

Role of coloration in antipredator strategies of *Pristidactylus achalensis* (Squamata: Leiosauridae) related to sex and stages of predation

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The interaction between behavioural and phenotypic traits, such as coloration, plays a specific role at different stages of the predatory sequence. Cryptic coloration involves a match to the background that reduces the risk of detection, and it is usually optimized by immobility behaviour. In lizards, sexual dichromatism and within-individual changes of colour can influence the level of their crypsis and thus influence antipredator behaviour and the decision to flee. Here, we examined variation in coloration and antipredator behaviour between the sexes of the Achala copper lizard (*Pristidactylus achalensis*). We measured sexual dichromatism and crypsis in accordance with avian vision. We also exposed lizards to a raptor dummy to assess the colour change and behaviour at the detection and approach stages of the predatory event. Finally, we tested escape behaviour in the natural habitat. We found that males were more conspicuous than females. Additionally, individuals showed distinct behaviours at different stages of the predation simulation, but there were no differences between the sexes. However, in their natural habitat males initiated flight at greater distances than females, which might be related to their more conspicuous coloration. In summary, this study shows how differences in crypsis between the sexes affect escape behaviour during the approach stage of predation.

ADDITIONAL KEYWORDS: colour change – crypsis – escape behaviour – predation – sexual dichromatism.

INTRODUCTION

Antipredator strategies in an evolutionary context are the result of interactions between the potential prey and its predator during different stages of the predation event that occur in a sequence of encounter, detection, identification, approach, subjugation and consumption (Endler, 1991). Coloration is one of the principal defence mechanisms, and behavioural responses can enhance the efficacy of this morphological trait against predators during the stages of detection, identification and approach (Endler, 1986; Abrahams, 1995). Other antipredator strategies, such as deimatic signals, involve the occurrence of an active behaviour to display colour signals only during the later predation stages (Umbers *et al.*, 2017; Perez-Martinez *et al.*,

2020). Animal behaviour thus varies in response to the specific stage of the predation sequence and the intrinsic phenotypic traits, such as coloration.

Coloration patterns, such as camouflage, aposematism, mimicry and deimatic displays, can serve as protection, acting at different stages of predation according to their function (Ruxton *et al.*, 2004; Umbers *et al.*, 2017; Yamazaki *et al.*, 2020). In particular, crypsis allows the prey to avoid detection, and one of its most common forms is background matching in which the appearance of the prey matches the colour, lightness and pattern of its background elements (Stevens & Merilaita, 2009). This animal–background relationship can be measured by determining the degree of visual contrast between the background and the colour of the animal (Stuart-Fox *et al.*, 2004). Owing to the specific colour perception of each species, crypsis must be evaluated by considering the visual system of the

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predator. Some birds that are important predators of lizards (Pianka & Vitt, 2003) can see in the ultraviolet (UV) spectrum (Hart, 2002; Osorio & Vorobyev, 2005; Scholtyšek & Kelber, 2017). Interestingly, some lizards have ultraviolet coloration, usually involved in intraspecific communication (Macedonia, 2001; Pérez i de Lanuza & Font, 2010; Badiane et al., 2020), and these signals might increase the probability of their detection if the colours are located in places visible to predators.

On the one hand, the risk of predation for each sex can be different owing to variations in colour (Husak et al., 2006; Cooper & Pérez-Mellado, 2011). Dichromatic lizard species that inhabit rocky environments are exposed to aerial predators owing to their requirement for basking and face a trade-off between predation risk and the opportunity of thermoregulation. In particular, a cold climate and a short reproductive season might affect sex differences in risk-taking and antipredator behaviours (Samia et al., 2015). For these reasons, lizards are excellent model organisms for the study of variability in antipredator strategies (Samia et al., 2016). If males contrast to a greater extent with their background, they will be detected and attacked by predators more frequently than females (Husak et al., 2006; Marshall et al., 2015). Although bright colours are often preferred in the sexual context (Sigmund, 1983; Bajer et al., 2010; Lisboa et al., 2017), the location of these visual signals is usually concealed from the view of predators (Endler, 1992). Generally, there is less conspicuousness in the dorsal region of diurnal lizards than in the ventral region (Stuart-Fox et al., 2004; Romero-Díaz et al., 2019), which could be because this decreases the predation risk, given that birds are common predators (Marshall & Stevens, 2014).

On the other hand, several lizard species show temporal variation of coloration (e.g. Smith et al., 2016; Cadena et al., 2018), which can fulfil functions such as thermoregulation, mate attraction and defence against predators (Stuart-Fox & Moussalli, 2008). Some species change to a more cryptic coloration when they perceive the risk of being predated (Stevens & Merilaita, 2009). Therefore, the ability to change colour might not be only a response to predator presence to improve crypsis but might also affect subsequent behavioural decisions.

Behavioural responses can make cryptic coloration patterns more effective (Houtman & Dill, 1994). Movement increases the probability of prey detection, and consequently, cryptic individuals tend to remain immobile in certain positions to maximize the camouflage (Webster et al., 2008; Cooper & Sherbrooke, 2010). Conspicuous individuals must use other behavioural responses to compensate for predation risks (Lima & Dill, 1990; Martín & López,

1999; Stuart-Fox & Moussalli, 2008), such as escape behaviour, aggressive behaviour or autotomy (Lailvaux et al., 2003; Nunes et al., 2012; Barr et al., 2019). A widespread behavioural response among lizards is the escape to a refuge (Martín & López, 1995; Whiting et al., 2003; Baxter-Gilbert et al., 2018). The flight initiation distance (FID; distance between predator and prey when the latter starts to flee) depends on the risk of predation (Cooper & Sherbrooke, 2010), which, in turn, can be affected by factors such as colour and the distance to the refuge (Cooper, 2003, 2016; Samia et al., 2016). Hence, FID is expected to be greater in more conspicuous than in cryptic individuals in the case that sexual dichromatism modifies crypsis. Likewise, the further an animal is from its refuge, the greater will be FID, because the predation risk is higher (Cooper, 1997).

The Achala copper lizard, *Pristidactylus achalensis* (Gallardo, 1964), belongs to the Leiosauridae family, with males generally having a green copper-coloured dorsum and females a dark brown dorsum (Fig. 1; Naretto & Chiaraviglio, 2020), making this species dichromatic to human vision. If this variation can be confirmed according to the vision of the predator, we can infer differences in crypsis between the sexes. There is evidence of aggressive encounters within this species (Torres et al., 2019), and colour change has been observed in males during agonistic encounters (S. Naretto, unpublished data). They live among rocks, which they use for thermoregulation during the day (Frutos, 2010). At that time, they are exposed to aerial predators, including avian raptors, such as the American kestrel (*Falco sparverius* Linnaeus, 1758) and the variable hawk (*Geranoaetus polyosoma* Quoy & Gaimard, 1824), and passerines, such as the black-billed shrike-tyrant (*Agriornis montana* D'Orbigny & Lafresnaye, 1837) (Salvador et al., 2017).

We hypothesized that the colour difference between the sexes, the ability of individuals to change colour and the stages of predation (detection and approach) would affect antipredator strategies in *P. achalensis* by changes in crypsis and behavioural responses. Intraspecific variability of these traits provides an opportunity to understand how the behavioural and phenotypic traits interact in predator avoidance. We assessed sexual dichromatism and differences of crypsis (colour contrast of individuals with the background) between sexes using the visual model of an avian predator. We also analysed their antipredator behaviours, in addition to colour change and its effects on crypsis in the presence of a raptor dummy (*Falco sparverius*) at the detection and approach stages of the predatory sequence. Finally, we compared escape behaviour between sexes by analysing FIDs and distances to refuge in the natural habitat.



Figure 1. Male (left) and female (right) Achala copper lizards (*Pristidactylus achalensis*) in their natural habitat.

MATERIAL AND METHODS

STUDY SPECIES AND AREA

The Achala copper lizard (*P. achalensis*) is endemic to the Sierras Grandes of Córdoba, Argentina. The species is found from 1800 m a.s.l. to the highest point at 3000 m. It is active during the warm, rainy months (October–April) and hibernates during the cold, dry months (May–September) (Etheridge & Williams, 1985). We studied lizards from populations located in the Pampa de Achala region, Argentina (31°36'S, 64°52'W) in October 2018. We captured 39 adult lizards (29 males > 92.5 mm snout–vent length; and ten females > 90 mm snout–vent length) by noosing (i.e. a pole with a loop of string, with a slipknot that tightens around the neck of the lizard) for colour analysis, and 20 of them (12 males and eight females) were used in behavioural trials in controlled conditions.

Trials were conducted in the field to minimize stress from transfer and to maintain natural temperature and light conditions during experiments. Lizards were kept individually in outdoor plastic enclosures (40 cm of length × 30 cm of width × 40 cm of height), with water *ad libitum* and were fed mealworm larvae (*Tenebrio* sp.) and flowers of *Taraxacum officinale* (L. Weber, 1780). Lizards had access to a refuge created with rocks. We provided to each individual the same amount of food and the same size of rocks for shelters. We performed behavioural trials during the 3 days after capture, after which the lizards were released at the site of capture (recorded with Garmin eTrex GPS).

Additionally, we observed and quantified the escape behaviour of 57 lizards (23 males and 34 females) in their wild environment.

We obtained appropriate permissions for conducting the study in the Pampa de Achala Nature Reserve from the Department of Fauna and Department of Natural Areas, both under the Secretaría de Ambiente y Cambio Climático, Córdoba Government. The research was approved by the Animal Ethics Committee of the Instituto de Diversidad y Ecología Animal IDEA (CONICET-Universidad Nacional de Córdoba; protocol numbers CICUAL 1/2015 and 3/2018) and adhered to the *Guidelines for the Treatment of Animals in Behavioural Research and Teaching* from the Association for the Study of Animal Behaviour (ASAB).

COLORATION

We used photographs to evaluate sexual dichromatism and contrast with the background in the visible and ultraviolet (UV) spectra, following the methodology proposed by Troscianko & Stevens (2015). This methodology is faster than spectrophotometry and requires less manipulation time, avoiding potential colour change. Immediately after the lizards were captured, we took digital photographs of the dorsum of males ($N = 29$) and females ($N = 10$). Also, we took photographs of the rocks ($N = 24$) that were representative of the background colour of habitat used by the lizards to compare the colours between a lizard and each rock and then averaged the contrast of each individual with the backgrounds. A Nikon D3400

camera was used, fitted with a Nikon 50 mm lens and a modified sensor to enable UV sensitivity, placed perpendicularly on a tripod 64 cm tall. We took two consecutive photographs, one with a filter that blocks UV (B+W, transmitting between 400 and 700 nm) and the other with a UV-pass filter (UVROptics, transmitting between 300 and 400 nm). We used a custom-built filter holder to switch each filter onto the end of the lens quickly, enabling us to keep the camera in the same position without modifying the light and distance to the specimen. We saved all the images in RAW format to prevent information loss or modification from automatic adjustments of the camera (Stevens *et al.*, 2007). We used constant diaphragm opening and ISO values ($F = 22$ and $ISO = 200$). We modified the shutter speed to control exposure and avoid oversaturation. For calibration purposes, each lizard was photographed alongside a ColorChecker Passport standard (mini X-Rite Inc., Grand Rapids, MI, USA), a white reflectance standard (Ocean Optics, Dunedin, FL, USA) and a black standard that reflected 87 and 8% of light between 300 and 700 nm, respectively.

We used the plugin 'Image Calibration and Analysis Toolbox' of the software IMAGEJ (v.1.52a), following the methodology proposed by Troscianko & Stevens (2015) to measure colour. First, the visible and UV photographs were combined into a single multispectral image. The multispectral images were analysed using a model of avian vision, and cone capture values were obtained. For cone mapping, we used a chart-based cone-catch model, consisting of a chart previously measured by a spectrophotometer used for calibrating the camera and including the predicted photoreceptors for the predator. The vision model used was that of the peafowl (*Pavo cristatus* Linnaeus, 1758), considering that it is representative of predatory birds (raptors) that hunt lizards (Marshall & Stevens, 2014; Marshall *et al.*, 2015). There are no published spectral sensitivity data for raptors in the ecosystem studied. However, the visual system is conserved between avian groups (Lind *et al.*, 2013; Ödeen & Håstad, 2013). The spectral sensitivities of peafowl were extracted from the paper by Hart (2002). We used the illumination of a clear sky ('bluesky') provided by the package for R PAVO2 (Maia *et al.*, 2019).

After mapping, we extracted the average photon catch values of long-wave (LW), medium-wave (MW), short-wave (SW), ultraviolet (UV) and luminance of the lizards and their backgrounds, selecting regions of interest with IMAGEJ. We obtained data for the following regions of interest: the dorsum of the lizards (including head and back, from the snout to the tail base, and excluding the eyes, flanks, tail and limbs) and the rock backgrounds (defined as rectangular patches that were representative of the rather uniform colours of the rocks). For assembling the regions of interest, we

verified that the patches had a uniform illumination, i.e. excluding zones with shadows.

Using these data, we calculated values of just noticeable differences (JNDs), considering the model of visual discrimination based on receptor noise (Vorobyev & Osorio, 1998; Siddiqi *et al.*, 2004), to make the comparison between the images. This model can be used to determine whether it is likely that two samples are discriminable by the animal. For the visual system, we used a Weber fraction value of 0.05, as in other studies with vertebrates (Vorobyev & Osorio, 1998; Vorobyev *et al.*, 1998). This chromatic and achromatic contrast grade is measured with the JND values. Several publications postulate that values below one indicate that two colours are indistinguishable within the particular visual system, and values between one and three are considered to be difficult to discriminate except in ideal controlled lighting conditions (Siddiqi *et al.*, 2004; Marshall & Stevens, 2014). With increasing value, the colours become gradually more distinct. Therefore, we adopted a conservative threshold of three JNDs to declare that two colours were discriminable to the lizards.

We plotted avian predator photon catches of the dorsum of males, females and their backgrounds in a tetrahedral colour space using the colspace function (PAVO2 package) and calculated the overlap between the volumes using the voloverlap function (PAVO2 package) (Stoddard & Prum, 2008). To analyse sexual dichromatism, we compared the chromatic and achromatic JNDs of males and females (Pérez i de Lanuza *et al.*, 2018). For crypsis, the chromatic and achromatic JNDs of individuals of both sexes with their backgrounds were compared using the Wilcoxon test. Henceforth, the significance threshold was set at 0.05. We verified data normality with the Shapiro–Wilk test and homogeneity variance with the Bartlett test. Statistical analyses were performed with the software R v.3.6.2 (R Core Team, 2018).

BEHAVIOURAL TRIALS AND COLOUR CHANGE

We evaluated behaviour and coloration change in a controlled experiment. We simulated the detection and approach stages of the predator attack with an avian raptor model. This methodology has been used to study diverse aspects of antipredator strategies (Leal, 1999; Fava & Acosta, 2018; Perez-Martinez *et al.*, 2020). The experiments were conducted at the study site between 10.00 and 18.00 h in similar climatic temperature and sky conditions. Each lizard was placed in an experimental arena (150 cm of length \times 62 cm of width \times 35 cm of height) and acclimated for 10 min. We simulated predation using a stuffed American kestrel (*Falco sparverius*) fixed to a rod (2 m), with no contact between the model

predator and the lizard ('Predator treatment'). The predator simulation lasted 180 s, consisting of a stimulus series with increasing predation risk intensity: the first phase of far gliding, with the hawk in a static position 2 m from the lizard for 90 s (stage 1), followed by an approach at a constant speed to 0.50 m from the lizard, maintaining close gliding for 30 s (stage 2), and finally, an intensive approach to 0.10 m from the lizard during 60 s (stage 3). There was a single model operator to ensure constant intensity and speed of the predator for all individuals. We conducted two control treatments of the same duration, one without the stimulus ('Baseline') and the other with the same simulation as the Predator treatment but using the rod without the stuffed model ('Control'). Each lizard participated in one treatment per day. The first treatment was always Baseline, and we randomized the order of Control and the Predator treatment. We took photographs immediately before and after to evaluate the colour change with the methodology previously described. The trials were also video-recorded (Sony HDR CX230) to analyse the common behaviours performed by lizards based on the literature (see [Table 1](#); [Leal, 1999](#); [Langkilde *et al.*, 2003](#); [Perez-Martinez *et al.*, 2020](#)). From the videos, we measured, for each experimental stage: (1) the duration (in seconds) of immobility, time in corporal motion, locomotion and escape behaviours; and (2) the frequency of aggressive behaviours, tongue flick and push-up. We analysed the videos using the software SOLOMON CODER (17.03.22) ([P  ter, 2011](#)).

To quantify the colour change, we compared the chromatic and achromatic JNDs of the individuals before and after the predation trial with the Kruskal–Wallis test. We compared the chromatic and achromatic JNDs of the individuals with their backgrounds before and after the trial to assess changes in crypsis.

To analyse the differences between sexes in antipredator behaviour, we plotted frequency histograms of the number of seconds of each behaviour during the trial. Additionally, we compared the frequency of behaviours between treatments, regardless of sex. In the Predator treatment, the frequency of the behaviours in each stage was compared for both sexes. Finally, the behaviours in the Predator treatment were compared between sexes. To test differences in the frequency of behaviours, we used the χ^2 test.

ESCAPE BEHAVIOUR

We measured FID and distance to refuge in the field in February and March 2019. For this trial, we searched for a lizard exposed or basking outside its refuge (rock crevices), and determined its sex by coloration. An operator approached slowly to a distance of ~5 m from the lizard and waited for 60 s to acclimate it to human presence. If the lizard did not flee, the operator simulated an attack by an avian predator, using the American kestrel model fixed to the end of a 4-m-long rod. Initially, the operator presented the stuffed American kestrel, raising it to ~5 m, simulating static gliding for 30 s. Next, the operator simulated a diving attack, with the model moving from its position towards the lizard in a direct line at a constant speed (~1 m/s), never attacking the lizard from behind. The movement of the model stopped when the animal fled to a crevice of any rock. Immediately, a second person measured the FID (distance between the predator model and the location of the lizard when it fled) and the distance to the refuge (distance between the lizard before fleeing and the site where it took refuge) ([Fig. 2](#)).

We conducted the same trial but using the rod without the predator model as a control. The individuals subjected to Predator treatment and Control were different and chosen randomly. We measured the ambient

Table 1. Ethogram of the behaviours analysed during the controlled trials

Behaviour	Description
Immobility	Lizard stays completely immobile for ≥ 2 s
Corporal movements without displacement	Movement of the head (to the sides or vertically), the tail or the limbs (scratching), while the body remains motionless
Locomotion	Lizard walks slowly and moves without stopping or with stopping for < 2 s
Flight	Lizard sprints and moves without stopping or with stopping for < 2 s
Escape attempt	Lizard jumps or stays against one of the enclosure walls, moving to climb
Aggressive behaviours	Lizard lifts the front part of its body, stretching its front limbs, and keeps its mouth open (gaping) or tries to bite
Tongue flick	Rapid movement of the tongue in and out of the mouth
Push-up	Lizard moves all its body or only the front part up and down quickly through a front-limb push-up

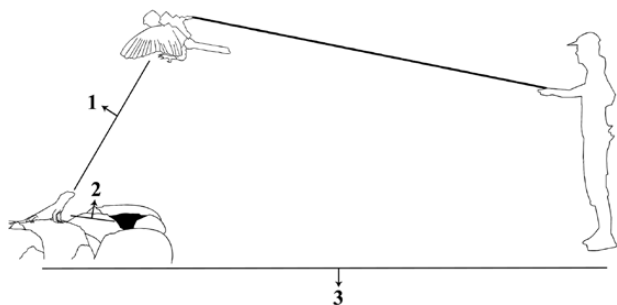


Figure 2. Schematic representation of the distances measured during escape behaviour trials. (1) flight initiation distance; (2) distance to the refuge; and (3) the distance between the predator model operator and the lizard.

temperature in the place where the lizard was located to analyse temperature effects on FID, because this is an important variable influencing defensive reactions (Hertz *et al.*, 1982; Senior *et al.*, 2019). Forty simulations were conducted with adults of both sexes (males, $N = 18$; females, $N = 22$) for the Predator treatment and 17 (males, $N = 5$; females, $N = 12$) for the Control. Having recorded the coordinates of each lizard with GPS, we moved > 50 m to avoid using the individual twice, considering the average home range areas (Naretto & Chiaraviglio, 2020). The trials were conducted only on sunny days with temperatures between 24 and 30 °C.

To analyse the distances, we used analysis of covariance (ANCOVA) to compare the FID between treatments and in the Predator treatment between sexes, considering temperature as a covariate. When this was not significant, it was removed, and we reiterated the analyses. Finally, we compared the distance to the refuge of males and females and determined how this affected the FID by linear regressions for each sex.

DATA AVAILABILITY

The data underlying this study are available to download from OSF (<https://osf.io/wm9qz>; Naretto, 2021) or from the corresponding author.

RESULTS

SEXUAL DICHROMATISM

Males and females differed in coloration. Chromatic perceptual distances between the sexes had a mean of 3.72 ± 2.07 JNDs, with 95.17% of comparisons above one JND and 56.90% above three JNDs (Fig. 3). Meanwhile, achromatic perceptual distances had a mean of 4.14 ± 2.99 JNDs, with 86.21% of distances above one JND and 58.28% of distances above three JNDs (Fig. 3).

In both sexes, the photon catches occupied the lower regions of the colour space, meaning a low UV stimulation (Fig. 4A). Avian predator photon catches of males and females occupied different areas in the tetrahedral colour space (Fig. 4). The relative stimulation of avian predator cones by males was shifted more towards the medium-wave region and by females towards the long-wave region (Fig. 4B). Also, males occupied a larger area in the colour space and were, therefore, more variable than females. There was no overlap between the colour space occupied by males and females (males–females, 0%).

CRYPISIS

Females were more cryptic than males. In the tetrahedral colour space, only avian predator photon catches of females barely overlapped with the background (females–background, 0.005%; and males–background, 0%; Fig. 4). Besides, sexes were spatially segregated from the background in a different axis (Fig. 4B). Chromatic JND values between females and their backgrounds had a mean less than three, whereas male JND had a mean higher than three (Table 2; Fig. 5). The achromatic JND of both was higher than three (Table 2; Fig. 5).

CHANGE OF COLOUR

Lizards did not change colour during the controlled trials. The chromatic and achromatic JNDs before and after the Predator treatment were less than three in both sexes (Table 3). Only 10% of chromatic distances were larger than one JND and 0% larger than three JNDs; meanwhile, 40% of achromatic distances were larger than one JND and 5% larger than three JNDs. Moreover, all the mean JND values in Baseline and Control were less than three (Table 3). No differences were observed between treatments in JNDs, except for females at the chromatic range, but the average values of JND were less than one (Table 3).

The Predator treatment did not produce changes in the contrast between individuals and their backgrounds when we compared crypsis before and after the simulation, in either the chromatic or achromatic range (Wilcoxon test: chromatic JND: males, $W = 0.29$, $P = 0.7728$; females, $W = -0.42$, $P = 0.6744$; achromatic JND: males, $W = -0.03$, $P = 0.9770$; females, $W = -0.26$, $P = 0.7927$; Fig. 6).

ANTIPREDATOR BEHAVIOUR

The frequency distributions of behaviour differed with the treatment (χ^2 test: $\chi^2 = 32.61$, d.f. = 8, $P < 0.0001$; Predator treatment, $N = 16$; Baseline, $N = 17$; Control, $N = 9$). Corporal movements without displacement and locomotion were more frequent in Baseline without any stimulus (10.91 and 9.24% of the time,

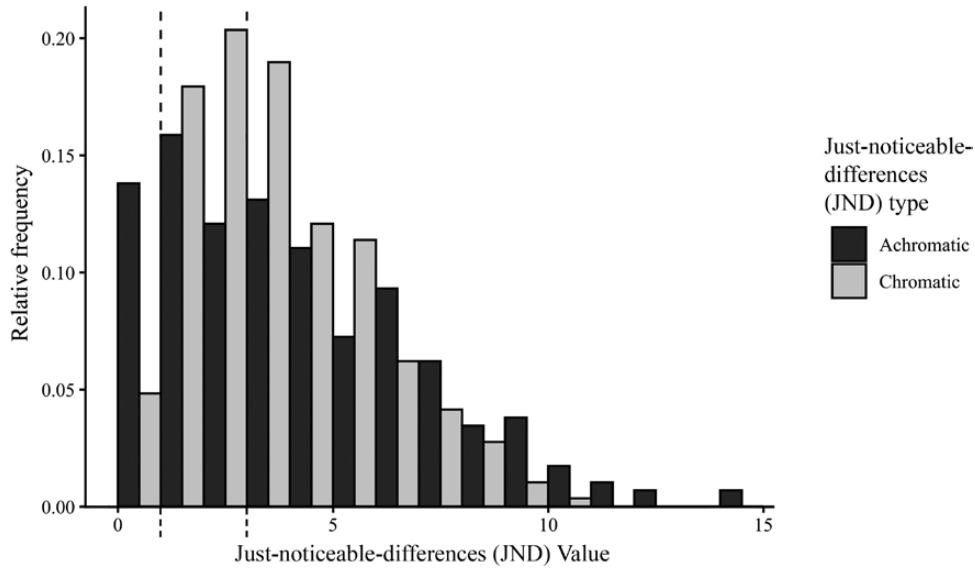


Figure 3. Histogram of relative frequencies of achromatic and chromatic just noticeable differences (JNDs) between males and females. Dashed lines indicate one and three JNDs.

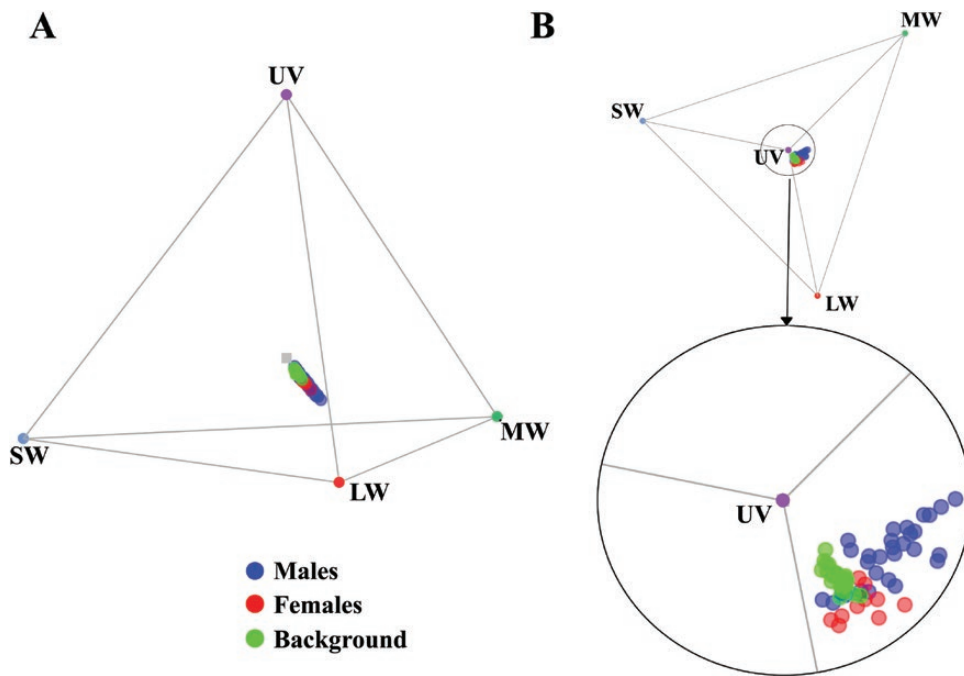


Figure 4. Distributions of avian-perceived coloration of male (blue points) and female (red points) Achala copper lizards (*Pristidactylus achalensis*) and their corresponding natural backgrounds (green points) in tetrahedral colour space. Each point in the tetrahedron is determined by the relative stimulation of the four cone colour channels: UV (ultraviolet), SW (short-wave), MW (medium-wave) and LW (long-wave). A, the entire tetrahedral colour space. B, detail of the space occupied by male, female and background points.

respectively). During the Predator treatment, flight behaviour increased (7.5% of the time in Predator treatment vs. 1.27% in Baseline and 0.8% in Control) as did escape attempts (4.5% of the time in Predator

treatment vs. 0.7% in Baseline and 0.5% in Control). Aggressive behaviours were observed only in the Predator treatment. The lizards performed tongue flick and push-up only during the Baseline and Control

Table 2. Comparison of chromatic and achromatic mean just noticeable differences between males and their backgrounds and between females and their backgrounds

JND type	Sex	Mean \pm SD JND	Median	JND > 1 (%)	JND > 3 (%)	W-value	P-value	N
Chromatic	Males	4.03 \pm 2.24	3.82	100	58.62	-1.96	0.0498*	29
	Females	2.44 \pm 0.92	2.12	100	20			10
Achromatic	Males	5.99 \pm 3.59	5.41	100	72.41	0.9169	0.3592	29
	Females	6.86 \pm 2.94	6.65	100	100			10

Abbreviation: JND, just noticeable difference; W-value, Wilcoxon test statistic.

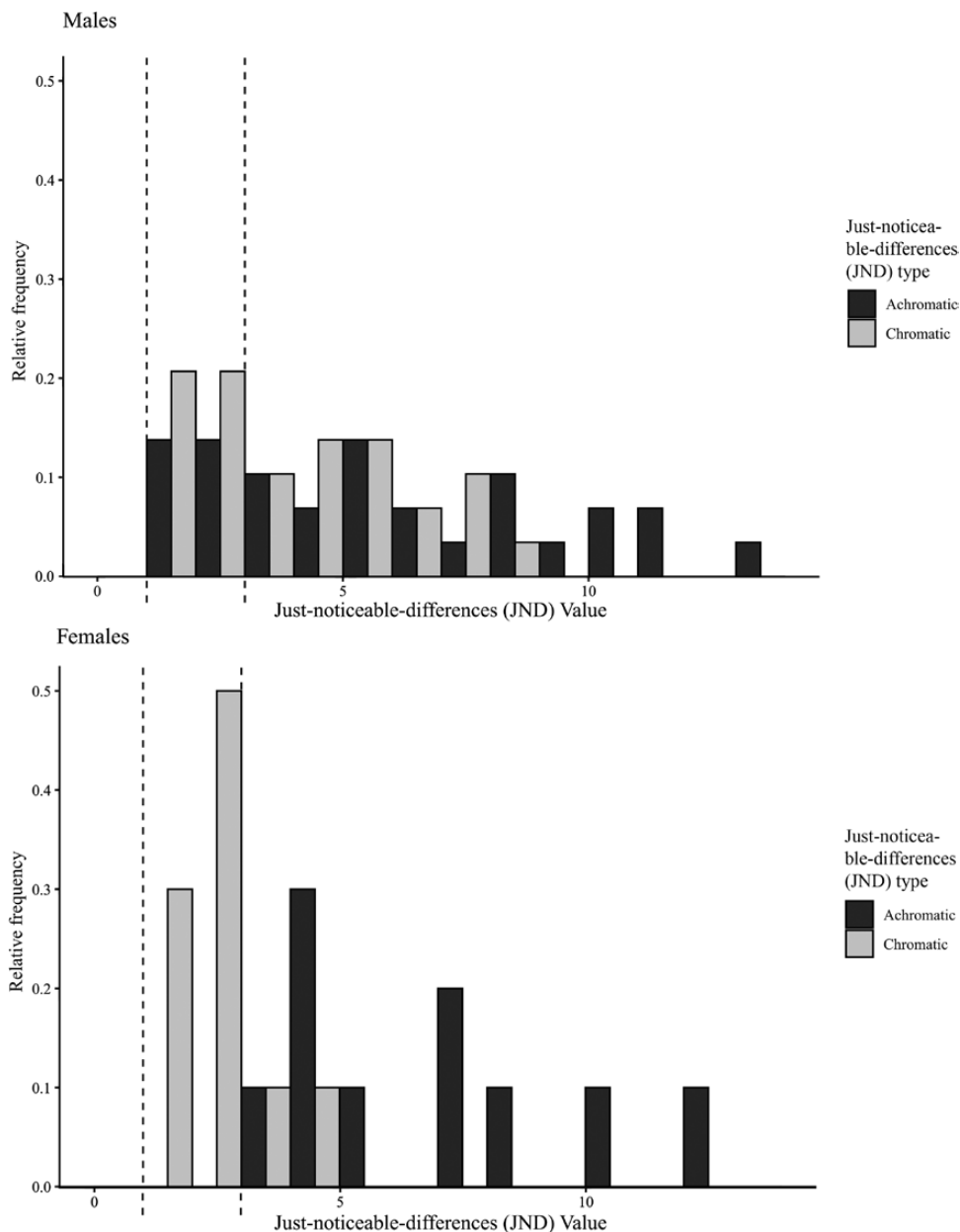
* $P < 0.05$.**Figure 5.** Histograms of relative frequencies of achromatic and chromatic just noticeable differences (JNDs) between males and their backgrounds and between females and their backgrounds. Dashed lines represent 1 and 3 JNDs.

Table 3. Comparison between treatments of controlled trials of chromatic and achromatic mean just noticeable differences of males and females before and after the experience

JND type	Sex	Predator treatment JND ± SD (N)	Baseline JND ± SD (N)	Control JND ± SD (N)	H-value	d.f.	P-value
Chromatic	Males	0.57 ± 0.39 (12)	0.96 ± 0.74 (6)	0.96 ± 0.54 (6)	3.28	2	0.1935
	Females	0.33 ± 0.21 (8)	0.54 ± 0.38 (6)	0.91 ± 0.36 (6)	8.24	2	0.0163*
Achromatic	Males	1.23 ± 1.10 (12)	1.79 ± 2.01 (6)	1.51 ± 0.86 (6)	0.67	2	0.7147
	Females	0.86 ± 0.81 (8)	1.21 ± 0.87 (6)	1.37 ± 0.62 (6)	2.70	2	0.2593

Abbreviation: H-value, Kruskal-Wallis test statistic; JND, just noticeable difference.
*P < 0.05.

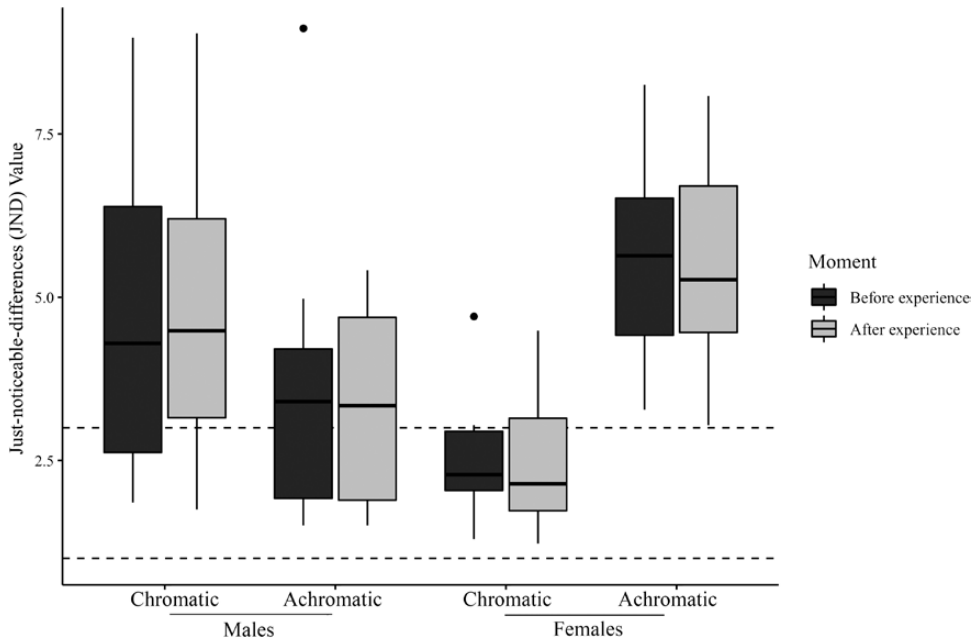


Figure 6. Boxplot of chromatic and achromatic just noticeable differences (JND) between individuals and their backgrounds before and after the Predator treatment. Dashed lines indicate one and three JNDs.

treatments, although all these had a low frequency (< 0.5%).

In the Predator treatment, the frequency distribution of behaviours differed according to the stages of predation simulation (χ^2 test: males, $\chi^2 = 159.80$, d.f. = 8, $P < 0.0001$, $N = 10$; females, $\chi^2 = 118.92$, d.f. = 10, $P < 0.0001$, $N = 6$), but did not differ by sex in each stage (χ^2 test: stage 1, $\chi^2 = 1.29$, d.f. = 2, $P = 0.5236$; stage 2, $\chi^2 = 1.29$, d.f. = 2, $P = 0.5236$; stage 3, $\chi^2 = 9.81$, d.f. = 5, $P = 0.0808$; Fig. 7). Flight and escape attempts were performed only when the predator model attacked intensively.

FLIGHT INITIATION DISTANCE

Lizards fled earlier in the Predator treatment than in the Control. The FID was shorter in the Control than

in the Predator treatment (Control, 83.41 ± 80.73 cm; Predator treatment, 327.20 ± 134.15 cm; Kruskal–Wallis test: $H = 28.40$, $P < 0.0001$; temperature covariance: $F_1 = 3.24$, $P = 0.0779$). In the Predator treatment, males had a greater FID than females (males, 404.33 ± 106.92 cm; females, 264.09 ± 122.05 cm; sex effect: $F_1 = 14.59$, $P = 0.0005$; temperature covariate effect: $F_1 = 0.05$, $P = 0.8250$), meaning that males fled earlier than females. Between sexes, there were no significant differences in the distances to refuge (males, 60.72 ± 86.83 cm; females, 56.73 ± 84.04 cm; Kruskal–Wallis test: $H = 0.03$, $P = 0.8701$). There was no significant relationship between the FID and the distance to refuge in either sex (linear regression FID vs. distance to refuge in each sex: males, $F_1 = 0.32$, $P = 0.5793$, $R^2 = 0.02$; females, $F_1 = 0.43$, $P = 0.5175$, $R^2 = 0.02$).

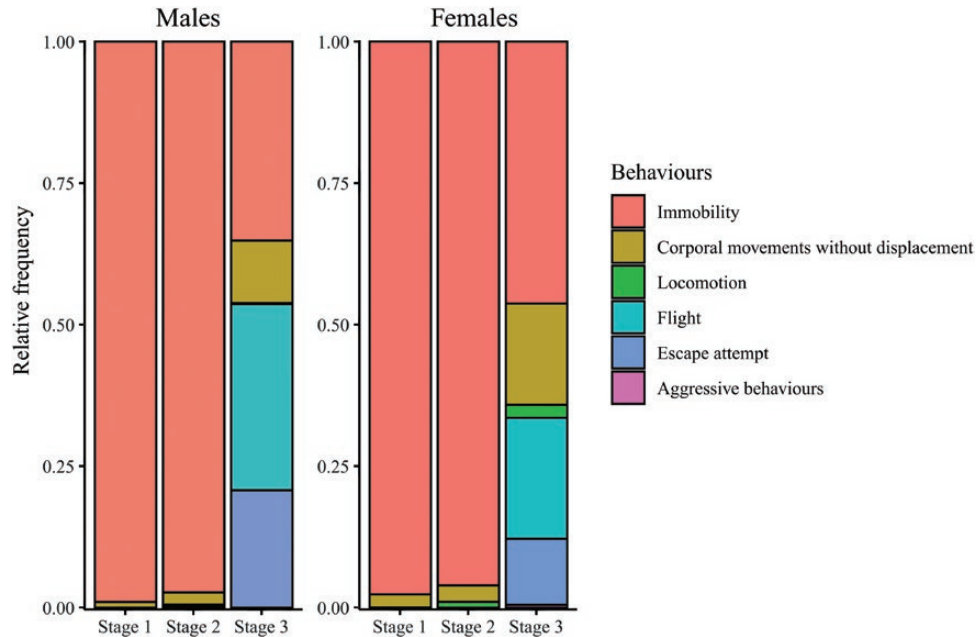


Figure 7. Distribution of relative frequencies of the behaviours during the Predator treatment for males and females, divided according to stages of predation simulation: stage 1, far gliding; stage 2, close gliding; and stage 3, intensive attack.

DISCUSSION

We found differences in coloration between the sexes of *P. achalensis* and distinct behavioural responses during the early stages of the predatory sequence, suggesting intraspecific variations of antipredator strategies. We used a study model in which sexual selection influences differences in body size, relative head size and coloration between sexes (Naretto & Chiaraviglio, 2020), but natural selection pressures also have a potential influence on sexual dichromatism.

To understand whether sexual dichromatism is associated with the antipredator strategies, we first needed to corroborate that the predators perceive the difference in coloration between sexes. We confirmed that *P. achalensis* is a species with sexual dichromatism according to avian vision. Our results showed that > 50% of the chromatic and achromatic JND values between males and females were higher than three. Males and females also occupied different regions in the tetrahedral colour space corresponding to the green (MW) and red (LW) colours, respectively. Hence, the predators will perceive different visual stimuli related to the sex of the prey. Regarding UV expression, both sexes showed low UV coloration in the dorsal region. A coloration that reflects less energy could be a benefit for a lizard living in high mountain habitats (Reguera *et al.*, 2014; Smith *et al.*, 2016; González-Morales *et al.*, 2021). Darker coloration enables faster heating, because it absorbs more solar radiation (Clusella-Trullas *et al.*, 2007);

therefore, being less reflective in the UV section might be advantageous in high-altitude environments with thermal constraints. Although this trait could improve thermoregulation of *P. achalensis*, the absence of UV expression in their dorsal region might also improve crypsis, because we have observed that the inhabited rocks showed low UV reflectance.

In addition to the sexual dichromatism, we also found differences in crypsis between males and females. On the one hand, the sexes were distinctly segregated in the colour space concerning their background. Notably, the males segregated along the MW–LW axis, whereas females segregated along the SW–LW axis. Furthermore, when the contrast with the background was evaluated in the chromatic range, females were more difficult to discriminate against their backgrounds (JND less than three) than males (JND more than three). According to avian predator vision, females are more cryptic than males. This pattern has been observed in numerous other lizard species (e.g. Macedonia *et al.*, 2009; Marshall & Stevens, 2014) where sexual selection is generally more intense in males. Sexual selection promotes conspicuousness and colour variability to attract mates and compete against conspecifics (Andersson, 1994). We also observed a remarkable variability of coloration and crypsis in males; meanwhile, the crypsis was similar among females, suggesting that predation risks among males might be more heterogeneous than in females.

On the other hand, we have analysed the crypsis of individuals against a rocky background because this is the landscape element most frequently used by lizards. Although we found that males were detected more easily and females were camouflaged better on these components, we cannot discard the possibility that vegetation cover or lichens might modify the observed cryptic patterns. Regarding the achromatic range, males and females were easily distinguishable by the predator (JND greater than three). Achromatic traits could facilitate detection of lizards, especially when they move. Achromatic mechanisms can mediate the detection of motion, form and pattern in various species, including avian raptors (Kemp *et al.*, 2015); therefore, both sexes of *P. achalensis* will benefit if they remain immobile to avoid detection. In contrast, the chromatic range is one determinant of the ability of an animal to determine how colours differ from backgrounds despite illumination conditions. These chromatic characteristics are the source of differences in crypsis between males and females of *P. achalensis* that influence intrasexual antipredator strategies, because they can be considered as the conjunction of colour and behaviour patterns.

Besides the modification of behaviour, a temporal colour change could compensate for the risks of being detected more easily. However, we found that neither of the sexes changed colour after a predation simulation to a degree detectable by avian vision, nor was the contrast to the background modified, as can occur in other species (e.g. Stuart-Fox *et al.*, 2006), suggesting that this is not a defence mechanism in *P. achalensis*. Nevertheless, in the present study the colour was analysed only through an avian vision model, whereas a potential minor colour change in *P. achalensis* could be related to intraspecific communication or it might improve the camouflage against other predators (Stuart-Fox *et al.*, 2008).

The behavioural responses at different stages of the predation sequence show how the risk of being detected modifies trade-off between costs and benefits of antipredator strategies. In controlled conditions, we observed that only the Predator treatment stimulated the lizards to perform specific behaviours (e.g. flight, escape attempt or aggressive behaviours), whereas behaviours not related to antipredator strategies (e.g. tongue flick) were performed at Baseline and Control. Both sexes showed behavioural variations between predation stages that might be closely related to crypsis. During the gliding stages (stages 1 and 2), lizards stayed immobile, which is consistent with a strategy using camouflage. Immobility increases the optimization of crypsis (Houtman & Dill, 1994; Ruxton *et al.*, 2004), especially for the type of hunting used by raptors, such as hawks, which remain in static flight to detect prey. Subsequently, in a stage of approach and

intensive attack where the prey was already detected (stage 3), the associated behaviours were mainly those of escape, because resemblance to the background was no longer a viable strategy for the lizard. During the field trials, the lizards also responded by fleeing when the raptor dummy attacked. The observed variations in behaviour during the predation sequence contribute to interpreting the prey–predator relationship as dynamic over time (Endler, 1986), suggesting that *P. achalensis* individuals evaluate the context and make behavioural decisions, as seen in many other species (Samia *et al.*, 2016).

During the controlled trials, both sexes performed the same behaviours; however, during the field trials the FID varied between the sexes, being greater in males than in females. Our results agree with the pattern presented by Samia *et al.* (2016), because cryptic lizards permitted a closer approach by predators than conspicuous lizards. We suggest that the compensation for the risk of having conspicuous colours is the behavioural response of fleeing at a greater distance from the predator. This pattern has been seen in several lizard species (Johnson, 1970; Stone *et al.*, 1994; Lailvaux *et al.*, 2003; Plasman *et al.*, 2007). When analysing the proximity to the refuge, which could affect animal predation risks, we found that this distance did not influence the distance at which the lizard initiated flight. This observation might be explained by a reduced perception of risk, usually observed in high-altitude environments (Samia *et al.*, 2016). Another explanation is the fact that Achala copper lizards were found to be active close to their refuge. Hence, flight seems to be influenced mainly by intrinsic sexual factors, such as coloration. Nevertheless, we must consider the existence of other factors affecting the escape behaviour, such as the costs of opportunities to obtain resources and to perform intraspecific interactions, in addition to predator traits. Additionally, Samia *et al.* (2016) observed that except for crypsis, morphological and physiological traits had weak influences on FID. Therefore, differences in crypsis between the sexes affect antipredator strategies through changes in escape behaviour during the approach stage of predation, as we have seen in *P. achalensis*.

In conclusion, we confirm, in part, our hypotheses regarding predation stages and different crypsis between sexes modulating antipredator strategies, whereas the ability of individuals to change colour was not found to be a defence mechanism. Our results also show that the distance at which lizards initiate flight is a key factor to compensate for the predation risks caused by the differential coloration between sexes. Finally, this study provides additional support to our understanding of antipredator strategies as a combination of behavioural and phenotypic traits.

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