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Orange ornamentation increases sex-specific conspicuousness of juvenile males to conspecifics and predators

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ABSTRACT

Many animal species have evolved striking colour patterns that attract the opposite sex and intimidate rivals. Although conspicuous coloration is usually restricted to adults in the context of reproduction, this is not always the case. Juvenile collared lizards (*Crotaphytus collaris*) are sexually dichromatic, wherein males exhibit 'dorsolateral bars' that are bright orange and showy, whereas females are light tan and inconspicuous. Given that adult male collared lizards suffer increased predation because of bright adult coloration, we hypothesized that juvenile males might also be more detectable to predators owing to the conspicuousness of their dorsolateral bars. To test this hypothesis, we measured the reflectance of the dorsolateral bars, non-bar background body regions, and the rocky habitat in which the lizards live. We modelled the vision of our study species and its dominant predators to quantify and compare statistically the contrasts of male and female dorsolateral bars against the natural rock background. We also calculated lizard survivorship over a 4 year study period. We found that male orange bars exhibited significantly higher chromatic contrast, but significantly lower achromatic contrast, than female bars when perceived through all visual models. However, the dorsolateral background colour of juvenile males and females did not differ significantly in chromatic or achromatic contrast from rocks in any visual model. Female lizards survived better than male lizards to the yearling (reproductive) stage. Our findings indicate that juvenile male bars are conspicuous both to conspecifics and to predators and that the bars probably increase predation on juvenile males.

Keywords: achromatic contrast; chromatic contrast; coloration; prey detection; reptile; vision; visual modelling

INTRODUCTION

Conspicuous coloration in animals can be used to attract mates, secure resources, and deter rivals via sexual selection (Andersson 1994), but maintaining these conspicuous signals can be costly. For carotenoid-dependent, conspicuous colour traits, early hypotheses proposed that the greatest cost can be in locating and securing food with abundant carotenoids, because animals cannot synthesize these pigments (Endler 1980, McGraw and Ardia 2003, Svensson and Wong 2011, Hill *et al.* 2023). Current literature suggests that this cost is not attributable to securing carotenoids in food, but instead being able to produce the carotenoid ornamentation through cellular processes (Hill *et al.* 2023). For other conspicuous colour traits, sometimes the cost is in finding a sufficient amount of food to supply the energy needed to produce the traits (Hill 2000, Scheuber *et al.* 2003, Barnett and Briskie 2007, Somjee 2021). Often, however, the leading cost will be increased predation risk from exhibiting the conspicuous trait (Magnhagen 1991, Zuk and Kolluru 1998, Montgomerie *et al.* 2001, Macedonia *et al.* 2002, Godin and McDonough 2003, Stuart-Fox *et al.* 2003, Husak *et al.* 2006, Ruiz-Rodríguez *et al.* 2013, Torres *et al.* 2021, Banfi *et al.* 2023).

In many cases, males have evolved colourful traits that attract females and that are selected through female mate choice, i.e. intersexual selection (Darwin 1871, Andersson 1994). Male–male competition can also be a driving force in the evolution of conspicuous coloration, which males can use to repel reproductive rivals or to secure better territories with resources that grant them access to females, i.e. intrasexual selection (Andersson 1994, Charles and Ord 2012). Importantly, the benefits of conspicuous coloration must outweigh its costs over the lifetime of

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the individual. Generally, natural selection favours cryptic over conspicuous coloration (Endler 1978, 1980, 1991, Slagsvold *et al.* 1995, Husak *et al.* 2006). Despite this fact, drivers other than sexual selection can underlie the appearance and maintenance of non-cryptic coloration (e.g. latitude, Karubian 2013; habitat, Medina *et al.* 2017). For example, Cain *et al.* (2019) used three-dimensional printed models of fairy wrens to demonstrate that dull-coloured models were attacked at a rate similar to conspicuously coloured models in a closed habitat, whereas in an open habitat, models of females (both dull and conspicuous) had a higher rate of predation than models of conspicuous males. The authors suggest that this lack of bias in predator attack towards conspicuous plumage could result from a complex interaction between conspicuousness against particular backgrounds, sex-specific vigilance, and predator behaviour. This idea shares some features with the unprofitable prey hypothesis for conspicuous bird plumage, which predicts that predators will avoid conspicuous prey because conspicuousness advertises prey unprofitability and should shift predation pressure to more cryptic individuals (Baker and Parker 1979). Like the unprofitable prey hypothesis for birds, some lizards (and other taxa) demonstrate their unprofitability by presenting pursuit deterrent signals that alert the predator to the readiness of the animal and its competency to escape (Hasson *et al.* 1989, Cresswell 1994, Clark 2005, Font *et al.* 2012, York and Baird 2016). Alternatively, other lizard species use conspicuous traits and colourful expendable tails to direct predator attacks away from vital parts of the body, thus allowing for escape (Castilla *et al.* 1999, Bateman and Fleming 2009, Murali and Kodandaramaiah 2016). Lastly, aposematic species, found in a variety of taxa, use conspicuous coloration to advertise their toxicity or harmfulness to deter predation (Blount *et al.* 2009, Summer *et al.* 2015). Regardless of the particular functions that conspicuous coloration can serve in interactions with predators, predation frequently is an important selective force in the evolution of colour signals in prey.

In the genus *Crotaphytus* Holbrook, 1842, various species possess both sexually dimorphic and dichromatic traits, with adult males being larger and more colourful (McGuire 1996). In *Crotaphytus collaris* Say, 1822, adult males use their exaggerated traits in displays to defend territories against other males and to secure mating opportunities (Baird *et al.* 1997, Husak 2004, Baird 2013). However, male coloration in some *Crotaphytus* species has been shown to increase their conspicuousness to predators (Husak *et al.* 2006, Macedonia *et al.* 2009).

Interestingly, juvenile male collared lizards also possess a sex-specific trait in the form of conspicuous dorsolateral orange bars (Fig. 1A), which juvenile females lack (McGuire 1996). In male *C. collaris*, the orange bars are lost upon reaching sexual maturity, when males begin to develop their adult blue–green coloration (Fox *et al.* 2020). Juvenile females have similar dorsolateral bar patterns, but the bars are a light, inconspicuous tan colour (female tan bars; Fig. 1B). Fox *et al.* (2020) hypothesized that the male orange bars are favoured via a form of precocial sexual selection. In this context, dorsolateral orange bars offer an early advantage to juvenile males by helping them: (i) to secure territories that later expand into breeding territories; and (ii) to attain pair bonds with nearby juvenile females that are retained into adulthood. In the present work, we offer findings that further our understanding of how predation pressure relates to the presence of male orange bars and female tan bars.

Our goal was to quantify the conspicuousness of juvenile male collared lizard orange bars against a natural background and to determine whether there is a difference in survivorship of juvenile males and females. Given that juvenile males present different sexually selected conspicuous traits than do adult males, and do so at a different time of the year, we wanted to learn whether the same potential predation pressures exist for juveniles as for adults. We addressed this question in two ways. First, we modelled reflectance spectra of the juvenile male orange bars and female tan bars using the visual systems of Eastern collared lizards (*C. collaris*) and those of relevant snake and avian predators. We predicted that juvenile male orange bars would be significantly more conspicuous against a natural background than would female tan bars when viewed through the eyes of conspecifics and predators. Second, we calculated the survivorship of male and female lizards captured over a previous 4 year time span on an adjacent study site. Here, we predicted that juvenile male survivorship would be lower than that of juvenile females over the sampling period.

MATERIALS AND METHODS

Measuring lizard and visual background reflectance

The study took place between August and October of 2019. We captured juvenile male and female collared lizards from the Sooner Lake dam of the Oklahoma Gas and Electric Sooner Generating Station in Pawnee County, OK, USA. We used a telescoping fibreglass pole and monofilament noose to capture lizards that were found along the concrete and stone embankment of the dam. Because these lizards had been used in a previous study, we used toe clips to identify individuals and prevent using the same lizard twice in our study. Given that male lizards achieve maximal dorsolateral bar development at a snout–vent length of 58–81 mm (Crosby 2015), we collected lizards only within that size range. We brought the captured lizards back to Oklahoma State University to measure spectral reflectance of the dorsolateral bars and body background coloration (body coloration adjacent to dorsolateral bars). After acclimating a lizard in a 37.9 L tank under a heat lamp for ≥1 h to raise body temperature to a typical range found in the field (35–40°C), we used a UV-VIS spectrometer (USB 4000, Ocean Optics), a deuterium-halogen light source (DH-2000-BAL, Ocean Optics), a reflectance probe (QR400-7-SR-BX, Ocean Optics), and SpectraSuite software (Ocean Optics) to collect the spectral reflectance data. We equipped the probe with an opaque hollow tube to standardize measurements from a 2-mm-diameter target at an angle of 90° and 7 mm from the surface. We took reflectance measurements of both the dorsolateral bars and the body background coloration adjacent to the bars on the right side of each lizard. Beginning with the dorsolateral bar nearest the collar, we measured reflectance at the widest point of the bar and continued caudally until we had measured three consecutive bars. We then took readings of body background reflectance, starting caudal to the first bar and repeating this measurement for the second and third bars while remaining centrally located between the two nearest bars. Several lizards (three males and 10 females) did not

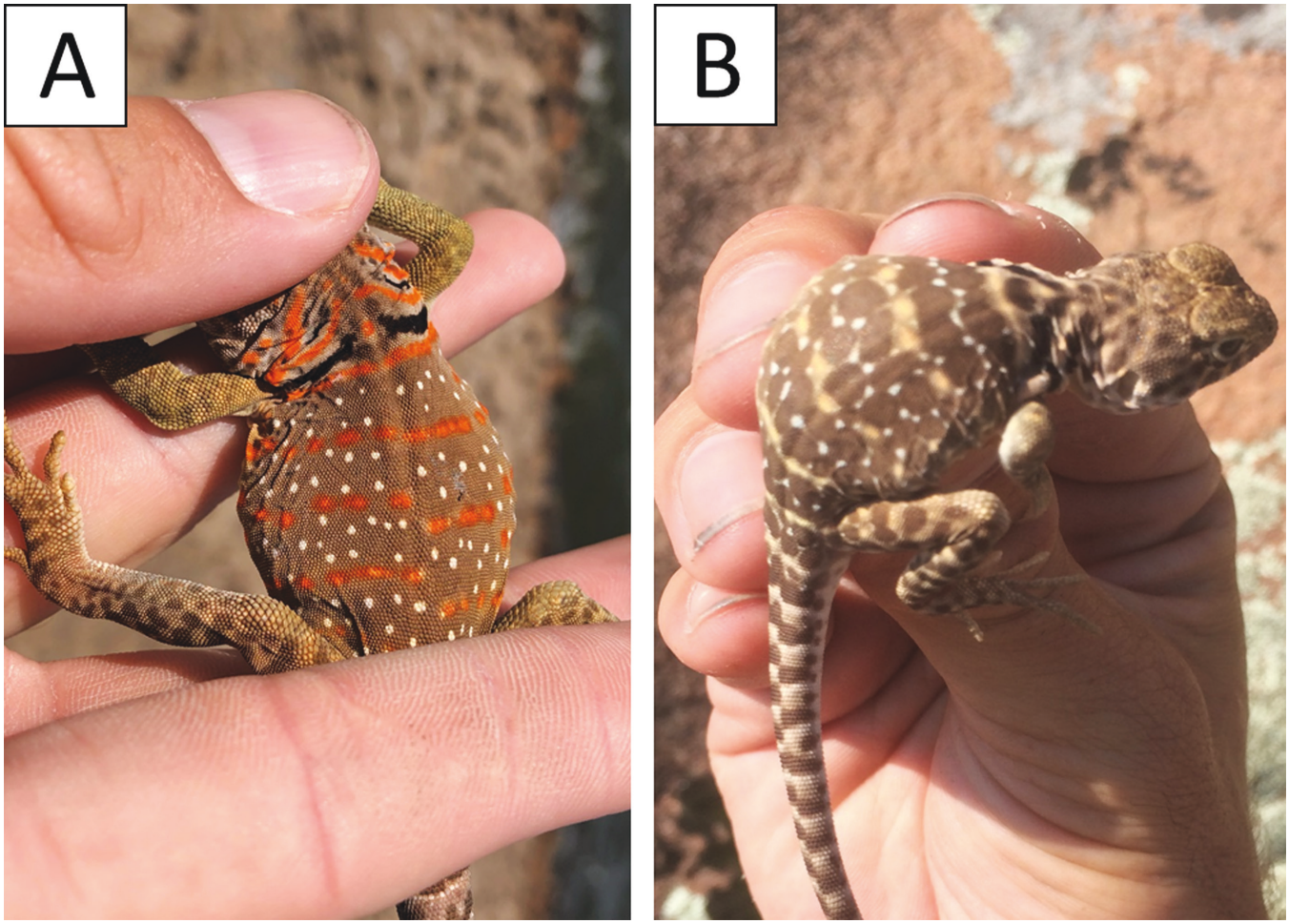


Figure 1. Photographs of juvenile male and female collared lizards, showing differences in dorsolateral bars. The male (A) has conspicuous orange dorsolateral bars, whereas the female (B) has inconspicuous tan dorsolateral bars.

have their body background reflectance recorded because we added this measurement after the study had begun. Reflectance spectra were also gathered from a sample of 20 large rocks collected from our study area. The study area harbours little vegetation, and the lizards spend most of their time on top of the rocks in direct sunlight. Rocks at the dam therefore constitute the relevant visual background for the collared lizards and their potential snake and avian predators.

Visual modelling

Photoreceptors of most vertebrates contain two types of light-sensitive cells: a single class of rods for vision in dim light and two or more classes of cones for colour perception. Each cone class possesses a unique visual pigment that absorbs light over a specific range of wavelengths (Loew *et al.* 2002). Luminance perception (achromatic vision) is achieved typically by a cone class that contains a long-wavelength-sensitive (LWS) visual pigment, whereas overlap between the absorption spectra of different cone classes provides the basic mechanism for colour discrimination (Osorio and Vorobyev 2005). Generally speaking, as the number of cone classes increases, so does the diversity of colours that can be perceived (Osorio and Vorobyev 2008).

Birds and non-avian reptiles exhibit four classes of single cones that are categorized by their wavelength region of peak absorption. In lizards, these photoreceptors include ultraviolet-wavelength-sensitive (UVS), short-wavelength-sensitive (SWS), middle-wavelength-sensitive (MWS), and LWS cones (Loew *et al.* 2002, Macedonia *et al.* 2009). Each cone also possesses an oil droplet which, with the exception of an optically transparent droplet in the UVS cone, acts as a long-pass cut filter by absorbing shorter wavelengths. Although this absorption of light reduces absolute photoreceptor sensitivity, it also narrows the absorption spectrum of each cone, reduces overlap between adjacent cone sensitivities, and can shift peak absorption to longer wavelengths (Loew *et al.* 2002). The most important functional effects of oil droplet filtering are an increase in colour discrimination, in addition to enhanced colour constancy across illumination conditions (Hart 2001, Vorobyev 2003).

Many avian taxa exhibit violet-sensitive (VS) cones rather than UVS cones. Methylation-specific PCR and opsin sequencing data (Ödeen and Håstad 2013) indicate that VS cones are ancestral for Aves (Hart and Hunt 2007) and that all raptors (Accipitridae and Falconidae) exhibit VS cones. The UVS and VS cones are homologues that contain the same SWS1 opsin (Lind *et al.* 2013, Ödeen and Håstad 2013, Toomey and Corbo 2017), and we refer to the two types collectively as SWS1 cones. As a rule, birds and non-avian reptiles also possess double cones for perception of luminance that contain the LWS pigment

in both members of the cone pair. In birds and diurnal lizards, the principal member of a double cone pair typically possesses an oil droplet with a shorter-wavelength cut-off than the single LWS cones, the effect of which broadens the absorption range of the double cones (Bowmaker *et al.* 1997, Osorio and Vorobyev 2005, Toomey and Corbo 2017). In contrast to non-raptorial birds, most raptor species studied to date (including the species used for our visual model) lack double cones (Mitkus *et al.* 2017, Perez-Martinez *et al.* 2020).

We generated Gaussian visual pigment absorptance curves using the peak absorptance (λ_{max}) value for each class of single cones and the photoreceptor template equations of Govardovskii *et al.* (2000). We then used the oil droplet template of Hart and Vorobyev (2005) to calculate cone oil droplet transmittance in our lizard and raptor visual models (snake photoreceptors do not possess oil droplets; Sillman *et al.* 1997, Simões *et al.* 2015). The reflectance spectra obtained from our lizard subjects, in addition to the rocks that constitute their visual background, exhibit very low UV reflectance (~5–8% from 330 to 700 nm). We therefore followed Fleishman *et al.* (2016a) in omitting UVS cones from our lizard and snake visual models and restricted our analyses of chromatic (i.e. colour) and achromatic (i.e. luminance or brightness) contrast to 400–700 nm. Likewise, we omitted the homologous VS cone from calculations in our raptor visual model, because ~40% of the absorptance by this cone from 330 to 700 nm lies in the UV (Lind *et al.* 2013). Figure 2 shows the reflectance spectra (400–700 nm) of juvenile male and female dorsolateral bars and dorsal backgrounds, in addition to the rocks that constitute the visual background.

Lizard visual model

Our lizard visual model, the Eastern collared lizard (*C. collaris*), possesses a pure cone retina with four classes of single cones and a double cone (E. R. Loew, pers. comm.). Spectral sensitivity of individual photoreceptors and oil droplets in *C. collaris* was determined with microspectrophotometry (MSP) and is virtually identical to that of *Crotaphytus dickersonae* Schmidt, 1922 (see Macedonia *et al.* 2009), with mean λ_{max} values for each

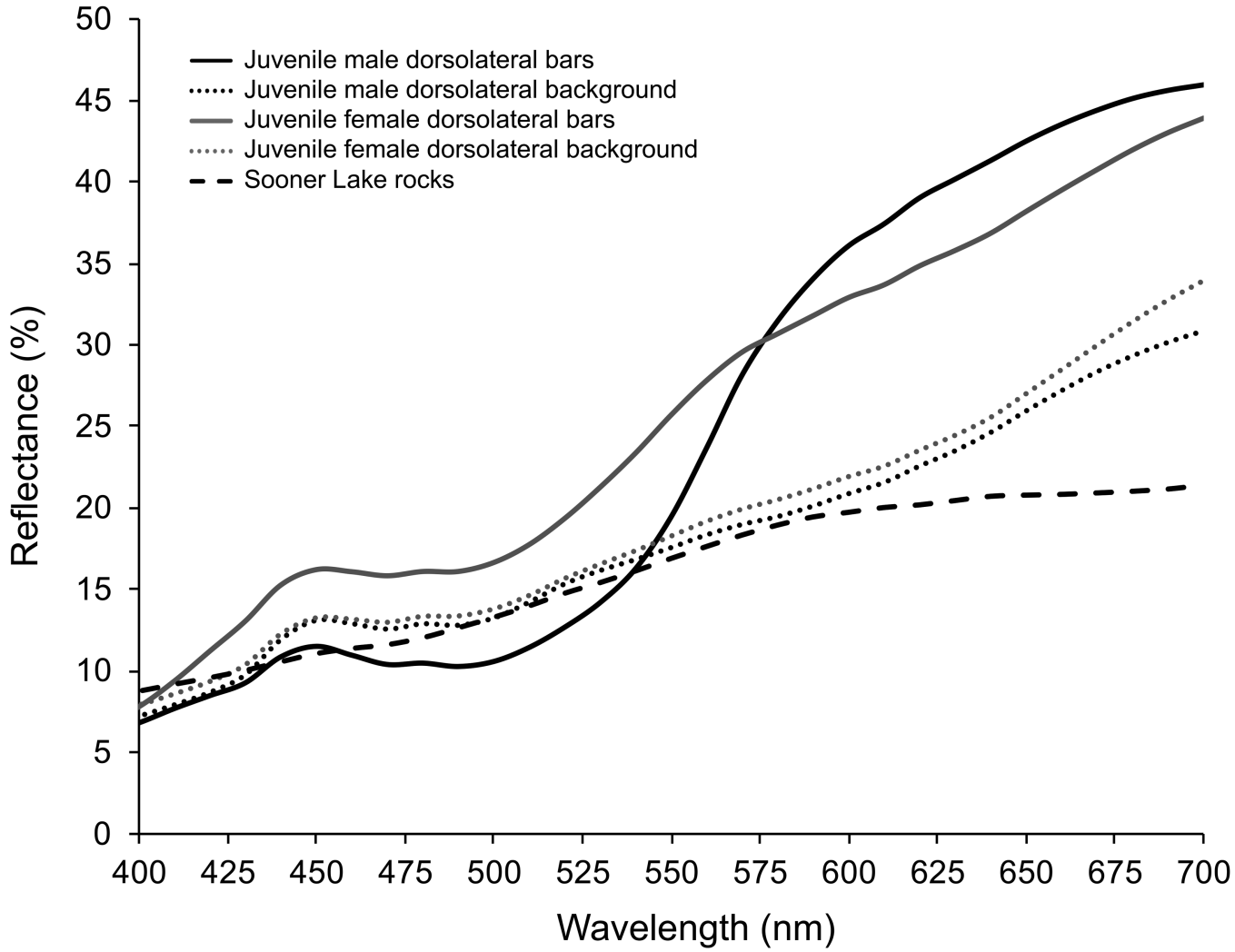


Figure 2. Mean reflectance spectra of juvenile *Crotaphytus collaris* and the rocks against which they are visually juxtaposed at the Sooner Lake study area. Sample sizes: male dorsolateral bars (N = 18; continuous black line), male dorsolateral background coloration (N = 15; dotted black line), female dorsolateral bars (N = 33; continuous grey line), female dorsolateral background coloration (N = 23; dotted grey line), and Sooner Lake rocks (N = 20; dashed black line).

of the four cone classes differing by 0–2 nm at most between the two species (*C. collaris*: UVS = 357 nm, SWS = 459 nm, MWS = 480 nm, and LWS = 556 nm; data courtesy of E. R. Loew, Cornell University).

Snake visual model

Most diurnal snakes exhibit two classes of single cones and one class of rods, where cones usually are UVS and LWS (Sillman *et al.* 1999, Simões *et al.* 2016) but in some cases are UVS and MWS (Sillman *et al.* 1997). In contrast, our visual model, the coachwhip (*Masticophis flagellum* Shaw, 1802), possesses a pure cone retina with three cone classes: UVS, SWS, and LWS (Macedonia *et al.* 2009: their fig. 4b). The highly active diurnal coachwhip hunts both moving and sedentary prey and is the most significant ophidian predator of collared lizards where the distributions of the two reptiles overlap (Macedonia *et al.* 2002, 2009), including our study site (S. Fox and J. Agan, pers. obs.). Secor and Nagy (1994) determined in a metabolic study that about half of the coachwhip diet consisted of lizards. Spectral sensitivity in *M. flagellum* was determined with MSP from a specimen collected at Sooner Lake dam. This individual was one of two subjects whose visual pigment λ_{max} values were averaged by Macedonia *et al.* (2009: their table 2). For the Sooner Lake specimen, the λ_{max} values were UVS = 359 nm, SWS = 458 nm, and LWS = 561 nm (data courtesy of E. R. Loew, Cornell University).

Avian visual model

The terrestrial greater roadrunner (*Geococcyx californianus* Lesson, 1829) might represent the most dangerous avian predator of collared lizards at our study site (J. Husak and S. Fox, pers. obs.), but spectral sensitivity has not been determined for this species. Given the distribution of VS and UVS cones in birds (Ödeen and Håstad 2013), it is highly likely that *G. californianus* possesses a VS cone type. In the absence of *G. californianus* spectral sensitivity data, we deferred to using a raptor visual model. Although raptors might not be as important as the greater roadrunner as lizard predators at our study site, raptors are common in areas with *C. collaris* (including our study site) and have been observed preying on lizards (Trauth *et al.* 2004, Husak *et al.* 2006, Ivanyi 2009). For our raptor visual model, we used cone pigment (λ_{max}) and oil droplet absorption data for the common buzzard (*Buteo buteo* Linnaeus, 1758) presented by Lind *et al.* (2013). The common buzzard has been used in a similar maner in visually modelling avian predator threat for the Australian frilled dragon (*Chlamydosaurus kingii* Gray, 1825) (Perez-Martinez *et al.* 2020).

Human visual model

Humans possess three classes of cone photoreceptors: an LWS 'red' cone, an MWS 'green' cone, and an SWS 'blue' cone. Bowmaker and Dartnall (1980) used MSP to determine the spectral sensitivities of each cone pigment from a single human eye that was removed owing to an intraocular malignancy. Results of that study showed an LWS cone with a mean λ_{max} of 563 nm, an MWS cone with a mean λ_{max} of 534 nm, and an SWS cone with a mean λ_{max} of 420 nm. Similar MSP work by Dartnall *et al.* (1983) on seven human retinae (also removed owing to malignant tumours) revealed average peak sensitivity values for the three cones (LWS λ_{max} = 558 nm, MWS λ_{max} = 531 nm, and SWS λ_{max} = 419 nm). For simplicity, in our human visual model we use the rounded values of LWS λ_{max} = 560 nm, MWS λ_{max} = 530 nm, and SWS λ_{max} = 420 nm.

Cone quantum catch

To determine the photoreceptor output in response to a target spectrum, we calculated quantum catch for each cone class, Q_i, as:

$$Q_i = \int_{400}^{700} R(\lambda)I(\lambda)S(\lambda)d\lambda \quad (1)$$

where $R(\lambda)$ is the reflectance spectrum of the target, $I(\lambda)$ is the irradiance spectrum illuminating the target, and $S(\lambda)$ is the spectral sensitivity of a given photoreceptor class, integrated over the wavelength range of interest, $d\lambda$. To convert lizard and rock reflectance to radiance (as would be perceived by viewers in the field), each reflectance spectrum was multiplied by a mean (N = 3) downwelling irradiance spectrum measured previously with an irradiance probe under clear skies in an open location (near Punta Chueca, Sonora, Mexico: for equipment, procedural details, and conversion of raw spectra to units appropriate for vision, see the methods and fig. 3a in the paper by Macedonia *et al.* 2009). We chose to calculate radiance from reflectance and irradiance rather than measuring it directly in the field to tightly control the lighting conditions in which we gathered spectral data for this study. We then simplified our lizard and rock radiance spectra for contrast calculations by extracting intensity values at 10 nm intervals from 400 to 700 nm (total of 30 values).

Before determining the response of a visual model to a calculated radiance input (dorsolateral bars, body background coloration, or rocks), we accounted for chromatic adaptation of the eye to the visual background as:

$$k_i = 1/\int_{400}^{700} A(\lambda)S_i(\lambda)d\lambda \quad (2)$$

where $A(\lambda)$ is the adapting spectrum (rock radiance) and $S(\lambda)$ is the spectral sensitivity of a given photoreceptor class. The response of each cone class in a visual model to a radiance input can then be summarized as q_i, where $q_i = k_i Q_i$. Our mathematical operations were performed in the following sequence. First, the spectral sensitivity of each cone class was multiplied by the adapting spectrum, and the outputs were summed within each class. Second, we calculated the von Kries correction (Fleishman *et al.* 2016a, b) for the visual response to the adapting spectrum as one divided by the sum of each cone class output (i.e. equation 2). When multiplied by this quotient, the summed output of each cone class equals one, thereby satisfying the assumption that the neural stimulation of each cone class is equal in response to a 'white' stimulus (Fleishman and Persons 2001, Fleishman *et al.* 2016a, b). Third, given that chromatic contrast is computed using cone output proportions, the relative output of each cone class was calculated by dividing the von Kries-corrected sum of each cone class output by the combined sum of the cone class outputs. For example, in a visual model with four outputs (each summing to one when von Kries corrected), each proportional output is 0.25.

Two different modelling approaches are frequently used to estimate colour perception in animals: the receptor noise model (Vorobyev and Osorio 1998) and the Euclidean distance model (Endler and Mielke 2005). In our study, we used the simpler Euclidean distance method. Fleishman *et al.* (2016a) have shown that the two approaches produce equivalent results, and the Euclidean distance approach is preferable when the ratios of different types of cones are uncertain, as is the case for some of our visual models.

Chromatic contrast calculations

For each subject, we calculated the chromatic contrast (CC) as the Euclidean distance between the targets (e.g. dorsolateral bar or body background radiance proportional cone output) and the visual background (rock radiance mean proportional output). For example, in a tetrachromatic visual model Euclidean distance is calculated as:

$$\mathrm{CC} = \sqrt{\begin{array}{l}(W_\mathrm{a} - W_\mathrm{b})^2 + (X_\mathrm{a} - X_\mathrm{b})^2 \\ +(Y_\mathrm{a} - Y_\mathrm{b})^2 + (Z_\mathrm{a} - Z_\mathrm{b})^2\end{array}} \quad (3)$$

where W is the UVS–VS (SWS1) cone, X is the SWS cone, Y is the MWS cone, and Z is the LWS cone. Our omission of the SWS1 cone (see above) simplifies the tetrachromatic model to three terms for our tetrachromats (*C. collaris* and *B. buteo*) and two terms for our trichromats (*M. flagellum* and *H. sapiens*). The subscript 'a' represents the proportional cone output of the target spectrum, and subscript 'b' represents the proportional cone output of the visual background spectrum.

Achromatic contrast calculations

Given that we lacked sufficient data for *M. flagellum* to use double cones in calculating achromatic contrast (AC) for the snake visual model, and because our raptor visual model (*B. buteo*) and human foveae lack double cones, we followed Perez-Martinez *et al.* (2020) in summing only outputs of single cones to calculate achromatic contrast. This quantity was calculated for each subject in each visual model as the mathematical difference between the perceived luminance of dorsolateral bar (or body background) radiance and the perceived luminance of rock radiance, divided by the sum of these two quantities:

$$\begin{aligned}\mathrm{AC_{DB}} &= (\mathrm{DB} - R) \,/\, (\mathrm{DB} + R) \quad \text{or } \mathrm{AC_{Back}} \\ &= (\mathrm{Back} - R) \,/\, (\mathrm{Back} + R)\end{aligned} \quad (4)$$

where 'DB' is dorsolateral bar radiance, 'Back' is dorsolateral background radiance, and '*R*' is rock radiance. In a visual model, positive values result when the target is perceived as being brighter than the rock background, and negative values result when the target is perceived as being darker than the rock background.

Statistical comparison of contrast between lizard body coloration and rocks

Preliminary data exploration (SPSS v.21) revealed that our data distributions (grouped by sex and visual model) for chromatic contrast exhibited significant unequal variance in Levene's tests. $\mathrm{Log_{10}}$-transformation of the data alleviated the problem of unequal variance, but Shapiro–Wilk tests showed that several distributions were non-normal. We therefore used Mann–Whitney *U*-tests for between-sex, within-visual-model comparisons of contrasts between dorsolateral bars (and body background coloration) against the visual background of rocks.

Survivorship

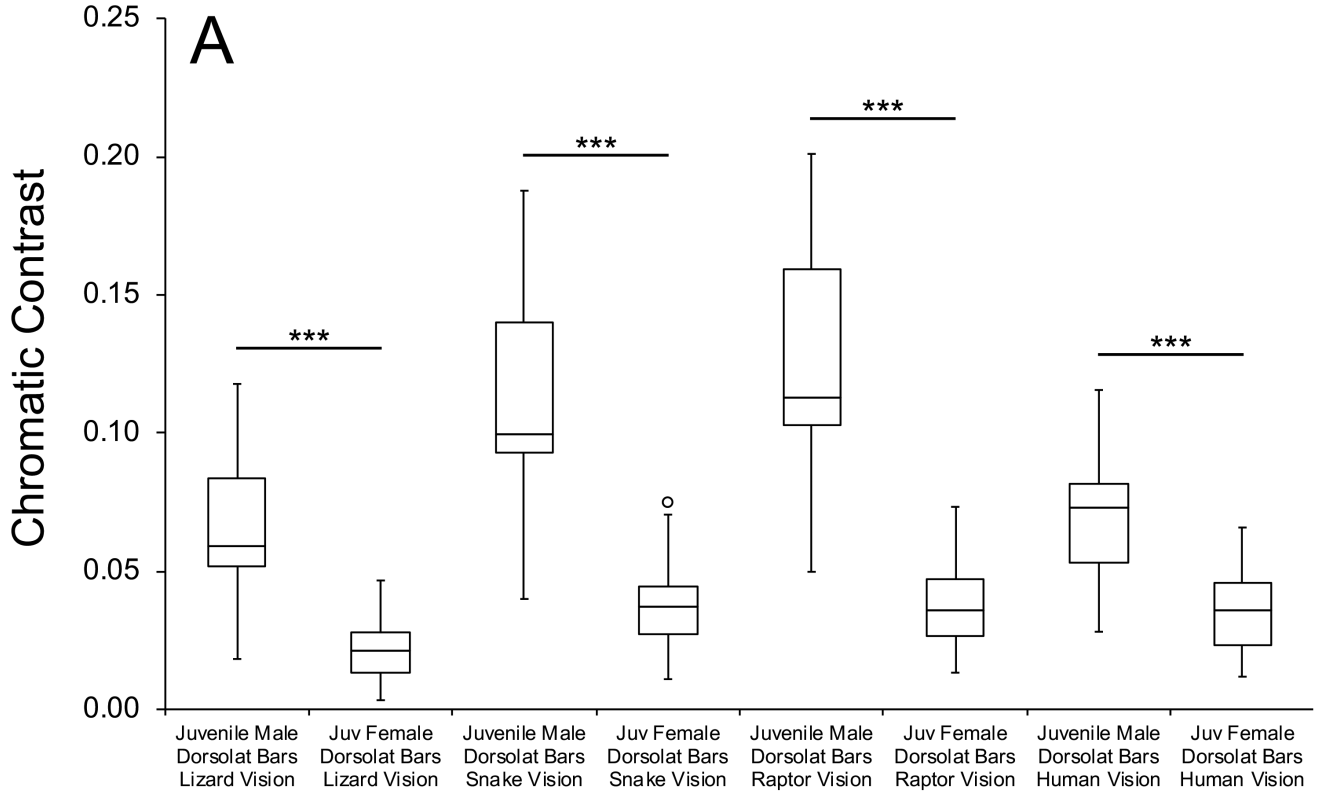
We used lizard data collected in a separate study at an adjacent site to analyse survivorship. Because we captured every lizard at our study site in the autumn as a juvenile and again in the next and subsequent spring/summer seasons, we were able to measure the survival of male and female lizards to the yearling (reproductive) stage directly. We classified as juveniles those subjects that hatched and were then active between August and November. Yearling lizards were those that emerged from brumation in early spring following the juvenile stage until they started brumation again in late summer to early autumn. Given that these lizards were used in a separate study that compared the male bar expression and lizard aggression by modifying how strongly the male bars and aggression were expressed, we initially tested to see whether these treatments had any impact on survival. All control and treatment lizards received a 2.5 mm Silastic implant that was either blank or contained 2.5 mg of dihydrotestosterone to increase lizard aggression (Agan 2021). Implants were placed using the same methods to insert larger passive integrated transponder tags, a procedure viewed as relatively safe for small amphibians and reptiles (Ott and Scott 1999, Le Galliard *et al.* 2011, Vesy *et al.* 2021). Given that implants were found to be safe for pilot lizards (Crosby 2015), receiving the implants was not likely to impact survival. Among treatment and control groups, male lizards did not survive differentially to the yearling stage (Pearson's χ^2 test; $\chi^2 = 0.974$, d.f. = 3, $P > 0.05$, total $N = 163$). Given the lack of significant differences in survivorship among treatment and control male lizards (females were untreated), we calculated survivorship between the sexes in R (R Core Team, 2019) as the number of individuals that survived to reproductive age (yearling stage). We used Pearson's χ^2 test to determine whether sex had a significant impact on survivorship.

RESULTS

Colour contrast of collared lizard dorsolateral bars and body background against rocks

In our four visual models, juvenile male dorsolateral bars are perceived as having significantly greater chromatic contrast with rocks than are juvenile female dorsolateral bars (Mann–Whitney *U* range = 6–59, $P < .001$ in all cases; Fig. 3A). Conversely, juvenile male dorsolateral bars are perceived as having significantly less achromatic contrast with rocks than juvenile female dorsolateral bars in all our visual models (Mann–Whitney *U* range = 102–186, *P*-value range: <.001–.029; Fig. 3B).

In comparison, juvenile male and female dorsolateral body backgrounds are not perceived as having significantly different chromatic contrast with rocks in any of our visual models (Mann–Whitney *U* range = 145–163, *P*-value range: .418–.787; Fig. 4A). Likewise, juvenile male and female dorsolateral body backgrounds are not perceived as having significantly different achromatic contrast with rocks in our four visual models (Mann–Whitney *U* range = 139–147, *P*-value range: .322–.453; Fig. 4B).



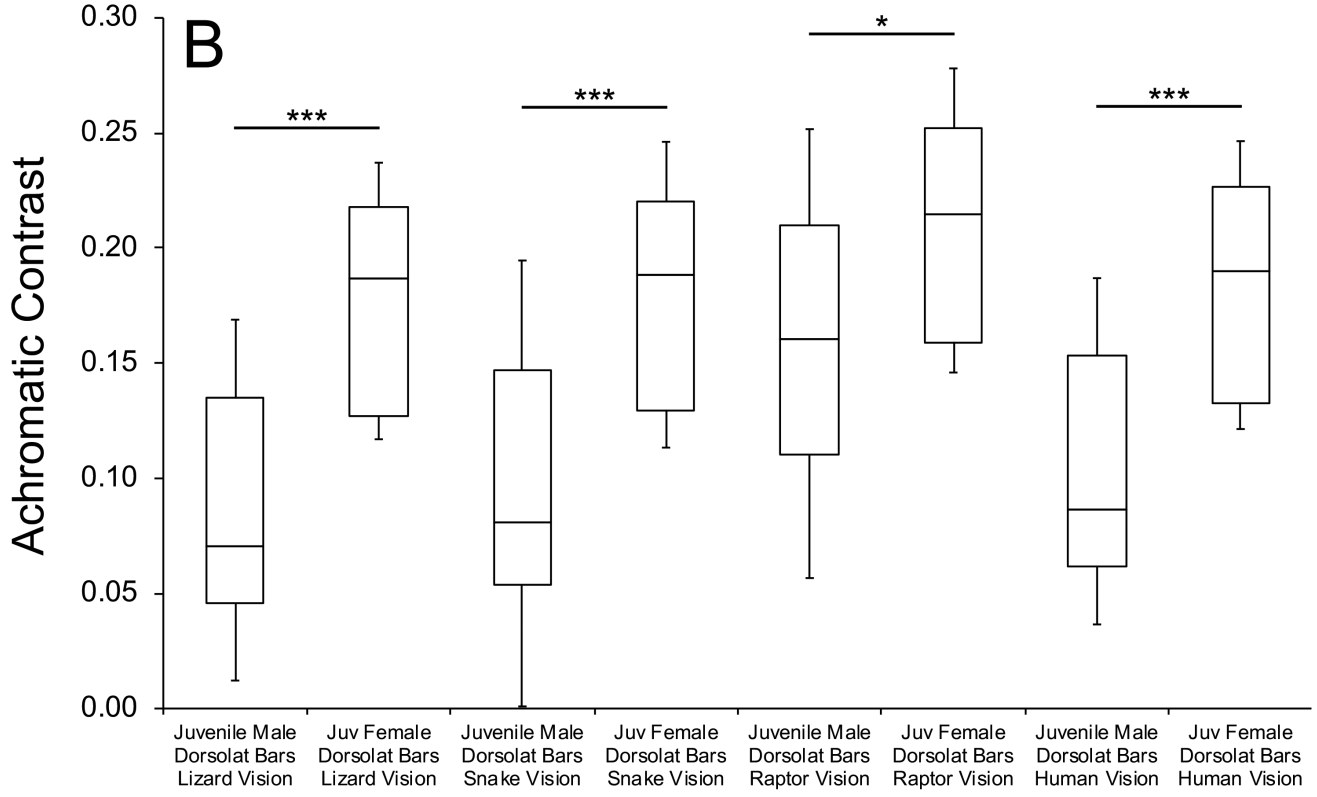


Figure 3. Box plots of chromatic (A) and achromatic (B) contrasts between juvenile dorsolateral bars and rocks. In each box, the central 50% of the data [i.e. the interquartile range (IQR)] are contained inside the box, and the horizontal line depicts the median. The end caps of the error bars are shown at the first quartile minus 1.5 IQR and the third quartile plus 1.5 IQR. Outliers are depicted as open circles. One outlier is not shown for achromatic contrast of juvenile male dorsolateral bars: lizard vision (−0.1). *$P < .05$; ***$P < .001$.

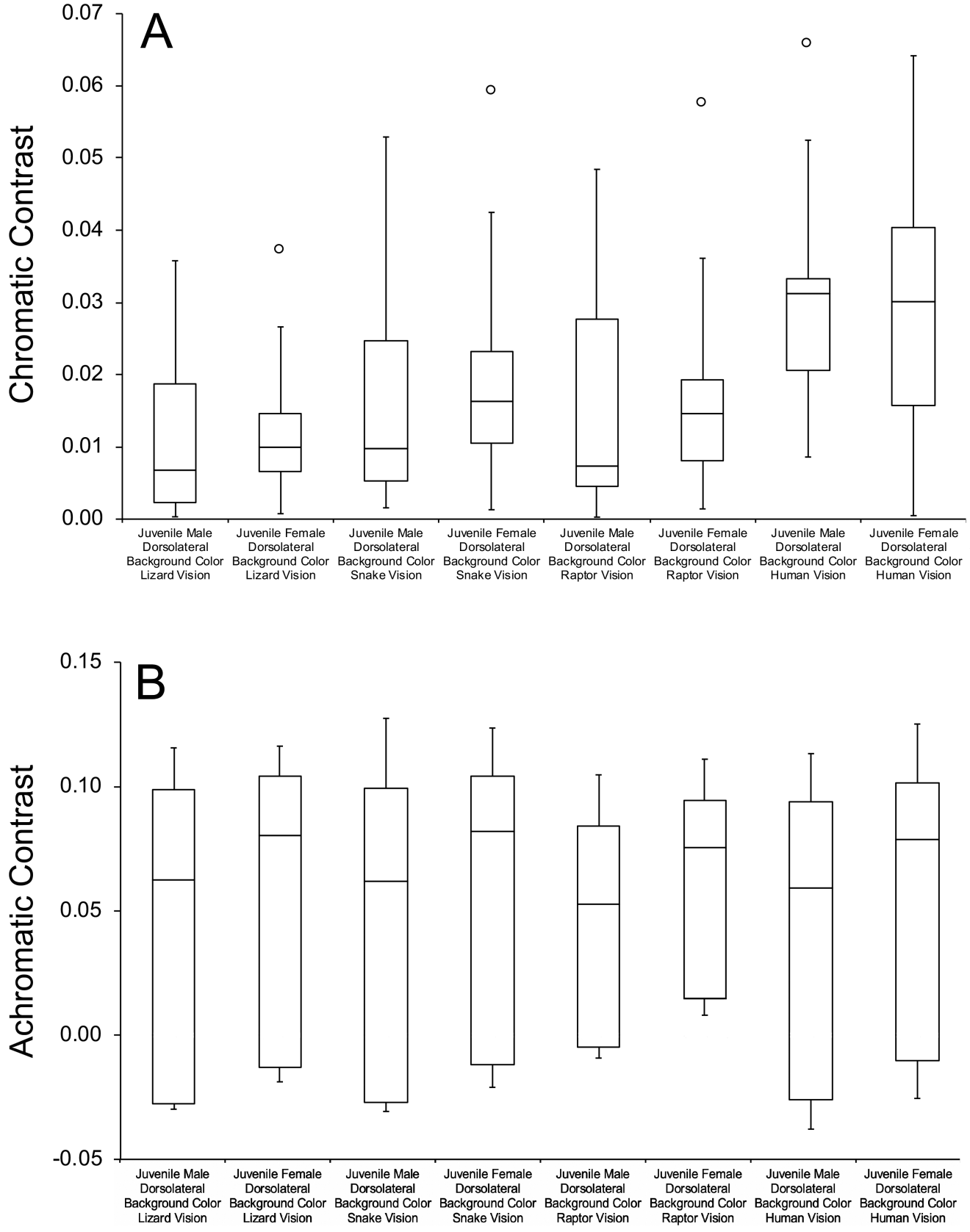


Figure 4. Box plots of chromatic (A) and achromatic (B) contrasts between juvenile dorsolateral background coloration and rocks. Three outliers are not shown for achromatic contrast of juvenile female dorsolateral background colour: raptor vision (0.21 and −0.16) and human vision (−0.17). Legend is as in Figure 3. No comparisons were statistically significant.

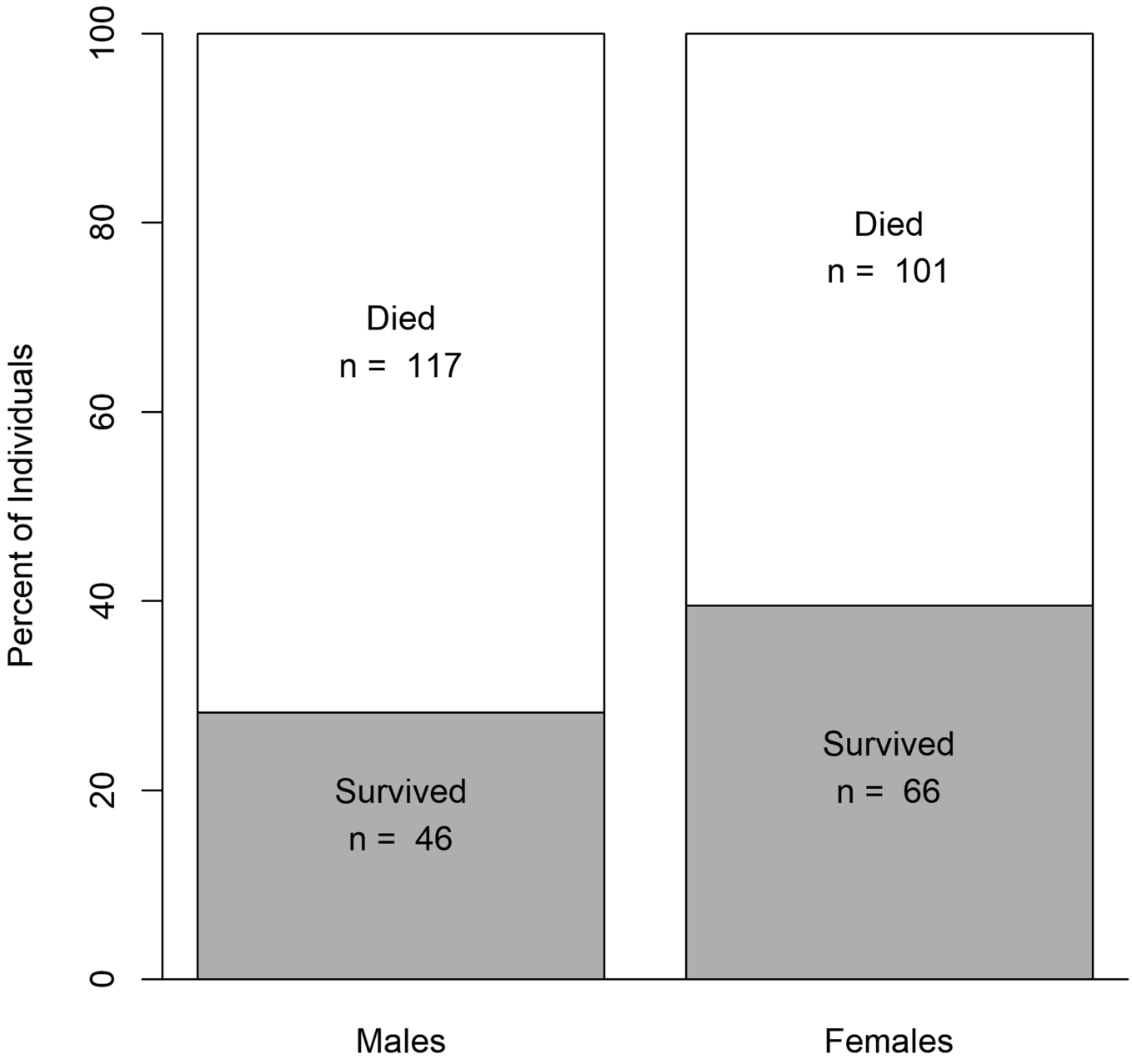


Figure 5. Number and percentage of males and females that survived to the yearling stage and those that died before the yearling stage.

Survivorship

Juveniles exhibited a near 50:50 sex ratio, totalling 163 males and 167 females over the 4 year study period. Significantly more females survived to become yearlings than did males (Pearson's χ^2 test with Yate's continuity correction, $\chi^2 = 4.21$, d.f. = 1, $P < .04$, total $N = 330$; Fig. 5).

DISCUSSION

The highly chromatic orange dorsolateral bars of male juvenile collared lizards are more conspicuous against the natural visual background of their rocky habitat than are the less chromatic tan dorsolateral bars of juvenile females. Moreover, juvenile males suffer decreased survival during the life stage in which the bars are present. It seems likely to us that juvenile males pay a survival cost from the orange bars through increased detection by predators. This interpretation follows from the fact that, for most visual systems, colours possessing strong chroma should be more detectable in natural environments than weakly chromatic colours (Endler 1990). As anticipated, we found no differences in contrasts between male and female background body coloration as viewed against the rocky substrate of the habitat of our study species. Somewhat surprisingly, female dorsolateral bars exhibited greater achromatic contrast than did male bars in all visual models. This result might stem from the larger difference between reflectance of the female bars and the rocks, compared with that of males, in the short and middle wavelengths (e.g. 425–550 nm; Fig. 2).

We must temper our conclusions on survivorship, because we reduced the number of predators at the study site. During

the second and third years of the study, the number of *G. californianus* (roadrunners) increased at the site. To prevent the reduction of our population size beyond what had occurred already (roadrunners are very efficient predators on collared lizards), we trapped and relocated several roadrunners away from our study site. We conducted this relocation in conjunction with another study, in which *M. flagellum* (coachwhips) were also captured and removed from a site adjacent to our study area. Our removal of predators in both locations might have suppressed predation pressure on collared lizards at our study site. Nevertheless, survival at our study site was still low overall, with only 28.2% of males and 39.5% of females surviving to become yearlings. During the 4 years of the population study, we found field evidence of predation on collared lizards and, in some cases, we observed attacks, but predation was probably lower than it might have been had we not removed any roadrunners or coachwhips. Overall, females survived significantly better than males, probably because females are less conspicuous in coloration and patrol less than males.

Colour vision plays important roles in ecological contexts such as foraging, intraspecific fighting, and mate choice, but highly chromatic visual signals favoured by sexual selection in attracting mates or repelling conspecific rivals can also attract predators (Endler 1978, Baker and Parker 1979, Husak *et al.* 2006, Karubian 2013, Cain *et al.* 2019). For example, in the Achala copper lizard (*Pristidactylus achalensis* Gallardo, 1964), males, which are visually more conspicuous than females, will retreat from predators at a greater distance than will females (Torres *et al.* 2021). In juvenile collared lizards, territorial defence and female pair bonding require that males exhibit conspicuous behaviour and approach the conspecific closely while displaying their striking dorsolateral bars (Fox *et al.* 2020). Unfortunately, frequent patrolling, intraspecific agonistic contests, and male courtship all increase exposure to potential predators (Andersson 1994). In a recent study, Wiggins *et al.* (2023) tested whether juvenile males were able to benefit immediately from the interactions they had with juvenile females by reproducing at the end of the juvenile period in the late autumn. Results showed that despite some males being able to produce sperm by late autumn, there was no evidence that they were reproducing before the spring (Wiggins *et al.* 2023). This finding emphasizes that any benefits to be gained from the conspicuous orange bars must be acquired outside of the juvenile period and, by extension, after males have lost the orange bars for their adult coloration.

Juvenile females do not advertise or defend territories, but instead reside on the developing territories of juvenile males. The less frequent and less vigorous movements by females reduce the risk of being seen by a predator. In comparison, juvenile males need to find and pair bond with juvenile females (Fox *et al.* 2020). Females might pay a price, nevertheless, by interacting with or simply being in the vicinity of an active, conspicuous male (Dawkins and Guilford 1991, Edomwande and Barbosa 2020). For example, in guppies (*Poecilia reticulata* Peters, 1859), Pocklington and Dill (1995) showed that when a cichlid predator was presented with mixed-sex guppy pairs, females were targeted first significantly more often than were males. The authors concluded that females were more profitable, because they were roughly three times the size of males and there was no difference in capture rate between the sexes. Pocklington and Dill (1995) speculated that in nature predators might shift their prey target to the female after initially detecting the conspicuous colour and behaviour of the male. Likewise, in a study with sand lizards (*Lacerta agilis* Linnaeus, 1758), predators tended to target cryptic female models over conspicuously coloured male models; a result which suggests that increased visual conspicuousness is not necessarily an indicator of predation risk (Olsson 1993).

In our study, for two reasons we suspect that the comparatively stronger achromatic contrast of juvenile collared lizard female dorsolateral bars does not translate into female-biased predation risk. First, given that juveniles of both sexes are approximately the same size, it is unlikely that females are more profitable prey than are males. Juvenile females also survived better than males to the yearling stage. Second, achromatic vision is important for mediating spatial resolution and motion detection (Gegenfurtner and Hawken 1996, Fleishman and Persons 2001, Jones and Osorio 2004, Hill and McGraw 2006, Olsson *et al.* 2018, Kaestner *et al.* 2019), and the rocks at our study site appear as a matrix of brownish-tan patches that vary in luminance (Supporting Information, File S1). From the perspective of viewers, the array of large rocks within the field of view forms a patchwork scene of light and shadows. In comparison, our spectrophotometric measurements of rock samples were taken from a very small area of rock surface, and all samples were illuminated equally. Dorsolateral bars that are brighter than a rock on which a collared lizard is perched might therefore be relatively inconsequential for detection by predators or conspecifics. It also seems possible that the dorsolateral bars could be functioning as disruptive coloration that breaks up the outline of the lizard against the rocks (e.g. Cuthill *et al.* 2005, Stevens and Merilaita 2009).

As adults, females develop orange dorsolateral bars during the reproductive season that appear similar to those of juvenile males. We speculate these orange bars serve the same function of attracting the opposite sex as in juvenile males. Originally, it had been proposed that this visual signal functioned to deter male aggression and courtship after females became gravid (Carpenter 1967, Cooper and Ferguson 1972) and that the orange bars of juvenile males served to mimic adult female coloration. Deterring aggression from adult males should be a priority for young males, given the much stronger bite force of mature males (Lappin and Husak 2005) that could harm or even kill juveniles (Fox 2009, Ivanyi 2009, Sievert and Sievert 2011). The adult female mimicry hypothesis was tested and rejected by Husak *et al.* (2004) when they showed that adult male aggression was not reduced by the presence of orange dorsolateral bars in juvenile males. It has also been shown that adult female orange bars stimulate, rather than deter, approach and courtship by adult males (Baird 2004). More recently, York and Baird (2019) discovered that females benefit from multiple sires of their offspring through increased hatching success and survivorship, which might be reduced if the orange bars inhibited male courtship.

To conclude, Fox *et al.* (2020) suggested that precocial sexual selection might have driven the development of dorsolateral orange bars in juvenile male collared lizards and continues to maintain them. Our visual modelling results have shown that

these orange bars are likely to be conspicuous, not only to the intended receivers (juvenile females and juvenile males) but also to unintended receivers, such as predators. This undesired attention increases predation on lizards bearing the orange bars, thus heightening the cost of displaying them. Emerging research is demonstrating that juvenile males with more developed dorsolateral orange bars leave significantly more offspring as adults than do juvenile males with less developed orange bars (Wiggins 2018). Moreover, males are not mating with females until the season after they have lost their orange ornamental coloration (Wiggins *et al.* 2023). These outcomes suggest that the bars might be a visual indicator of potential future reproductive success. The benefit of the attraction of this signal to prospective mates and repulsion of prospective rivals indicates that it has outweighed the likely cost from predation over evolutionary time.

SUPPLEMENTARY DATA

Supplementary data is available at *Biological Journal of the Linnean Society* online.

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DATA AVAILABILITY

The data underlying this article will be shared on reasonable request to the corresponding author.

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