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A potential deimatic display revealed in a lizard

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Conspicuously coloured signals may evolve via sexual selection to be ornaments or armaments, thereby conferring a fitness advantage to their bearer. Conversely, conspicuous colours may also evolve under natural selection as either aposematic signals or deimatic displays that deter attacks from predators. While conspicuous colour patches may evolve for one purpose (e.g. quality indicators), they may later be co-opted for another (e.g. anti-predator defence). *Phrynocephalus mystaceus* is a cryptic agamid lizard with flaps in both sexes that when folded against the head are inconspicuous, but when deployed are predicted to be highly conspicuous and to increase the appearance of body size. We tested whether head flaps play a role in social signalling via courtship or as status signals during contests in both sexes. We also tested whether the head flaps have an anti-predator function by simulating predatory encounters. Head flaps were never deployed in courtship or during contests and, therefore, are unlikely to be under sexual selection. However, head flaps and their deployment during simulated predatory encounters were consistent with the predictions associated with deimatic display theory. First, head flaps were similar in form and function between sexes. Second, they were highly conspicuous to both avian and snake predators. Third, there was a rapid transition from crypsis to conspicuousness when they deployed their head flaps during a late stage of predation, the subjugation phase, consistent with an ambush. Confirmation of the deimatic display hypothesis will require future testing of receiver responses.

ADDITIONAL KEYWORDS: anti-predator behaviour – deimatic display – lizard – lizard behaviour – signal.

INTRODUCTION

Conspicuous signals typically evolve because they confer a reproductive advantage to the bearer (sexual selection) or because they improve survival, such as aposematic signals (natural selection) (Darwin, 1859, 1871; Andersson & Iwasa, 1996; Stevens, 2015; Loeffler-Henry *et al.*, 2021; White & Umbers, 2021). Signals that evolve under natural selection convey that the bearer represents unprofitable prey either because they are distasteful and/or have physical defences such as spines or armour (e.g. aposematism; Bates, 1862; Pekár *et al.*, 2017) or because pursuit or attack is risky or has a low probability of reward (sometimes referred to as pursuit deterrent signals; e.g. Caro, 1995; Font *et al.*, 2012). Some conspicuous defensive displays are flashed by normally cryptic prey while fleeing and serve to misdirect predators because they continue searching for conspicuous prey when the prey has already settled and returned to its cryptic state (Loeffler-Henry *et al.*, 2021). Conversely, startle or deimatic behaviour also involves flashing conspicuous displays, but this occurs when the animal is stationary and not fleeing (Umbers *et al.*, 2015, 2017).

Part of the effectiveness of deimatic displays is that they rapidly transition from being cryptic to being predicted to be highly conspicuous and/or because they change shape or increase in size. Deimatic displays may occur in animals that are either defended (as in aposematism) or undefended. However, a key difference between the two is that aposematic signals must be associated with a cost to the attacker because of an unpleasant experience (White & Umbers, 2021) while a deimatic display can be a bluff (i.e. dishonest; Umbers & Mappes, 2016) that seeks to exploit the sensory system of the receiver and elicit a startle or fear response in a potential predator, thereby discouraging or halting an attack (Umbers *et al.*, 2017).

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Deimatic displays have evolved many times independently in a wide range of species from diverse invertebrate and vertebrate lineages, including cuttlefish (Langridge, 2009), lepidopterans, phasmids, mantids and various orthopterans. These species may rapidly change shape (e.g. lepidopteran larvae) or flash a conspicuous colour patch such as an eye spot (Cott, 1940; Bedford & Chinnick, 1966; Maldonado, 1970; Edmunds, 1974; Stevens, 2015) or even use auditory cues such as in the tettigoniid *Poecilimon ornatus* (Kowalskia *et al.*, 2014). The effects of deimatic displays are also amplified by the animal's behaviour. For example, newts use the unken reflex to contort their body and display their orange venter (Johnson & Brodie, 1975), bluetongue skinks gape, inflate their bodies and hiss (Badiane *et al.*, 2018), and frill-neck lizards (*Chlamydosaurus kingii*) rapidly deploy conspicuous frills while gaping their mouth and responding aggressively (Perez-Martinez *et al.*, 2019).

Unlike aposematic signals, deimatic displays are much less well understood and many suspected deimatic displays have not been objectively studied (Umbers *et al.*, 2015, 2017). Furthermore, we need more data on the context in which species use deimatic displays and at what stage during an encounter with a potential predator an individual will resort to a deimatic display. The stage at which a startle response is initiated could be important because late-stage displays may have a greater effect on the sensory system of a potential predator by virtue of their proximity (Umbers & Mappes, 2015; but see Vallin *et al.*, 2006).

In contrast to natural selection, signals under sexual selection are costly when they increase conspicuousness or detectability and thereby reduce survival, although this is traded-off against reproductive fitness (Ryan *et al.*, 1982; Andersson, 1994; Stuart-Fox *et al.*, 2003). One way to ameliorate the costs of conspicuous social signalling is to only expose signals to conspecific receivers during key moments such as courtship or when settling a contest with a rival (Hutton *et al.*, 2015; White *et al.*, 2015; Whiting *et al.*, 2003). By 'flashing' a signal, the emitter may be more likely to gain the attention of the receiver while also reducing the time they are conspicuous to a predator (Whiting *et al.*, 2003).

Whatever their form, signals frequently have a dual function and contain different sources of information for multiple receivers. For example, bright colours in males may signal information about fighting ability to rivals while signalling some aspect of quality to females (Berglund *et al.*, 1996). There has been considerable interest in signals used in social and sexual selection, but very little investigation of signals or displays that may function in multiple contexts such as anti-predator behaviour and conspecific social signalling (but see Cott, 1940; Caro, 2009). For example, conspicuous structures such as ornaments or armaments may evolve for one purpose (sexual selection) and later be co-opted for another, such as surviving a predation attempt (natural selection). Any survival benefit from one of these structures could set the stage for selection.

The secret toad-headed agama *Phrynocephalus mystaceus* (Fig. 1) is a central Asian lizard in which both sexes have conspicuous red cheek flaps that fold against the side of their head. The dorsal or posterior surfaces of the cheek flaps are brown, while the ventral or anterior surfaces are red. Consequently, when the lizard is at rest and the flaps are folded it is cryptic (Fig. 1A), but when the flaps are deployed they are red and also serve to increase the lizard's perceived size (Fig. 1B; Supporting Information Video S1). Given the

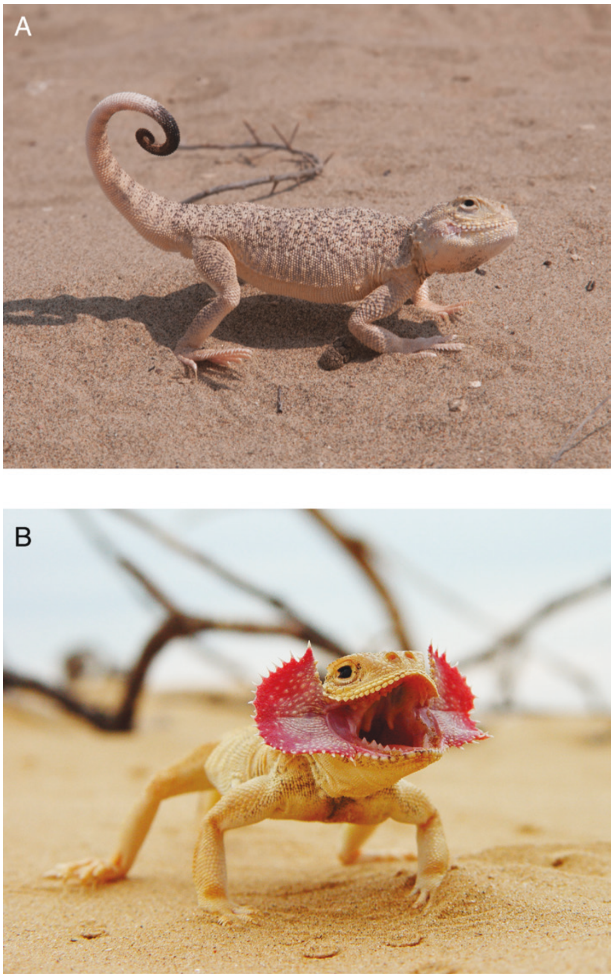

Figure 1. A, a male *Phrynocephalus mystaceus* with head flaps concealed against the side of his head in a cryptic state. Photo by Martin Whiting. B, an individual that has deployed its head flaps, while also gaping. Photo by Qiang Dai.

conspicuous nature of these flaps, they may also have evolved to signal some aspect of quality regardless of whether this was the original driver of selection or whether they were co-opted through sexual selection. This species also uses complex tail waving, which has previously been suggested to play a role in social communication, particularly in males (Panov *et al.*, 2004), but the function of the head flaps is unknown. We experimentally tested two non-mutually exclusive hypotheses: first, we tested the social signalling hypothesis – that flaps play a role in mate choice and/or intrasexual competition (i.e. potentially in sexual selection). Under this hypothesis, we predicted that the flaps would be deployed by males when courting females and/or during male–male contests. We also predicted that males would have larger head flaps than females if they played a role in contest competition. Alternatively, flaps may have an anti-predator function. The anti-predator hypothesis predicts that flap flaring would be used during predatory threats and may or may not exhibit sexual dimorphism/dichromatism. In the context of anti-predatory behaviour, we also conducted a *post hoc* examination of our anti-predator data to examine whether they conformed to the predictions associated with deimatic display theory, which have recently been refined (Umbers *et al.*, 2015, 2017; Umbers & Mappes, 2016). In the case of the deimatic display hypothesis, following Umbers *et al.* (2017), we predicted: (1) the head flaps are perceived as highly conspicuous and novel in the case of a visual display; (2) they are dynamic and need to be activated, thereby transitioning from a cryptic to conspicuous state; and (3) they are more likely to be deployed late in an encounter with a predator such as immediately preceding attack or during contact or subjugation, thereby providing greater impact on a receiver's sensory system albeit at greater risk. These are not mutually exclusive hypotheses and they do not address how head flaps evolved initially, but merely their current function.

MATERIALS AND METHODS

EXPERIMENTAL SUBJECTS AND STUDY AREA

This study was carried out in the Tukai Desert ~10 km south-west of Huocheng, Xinjiang Province, China, during June–July 2012. This habitat is a sandy desert with shifting dunes and sparse vegetation. *Phrynocephalus mystaceus* were most common in the dune streets – the low-lying areas between adjacent dunes, typically in slightly sheltered areas, where they live in burrows. Lizards of this body size, in open sandy habitats, are vulnerable to predation by a range of avian (e.g. kestrels) and snake (either through ambush or active searching) predators (De Schauensee, 1984; Pianka, 1986; Greene, 1988; Pianka & Vitt, 2003; Shi *et al*, 2007; Yang & Chen, 2021). This study had two components used to test our hypotheses: first, we captured lizards and used them in controlled experiments in outdoor enclosures. Second, we conducted a series of behavioural experiments on free-ranging individuals in the wild. Lizards were caught by lassoing using a 3-m telescopic pole with a 10–15-cm dental floss lasso. The lasso was dropped over the lizard's head and the lizard was then lifted off the ground. This is a standard procedure for catching many species of lizards and does not harm the animal (Medica *et al.*, 1971; Wilson, 2016). Lizards were placed in a numbered cotton bag and kept in the shade until they were processed on the same day. On the day of capture, we measured snout–vent length (SVL) to the nearest 1 mm using a plastic ruler and the length and width of the right head flap using digital calipers (nearest 0.01 mm). To examine how conspicuous the display was, we measured the spectral reflectance of the head flaps (proximal and distal surface) in addition to the dorsum and mouth of the lizard (Supporting Information Fig. S1) using a Jaz spectrometer (Ocean Optics Inc., Dunedin, FL, USA) with a PX2 light source. We took two or three measurements per body region using a fixed probe holder at a constant distance of 5 mm and held at 90° to the skin surface, encompassing an area of 6 mm^2. Measurements were relative to a dark and white 99% WS-1 (Labsphere) standard between 320 and 700 nm, which is the broadest range of wavelengths known to be visible to lizards (Loew *et al*., 2002). To quantify the lizards' signalling environment, we also measured the spectral reflectance of the desert sand as a background ($N = 10$) and we measured irradiance using a separate irradiance channel held at ground level and parallel to the ground ($N = 42$), thereby capturing side-welling light. Measurements were taken during the peak of the lizard's activity period (10:00–12:00 h). Lizards were used in behavioural experiments the day following capture and released at their point of capture immediately following the experiments, using GPS coordinates. We added a small mark using a xylene-free paint pen to ensure that we did not reuse the same lizard.

FIELD ENCLOSURE EXPERIMENTS

Courtship and/or male contest competition

To test the social signalling hypothesis, we conducted staged interactions in outdoor arenas within sexes (male–male, $N = 14$; female–female, $N = 17$) and between males and females to test whether the flaps were used in contests and/or during courtship. We were not able to elicit courtship behaviour (opposite sex trials) in the arenas and thus did not analyse and report these data. For their first contest, same-sex individuals were paired with the individual next closest in size. Following their first trial, lizards were paired randomly against the remaining individuals. This design is appropriate because we were simply interested in whether they use their head flaps during contests and not how physical traits influenced contest outcome. Each individual was restricted to two contests per day and no more than three contests in total except for a single male which was used in four contests. We conducted a total of 14 male–male and 17 female–female contests over a 4-day period. All trials were 15 min in duration and conducted in a neutral arena (i.e. novel to trial participants) measuring 74 × 62 cm. The enclosures were outdoors at the study site, in the same habitat (sandy desert substrate) where lizards were field-collected. We conducted trials within the normal lizard activity period under the shade of a tree, which provided mixed shade during the late morning and prevented heat stress. All lizards were released after 1–2 days.

ANTI-PREDATOR HYPOTHESIS

We tested each lizard ($N = 38$: 14 males, 17 females, seven juveniles) in a 2.4 × 2.4-m arena in the field, on their natural sand substrate. We used a larger arena than for the social trials to enable us to manipulate the model predator more easily and to give the lizards adequate space to respond and run, if necessary. Each lizard had 1 min to acclimatize before being presented with either the bird predator or a stick (control) (balanced presentation order). Both were attached to 2-m poles with tape. The stick was T-shaped and the same width as the bird (70 cm). The bird was a colour-printed image of a common kestrel in flight, ventral view, with wingspan of 70 cm, 30 cm from head to tail and mounted on a laminated board. We filmed all trials starting with 1 min of acclimatization followed by 2 min of scaring, during which the bird/stick was repeatedly 'flown' over the lizard (~8-10 times) and also held in a 'hover' above them (~50 cm, 10 s). The researcher kept low outside the arena and was not easily visible to the lizard. If they flared their head flaps before the 2 min were up, we terminated the trial. After 2 min we gently pinned the lizard in the sand, behind the neck, with the bird or stick, to see if they would flare their flaps. If they did not, we then picked them up and gently tapped their snout ten times with a finger.

FIELD EXPERIMENTS WITH FREE-RANGING INDIVIDUALS IN THE WILD

We conducted a second experiment to verify the results from our enclosure trials. Although lizards used tail signalling in the enclosure trials, we wished to exclude the possibility that natural behaviour was constrained by the experimental setup. Therefore, we tested for head-flap displays in free-ranging individuals by presenting them with (1) a same-sex individual ($N = 13$ male–male; 12 female–female); (2) an opposite sex individual (nine male–female; 15 female–male); and (3) a model predator ($N = 25$, seven males, 11 females, seven juveniles). Trials were 5 min long and terminated if there was fighting. Test lizards were attached to ~1 m of dental floss and lowered on the end of a 3-m pole to ~1 m from the resident. We alternated in presenting the same sex or different sex first in a balanced order after randomizing the first trial. Tethered lizards were used no more than three times. After each lizard was presented with the same and opposite sex, we then performed a bird-predation trial in which a researcher (M.J.W.) rapidly approached and chased the lizard with the model bird in hand. We scored gaping, flaring of flaps and lunge-bites. Once lizards were caught and in hand, we lightly tapped the nose ten times if they had not already flared their head flaps.

Finally, we conducted a third experiment with free-ranging lizards ($N = 25$: six males, nine females, 12 juveniles) that we had not previously worked with. In these trials, we simulated a 'surprise' predator attack by lassoing the lizard (method as before). During this process, lizards were aware of the researcher's presence but the researcher was crouched at a distance at which they did not appear to be threatened by our presence because they behaved normally. We gave the lizards 2 min to get used to our presence. We also planned to record tail displays, in case they were used as a pursuit deterrent signal (e.g. Cooper, 2001), but none did. When lizards were presented with a lasso they either ignored it completely or some lizards jumped and attempted to bite the noose in the same way they would attack a flying insect. Once in the lasso, the lizard was rapidly lifted off the ground and at this point they reacted defensively. We simply scored whether the lizard exposed its flaps before applying a small paint mark to the side of the body to ensure we did not sample the same lizard twice following release at the point of capture.

VISUAL MODELLING

We conducted visual modelling to determine if the head flaps were conspicuous to a snake or bird predator (deimatic display hypothesis) and also to another lizard (social signalling hypothesis). We calculated chromatic (ΔS) and luminance (ΔL) contrast for the mouth, flap and dorsal regions against an average sand background ($N = 10$ spectral reflectance curves) to assess conspicuousness using knowledge of the lizard, avian and snake visual system (Sillman *et al.*, 1997; Vorobyev & Osorio, 1998; Barbour *et al.*, 2002; Stuart-Fox *et al.*, 2008). We applied the receptor noise model of Vorobyev & Osorio (1998) (VO) in the *R* package *pavo* (Maia *et al.*, 2013). Prior to analysis, we smoothed each individual's spectral reflectance curve for each body region (LOESS smoothing = 0.2) to remove electrical noise and correct negative reflectance values (added minimum value). From the VO model, we calculated discrimination thresholds as 'just noticeable differences' (JNDs) from each colour patch and individual spectral reflectance curve. The VO model requires data on spectral sensitivities of cone pigments for the UV (UVS), short (SWS), medium (MWS) and long wavelengths (LWS) for each visual system along with environmental irradiance measures which we obtained in the field (average of $N = 23$ spectral curves). Spectral sensitivities for *P. mystaceus* are not available so we used those of another agamid lizard, *Ctenophorus ornatus* (Barbour *et al.*, 2002). We assumed λ_{max} for the UVS, SWS, MWS and LWS to be 360, 440, 493 and 571 nm, respectively, along with photoreceptor class densities of 1:1:3.5:6 (UVS:SWS:MWS:LWS). In addition, we modelled visual discrimination thresholds for an average avian predator with a UV photoreceptor (λ_{max}: UVS = 372 nm; SWS = 456 nm; MWS = 544 nm and LWS = 609 nm) with photoreceptor densities of 1:2:3:3 (UVS:SWS:MWS:LWS). While avian predators are the most likely threat to *P. mystaceus*, a few snake species also co-exist, so we also calculated the discrimination of body regions against a sand background under a snake visual system with λ_{max} = 360, 482 and 554 nm (UVS, SWS, LWS) and photoreceptor densities of 1:1.6:7.3. In all cases, we derived receptor quantum catches between 300 and 700 nm wavelengths and applied the von Kries transformation to the spectral curves. In all cases, we assumed a signal-to-noise ratio (Weber fraction) of 0.10.

STATISTICAL ANALYSIS

Given the low frequency of flap flaring under most experimental conditions, we qualitatively report the frequency of behaviours during trials. For subjugation analysis, flaps were flared quite frequently, so we compared the frequency of flap flaring using Fisher's exact tests on a 2 × 2 contingency table comparing our observed to expected frequencies assuming flap frequency was random (Agresti, 2007). Sex differences in chromatic and achromatic conspicuousness (i.e. ΔS and ΔL) along with sexual dimorphism in flap height and length were tested using multi-response models in the *MCMCglmm* package (Hadfield, 2010). Multi-response models explicitly model trait covariance (i.e. covariance between flap height and length, as well as ΔS and ΔL) in a single model for each body region of interest. For contrast (ΔS and ΔL models), we included body mass to account for the possibility of condition-dependent expression of these traits. In models exploring sexual dimorphism of flap morphology, we included log-transformed body size to account for scaling between body size and flap morphology. Overall, we ran 1 000 000 Markov chain Monte Carlo (MCMC) iterations and a thinning interval of 100, discarding the first 3000 iterations (as burn in). We also checked that autocorrelation between samples of the posterior distribution was low (i.e. lag values < 0.10), and that the chain was mixing well (visual inspection and evaluating effective sample size of the posterior distribution). In all cases, chains were mixing well (effective sample sizes >5000) and there was low autocorrelation (lag < 0.05). For our models, we used default uniform priors for the fixed effects and inverse-Wishart priors for the variance–covariance matrix.

ETHICAL NOTE

We obtained animal ethics approval for this study from the Chengdu Institute of Biology (Chinese Academy of Sciences; approval number: 2018016). We also followed the guidelines of the Animal Behavior Society (ABS)/Association for the Study of Animal Behaviour (ASAB) Guidelines for the treatment of animals in behavioural research and teaching. Our project was non-invasive and we minimized handling and stress as much as possible. Lizards were all returned to the wild as soon as an experiment was complete.

RESULTS

SOCIAL SIGNALLING HYPOTHESIS

Courtship and/or male contest competition

If the flaps were used in males contests, we would expect larger flaps in males. When controlling for body size (SVL), we did not find significant differences in flap morphology between the sexes [$B_{male–female} = –0.023$, 95% confidence interval (CI) = –0.095–0.049, pMCMC = 0.529]. We would also expect that the flap and mouth colour would be sexually dichromatic. However, chromatic contrast of the mouth (contrast: $B_{male–female} = –0.133$, 95% CI: –0.38 to 0.09, pMCMC = 0.27) and flap ($B_{male–female} = 0.33$, 95% CI: –0.07 to 0.726, pMCMC = 0.10) did not differ significantly between males and females when using a lizard visual system. In contrast, luminance contrast was higher in males compared to female flaps ($B_{male–female} = 1.92$, 95% CI: 0.95–2.88, pMCMC < 0.001), whereas this was not the case for the mouth ($B_{male–female} = –0.43$, 95% CI: –1.48 to 0.548, pMCMC = 0.41)

In both neutral arena trials and tethering trials where free-ranging individuals in the wild were presented with either a member of the same or opposite sex, we did not observe a single individual expose or flare their head flaps. With the exception of courtship trials in neutral arenas, we observed a high frequency of behavioural responses through signalling using tail waving (Fig. 2). This strongly suggests that we were able to elicit behavioural responses but that tail-waving, and not the flaring of flaps, is used to signal in a social context.

ANTI-PREDATOR HYPOTHESIS

Response to a bird model predator

When lizards in an outdoor arena were presented with a bird model predator most individuals responded by running (61%) and a low proportion by defensive behaviour (gape–lunge–bite, 8%) but only a very small proportion flared their flaps (3%; Supporting Information, Table S1). Conversely, in response to the stick (control), 10% ran a short distance, one individual gaped but none flared their flaps. During trials with free-ranging lizards in the wild, all lizards responded by initially running. Thereafter, they responded by gaping (20%) and then by a lunge–bite (20%), but only 12% responded by flaring their flaps (Fig. 3). None responded with tail waving.

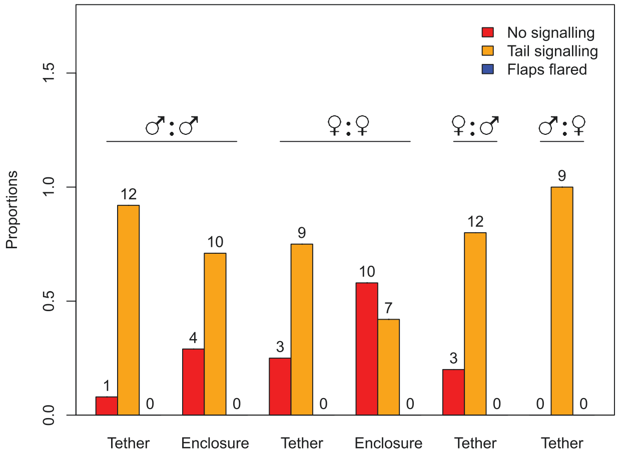

Figure 2. Results of social trials in which same- and opposite-sex individuals were paired either in outdoor arena trials or in the wild through the introduction of another individual to a free-ranging lizard. The proportion of individuals that responded by either deploying their flaps, using signalling via tail waves or that did not respond are presented. We do not present results for opposite-sex arena trials because these lizards were less responsive, probably because of the artificial environment. Sample sizes are given above bars.

Conspicuousness to an avian and snake predator and sexual dichromatism

Males and females had similar spectral reflectance curves for the mouth, head flaps and dorsum, and both sexes had a sharp peak in the UV of the mouth (Fig. 4). When the head flaps are deployed (Fig. 1B), the proximal surface of the flap is predicted to be highly conspicuous to an avian predator (Fig. 5A). Luminance and chromatic contrast of the flaps, under an avian visual system, differed between males and females, but only significantly so for luminance (Luminance: $B_{\text{male–female}} = 1.48$, 95% CI = 0.64–2.33, pMCMC < 0.001; Chromatic: $B_{\text{male–female}} = 0.55$, 95% CI = –0.05 to 1.13, pMCMC = 0.06; Fig. 6A), whereas the same was not true of the mouth (Luminance: $B_{\text{male–female}} = -0.80$, 95% CI = –1.97 to 0.38, pMCMC = 0.18; Chromatic: $B_{\text{male–female}} = -0.28$, 95% CI = –0.67 to 0.10, pMCMC = 0.16; Fig. 5B). The dorsum differed in chromatic but not luminance contrast (Luminance: $B_{\text{male–female}} = -0.28$, 95% CI = –1.02 to 0.49, pMCMC = 0.47; Chromatic: $B_{\text{male–female}} = 1.48$, 95% CI = 0.01–2.06, pMCMC = 0.16; Fig. 5C). In contrast, chromatic contrast under the snake visual system only differed significantly between the sexes in the dorsum (Flap: $B_{\text{male–female}} = 0.36$, 95% CI = –0.04 to 0.71, pMCMC = 0.056, Fig. 5D; Mouth: $B_{\text{male–female}} = -0.09$, 95% CI = –0.29 to 0.11, pMCMC = 0.36, Fig. 5E; Dorsum: $B_{\text{male–female}} = 0.98$, 95% CI = 0.14–1.77, pMCMC = 0.02, Fig. 5F), whereas flaps differed significantly between the sexes in luminance contrast (Flap: $B_{\text{male–female}} = 1.94$, 95% CI = 0.90–2.92, pMCMC < 0.001, Fig. 5D; Mouth: $B_{\text{male–female}} = -0.39$, 95% CI = –1.29 to 0.56, pMCMC = 0.39, Fig. 5E; Dorsum: $B_{\text{male–female}} = -0.38$, 95% CI = –1.14 to 0.41, pMCMC = 0.34, Fig. 5F).

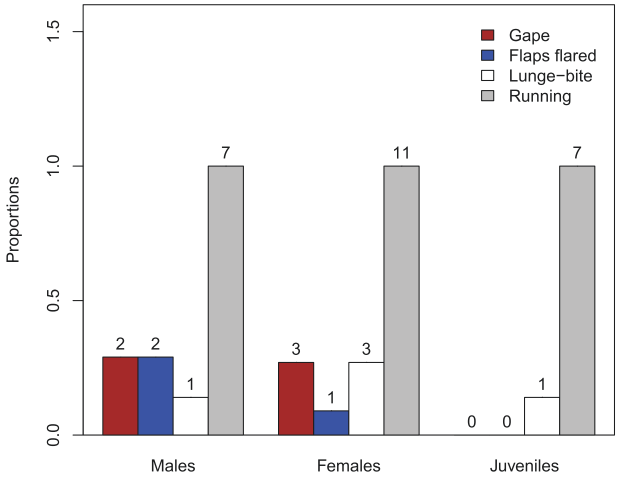

Figure 3. Behavioural responses of free-ranging lizards in the wild to a bird model predator on the end of a pole.

Response to 'subjugation'

We lassoed 25 lizards and 21 (84%) of these responded by flaring their flaps (but not tail waving). The frequency with which lizards flared their flaps was different than expected by chance (Fisher's exact test; odds ratio = 5.06, $P = 0.016$; Fig. 6). In the process of flaring their flaps, all lizards also gaped.

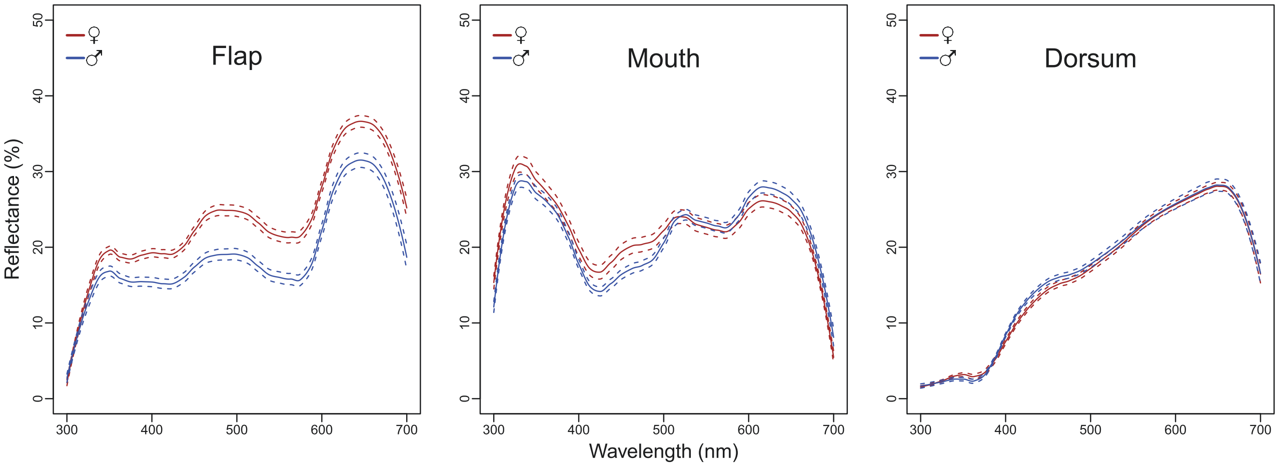

Figure 4. Mean spectral reflectance curves for male and female lizards for (A) flap, (B) mouth and (C) dorsum.

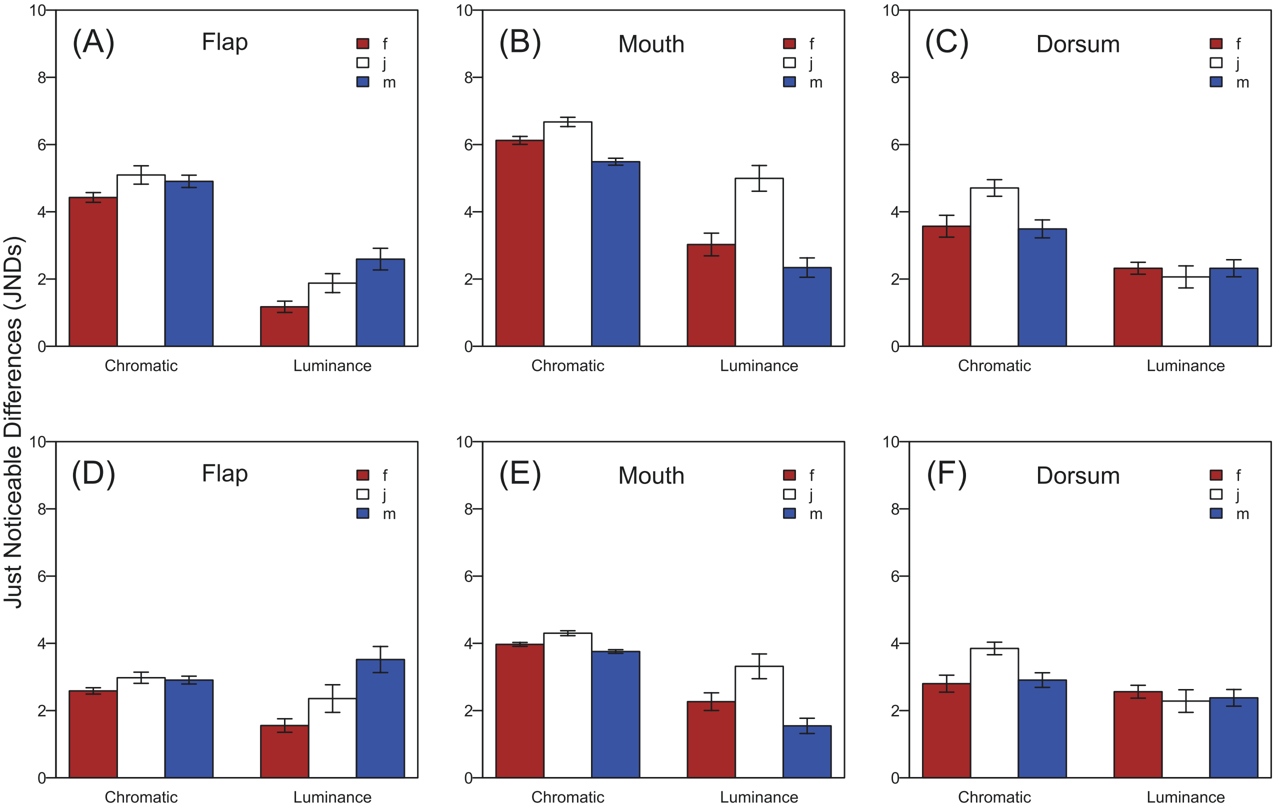

Figure 5. Conspicuousness of the lizards' head flaps, mouth and dorsum in Just Noticeable Differences (JNDs) in relation to a bird (A–C) and snake (D–F) visual system for the chromatic and luminance channels as viewed against a sand substrate for males ('m'), females ('f') and juveniles ('j').

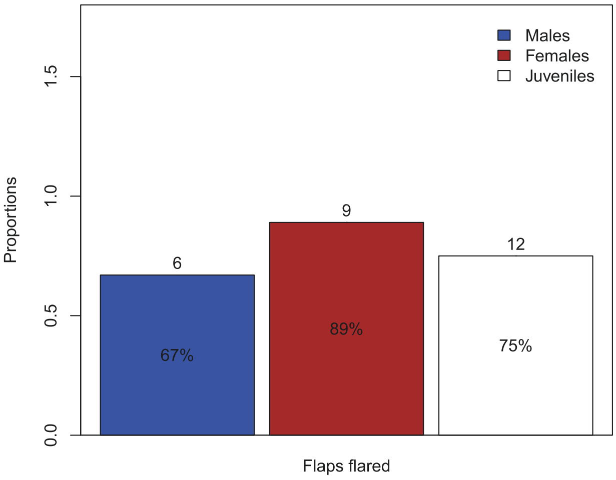

Figure 6. Proportion of individuals that responded by deploying their head flaps when a 'predator ambush' was simulated by lassoing the lizard.

DISCUSSION

In two different experiments in which lizards encountered same-sex rivals either in outdoor neutral arenas in the field or as free-ranging individuals in the wild, they never deployed their head flaps. In a large proportion of these trials they used aggressive tail waving, confirming that the design of the experiments was sufficient for eliciting social responses. We also paired males and females to test whether the head flaps were used in courtship and as a potential signal of male quality to females. Again, males in the wild approached and signalled to females in presumed courtship using tail waves but did not expose their head flaps. Furthermore, head flaps were similar in size between males and females. If head flaps played a role in social signalling in one sex more than the other (typically males), we would predict larger flaps in that sex. We found no evidence that their head flaps are used in any form of social signalling and therefore they are not under sexual selection. We then focused on the hypothesis that the head flaps have an anti-predator function. Interestingly, males had head flaps that were predicted to be more conspicuous to an avian visual system than the flaps of females. This was not the case for other body regions (mouth, dorsum) or for the snake visual system. This difference was surprising. It might be that males are more vulnerable to predation because of their behaviour, and perhaps experience stronger selection as a consequence. This is a question worth investigating in the future.

We conducted three different experiments which ultimately confirmed that head flaps were used in anti-predatory behaviour but only under specific circumstances, suggesting context-specific responses consistent with deimatic display theory. In the first two experiments (outdoor arena and in the wild) we flew a life-sized cut-out of a local raptor attached to the end of a long pole and gradually increased the level of threat by flying the bird closer to the lizard and with greater intensity. The typical response was to run. Lizards appeared highly reluctant to expose their flaps and only a small percentage did so. It was only in the final experiment when lizards were lassoed from a distance that lizards consistently responded by flaring their flaps and gaping at the same time. In this experiment, we simulated an ambush attack from a predator, which is what might occur with an aerial attack by a bird or an ambushing snake in which they immediately find themselves in a subjugation phase of predation or at very close proximity to a predator. This response is consistent with what we predicted (*post hoc*) for deimatic displays. First, in deimatic displays there is a rapid transition from a cryptic to a conspicuous state (Umbers *et al.*, 2017). *Phrynocephalus mystaceus* are cryptic (all brown) until they rapidly deploy their head flaps. Second, the effect of a startle response that depends on overwhelming the sensory system of a receiver could be more effective in close proximity to the predator. The lizards only deployed their head flaps during a simulated subjugation phase. Third, the form of the display and associated behavioural responses of the prey can amplify the effect of the display. To this end, the flaps need to be highly conspicuous to a potential predator. Our modelling showed that the flaps were predicted to be more conspicuous to both a bird and snake predator. Furthermore, the conspicuous flaps in conjunction with an open-mouth gape also greatly increases the perceived size of the head. At the same time, the lizard will also inflate its body. The lizards thus use a rapidly deployed and a predictably conspicuous display at very close range to a potential predator in a way that has a high probability of overwhelming the sensory system of the receiver in a fashion similar to what occurs in blue-tongue skinks and frill-neck lizards (Badiane *et al.*, 2018; Perez-Martinez *et al.*, 2019).

We found that *P. mystaceus*, once detected, used flight as their first response. These lizards are capable of rapid sprinting that quickly gives them some distance from a predator (our pers. obs). It was only when we simulated a surprise attack similar to an early stage of subjugation during an ambush that they consistently deployed their head flaps. This context-specific response is reminiscent of what happens in cuttlefish, which have species-specific anti-predator responses and only use deimatic displays for a smaller class of non-threatening fish species while otherwise using rapid swimming to escape (Langridge, 2009). Cuttlefish also were more likely to flee from predatory fish that are less visually oriented and more reliant on chemical cues (Langridge *et al.*, 2007). We did not experiment with different predator types except for a pilot study in which we presented lizards ($N < 10$) in outdoor arenas in their natural habitat with a model snake predator. We were unable to elicit a response, which could be because rapid flight is a logical reaction to a snake. Animals that are capable of rapid flight, such as cuttlefish, may have more escape options and be more likely to have context- or predator-specific escape responses (Langridge *et al.*, 2007).

Currently, we need more empirical studies testing the predictions of deimatic display theory and how context may influence an animal's decision to deploy a deimatic display. Our *post hoc* analysis focused on the first stage of this process, which is to test whether anti-predator behaviour conforms to the predictions of deimatic display theory. Our experiments and measures of anti-predator responses were very much focused on the perspective of potential prey. The next stage is to test the response of a potential predator to establish whether the display does indeed induce a startle response by overwhelming their sensory system. Additionally, although we did not detect a dual function for this display, testing for multiple signals or displays across social and predation contexts will help uncover the evolution of complex displays. Lizards may well be a good model in this respect. For example, the frill-neck lizard uses its frill in an anti-predator context in a similar fashion to *P. mystaceus* (Perez-Martinez *et al.*, 2019). However, the frill is sexually dimorphic (larger in males) and also used in male–male contests and by females during social signalling (Shine, 1990), suggesting a rare example of a potential deimatic display also used in social signalling. Furthermore, both sexes of many species of lizards have brightly coloured mouths that are exposed during encounters with potential predators (M.J.W., unpubl. data). It may be that deimatic displays are more common than we think. Future work on deimatic displays could make a significant contribution to our understanding of sensory ecology more broadly.

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DATA AVAILABILITY

Data and code used to reproduce the results in this paper can be found on the Open Science Framework (OSF) at https://osf.io/2ungd/.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Video S1. An adult *P. mystaceus* extending its head flaps while inflating its body and giving an open-mouth threat. In this case the individual did not fully extend its flaps.
Figure S1. Location of spectral reflectance readings.
Table S1. Response of lizards to a model bird predator in arena trials.