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SEXUAL SELECTION, ALTERNATIVE REPRODUCTIVE TACTICS AND SEXUAL CONFLICT IN COLLARED LIZARDS: INTEGRATION OF MOLECULAR AND BEHAVIORAL ECOLOGY

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SEXUAL SELECTION, ALTERNATIVE REPRODUCTIVE TACTICS AND SEXUAL CONFLICT IN COLLARED LIZARDS: INTEGRATION OF MOLECULAR AND BEHAVIORAL ECOLOGY

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ABSTRACT OF THESIS

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TITLE OF THESIS: Sexual Selection, Alternative Reproductive Tactics and Sexual Conflict in Collared Lizards: Integration of Molecular and Behavioral Ecology

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ABSTRACT: Sexual selection theory often predicts that socially dominant males should sire more offspring than males adopting subordinate social tactics. However, it is often difficult to determine the extent to which this expected distribution of male reproductive success is influenced by intra- and intersexual selection. Using a combination of field behavioral studies and molecular genetic techniques, I first tested the extent to which observations of social and spatial behavior predicted the distribution of reproductive success among female collared lizards and males displaying alternative social tactics (territorial and non-territorial) during a single reproductive season. I also examined the strength of sexual selection acting on male morphological and behavioral traits. Contrary to expectations, male social status did not accurately predict patterns of reproductive success: non-territorial males obtained reproductive success equal to that of territorial males and females were highly promiscuous, mating with a similar number of territorial and non-territorial males, both within and among successive clutches. None of the traits that I examined were significant targets of sexual selection among non-territorial males. However, male snout-vent-length was under positive directional selection among territorial males.

To test the generality of my earlier findings, I expanded my analyses to encompass three seasons to examine how the number of female mates and offspring sired among males varied with marked natural variation in the intensity of intra- and intersexual selection within and among seasons, and the influence of behavioral traits on male fitness. I also examined how the degree of female promiscuity varied with changes in the intensity of sexual selection and the influence of female promiscuity on offspring survivorship. Unexpectedly, results from all seasons confirmed that non-territorial males consistently mated with similar numbers of females and sired similar numbers of offspring as territorial males. Moreover, females were promiscuous in all three seasons with similar numbers of territorial and non-territorial males. However, promiscuity decreased offspring survivorship. Together, my results suggest that mating relationships among collared lizards contrast sharply with predictions from classical mating system theory and likely represent the outcome of sexual conflict. Both sexual conflict and the high reproductive success of non-territorial males appear to be promoted by the homogeneous and continuous topography of the semi-natural habitat at my study site, which differs markedly from the natural habitat of collared lizards.

THESIS INTRODUCTION

Biologists have long recognized sexual selection as a pervasive and powerful evolutionary force, with strong potential to shape behavioral, morphological, and physiological traits that influence individual reproductive success (Fisher 1915; Williams 1966; Trivers 1972; Andersson 1994). For males, reproductive success is generally limited by their ability to obtain access to limited female mates, which often results in intense intrasexual competition (Williams 1966; Trivers 1972). By contrast, because female reproductive success is usually not limited by access to males, selection often acts on females to choose mates based upon one or more phenotypic attributes that vary among numerous competing males (intersexual selection; Andersson and Simmons 2006). The particular mating system (e.g., monogamy, polygyny, polygynandry) that evolves in natural populations is often viewed as a balance between intra- and intersexual mechanisms (Reynolds 1996).

One possible consequence of strong intrasexual selection on males is the monopolization of mating opportunities by a subset of males that utilize dominant social tactics. Such tactics may range from intense physical contests and wars of attrition, to defense of territories and conspicuous patterns of display (LeBoef 1974; Dewsbury 1984; Stamps 1994). The inevitable outcome of mate monopolization by socially dominant competitors is that other males will be excluded from mating opportunities (Shuster 2010). Less successful males are often sexually mature, but as a consequence of size and/or age constraints, may not be able to compete effectively against males employing dominant social tactics, and/or may not possess suites of morphological traits that are attractive to females (Dominey 1984; Caro and Bateson 1986; Andersson 1994). Consequently, selection may favor the evolution of one or more alternative tactics that promote the ability of such males to increase their reproductive success by adopting subordinate patterns of behavior (e.g., sneaking copulations, female mimicry) (Dawkins 1980; Shuster and Wade 2003).

Alternative social tactics among males have been documented in almost every major vertebrate taxon, including fish, amphibians, reptiles, mammals, and birds (reviewed by Gross 1996; Shuster and Wade 2003). In most cases, alternative tactics are expressed in a condition-dependent (= plastic) manner, such that individual males are capable of switching between/among two or more tactics during ontogeny (Dominey 1984; Gross 1996; Neff and Svennson 2013). Plastic tactics most often correlate with age and are characterized by individuals utilizing subordinate tactics when they are younger and smaller, and then switching to dominant social tactics when they are older and larger (Caro and Bateson 1986). A key prediction of classical mating system theory is that the evolutionary stability of plastic tactics is conditional upon reproductive success being disproportionately skewed toward males that are socially dominant in order to balance the high costs incurred (Andersson 1994; Ellis 1995). By contrast, males adopting subordinate tactics are predicted to have low reproductive success and ‘make the best of a bad job’ until they are old or large enough to compete via dominant tactics (Dawkins 1980).

Historically, the expected relationship between social dominance and fitness has been well-supported by a wealth of studies (reviewed by e.g., Dewsbury 1982; Andersson 1994; Ellis 1995). These studies have relied primarily on detailed observations of individual social and spatial behavior, and formed the basis for much of classical mating system theory (Krebs and Davies 1997). However, the reliability of these techniques has been strongly criticized, primarily due to the findings of studies which incorporate molecular genetic tools into behavioral ecological research on social and mating systems (Hughes 1998; LeBas 2001; Byers and Dunn 2012). Molecular studies have increased the precision with which investigators can measure individual variation in fitness. Surprisingly, these molecular estimates of fitness have produced results that often conflict strongly with behavioral estimates. For example, dominant males do not always monopolize females as predicted. Males employing subordinate tactics may achieve higher-than-expected levels of fitness by outcompeting socially dominant males through the use of sneaking or satellite tactics, the success of which may be promoted by social or ecological factors that render monopolization difficult for dominant males (Kvarnemo and Ahnesjö 1998; LeBas 2001; Rodriguez-Munoz et al. 2010). Alternatively, subordinate males may be relatively unsuccessful in precopulatory mating competition, but succeed in sperm competition against socially dominant rivals (Bilde et al. 2009). These discrepancies have shown that the assumption that socially dominant males will monopolize matings is not always supported, and in turn are altering our views of the fundamental processes underlying the evolution of mating systems and sexually selected traits.

Another surprising pattern to emerge from studies combining molecular and behavioral techniques is that female promiscuity is common (Parker and Birkhead 2013; Shuster et al. 2013). This finding stands in stark contrast to the long-held view that females behave passively during the mating process. Indeed, recent studies that highlight numerous instances where females not only influence mating system structure, but may also be the primary determinants of male reproductive success, completely dispel this notion (Fisher et al. 2006; Pölkki et al. 2012; Shuster et al. 2013). For example, females in many species actively pursue multiple copulations at the expense of dominant males that attempt to defend them. Their doing so likely promotes sexually antagonistic coevolution of male and female morphological and behavioral traits (Chapman et al. 2003). Females may possess morphological adaptations that promote sperm competition and/or manipulate sperm from individual males to control which ones fertilize their eggs (Eberhard 1996). Although such findings provide fresh theoretical and empirical insights, they also complicate the task for evolutionary biologists to disentangle the effects of intra- and intersexual selection on individual fitness.

Reptiles have emerged as excellent model systems for studies of sexual selection on social behavior (reviewed by e.g., Fox et al. 2003; Baird 2013a, b). Lizards in particular show remarkable flexibility in mating system structure both within and among species, as well as a wide range of sexually-selected variation in behavioral and morphological traits (Fox et al. 2003; Baird 2013a, b). Moreover, molecular studies reveal that many lizard species with diverse social mating system structure have exceptionally high rates of multiple paternity (Uller and Olsson 2008), even in species where males appear to monopolize groups of females socially. Offspring production has even been detected between males and females that have no known behavioral relationships (LeBas 2001). Such findings are also the source of controversy regarding the extent to which intra- and intersexual selection influence patterns of observed mating relationships (Uller and Olsson 2008; Madsen 2011). Adequate answers to these problems are lacking, and this deficit is exacerbated by the fact that many mating system studies continue to rely solely on behavioral or molecular measures to estimate fitness. Moreover, many tests have been conducted in controlled laboratory settings, where ecological and social variables that likely influence sexual selection on mating system dynamics may be confounded. These problems highlight the need for investigators to combine behavioral and molecular data in free-ranging populations to gain insight into the processes governing the evolution of social behavior and sexually selected traits in the wild.

Using the Eastern collared lizard (*Crotaphytus collaris*) as a model system, my thesis integrates extensive observations of social and spatial behavior in the field with molecular genetic determination of reproductive success in males and females to test: 1) the extent to which social and spatial relationships among females and males employing alternative tactics predicts actual mating relationships, and 2) the extent to which intra- and intersexual selection influence male fitness, female promiscuity, and the evolution of sexually selected traits. Below, I present my research in two chapters that are each formatted as papers for publication in two different journals. Chapter 1 is formatted for, and is now in press in, the journal *Animal Behaviour*. Chapter 2 is formatted for submission to the journal *Evolution.*

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UNEXPECTED HIGH FITNESS PAYOFF OF SUBORDINATE SOCIAL TACTICS IN MALE COLLARED LIZARDS

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ABSTRACT

Sexual selection theory often predicts that dominant males will sire more offspring than males displaying subordinate social tactics. I combined the records of space use by collared lizard (*Crotaphytus collaris*) females and records of social and spatial behaviour of males displaying two markedly different social tactics (territorial and non-territorial) with genetic determination of parentage to test how variation in male social tactics influences the distribution of reproductive success. In marked contrast with predictions based on their social and spatial behaviour, territorial males did not monopolise paternity of offspring with the females that they defended, and on average, non-territorial males obtained reproductive success equal to that of territorial males, both within and among successive clutches. When all males were analysed together, none of the traits that are often hypothesized to promote fitness in other lizards were under strong sexual selection in collared lizard males. Among territory owners alone, however, there was positive directional selection on body size. Both the unexpected success of non-territorial males and exceptionally high levels of multiple paternity appear linked in part to features of the habitat at my study site that diminish the ecological potential for territorial males to monopolise mating opportunities with females that resided in their

defended areas. If female collared lizards derive any fitness benefits by mating with multiple males, it is likely that these are genetic rather than material.

INTRODUCTION

In populations under strong sexual selection, males having high resource holding potential (RHP; Parker, 1974) often attempt to monopolise groups of females or the resources that females require for reproduction (Andersson, 1994; Candolin & Voigt, 2001; Pryke & Andersson, 2003). By contrast, unless they can disperse and establish territories elsewhere (Lawrence, 1987; Pasinelli & Walters, 2002), males having lower RHP typically remain within neighbourhoods composed of adjacent breeding territories by adopting alternative social tactics characterised by inconspicuous behaviour (Gross, 1996; Shuster & Wade, 2003; Taborsky, Oliviera, & Brockmann, 2008). Inconspicuousness allows lower RHP males to avoid costly aggression, but still maintain proximity to females, which may promote their ability to sneak copulations (Krebs, 1971; Mills & Reynolds, 2003; Whiting et al., 2006). Because territorial males typically interact with females more frequently and conspicuously than subordinate males, mating system studies based solely on observations of behaviour have often concluded that male territory owners monopolise matings and obtain much higher reproductive success than males utilising subordinate social tactics (Cox & Le Bouef, 1977; Andersson, 1994). In such systems, subordinate males are assumed to be ‘making the best of a bad job’ until they attain sufficient RHP to acquire territories (Dawkins, 1980; Andersson, 1994; Baird, Acree, & Sloan, 1996).

Inherent in studies that rely on behaviour to estimate mating relationships and reproductive success is the assumption that the behaviour of males accurately predicts mating and fertilisation (Wiley, Hatchwell, & Davies, 1991; Hughes, 1998; Baird, Hranitz, Timanus, & Schwartz, 2007). Moreover, females are often assumed to remain passive during the mating process, even though there is abundant evidence in several taxa that they preferentially interact and perhaps mate with males having certain morphological and/or behavioural characteristics (Kodric-Brown, 1985; Sullivan & Hinshaw, 1992; Ophir & Galef, 2003). The possibility for error in mating assignments based solely on observations of behaviour may be worsened because free-ranging animals often copulate quickly and secretively. Even when reliable observation of copulation is possible, post-copulatory mechanisms (e.g., sperm competition, cryptic female choice) may confound parentage assignments (Eberhard, 1996; Birkhead & Pizzari, 2002). Indeed, the difficulty of determining parentage assignments accurately is accentuated by mounting evidence that females choose to mate with and/or select sperm from multiple males, even in species where males judged to have to high RHP monopolise females socially (Gibbs et al., 1990; Olsson, Madsen, Shine, Gullberg, & Tegelstrøm, 1994; Hughes, 1998). By mating with multiple males, females may gain increased paternal care, access to resources required for reproduction, or increased quantities of sperm to ensure fertilisation of all eggs (Andersson & Simmons, 2006; Slatyer, Jennions, & Blackwell, 2012). Alternatively, by mating with multiple males females may derive genetic benefits that promote the survivorship and/or attractiveness of their offspring (Kokko, Jennions, & Brooks, 2006; Byrne & Keogh, 2009; Kuijper, Pen, & Weissing, 2012).

Genetic determination of parentage coupled with observations of social interactions among all potential parents, provides a much more accurate estimate of mating relationships and the distribution of reproductive success, especially in social systems where individuals use more than one reproductive tactic (Double & Cockburn, 2003; Zamudio & Sinervo, 2003). The necessity of combining genetic with behavioural measures is accentuated by studies demonstrating marked discrepancies between mating relationships established using genetic techniques versus those estimated using behavioural observations (Gibbs et al., 1990; Hughes, 1998; LeBas, 2001).

I combined genetic determination of parentage with detailed observation of the social and spatial behaviour of individual collared lizards to test whether defence of territories by high RHP males promotes monopolisation of females, or whether females mate with multiple males, including those that do not defend territories. Higher RHP and prolonged, frequent courtship predict that territorial males should garner a reproductive advantage over mature, but non-territorial males (Baird et al., 1996; Lappin & Husak, 2005), and that females should preferentially mate with the males that defend areas overlapping their home ranges (Baird, Fox, & McCoy, 1997; Baird et al., 2007; Baird, 2013a). In my study population, however, the possibility that spatial overlap and courtship frequency do not accurately predict mating relationships may be especially high. Female home ranges are partially overlapped by up to three territorial and numerous non-territorial males (Baird et al., 1996). Moreover, because the habitat consists of continuous boulder fields having nearly unlimited crevices (Baird & Sloan, 2003), non-territorial intruders can readily hide to avoid attacks by territory owners without leaving the vicinity of female home ranges. Increased access to females while being able to avoid aggression may promote opportunities for mate choice and multiple mating by females.

METHODS

Study population

This study was conducted from 20 March–31 October, 2007 and 2008 at the Arcadia Lake (AL) Dam flood control spillway located 9.6 km east of Edmond, Oklahoma Co., OK (Baird, Timanus, & Sloan, 2003). Collared lizards at AL occupy three topographically homogeneous patches of boulders (1 230–19 853 m^2) used to construct flood-control channels (Curtis & Baird, 2008). This study site is well-suited for documentation of behavioural interactions among individuals because human access is restricted, lizards are undisturbed, the homogeneity of rock patches allows prolonged and unobstructed observation, and rock patches are 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). All lizards have been noosed as hatchlings, the terminal phalanges of three digits clipped for permanent identification, and unique combinations of non-toxic acrylic paint spots applied to the dorsum for identification of individuals from a distance (see *Ethical note*). I know the ages of all of the lizards used in the present study because they were periodically recaptured for remarking and measurement since their first capture as hatchlings.

Previous studies on social and spatial behaviour have shown that females maintain strong philopatry to small non-defended home ranges where they spend most of their time scanning for arthropod prey from elevated perches (Baird et al., 1996; Baird & Sloan, 2003). Males typically acquire territories at the beginning of their second season. Territorial males rely on high rates of patrol and broadcast display punctuated by occasional chases and fights to advertise and defend territories (Baird, 2013a). Territories partially or completely overlap the home ranges of up to eight females that these males interact with frequently during prolonged (up to 30 min) courtship encounters throughout the reproductive season (Baird, Sloan, & Timanus, 2001; Baird et al., 2007). Even though they are sexually mature during their first year, males typically adopt inconspicuous subordinate social tactics characterised by low patrol and display rates. When detected by territory owners, non-territorial males flee and hide in crevices which are abundant at AL (Baird & Sloan, 2003). Nonetheless, first-year males interact with females when territory owners have not detected them (Baird et al., 2003).

Recording spatial and social data

During the reproductive season (1 May–15 July), mapped census sightings and focal individual observations (both described below) were recorded to document the spatial and social behaviour of lizards in the AL population. For the present study, both types of data were recorded on all mature males (*N* = 27), and census data on all females (*N* = 28). 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). Behavioural data were recorded (described below) from 1 May–30 June, when females produce up to three successive clutches (see *Schedule of egg production and hatching*; Baird et al., 2001).

Censuses of the entire study site (*N* = 30; 15 during May, 15 during June) involved recording the point locations and identities of all emergent lizards on scale-drawn maps. Census sightings for males were combined with the beginning and ending points of focal traces (described below) to construct maps of territories and home ranges using the minimum convex polygon technique (Turner, 1971). The number of points used to construct the composite maps of male territories (*N* = 60–65), as well as female home ranges (*N* = 30–40), equalled 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 method of Rose (1982).

Focal observations (*sensu* Altmann, 1974) involved tracing the path of travel and recording all of the social acts initiated by subject males on scale drawn maps (Baird, 2013a). Twenty-minute focal observations (*N* = 10/male) were recorded on different days throughout the reproductive season. Male collared lizard activity does not vary as a function of time of day from 900–1300 h when focal observations were recorded (Baird et al., 2001). However, to control for any possible temporal bias, individual males present on the study site each day were observed in random order.

Social behaviour is initiated by male collared lizards in two distinct contexts. Displays that are broadcast when males are on elevated perches at least 5 m from conspecifics are the most common (Baird & Curtis, 2010; Baird, 2013a). Most broadcast displays involve males extending all four legs to elevate the torso which is compressed laterally while the dewlap is extended (see photographs in Baird, 2013a, 2013b). While holding this full-show posture, males almost always flex their legs to raise and lower the head and torso 1–12 times (= push-ups) in succession. Much less frequently (2%), males display by walking in a circular or figure-eight pattern while remaining on a single perch (Baird & Curtis, 2010; Baird, 2013a, 2013b).

In contrast to broadcast displays, proximal aggressive encounters with male rivals (= contests) involve one male running to within 1 m of a male rival which always escalates into one or more of the following: an exchange of displays (full shows, push-ups) while the two males remain in close proximity (1 m), the recipient fleeing, reciprocal chases (up to 40 m) back-and-forth, and occasionally attacks involving wrestling and biting (Baird, 2013a, 2013b). Because broadcast displays are given when males pause on perches and are distant from all conspecifics, they are readily distinguished from contests when males are charging, chasing, or fighting a rival, or when males are displaying to a rival in close (1 m) proximity that is reciprocating by also giving displays.

Males also initiate proximal encounters with females that function for courtship (Baird et al., 2007; Baird & Curtis, 2010; Baird, 2013a). Courtship encounters involve the same displays that males broadcast from a distance (described above), but these are also given when one male and female are within one body length of one another, and when both lizards are making frequent and prolonged physical contact (Baird, 2004). Physical contact includes 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, 2013b), or simply perching adjacent while touching the other lizard (Baird & Sloan, 2003; Baird, 2004). Males sometimes grasp the dorsal skin of the female’s neck and attempt to juxtapose their vent with that of the female, presumably to attempt copulation. However, because attempts at copulation usually result in both lizards moving into a refuge (Baird et al., 2003), it was not possible to reliably determine whether or not mounting resulted in successful intromission.

Using the cumulative focal observations recorded on each male, I calculated hourly frequencies of broadcast displays, contests between rival males, and courtship encounters with females (separately) by dividing the total number of these acts/events by the total focal observation time (Baird et al., 2007). I measured mapped traces using a digital planimeter (Planix 2000) and calculated the hourly rate of patrol by dividing the total distance travelled by the cumulative observation time on individual males (Baird et al., 2007).

Schedule of egg production and hatching

Adult lizards typically emerge from hibernacula from late March to early April and remain reproductively active until 15 July (Baird et al., 2001). In 2007, the schedule of egg development and oviposition was documented by capturing all females ($N = 28$) present on the site every 7–10 d to weigh and measure them, and palpate their abdomens. At each palpation, follicular/egg development was characterised 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 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 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), which are oviposited throughout June, into the first two weeks of July. 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 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 emerged hatchlings. For each individual, 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 was recorded on scale-drawn maps, and a blood sample was collected (see *Collection of DNA samples and determination of genotypes*). Hatchlings were then released unharmed by placing them in rock crevices at their precise capture locations (see *Ethical note*).

Genetic assignment of hatchlings to individual mothers (see *Parentage assignments and patterns of reproductive success in females and males*) of known age, combined with the schedule of oviposition for serial clutches and hatchling SVL at first capture, allowed me to estimate whether offspring were from first or subsequent (second or third) clutches. Assignment of offspring to first clutches was obvious using these criteria for both 2Y+ and first-year females. Because third clutches sometimes begin maturation before oviposition of second clutches, and third clutches develop rapidly (Baird, 2004), I could not distinguish hatchlings from second or third clutches. Therefore, I pooled hatchlings from second and third clutches for analyses.

Collection of DNA samples and determination of genotypes

Blood samples were collected for isolation of nuclear DNA from all adult lizards (*N* = 55) when they emerged from hibernacula in early April 2007 and from 86 hatchlings from August 2007–May 2008 (for details see *Schedule of clutch production and hatchling emergence*). Blood samples (50 µl) were collected from the orbital sinus using heparanised micro-hematocrit tubes, 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 with a cloth. Lizards were returned to their exact capture locations within 15 min (see *Ethical note*).

Genomic DNA was isolated from blood samples using a DNeasy blood and tissue extraction kit (Qiagen, Venlo, Netherlands). Using PCR, I amplified eleven microsatellite loci with primers developed for *C. collaris* (Hutchison, Strasberg, Brission, & Cummings, 2004) that were labeled with fluorescent dyes. PCR amplification reactions (15 µl) contained 4.75 µl of genomic DNA, 0.50 µl of forward and reverse primers, 9 µl of True Allele Premix (Perkin-Elmer Applied Biosystems, Foster City, CA), and 0.25 µl of GoTaq DNA polymerase (Promega, Madison, WI). All PCR products were optimised according to the thermal profile and annealing temperatures described in Husak, Fox, Lovern, & Van Den Bussche (2006). I visualised amplicons for all loci on an automated DNA sequencer (model ABI 3130, Perkin-Elmer Applied Biosystems, Foster City, CA) after loading a mixture of 9.25 µl formamide, 0.25 µl of ROX 500 HD size standard, and 0.50 µl of PCR product. Each mixture was denatured at 96˚C for 5 min and then immediately chilled on ice for 3 min prior to loading. I scored all genotypes using GeneMapper software v. 4.0 (Perkin-Elmer Applied Biosystems, Foster City, CA). To test for the presence of null alleles, large-allele dropout, and stutter-induced typing errors at each locus, I used Microchecker software v. 2.2.1 (University of Hull, UK; Van Oosterhout, Hutchinson, Willis, & Shipley, 2004).

All adult males ($N = 27$) and hatchlings ($N = 86$) in the 2007 cohort were genotyped for all eleven loci. I genotyped all 28 females that were present in 2007, but only included in my parentage analyses the 18 that produced clutches (see *Schedule of clutch production and hatchling emergence*). Two loci (Orig11, ENR21) showed a high frequency of null alleles. Null alleles can confound parentage assignments when a true heterozygote is incorrectly typed as a homozygote, potentially resulting in a genetic mismatch and false exclusion of the true parent (Dakin & Avise, 2004). However, because both loci were polymorphic, I retained them in analyses. To avoid false exclusion of potential parents, all hatchlings that were homozygotes at these two loci ($N = 66$) were typed at only one allele for parentage analyses following the methods of LeBas (2001) and Husak et al. (2006).

Parentage assignments and patterns of reproductive success in females and males

Both adult female and male collared lizards maintain strong philopatry to home ranges and territories, 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 (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). The two smallest habitat patches (1 230 and 1 505 m^2) are separated by only 40 m of grass, and there is a concrete wall running between them along which lizards have been observed to travel two to four times per season (Curtis & Baird, 2008). I pooled lizards from these two patches for parentage analyses because the potential for gene flow is high. A much larger (19 583 m^2) habitat patch is 260 m from the other two at the closest point (Baird & Curtis, 2010), no more than one lizard per season has moved among this larger patch and the other two during 17 seasons, and no such movements were recorded in 2007. Consequently, I considered the larger patch separate from the small patch for parentage analyses.

For these two pools of potential parents and offspring, I used the maximum-likelihood program CERVUS v. 3.0 (Marshall, Slate, Kruuk, & Pemberton, 1998; Kalinowski, Taper, & Marshall, 2007) to assign a mother and father for all hatchlings at 80% confidence. My simulation parameters for parentage assignments were: 1) mean proportion of candidate fathers (or mothers) sampled = 0.98, 2) proportion of loci mistyped = 0.01, and 3) number of simulation cycles = 100 000. For hatchlings that CERVUS could not assign to a mother and/or father with at least 80% confidence, I compared the genotypes of the two most-likely parents to the hatchling genotype, and excluded the parent candidate that mismatched at any locus (genetic exclusion, Haynie, Van Den Bussche, Hoogland, & Gilbert, 2003). If the two most-likely parents did not mismatch, or shared the same number of mismatches with that of the hatchling at any locus, I measured the minimum linear distance between the mapped 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.

I estimated relative fitness for individual males for all clutches pooled, and for the first and subsequent (second and third) clutches separately by dividing absolute reproductive success (number of offspring sired) by the population mean reproductive success for males. I estimated the number of different males that females mated with by determining the identities of sires for the offspring assigned to individual females, and the number of different males that inseminated individual clutches by determining the identity of sires for hatchlings from individual clutches.

Statistical analysis

All analyses were performed in the program R v. 3.0.1 (R Development Core Team, 2013). I used generalised linear models (GLM) to compare the following variables in 2Y+ males that were defending territories and first-year males that were not: hourly rate of patrol (m/h); hourly frequencies of broadcast display; courtship encounters with females; and contests with rival males; territory/home range area (m^2); the number of females that males overlapped spatially; and SVL (mm). Because the number of females overlapped was a discrete variable, I used a GLM with Poisson error structure and log link function. The response variables for all other GLM were continuous, so I used a Gaussian error structure and identity link function. I also used GLM to compare relative fitness in territorial and non-territorial males by including sire social status (territorial or non-territorial) as a categorical predictor and relative fitness as a response variable with Gaussian error structure and identity link function. I used the package ‘compute.es’ to calculate standardised (mean = 0, standard deviation = 1) effect sizes (Cohen’s *d*) and associated 95% confidence intervals (CI) for all models.

To determine the strength of selection acting on phenotypic traits that are hypothesized to promote fitness in male lizards (reviewed by Baird, 2013c), I calculated standardised linear selection differentials (*s′*) using the methods of Morrissey & Sakrejda (2013). This approach employs spline-based generalised additive models to model absolute fitness as a function of unstandardised traits, and converts regression coefficients of unstandardised traits into standardised linear selection differentials. To avoid problems with model over-fitting and multicolinearity among independent variables, I conducted separate univariate analyses of selection for individual traits (see similarly Bolund, Bouwhuis, Pettay, & Lummaa, 2013). I used the package ‘mgcv’ to model absolute reproductive success as a function of male phenotypic traits. Standardised linear selection differentials and standard errors were estimated from models after 1000 parametric bootstrap replicates in the package ‘gsg’ (Morrissey & Sakrejda, 2013).

For my selection analyses, I chose traits that are hypothesized to be important components of male fitness in my study population (Baird et al., 2003, 2007) and lizards in general (Andersson, 1994; Zamudio & Sinervo, 2003; reviewed by Baird, 2013c). Baird et al. (2007) showed that broadcast display, patrol, and courtship behaviours were positively associated with annual male mating success as estimated by relative courtship frequency in the AL population, whereas intrasexual contests and large body size (SVL) did not influence mating success. Especially in territorial polgynous species such as collared lizards, the number of females overlapped has been used as an estimate of male fitness because males overlapping more females are assumed to mate more frequently and hence achieve higher reproductive success (Andersson, 1994; Lappin & Husak, 2005). Therefore, on the basis of previous behavioural studies I predicted that the frequency of broadcast display, patrol rate, frequency of courtship and the number of females overlapped would be under positive directional selection, whereas traits that previous studies have not linked with behavioural estimates of mating success (male SVL, frequency of contests initiated) would not.

For all analyses, my primary means for evaluating statistical significance involved determining whether the 95% CI of predictor variables did not include zero. However, because my selection analyses involved multiple univariate tests, I also used Bonferroni correction for *P*-values as a supplementary measure of statistical significance. For all other analyses, 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 use standardised effect sizes with CI because they provide both biologically and statistically meaningful inference at a specified degree of certainty (Colegrave & Ruxton, 2003), and have the additional advantage of facilitating direct comparisons of the influence of variables in my system with other systems (Nakagawa & Cuthill, 2007).

Ethical Note

All procedures performed on live lizards were conducted with approval of the Institutional Animal Care and Use Committee at the University of Central Oklahoma (IACUC, permit number 13009) and the Oklahoma Department of Wildlife (permit number 5553). Longitudinal studies of collared lizard behaviour, growth and survival in this population have been conducted over 17 consecutive seasons. Throughout, the terminal phalanges of three digits were clipped for permanent identification of individuals, non-toxic acrylic paint has been applied to the dorsum for identification of individuals from a distance, individuals have been repeatedly captured by noosing, female abdomens have been palpated to monitor reproductive cycles, and morphometric measurements have been made on lizards at each capture. Subsequent monitoring of the behaviour of lizard subjects confirmed that these techniques have had no adverse effects on the health of adult or hatchling collared lizards (Baird et al., 2001, 2003, 2007; Baird, 2004). Collection of blood from the orbital sinus using a micro-hematocrit tube is the most humane technique, because samples are taken within 1 min of capture, and bleeding is staunched quickly (≤ 1 min) by applying gentle pressure to the orbit with the eyelids closed. Alternative collection techniques (e.g., from clipped toes, needle puncture) are more invasive and/or would require much longer handling. Rapid blood collection from the orbital sinus is especially important to protect hatchlings because they are the most susceptible to over-heating (high surface area/volume) during handling. Hundreds of hatchlings from 2007–2013 have had blood samples obtained in this manner and their behaviour has been subsequently monitored for the balance of these seasons and beyond with no indication of ill effects. Hatchlings are almost always re-sighted behaving normally within 1 h of blood sampling, and the others are sighted no more than 2 d later. There has not been a single observed incidence of eye infection in the hundreds of lizards that have been bled.

RESULTS

Male spatial and social behaviour

Consistent with findings of past studies on male behaviour at AL, all 2Y+ males ($N = 17$) defended territories, whereas even though they were sexually mature, first-year males ($N = 10$) did not. Average rates of patrol and broadcast display in territorial males were 5.2 times and 3.1 times higher, respectively (patrol, GLM: $t_{2, 25} = 7.27$, Cohen's *d*, 95% CI = 2.90, 1.74 to 4.05; broadcast display, GLM: $t_{2, 25} = 6.50$, Cohen's *d*, 95% CI = 2.59, 1.49 to 3.68; Table 1). On average, territorial males courted females 3.2 times more frequently (GLM: $t_{2, 25} = 2.59$, Cohen's *d*, 95% CI = 1.03, 0.16 to 1.90) than did non-territorial males (Table 1). Not only did territorial males initiate aggressive contests more frequently (GLM: $t_{2, 25} = 3.71$, Cohen's *d*, 95% CI = 1.48, 0.56 to 2.40 (Table 1), in most contests (95%) they engaged non-territorial males that fled immediately. Territorial males were significantly larger (GLM: $t_{2, 25} = 5.58$, Cohen's *d*, 95% CI = 2.33, 1.28 to 3.38) than non-territorial males (Table 1). In marked contrast, both the size of areas used (GLM: $t_{2, 25} = 0.34$, Cohen's *d*, 95% CI = 0.14, - 0.69 to 0.96), and the number of females overlapped (GLM: $z_{2, 25} = 0.03$, Cohen's *d*, 95% CI = 0.01, - 0.81 to 0.83), were similar in the two social classes of males (Table 1).

Schedule of clutch production and hatchling emergence

Of the 28 females that emerged from hibernacula in early April of 2007, ten died before they produced a first clutch as indicated by their abrupt and continued absence. The reproductive cycles of the remaining 18 females were monitored using recaptures from 1 May–15 July during which the abdomen was palpated to assess developmental stages and oviposition of one to three clutches of eggs. These 18 females produced 25 clutches total. Eight females produced only one clutch because they died before the reproductive season was completed, whereas seven and three females that survived the entire season produced two and three clutches, respectively. The eight females that died early were each captured and palpated three to four times. The remaining ten females were palpated 8–12 times distributed throughout the season.

Daily monitoring revealed that 2007 hatchlings began emerging from the earliest clutches on 13 August. Seventy hatchlings were captured from then until October 2007. Sixteen more 2007 hatchlings were captured from 19 April–15 May in 2008. Hatchlings that were captured first in 2007, as well as those captured in early 2008, were distributed randomly throughout the entire site. Therefore, the fact that 19% of hatchlings were not captured until 2008 does not introduce systematic bias into my estimates of male reproductive success. Hatchlings from later clutches began to emerge on 10 September, which resulted in their being substantially (< 20 mm) smaller than already emergent hatchlings from first clutches. Based on the different reproductive schedules of first-year and 2Y+ females (see *Schedule of egg production and hatching*), and the marked difference in the size of hatchlings when they first emerged, I was able to assign 68 offspring to first clutches, and 18 offspring to subsequent (second or third) clutches.

Parentage assignments, mating relationships and reproductive success in males and females

I assigned a father and mother for all hatchlings on the small habitat patch using CERVUS. On the large habitat patch, I assigned 37 (62%) hatchlings a father and 35 (56%) hatchlings a mother using CERVUS. Of the 25 hatchlings that I could not assign a father using CERVUS, eight were assigned using genetic exclusion, whereas 17 were assigned by exclusion based on spatial proximity (see *Parentage assignments and patterns of reproductive success in females and males*). Twenty-seven hatchlings could not be assigned a mother using CERVUS. Of these, seven were assigned based upon genetic exclusion, and the other 20 were assigned using spatial proximity.

When I pooled data for all clutches, the relative fitness of territorial and non-territorial males was similar (GLM: $t_{2,\,25} = -0.17$, Cohen's *d*, 95% CI = - 0.07, - 0.89 to 0.75, Fig. 1). All non-territorial males sired at least one offspring, whereas three territorial males did not sire any offspring. Because survivorship of hatchlings from first clutches appears to be higher than that from second and third clutches in the AL population (unpublished data), I examined reproductive success of the two social classes of males from first versus later clutches separately. Relative fitness of males employing the two social tactics was also similar for the first clutch alone (GLM: $t_{2,\,25} = -0.34$, Cohen's *d*, 95% CI = - 0.13, - 0.96 to 0.69, Fig. 1), as well as for later clutches (GLM: $t_{2, 25}$ = 0.27, Cohen's *d*, 95% CI = 0.11, - 0.71 to 0.93, Fig. 1).

Sixteen females (89%) copulated with two to six males, whereas only two females (11%) mated exclusively with one male (Fig. 2). Of the 16 females mating with multiple males, 13 (81%) mothered hatchlings sired by both territorial and non-territorial males (Fig. 2). Seventy-six percent (19 of 25) of individual clutches were fertilised by multiple (up to six males) males, and eggs in 15 (60%) clutches were fertilised by both territorial and non-territorial males (Fig. 3).

Because the number of offspring sired by territorial and non-territorial males was not different, I pooled them for my estimates of the strength of sexual selection on male phenotypic traits even though behavioural and morphological traits were markedly different. As a consequence of these differences, none of the seven traits that I examined were significant targets of selection for all males pooled (Table 2; *P*'s 0.22 to 0.90). When only territorial males were considered, I found positive directional selection on male SVL (Table 2; *P* = 0.02), but Bonferroni correction rendered this result nonsignificant.

DISCUSSION

As expected, 2Y+ males vigorously defended territories and courted females that resided within these territories far more frequently and conspicuously than first-year males that displayed subordinate non-territorial tactics. Nonetheless, genetic parentage analyses did not support predicted patterns of reproductive success based on these patterns of male behaviour. Territorial males did not effectively monopolise matings with the females that resided within their territories. Instead, females were highly promiscuous, producing offspring with several other males (even for individual clutches), both territorial and non-territorial. Non-territorial males obtained unexpectedly high reproductive success, siring equal numbers of offspring on average relative to territory owners. That non-territorial males had equal reproductive success while avoiding the costs of territory defence incurred by territory owners (Baird et al., 2001), and that females did not maintain high mating fidelity to territory owners, calls into question the adaptive value of territory defence in this population. These results are surprising, because field studies in all populations of *C. collaris* examined to date show that the largest males incur substantial costs by defending reproductive territories, and hence are expected to obtain a disproportionate reproductive advantage over non-territorial males to balance these costs (Baird et al., 2003; McCoy, Baird, & Fox, 2003; Lappin & Husak, 2005).

One possible explanation of the unexpectedly high reproductive success of non-territorial males is that the habitat topography at AL promotes exceptional opportunities for them to travel to contact females and mate by stealth. Habitat patches at AL are large and continuous and contain nearly unlimited crevices in which non-territorial males can hide to evade attacks by territorial males without being forced to disperse away from females (Baird & Sloan, 2003). Especially when territorial males are patrolling and displaying at distant boundaries, there appear to be opportunities for non-territorial males to sneak copulations. By contrast, the natural habitat of collared lizards is fundamentally different from that at AL. It consists of smaller discontinuous rock patches that contain fewer crevices, and patches are separated by expanses of prairie grass. Travel among patches is infrequent due to increased predation risk when lizards are distant from cover. This habitat distribution and scarcity of crevices provides territory owners with smaller, more economically defensible areas from which to repel intruders that cannot readily hide. The features at AL that appear to promote the success of non-territorial males are diminished in natural habitats (McCoy et al., 2003), and territorial males are probably better able to monopolise matings with the females that they overlap spatially.

Relatively high reproductive success in non-territorial males and high levels of multiple paternity may also be a consequence of females increasing their own fitness by choosing to mate with multiple males (Arnqvist & Nilsson, 2000). With a few exceptions (Uller & Olsson, 2005), there is little support for the hypothesis that female squamates mate multiply to gain access to material benefits (e.g., increased paternal care, access to high quality resources, fertilisation assurance; Uller & Olsson, 2008). Collared lizards do not provide parental care for offspring. It is also unlikely that female collared lizards mate multiply to obtain access to important resources such as elevated perches that they use for foraging and basking, or rock crevices that function as refuges from predators and heat. Both are abundant at AL (Baird & Sloan, 2003), and females mated frequently with non-territorial males that did not control access to these resources. For the few females that sired offspring with only one male, the fact that these same males also produced offspring with other females indicates that mating with multiple males is not selected in females to avoid sperm depletion (Preston, Stevenson, Pemberton, & Wilson, 2001).

Multiple mating may also promote female fitness by increasing the viability or attractiveness of their offspring (Jennions & Petrie, 2000) through post-copulatory mechanisms such as sperm competition (Birkhead & Pizzari, 2002) or cryptic female choice (Eberhard, 1996). In several taxa, including squamate reptiles, females either promote competition among sperm acquired from multiple males (sperm competition), or bias fertilisation by sperm obtained from particular males (cryptic female choice) (Uller & Olsson, 2008). Both of these mechanisms are possibilities in collared lizards. However, differences in relative testis size between males employing different social tactics, which is often observed in species with sperm competition (Birkhead & Møller, 1998), was not observed in territorial and non-territorial males from the AL population (Baird et al., 2003). In many female squamates having cryptic female choice, there are morphological specialisations for sperm storage and/or manipulation, but these are also lacking in female collared lizards (Telemeco & Baird, 2011). Moreover, both sperm competition and cryptic choice models predict random mating by females, but non-random biases in paternity (Uller & Olsson, 2008). The distribution of paternity observed in our study did not support either prediction.

Females mated with males displaying a wide range of phenotypic traits. When all males were pooled, none of the traits that are typically hypothesized to promote fitness in male lizards (Baird et al., 2003, 2007; Zamudio & Sinervo, 2003; reviewed by Baird, 2013c), were under strong sexual selection. However, when I restricted the analysis to only males that controlled territories, I found positive directional selection on sire SVL. Large body size among territory owners may promote success in intra-sexual contests among males. In many lizard species, larger males often defend larger or higher-quality territories and/or monopolise mating opportunities with more females (Andersson, 1994; Sinervo & Lively, 1996). Sexual selection on body size may be particularly important in species such as collared lizards where males exhibit alternative tactics, because traits characterising each tactic may be under correlational selection. Such a case is evident in water skinks in which male SVL interacts with a suite of behavioural traits that promote the evolution of divergent social tactics through disruptive selection (Noble, Wechmann, Keogh, & Whiting, 2013).

Sexual selection for large body size among territorial males may also be explained by female choice. If females derive fitness benefits by mating with multiple males, then benefits derived by mating with territorial versus non-territorial sires are likely different. Females may use body size as an indicator of superior genetic quality in the case of territorial sires (Kirkpatrick, 1982; Andersson & Simmons, 2006), but be choosing one or more different traits displayed by non-territorial males. Mating with non-territorial males also may be advantageous because it promotes genetic compatibility or diversity, both of which may enhance offspring survivorship (Stockley, Searle, Macdonald, & Jones, 1993; Yasui, 1998; Mays & Hill, 2004). Especially when selection varies spatially and temporally, the adaptive significance of mating preferences by females may fluctuate depending upon the ecological and social conditions experienced in local neighbourhoods

(Cornwallis & Uller, 2010). For example, females may prefer dominant males during one season, whereas preferences may change or vary among seasons (Gosden & Svensson, 2008; Robinson, Pilkington, Clutton-Brock, Pemberton, & Kruuk, 2008). The possibility that variation in operational sex ratios in local neighbourhoods influences the distribution of reproductive success among males, and the potential for females to evaluate and choose mates remains to be tested in collared lizards.

My results contrast sharply with predictions from classical mating system theory and with many findings on reproductive success in other systems where males adopt alternative social tactics (Dawkins, 1980; Andersson, 1994; Ellis, 1995; Qvarnström & Forsgren, 1998). Moreover, my estimate of the strength of sexual selection on male SVL among territory owners was high relative to studies that examined similar morphological traits, but in larger samples recorded over longer periods (Kingsolver et al., 2001; Kingsolver, Diamond, Siepielski, & Carlson, 2012). Thus, my small sample size warrants that my results should be interpreted with caution. Smaller sample sizes coupled with univariate models of selection have been shown to inflate the estimated strength of selection (Kingsolver et al., 2001; 2012). Moreover, estimates of selection and the high success of non-territorial males over short time scales may not accurately reflect selective regimes and mating system dynamics over the long term (Kingsolver et al., 2001; but see Morrissey & Hadfield, 2012). Analyses of larger sample sizes within individual seasons, combined over longer time scales, will clarify the extent to which patterns of reproductive success and strength of selection vary temporally among male collared lizards at AL, providing much needed insight into the evolution and maintenance of alternative tactics in natural populations.

Conclusion

As expected, I found that territory defence, the dominant social tactic in male collared lizards, promoted increased courtship opportunities relative to the subordinate, non-territorial social tactics employed by first-year males. Nonetheless, on average, relative fitness among territorial and non-territorial males was similar, both within and among successive clutches. None of the phenotypic traits I analysed were significant targets of selection when all males were pooled. However, there was positive directional selection on large body size when only territory owners were considered, possibly to promote success in intra-sexual competition, or because females prefer to mate with larger territorial males. The homogenous, continuous topography of the human-constructed habitat at my study site appears to promote exceptional opportunities for subordinate males to sneak matings, and for females to mate with multiple males, perhaps to gain genetic benefits that promote the survivorship and/or attractiveness of their offspring.

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Table 1. Summary of GLM analyses comparing social, spatial and morphological data in territorial and non-territorial collared lizard males at Arcadia Lake in 2007. Data are means with standard errors in parentheses.

Variable	**Territorial Males**		**Non-Territorial Males**
Rate of Patrol (m/h)	76.07 (5.21)	*	14.58 (6.57)
Broadcast Displays/h	51.00 (5.49)	*	3.90 (0.85)
Courtship Encounters/h	0.79 (0.15)	*	0.25 (0.09)
Contests/h	0.27 (0.05)	*	0.00 (0.00)
SVL (mm)	112.00 (0.72)	*	94.35 (3.71)
Territory/Home Range Area (m^2)	2 094.00 (409.00)		1 867.00 (518.00)
Number of Females Overlapped	2.10 (0.30)		2.10 (0.50)

[1] Asterisks indicate statistically significant differences between columns (95% CI did not include zero).

Table 2. Standardised linear selection differentials (*s′*), standard errors (SE) and 95% CI from univariate linear selection analyses of phenotypic traits for all males pooled, and for only territorial males.

All Males Pooled (*N* = 27)	***s′* (SE)**	**95% CI**
Trait		
Rate of Patrol (m/h)	0.11 (0.17)	- 2.33 to 9.82
Broadcast Displays/h	0.09 (0.16)	- 0.25 to 0.43
Courtship Encounters/h	0.22 (0.15)	- 0.21 to 0.68
Contests/h	0.18 (0.15)	- 0.57 to 0.69
Number of Females Overlapped	0.07 (0.18)	- 0.36 to 0.66
SVL (mm)	0.65 (0.40)	- 0.85 to 1.49
Territorial Males Only (*N* = 17)		
Rate of Patrol (m/h)	- 0.11 (0.42)	- 1.03 to 6.40
Broadcast Displays/h	0.27 (0.24)	- 0.20 to 0.75
Courtship Encounters/h	0.42 (0.23)	- 0.09 to 0.86
Contests/h	0.15 (0.23)	- 0.66 to 1.04
Number of Females Overlapped	0.33 (0.35)	- 0.57 to 2.12
SVL (mm)	0.60 (0.23)	* 0.13 to 0.95

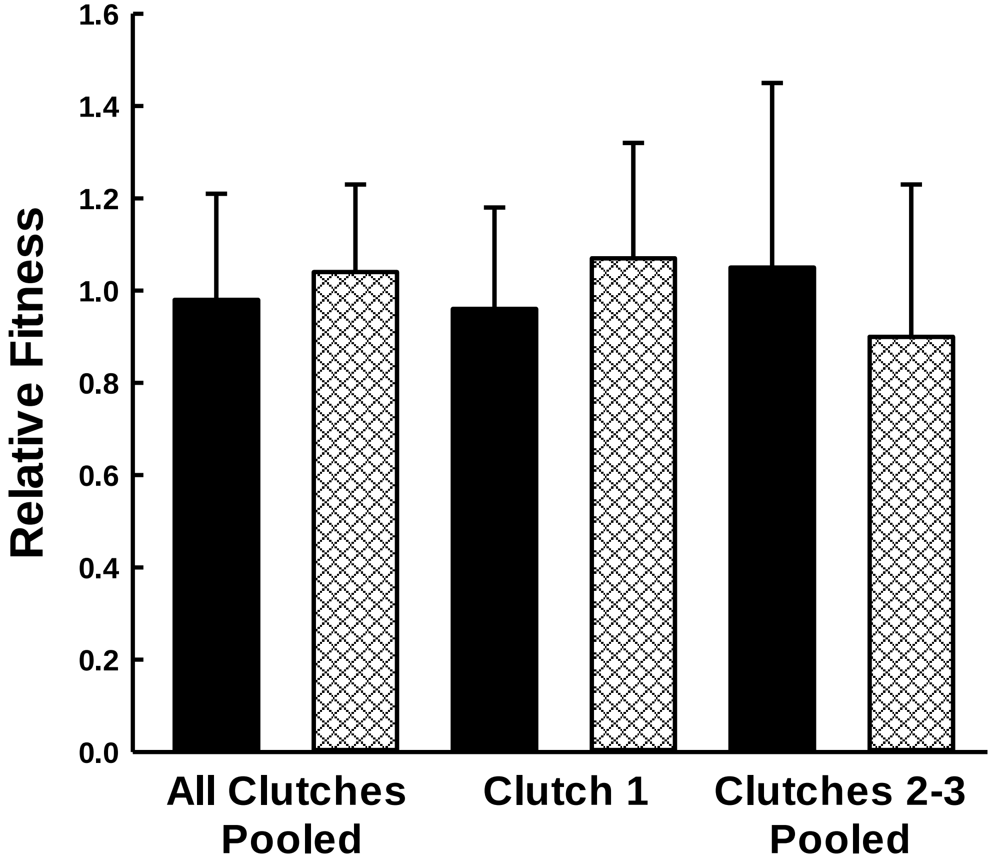
[1] Asterisk indicates a statistically significant difference (95% CI did not include zero).

FIGURE LEGENDS

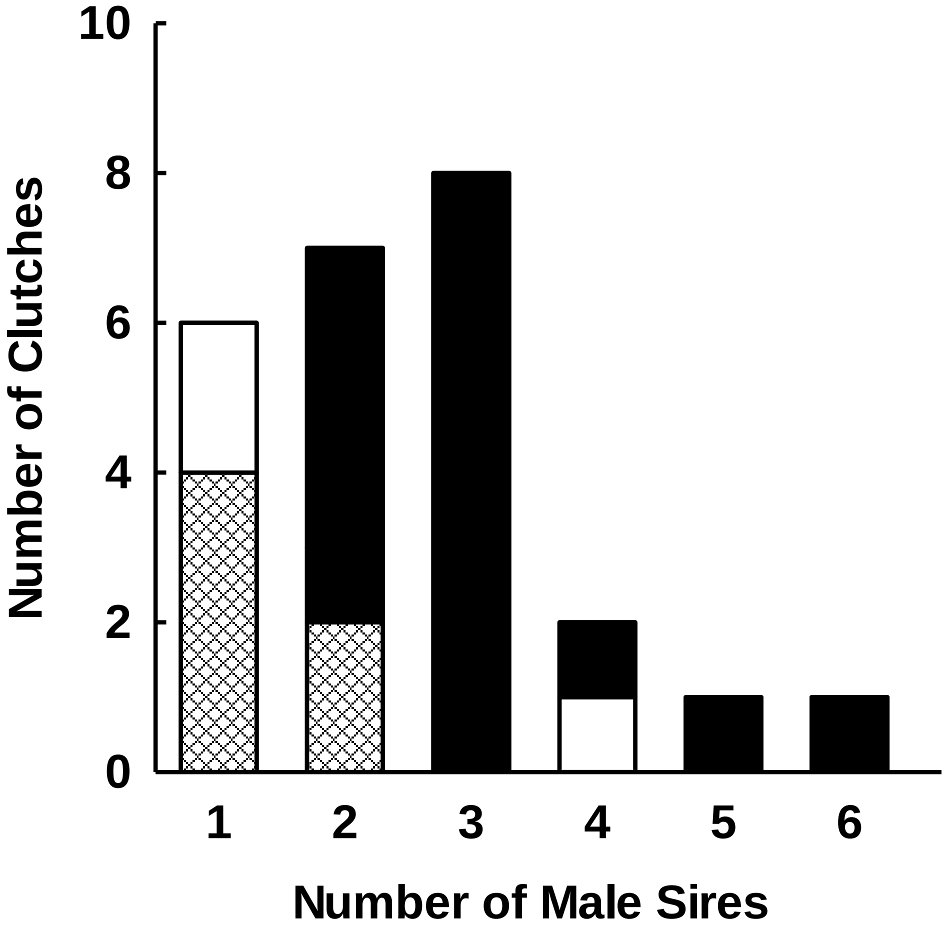
Fig. 1. Relative fitness in territorial males (solid bars) and non-territorial males (hatched bars) for all clutches pooled, first clutches only, and the second and third clutches pooled. Data are means ± 1.0 SE.

Fig. 2. The number of females that produced offspring with only one versus multiple males. Hatched bars indicate females that mated only with territorial males, open bars indicate females that mated with only non-territorial males, and solid bars indicate females that mated with males employing both social tactics.

Fig. 3. The number of individual clutches inseminated by only one versus multiple males. Hatched bars indicate clutches inseminated by only territorial males, open bars indicate clutches inseminated by only non-territorial males, and solid bars indicate clutches inseminated by males employing both social tactics.


Relative Fitness
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
All Clutches Pooled
Clutch 1
Clutches 2-3 Pooled


6
5
4
3
2
1
0
Number of Females
1
2
3
4
5
6
Number of Male Sires


10
8
6
4
2
0
Number of Clutches
1
2
3
4
5
6
Number of Male Sires

FEMALE PROMISCUITY AND SUCCESS OF SUBORDINATE MALES PROMOTE SEXUAL CONFLICT IN COLLARED LIZARDS

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ABSTRACT

Disentangling the effects of intra- and intersexual selection in natural populations is a long-standing goal of research in evolutionary biology. I tested the extent to which these sexual selection mechanisms influenced mating relationships among collared lizards over three seasons when sex ratios in local neighborhoods (LSR) varied markedly. Surprisingly, neither the number of offspring sired, nor the number of females that males mated with, varied as a consequence of highly variable LSR. Moreover, non-territorial and territorial males sired similar numbers of offspring by mating with similar numbers of females in all three years. For territorial males, courtship frequency was positively associated with both the number of female mates and offspring sired, but none of the factors examined predicted either fitness estimate in non-territorial males. Females mated promiscuously with similar numbers of territorial and non-territorial males during all three seasons, and survivorship of offspring produced by individual females decreased with the degree of female promiscuity. Because females do not appear to garner material or genetic benefits that balance this offspring survival cost, it appears that they are 'making the best of a bad job' by accepting multiple copulations. Sexual conflict and the high success of non-territorial males may be promoted by the homogenous, continuous

topography of the human-constructed habitat occupied by this population, which differs substantially from that of the natural habitat of collared lizards in Oklahoma.

INTRODUCTION

Sexual selection is a powerful evolutionary force responsible for shaping sex-specific patterns of mating behavior, but is also capable of generating substantial intrasexual diversity in mating phenotypes known as alternative reproductive tactics (Gross 1996; Oliveira et al. 2008; Neff and Svensson 2013). In many populations under strong sexual selection, males having high resource holding potential (RHP, Parker 1974) attempt to monopolize females using dominant tactics such as territory defense (Stamps 1994; Calsbeek and Sinervo 2002). When males having lower RHP cannot disperse, they may adopt socially subordinate tactics that allow them to avoid aggressive encounters with territorial rivals, but still remain near to females to sneak copulations (Lawrence 1987; Baird et al. 2003). Classical mating system theory predicts that selection will favor dominant tactics when the fitness benefits gained balance the costs incurred (Dewsbury 1982; Andersson 1994; Ellis 1995). Therefore, both higher RHP and extensive social interactions with females predict that territorial males should obtain a reproductive advantage over non-territorial males to balance costs imposed by territory maintenance. Non-territorial males are often hypothesized to be ‘making the best of a bad job’ earning relatively low reproductive success (Dawkins 1980; Gross 1996; Shuster and Wade 2003).

The expectation that territorial males monopolize matings has become increasingly difficult to reconcile with strong evidence that females in many species are highly promiscuous, even when males are strongly territorial and attempt to deny access by same-sex competitors to certain females (Hughes 1998; Uller and Olsson 2008; Pizzari and Wedell 2013; York et al. 2014). Mating promiscuously may increase female fitness, or the fitness of their offspring (Gray 1997; Newcomer et al. 1999; Fisher et al. 2006), which acts to counter the purposes of males that are using territorial tactics to monopolize females (Qvarnström and Forsgren 1998; York et al. 2014). Female promiscuity may also arise as a consequence of ecological factors that promote such ready access by subordinate males because females cannot avoid harassment by several males without incurring other costs without simply mating with them. Either scenario predicts the evolution of different mating strategies in the sexes that are in conflict with one another (Chapman et al. 2003; Fricke et al. 2010).

Both the intensity of intrasexual male competition and the potential for females to exercise adaptive mating choices are hypothesized to be influenced by variation in the number of male competitors relative to the number of receptive females in local neighborhoods (hereafter, local sex ratio = LSR) (sometimes referred to as operational sex ratio = OSR by Emlen and Oring 1977; Kvarnemo and Ahnesjø 1996; Weir et al. 2011). Estimating LSR is particularly important for species that display low vagility and maintain strong philopatry to certain habitat patches (Zamudio and Sinervo 2000). Sex ratio-based hypotheses predict that when LSR is male-biased, more males will compete for and court each available female. Both increased pressure from rivals and opportunities for females to interact with more males should decrease the ability of territorial males to monopolize matings with individual females. By contrast, lower LSR should enhance opportunities for mate monopolization by territorial males, and decrease opportunities for females to mate promiscuously. I combined detailed observations of social and spatial behavior made in the field with genetic determination of parentage to test the extent to which mating relationships in collared lizards are influenced by intrasexual competition among males displaying territorial and non-territorial social tactics, and adaptive mating choices by females. My test involved 1) determining the number of females that males mated with and the number of offspring sired by all males in the population and 2) determining variation in the degree of female promiscuity in response to marked natural variation in LSR within and among three seasons. Because females have been hypothesized to mate with multiple males to increase the survival of their offspring (Yasui 1997; Ivy and Sakaluk 2005), I also examined survival of offspring as a function of the degree that females mated promiscuously.

MATERIALS AND METHODS

Study site and population

Field work for this study was conducted from 20 March–15 July 2007–2010 at the Arcadia Lake (AL) Dam flood-control spillway located 9.6 km east of Edmond, OK, where collared lizards occupy three topographically homogeneous patches of boulders (1,230–19,853 m^2) used to construct flood-control channels (Curtis and Baird 2008). The

AL site is well-suited for studying the social and spatial behavior of individual lizards because human access is restricted, the homogeneity of rock patches allows prolonged and unobstructed observation of all individuals (Baird et al. 1996; 2003), and the entire site is mapped to scale using GIS measurements of mapping markers arranged in 10 m grids made with USAF equipment (Baird and Timanus 1998; Baird et al. 2003). All social and spatial data (see below) were recorded on these scale-drawn maps. Since 1990, all lizards at AL have been noosed after hatching, the terminal phalanges of three digits clipped for permanent identification, and unique combinations of non-toxic acrylic paint spots applied to the dorsum for identification of individuals from a distance. Because lizards have been periodically recaptured for remarking and measurements over 24 consecutive seasons, I knew the ages of all subjects used in this study.

Previous findings on individual social and spatial behavior have shown that females maintain strong philopatry to small non-defended home ranges where they spend most of their time scanning for arthropod prey from elevated perches (Baird et al. 1996; Baird and Sloan 2003). Females may produce one to three successive clutches of eggs each reproductive season (Baird et al. 2001; Telemeco and Baird 2011). Males typically acquire territories at the beginning of their second season that they defend until they die (Baird et al. 1996; Baird 2013a). Defense of territories involves high rates of patrol, frequent broadcast display, and occasional chases and fights (described below; Baird et al. 2007; Baird 2013b). Territories of males partially or completely overlap the home ranges of up to eight females, with whom the males interact frequently during prolonged (up to 30 min) courtship encounters throughout the reproductive season (Baird 2013b, c).

Even though males are sexually mature during their first year, they typically adopt inconspicuous subordinate social tactics characterized by low patrol and display rates. When detected by territory owners, non-territorial males flee and hide in crevices, which are abundant at AL (Baird & Sloan, 2003). Nevertheless, first-year males interact with females and attempt to sneak copulations when territory owners have not detected them (Baird et al., 2003). Females frequently reject their advances by fleeing (Baird and Timanus 1998). By contrast, females almost always engage in courtship involving prolonged physical contact by territorial males (Baird 2013c).

Spatial and Social Data

During each reproductive season (1 May–15 July), mapped census sightings and focal individual observations (both described below) were recorded to document the spatial and social behavior of lizards. We recorded both types of data on all mature territorial (2007, N = 17; 2008, N = 12; 2009, N = 9) and non-territorial (2007, N = 10; 2008, N = 3; 2009, N = 9) males, and census data on all mature females (N = 64). 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). Behavioral data (described below) were collected from 1 May–30 June when female collared lizards produce one to three successive clutches, and 2Y+ males actively defend territories (Baird et al. 2001).

Censuses of the entire study site (*N* = 30; 15 during May, 15 during June of each year) involved recording the point locations and identities of all emergent lizards on scale-drawn maps. I combined census sightings for males with the beginning and ending points of their focal traces (described below) to construct composite maps of territories and home ranges using the minimum convex polygon technique (Turner 1971). The number of points used to construct composite 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 territory/home range areas were graphed against the number of sightings (Stone and Baird 2002; Baird and Sloan 2003), following the method of Rose (1982).

Focal observations (sensu Altmann 1974) involved tracing the path of travel and recording all of the social acts initiated by subject males on scale drawn maps (Baird 2013a). Twenty minute focal observations (Baird et al. 2003; *N* = 10–15 per male) were recorded on different days during May and June of each year. Male collared lizard activity does not vary as a function of time of day from 0900–1300 h when focal observations were recorded (Baird et al. 2001). However, to control for any possible temporal bias during this 4 h time period, individual males were observed each day in random order.

Previous studies have shown that collared lizard males initiate social behavior in two distinct contexts. Displays that are broadcast when patrolling males are on elevated perches at least 5 m from conspecifics are the most common (Baird and Curtis 2010;

Baird 2013a). Most broadcast displays involve males extending all four legs to elevate the torso which is laterally compressed while the dewlap is extended (see photographs in Baird 2013a, b). While holding this ‘full-show’ posture, males typically flex their legs to raise and lower the head and torso multiple times (= pushups) in succession. Much less frequently, males display by walking in a circular or figure-eight pattern while remaining on a single perch (Baird 2013a, b; Baird and Curtis 2010).

In contrast to distant broadcast displays, proximal aggressive encounters with male rivals (= contests) involve one male running towards another male to within 1 m, followed by escalation into one or more of the following: an exchange of displays (full shows, push-ups) while the two males remain in close proximity (1 m), the recipient fleeing, reciprocal chases (up to 40 m) back-and-forth, and occasionally attacks involving wrestling and biting (Baird 2013a, c). Because broadcast displays are given when males pause on perches and are distant from all conspecifics, they are readily distinguished from contests when males are charging, chasing, or fighting a rival, or when males are displaying to a rival in close proximity that is reciprocating by also giving displays (Baird 2013a, c).

Males also initiate proximate encounters with females that function in courtship. Courtship encounters involve the same displays that males broadcast from a distance (described above), but these are also given when one male and female are within one body length of one another, with both lizards making frequent and prolonged physical contact (Baird and Sloan 2003; Baird 2004). Physical contact includes one lizard mounting and sitting on their partner’s dorsum, superimposition of the legs and/or tails, nudging their partner with the snout, or perching adjacent to and touching the other lizard (Baird and Sloan 2003; Baird 2004). Occasionally, males grasp the dorsal skin of the female’s neck and attempt to juxtapose their vent with that of the female, presumably to attempt copulation. Because such mounting usually results in both lizards moving into a crevice (Baird et al. 2003), we could not reliably determine whether or not mounting resulted in successful intromission.

I used cumulative focal observations recorded on each male to calculate hourly frequencies of broadcast displays, contests initiated with rival males, and courtship with females (separately) by dividing the total number of these acts/events by the total focal observation time (Baird et al. 2007). I measured mapped spatial traces using a digital planimeter (Planix 2000)) and calculated the hourly rate of patrol for each male by dividing the total distance traveled by the total observation time on individual males (Baird et al. 2007).

Local Ratios of Male Competitors to Females

In species such as collared lizards where adults show strong intra- and interseasonal philopatry to their territories and home ranges, determining the ratio of male competitors to available females that individual males experience in local neighborhoods is a powerful method to quantitatively estimate the intensity of sexual selection (Baird et al. 2001; Baird and Sloan 2003; Baird 2013a). Using mapped census sightings and focal observations (described above), I determined the ratio of the number of mature males that abutted or partially overlapped each male territory/home range to the number of mature females partially overlapped by each territorial (2007, *N* = 17; 2008, *N* = 12; 2009, *N* = 9) and non-territorial (2007, *N* = 10; 2008, *N* = 3; 2009, *N* = 9) male present in the AL population during these three seasons. I used census data recorded on all females (*N* = 64) during this period to document spatial relationships between each female and the males in their neighborhoods.

Schedule of egg production and emergence of hatchlings

Adult lizards at AL typically emerge from hibernacula from late March to early April and remain reproductively active until 15 July (Baird et al. 2001). During all three study seasons, the schedule of egg development and oviposition was documented by capturing all females present throughout the site every 7–10 d to weight and measure them, and palpate their abdomens. At each palpation, follicular/egg development was characterized using egg size and shape criteria developed for females in this population (Baird 2004; Telemeco and Baird 2011). The abdomen becomes increasingly swollen as females ripen their eggs, whereas oviposition is marked by 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 between first-year females and females that are two years old or older (2Y+ females) (Baird et al. 2001; Telemeco and 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 and Baird 2011), which are oviposited throughout June, into the first two weeks of July. Once the last clutches of the season are oviposited, females feed more frequently and become progressively less active (Baird and Sloan 2003), presumably to store energy for winter.

Eggs from the earliest clutches begin to hatch in mid-July, followed by hatchlings from later clutches emerging until mid-October. Offspring are 38.0–40.0 mm 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, 2007–2009, the entire study site was surveyed at least three times per week to capture, mark and measure newly emerged hatchlings. At first and subsequent captures standard measurements (SVL, body mass) were recorded, sex was determined by examination of the post-anal scales (enlarged in males), and capture locations were recorded on scale-drawn maps. A blood sample was collected at the first capture. Hatchlings were then released unharmed by placing them in rock crevices at their precise capture locations.

Genetic assignment of hatchlings to individual mothers (see *Parentage assignments and estimates of male fitness*) of known age, combined with the schedule of oviposition for serial clutches and hatchling SVL at first capture, allowed me to estimate whether offspring were from first or subsequent (second or third) clutches. Assignment of offspring to first clutches was obvious using these criteria for both 2Y+ and first-year females. Because third clutches sometimes begin maturation before oviposition of second clutches, and third clutches develop rapidly (Baird 2004), I could not distinguish hatchlings from second or third clutches. Therefore, I pooled offspring from second and third clutches for analyses.

Collection of blood samples and DNA genotyping

Blood samples (50 µl) were collected from all adults when they emerged from hibernacula in the spring, and from all hatchlings (*N* = 251) at their first capture by puncturing the orbital sinus with heparinized micro-hematocrit tubes. Blood samples were immediately transferred into 15 ml tubes containing lysis buffer for storage until DNA extraction. Bleeding was staunched by applying slight pressure to the orbit with a clean cloth. Lizards were released unharmed by placing them in a rock crevice at their precise capture location.

I isolated genomic DNA from blood using a DNeasy blood and tissue extraction kit (Qiagen, Venlo, Netherlands). Using fluorescently-labeled primers developed for *C. collaris* (Hutchison et al. 2004), I amplified eleven microsatellite loci. PCR amplification reactions (15 µl) contained 4.75 µl genomic DNA, 0.50 µl forward and reverse primers, 9 µl True Allele Premix (Perkin-Elmer Applied Biosystems, Foster City, CA), and 0.25 µl GoTaq DNA polymerase (Promega, Madison, WI). PCR products were optimized according to the thermal profile and annealing temperatures used by Husak et al. (2006) for *C. collaris*. Mixtures of 9.25 µl Hi-Di formamide, 0.25 µl ROX 500 HD size standard, and 0.50 µl PCR product were denatured at 96˚C for 5 min and then immediately chilled on ice for 3 min prior to loading. Amplicons were visualized on an automated DNA sequencer (model ABI 3130, Perkin-Elmer Applied Biosystems) using GeneMapper software (Perkin-Elmer Applied Biosytems). I used Microchecker (University of Hull, U.K., Van Oosterhout et al. 2004) to test for the presence of null alleles, large-allele dropout, and stutter-induced typing errors at each locus.

All adult and hatchling lizards were genotyped for all eleven loci. Microchecker revealed that one locus (Orig11) contained null alleles. Null alleles can confound parentage assignments when a true heterozygote is incorrectly typed as a homozygote, potentially resulting in false exclusion of the true parent (Dakin and Avise 2004). Because this locus was polymorphic, it was still informative for determination of offspring-parent relationships. Therefore, I retained it for parentage analyses. To avoid false exclusions, all hatchlings that were homozygous at this locus were typed at only one allele following the methods of LeBas (2001) and Husak et al. (2006).

Parentage assignments and estimates of male fitness

Because 24 years of mark-recapture studies on collared lizards at AL have shown that adults occupy the same home ranges/territories over multiple seasons (Baird and Sloan 2003), and hatchlings remain within 20 m of where they first emerged for 1–1.5 months (T. A. Baird unpublished data), I used the spatial relationships of hatchlings relative to potential parents as my first criterion to guide parentage assignments (see similarly, Zamudio and Sinervo 2000). The two smallest habitat patches (1,230, 1,505 m^2) at AL are separated only by 40 m of grass, and there is a concrete wall running between them. Several lizards each season have been observed to use this wall to travel between these two patches (Curtis and Baird 2008). Because the potential for gene flow is high, I pooled these two patches for parentage analyses. By contrast, the third much larger (19,583 m^2) habitat patch at AL is separated from the two smaller patches by 260 m at the closest point (Curtis and Baird 2008). No more than one lizard per season has moved between the larger patch and the two smaller patches during 24 seasons, and no such movements were recorded during 2007–2009. For parentage analyses, therefore, I considered the larger patch separate from the pooled smaller patches.

I used CERVUS 3.0.3 (Marshall et al. 1998; Kalinowski et al. 2007) to assign a mother and father to all hatchlings at a minimal 80% confidence level. My simulation parameters for parentage assignments were: 1) mean proportion of candidate fathers (or mothers) sampled = 0.98; 2) proportion of loci mistyped = 0.01; 3) number of simulations = 100,000. For cases in which hatchlings could not be assigned a mother and/or father by CERVUS alone, I compared the genotypes of the two most-likely parents to the hatchling genotype. I excluded a parent candidate when it mismatched the genotype of the hatchlings at any locus (genetic exclusion, Haynie et al. 2003). For the few hatchlings that both candidate parents did not mismatch the genotype of the hatchling at any locus, but still had positive logarithm of the odds (LOD) scores (I did not used LOD scores that were negative), I used spatial locations of hatchlings relative to putative parents as my guide. Specifically, I compared the minimum linear distance from the first capture location of the hatchling to the boundaries of the home ranges/territories of each candidate parent, and assigned the hatchling to the parent that was closest. I then determined the number of offspring sired and the number of different females mated with in all territorial and non-territorial males.

Female promiscuity and offspring survivorship

I determined whether or not offspring produced by individual females survived to the following season in relation to the number of different males that sired their offspring to test the hypothesized positive effect of female promiscuity on the survivorship of their offspring. I determined the number of males that females mated with by determining the identity (territorial or non-territorial) of sires that inseminated individual clutches. Hatchlings that were captured during one season, but absent throughout the following season were considered non-survivors.

Statistical analyses

All analyses were performed in the program R v. 3.0.1 (R Development Core Team 2013) using a Bayesian statistical framework in the package ‘MCMCglmm’ (Hadfield 2010). Similar to traditional statistical approaches, Bayesian models determine effect sizes (β), standard errors (SE), and 95% credible intervals (CI, Bayesian analogue of confidence intervals) for evaluating the significance of predictor variables (Ellison 2004; Kruschke et al. 2012). However, because these parameters often cannot be calculated directly, they must be estimated using a simulation technique known as Markov Chain Monte Carlo (MCMC). MCMC simulations are iterated until a point is reached where estimates of all parameters are unbiased (convergence). Because the first batch of simulation runs are usually far from convergence, retaining them produces biased estimates. Consequently, these runs are discarded (burn-in). Because the total number of simulation iterations is often very large, only a fraction are kept as samples for parameter estimates after burn-in (thinning interval). This entire process yields an 'effective sample size' that provides a robust estimate of effect size, SE, and 95% CI for predictor variables. For all models (described below), MCMC simulations consisted of 13,000 iterations in total. I discarded the first 3000 iterations as burn-in, and retained a sample at every tenth iteration (thinning interval = 10). In total, this yielded an effective sample size of 1000 for each model.

I used generalized linear mixed models (GLMM; Bolker et al. 2009) to compare behavioral traits (rate of patrol (m/h), broadcast displays/h, courtship encounters/h, and contests/h), the number of different females mated with, and the number of offspring sired by territorial and non-territorial males. I also used GLMM to examine the effects of LSR within each season (intraseasonal LSR) and male behavioral traits on the numbers of female mates and the number of offspring sired by territorial and non-territorial males. Because some males controlled territories for more than one season, I included paternal identity as a random effect to control for pseudoreplication. I also used GLMM to determine annual variation in female promiscuity, and the potential effects of female promiscuity, sire social status, and variation in LSR among seasons (interseasonal LSR) on offspring survivorship. For these analyses, I included both paternal and maternal identity as random effects. Predictor variables having 95% CI that did not include zero were considered statistically significant. 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 tested (Colegrave and Ruxton 2003; Nakagawa and Cuthill 2007). Instead, I report effect sizes (β), SE, and 95% CI for predictor variables, which provide both biologically and statistically meaningful inference at a specified degree of certainty (Colegrave and Ruxton 2003).

RESULTS

Male social behavior

Consistent with all previous studies on the AL population (reviewed by Baird 2013c), territorial males in 2007–2009 had markedly higher rates of patrol (β = 51.7, SE = 7.12, 95% CI = 38.87–65.85) and broadcast display (β = 55.15, SE = 8.62, 95% CI = 39.30–72.29). They also courted females (β = 0.78, SE = 0.18, 95% CI = 0.44–1.45), and initiated aggressive contests more frequently than non-territorial males did (β = 0.18, SE = 0.05, 95% CI = 0.09–0.27).

Emergence of hatchlings, determination of genotypes, and parentage assignments

Eighty-six percent (215 of 251) of hatchlings were captured from 15 July–15 October (2007, *N* = 70; 2008, *N* = 76; 2009, *N* = 69). Thirty-six more (14% of total) hatchlings (2007, *N* = 16; 2008, *N* = 8; 2009, *N* = 12) were not captured until April to May, 2008–2010. In all three seasons, these additional hatchlings were randomly distributed throughout the entire study site instead of being localized on the territories/home ranges of only some males on areas of some males. The fact that a small percentage of hatchlings were captured later, therefore, does not introduce bias into my estimates of the number of offspring sired and the number of different mates for males and females.

Of the 251 total hatchlings, 168 were assigned a mother, and 189 assigned a father, using CERVUS alone. I used genetic exclusion to assign mothers for 13 hatchlings, and fathers for 14 hatchlings. Forty-five hatchlings were assigned mothers, and 31 were assigned fathers using exclusion based on spatial proximity. As a consequence of negative LOD scores for one or both parents, I did not assign 25 and 17 hatchlings mothers and fathers, respectively. Both parents shared negative LOD scores for the same hatchlings in ten of these 42 cases. Therefore, only 15% of hatchlings (*N* = 32) were not assigned parents, whereas I assigned a mother and father to 214 of 251 (85%) hatchlings using a combination of the three described methods. Of these 214 hatchlings, 117 (55%) were assigned to territorial males, and 97 (45%) were assigned to non-territorial males.

Influence of local sex ratio and behavioral traits on male fitness

Despite marked variation in the LSR values among individual males within each season (range = 0.00–7.00), LSR did not influence the number of female mates, or the number of offspring sired in either territorial or non-territorial males (Tables 1, 2). None of the behavioral variables that I examined significantly predicted the number of female mates or offspring sired for non-territorial males (Tables 1, 2). For territorial males considered alone, however, courtship frequency was positively associated with both the number female mates and offspring sired (Tables 1, 2).

Although LSR varied significantly among seasons (β = -0.99, SE = 0.23, 95% CI = -1.46 – -0.55, Fig. 1), both the numbers of female mates and offspring sired were similar (95% CI's included zero) in all three years when all males were pooled, and when territorial and non-territorial males were considered separately (Table 3). Moreover, comparisons between territorial and non-territorial males revealed that social status had no significant effect on the number female mates or offspring sired in all three seasons (Table 3, all 95% CI included zero).

Female promiscuity and offspring survivorship

Neither the degree of female promiscuity, nor the number of offspring produced from matings with territorial versus non-territorial sires differed by year (Table 1). Survivorship of offspring produced by individual females did not vary among years, and was independent of sire social status (Table 4). However, offspring survivorship decreased with the degree of female promiscuity (Table 4).

DISCUSSION

Consistent with previous studies on male collared lizards at AL, territorial and non-territorial males differed markedly in patterns of social and spatial behavior. Although territory ownership promoted increased courtship opportunities relative to the subordinate, non-territorial social tactics employed by first-year males, my results show that male social status had no effect on the numbers of females that males mated with or offspring sired, regardless of significant variation in LSR. Despite attempts by territory owners to monopolize females that they overlapped spatially by courting them frequently, females showed little mating fidelity, producing offspring with multiple territorial and non-territorial males in each season. This finding is surprising. In the four populations of *C. collaris* that have been studied quantitatively to date, the oldest and largest males incurred substantial costs by defending territories (Baird et al. 1997; McCoy et al. 2003; Baird et al. 2003; Husak et al. 2006). Theory predicts that territoriality should only evolve when those individuals defending territories obtain a reproductive advantage that balances the cumulative costs (Brown 1964; Davies and Houston 1981; Stamps 1994). The fact that non-territorial male collared lizards in our population consistently achieved reproductive success equal to that of territory owners without incurring the costs of territory maintenance contradicts this widely-held expectation. My results raise the question, is territory defense by males adaptive and evolutionarily stable in the AL population?

One possible explanation of my results is that the success of non-territorial males and high degree of female promiscuity may be linked to features of the human-constructed AL habitat that promote the ability of non-territorial males to access mating opportunities with several females despite the defensive efforts of territory owners. The rock habitat patches at AL are large and continuous and offer almost unlimited crevices within which non-territorial males take refuge when threatened by larger territory owners (Baird and Sloan 2003). Inconspicuous behavior coupled with ready access to refuges, appears to promote the ability of non-territorial males to evade attacks by territory owners without leaving the vicinity where females reside. Maintaining proximity to females likely allows subordinate males to sneak copulations, especially when territory owners are patrolling distant boundaries. The frequent, prolonged and intimate courtship behavior that characterizes territorial male interactions with females at AL may better promote mate monopolization in smaller, much less topographically homogeneous and continuous rock outcroppings and washes in the natural habitat of collared lizards in which mate monopolization is more economical (Baird and Sloan 2003; McCoy et al. 2003). The markedly different features of the AL habitat that promote both matings by non-territorial males and female mating with multiple males, both diminish a higher degree of mate monopolization through territory defense that may be possible under the habitat conditions in which the social structure of this species evolved.

What explains the persistence of territorial tactics at AL even though defense did not result in higher reproductive success than that achieved using non-territorial tactics? In some other vertebrates, intense intrasexual competition and female promiscuity appears to force socially dominant males to abandon territory defense temporarily (Grant 1993; Weir et al. 2010). Adopting subordinate tactics over short periods may allow such males to increase their reproductive success with much lower costs. There is no evidence that territorial collared lizard males revert to non-territorial social tactics in the AL population. Even in local neighborhoods having strongly male-biased LSR, territorial males have not been observed to revert to non-territorial tactics during longitudinal studies spanning 24 seasons (T. A. Baird unpublished data), but there are numerous examples of non-territorial males becoming territorial when opportunities arise through experimental removal or natural mortality of territory owners (Baird and Timanus 1998; Baird and Curtis 2010). Features of the AL habitat that distinguish it from this species' natural habitat over time may promote the diminution of a territorial male advantage in mating competition enough that territorial tactics are lost in the AL population. The loss of sexually selected traits is common in many vertebrate clades, including lizards (Wiens 2001; Hews and Quinn 2003). However, if territory defense is under strong phylogenetic inertia and has become fixed in the AL population (Wilson 1975; Blomberg and Garland Jr. 2002), it seems highly unlikely that short-term reproductive disadvantages for territorial males will rapidly lead to the loss of territoriality and/or its replacement by an alternative tactic.

The adaptive significance of multiple paternity in reptiles remains a controversial issue (Uller and Olsson 2008; Madsen 2011). Uller and Olsson (2008) hypothesized that female multiple mating is selected because mating with numerous females increases male fitness, and costs to females of copulating with several males are probably negligible. Alternatively, females may mate promiscuously to promote their own fitness, or that of their offspring (Keogh et al. 2013; Noble et al. 2013; York et al. 2014). My results do not support either hypothesis. The negative effect of female multiple mating on survivorship of offspring strongly suggests that different factors promote fitness of the sexes in this population, and that these factors act antagonistically in females and males (i.e., sexual conflict, sensu Parker 1979; Chapman et al. 2003; Arnqvist and Rowe 2005). Importantly, the negative effect on female fitness was independent of the social status of males that sired their offspring, ruling out the possibility that mating with territorial and non-territorial males imposes differential offspring survival costs for females. Although the genetic basis of sexual conflict remains unknown in collared lizards, recent theoretical work and empirical findings on zebra finches have revealed that female promiscuity may arise incidentally via indirect sexual selection on males (Forstmeier et al. 2011; Reid 2011a, b). Alleles that promote multiple mating by males may be inherited by both male and female offspring (Halliday and Arnold 1987). Consequently, female promiscuity may be selected, despite the potential for significant fitness costs incurred by females (Reid et al. 2011a, b).

Females may also mate promiscuously to acquire material and/or genetic benefits (Jennions and Petrie 2000; Head et al. 2005; Slatyer et al. 2011). There is little evidence that material benefits explain multiple mating by female collared lizards because the resources that females require to produce eggs (foraging perches, arthropod prey, refuges) are not limiting at AL and neither sex provides parental care (Baird and Sloan 2003). Genetic benefits acquired through multiple mating are also unlikely because female *C. collaris* appear to lack mechanisms that, in other species, promote sperm competition and/or cryptic female choice (Birkhead and Pizzari 2002; Telemeco and Baird 2011), paternity was not biased toward a subset of males (Uller and Olsson 2008), and females decreased, rather than increased, offspring survivorship by mating multiply. Although females may reject male advances by fleeing (Baird et al. 2003; Baird 2004), doing so likely detracts from other important activities such as effective foraging and thermoregulation, and may increase their risk of being noticed by predators. Fleeing would require females to abandon locations that they had chosen because they were favorable for one or more of these activities (Rowe 1992; Magurran and Seghers 1994; Arnqvist and Rowe 2005). Given the lack of evidence for material and genetic benefits to counter the likely costs, the most parsimonious explanation for sustained multiple copulations by female collared lizards is that they are 'making the best of a bad job' by accepting copulations from males that attempt to maximize their fitness by mating with as many females as possible (convenience polyandry; Lee and Hays 2004). Convenience polyandry may be the only viable strategy for females to manage such costs, given the high rate at which males encounter them in the AL population.

Variation in courtship frequency was positively associated with both the number of female mates and the number of offspring sired by territorial males, whereas variation in LSR and behaviors that are hypothesized to promote defense of territories (e.g., patrol, frequency of contests with rivals) had no significant effect on genetic measures of male fitness. This finding is consistent with those of previous behavioral studies suggesting that territory ownership increases access to females by AL males (Baird 1996; 2013b, c). Male performance traits that are likely important in competitive contests (bite force, sprint speed) were positively correlated with behavioral and genetic estimates of territorial male fitness in another Oklahoma population of collared lizards (Lappin and Husak 2005; Husak et al. 2006). I did not measure performance traits in this study. However, the success of non-territorial males clearly indicates that correlates of success in intrasexual contests are not the only determinants of male fitness in the AL population. Non-territorial males almost always fled instead of fighting, and almost certainly exhibit lesser performance traits (bite force, sprint speed; Lappin and Husak 2005; Husak et al. 2006) owing to their small size, and neither the frequency with which territorial males initiated contests or their size were correlated with fitness. Instead, I hypothesize that frequent close-contact courtship may be functional for two possible reasons in the AL population. Territorial males may use courtship to advertise genetic quality, resulting in offspring that are more viable and/or attractive to the opposite sex (Candolin 2003; Kokko et al. 2003; Andersson and Simmons 2006). Males that court most persistently may also sire more offspring borne by more different females. Frequent courtship may carry advantages for territorial males, but such harassment may also be costly to females (Clutton-Brock and Langley 1997; Rowe and Arnqvist 2002; Crudgington et al. 2009). Females may endure the persistent courtship efforts of territorial males because evading them would impose even greater costs.

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Table 1. Summary statistics from analyses examining the effects of intraseasonal local sex ratios (LSR) and male behavioral traits on the number of females mated by territorial and non-territorial males. The asterisk indicates a statistically significant effect (95% CI did not include zero).

Territorial Males (*N* = 38)	**β**	**SE**	**95% CI**
Intraseasonal LSR	0.08	0.07	-0.03–0.23
Rate of Patrol (m/h)	0.003	0.007	-0.009–0.01
Broadcast Displays/h	-0.002	0.004	-0.01–0.004
Courtship Encounters/h	0.47	0.19	* 0.11–0.83
Contests/h	-0.006	0.59	-1.01–1.20
Non-Territorial Males (*N* = 22)			
Intraseasonal LSR	0.04	0.15	-0.25–0.32
Rate of Patrol (m/h)	0.007	0.01	-0.01–0.03
Broadcast Displays/h	-0.09	0.08	-0.23–0.06
Courtship Encounters/h	0.81	0.65	-0.29–2.12
Contests/h	2.03	2.05	-1.69–5.70

Table 2. Summary statistics from analyses examining the effects of intraseasonal local sex ratios (LSR) and male behavioral traits on the number of offspring sired by territorial and non-territorial males. The asterisk indicates a statistically significant effect (95% CI did not include zero).

Territorial Males (*N* = 38)	**β**	**SE**	**95% CI**
Intraseasonal LSR	0.01	0.08	-0.14–0.17
Rate of Patrol (m/h)	0.007	0.007	-0.008–0.02
Broadcast Displays/h	-0.001	0.005	-0.01–0.008
Courtship Encounters/h	0.51	0.23	* 0.06–0.94
Contests/h	0.08	0.68	-1.21–1.34
Non-Territorial Males (*N* = 22)			
Intraseasonal LSR	0.04	0.12	-0.23–0.29
Rate of Patrol (m/h)	0.008	0.01	-0.007–0.03
Broadcast Displays/h	-0.09	0.06	-0.21–0.02
Courtship Encounters/h	0.54	0.65	-0.43–1.76
Contests/h	2.05	1.71	-0.77–0.03

Table 3. Summary statistics from analyses examining the effects of variation in interseasonal local sex ratios (LSR) for each year and sire social status (territorial or non-territorial) on the number of female mates, and number of offspring sired by male collared lizards, and the effects of year and sire social status on the number of different territorial and non-territorial males that female collared lizards produced offspring with for individual clutches. Data in columns for territorial and non-territorial males are means with standard errors in parentheses.

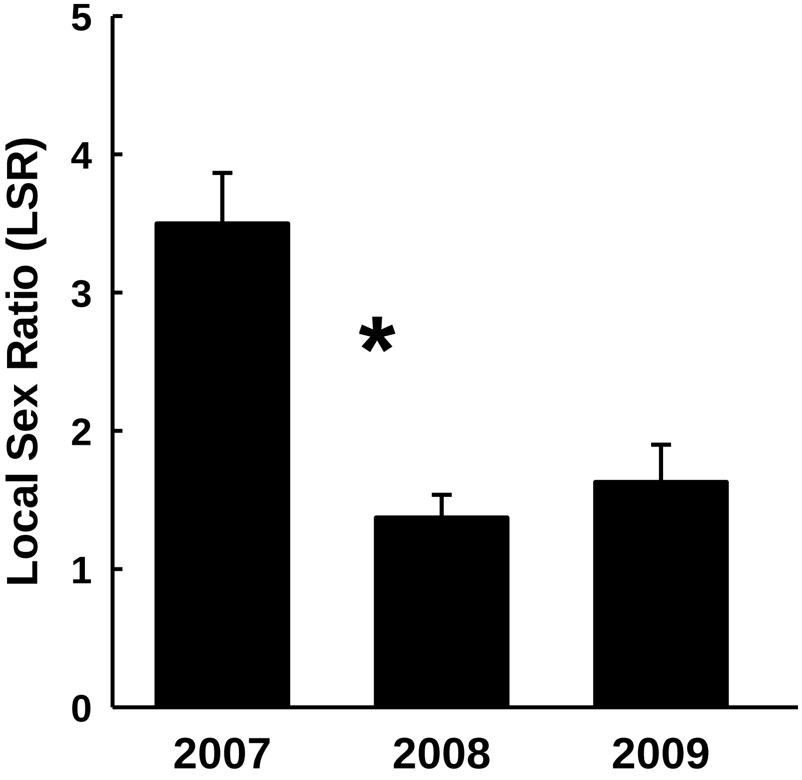
		Territorial	**Non-Territorial**	**Effect of Year**		**Effect of Sire Status**	
Dependent Variable	**Year**	**Males**	**Males**	**β (SE)**	**95% CI**	**β (SE)**	**95% CI**
Number of Female Mates	2007	1.94 (0.34)	2.10 (0.41)	-0.11 (0.13)	-0.37–0.14	-0.15 (0.40)	-0.72–0.50
	2008	2.33 (0.31)	2.33 (0.58)	—	—	-0.18 (0.38)	-0.49–0.44
	2009	1.64 (0.50)	1.68 (0.41)	—	—	-0.03 (0.43)	-0.80–0.81
Number of Offspring Sired	2007	2.94 (0.74)	2.70 (0.52)	-0.17 (0.20)	-0.56–0.22	0.0001 (0.38)	-0.74–0.75
	2008	3.67 (0.64)	3.00 (0.80)	—	—	0.16 (0.23)	-0.20–0.62
	2009	2.09 (0.67)	2.26 (0.66)	—	—	0.03 (0.39)	-0.73–0.83
Number of Male Sires	2007	1.48 (0.20)	0.84 (0.16)	-0.10 (0.07)	-0.22–0.04	0.04 (0.08)	-0.25–0.08
	2008	1.07 (0.19)	0.85 (0.16)	—	—	0.11 (0.11)	-0.13–0.28
	2009	0.67 (0.13)	1.19 (0.19)	—	—	-0.03 (0.05)	-0.09–0.03

Table 4. Summary statistics from analysis examining the effects of interseasonal variation in local sex ratios (LSR) among years, sire social status (territorial or non-territorial) and female promiscuity (number of male mates for individual clutches) on the survivorship of offspring produced by individual females. Asterisk indicates a statistically significant effect (95% CI did not include zero).

Variable	**β**	**SE**	**95% CI**
Year	-0.48	0.23	-0.91–0.008
Sire Social Status	-0.41	0.38	-1.11–0.37
Female Promiscuity	-0.31	0.14	*****-0.58– -0.04

FIGURE LEGEND

Fig. 1. Annual variation in local sex ratios (LSR) for individual males. Data are means ± 1.0 SE. The asterisk indicates a statistically significant effect (95% CI did not include zero).



Local Sex Ratio (LSR)
0
1
2
3
4
5
*
2007
2008
2009

GENERAL SUMMARY

My results add to an extensive body of work documenting marked differences in social and spatial behavior among territorial and non-territorial male collared lizards at Arcadia Lake that appear to be linked to sexual selection pressures (Baird et al. 1996; 2003; Baird 2013). According to classical mating system theory, these differences should result in a disproportionate reproductive advantage for territorial males (Dewsbury 1982; Andersson 1994; Ellis 1995). My results contradict this prediction. Male social status had no influence on the numbers of female mates or hatchlings sired, regardless of significant intra- and interseasonal variation in the intensity of sexual selection, and females showed little mating fidelity to territorial males that appeared to monopolize them socially. Rather than modifying their behavior patterns to reduce costs, 2Y+ males continued to invest in costly behaviors that promote ownership of territories, but did not achieve higher reproductive success. Together, these findings question the evolutionary stability of territorial tactics in the AL population. Mine is a startling result given that studies on all four populations of *C. collaris* to date have revealed that the oldest and largest males control territories and attempt to monopolize social access to female residents (Baird et al. 1996; McCoy et al. 2003; Lappin and Husak 2005; Husak et al. 2006).

My earliest results based on a single season (Chapter 1) raised the possibility that females at AL mate promiscuously to gain genetic benefits. However, results over three consecutive seasons (Chapter 2) showed that this was not the case. Indeed, a strong negative impact of mating with multiple males on the survivorship of offspring produced by individual females indicated significant fitness costs of promiscuity for females. Because females do not appear to possess any behavioral or morphological adaptations to balance these costs, or appear to obtain any material or genetic benefits by copulating with multiple males, the most parsimonious explanation of this pattern is that mating relationships in AL collared lizards are influenced strongly by sexual conflict. Although the ‘best of a bad job’ hypothesis has been applied to male collared lizards (Baird and Timanus 1998), it appears to apply well to females.

An important component of sexual selection theory is how non-random variation in reproductive success is linked to variation in the expression of phenotypic traits, especially those in males (Lande and Arnold 1983; Andersson 1994; Kingsolver et al. 2001). None of the behavioral variables that I measured significantly influenced the fitness of non-territorial males. This result is not surprising given the low level of investment by these males in traits that are associated with social dominance, and a wealth of data indicating that non-territorial males attempt to increase their reproductive success by sneaking copulations, especially when 2Y+ males are patrolling distant territorial boundaries. Despite the fact that they achieved reproductive success no better than that of socially subordinate non-territorial males, territorial males continued to engage in prolonged intimate courtship encounters with females. Doing so may be a long-term bet-hedging strategy to ensure some degree of reproductive success, even when intense intrasexual competition renders monopolization of multiple females difficult. However, it may also indicate low potential for behavioral plasticity owing to genetic constraints and canalization (Baird and Baird 2006; Baird and Baird 2014). Contrary to studies on other populations of *C. collaris* in Oklahoma that incorporated behavioral and/or genetic estimates of male fitness (Lappin and Husak 2005; Husak et al. 2006), my results show no support for the hypothesis that traits associated with intrasexual male aggression are important components of male fitness. Instead, my findings reveal that social dominance in general is not an effective strategy for maintaining exclusive access to mating opportunities with females, especially against non-territorial males.

My results also conflict with current hypotheses regarding the evolutionary origin of multiple paternity in squamate reptiles (Uller and Olsson 2008), suggesting an alternative hypothesis rooted in sexual conflict. In my study population, the common factor that explains both the cause of sexual conflict and high success of non-territorial males appears to be the homogenous, continuous topography of the human-constructed habitat. The habitat at AL is markedly different from the natural habitat of collared lizards, which is characterized by much smaller, more discontinuous rock outcroppings that likely decrease female encounter rates with multiple males, make territories more economically defensible, and promote a higher degree of mate monopolization by territory owners (McCoy et al. 2003). Although territory defense may promote high reproductive success in such natural rock habitats, my results indicate that mate monopolization by territory owners is much less feasible when habitat structure renders mate monopolization more difficult.

The incongruence between behavioral and genetic estimates of reproductive success in collared lizards highlights the unreliability of using social and spatial interactions among individuals alone to determine fitness. My results are certainly not the first that document this incongruence. Indeed, similar findings have been reported in almost every major vertebrate and invertebrate taxon in which behavioral and genetic estimates of fitness have been integrated (reviewed by Hughes 1998; Birkhead and Pizzari 2002; Shuster et al. 2013). It is obvious that the inclusion of contemporary molecular techniques in behavioral ecology has provided a heretofore unparalleled level of precision for determining individual variation in fitness, and revealed subtle, yet important features underlying the evolution of sexually selected traits that are simply undetectable using behavioral methods alone. Although the application of molecular techniques presents clear advantages, it should be noted that these techniques are also prone to pitfalls unless they are coupled with detailed information on behavioral or morphological traits that are hypothesized to influence reproductive success. Molecular data will be of limited use unless investigators combine behavioral and genetic measures over the long term to test important evolutionary hypotheses.

Although the results presented here provide important and surprising insights into the mechanisms underlying individual variation in fitness in collared lizards, there are still numerous questions remaining to be answered. Future work should focus on determining the genetic basis of sexual conflict, and the extent to which behavioral traits, social dominance, fitness, and multiple mating in males and females, are heritable. Answers to such questions have strong potential to shed light on how behavioral traits respond to spatial and temporal variation in selection, as well as the role of genotype-environment interactions on sexually selected traits, an area that remains largely unexplored (Cornwallis and Uller 2010; Forstmeier et al. 2011). Lastly, although logistically difficult, studies combining behavioral and molecular techniques should ultimately be conducted in the fully natural habitats occupied by collared lizards to test the hypothesis that habitat topography and ecology are key factors influencing the distribution of reproductive success and mating system evolution that I have documented in a human-constructed habitat.

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