

# Juvenile-juvenile social signalling: a case for precocial sexual selection in the collared lizard, *Crotaphytus collaris* (Squamata: Crotaphytidae)?

STANLEY F. FOX<sup>1\*</sup>, FELIPE DE JESÚS RODRÍGUEZ-ROMERO<sup>2</sup>, and ANDREA ACEVEDO CROSBY<sup>1</sup>

<sup>1</sup>Department of Integrative Biology, Oklahoma State University, Stillwater, OK 74078, USA

<sup>2</sup>Laboratorio de Sistemas Biosustentables, Facultad de Ciencias, Universidad Autónoma del Estado de México, El Cerrillo Piedras Blancas, Carretera Toluca-Ixtlahuaca Km 15.5, CP 50200, Toluca, Estado de México, México

Received 16 January 2020; revised 11 March 2020; accepted for publication 11 March 2020

Sexual selection is widespread in animals, but quite naturally studied in adults. Juvenile males in most animals are not differentiated from females and coloration is usually drab. However, there is no reason to suspect that sexual differences cannot develop before puberty, influence social interactions, and then have fitness pay-offs later in life. Juvenile collared lizards (*Crotaphytus collaris* (Say, 1822)) show marked dichromatism: males develop bright dorsolateral orange bars whereas females do not. These juvenile orange bars (JOB) disappear at sexual maturity, when males develop different colour traits maintained by sexual selection. We conducted field experiments with juvenile males on their developing territories in which we utilized staged intruders of juvenile males (with JOB) and juvenile females (lacking JOB) and also juvenile male intruders whose JOB were manipulated. Residents reacted significantly more aggressively toward males vs. females, and also toward males whose JOB were emphasized with paint than those whose JOB were masked by paint. These JOB are used in signalling among juveniles and we suggest the social relations established then are retained until sexual maturation the next spring (after the JOB are lost) to benefit males that previously displayed strong JOB by increased matings in the spring as sexually mature yearlings as per a phenomenon we call precocial sexual selection.

**ADDITIONAL KEYWORDS:** aggression – delayed fitness – dichromatism – field manipulation – intrasexual selection – intersexual selection – puberty.

## INTRODUCTION

Sexual selection is widespread in animals and is well studied (Andersson, 1994; Stuart-Fox & Ord, 2004). In most sexually reproducing animals, males experience strong competition for mates and display greater variation in reproductive success than females. Females typically prefer conspicuously coloured males as mates (Hill, 1990; Houde, 1997) and such males often achieve greater social dominance or greater access to resources (e.g. females) or both (Baird *et al.*, 1997; Zamudio & Sinervo, 2003). This differential mating advantage of conspicuous coloration in one sex results in sexual dichromatism via sexual selection. Furthermore, if the

bright colours of males are condition-dependent, then the effectiveness of sexual selection is enhanced (Hill, 1990, 1991, 1999, 2011; Houde & Torio, 1992). Usually, sexual dichromatism and sexual differences in behaviour arise at the time when individuals become sexually mature (puberty). This synchrony among secondary sexual characteristics, behaviour and sexual maturation is logical given that sex steroids frequently are critical to the development and maintenance of both primary and secondary sexual characteristics (e.g. Cooke *et al.*, 1998; Adkins-Regan, 2005). However, there is no logical reason to suspect that sexual differences in morphology, colour or behaviour cannot develop before puberty, influence social interactions before puberty, and then have adaptive significance later in life, realized as increased reproductive success.

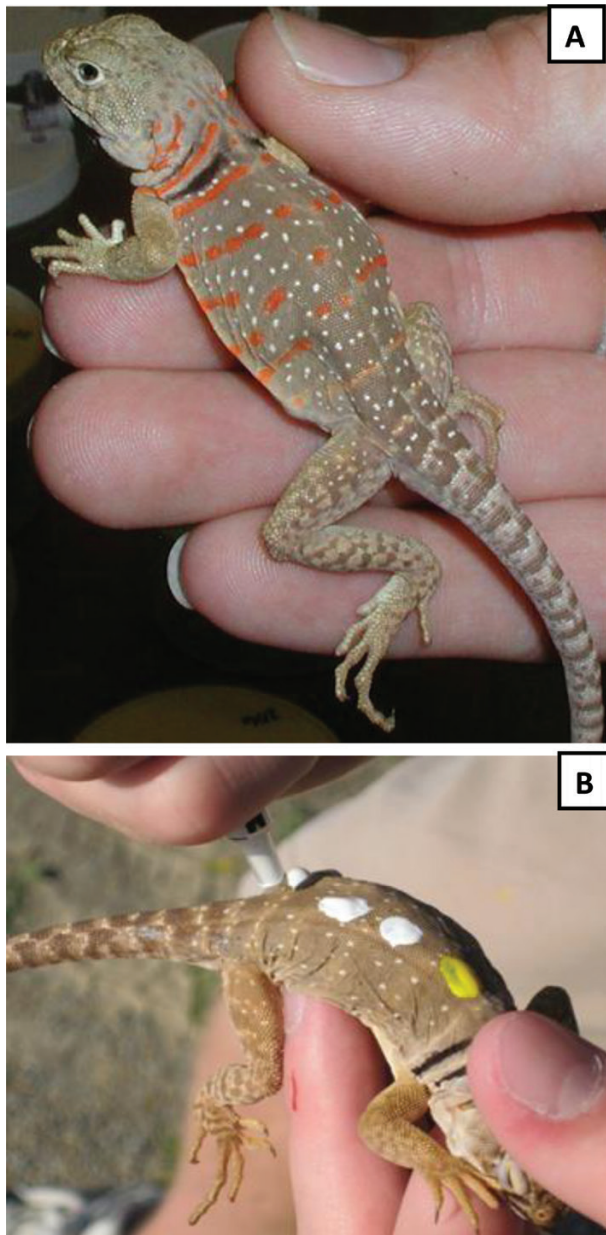
\*Corresponding author. E-mail: [stanley.fox@okstate.edu](mailto:stanley.fox@okstate.edu)

Nevertheless, pre-reproductive juveniles in most vertebrate species are not differentiated in appearance or behaviour. Generally juveniles resemble one another and treat one another the same with respect to sex. In species that show strong sexual dimorphism as adults, juveniles generally resemble cryptic adult females and not conspicuous adult males. This inconspicuous, cryptic coloration and non-flashy behaviour are thought to decrease predation pressure on juveniles and similarly coloured adult females (Houde, 1997; Husak *et al.*, 2006). In some cases in which juveniles differ from adults in coloration and behaviour, it is clearly due to predation pressure exerted on the juvenile life stage. For example, in lizards that have a strongly developed tail autotomy adaptation, the tail of the more predation prone juveniles is more brightly coloured and is easily lost to a would-be predator (Cooper & Vitt, 1985; Pianka & Vitt, 2003; Hawlena *et al.*, 2006; Bateman & Fleming, 2009). Such cases of specific juvenile coloration and behaviour can be explained by natural selection. It is unknown if there are cases of juvenile trait expression that can be explained by sexual selection; however, existing data are intriguing. For example, some traits in juvenile male jumping spiders are more brightly coloured than in juvenile females (Taylor *et al.*, 2014). Some bird species show sex-specific colour differences in the juvenile life stage, including European bee-eaters (Kapun *et al.*, 2011), red and Scottish crossbills (Edelaar *et al.*, 2005), Florida scrub-jays (Siefferman *et al.*, 2008) and bearded reedlings (Marin *et al.*, 1994; Surmacki *et al.*, 2015), the latter of which even form pre-reproductive pair bonds possibly in part based on this sexual dichromatism. Such data beg further study and consideration in the realm of sexual selection, as detailed below. If the benefits of sexually dimorphic coloration or behaviour in juveniles carry over and increase the fitness of sexually mature adults in the context of increased matings, then that is sexual selection on pre-reproductive individuals and might be called precocial sexual selection. Precocial sexual selection could logically exist in many species that later show strong sexual selection, but the phenomenon apparently has not been sought or documented in the literature. However, one apparent case is seen in the collared lizard (*C. collaris*) and is the focus of this study.

Collared lizards (*C. collaris*) are highly territorial and adults exhibit strong sexual dimorphism (McCoy *et al.*, 1994; McGuire, 1996) and dichromatism, with males being bright bluish-green dorsally and with a pale to near-fluorescent yellow head and/or throat, whereas adult females are wholly brown to dull olive (McGuire, 1996; McCoy *et al.*, 1997). Interestingly, during the reproductive cycle, females develop orange dorsolateral bars (McGuire, 1996) that presumably cycle in intensity with ovarian steroid hormones

(Cooper & Ferguson, 1972). Many authors have suggested that these orange bars of female *C. collaris*, which appear only when the female is gravid, inhibit male aggression (e.g. Carpenter, 1967; Cooper & Ferguson, 1972; Cooper & Greenberg, 1992; McGuire, 1996; Ivany, 2009). Baird (2004) directly tested this aggression hypothesis, expecting that females lacking the orange bars would be courted more frequently and intensely by males than females with them. However, using both natural variation in orange female markings and experimentally altering them in the field, he found that males, instead of being repelled, were attracted to females with lateral orange bars by courting longer and initiating more displays and contacts with orange than with brown females. Interestingly, in the same species, males develop conspicuous dorsolateral orange bars (juvenile orange bars (JOB), Fig. 1) 2 to 3 weeks after hatching. These JOB fade after several months while the maturing males begin to attain their typical adult green and yellow coloration, although they are still seen in some small yearlings early the next season. These same JOB are observed in at least seven of the other eight species of *Crotaphytus* (McGuire, 1996). Husak *et al.* (2004) tested the long-standing hypothesis that JOB in small male yearling *C. collaris* serve as a form of female mimicry, reducing aggression from adult males; however, they found no support for this function of the bars. Their result is not surprising since we now know that the orange bars in adult female *C. collaris* do not serve the purpose of dissuading adult males (Baird, 2004). Also, at the time of the year when juvenile males (pre-reproductive individuals before their first brumation) develop the most intense JOB (September and first part of October), most adults (male and female) have already retreated underground for the winter (Trauth *et al.*, 2004; A. Crosby and S. Fox, pers. obsv.). Thus, it seems reasonable that the JOB are a visual signal directed against other juveniles (and not adult males) and the JOB may have evolved and are now maintained by precocial sexual selection. In fact, work performed recently in the laboratory of S. Fox has shown this precocial sexual selection in *C. collaris*. Juvenile males with more developed JOB were significantly preferred by juvenile females in choice tests in the laboratory, were significantly more aggressive than juvenile males with more weakly expressed JOB, and eventually sired significantly more offspring than their counterparts with less developed JOB (Wiggins, 2018).

The objective of this study was to test if the JOB are a male-indicative signal in juvenile collared lizards. Specifically, we tested if juvenile intruders with JOB (males) and juvenile male intruders with JOB emphasized with orange paint would elicit stronger aggression by juvenile males in the field in staged, tethered intrusions than juvenile intruders without



**Figure 1.** (A) Juvenile male *C. collaris* 4–5 weeks old with JOB, and (B) juvenile female *C. collaris* 4–5 weeks old without JOB. Paint marks on back are used for individual identification.

JOB (females) or juvenile male intruders with JOB masked with background-matching paint.

## MATERIALS AND METHODS

We conducted a series of staged intrusions after hatchlings emerged (August–October) at Sooner Lake Dam in Pawnee County, Oklahoma, USA (36° 27'28.0" N, 96° 59'39.8"W), in 2006–2010. This is a rip-rap dam,

1.7 km long with an average width of 15 m. The granite rocks on the dam were sprayed with a concrete slurry upon construction to hold them in place; however, there are still numerous crevices and refuges for the lizards. The other side of the dam is a grassy slope where lizards are rarely found. Once juvenile males reach a size of 65–70 mm snout-vent length (SVL), they have maximally expressed JOB and they begin to show territorial behaviour (Crosby, 2015). We conducted staged intrusions into the territory of residents 70 mm SVL and larger and with well-developed JOB. On clear warm days with little to no wind when lizards were active on the site between 09:00 and 18:00, an intruder was introduced 50–100 cm from a resident male juvenile using a 15-m pole with the intruder tethered at the tip in a soft cotton thread harness around its waist. The observer backed away 12–15 m and started the 10-min trial immediately. All agonistic behaviour patterns of the resident were observed and recorded, following Fox & Baird (1992). We analysed: 1) total aggressive acts, 2) total of weighted aggressive acts (+1: approach; +2: throat display, lateral throat display, headbob, push-up, circle, gape, superimposition; +3: attack, bite, fight) less weighted submissive acts (-1: retreat, flee), 3) trial intensity (0 = flee, 1 = no response, 2 = display then flee, 3 = display no fight, 4 = display then fight, 5 = fight then display), and 4) elapsed time to first aggression by the resident. Each resident was tested only once on a given day. Intruders, however, were sometimes used more than once on a given day, but never more than three times. We maintained duplicate sets of small, medium and large-sized intruders in captivity and used them opportunistically against intruders of known body size in order to match the body size of intruder and resident within a couple of millimetres SVL and to ensure that we did not use an intruder originally from nearby the resident to avoid any 'Dear Enemy' effect (Fox & Baird, 1992). All the residents and intruders had full tails. Old intruders were replaced with new intruders if they showed any negative effects of captivity or use in multiple trials. Negative effects were not assessed from the reaction of residents during trials, rather these effects were seen as subtle decreases in activity in captivity, even though they continued to feed well and react normally to handling. Old intruders (and all intruders at the end of the year) were returned to their point of original capture. No lizards died nor showed any signs of ill health during the research.

In the first set of 25 trials, the intruder was either male (possessing the JOB) or female (lacking the JOB). In the second set of 24 trials, both kinds of intruders were juvenile males. In 12 of the intruders of this second set, we emphasized JOB with matching non-toxic, acrylic orange paint. In the other 12 of this set, we masked JOB with non-toxic acrylic brown paint,



which matched the background coloration of the lizard (i.e. these resembled juvenile females, but retained the behaviour and any scent signals of males). In both sets of trials, the order of intruder presentation was random. Because we limited trials to only ideal weather conditions, we conducted trials over multiple years to gather sufficient data for statistical analysis.

We analysed the spectral qualities of the natural JOB, natural background coloration, and emphasized and masked JOB via painting with reflectance spectrophotometry. We used a UV-Vis spectrometer (USB 4000), deuterium-halogen light source (DH-2000-BAL), probe (QR400-7-SR-BX) and SpectraSuite software (all Ocean Optics) to quantify spectral reflectance of these natural and painted body areas. The probe was mounted within a custom-designed probe holder that excluded ambient light and ensured readings were taken from areas 2 mm in diameter at a constant 7-mm distance from the surface with both illumination and reflectance measurement at a 90° angle to the surface. JOB are approximately 2 mm in width, so colour only of JOB was measured. Spectral reflectance was measured at 320–700 nm as this represents the broadest range of wavelengths known to be visible to lizards (Loew *et al.*, 2002). Measurements were taken with lizards at an optimal body temperature (35–40 °C).

Research procedures were reviewed and approved by the Oklahoma State IACUC Protocol #AS-06-15.

## RESULTS

We first compared the spectral reflectance of natural JOB against the acrylic orange paint used to emphasize JOB, and the natural female coloration against the brown paint used to mask JOB on the male intruders. Spectral reflectance of painted individuals closely matched those of real animals with and without JOB (Fig. 2).

We tested for any possible year effects because data were collected in multiple years. For the first set of 25 trials in which intruders were male or female, no response was significantly different between the 2 years in which data were collected (Mann-Whitney U-tests, all  $P > 0.05$ ). For the second set of 24 trials in which intruders were males with and without JOB, no response was significantly different among the 4 years in which data were collected (Kruskal-Wallis tests, all  $P > 0.05$ ).

We used non-parametric Wilcoxon matched-pairs signed-ranks tests to analyse the responses of the resident to different kinds of tethered intruders. First, for 25 trials with male and female intruders, juvenile male residents showed significantly more total aggression ( $Z = 2.78$ ,  $P < 0.01$ ) and graded aggression

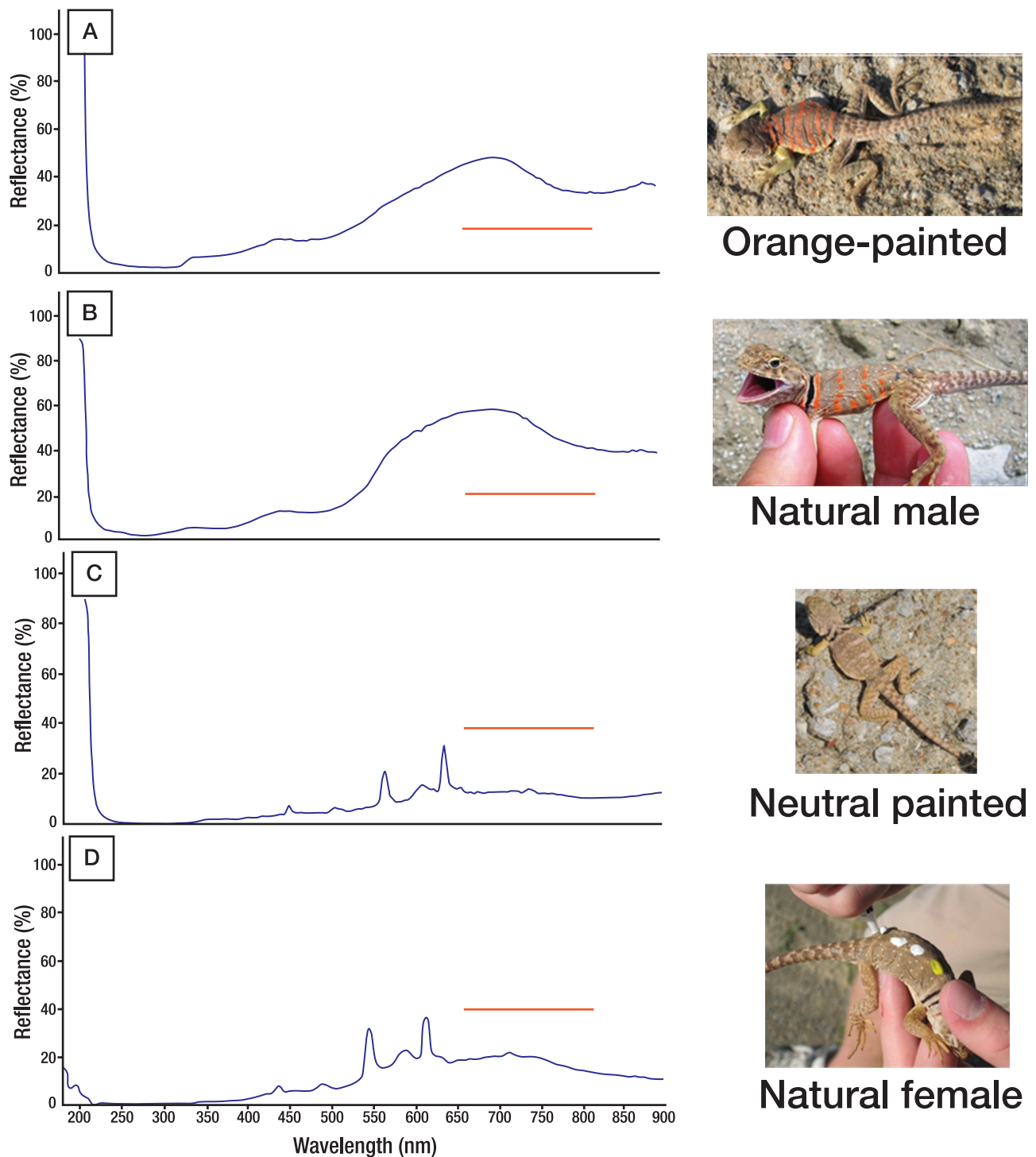
( $Z = 3.54$ ,  $P < 0.001$ ), and displayed significantly more trial-wide aggressive intensity ( $Z = 2.13$ ,  $P = 0.03$ ) to male than female intruders (Fig. 3). Second, for the 24 trials consisting of only juvenile male intruders (half with JOB emphasized orange paint and half with JOB masked brown paint), juvenile male residents showed significantly more total aggression ( $Z = 3.67$ ,  $P < 0.001$ ) and graded aggression ( $Z = 3.60$ ,  $P < 0.001$ ), displayed significantly more trial-wide aggressive intensity ( $Z = 3.07$ ,  $P < 0.01$ ), and waited significantly less time to show aggression ( $Z = 2.39$ ,  $P = 0.02$ ) to juvenile males with JOB vs. those without JOB (Fig. 4).

## DISCUSSION

These results strongly suggest a phenomenon we call precocial sexual selection: sexually immature (juvenile) *C. collaris* males compete against future reproductive competitors and allow close presence of future reproductive mates. Moreover, recent observations of male juveniles courting female juveniles (and even the female-looking male intruders in a few cases in the present study), suggest that they could be spending a large portion of the fall (autumn) season pair bonding. Juvenile males with JOB are frequently seen in the field in near proximity to juvenile females (even touching them and in some cases, performing courtship displays), which is similar to behaviour of adult and yearling males with females in the spring and summer, and they do not show this behaviour toward juvenile males, to whom they react aggressively and repel. Previous and on-going mark-recapture investigations show that juveniles confine their movements to a small area and do not stray far from their home site later as yearlings and older adults (S. Fox, pers. obsv.) Thus, it is quite possible that yearling males encounter the same females with whom they consorted the fall before as juveniles.

Adult male collared lizards appear to establish/strengthen social bonds with females and repel rival males in the summer after breeding, not before, probably for mating advantages early the next spring (S. Fox, pers. obsv.). Collared lizards have individual recognition (Husak & Fox, 2003), so it appears that pairs that bonded in the summer after mating can retain recognition until the next year and benefit by early spring copulation and increased time for multiple clutches (Baird *et al.*, 2001; Trauth *et al.*, 2004). Juveniles appear to follow the same pattern, with the expression of juvenile-specific social coloration and behaviour the year before the reproductive pay-off.

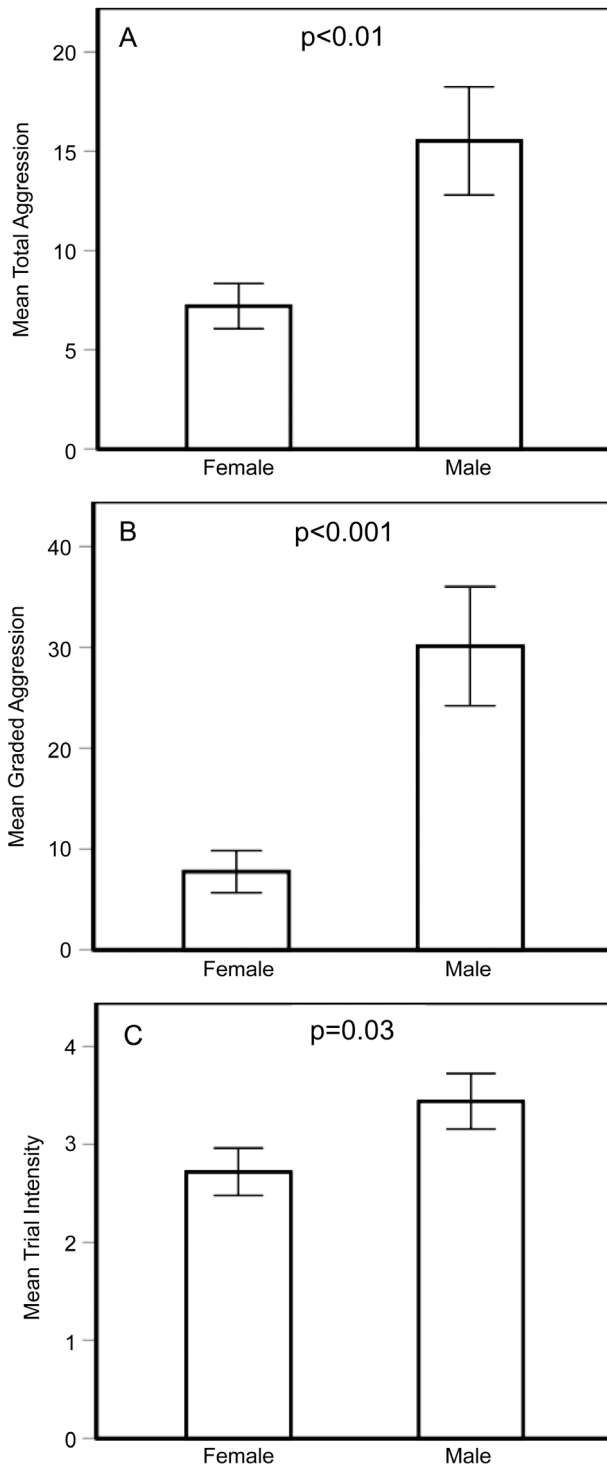
Juvenile males establishing territories appear to use the JOB to distinguish males from females and then treat male intruders more aggressively than female intruders and even promote social bonds with juvenile



**Figure 2.** Orange-painted male juvenile (A) with same reflectance spectrometry as natural male (B) and neutral-painted female juvenile (C) with same spectrometry as natural female (D). Orange bars represent the orange-red wavelengths (650–800 nm) representative of the JOB.

females. We suggest that the differential treatment of male and female juvenile interlopers benefits the male juvenile residents; however, the benefits are delayed in time (Fig. 5). The aggressive response of juvenile

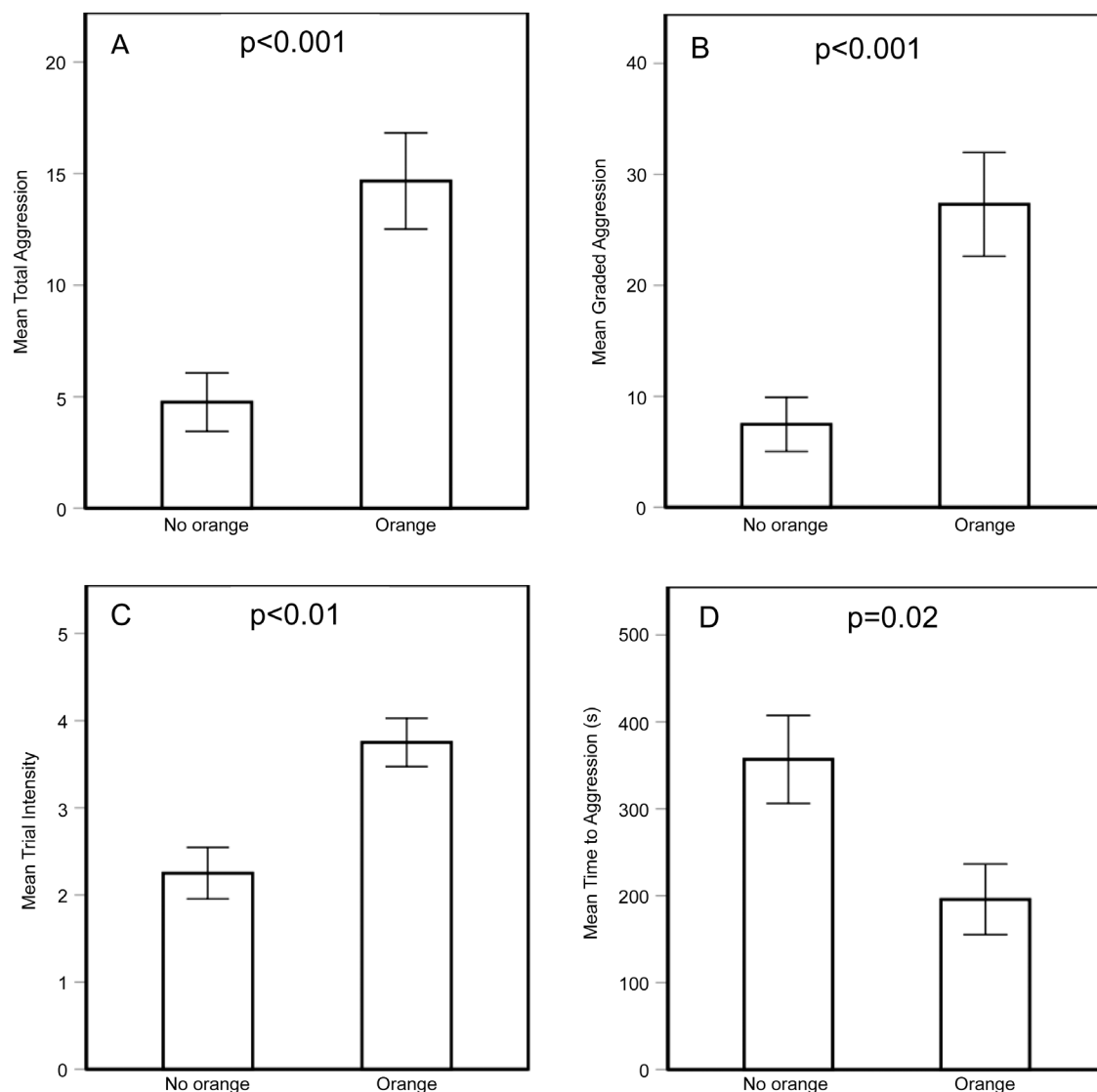
male residents to male intruders serves to repel them spatially such that competition with them as sexual rivals for females the next spring is reduced; and the non-aggressive treatment of female intruders serves



**Figure 3.** Juvenile male residents were significantly more aggressive to male than female intruders with respect to (A) total aggression, (B) graded aggression, and (C) trial intensity. Error bars represent  $\pm 1$  SE.

to initiate a pair bond that extends to the next spring and gives that male a subsequent mating advantage. This suggests precocial sexual selection with both intra- and intersexual components. The authors have recently shown exactly this in *C. collaris* (Wiggins, 2018). Juvenile males with more developed JOB were significantly preferred by juvenile females in choice tests in the laboratory, i.e. intersexual selection; were significantly more aggressive than juvenile males with less endowed JOB, i.e. intrasexual selection; and eventually sired significantly more offspring the next year than their counterparts with less developed JOB, i.e. fitness advantage to those trait-bearing males.

It is important to point out that the JOB expressed in juvenile males in their first year of life and used to signal both other juvenile males and females are completely different colour signals to those expressed and used by adult males. Adults are extremely sexually dimorphic and dichromatic (McCoy *et al.*, 1994; McCoy *et al.*, 1997); however, adult males do not have dorsolateral orange bars. Juvenile males start to lose their JOB in the late fall season before brumation as they begin to develop adult-specific sexual colours. The next spring, after brumation, the JOB have disappeared from most males and are present only in diminished state in a few individuals. In the late fall (October in Oklahoma), after juvenile males are beginning to lose their juvenile-specific JOB and after they have been functional in repelling competitor juvenile males and attracting juvenile females as potential future mates, juvenile males begin to produce mature sperm (Wiggins, 2018). Nevertheless, we have no evidence that these juveniles mate then. By this time, virtually all adult and yearling females are underground in brumation (in most years none of these females are above ground and active [S. Fox *et al.*, unpubl. data]). None of the juvenile males with JOB and behaving aggressively toward other males before October had mature sperm; however, perhaps their levels of androgens were at this time increasing and sufficient so as to invoke the aggressiveness and territoriality we observed. In fact, the authors found in pre-reproductive, unmanipulated juveniles from subsequent studies that JOB area (proportion of lateral exposition) is significantly positively related to both testosterone and aggression (Wiggins, 2018). It is the fact that the JOB are juvenile-specific and pre-reproductive, used to signal to other juveniles when adults are not present due to early brumation, fade and are replaced by different, adult-specific male coloration as juveniles sexually mature, exhibit inter-individual variation in expression, and this juvenile trait variation is subsequently related to



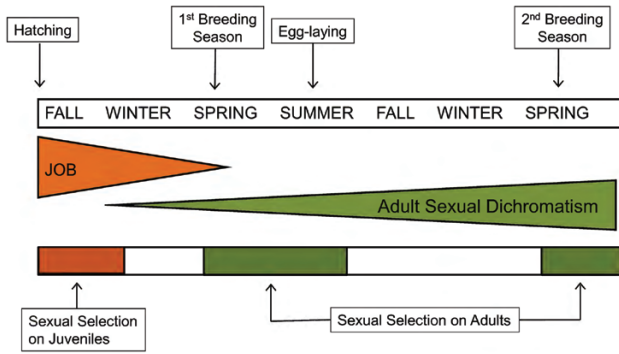
**Figure 4.** Juvenile male residents were significantly more aggressive toward male juvenile intruders with painted JOB than those with masked JOB with respect to (A) total aggression, (B) graded aggression, (C) trial intensity and (D) time to aggression. Error bars represent  $\pm 1$  SE.

fitness once these males mature, that we call this precocial sexual selection. Even so, we recognize that the JOB and associated behaviour can be interpreted as an alternative reproductive tactic (ART) as seen in many other animals (Gross, 1996; Oliveira *et al.*, 2008), although no such ART with one divergent tactic expressed in pre-reproductive juveniles has, to our knowledge, been heretofore described. Thus, in *C. collaris*, there exists a mating strategy specific to the juvenile life stage, in addition to the documented dominant and subordinate ARTs that occur among adult and yearling males (York & Baird, 2015).

Ontogenetic colour changes among lizards have received little attention (Cooper & Greenberg,

1992), and few studies exist that detail the adaptive significance of juvenile coloration (e.g. Clark & Hall, 1970; Huey & Pianka, 1977; Cooper & Vitt, 1985). *C. collaris* represents a good model to examine the adaptive significance of juvenile coloration, especially as it relates to sexual selection. For selection to favour the development of JOB and the differential treatment of those with and without them (i.e. males and females) in sexually immature individuals, there must be a fitness advantage, which occurs later with subsequent sexual maturation (Andersson, 1994). In collared lizards, even though a juvenile is far removed temporally from sexual activity, it would ultimately benefit juvenile males the next spring when they first mate (Wiggins, 2018) to drive





**Figure 5.** The proposed relationship among JOB, adult-typical sexual dichromatism and sexual selection. We suggest that this represents an example of a sexually dimorphic trait—JOB, present only in males—acted upon by sexual selection prior to sexual maturation.

away other juvenile males (current resource competitors and future reproductive competitors) and accept the presence of nearby female juveniles (future mates). It is quite possible that the precocial territoriality and pair-bonding do not negatively affect growth and survival of the juveniles, especially since there are few to no males present at that time. Baird (2018) compared life history parameters like growth and survival in yearling male collared lizards that adopted territoriality vs. those who did not (and instead used sneaking to fertilize females), and found no negative consequences of first-year territoriality. The presence of this conspicuous JOB coloration in male juveniles offers a unique opportunity to study precocial sexual signalling, a heretofore undocumented phenomenon in nature. We believe this phenomenon has not been documented before because investigators have not looked for it in other taxa, and also because there might be some limitations to its presence. First, there cannot be dispersal from between the time juveniles use their sex-specific signals and the time they first mate. Indeed, many animals do disperse as juveniles (Dobson, 1982; Clobert *et al.*, 2001; Bowler and Benton, 2005; Ronce, 2007). Second, there must be the capacity for individual recognition and memory of individuals from juvenile to adult life stages. Third, costs to conspicuous sexual signals and behaviour must be overcome by the benefits reaped when these animals begin to reproduce. Nevertheless, we believe that the phenomenon of precocial sexual selection suggested in *C. collaris* is not restricted to that taxon and we encourage investigators to seek its presence in other animals.

## ACKNOWLEDGEMENTS

We thank the Sooner Lake Power Plant of the Oklahoma Gas and Electric Company for permission

to conduct the research on their property. We also thank the Department of Integrative Biology (formerly Zoology), Oklahoma State University, and the Facultad de Ciencias, Universidad Autónoma del Estado de México, for financial support. Fig. 5 was composed by Matt Lovern and we thank him as well as Justin Agan and Taylor Carlson for help with other figures. We express our gratitude to many field assistants: Susana Perea, Matt Anderson, Enrique Santoyo-Brito, Gil Martínez, Adam Simpson, Erin Roberts, Lauren White, Brent Linihan, Rob Seal, Boe Ray, Chris Brown and Megan Reidy. We thank two anonymous reviewers for their helpful comments.

## REFERENCES

- Adkins-Regan E. 2005. *Hormones and animal social behavior*. Princeton: Princeton University Press.
- Andersson MB. 1994. *Sexual selection*. Princeton: Princeton University Press.
- Baird TA. 2004. Reproductive coloration in female collared lizards, *Crotaphytus collaris*, stimulates courtship by males. *Herpetologica* **60**: 337–348.
- Baird TA. 2018. Live fast and prosper: early territory defence is not costly in male collared lizards (*Crotaphytus collaris*). *Biological Journal of the Linnean Society* **123**: 628–635.
- Baird TA, Fox SF, McCoy JK. 1997. Population differences in the roles of size and coloration in intra- and intersexual selection in the collared lizard, *Crotaphytus collaris*: influence of habitat and social organization. *Behavioral Ecology* **8**: 506–517.
- Baird TA, Sloan CL, Timanus DK. 2001. Intra- and interseasonal variation in the socio-spatial behavior of adult male collared lizards, *Crotaphytus collaris* (Reptilia, Crotaphytidae). *Ethology* **106**: 1–19.
- Bateman PW, Fleming PA. 2009. To cut a long tail short: a review of lizard caudal autotomy studies carried out over the last 20 years. *Journal of Zoology* **277**: 1–14.
- Bowler DE, Benton TG. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological Reviews of the Cambridge Philosophical Society* **80**: 205–225.
- Carpenter CC. 1967. Aggression and social structure in iguanid lizards. In: Milstead WW, ed. *Lizard ecology: a symposium*. Columbia: University of Missouri Press, 87–105.
- Clark JR, Hall RJ. 1970. Function of the blue tail-coloration of the five-lined skink (*Eumeces fasciatus*). *Herpetologica* **26**: 271–274.
- Clobert J, Danchin E, Dhondt AA, Nichols JD, eds. 2001. *Dispersal*. New York: Oxford University Press.
- Cooke B, Hegstrom CD, Villeneuve LS, Breedlove SM. 1998. Sexual differentiation of the vertebrate brain: principles and mechanisms. *Frontiers in Neuroendocrinology* **19**: 323–362.
- Cooper WE Jr, Ferguson GW. 1972. Steroids and color change during gravidity in the lizard *Crotaphytus collaris*. *General and Comparative Endocrinology* **18**: 69–72.



- Cooper WE, Greenberg N. 1992.** Reptilian coloration and behavior. In: Gans C, Crews D, eds. *Biology of the Reptilia, Vol. 18 Physiology E, Hormones, brain and behavior*. Chicago: University of Chicago Press, 298–422.
- Cooper WE, Vitt LJ. 1985.** Blue tails and autotomy: enhancement of predation avoidance in juvenile skinks. *Zeitschrift für Tierpsychologie* **70**: 265–276.
- Crosby AA. 2015.** Possible sexual selection in pre-reproductive juvenile collared lizards (*Crotaphytus collaris*). Unpublished PhD Thesis. Stillwater: Oklahoma State University.
- Dobson FS. 1982.** Competition for mates and predominant juvenile male dispersal in mammals. *Animal Behaviour* **30**: 1183–1192.
- Edelaar P, Phillips RE, Knops P. 2005.** Sexually dimorphic body plumage in juvenile crossbills. *Wilson Bulletin* **117**: 390–393.
- Fox SF, Baird TA. 1992.** The dear enemy phenomenon in the collared lizard, *Crotaphytus collaris*, with a cautionary note on experimental methodology. *Animal Behaviour* **44**: 780–782.
- Gross MR. 1996.** Alternative reproductive strategies and tactics: diversity within sexes. *Trends in Ecology & Evolution* **11**: 92–98.
- Hawlena D, Bochnik R, Abramsky Z, Bouskila A. 2006.** Blue tail and striped body: why do lizards change their infant costume when growing up? *Behavioural Ecology* **17**: 889–896.
- Hill GE. 1990.** Female house finches prefer colorful males: sexual selection for a condition-dependent trait. *Animal Behaviour* **38**: 563–572.
- Hill GE. 1991.** Plumage coloration is a sexually selected indicator of male quality. *Nature* **350**: 337–339.
- Hill GE. 1999.** Mate choice, male quality, and carotenoid-based plumage coloration. In: Adams N, Slowtow R, eds. *Proceedings of the 22nd International Ornithological Congress*. Durban: University of Natal, 1–11.
- Hill GE. 2011.** Condition-dependent traits as signals of the functionality of vital cellular processes. *Ecology Letters* **14**: 625–634.
- Houde A. 1997.** *Sexual selection and mate choice in guppies*. Princeton: Princeton University Press.
- Houde AE, Torio AJ. 1992.** Effect of parasitic infection on male colour pattern and female choice in guppies. *Behavioral Ecology* **3**: 346–351.
- Huey RB, Pianka ER. 1977.** Natural selection for juvenile lizards mimicking noxious beetles. *Science* **195**: 201–203.
- Husak JF, Fox SF. 2003.** Adult male collared lizards, *Crotaphytus collaris*, increase aggression towards displaced neighbours. *Animal Behaviour* **65**: 391–396.
- Husak JF, Macedonia JM, Fox SF, Saucedo RC. 2006.** Predation cost of conspicuous male coloration in collared lizards (*Crotaphytus collaris*): an experimental test using clay-covered model lizards. *Ethology* **112**: 572–580.
- Husak JF, McCoy JK, Fox SF, Baird TA. 2004.** Is coloration of juvenile male collared lizards (*Crotaphytus collaris*) female mimicry?: an experimental test. *Journal of Herpetology* **38**: 156–160.
- Ivany CS. 2009.** Eastern collared lizard, *Crotaphytus collaris* (Say, 1823). In: Jones LC, Lovitch RE, eds. *Lizards of the American southwest: a photographic field guide*. Tucson: Rio Nuevo Press, 104–107.
- Kapun M, Darolová A, Křištofik J, Mahr K, Hoi H. 2011.** Distinct colour morphs in nestling European bee-eaters *Merops apiaster*: is there an adaptive value? *Journal of Ornithology* **152**: 1001–1005.
- Loew ER, Fleishman LJ, Foster RG, Provencio I. 2002.** Visual pigments and oil droplets in diurnal lizards: a comparative study of Caribbean anoles. *Journal of Experimental Biology* **205**: 927–938.
- Marin G, Marchesini M, Tiloca G, Pagano A. 1994.** DNA fingerprinting fails to reveal inbreeding in a small, closed population of bearded tits (*Panurus biarmicus* L.). *Ethology, Ecology, and Evolution* **6**: 243–248.
- McCoy JK, Fox SF, Baird TA. 1994.** Geographic variation in sexual dimorphism in the collared lizard, *Crotaphytus collaris* (Sauria: Crotaphytidae). *Southwestern Naturalist* **39**: 328–335.
- McCoy JK, Harmon HJ, Baird TA, Fox SF. 1997.** Geographic variation in sexual dichromatism in the collared lizard, *Crotaphytus collaris* (Sauria: Crotaphytidae). *Copeia* **1997**: 565–571.
- McGuire JA. 1996.** Phylogenetic systematics of crotaphytid lizards (Reptilia: Iguania: Crotaphytidae). *Bulletin of the Carnegie Museum of Natural History* **32**: 1–143.
- Oliveira RF, Taborsky M, Brockmann HJ. 2008.** *Alternative reproductive tactics*. Cambridge: Cambridge University Press.
- Pianka ER, Vitt LJ. 2003.** *Lizards: windows to the evolution of diversity*. Berkeley: University of California Press.
- Ronce O. 2007.** How does it feel to be like a rolling stone? Ten questions about dispersal evolution. *Annual Review of Ecology, Evolution, and Systematics* **38**: 231–253.
- Siefferman L, Shawkey MD, Bowman R, Woolfenden GE. 2008.** Juvenile coloration of Florida scrub-jays (*Aphelocoma coerulescens*) is sexually dichromatic and correlated with condition. *Journal of Ornithology* **149**: 357–363.
- Stuart-Fox DM, Ord TJ. 2004.** Sexual selection, natural selection and the evolution of dimorphic coloration and ornamentation in agamid lizards. *Proceedings. Biological sciences* **271**: 2249–2255.
- Surmacki A, Stępniewski J, Stępniewska M. 2015.** Juvenile sexual dimorphism, dichromatism and condition-dependent signaling in a bird species with early pair bonds. *Journal of Ornithology* **156**: 65–73.
- Taylor LA, Clark DL, McGraw KJ. 2014.** From spiderling to senescence: ontogeny of color in the jumping spider, *Habronattus pyrrithrix*. *Journal of Arachnology* **42**: 268–276.
- Trauth SE, Robison HW, Plummer MV. 2004.** *The amphibians and reptiles of Arkansas*. Fayetteville: University of Arkansas Press.
- Wiggins JM. 2018.** *Precocial sexual selection in Crotaphytus collaris*. Unpublished PhD Thesis. Stillwater: Oklahoma State University.
- York JR, Baird TA. 2015.** Testing the adaptive significance of sex-specific mating tactics in collared lizards (*Crotaphytus collaris*). *Biological Journal of the Linnean Society* **115**: 423–436.
- Zamudio K, Sinervo B. 2003.** Polygyny, mate-guarding, and posthumous fertilization as alternative male mating strategies. *Proceedings of the National Academy of Sciences USA* **97**: 14427–14432.