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Sexual Selection Dynamics In A Smoky Hills Population Of Crotaphytus Collaris

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SEXUAL SELECTION DYNAMICS IN A
A SMOKY HILLS POPULATION OF
CROTAPHYTUS COLLARIS

being

A Thesis Presented to the Graduate Faculty
of the Fort Hays State University in
Partial Fulfillment of the Requirements for
the Degree of Master of Science

by

Katherine Talbott
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This Thesis for

The Master of Science Degree

By

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PREFACE

This thesis is written in the style appropriate for publication in *The American Midland Naturalist.*

ABSTRACT

Recent studies in behavioral ecology have suggested environmental pressures might influence sexual selection dynamics to the extent that sexually-selected signals reflect local adaptation. I experimentally tested this hypothesis by manipulating a potential male ornament and observing the sexual selection dynamics in a Smoky Hills population of eastern collared lizards (*Crotaphytus collaris*). Sexual selection dynamics were investigated by characterizing habitat structure, describing individual lizard spatial distribution, and investigating morphological predictors of adult male territorial success. Habitat occupied by lizards had significantly different and higher percentages of rock cover, and significantly different and lower percentages of vegetation cover, than unoccupied habitat. No differences in habitat structure were detected between areas occupied by both sexes and areas occupied only by males. Experimental enlargement of the male gular ornament did not affect the spatial distribution of sexually mature lizards. Potential male fitness was estimated using several indices, which were then used to predict which morphological characters might affect male intrasexual success. Measures of body size, particularly mass, snout-vent length, and head width, were the strongest predictors of successful territory defense in adult males. The potential for sexual selection for this population is analyzed with respect to previous studies of sexual selection in *C. collaris*. This study supports previous observations of geographic variation in behavior in this species, and constitutes one of the first behavioral studies of *C. collaris* in the Smoky Hills portion of its range.

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INTRODUCTION

In his landmark work, *On the Origin of Species*, Charles Darwin outlined his hypotheses on the selective pressures that lead to speciation. He described natural and sexual selection as forces that influence survivorship and reproduction, respectively (Darwin, 1859). In the *Origin*, Darwin predicted natural selection operates through environmental forces, such as drought or predation, while sexual selection affects a population through the mating decisions of the choosy sex. When investigating the impact of environmental forces on speciation, biologists have traditionally retained this Darwinian paradigm.

Relatively recently, researchers began to investigate the influence of environmental factors on sexual selection (Van Valen, 1962; Hamilton and Zuk, 1982; Endler and Houde, 1995; Maan *et al.*, 2010). In addition, investigators have proposed mechanisms by which sexual selection itself might lead to speciation (*e.g.*, Lande, 1981), and have even identified populations thought to be in the process of such divergence (Masta and Maddison, 2002; Boul *et al.*, 2006). Together, these two paths of research support the emerging hypothesis that sexually-selected signals might reflect local adaptation (Mank, 2009; Van Doorn *et al.*, 2009).

Darwin thought sexual signals, such as elaborate male ornaments, evolved somewhat arbitrarily; however, he realized this assumption violated the principles of natural selection (Darwin, 1871). More recent interpretations of Darwin's theory describe how such sexually selected characteristics provide information on male quality. The handicap hypothesis is one such modification, and suggests conspicuous, energetically costly ornaments illustrate a male's quality simply through his ability to survive with the ornament (Zahavi, 1975). Additional hypotheses, including good genes (e.g., Van Valen, 1962; Hamilton and Zuk, 1982) and truth in advertising (Kodric-Brown and Brown, 1984), predict the degree of ornament expression reflects a male's quality as a function of the current environment and his genome. These models have been well-tested and supported, although it is clear they might not be mutually exclusive. Furthermore, one theory might not be sufficient to describe the nature of sexual selection in all species, or of all populations within a species. For example, geographic variation in characteristics under sexual selection has been observed among populations of the same species (Baird *et al.*, 1997; Kwiatkowski and Sullivan, 2002; Rosenblum, 2008).

Studying sexual selection in geographically variable species provides an opportunity to investigate whether the selection of specific characteristics is a result of local adaptation. Often, the species used as models for these questions also are sexually dimorphic, as such dimorphisms reflect differing selection pressures between the sexes (*e.g.*, Shine, 1989; Butler and Losos, 2002). The focal species of this study, the eastern collared lizard (*Crotaphytus collaris*), is an excellent model for investigating the interplay of sexual selection and local adaptation, as it displays both geographic variation and sexual dimorphism.

The range of *C. collaris*, a member of the family Crotaphytidae, covers much of the southwestern United States, extending from western Arizona to eastern Missouri, and from northern Kansas to central Mexico (McGuire, 1996; Stebbins, 2003; Figure 1). Suitable habitat for this predatory reptile is often discontinuous, leaving many populations in relative isolation. This species is generally territorial and polygynous, with males defending large territories containing the home ranges of one to several females

(Fitch, 1956). Males regularly patrol these territories, reinforcing territory ownership through classic iguanid (sensu lato) behaviors including head bobbing, gular extension, and gaping (Fitch, 1956). Occasionally, intrasexual contests result in direct physical confrontation (Fitch, 1956; Stamps, 1983). Throughout its range, this species is sexually dichromatic; males display geographically variable blue, green, and yellow markings, while females are more cryptically colored (McCoy *et al.*, 1994; McCoy *et al.*, 1997; Stebbins, 2003). Males are also larger than females, with increased head musculature and relatively longer hindlimbs, although the degree of these dimorphisms also is geographically variable (Fitch, 1956; McCoy *et al.,* 1994; McCoy *et al.*, 1997; Stebbins, 2003).

In territorial polygynous lizards, sexual dimorphism might be influenced by male intrasexual selection (Stamps, 1983). This is probably the case in *C. collaris*, and previous authors have found support for the role of body size (Baird *et al.*, 1997), bite force (Lappin and Husak, 2005), and sprint speed (Peterson and Husak, 2006) in male intrasexual interactions. In terms of intersexual selection, female choice rarely has been documented in lizards (*e.g.*, Olsson and Madsen, 1995). However, variations in environmental pressures, including predation pressure, food and mate availability, and intrasexual competition pressure, have been suggested to affect the social dynamics of iguanid lizards, including this species (Emlen and Oring, 1977; Stamps, 1983; Baird *et al.*, 1997; Kwiatkowski and Sullivan, 2002). Furthermore, previous authors have shown bright coloration in this species to be under sexual selection in populations with high environmental potential for polygyny (Baird *et al.*, 1997; McCoy *et al.*, 2003). Taken together, these observations suggest the intensity of sexual selection, as well as the characteristics under sexual selection, might vary within species in response to local environmental pressures. Thus, there is a need for further studies investigating the dynamics of sexual selection in ecologically disparate populations, even in species that already have been well studied (McCoy *et al.*, 2003).

The population of *C. collaris* selected for this study was located southeast of Liebenthal, Kansas, within the northeastern periphery of this species' range. Population density at the site appears to be high, and males possess bright yellow gular coloration, which is present only in the northeastern portion of this species' range (McGuire, 1996; Stebbins, 2003). The restricted geographical distribution of this ornament suggests it might be locally adaptive. The presence of the gular ornament, in combination with the high density of individuals, suggests there might be strong environmental potential for polygyny in this population, making it an excellent model for investigating sexual selection and local adaptation.

Little literature exists regarding the behavioral ecology of *C. collaris* in the Smoky Hills portion of its range. Much might be gained by studying this population, as most of our knowledge of *C. collaris* behavior comes from studies conducted in the Crosstimbers and Central Great Plains regions of Oklahoma (*e.g.,* McCoy, 1994; Baird 1997; McCoy, 1997; but see Fitch, 1956), yet geographic variation in form and behavior is known to occur in iguanids , including this species (Baird *et al.*, 1997; Kwiatkowski and Sullivan, 2002). Environmental pressures of the Smoky Hills in Kansas, being quite distinct from those of the Crosstimbers and Central Great Plains regions in Oklahoma, might have differently affected the dynamics of sexual selection in the Liebenthal population.

The objective of this study is to investigate the sexual selection dynamics of the Liebenthal population by characterizing habitat structure, describing lizard spatial distribution, investigating morphological predictors of male fitness, and manipulating a potential male ornament. I predict habitat structure to differ significantly between unoccupied areas and areas occupied by lizards, particularly in relative percentages of rock and vegetation. Because females and males are likely to have the same habitat requirements, I do not predict significant differences in habitat structure between areas occupied by both sexes and areas occupied by males only. In addition, I predict the male gular ornament is a strong signal of male quality, and manipulation will cause a shift in male territories. Specifically, I predict males manipulated to have larger ornaments will successfully enlarge their territories, causing simultaneous contractions or shifts in neighboring males' territories. If such redistribution of male territories occurs, I predict adult females will redistribute themselves as well, to associate with males manipulated to have larger gular ornaments.

METHODS

STUDY SITE

The study site is located 1.6 km southeast of Liebenthal, Kansas (38°39.18”N, 99°19.14”W), on a westward-facing hill approximately 415 m in length and 60 m in width at the widest point. Limestone outcroppings, mulberry trees (*Morus* sp.), yucca (*Yucca glauca*), and forbs and grasses typical of mixed-grass prairie, such as Missouri evening primrose (*Oenothera macrocarpa*), catclaw sensitive briar (*Mimosa quadrivalvis*), palm-leaf scurf-pea (*Pediomelum digitatum*), little bluestem (*Schizachyrium scoparium*), blue grama (*Bouteloua gracilis*), and sideoats grama (*Bouteloua curtipendula*), dominate the landscape. Because the site is used for livestock grazing, cattle were observed occasionally on the study site from late April to late September each year. Historically, the site has been used only for cattle grazing and limestone quarrying; there is no known record of the study site being cultivated for agricultural purposes (G. Anders, pers. comm.).

The perimeter of the study site was fenced with limestone posts, upon which lizards occasionally were observed displaying. The western edge was open to a field of prairie grasses along the northwestern border, and lined by a stand of deciduous trees along the southwestern border of the site. These areas of dense vegetation might present a barrier to westward lizard dispersal. Cattle pastures containing limestone outcroppings bordered the site to the north, east, and south. These habitats present potential corridors for lizard dispersal, and individual lizards were observed moving between the study site and pastures to the north and east.

HABITAT CHARACTERIZATION

In August and September 2011, I used lizard capture location data (see below) to identify 29 areas of habitat as having been occupied by males only (n = 7), by males and females (n = 11), or unoccupied by either sex (n = 11). From these areas, I randomly selected a total of 105 quadrats, each measuring 2.5 x 2.5 m, to sample abitat structure. I recorded the percentage of the following categories of ground cover in each sample: bare ground, rock, and vegetation. When I detected rock, I recorded the percentage of each rock size category: <100 cm^2, 100 cm^2–500 cm^2, and >500 cm^2. Similarly, when vegetation was detected, I recorded the percentage of each type (forb, grass, or shrub), and each height category (0–10 cm, 11–30 cm, 31–50 cm, and >50 cm) present. *Yucca glauca* and *Morus* sp. were included in the shrub category (individual *Morus* sp. included were ≤2 m), as vegetation was categorized based on physical structure, rather than taxonomy.

LIZARD CAPTURE, MARKING, AND MEASUREMENTS

The 2010 field season began in mid-May, by which time all adults and yearlings had already been active for some weeks, and extended to early September. In 2011, I began field observations in late April, and the majority of adults and yearlings became active by the end of the first week in May; the 2011 field season extended to early August. During both field seasons, I observed individuals by walking the perimeter of the study site and scanning with 8 x 40 mm binoculars. When possible, individuals were captured by using a noose pole, or by hand after turning over rocks. Individuals captured in 2010 were toenail-clipped for semipermanent identification, and marked for field identification using unique acrylic paint patterns (sensu Baird *et al.*, 1996). During the 2011 field season, captured individuals were toe-clipped for permanent identification and marked with unique acrylic paint patterns. Toes and toenails were retained for potential future use in genetic analyses.

Males were distinguished from females by coloration, head musculature, and femoral pore enlargement (*e.g.*, Fitch 1956). Sexual maturity was assessed using body length measurements taken on or before 1 June (adult females ≥75 mm SVL; adult males ≥85 mm SVL) and presence of juvenile markings, adult male coloration, or adult female nuptial markings. Means of body size measurements for each age and sex class were calculated using data collected during the same time interval (Table 2). Individuals captured for the first time after 1 June were assigned maturity status based on estimated SVL on 1 June, however these individuals were not included in calculations for Table 1.

I collected data from each individual on a daily basis when possible, but did not handle an individual more than twice per day. Each field day, I entered the study site either at the northern or southern border; from day to day, I alternated between entrances to minimize the likelihood of individuals becoming habituated to my behavior or shifting their territories. Data recorded for each capture event included: snout-vent length (SVL), total length (TL), mass, presence of ectoparasites, reproductive condition, progression of shedding, and presence of wounds. Reproductive condition was assessed in males by checking for adult markings and the presence of enlarged femoral pores, and in females by checking for nuptial markings and palpating the abdomen to detect oviductal eggs (sensu Fitch 1956).

In 2011, the same observation and capture methods were used, but additional data were recorded: capture or observation location, number of femoral pores on each hind limb, gular width and length (adult males only), head width (adult males only), and hindlimb length (adult males only). To identify capture locations, I erected a grid on the study area by placing marked 30.5 x 2.5 x 3.8 cm wooden stakes every 5 m. A capture location was noted as being within the northeastern, northwestern, southeastern, or southwestern quarter of a grid cell as identified by the nearest southeastern-most stake. In early June 2011, before male ornament manipulation (see below), I increased the number of observed location points for each individual using the following procedure, modified from a method designed by Wiens (1969): the individual was flushed from under a rock, and the locations at which it paused, or burrowed under another rock, were recorded. When an individual ceased to flee, I captured it, took any appropriate measurements, and released it near the location at which it was observed before it was flushed. Female home range and adult male territory maps were generated by hand by plotting location data on a grid in Microsoft Excel. Each male's territory map was delineated by connecting the outermost location points to produce a polygon. Three sets of territory and home range maps were generated using premanipulation location data, postmanipulation location data, and combined location data from the entire 2011 season.

On 5 September 2010, I captured all hatchlings encountered within a 5 h time period. Hatchlings were located using the same procedure used earlier in the field season to locate overwintered individuals. Mass and TL were recorded for each captured individual, and a line of paint was applied to each individual's tail to avoid resampling the same individual. On 5 September 2011, I captured all hatchlings encountered within a

7.5 h time period using the same procedure as in 2010. Mass, SVL, TL, and capture location were noted for each hatchling. The fifth digit of the left hind limb was removed to avoid resampling the same individual, and these digits were retained for potential future genetic analyses.

MALE ORNAMENT EXPERIMENT

From 15–17 June 2011, after six weeks of accumulating location data, I experimentally enlarged the gular ornaments of five adult males. Six pairs of the most frequently observed males were selected; each pair consisted of individuals size-matched within ≤2mm SVL, one of which had a larger (≥5mm width or length) gular ornament than the other. In each pair, the male with the smaller ornament was painted with an artificially enlarged ornament, and the male with the naturally larger ornament was painted as a control (Figure 2). To control for any effect of color or texture of the paint, I used the same paint mixture to fill in, but not enlarge, the gular ornaments of the six control males. Using a mixture of acrylic paint (Folk Art acrylic paints, #455 Medium Yellow, #437 Lipstick Red, and #484 Brilliant Ultramarine) color-matched to the male gular ornament, experimental males were manipulated by applying a coat of paint from the lower border of the ornament to the mental scale, and from the left to the right corners of the mouth. For one pair of males, the male with the larger gular ornament could not be located, resulting in a total of five males being painted with enlarged gular ornaments, and six males being painted as controls. After manipulation, I continued to observe, capture, and record data from all individuals. When painted males were captured, I checked the condition of the paint, and reapplied paint as necessary. After three weeks I ceased reapplying paint, but continued to observe and capture all individuals until 9 August 2011.

STATISTICAL ANALYSES

I used a Kruskal-Wallis test to detect differences in habitat structure among unoccupied areas, areas occupied by males only, and areas occupied by both males and females. When analyzing the three categories of ground cover, the significance level was adjusted to 0.017 using a Bonferroni correction (sensu McCoy *et al*. 1994). This adjustment was repeated when analyzing the three categories of vegetation type (α = 0.017), four categories of vegetation height (α = 0.013), and three categories of rock size (α = 0.017). When differences were detected, the data were further discriminated using Tukey's nonparametric HSD tests. Microsoft Excel 2007 and SPSS 12.0 were used for statistical analyses.

Responses to the 2011 male manipulation experiment were assessed by comparing premanipulation and postmanipulation territory maps of sexually mature males, and home range maps of sexually mature females. Following male manipulation, when an individual was detected outside its premanipulation territory, the distance between its observed location and the nearest premanipulation locality point was calculated. For adult males, a postmanipulation location greater than 20 m from the nearest premanipulation location was considered a departure from the premanipulation territory. An adult female observed more than 10 m from her nearest premanipulation location was considered to have moved outside her premanipulation home range.

Using these maps, I assessed potential male fitness in those individuals for which sufficient data ($n \geq 6$ locations) were available. Potential fitness was estimated by analyzing the proximity of females to each male (Figure 3). A female was considered accessible to a particular male if she was detected within approximately 10 m of any of his locality points or within approximately 10 m of a line connecting two of his locality points. These data were used to calculate five different indices of male fitness: number of accessible adult females, number of accessible juvenile females, fitness score calculated with adult females, fitness score calculated with juvenile females, and fitness score calculated with all females. Fitness scores (x) are given by the formula:

$$x = {}^{1}/m_{x} + {}^{1}/m_{y} \ldots {}^{1}/m_{z}$$

where x-z represent the individual females a male defends, and m is the number of males defending an individual female. Each female was given a value of 1, and the value assigned to a particular male represents this value divided by the total number of males sharing that female. An individual female detected within approximately 10 m of only a single male's territory was interpreted as being accessed exclusively by that male, and was therefore assigned a value of 1. For a female shared by two or more males, the value assigned to each male was calculated by dividing 1 by the number of sharing males. Although female access in such cases is likely not equal among sharing males, this procedure provides the most accurate estimate of potential male access.

Principal components analysis (PCA) was used to assess which morphological characteristics described the most variation in male measurements. These characteristics included mass, SVL, head width, hindlimb length, gular ornament width, and gular ornament length. The resulting component scores were entered into single linear regressions to assess the relationship between male characteristics and various fitness indices.

RESULTS

HABITAT STRUCTURE

The results of the Kruskal-Wallis test suggested differences in total vegetation cover ($X^2 = 22.44$, df = 104, P = 0.00), total rock cover ($X^2 = 27.47$, df = 104, P = 0.00), grass ($X^2 = 24.13$, df = 104, P = 0.00), 100–500 cm^2 rock ($X^2 = 18.80$, df = 103, P = 0.00), and <100 cm^2 rock ($X^2 = 33.76$, df = 103, P = 0.00) among occupancy categories. No differences in percent forb, shrub, 31–50 cm vegetation, >50 cm vegetation, or >500 cm^2 rock were detected (Table 1).

Results of Tukey's HSD tests indicated differences in habitat structure existed only between occupied and unoccupied habitat, as no significant differences were detected between habitat occupied by both sexes and habitat occupied only by males. Significant differences in percent vegetation cover, rock cover, grass, <100 cm^2 rock, and 100 cm^2–500 cm^2 were detected between unoccupied habitat and both types of occupied habitat (all P's < 0.01). Significant differences in percent of 10–30 cm vegetation also were detected between unoccupied habitat and that occupied only by males (P < 0.05), although no difference was detected between unoccupied habitat and habitat occupied by both sexes. No significant differences were detected in percentage of bare ground between the categories of occupancy.

POPULATION DESCRIPTION

In 2010, 50 individuals were marked and measured, consisting of four adult males, eight adult females, seven juvenile males, five juvenile females, and 26 hatchlings.

In 2011, 122 individuals were marked and measured, consisting of 16 adult males, 27 adult females, 25 juvenile males, 19 juvenile females, five juveniles of unknown sex, and 30 hatchlings. Population density, calculated using all overwintered individuals that emerged in the spring of 2011, was approximately 1 individual per 270 m^2. Previous authors, working with similar numbers of individuals within habitat patches of similar size, have characterized these population densities as high (Baird *et al*., 1997; Hranitz *et al.*, 2000).

The first seasonal observations of a female with nuptial coloration occurred on 21 May 2010 and 31 May 2011. In 2011, mean adult female mass peaked at 32 ± 0.5 g (± 1 SE) between 28 May and 4 June, and sharply decreased to 26 ± 1.3 g between 13 and 20 June (Figure 4). This suggests most adult females oviposited during or near the 13–20 June interval. Hatchlings without egg teeth or external yolk sacs (mean mass 2 ± 0.2 g, n = 6) were observed on 8 August, 54 d after the earliest estimated oviposition date.

Frequencies of hatchling TL and mass exhibited bimodal peaks in 2010 and 2011 (Table 3). The mean TL and mass for all hatchlings captured in 2010 (n = 26) was 140 ± 3.7 mm and 7 ± 0.4 g, respectively, and the mean TL and mass for hatchlings captured in 2011 (n = 23) was 135 ± 3.8 mm and 6 ± 0.4 g, respectively. When separated into cohorts by TL, the mean TL and mass of cohort I (135–160 mm TL, n = 22) in 2010 was 148 ± 1.3 mm and 8 ± 0.3 g, respectively, and the mean TL and mass of cohort II (85–110 mm TL, n = 4) was 100 ± 5.3 mm and 4 ± 1.1 g. In 2011, cohort I (148–158 mm TL, n = 9) had a mean TL and mass of 154 ± 1.2 mm and 8 ± 0.3 g, and cohort II (101–140 mm TL, n = 14) had a mean TL and mass of 122 ± 2.8 mm and 4 ± 0.2 g. The distinct peaks in hatchling body size frequency are probably attributable to differing dates of oviposition between yearling females and older individuals (Baird *et al.*, 2001), as there is no evidence for double clutching at the northern extent of this species' range (W. Meshaka *et al.*, in litt.).

Growth rates of juveniles during the 2011 season were similar between sexes, with males (n = 13) and females (n = 6) growing a mean of 0.31 ± 0.02 mm SVL/d. The mean SVL for juveniles at the beginning of the field season (4–31 May) was 63 ± 1.7 mm for females (n = 10) and 67 ± 0.9 mm for males (n = 21). By the end of the field season (7 July–9 August), mean SVL for individuals which overwintered as juveniles equaled 80 ± 1.4 mm for females (n = 6) and 87 ± 1.5 mm for males (n = 5).

TERRITORIALITY AND MALE ORNAMENT EXPERIMENT

In 2011, sufficient data ($n \geq 6$ locations; $n \geq 3$ pre– and postmanipulation locations each) were collected to generate maps of pre– and postmanipulation territories for six control males and two males with enlarged gular ornaments. Male territories overlapped in all cases, although the extent of overlap varied among individuals. Three control males and one male with an enlarged gular ornament were detected more than 20 m outside their premanipulation territories on at least one occasion. One control male and one male with an enlarged ornament were detected outside their premanipulation territories directly following male manipulation (17–24 June), and two control males were detected outside their premanipulation territories later in the season (27 June–9 July). All individuals were subsequently found within their premanipulation territories on at least one occasion.

Immediately following male manipulation, most experimental males detected outside their premanipulation territories did not approach any previously inaccessible females, with one exception. A control male gained potential access to four juvenile females following male manipulation when he moved outside his premanipulation territory. Because this male was a control, I assume his movement out of his premanipulation territory was not a result of the male manipulation experiment. Therefore, it is unlikely any male experienced an increase in his potential fitness, as quantified by number of accessible females, as a result of the experiment. Because of this apparent lack of movement, premanipulation and postmanipulation location points were pooled for each individual to produce the territory and home range maps used in assessing male fitness.

Sufficient data were collected to estimate premanipulation and postmanipulation territories for five sexually mature females ($n \geq 4$ locations; $n \geq 2$ pre– and postmanipulation locations each during the same time period used to quantify male movement). Before male manipulation, one female was captured approximately 200 m away from the area where she was most frequently detected. On one occasion following male manipulation, this same individual was captured 20 m away from her nearest observed premanipulation location; however, she was subsequently detected within her main premanipulation territory. The four remaining females were observed within 10 m of their nearest premanipulation locations. These results suggest any female movement was unlikely attributable to male manipulation.

MALE MORPHOLOGY AND FITNESS

Differences in fitness scores among experimental males suggest two distinct reproductive strategies in adult males: defending exclusive females (‘defenders’) and mating with as many shared females as possible (‘floaters’). All juvenile females were thought to be shared by more than one male. Defending males (n = 3) were estimated to have access to a mean of 10 ± 2.2 females, consisting of 2 ± 0.3 defended adults, 5 ± 1.2 shared adults, and 3 ± 1.5 juveniles. Floating males (n = 5) were estimated to have access to a mean of 8 ± 1.2 females, consisting of 6 ± 0.9 shared adults, and 3 ± 0.6 juveniles (Table 4).

For the eight analyzed males, differences in morphological measurements indicated defending males were generally larger than floating males. Defending males (n = 3) possessed a mean mass of 37 ± 0.6 g, SVL of 93 ± 0.5 mm, head width of 27 ± 0.3 mm, and left hind limb length of 85 ± 1.1 mm. Floating males (n = 5) had a mean mass of 33 ± 1.1 g, SVL of 90 ± 1.2 mm, head width of 27 ± 0.4 mm, and left hind limb length of 83 ± 1.2 mm. Total length measurements were not calculated because two of the three defending males had broken tails. Defending and floating males did not differ notably in gular ornament size, with defending males exhibiting a mean gular length and width of 18 ± 1.4 mm and 30 ± 1.7 mm, respectively, and floating males possessing a mean gular length and width of 17 ± 0.5 mm and 30 ± 1.2 mm, respectively.

The PCA produced two components representing male morphometrics. Together, these two components explained 84.5% of data variation, with the most variation described by component one (57.4%). Male mass (0.96), head width (0.94), and SVL (0.90) produced the highest loading values for component one. Component one was a significant predictor of fitness score calculated with adult females (adjusted $R^2 = 0.59$, $P = 0.02$), but not of fitness score calculated with juvenile females (adjusted $R^2 = -0.13$, $P = 0.69$) or total females (adjusted $R^2 = 0.10$, $P = 0.23$). In addition, component one was not a strong predictor of the number of adult (adjusted $R^2 = 0.31$, $P = 0.09$) or juvenile (adjusted $R^2 = -0.13$, $P = .67$) females detected near each male.

DISCUSSION

HABITAT STRUCTURE

The geographic range of *C. collaris* encompasses much of the southwestern United States and northern Mexico (Fitch, 1956; Hutchinson *et al*., 1999). Across such a relatively large geographic range, there exists great variation in geographic features, predominant vegetation, and prevailing climate of areas inhabited by different lizard populations. Although geographic variation in form and behavior has been observed among lizard populations (Burt, 1928a; McCoy *et al*., 1994; Baird *et al*., 1997; Macedonia *et al*., 2004), several common habitat features among these seemingly disparate environments also have been detected. These features include sparse vegetation and outcroppings of rock (Fitch, 1956; Hutchinson *et al*., 1999).

These habitat preferences reflect the general ecology of *C. collaris*. Rocks are used for thermoregulation, spotting prey, performing territorial displays, and detecting potential predators (Fitch, 1956). A certain amount of visibility is required for these behaviors to be effective, and any vegetation present in areas preferred by this species must be sparsely distributed. Habitat structure analyses of the Liebenthal population support these observations. Significantly different ($P<0.01$) and higher percentages of mean overall rock cover were detected in occupied ($\bar{x} = 28.4 \pm 2.8\%$) versus unoccupied areas ($\bar{x} = 13.2 \pm 2.3\%$). Furthermore, significantly different ($P<0.01$) and lower percentages of mean total vegetation cover, including grass, were detected in occupied areas (total vegetation $\bar{x} = 53.8 \pm 3.5\%$, grass $\bar{x} = 40.8 \pm 3.3\%$) than in unoccupied areas (total vegetation $\bar{x} = 76.6 \pm 3.3\%$, grass $\bar{x} = 64.1 \pm 3.5\%$). Thus, the overall trend was more rock and less vegetation in occupied habitat than in unoccupied habitat.

Included in ratios of rock to vegetation were two size classes of rock: rock less than 100 cm^2 and rock between 100 cm^2–500 cm^2. In occupied areas, mean cover of rock smaller than 100 cm^2 ($\bar{x} = 11.2 \pm 1.8\%$) is similar to mean coverage of larger rock ($\bar{x} = 13.1 \pm 1.7\%$), and both of these means are significantly ($P<0.01$) higher than the means of >100 cm^2 ($\bar{x} = 2.3 \pm 0.7\%$) and 100 cm^2–500 cm^2 rock ($\bar{x} = 5.2 \pm 1.3\%$) detected in unoccupied areas. Larger rocks measuring 100 cm^2–500 cm^2 appeared to be used for basking, surveillance, and as refuges from excessive heat and predators. Most rocks smaller than 100 cm^2 are not amenable to these activities, and might inhibit the growth of dense vegetation. Thus, for the Liebenthal population, both groups of rock probably play a role in fulfilling the general habitat requirements of *C. collaris*.

Although a higher percentage of rock than vegetation was detected in occupied areas, the vegetation present has probably affected the ecology of this population. In most populations studied to date, insects, mainly in the Order Orthoptera, make up the bulk of *C. collaris'* diet (Burt, 1928b; Blair and Blair, 1941; Fitch, 1956; McAllister, 1985). In the Liebenthal population, grasshoppers (Family Acrididae) probably constituted the main diet of *C. collaris*. In fact, individual lizards were observed ingesting grasshoppers, and often were captured with grasshopper tibiae projecting from their mouths.

Competition for space might exist between forbs and grasses (Dwyer, 1958). Because mean grass cover was higher in unoccupied areas ($\bar{x} = 64.1 \pm 3.5\%$) than in occupied areas ($\bar{x} = 40.8 \pm 3.3\%$), the lower density of grasses in occupied areas might be conducive to forb growth. If the main orthopteran prey of *C. collaris* are forb specialists, lower densities of grasses might correlate with a higher density of prey. Thus, significantly lower means of grass cover in occupied versus unoccupied areas might provide individual lizards not only with increased visibility, but also might indirectly support higher densities of prey for this population.

Although no significant differences in percent shrub cover were detected between occupied and unoccupied areas, plants included in the shrub category probably are used by *C. collaris* in some capacity. To evade approaching humans, many individual lizards fled into *Yucca glauca* foliage. Small *Morus* sp. trees also were used to escape approaching humans. In addition, individual lizards were detected within these trees on several occasions, perched on branches ~1 m above the ground. Solitary adult males, as well as pairs of adult males and females, were observed in this position. This behavior provides a substantial cooling effect, and has been documented as a thermoregulatory behavior in lizards (*e.g*., Bauwens *et al*., 1996; Angert *et al*., 2002). Although larger (>2 m) *Morus* sp. trees were detected along the perimeter of the study site, individuals observed in these trees were never detected more than ~1.5 m above the ground.

In addition to serving as refugia from predators and structures for thermoregulation, *Morus* sp. trees also might provide some nutritive value. Previous authors have observed *C. collaris* placing themselves under vegetation that might attract insect prey (McAllister, 1985), although this behavior has not been confirmed in the Liebenthal population. Moreover, on one occasion, an individual was observed feeding on *Morus* sp. fruit (J. Carter, pers. comm.). Analyses of scat from this population might confirm this observation as a regularly occurring behavior. Ingesting plant matter has been documented in the genus *Crotaphytus*, although rarely, and has included flower heads, seeds, stems, leaves, and *Lycium* sp. berries (Burt, 1928b; Blair and Blair, 1941; McAllister, 1985). The observation of an individual in the Liebenthal population ingesting *Morus* sp. fruit is the first report of frugivory in northern populations of *C. collaris*.

C. collaris might avoid certain types of vegetation that inhibit predator detection. This is supported by significantly different, and higher, percentages of grass in unoccupied than in occupied areas. Grass often grows densely and relatively tall with respect to *C. collaris*, and therefore might reduce detection of potential mammalian predators, such as coyote (*Canis latrans*), opossum (*Didelphis virginiana*), raccoon (*Procyon lotor*), bobcat (*Lynx rufus*), skunk (*Mephitis mephitis*), domestic dog (*Canis lupus familiaris*), and domestic cat (*Felis catus*). All of these species, except *P. lotor* and *F. silvestris*, have been detected on or near (within ~800 m) the study site, although these species probably occur on the site as well.

These analyses focused on habitat structure of areas inhabited by lizards of unknown social rank. Investigating social dynamics was a primary objective for this study, therefore, data regarding social hierarchies were not available *a priori* when habitat structure samples were selected. Furthermore, the distinction between occupied and unoccupied areas was based on occupancy by individuals at any stage of maturity. Studies of habitat use by individuals of different age classes and hierarchical cohorts in this population would be needed to detect any differences in habitat structure among areas inhabited by each demographic class.

TERRITORIALITY AND POTENTIAL FOR FEMALE CHOICE

Analyses of territory maps for males indicated movement in only two non-neighboring individuals immediately following male manipulation. These movements involved one control male and one experimental male. Because these individuals were not neighbors, it is unlikely their movements were related. Furthermore, there were no observations of territory expansions coupled with adjacent territory contractions, which was a predicted outcome of the experiment. These results suggest it is unlikely manipulation of male gular ornamentation affected the pattern of movement among experimental males.

Although I had limited data for mapping individual territories, my interpretation is they were sufficient to detect changes in individual movement, as manipulating easily detectable signals usually illicits a clear response (Rohwer, 1977). Previous authors have mapped crotaphytid territories using anywhere from 8–≥80 location points per individual (Werth, 1972; Baird *et al*., 1996; Warrick *et al*., 1998; Husak, 2005). Stone and Baird (2002) estimated approximately 80 location points are necessary to accurately map the territory of an adult male *C. collaris*, and warned using fewer locations might result in underestimating territory sizes and the extent of territory overlap. For my study, 4–13 premanipulation points and 2–10 postmanipulation points, resulting in 6–17 total points, were recorded for each of the eight experimental males.

Analyses of female distribution suggest only one experimental male expanded his territory in such a manner as to gain access to previously uncontacted females. Territory enlargement carries a high risk in terms of aggressive intrasexual interactions (Fitch, 1956; Husak and Fox, 2003), making it unlikely a male would expand his territory without a considerable potential benefit, such as access to potential mates. The other male’s territory expansion might have provided access to females I was unable to capture and mark. However it is unlikely, given the amount of time I spent in the study site, that there were enough unmarked females in the site to support this explanation. It is more likely the two apparent territory expansions reflected territory boundaries established before male manipulation.

The lack of territorial response in adult males suggests the male gular ornament might not constitute a sexually selected signal. This suggestion is plausible, as the expression of the yellow gular ornament is highly variable among populations of this species, and it is even absent in some portions of its range (McGuire, 1996; Stebbins, 2003). Previous authors have documented geographic variation in morphological features under sexual selection, including male coloration, in *C. collaris* (Baird *et al*., 1997). These authors have suggested the physical and social environment specific to each population might influence which morphological features are affected by sexual selection. A review of the mechanisms underlying sexually selected signals further supports this prediction.

In many territorial vertebrates, sexually selected signals, such as elaborate ornaments, convey information regarding male quality (*e.g*., Zahavi, 1975; Kodric-Brown and Brown, 1984). Males use these ornaments to assess dominance and fighting ability in conspecifics, thereby avoiding potentially dangerous and energetically costly conflicts (Parker, 1974). In addition to serving as intrasexual signals, ornaments are often used by females in mate selection (Kodric-Brown and Brown, 1984). This is thought to occur because males expressing energetically costly ornaments must be in good health (Zahavi, 1975; Zuk *et al.*, 1990) and probably possess good genes that make them successful in the context of their environment. Therefore, mating with such males presents a potential fitness benefit for a choosy female (*e.g.*, Van Valen, 1962; Hamilton and Zuk, 1982; Kodric-Brown and Brown, 1984).

In this population, the male gular ornament might serve several functions. Greenberg (1945) observed adult males were notably more aggressive towards other males positioned with their gular ornaments clearly visible; he also predicted the function of the ornament might be sex recognition. Additionally, the yellow coloration of the gular area might possibly accentuate male displays through automimicry (West-Eberhard, 1979). Adult males use gular extensions during aggressive intrasexual interactions as well as courtship displays (Greenberg, 1945; Fitch, 1956); thus, an ornament that could draw attention to these displays might be sexually selected. Analyses of integument coloration have shown yellow to be expressed through carotenoid pigments in some lizard species (Macedonia *et al*., 2000; but see Morrison *et al.*, 1995). Carotenoids can only be acquired through diet (Macedonia *et al*., 2000), which suggests the expression of a yellow gular ornament might signal resource quality in a male's territory. Although both sexes perform gular extensions, only adult males possess the yellow ornament (Fitch, 1956). This supports the suggestion that some degree of sexual selection might operate on the gular ornament.

If the male gular ornament is truly a strong intrasexual signal, the results of the experiment might reflect the fact that only the ornament was manipulated, when in practice, the ornament is connected with a behavioral display. A previous experiment enlarging the ornaments of low ranking Harris' sparrows (*Zonotrichia querula*) also was ineffective in advancing their social rank (Rohwer, 1977). This probably was because the manipulated individuals lacked the behavioral attributes needed for success in intrasexual contests. Results of a further experiment support this conclusion: when individual sparrows were manipulated with enlarged ornaments as well as testosterone implants, which modified their behavior, they did advance in social rank (Rohwer and Rohwer, 1978).

These observations support the prediction that males with enlarged gular ornaments might have failed to enlarge their territories because they lacked the other physical attributes that would accompany a strong signal of quality. Male territoriality is strongly developed in this species; even subordinate or juvenile individuals have been observed to react aggressively when other individuals attempt to enter their territories (Fitch 1956). Furthermore, the dear enemy phenomenon, well documented in *C. collaris*, predicts neighboring individuals are likely to be less aggressive towards one another than they would be towards non-neighbors (Husak and Fox, 2003). Therefore an experimental male with an enlarged ornament, of which he is unaware, might be even less likely than other males to attempt an invasion of his neighbor’s territory. Without initiating a challenge to his neighbor, it is unlikely his neighbor would flee in response to the enlarged gular ornament. If the gular ornament is a strong signal, the neighbor of a manipulated male might display more frequently in an effort to defend his territory from a perceived threat. In such a situation, the effect of the experiment might be to solidify existing territory boundaries. If the male gular ornament is in fact under sexual selection, the behavior of this species probably was not conducive to the methods used in this study.

The importance of the male gular ornament as an intrasexual signal might be better assessed in future studies with revised methods. Because individuals are highly territorial, experiments investigating dominance between paired males should be conducted in areas outside both individuals' territories. This might be accomplished in the Liebenthal population using tethering experiments (Fitch, 1956; Husak and Fox, 2003), or, after further investigation of the natural history of this population, in a laboratory setting.

In an unfamiliar setting, each male would be expected to perform displays to establish a territory. The importance of the gular ornament in determining the outcome of such contests might be investigated using males of comparable appearance, differing only in ornament size. If the gular ornament were under intrasexual selection pressure, males with smaller ornaments would retreat more often than males with ornaments of similar or larger size.

The role of the gular ornament also could be studied by quantifying aggressive displays (*e.g.*, Baird *et al*. 1997; Husak and Fox 2003). Comparing the level of aggression displayed by males towards individuals with smaller, larger, or similarly-sized ornaments might reveal whether males perceive the gular ornament as a signal of quality. Furthermore, to fully understand the role of the gular ornament in the social dynamics of this species, additional research is needed to assess the factors that affect ornament expression. Future research should address the possibility that ornament size might be influenced by parasite load (Zuk *et al*., 1990), age, head size, body temperature (Cole, 1943), androgen levels (Ligon *et al*., 1990), or carotenoid levels (Steffen and McGraw, 2007).

Comparisons of premanipulation and postmanipulation home range maps of adult females indicate little quantifiable movement in response to male manipulation. Only one individual was detected more than 10 m outside her premanipulation home range, and this same individual was detected far outside her home range (≥200 m) before male manipulation. Therefore, this individual's postmanipulation movement was probably not a response to male manipulation. As with males, relatively few location points were collected for each individual: 2–5 premanipulation and postmanipulation points, totaling 4–10 total points. However, the data available were probably sufficient to estimate female home ranges, as females occupy smaller areas than males, and therefore probably move less (Fitch, 1956; Baird *et al*., 1996).

I originally predicted that if the male gular ornament is under intersexual selection, females might redistribute themselves following the male manipulation experiment. Because little movement occurred after male manipulation, the gular ornament might not be a factor used in female choice, assuming female choice does exist in this population. After reviewing the behavior of this species, such a conclusion is not necessarily supported by a lack of female movement. In many vertebrate taxa, including other iguanid species, females are known to distribute themselves with respect to food resources rather than mates *per se* (Ims, 1988; Hews, 1990; Hews, 1993; Perry and Garland, 2002; Anderholm *et al*., 2004). When this occurs, females are predicted to have a clumped distribution, which is conducive to male territoriality and polygyny (Emlen and Oring, 1977). This is probably the type of mating system employed by *C. collaris*, considering females are generally not territorial and often have a clumped distribution (Baird *et al.*, 1996), while males are highly territorial in defense of areas containing potential mates (*e.g*., Fitch, 1956). If females do distribute themselves independently of male distribution, it is unlikely females would shift their home ranges following male manipulation.

In territorial polygynous species, including *C. collaris*, females have been observed to mate with the male whose territory intersects their home ranges, with little evidence of direct female choice (Olsson and Madsen, 1995; Anderholm *et al.*, 2004; Lappin and Husak, 2005). In the Liebenthal population, females might mate only with the territorial males that defend their home ranges. There is potential, however, for female choice even in this situation, as male territories often overlap in such a way that two or more males might share access to a particular female (Baird *et al.*, 1996; Lappin and Husak, 2005). Comparison of adult male premanipulation and postmanipulation territories reveals territory overlap among many adult males. Furthermore, the degree of territory overlap is probably underestimated as a result of the limited available individual location data (Stone and Baird, 2002). All eight males shared access to at least one potential mate, and only three males defended territories containing females thought to be inaccessible to other males (Table 4). When mate sharing occurs, it is unlikely each male sires an equal number of offspring through the shared female, which indicates females have some level of choice in deciding which male sires the majority of their offspring. This is supported by the observation that copulations are not coerced in this species (but see Greenberg, 1945), as females have been observed to reject male courtship displays (Fitch, 1956; Baird *et al.*, 1996).

Another potential mechanism for female choice is extra-pair copulation, which has been widely reported in territorial polygynous species (*e.g.*, Gibbs *et al.*, 1990; Abell, 1997; Double and Cockburn, 2000; Morrison *et al.*, 2002). Although females reside in close proximity to the males that defend them, and even copulate or form pair bonds with these males, securing a territory does not necessarily assure paternity to the territorial male (Gibbs *et al.*, 1990; Abell, 1997; Baird *et al.*, 1996). The likelihood of extra-pair copulation in this population is supported by separate observations of an adult female and an experimental male far outside (≥200 m) their home ranges during the mating season (Fitch, 1956), prior to male manipulation.

These observations suggest there is potential for female choice in this population. A previous study on iguanid mate selection suggested high-density populations of lizards might have greater potential for female choice than low-density populations (Kwiatkowski and Sullivan, 2002). This is thought to be attributable to the increased cost to females of searching for mates in low-density populations. Therefore, given the relatively high population density, high frequency of male territory overlap, and potential for extra-pair copulation (Husak *et al.*, 2008), some level of female choice probably operates in the Liebenthal population. Whether the male gular ornament is a factor in female choice remains unknown. If the ornament is influential in male intrasexual contests, the ornament is probably under intersexual selection as well (*e.g.*, Kodric-Brown and Brown, 1984).

SELECTION PRESSURES ON MALE MORPHOLOGY

To assess which male characteristics might be under intersexual selection, accurate indices of male fitness are needed. Male-female proximity, number of females defended, and observations of copulation have traditionally been used as indices of male mating success (*e.g.*, Stamps, 1983). However, the only study to employ molecular analyses of paternity in this species estimated 39% of offspring were sired by males that did not defend their mothers (Husak *et al.*, 2008). Molecular analyses in other species of territorial polygynous lizards also have shown territorial males do not necessarily sire all offspring produced by females residing within their territories (Abell, 1997; LeBas, 2001; Morrison *et al*., 2002; Uller and Olsson, 2008). Therefore, the methods used in this study to estimate male fitness are limited, and preclude an assessment of male characteristics under intersexual selection.

Conversely, male intrasexual selection might be assessed in territorial polygynous species by analyzing the territories themselves, as they reflect the results of male-male contests (*e.g.*, McCoy *et al.*, 2003). Although extra-pair copulation might occur, it is clear males with the highest fitness are those that successfully defend territories (McCoy *et al.*, 2003; Lappin and Husak, 2005; Husak *et al.*, 2008). Therefore, most individuals probably attempt to use the territorial strategy by excluding all surrounding males from their territories. Territory overlap by another male might reduce a male's chances of siring resident females' offspring; therefore, a male's intrasexual success might be assessed by analyzing the exclusivity of females residing within his territory. While a male could potentially fertilize any female detected near his territory, a female detected solely in one male's territory is thought to be successfully guarded from other males. Therefore, the presence of such a female might indicate a higher level of success in intrasexual contests than would the presence of a female shared with neighboring males.

This interpretation is supported by analyses assessing the connection between male morphological characteristics and male intrasexual success. Results of analyses using the number of females detected in each male's territory as an index of intrasexual success did not suggest a relationship between male morphological characteristics and fitness. Because both exclusive females and shared females are assigned equivalent values in this estimate, the results are probably attributable to asymmetry in female sharing. Therefore, fitness scores, which take into account the number of males sharing each female, might provide more accurate depictions of mate guarding success. In fact, relationships between male morphometrics and intrasexual success were detected in analyses using fitness scores calculated with adult females. Although similar results were not detected in analyses using fitness scores calculated with juvenile females or total females, this is probably attributable either to differences between juvenile and adult female behavior, or to my sampling methods. Further references to fitness score will refer to scores calculated with adult females, unless otherwise specified.

Those morphological characteristics shown to predict fitness score, therefore, are most likely to be characteristics under male intrasexual selection. Two such characteristics, mass and SVL, are metrics of body size, which correlates with intrasexual success in many taxa, including *C. collaris* (Baird *et al*., 1997). In this species, which has indeterminate growth and displays territory fidelity (Baird *et al.*, 2001), large body size might indicate an older, experienced individual with a well-established territory (Stamps, 1983). Large mass also might reflect resource-holding potential (Parker, 1974), as a heavy individual's territory must contain sufficient resources for him to gain mass. Furthermore, a larger individual might be more likely to prevail in an intrasexual contest simply through his strength or bulk, and might therefore be avoided by smaller males (Baird *et al.*, 1997).

Head width, also a significant predictor of fitness score, represents a potential weapon used in intrasexual contests. Lappin and Husak (2005) showed bite force to be a strong predictor of mating success in *C. collaris*, which they attributed to the weapon's influence on intrasexual contests. In addition, head width has been shown to affect intrasexual success in other lizard species (*e.g.,* Hews, 1990). Given the relatively high density of individuals in the Liebenthal population, there is probably a high level of aggression among individuals establishing and maintaining territories. The importance of weapon size and bite force, potentially correlated with head width, is further supported by frequent observations of males with bite-inflicted wounds. Individuals might therefore use a signal reflecting weapon size and bite force to avoid potentially costly fights (*e.g.*, Maynard Smith, 1974).

Gular ornament size appears to have to have little direct effect on fitness score. Little is known regarding the expression of this ornament, and size probably varies in response to individual condition or environmental factors such as temperature. If this is correct, the field measures used in this study might not have accurately reflected each male's maximum ornament size, and this might have influenced the accuracy of the analysis. Assuming the ornament does influence intrasexual selection, it might be one of several characteristics simultaneously assessed in intrasexual contests (Hamilton and Sullivan, 2005). In addition, absolute ornament size, which was analyzed in this study, might not be as influential as proportional size, or perhaps aspects of ornament color might be more influential than size. Furthermore, the gular ornament simply might not be under sexual selection in this population (*e.g.*, Baird, 1997).

Another approach to assess which morphological characteristics predict male intrasexual success is to compare measurements of defending and floating males. Although the small sample size of defending males precluded the use of inferential statistics, some trends are apparent when comparing means of each group's measurements. Defending males had notably longer SVL and larger masses. This supports the positive relationship between fitness score and body size. Defending and floating males had similar hindlimb lengths and gular ornament measurements, which also corresponds to the previously described relationships between morphometrics and fitness score.

However, average head width was similar between floating and defending males, which does not corroborate the previous results suggesting a relationship between fitness score and head width. Within each type of mating strategy, some individuals are likely to be more successful than others (Dominey, 1984). The development of certain characteristics, such as SVL or mass, might predict which mating strategy a male adopts, while other characteristics, such as head width, might predict his success in that strategy.

SEXUAL SELECTION IN THE LIEBENTHAL POPULATION

Studies investigating sexual selection in other populations of *C. collaris* have suggested the level of selection intensity varies according to environmental factors (McCoy *et al.*, 1994; Baird *et al.,* 1997; McCoy *et al.*, 1997). Habitat quality, patch size, predation intensity, female distribution, and population density varied among three populations in Oklahoma, producing unique combinations of morphological and behavioral characteristics in terms of sexual dimorphism, intrasexual aggression, and degree of territory and home range overlap (McCoy *et al.*, 2003). Based on these factors, the Liebenthal population most closely parallels the Arcadia Lake population, which was thought to have the highest environmental potential for polygyny (Emlen and Oring, 1977) of the three Oklahoma populations (McCoy *et al.*, 1994; Baird *et al.,* 1997; McCoy *et al.*, 2003).

In both the Liebenthal and Arcadia Lake populations, females were distributed in a clumped pattern. Although home range size and overlap were not calculated in my study, I have interpreted female home range overlap in the Liebenthal population to be more similar to the Arcadia Lake population than the other two populations investigated by McCoy *et al*. (2003). In addition, female territoriality was thought to be absent in the Arcadia Lake population, which is conducive to male polygyny (McCoy *et al.*, 2003).

At the Liebenthal study site, I often detected multiple females resting under a single rock, which suggests female territoriality also was not strongly developed in this population. Of the three Oklahoma populations, the Arcadia Lake population also had the highest degree of male territory overlap (McCoy *et al.*, 2003). As in females, territory size and overlap were not calculated for adult males, although these patterns in the Liebenthal population were interpreted to be most similar to the Arcadia Lake population than the remaining two Oklahoma populations (McCoy *et al.*, 2003). Furthermore, habitat patch sizes and population densities were similar between both the Liebenthal and Arcadia Lake populations (Baird *et al.*, 1996; McCoy *et al*., 2003). These observations suggest males were polygynous in both populations, which in turn supports the prediction of strong sexual selection pressure.

A laboratory study of the three Oklahoma populations showed body size to be influential in male intrasexual contests among all populations, while male coloration was influential only in the Arcadia Lake population (Baird *et al*., 1997). It should be noted, however, that estimates of brightness were based on overall coloration, without particular reference to the gular ornament (Baird *et al*., 1997). Based on the observations of Baird *et al*. (1997), McCoy *et al.* (2003), and the results of this study, the most likely characteristics under intrasexual selection in the Liebenthal population include: SVL, mass, and head musculature. Some aspect of coloration might also be under intrasexual selection, although the results of my study do not support this conclusion. Future studies of intrasexual selection in this population would do well to further examine these characteristics, as well as the importance of behavioral attributes in intrasexual contests. A detailed comparison of floating and defending males also might reveal which morphological characteristics function as honest signals.

McCoy *et al.* (1997) also investigated the possibility of female choice in *C. collaris*; they reported no female preference for male size in any population, although they did detect a preference for male coloration in the Arcadia Lake population. This result is reasonable, considering the Arcadia Lake population was thought to be the most polygynous, and the environmental potential for polygyny is often correlated with the intensity of sexual selection pressure (McCoy *et al.*, 2003). Therefore, (McCoy *et al.*, 1994) female preference for some aspect of color might exist in the Liebenthal population, as the social dynamics appear to be similar to the Arcadia Lake population. Future studies that include paternity analyses or a laboratory assessment of field preference might support this suggestion. The presence of the male gular ornament, combined with the potential for extra-pair copulation, indicates some degree of female preference (McCoy *et al.*, 2003) is possible in the Liebenthal population.

Additional characteristics, such as male femoral pore secretions, might be also analyzed as potential criteria for female preference. These secretions have been shown to convey information regarding male quality and individual identity in lizard species (*e.g.*, Alberts *et al.,* 1993; Martín and López, 2000; López *et al.*, 2003), but similar studies have yet to be conducted in *C. collaris*. These secretions might influence intersexual interactions, as this species possesses the anatomical capacity to process chemical information; for example, individuals have been shown to distinguish sex using chemical information from fecal pellets (Simon, 1983; Wilgers and Horne, 2009). If male femoral pore secretions do function as a chemical ornament, it could provide a mechanism for female choice in populations where environmental potential for intersexual selection is high, but no morphological criteria for female choice have yet been identified by researchers (Baird *et al.*, 1997; López *et al.*, 2002).

Although sexual selection dynamics of the Liebenthal population warrant further investigation, the results of such studies might corroborate previous authors' observations of geographic variation in sexual selection dynamics in this species. Because the Arcadia Lake and Liebenthal populations share many similarities, including degree of male and female territoriality, population density, habitat size, and territory overlap, they probably also share similar sexual selection dynamics, such as relatively strong polygyny, strong male intrasexual competition, and strong potential for female choice. Whether future studies on the Liebenthal population support or refute this prediction, it is clear geographic variation in environmental pressures has produced unique combinations of morphological and behavioral characteristics in the Liebenthal population, as well as several Oklahoma populations, which might constitute local adaptation.

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TABLE 1.— Results of Kruskal-Wallis tests of differences in habitat structure among categories of occupancy in the Liebenthal, KS population of *Crotaphytus collaris*. Asterisks indicate differences between categories of occupancy are significant with a Bonferroni correction. Means ± 1 SE of percentage substrate cover in: unoccupied areas (x̄ UO), areas inhabited by males and females (x̄ MF), areas inhabited only by males (x̄ MO), and the combined percentages of MF and MO (x̄ O). Sample sizes in parentheses.

	X^2	P	df	x̄ UO	x̄ O	x̄ MF	x̄ MO
Overall habitat structure							
Total vegetation	22.44	0.00*	104	76.6 ± 3.3 (32)	53.8 ± 3.5 (73)	54.4 ± 3.9 (34)	53.1 ± 3.1 (39)
Total rock	27.47	0.00*	104	10.2 ± 2.4 (32)	28.4 ± 2.8 (73)	26.6 ± 3.1 (34)	30.1 ± 2.4 (39)
Total bare	7.30	0.03	104	13.2 ± 2.3 (32)	17.9 ± 1.9 (73)	19.0 ± 1.9 (34)	16.8 ± 1.9 (39)
Vegetation type							
Shrub	2.18	0.34	104	00.4 ± 0.4 (32)	01.0 ± 0.7 (73)	01.1 ± 0.6 (34)	00.8 ± 0.7 (39)
Forb	0.43	0.80	104	12.1 ± 1.5 (32)	12.1 ± 1.9 (73)	11.5 ± 1.9 (34)	12.6 ± 1.8 (39)
Grass	24.13	0.00*	104	64.1 ± 3.5 (32)	40.8 ± 3.3 (73)	41.8 ± 3.8 (34)	39.7 ± 2.7 (39)
Vegetation height							
0–10 cm	8.29	0.02	103	41.0 ± 3.5 (32)	28.9 ± 2.8 (72)	29.3 ± 3.2 (33)	28.4 ± 2.3 (39)
10–30 cm	6.43	0.04	103	17.9 ± 1.6 (32)	13.8 ± 1.6 (72)	15.4 ± 1.9 (33)	12.2 ± 1.2 (39)
30–50 cm	4.66	0.10	103	14.1 ± 2.3 (32)	09.9 ± 1.4 (72)	08.4 ± 1.2 (33)	11.3 ± 1.6 (39)
>50 cm	5.10	0.08	103	02.8 ± 0.6 (32)	02.5 ± 0.7 (72)	01.7 ± 0.5 (33)	03.2 ± 0.8 (39)
Rock size							
<100 cm^2	33.76	0.00*	103	02.3 ± 0.7 (31)	11.2 ± 1.8 (73)	10.0 ± 1.6 (34)	12.4 ± 1.9 (39)
100 cm^2*–500 cm*^{2}	18.80	0.00*	103	05.2 ± 1.3 (31)	13.1 ± 1.7 (73)	12.7 ± 1.8 (34)	13.4 ± 1.6 (38)
>500 cm^2	1.93	0.38	103	01.7 ± 0.9 (31)	04.2 ± 1.8 (73)	04.0 ± 1.5 (34)	04.3 ± 2.0 (39)

TABLE 2.—Mean body size measurements ± 1 SE of individuals captured from 4 May–1 June 2011 in Liebenthal, KS population of *Crotaphtyus collaris*.

	Adult males (n = 13)	Adult females (n = 18)	Juvenile males (n = 21)	Juvenile females (n = 10)
SVL (mm)	91.5 ± 1.4	85.9 ± 0.8	66.6 ± 0.9	63 ± 1.7
TL (mm)	269.5 ± 3.9	248.2 ± 1.8	194. 7 ± 2.8	183.6 ± 4.9
Mass (g)	33.8 ± 1.3	30.9 ± 0.7	12.7 ± 0.5	10.6 ± 0.6

TABLE 3.—Body size measurements of 2010 and 2011 hatchlings in the Liebenthal, KS population of *Crotaphytus collaris*.

Mass (g)	2010 (n = 26)	2011 (n = 23)	TL (mm)	2010 (n = 26)	2011 (n = 23)	SVL (mm)	2011 (n = 23)
1–≤2	1	0	81–90	1	0	43–45	2
>2–≤3	1	0	91–100	1	0	46–48	5
>3–≤4	2	6	101–110	2	2	49–51	5
>4–≤5	1	7	111–120	0	3	52–54	2
>5–≤6	0	1	121–130	0	6	55–57	2
>6–≤7	7	3	131–140	3	3	58–60	6
>7–≤8	6	2	141–150	10	2	61–63	1
>8–≤9	7	4	151–160	9	7		
>9–≤10	1	0					

TABLE 4.—Male fitness scores and numbers of females detected near each 2011 experimental male in the Liebenthal, KS population of *Crotaphytus collaris*. See text for fitness score calculation details.

Male	Exclusive adult females	Nonexclusive adult females	Total adult females	Total juvenile females	Total females	Fitness score (juvenile females)	Fitness score (adult females)	Fitness score (total females)
61	2	3	5	3	8	1.33	2.3	2.6
10	2	4	6	1	7	0.33	2.4	2.5
25	1	7	8	6	14	2.50	1.7	2.3
20	0	7	7	4	11	1.83	0.7	1.1
41	0	7	7	4	11	1.83	0.7	1.1
22	0	7	7	1	8	0.33	0.7	0.8
23	0	4	4	3	7	1.17	0.4	0.7
65	0	3	3	2	5	0.67	0.3	0.5

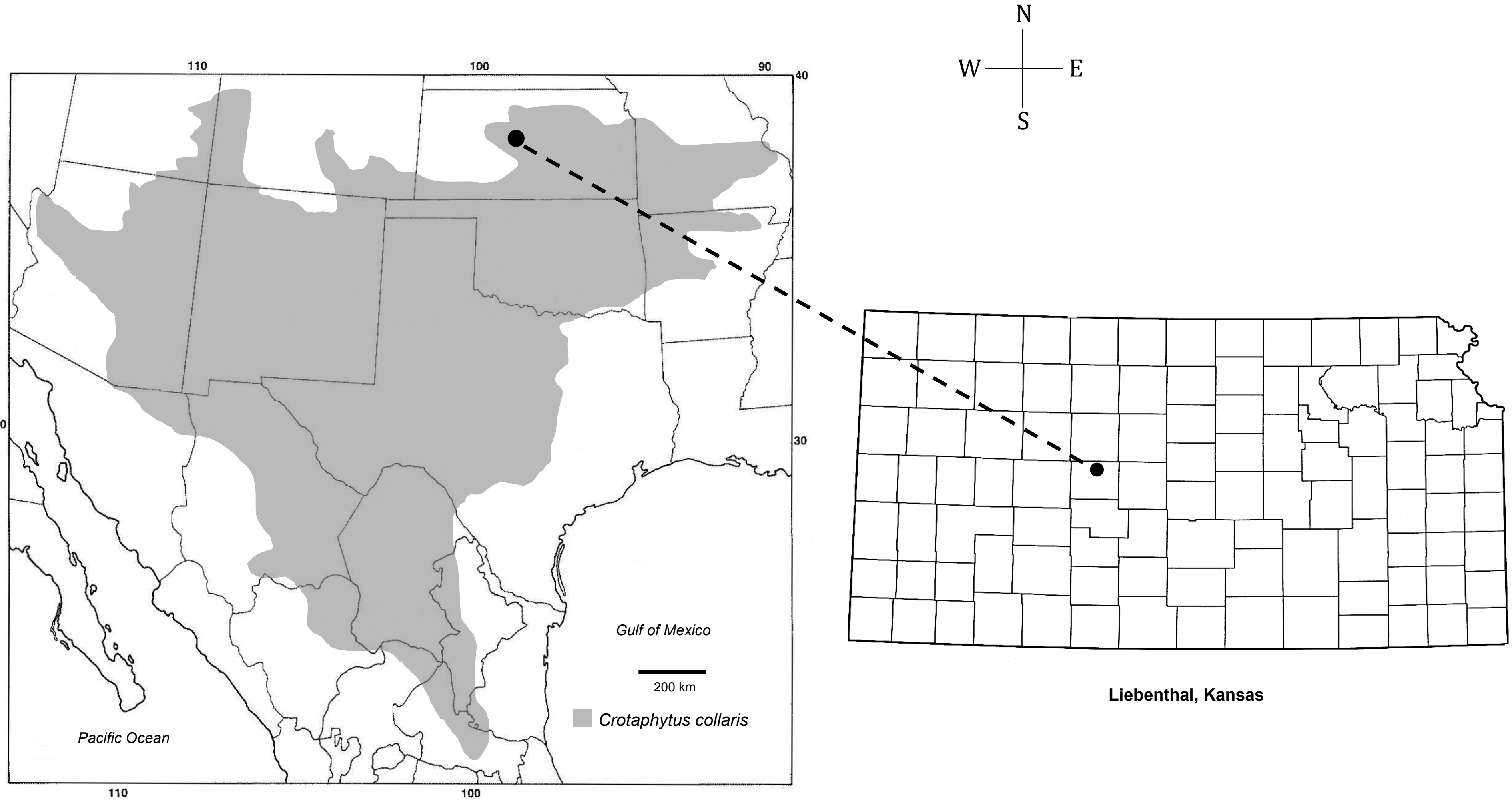


FIGURE 1.—Range map of *Crotaphytus collaris* and location of Liebenthal, KS study site. Adapted from McGuire (1996).

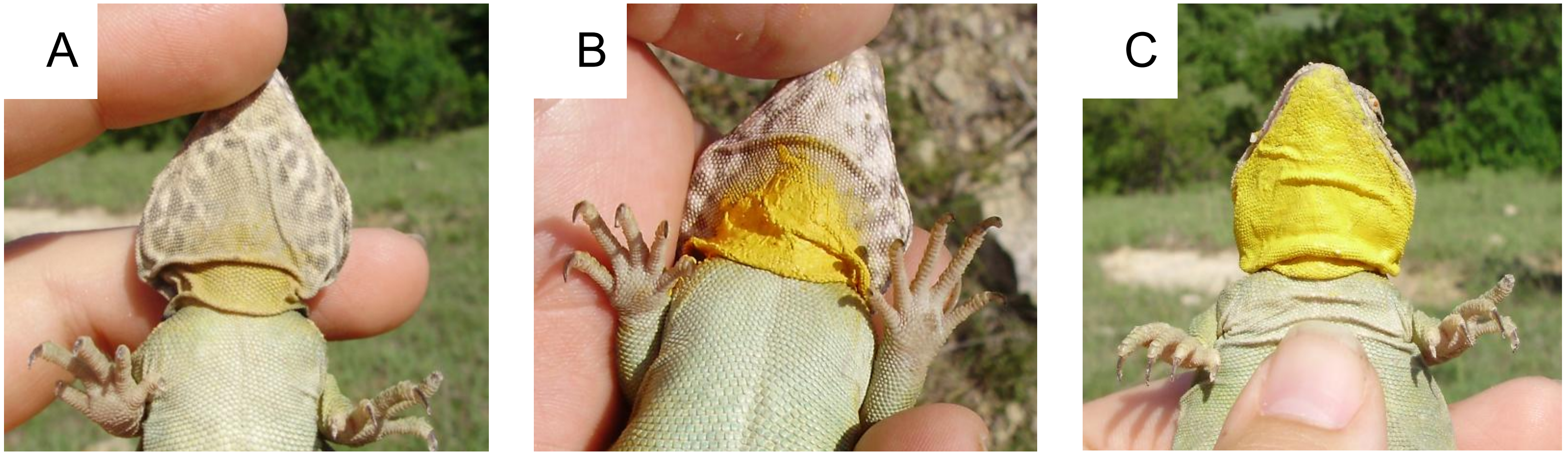


FIGURE 2.—Gular ornaments in males from 2011 in the Liebenthal, KS population of *Crotaphytus collaris*; (a) unmanipulated male, (b) male painted as control, and (c) male with an experimentally enlarged ornament.

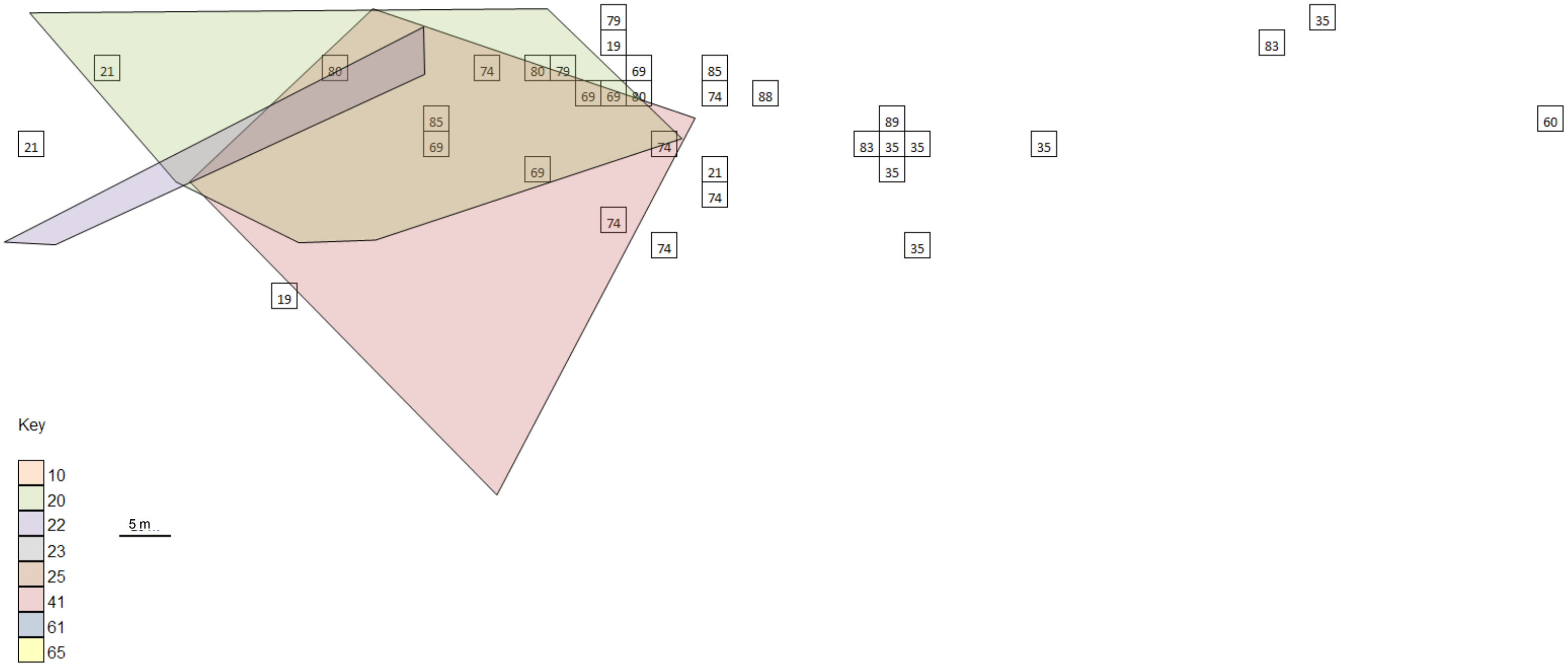
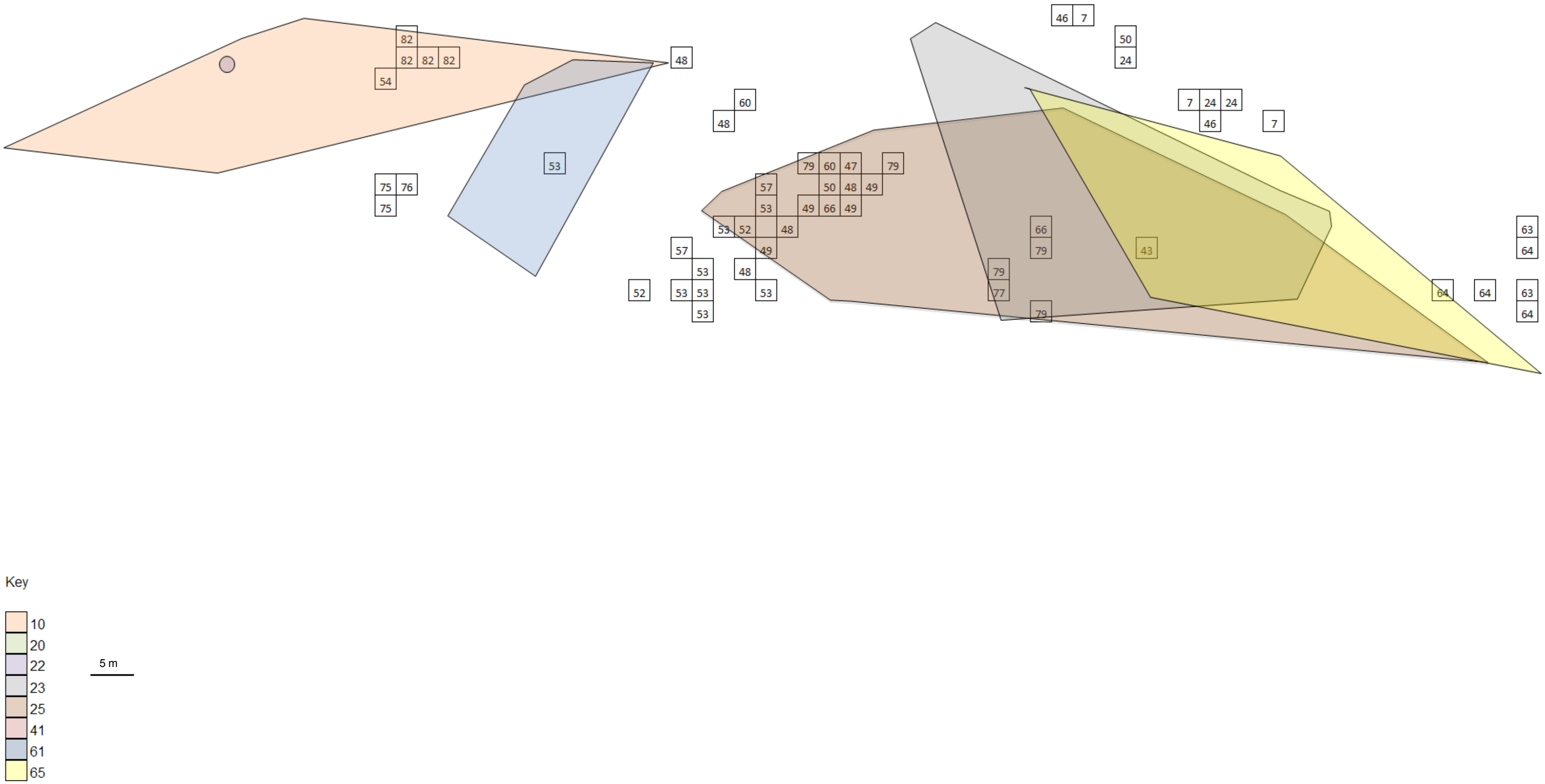


FIGURE 3.—Territory maps of experimental males and observed locations of accessible females in the Liebenthal, KS population of *Crotaphytus collaris*. Polygons represent male territories, and open squares represent observed locations of females. Numbers in open squares indicate individual female identity; the numbers adjacent to colored boxes in the key, which correspond to polygon colors, indicate individual male identity.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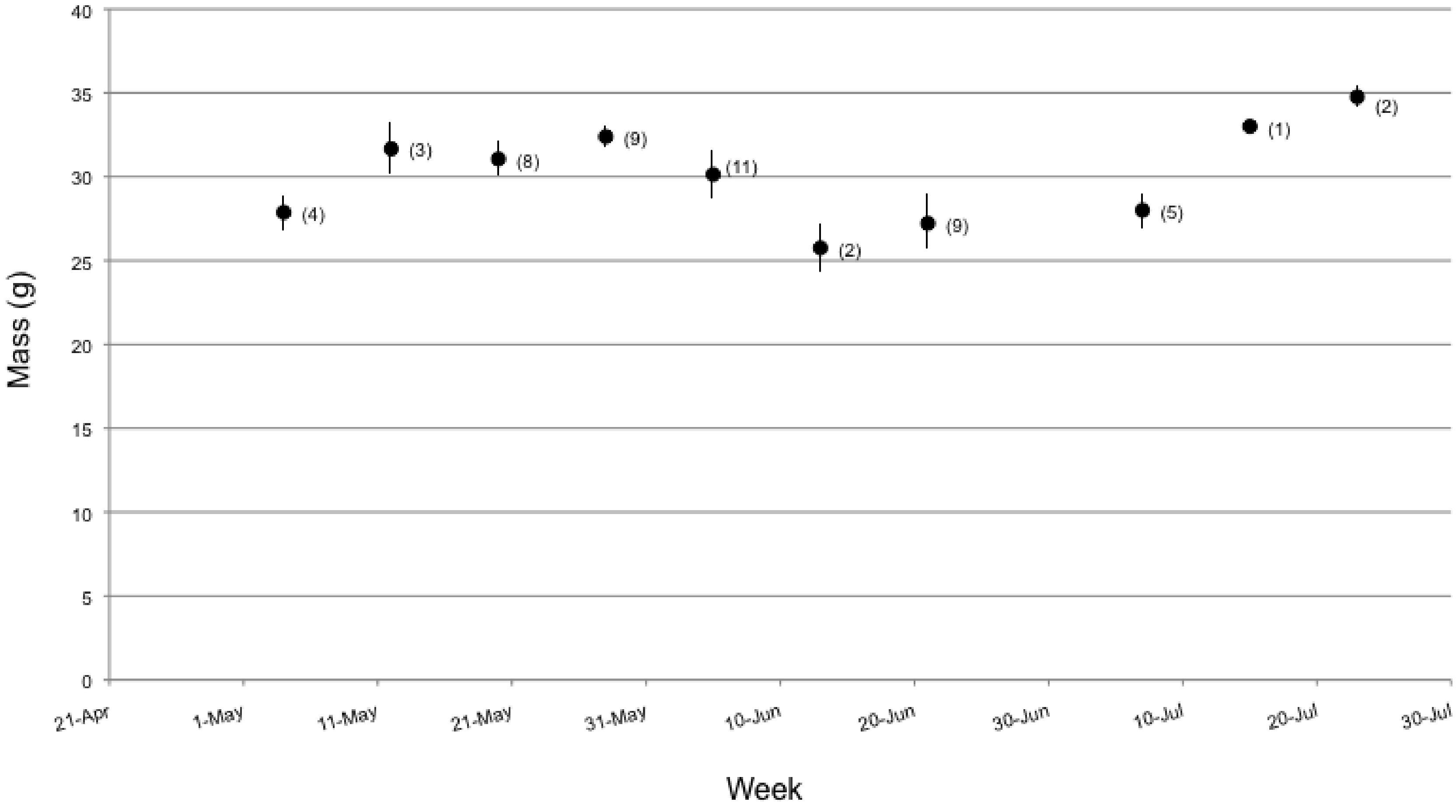

FIGURE 4.—Mean mass ± 1 SE calculated each week for sexually mature females captured between 4 May and 23 July 2011 in the Liebenthal, KS population of *Crotaphytus collaris*. No data are available for the week of 30 June. Sample sizes are in parentheses.