspring produced by their female mates. Neither the number of offspring sired nor the number of female mates differed as a function of male social status on simple patches. By contrast, territorial males on complex patches sired more offspring total than non-territorial males, and also tended to mate with more females. My results suggest that mate monopolization through territory defense is more feasible on microhabitats that are less topographically complex, and that the adaptive value of territorial social tactics in male collared lizards may be promoted by microhabitat simplicity because it enhances monopolization of female mates.

INTRODUCTION

In populations under strong sexual selection, males having high resource holding potential (RHP; Parker 1974) often defend territories to attempt to monopolize the reproductive efforts of females that they spatially overlap (Andersson 1994; Candolin & Voigt 2001; Pryke & Andersson 2003). Territory defense typically involves time and energy intensive advertisement displays (Marler & Moore 1989; Marler et al. 1995; von Kuerthy et al. 2015), as well as contesting intruders physically (Beck 2005; Baird et al. 2012). By contrast, unless they can disperse and establish territories elsewhere (Lawrence 1987; Pasinelli & Walters 2002), males having lower RHP typically remain within neighborhoods composed of several adjacent breeding territories by adopting alternative social tactics characterized by inconspicuous behavior (Gross 1996; Shuster & Wade 2003; Taborsky et al. 2008). One key prediction of mating system theory based

upon these behavior patterns is that reproductive success among males should be disproportionately skewed toward those individuals that maintain social dominance over territories which compensates the high costs of defense. Socially subordinate males, on the other hand, are expected to obtain relatively low reproductive success (Andersson 1994; Ellis 1995).

Mating system studies based solely on observations of behavior often have supported the prediction that territory owners monopolize matings and obtain higher reproductive success because they interact with females more frequently and conspicuously, and drive subordinate males away from where females reside (reviewed by Dewsbury 1982; Andersson 1994; Ellis 1995). However, studies that have combined observations of social interactions and spatial overlap with genetic measures of parentage have shown increasingly that mating systems expected on the basis of social interactions do not always accurately predict mating systems revealed by genetic parentage analyses for several reasons (reviewed by Hughes 1998). It is impossible to monitor all individuals in a free-ranging population continuously, and free-ranging animals often copulate quickly and secretively. It also is clear that socially dominant males do not always sire all of the offspring produced by females that these males appear to monopolize on the basis of behavioral interactions (Qvarnström & Forsgren 1998; York & Baird 2015). In addition, territorial males may sire offspring with females that they do not share space with (Travis et al. 1996; LeBas 2001) and males employing subordinate social tactics may achieve mating success equal to or exceeding that of dominant males using alternative social tactics (Franco-Trecu et al. 2014; York et al. 2014). Further confounding fitness estimates based on observations of behavior alone is the fact that

females may solicit matings with multiple males and then play an active role in determining paternity after copulation has occurred via sperm competition (Birkhead & Pizzari 2002) and/or cryptic female choice (Eberhard 1996; Calsbeek & Sinervo 2004). For all of these reasons, it has become evident that accurate characterization of mating system dynamics requires a combination of quantitative records of interactions between individual males and females and genetic determination of parentage (Double & Cockburn 2003; York et al. 2014).

Reproductive monopolization of mates also may be rendered difficult if one or more ecological and social factors diminish the ability of socially dominant males to exclude competitors from areas where females settle (Emlen & Oring 1977; Davies & Lundberg 1984; Hews 1993) and prevent extra-pair copulations by rivals (Goossens et al. 1998; Westneat & Stewart 2003). Multiple paternity is frequent particularly in squamate reptiles, and appears to be driven largely by frequent encounters with males and relatively low costs to females of mating repeatedly, instead of females deriving material or genetic benefits from mating with multiple males (Lee & Hays 2004; Uller & Olsson 2008). High local population densities likely increase encounter rates between the sexes (Kokko & Rankin 2006). When local densities are high, it may become exceedingly difficult for territory holders to prevent other males from interacting with females (Mills & Reynolds 2003; Byrne & Roberts 2004), in which case females may initially reject but ultimately accept copulation attempts by multiple males in order to reduce harassment and other possible costs (e.g. forced copulation, punishment) incurred by resisting male advances (Thornhill & Alcock 1983; Clutton-Brock & Parker 1995).

The efficiency of mate monopolization may be influenced especially by the dimensions and structural complexity of patches of suitable microhabitat. Smaller patch dimensions likely will crowd females and males (Baird et al. 2003; Zamudio & Sinervo 2003), whereas structural topography may affect visibility, and therefore the ability of territory owners to detect and repel intruders (Eason & Stamps 1992, 2001) as well as locate and interact with females. As a consequence, variation in the structural complexity of microhabitats may have significant effects on the ability of territory owners to effectively monopolize the reproductive efforts of females that they are attempting to defend (Westneat & Sherman 1997; York & Baird 2015). Because selection on males is expected to result in their establishing territories and adopting behavior patterns that maximize fitness in their local environments (Grant 1993; Both & Visser 2003), optimal behavioral tactics may differ among groups that occupy structurally dissimilar microhabitats.

In Chapter 1, I showed that the basic social structure among male eastern collared lizards (*Crotaphytus collaris*) occupying microhabitats that differed markedly in complexity was not changed; some males defended territories whereas others were relegated to using stealthy, non-territorial social tactics. There was, however, a strong effect of microhabitat complexity on the behavior of territorial males. On simple patches, males courted more and different females more frequently, but did so without increasing the frequencies of the most common advertisement behavior pattern (broadcast display) or intrasexual contests that might both be expected to increase defense costs caused by a higher density of rivals. The observation that costs of defense did not appear higher on simple patches suggests that access to and monopolization of female mates might be

more cost effective for these males as a consequence of the smaller patch dimensions, increased visibility, and the absence of a subsurface network of crawlspaces that non-territorial males could use to hide and travel surreptitiously. If territory defense is more cost effective for males on simple microhabitats, then they should sire more hatchlings and monopolize the reproductive efforts of females to a higher degree than their counterparts on patches having higher complexity. Non-territorial males on the other hand are expected to be less successful under this hypothesis. The alternative possibility is that microhabitat simplicity makes it more difficult for territorial males to repel rivals which are more abundant. This hypothesis was not supported by the observation that neither displays nor contests were more frequent in males defending territories on simple microhabitat patches. Nevertheless, because behavioral dynamics do not always accurately predict reproductive consequences it also is necessary to test the alternative prediction that the number of mates and hatchlings sired by individual males on simple patches is lower, and that territorial males are less able to monopolize the reproductive efforts of females, which might increase mating opportunities for non-territorial males. I tested these alternative predictions by using genetic techniques to determine parentage of all hatchlings produced over four seasons, and comparing reproductive success in the males for which behavioral data were presented in Chapter 1.

METHODS

The study population and field site, including physical features of the two microhabitats that were used as the independent variable; the methods for recording male

advertisement displays, contests with rival males, and interactions with females; and the comparative results for territorial and non-territorial male socio-spatial behavior on simple and complex patches are all described in detail in Chapter 1 and will not be repeated here. Below, I focus on the methods necessary to assign parentage of offspring, and estimate male reproductive success and mate monopolization using genetic techniques.

Schedule of Egg Production and Emergence of Hatchlings

Adult lizards typically emerge from hibernacula from late March to early April and remain reproductively active until 15 July (Baird et al. 2001; York & Baird 2015). The schedule of egg development and oviposition was documented by capturing all females present on both microhabitat types ($N = 228$) every 7–10 d to weigh and measure them, and to palpate their abdomens. At each palpation, follicular/egg development was characterized using the egg size and shape criteria developed for females in this population (Baird 2004; Telemeco & Baird 2011). The abdomen becomes increasingly swollen as females ripen their eggs, whereas oviposition is marked by a pronounced loss in body mass (30–50% of total mass) and mud caked on the toes and integument from digging nests (Baird 2004). The temporal schedule of oviposition of first and subsequent clutches differs in first-year and two-year and older (2Y+) females (Baird et al. 2001; Telemeco & Baird 2011). First clutches produced by 2Y+ females typically begin to develop in early May and are oviposited about two weeks later during the third week of May. First-year females ripen their first clutches 10–15 d later in mid-May, and lay them

at the end of May or the first week of June. Females of both age groups may produce second or third clutches (Baird 2004; Telemeco & Baird 2011; McGill et al. in preparation), which are oviposited throughout June, into the first two weeks of July. Above average temperatures in March and April of 2012 resulted in an earlier than usual onset of clutch production in both female age classes, and some 2Y+ females produced a fourth clutch (McGill et al. in preparation). Once the last clutches of the season are oviposited, females feed heavily and become progressively less active (Baird & Sloan 2003), presumably to store energy for winter.

Eggs from the earliest clutches begin to hatch in mid-July, and hatchlings from later clutches continue to emerge until mid-October. Offspring are 38.0–40.0 mm snout-to-vent length (SVL) when they hatch, and may grow to 70.0–85.0 mm SVL by the end of the activity season in late October. From 15 July–15 October, the study site was surveyed at least three times per week to capture, mark, and measure newly emergent hatchlings. Standard measurements (SVL, tail length, body mass) were recorded at first and subsequent captures, sex was determined by examination of the post-anal scales (enlarged in males), the location of the first and subsequent captures were recorded on scale-drawn maps, and a blood sample was collected. Hatchlings were then released unharmed by placing them in rock crevices at their precise capture locations.

Collection of DNA and Genotyping

Blood samples were collected for isolation of genomic DNA from 2010 adult lizards prior to the 2010 reproductive season (York & Baird 2015), and from all

hatchlings that emerged in 2010–2013. Blood samples (50 μ l) were collected by puncturing the orbital sinus using a heparinized micro-capillary tube, and immediately transferred into 15 ml tubes containing standard lysis buffer for storage until DNA extraction. Bleeding was staunched by applying slight pressure to the orbit using a clean cloth. Collection of blood samples was conducted with approval of the Institutional Animal Care and Use Committee (IACUC) at the University of Central Oklahoma (permit number 13009).

Genomic DNA was isolated from blood samples using a DNeasy Blood and Tissue Kit (Qiagen). I amplified 11 microsatellite loci using polymerase chain reaction (PCR) primers developed for *C. collaris* (Hutchison et al. 2004) that were labeled with fluorescent dyes. Amplification reactions (15 μ l) contained 4.75 μ l of genomic DNA, 0.50 μ l of forward and reverse primers, 9 μ l of Applied Biosystems (ABI) True Allele PCR Premix (Thermo Fisher Scientific), and 0.25 μ l of GoTaq DNA polymerase (Promega). All PCR products were amplified according to the thermal profile and annealing temperatures described in Husak et al. (2006). Mixtures of 9.25 μ l of Hi-Di formamide (ABI, Thermo Fisher Scientific), 0.25 μ l of ROX 500 HD size standard (ABI, Thermo Fisher Scientific), and 0.50 μ l of PCR product were denatured at 96°C for 5 min and then immediately chilled on ice for 3 min prior to loading. I visualized amplicons for all loci using an automated DNA sequencer (model ABI 3130; Thermo Fisher Scientific) and GeneMapper software (v. 4.0; ABI, Thermo Fisher Scientific). I used ML-NullFreq software (Kalinowski & Taper 2006) to test for the presence of null alleles at each locus.

All adult and hatchling lizards present on the study site from 2010–2013 were genotyped for all 11 loci. I included in parentage analyses all females that produced at least one clutch of eggs ($N = 201$), all sexually mature males ($N = 198$) that were present on the study site during at least part of the reproductive season (1 May – 15 July, 2010–2013), and all offspring ($N = 869$). Ninety-one percent (790 of 869) of offspring were captured from late July – Oct of the season that they hatched (2010, $N = 144$; 2011, $N = 162$; 2012, $N = 257$; 2013, $N = 257$). The other 79 hatchlings (9% of total; 2010, $N = 19$; 2011, $N = 13$; 2012, $N = 27$; 2013, $N = 20$) were not captured until early spring (20 March – 30 April) of the following activity season. Since hatchling first capture locations were sometimes used to inform maternity/paternity assignments, I plotted the capture locations of these hatchlings on maps to determine if they appeared clumped in any particular portion of their respective parentage group. Because their capture locations appeared to be randomly distributed throughout each parentage group, their delayed capture most likely did not significantly bias parentage assignments or estimates of mating relationships.

Two loci (Orig21, ENR21) showed a high frequency of null alleles. Null alleles may confound parentage assignments because true heterozygotes may be incorrectly typed as homozygotes, potentially resulting in genetic mismatches and false exclusion of the true parents (Dakin & Avise 2004). Because both loci were polymorphic, I retained them in analyses, and minimized the probability of false exclusion of potential parents by typing hatchlings that were homozygotes at one or both of these loci ($N = 614$) at only one allele for parentage analyses (LeBas 2001; Husak et al. 2006). The high frequency of null alleles at locus Orig21 in my dataset (2010–2013) was unexpected because this locus

did not show null alleles in previous seasons (2007–2009; York & Baird 2015). In 2007–2009, Orig21 had four alleles, although one was exceedingly rare. Only three potential parents carried the rare allele in 2010, it was not passed on to any offspring, and these three parents died prior to the 2011 season. The other three alleles appeared regularly in all generations (2010–2013). Consequently, it is likely that excess homozygous genotypes at locus Orig21 in my data set was the result of random genetic drift, and not the failure of one or more alleles to amplify. Analyses based upon parentage assignments using both one and two null alleles yielded similar results. Because results based upon two null alleles are more conservative, I used these.

Parentage Assignments and Patterns of Male Reproductive Success

Both adult female and male collared lizards maintain strong philopatry to home ranges and territories (Baird 2013a), and mark-recapture/mapping studies since 1990 have shown that hatchlings remain within 20 m of their first capture location for 1–1.5 months (Baird unpublished data). Therefore, I used the locations of adults relative to hatchlings as the first criterion to inform my analysis of possible parents (see similarly Zamudio & Sinervo 2000; York et al. 2014; York & Baird 2015). Only the width of a service road (8 m) separated one of the simple microhabitat patches from the largest complex patch (see Figure 2 in Chapter 1). Each season 2–3 females and 2–7 males moved between the south end of this simple patch and the largest complex patch. Because gene flow between these two patches was likely, I pooled lizards from them for parentage analyses (Parentage Group 1; Figure 1, Table 1). The 16 males that moved

between this simple and adjacent complex patch were assigned to the complex treatment group because the area-to-perimeter ratios of their territories/home ranges were similar to those of lizards on the other complex microhabitat patches (Chapter 1). Lizards on an entirely separate simple microhabitat patch were considered a second group of potential parents and offspring (Parentage Group 2; Figure 1, Table 1), because they were separated by at least 285 m from conspecifics residing on the nearest patch. A third Parentage Group consisted of two smaller complex patches that are separated by only 40 m of grass with a concrete wall running between them (see Figure 2 in Chapter 1), along which lizards have been observed to travel two to four times per season (Curtis & Baird 2008). Because the potential for gene flow here was high, I pooled lizards from these two patches for parentage analyses (Parentage Group 3; Figure 1, Table 1). A small number of males moved between patches included in two different parentage groups (2010, $N = 1$; 2011, $N = 3$). Because these males may have mated with female residents of both patches, to be conservative I included them in both parentage analysis groups.

For each of these three parentage analysis groups separately, I used the maximum likelihood program CERVUS v. 3.0.3 (Marshall et al. 1998; Kalinowski et al. 2007) to assign a mother and father for all hatchlings at 80% confidence. My simulation parameters for parentage assignments were a mean proportion of candidate fathers (or mothers) sampled of 0.98, a proportion of loci mistyped of 0.01, and a number of simulation cycles of 100,000. For hatchlings that CERVUS could not assign to a mother and/or father with at least 80% confidence, I next compared the genotypes of the two most-likely parents to the hatchling genotype, and excluded the candidate parent that mismatched at any locus (i.e. genetic exclusion; Haynie et al. 2003; York et al. 2014;

York & Baird 2015). When the two most-likely parents did not mismatch, or shared the same number of mismatches with that of the hatchling at any locus, I used mapped location data to guide parentage assignments. Specifically, I measured the minimum linear distance between the first hatchling capture location and the nearest boundaries of the home ranges (or territories) of each candidate parent, and assigned the hatchling to the parent that was closest (= spatial proximity; York et al. 2014; York & Baird 2015). Using this highly prioritized hierarchy of parentage assignment methods, I first assigned hatchlings to individual mothers and fathers, separately, then determined the parent pair of each hatchling. For all hatchlings that were assigned both parents, I determined the total number of offspring sired, as well as the number of different females that males mated with for all males on complex and simple microhabitat patches. Using all males for which I had sufficient behavioral data to determine social status (territorial, $N = 62$; non-territorial, $N = 28$; Chapter 1), I compared the number of mates and number of hatchlings sired as a function of microhabitat type and male social status.

Degree of Mate Monopolization

To determine the extent to which territorial males monopolized the reproductive efforts of their female mates, I divided the number of hatchlings assigned to each pair of parents by the total number of offspring produced by each female (monopolization index). I tested the influence of habitat complexity on mate monopolization by comparing these monopolization indices for territorial males on simple versus complex microhabitat patches.

Statistical Analyses

All statistical analyses were performed in the program R v. 3.1.2 (R Core Team 2014) using generalized linear models (GLM). I used GLM's rather than traditional (parametric) linear models because several fitness variable estimates were non-normally distributed among both territorial and non-territorial males within each microhabitat type. To test for effects of microhabitat patch complexity on male reproductive success, I used patch type (simple versus complex) as the independent variable to compare the total number of offspring sired and the number of different female mates for territorial and non-territorial males (separately). To test for effects of social status on male reproductive success within each microhabitat type, I compared these two dependent variables (total number of offspring, number of female mates) for territorial versus non-territorial males on simple and complex patches.

To test the hypothesis that microhabitat complexity influences the extent to which territorial males monopolize females, I used patch type (simple versus complex) as a categorical predictor, and the proportion of offspring that individual territorial males sired with each of their female mates as the dependent variable. I used a generalized linear mixed model (GLMM) for this analysis because it allowed me to include a random effects term to control for individuals with multiple monopolization index values (one for each female mate).

Because total number of offspring sired and number of female mates were discrete dependent variables, I used a GLM with Poisson error structure and log link function for each analysis involving these variables. The response variable in the analysis

of mate monopolization was continuous, so I used a Gaussian error structure and identity link function. I used the package ‘compute.es’ to calculate standardized (mean = 0, standard deviation = 1) effect sizes (Cohen’s d) and associated 95% confidence intervals (CI) for all models.

For all analyses, I evaluated statistical significance by determining whether or not the 95% CI of predictor variables overlapped zero. Specifically, if the 95% CI of predictor variables did not overlap zero, predictor (independent) variables were deemed to have a significant effect on the dependent fitness variable being examined. I do not report P -values, because they are subject to sample size variation and do not reveal the biological significance or statistical uncertainty of the variables of interest (Colegrave & Ruxton 2003; Nakagawa & Cuthill 2007). Instead, I report standardized effect sizes with CI because they provide both biologically and statistically meaningful inference at a specified degree of certainty (Colegrave & Ruxton 2003). I also report z values for tests involving the total number of offspring sired and the number of female mates, and t values for my analysis of mate monopolization, which are GLM and GLMM test statistics derived by R for analyses involving discrete and continuous data, respectively.

RESULTS

Parentage Assignment

In Parentage Group 1, I assigned 216 (48.5%) hatchlings a father and 284 (63.8%) hatchlings a mother using CERVUS. An additional 21 (4.7%) hatchlings were assigned

fathers and five (1.1%) mothers using genetic exclusion. One-hundred seventy-five (38.5%) hatchlings having positive LOD scores for both candidate parents were assigned fathers and 146 (32.8%) were assigned mothers using exclusion based on spatial proximity. I did not assign fathers for 33 (7.4%) and mothers for 10 (2.2%) hatchlings as a consequence of either negative LOD scores for one or both parents, or because hatchling first capture locations were either equidistant from the two most-likely mothers/fathers, or overlapped by both most-likely mothers/fathers. Altogether for Parentage Group 1, only 9.7% of hatchlings ($N = 43$) were not assigned parents, whereas I assigned a mother and father for 402 of 445 (90.3%) hatchlings using a combination of the three assignment methods applied hierarchically.

In Parentage Group 2, I assigned 145 (38.9%) hatchlings a father and 135 (36.2%) hatchlings a mother using CERVUS. I used genetic exclusion to assign fathers for an additional 19 (5.1%) hatchlings and mothers for an additional six (1.6%) hatchlings. One-hundred seventy (45.6%) hatchlings having positive LOD scores for both candidate parents were assigned fathers and 195 (52.3%) were assigned mothers using exclusion based on spatial proximity. As a consequence of either negative LOD scores for one or both parents or indeterminate spatial assignments, I did not assign fathers for 39 (10.5%) and mothers for 37 (9.9%) hatchlings. However, both parents shared negative LOD scores or indeterminate spatial criteria for the same hatchlings in 9 of 76 cases. Therefore, altogether only 18.0% of hatchlings ($N = 67$) were not assigned parents, whereas I assigned a mother and father to 306 of 373 (82.0%) hatchlings in Parentage Group 2 using a combination of the three assignment methods applied hierarchically.

Each year from 2011 to 2013, there was only one female on the two smaller complex microhabitat patches that composed Parentage Group 3 that spent some time on each patch. The same lizard was present in 2011 and 2012, whereas a different female used these two patches in 2013. CERVUS requires at least two candidate mothers (or fathers) to perform maternity/paternity simulations and analyses. Although there were at least two potential fathers in 2011–2013, I could not assign maternity using CERVUS because there was only one female present each season. These females were almost certainly the mothers of the hatchlings captured on these two patches because they were the sole residents. Of the 23 hatchlings in Parentage Group 3 in 2010, all (23) were assigned a mother and 22 assigned a father using CERVUS. The one hatchling not assigned paternity using CERVUS had positive LOD scores for two potential fathers, but paternity could not be assigned using spatial proximity because the territories of both potential fathers overlapped the first capture location for this hatchling. Of the 28 remaining hatchlings (2011–2013) in Parentage Group 3, all (28) were assigned a father using CERVUS. Altogether, I assigned a mother and father to 50 of 51 (98.0%) hatchlings in Parentage Group 3.

Influence of Microhabitat Complexity on Male Fitness Estimates

On average, males defending territories on complex microhabitat patches sired 1.6 times more offspring total (GLM: $z_{2, 59} = 5.44$; Cohen's $d = 1.63$, 95% CI = 1.03–2.23) than territorial males on simple patches (Figure 2). Territorial males on complex patches also mated with 1.4 times more females on average (GLM: $z_{2, 59} = 3.08$; Cohen's $d =$

0.84, 95% CI = 0.3–1.39) than their counterparts on simple patches (Figure 3). By contrast, the average proportion of offspring produced by female mates that were sired by males defending territories on simple microhabitat patches was 1.3 times higher (GLMM: $t_{2,54} = 2.35$; Cohen's $d = 0.64$, 95% CI = 0.08–1.20) than that of territorial males on complex patches (Figure 4).

Consistent with previous parentage studies at Arcadia Lake (AL), non-territorial males on complex microhabitat patches mated successfully using stealthy tactics, and in 2010–2013 they continued to do so on microhabitat patches having a simpler structure. Neither the number of offspring sired (GLM: $z_{2,25} = 1.12$; Cohen's $d = 0.46$, 95% CI = –0.38 to 1.30) nor the number of female mates (GLM: $z_{2,25} = 0.14$; Cohen's $d = 0.06$, 95% CI = –0.77 to 0.89) differed for non-territorial males in the two microhabitat types (Figures 2 and 3, respectively).

Influence of Male Social Status on Fitness Estimates Within Types of Microhabitat

On complex microhabitats, territory owners sired 1.7 times more offspring total (GLM: $z_{2,32} = 2.79$; Cohen's $d = 1.06$, 95% CI = 0.29–1.84) than their non-territorial rivals (Figure 2). Territorial males on complex patches also tended to mate with more, different females than non-territorial males, although the difference was not statistically significant (GLM: $z_{2,32} = 1.82$; Cohen's $d = 0.67$, 95% CI = –0.07 to 1.41; Figure 3). By contrast, male social status did not have a significant effect on either the total number of offspring sired (GLM: $z_{2,52} = 1.18$; Cohen's $d = 0.33$, 95% CI = –0.23 to 0.89) or the

number of female mates (GLM: $z_{2, 52} = 0.67$; Cohen's $d = 0.19$, 95% CI = -0.37 to 0.75) on simple microhabitat patches (Figures 2 and 3, respectively).

DISCUSSION

My results support the hypothesis that the structural complexity of microhabitats influences the ability of male collared lizards to monopolize the reproductive efforts of females within their territories. Even though they produced fewer total offspring with fewer females, territorial males on simple patches sired a greater proportion of the offspring produced by their mates. Several physical features of simple microhabitats likely promoted a higher degree of mate monopolization. The extreme narrowness of these patches concentrated females spatially much more than on complex patches, and as a consequence males defended much smaller territories on simple patches (Chapter 1). The relatively flat and unobstructed surface topography also enabled territory owners to detect rivals more efficiently, and non-territorial males were not able to travel inconspicuously because the network of subsurface crawlspaces that was present on complex patches was absent on simple patches.

Contrary to the expectation that increased mate monopolization by territorial males would decrease mating opportunities for non-territorial males on simple patches, these males did not sire fewer offspring or mate with fewer females. Similar reproductive success by non-territorial males is not entirely surprising given that lizard densities on simple patches were nearly an order of magnitude higher than those on complex patches for all years combined. High densities are expected to increase

encounter rates between the sexes (Kokko & Rankin 2006), perhaps even for stealthy non-territorial males. Indeed, non-territorial collared lizard males on simple patches tended to court more different females than their counterparts on complex patches (Chapter 1). Past studies on complex patches showed that females often rejected unwanted advances from males by fleeing into the network of subsurface crevices (Baird & Timanus 1998). This avenue of evasion was not available to females on simple patches because subsurface crawlspaces were lacking. Therefore, repeated courtship by both territorial and non-territorial males on simple patches appears to have resulted in females accepting copulations from multiple males, independent of social status, in order to avoid harassment (York & Baird 2015). That females apparently mated independent of male social status seems likely given that multiple paternity among other squamates appears to be driven by frequent encounters between the sexes and relatively low costs to females of mating repeatedly (Lee & Hays 2004; Uller & Olsson 2008). It also is probably unrealistic to expect that territorial males could prevent non-territorial rivals from mating altogether because territories on simple patches were long ($\bar{x} = 172.5$ m), and overlapped the home ranges of up to 19 females and just as many competitors.

The observation that territorial males on complex patches mated with more females and sired more offspring total is difficult to reconcile with higher frequencies of courtship of more females by territorial males on simple patches (Chapter 1). One possible explanation is that prolonged bouts of courtship do not necessarily ensure that males will secure matings (York et al. 2014; York & Baird 2015). Courtship interactions between territorial males and their potential mates on simple patches might also have been interrupted by the necessity to chase-off non-territorial competitors, given the

extremely high density of such rivals. If this were the case, however, territory owners on simple patches would be expected to initiate intrasexual contests more frequently than their counterparts on complex patches. Although the frequency of contests initiated with rivals was somewhat higher on simple patches, the difference was not statistically significant (Chapter 1). It also is possible that territorial males on complex patches mated with females that they were not observed courting. Offspring production by parents not observed to interact socially are increasingly common in studies on vertebrates (LeBas 2001; Griffith et al. 2002; Cohan & Allainé 2009). My results therefore, add to a growing body of evidence indicating that social interactions alone do not accurately predict mating relationships.

Territorial males on complex microhabitat patches sired more offspring total, and also tended to mate with more females than non-territorial males. In the only previous genetic parentage studies at AL, males that defended territories on complex patches did not achieve higher annual reproductive success than non-territorial males during the 2007–2009 seasons (York et al. 2014; York & Baird 2015). Different results from these two sampling periods suggests that the relative reproductive success of males displaying the two alternative social tactics varies enough annually that the average success of either tactic may end up being higher depending upon fluctuating social conditions. In each of the 2007–2009 seasons, sex ratios (the number of male competitors relative to the number of receptive females in local neighborhoods) were male-biased, and in one year (2007) males were 3.5 times more abundant (York & Baird 2015). By contrast, sex ratios on complex microhabitats were decidedly male-biased only during 2011 (ratio of males to females ± 1.0 SE = 2.60 ± 1.05), were nearly equal in both 2010 (1.19 ± 0.47) and 2013

(1.17 ± 0.48), and female-biased (0.74 ± 0.20) in 2012. These results suggest that the relative success of territorial males may increase during seasons when there are fewer competitors relative to receptive females within local neighborhoods, whereas the relative fitness of non-territorial males appears to increase when the number of rival males exceeds the local number of females.

Territorial behavior is expected to evolve and be maintained by selection when the net benefits over the entire lifespan of individuals acquired through resource defense exceed those that could be obtained using alternative mating tactics not involving defense of space (Maynard Smith 1974; Dominey 1984). The lifetime reproductive success of individual collared lizard males has not been determined in any population occupying either natural or human-constructed microhabitats. Moreover, territory defense appears to be a fixed tactic in male collared lizards, because at least some males defend territories in all populations examined to date (Fitch 1956; McCoy et al. 2003; Husak et al. 2006; Baird 2013a). My results showing more efficient mate monopolization by males on simple habitats without incurring higher defense costs indicates that the structural complexity of microhabitats is one factor that influences the relative success of territorial versus non-territorial tactics for male collared lizards, and may have played a role in the evolution of territorial behavior in this species.

Increased mate monopolization on simple microhabitat patches is important with respect to the adaptive value of territory defense, because simple patches share some similarities with the natural ancestral habitat of *C. collaris*. Collared lizard social behavior evolved on relatively small, discrete rock outcroppings or washes having

relatively few crevices and crawlspaces (Fitch 1956; Baird & Sloan 2003). Natural rock habitats have only a few markedly elevated perches that afford territory owners high visibility over relatively small surrounding areas, and the scarcity of crevices likely inhibits the ability of non-territorial males to move through such habitats without being detected by territory owners. Simple microhabitat patches at AL resemble the natural habitat of *C. collaris* because the dimensions of patches are small, visibility is high, and hiding places are scarce. Although past studies conducted on complex microhabitat assumed that territorial males were able to prevent matings by non-territorial males (Baird 2013a), parentage analyses combined with behavioral data have revealed that the highly modified structure of these human-constructed habitats severely jeopardized the potential for mate monopolization (York et al. 2014; York & Baird 2015; this study). Enhanced mate monopolization on simple patches may promote the adaptive value of territorial behavior, especially if males can achieve high levels of success without increasing chronic energy expenditure on advertisement and aggression (Chapter 1), thereby increasing reproductive longevity (more seasons).



Figure 1. Parentage Groups (1–3) at the Arcadia Lake spillway site that lizard hatchlings and potential parents were placed in for parentage analyses. Individual lizards were placed in their respective parentage group based upon their first capture location (hatchlings) and the rock patches they occupied during the reproductive season (adult males and females). See text for justification of the three parentage groups.

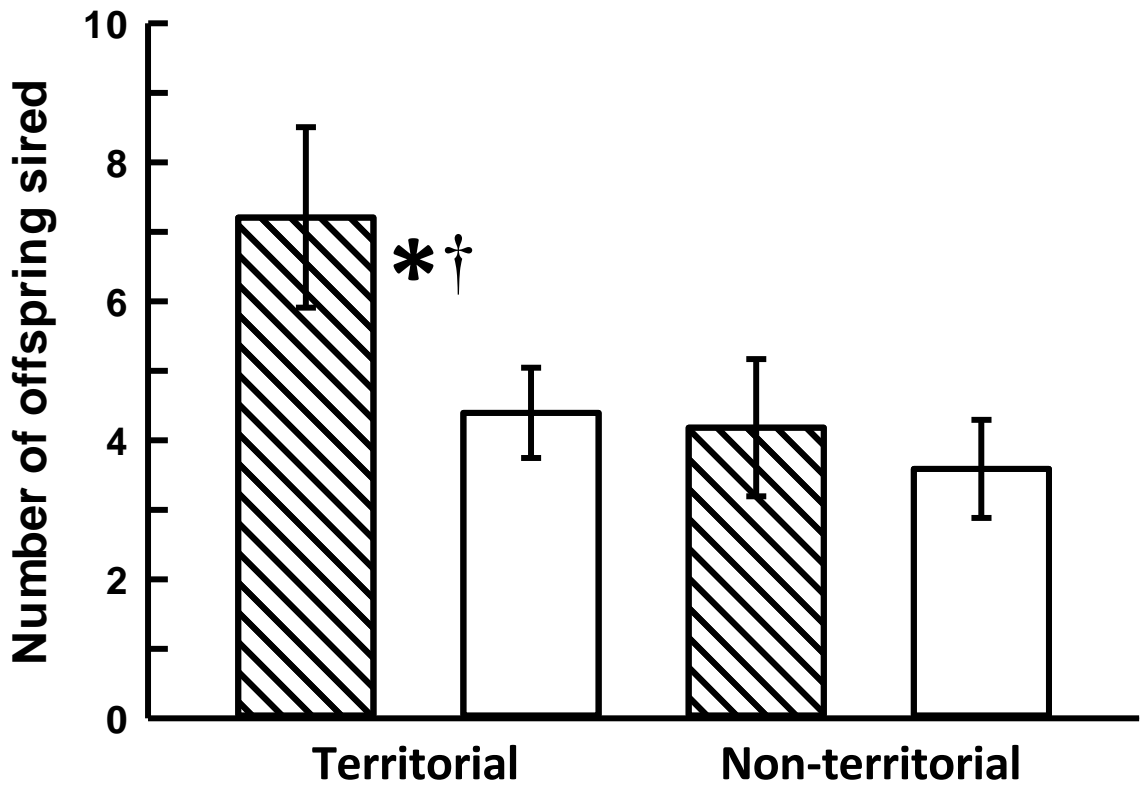


Figure 2. Average total number of offspring sired by territorial and non-territorial males on complex (hatched bars) and simple (open bars) microhabitat patches from 2010–2013. Data are means \pm 1.0 SE. The asterisk indicates statistically more (95% CI did not include zero) offspring sired by territorial males on complex patches relative to their counterparts on simple patches, whereas the dagger indicates statistically more offspring sired by territorial males relative to non-territorial males on complex patches.

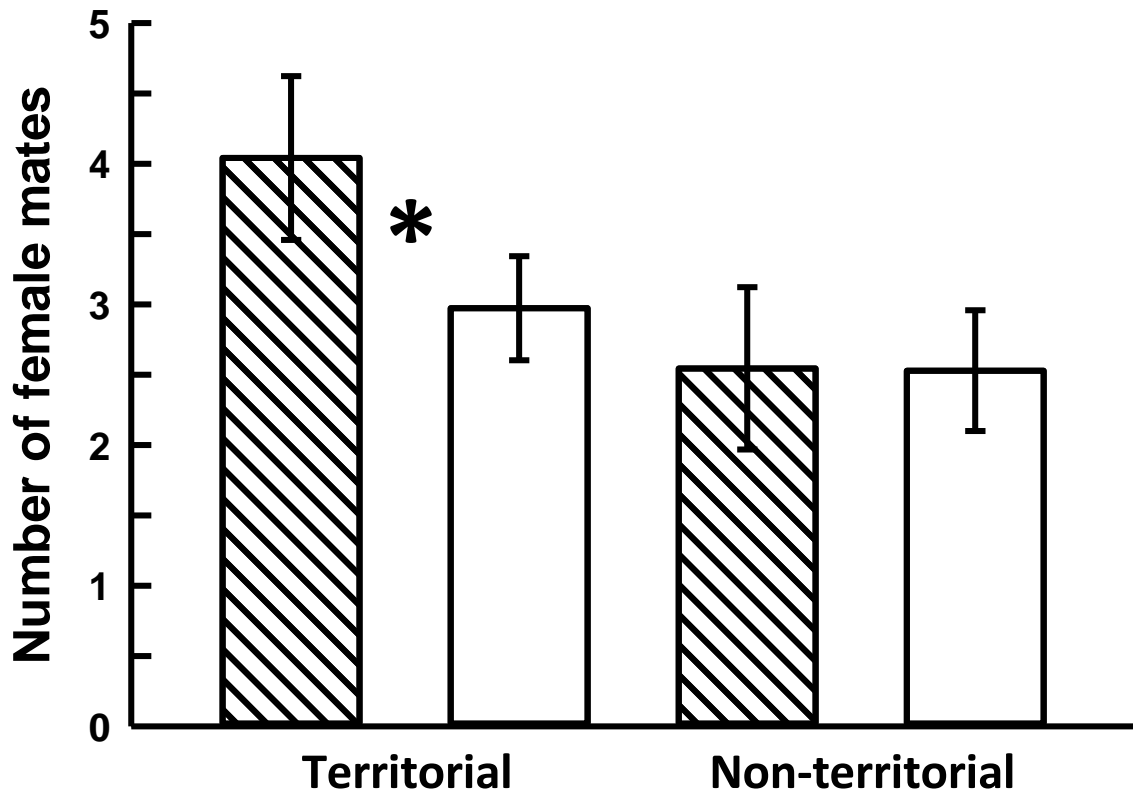


Figure 3. Average number of female mates for territorial and non-territorial males on complex (hatched bars) and simple (open bars) microhabitat patches from 2010–2013. Data are means \pm 1.0 SE. The asterisk indicates statistically more (95% CI did not include zero) mates for males in the complex microhabitat.

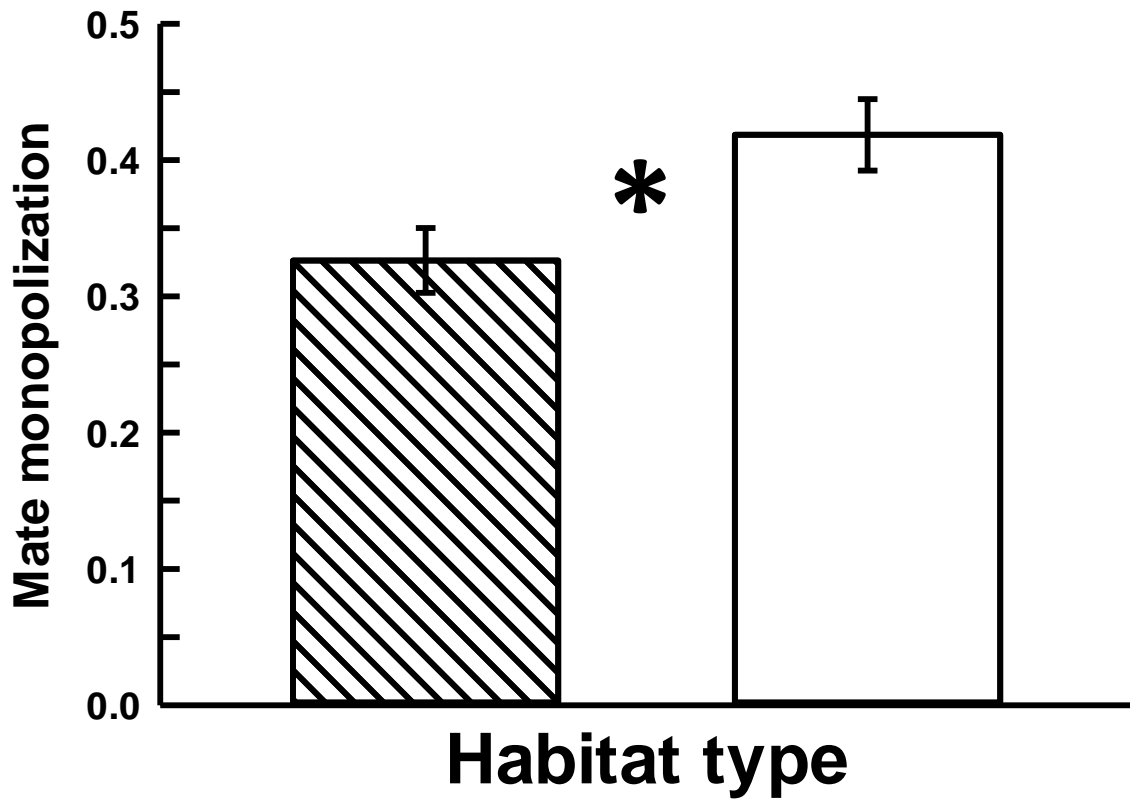


Figure 4. Proportion of total offspring produced by each female sired by territorial males (mate monopolization) on complex (hatched bar) and simple (open bar) microhabitat patches from 2010–2013. Data are means \pm 1.0 SE. The asterisk indicates a statistically higher (95% CI did not include zero) degree of mate monopolization by males on simple patches.

Table 1. Number of potential fathers, potential mothers, and hatchlings included in parentage analyses for the three Parentage Groups at Arcadia Lake Dam.

	2010	2011	2012	2013	Total
Parentage Group 1					
Potential fathers	15	24	17	25	--
Potential mothers	11	8	31	36	--
Hatchlings	60	99	144	142	445
Parentage Group 2					
Potential fathers	12	21	23	44	--
Potential mothers	13	16	32	45	--
Hatchlings	50	71	130	122	373
Parentage Group 3					
Potential fathers	10	2	3	3	--
Potential mothers	6	1	1	1	--
Hatchlings	23	5	10	13	51

GENERAL SUMMARY

My results are the first data presented on the social and spatial behavior of male eastern collared lizards (*Crotaphytus collaris*) occupying simple microhabitat patches at the Arcadia Lake (AL) Dam spillway study site. Although the basic social structure on simple patches remained unchanged relative to that documented on complex patches in the present study (Chapter 1) and previously (Baird et al. 1996, 2003; Baird 2013a), behavior patterns exhibited by territorial males differed in some important respects that provide insight into likely sexual selection pressures acting on the adaptive value of territory defense in collared lizards. Frequencies of direct contests among males were not higher when the density of rival males was higher on simple microhabitats, nor were frequencies of broadcast display. By contrast, males defending territories on simple patches traveled throughout their territories at higher rates and courted more different females, more frequently. Sexual selection theory often predicts that males should compete more intensely for mates when population density is high (Shuster & Wade 2003; Kokko & Rankin 2006). Furthermore, some have argued that aggression with rivals should take precedence over courtship because rivals can interfere with mating opportunities (Warner & Hoffman 1980; Berglund et al. 1996). My results show the opposite to be the case in the AL population, suggesting that male behavior is shaped more by opportunities to court and perhaps form social bonds with females, than by intrasexual aggressive activities.

Microhabitat complexity also had a significant influence on correlates of fitness in males that defended territories. Although territory owners on complex patches mated

with more females and sired more offspring total, their counterparts on simple patches monopolized the offspring that their female mates produced to a higher degree. The efficiency of mate monopolization may be enhanced in less structurally complex habitats because there is less visual obstruction which increases male visual detection of competitors as well as female mates. Because simple microhabitat patches are flatter, the surface is less topographically variable, and an extensive network of subsurface crawlspaces is absent, non-territorial males are less able to travel stealthily the way that they are able to on complex patches at the AL site. In this way, the simple patches at AL more closely resemble the natural ancestral habitat of collared lizards which were (and still are) relatively small discontinuous rock outcroppings or washes with only a few prominent elevated perches and relatively few crevices and crawlspaces (Fitch 1956). Similar to these natural habitats, human-constructed simple patches at AL may promote both increased economic defensibility of territories and a higher degree of mate monopolization by territory owners (McCoy et al. 2003; York et al. 2014). My study is the first to integrate molecular parentage assignments with behavioral data on free-ranging males to demonstrate that such attributes of the microhabitats where male collared lizards defend territories likely have a strong influence on the behavior and fitness of lizards displaying this social tactic.

Previous genetic parentage data recorded over three seasons on collared lizards occupying complex patches at AL found no difference in the number of female mates or the number of offspring sired by males utilizing territorial and non-territorial tactics (York & Baird 2015). Similarly, this measure of annual reproductive success did not differ between the two alternative social tactics on simple patches during my study. The

observation that territorial males do not sire more offspring annually might appear to cast doubt on territory defense as an adaptive social tactic in this population. Nevertheless, some results from my study combined with those of a previous study (York & Baird 2015) support the hypothesis that spatial defense confers fitness advantages for some males at AL over individual reproductive seasons. Although males that defended territories on complex patches sired more offspring total and tended to mate with more females than non-territorial males, territorial males on simple patches monopolized females to a higher degree, siring nearly one-half of the offspring produced by their mates. Increased mate monopolization, apparently without increased defense costs despite much higher rival densities, strongly suggests simple patches promoted more economical spatial defense. York & Baird (2015) also showed that monogamous matings (i.e. mate monopolization) appear to promote survival of offspring. Increased mate monopolization in simple microhabitats, therefore, may promote the adaptive value of territory defense if offspring survive at a higher rate even though fewer offspring total are produced from monogamous pairings.

The relative success of non-territorial mating tactics at AL appears to be the result of ecological and social factors that increase encounter rates between females and males, both territorial and non-territorial. Territorial males court females vigorously throughout the 2.5-month reproductive season, both at AL and in other Oklahoma populations occupying natural rock outcroppings (Baird et al. 1997; Baird 2013a). The topography of complex microhabitat patches at AL, especially the interconnected subsurface network of crevices, clearly also promotes the ability of non-territorial males to encounter and mate with females, even though these interactions are not readily observed (York et al. 2014;

York & Baird 2015; Chapter 2). High densities on simple patches during the present study likely promoted frequent intersexual encounters by territorial males, but perhaps also by non-territorial males even though subsurface passages were lacking. Rejecting male advances by hiding in crevices (Baird & Timanus 1998) may be costly for females because it forces them to abandon favorable perches (Baird & Sloan 2003), and movement may increase predation risk (Magurran & Seghers 1994; Arnqvist & Rowe 2013). Because subsurface crawlspaces are lacking in crowded simple patches, females cannot evade unwanted courtship advances unless they flee into the surrounding grass, which probably also increases predation risk. In both semi-natural habitat types, therefore, females appear to be accepting copulations from both territorial and non-territorial males (convenience polyandry; Lee & Hays 2004) in order to manage the potential costs imposed by chronic male harassment including interruption of foraging and thermoregulation, and increased risk to predators (York & Baird 2015). Since offspring survival is inversely related to the number of male partners (York & Baird 2015), this hypothesis raises the interesting possibility that increased mate monopolization may also enhance female fitness, which my results suggest is likely promoted in smaller, more topographically simple microhabitats that do not support large numbers of conspecifics. Studies combining behavioral and molecular techniques should be conducted in natural habitats occupied by collared lizards which also appear to promote more economical spatial defense, to test the possible effects of habitat structure and local population density on male behavior and the distribution of reproductive success documented for males in the semi-natural microhabitats in the AL population.

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