



Unexpected high fitness payoff of subordinate social tactics in male collared lizards



Joshua R. York*, Troy A. Baird¹, Michelle L. Haynie²

Department of Biology, University of Central Oklahoma, Edmond, OK, U.S.A.

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Sexual selection theory often predicts that dominant males will sire more offspring than males displaying subordinate social tactics. We 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 nonterritorial) 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 monopolize paternity of offspring with the females that they defended, and on average, nonterritorial 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 nonterritorial males and exceptionally high levels of multiple paternity appear linked in part to features of the habitat at our study site that diminish the ecological potential for territorial males to monopolize mating opportunities with females that reside 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.

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In populations under strong sexual selection, males having high resource-holding potential (RHP; Parker, 1974) often attempt to monopolize 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 characterized by inconspicuous behaviour (Gross, 1996; Shuster & Wade, 2003; Taborsky, Oliviera, & Brockmann, 2008). Inconspicuousness allows males with lower RHP 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 do, mating system studies based solely on observations of behaviour have often

concluded that male territory owners monopolize matings and obtain much higher reproductive success than males utilizing subordinate social tactics (Andersson, 1994; Cox & Le Bouef, 1977). In such systems, subordinate males are assumed to be ‘making the best of a bad job’ until they attain sufficient RHP to acquire territories (Andersson, 1994; Baird, Acree, & Sloan, 1996; Dawkins, 1980).

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 fertilization (Baird, Hranitz, Timanus, & Schwartz, 2007; Hughes, 1998; Wiley, Hatchwell, & Davies, 1991). 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; Ophir & Gafel, 2003; Sullivan & Hinshaw, 1992). 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, postcopulatory mechanisms (e.g. sperm competition, cryptic female choice) may confound parentage assignments (Birkhead & Pizzari, 2002; Eberhard, 1996). Indeed, the difficulty of

* Correspondence: J. R. York, Department of Biology, University of Central Oklahoma, Edmond, OK 73034, U.S.A.

E-mail address: jyork7@uco.edu (J. R. York).

¹ E-mail address: tbaird@uco.edu (T. A. Baird).

² E-mail address: mhaynie@uco.edu (M. L. Haynie).

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 monopolize females socially (Gibbs et al., 1990; Hughes, 1998; Olsson, Madsen, Shine, Gullberg, & Tegelström, 1994). By mating with multiple males, females may gain increased paternal care, access to resources required for reproduction, or increased quantities of sperm to ensure fertilization 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 (Byrne & Keogh, 2009; Kokko, Jennions, & Brooks, 2006; 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 and 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).

We 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 monopolization 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 nonterritorial, 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, 2013a; Baird, Fox, & McCoy, 1997; Baird et al., 2007). In our 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 males and numerous nonterritorial males (Baird et al., 1996). Moreover, because the habitat consists of continuous boulder fields having nearly unlimited crevices (Baird & Sloan, 2003), nonterritorial 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

We conducted this study during 20 March–31 October in 2007 and 2008 at the Arcadia Lake Dam flood control spillway located 9.6 km east of Edmond, Oklahoma Co., OK, U.S.A. (Baird, Timanus, & Sloan, 2003). Collared lizards at Arcadia Lake occupy three topographically homogeneous patches of boulders (1230–19853 m²) 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 at this study site are noosed as hatchlings and marked (the terminal phalanges of three digits are clipped for

permanent identification, and unique combinations of nontoxic acrylic paint spots are applied to the dorsum for identification of individuals from a distance; see [Ethical Note](#) below). The ages of all lizards used in the present study were known 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 nondefended 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 of males partially or completely overlap the home ranges of up to eight females, with whom the males frequently interact during prolonged (up to 30 min) courtship encounters throughout the reproductive season (Baird, Sloan, & Timanus, 2001; Baird et al., 2007). 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, nonterritorial males flee and hide in crevices, which are abundant at Arcadia Lake (Baird & Sloan, 2003). Nevertheless, 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), one of the authors recorded mapped census sightings and focal individual observations (both described below) to document the spatial and social behaviour of lizards in the Arcadia Lake population. For the present study, we recorded both types of data 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, over which collared lizard activity is independent of substrate temperature (Baird et al., 2001). We recorded behavioural data (described below) from 1 May to 30 June, when females produce up to three successive clutches (see [Schedule of Egg Production and Hatching](#) below; Baird et al., 2001).

Censuses of the entire study site ($N = 30$; 15 censuses during May, 15 censuses 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 (Baird & Sloan, 2003; Stone & Baird, 2002), 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). We recorded 20 min focal observations ($N = 10$ /male) on different days throughout the reproductive season. Male collared lizard activity does not vary as a function of time of day from 0900 to 1300 hours when we recorded focal observations (Baird et al., 2001). However, to control for any possible temporal bias, each day we observed individual males that were present on the site 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

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