Mirrored images but not silicone models trigger aggressive responses in male Common wall lizards

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Abstract. Disentangling the effects of single releasers in animal communication is a demanding task because a releaser often consists of a combination of different key stimuli. Territorial communication in reptiles usually depends on visual, chemical, and acoustic stimuli, but the role of each of them depends on phylogeny. Lacertids are modern lizards that rely mainly on chemical cues for their communication, but they also use aggressive displays based on visual recognition. We experimentally tested the visual stimuli that release an aggressive response in the males of a typical lacertid, the common wall lizard (*Podarcis muralis*), testing the effects of silicone models and mirrored images in captivity. The response to models and control (a blank sheet) was not significantly different and these stimuli did not release any aggressive behaviour. On the contrary, the reflected image in a mirror caused overt aggression (i.e., bites against it) in 63% of tested individuals. The results clearly demonstrate the role of visual stimuli in territorial communication, but only as a combined effect of shape and motion, differently from other lizard families for which shape is enough to stimulate aggressive responses. Mirrors can be useful tools to investigate aggression related to physiological and morphological aspects in lacertid lizards.

Keywords. visual stimulus, aggression releaser, mirrored image, plaster model, Lacertidae.

INTRODUCTION

Animal communication systems have evolved so that individuals can make decisions based upon the behaviour, morphology, and physiology of other individuals (Endler, 1993). Communication depends on signal transmission between a signaller and a receiver and in order for the signal to be successful, it must be detected by the receiver against a background of other potential stimuli (Fuller and Endler, 2018). Signals act as releasing mechanisms, intended as the totality of all parts of the nervous system that are involved in the filtering of incoming stimuli and it ensures that only the "appropriate" stimuli release a specific behaviour pattern (Immelmann, 1983). The key stimulus or releaser may consist of single or complex cues and disentangling their effect to fully understand which of them releases certain behaviours could be challenging. The majority of releasers consists of a combination of motor patterns acting as a signal and a morphological structure enhancing the signal's effect (Lorenz, 1981), so a single portion of a key stimulus could be insufficient to release a particular behaviour. Notably, when the behaviour pattern is simple and the risk of error is low, releasers are extremely simplified, such as the pecking at the red spot on the beak triggering the regurgitation of food by adult herring gulls (Tinber-

gen, 1951). By contrast, when costs associated with errors are high, the releasers are more complex to ensure that behavioural patterns start only when they are necessary. This especially applies to aggressive behaviours, whose primary function is releasing of aggression against fellow members of the species and to avoid unnecessary fighting against heterospecific opponents (Immelmann, 1983).

Aggressive behaviours are most common in territorial species, because individuals are forced to compete for limited resources, such as partners, food, shelters and reproductive sites, even if territoriality can be also assessed without overt aggression (Brown, 1964; Myrberg and Thresher, 1974; Van den Berghe, 1974; Stamps, 1977; Kaufmann, 1983). Among reptiles, many cases of territorialism are well documented for chelonians, crocodiles, tuataras, and, particularly, for lizards (Pough et al., 2004). Three main kinds of stimuli can be used for territorial communication by reptiles: visual, chemical, and acoustic. The latter is typical of species living in habitats where visual displays are ineffective and it is used only by nocturnal geckoes (Marcellini, 1977), terrestrial tortoises (Galeotti et al., 2005a; Galeotti et al., 2005b) and crocodilians (Vliet, 1989). Chemical cues are effective communication tools, used by most reptiles, but particularly developed in modern species, like snakes and most scleroglossan lizards, thanks to the evolution of a complex vomeronasal system that freed the tongue from its ancestral role and allowed the transformation to a chemosensory organ (Mason, 1992; Schwenk, 1993; Cooper, 1994).

Disentangling the role of intraspecific communication channels needs experiments analysing the single cues separately. For example, numerous studies have been done on iguanians (in particular on agamids and iguanids), a reptile clade that bases most of its territorial communication on visual stimuli, like posture, dewlap extension, colour patches and colour changes (Yang et al., 2001; Yang and Wilczynski, 2002; Van Dyk and Evans, 2008; Norfolk et al., 2010; Osborne et al., 2012; Dunham and Wilczynski, 2014; Yewers et al., 2016). On the contrary, information is still lacking on the role of visual cues in lacertids, a family of scleroglossan lizards that relies mostly on chemical communication by means of femoral pores to assess territoriality (Cooper, 1994; Martin and López, 2015; Mangiacotti et al., 2017; Baeckens et al., 2018).

Visual stimuli can be tested using four kinds of methods: silicone models that mimic shape and colours of the species, the reflected image in a mirror of the subjects involved in the experiments, video playbacks showed to lizards, and direct staged encounters with another male. The latter method has been often used, but many factors can affect results, such as opponent size, residence status, and individual motivation (Sacchi et al.,

2009). Video playbacks have been successfully used for some species (Macedonia and Stamps, 1994; Yang et al., 2001; Ord et al., 2002; Van Dyk and Evans, 2008; Frohnwieser et al., 2017), but they require a long preparation time to acquire video sequences or to prepare animated images after 3D scanning. Hence, it requires a substantial *a priori* knowledge of the species' stereotyped behaviours to present a complete sample set to the subjects. Silicone models have been used, for example, with *Stellagama stellio* and *Pseudotrapelus sinaitus* (Norfolk et al., 2010), *Platysaurus minor* and *P. monotropis* (Korner et al., 2000) and they proved to be adequate cues for territorial behaviours both for agamids and cordylids.

Mirrors are the most used visual stimuli in experimental designs because they are easy, cheap, and typically stimulate aggressive behaviours against the reflected image (Balzarini et al., 2014). Furthermore, the signal is enhanced by positive feedback, because an aggressive posture or behaviour is immediately replicated by the mirrored lizard. Numerous species have been successfully tested using this methodology, particularly from families Agamidae, Phrynosomatidae, and Dactyloidae (Korzan et al., 2000; Brandt, 2003; Farrell and Wilczynski, 2006; Osborne et al., 2012; Dunham and Wilczynski, 2014).

Podarcis muralis, our model species, is a typical representative of this family. It is a small (snout to vent, SVL up to 7.5 cm) and sexually dimorphic lizard, with males stouter and with bigger heads than females; males show a marked territorial behaviour (Edsman, 1990; Sacchi et al., 2009), as supported also by data about testosterone levels and homing behaviour in previous works (Scali et al., 2013; Sacchi et al., 2017). As a consequence, intraspecific communication in this species has been intensively studied as far as chemical cues are concerned (Martin et al., 2008; Heathcote et al., 2014; Pellitteri-Rosa et al., 2014; Baeckens et al., 2017; Mangiacotti et al., 2017, 2019), but no information is available about visual stimuli and communication during intraspecific encounters (but see Zagar et al., 2015). Since aggressive displays and postures of *Podarcis muralis* have never been detailed before (but see Sacchi et al., 2009 and Abalos et al., 2016 for some information), we discarded playback videos and chose a dual experimental approach based on silicone models and mirrors as visual stimuli to boost and record aggressive behaviours. The specific aim of our work was to assess if visual stimuli can trigger an aggressive response in a typical lacertid lizard that bases most of its intraspecific communication on chemical cues. We did this by comparing the aggressive response to: i) a static and oversimplified visual cue (i.e., a silicone model); ii) a more complex and realistic visual stimulus combining movement, behaviour, and posture (i.e., a mirrored image).

MATERIALS AND METHODS

Ninety *P. muralis* adult males (SVL > 50 mm) were captured by noosing in various localities in Lombardy (northern Italy) between April and June 2016, to maximize territorial response in accordance with reproductive season (Corti and Lo Cascio, 2002; Sacchi et al., 2017). The capture sites were located within 50 km each other and had similar ecological conditions, being all peripheral urban habitats, with comparable habitats, presence of predators and densities. Lizards were carried to the Natural History Museum of Milan and housed in individual plexiglas boxes (40 × 40 × 30 cm) with a refuge positioned near one box's wall, water *ad libitum* and fed with three mealworms (*Tenebrio molitor*) per/day. A sheet of absorbent paper was used as substrate, to keep the resident odour in each terrarium and thus lizards could consider it as their own territory. The vertical sides of the boxes were also covered externally with white paper sheets, to avoid external stimuli and wall reflectance. The room was exposed to a natural day/night cycle.

After an acclimation period lasting between three and seven days, lizards were tested in the same terrarium where they were kept, after removing water and food. A heating lamp (ZooMed Repti Basking spot lamp, 150 W) was turned on for 15 minutes to achieve a plateau body temperature similar for all the individuals (Sannolo et al., 2014), then it was turned off and a cold led lamp (Greenergy, 8 W, 600 lm) was lighted to ensure uniform lighting in the terrarium. A surveillance camera (SONY Super Night Vision Camera, M020-s53-001, located near the heating lamp) was turned on and lizard behaviour was recorded for 15 minutes immediately after inserting a visual stimulus in the box. Individuals were randomly assigned to the following three different stimuli (n = 30 for each treatment without replicates): i) a white paper sheet covering one side of the box, and used as control to simulate the insertion of an object by researcher's hand; ii) a silicone model simulating a new lizard invading the resident's territory; iii) a mirror covering one side of the box, reflecting lizard image and movements. All the stimuli were positioned inside the terrarium near the wall of the box opposite to the refuge.

The lizard model was a silicon-rubber cast prepared by the museum taxidermist using a dead male *P. muralis* specimen that was painted brown on the back and white on the belly and throat using water-based tempera colours (Fig. A1 in Supplementary materials). The model was painted one month before starting the experiment to perfectly dry the paint. A push-up stance was obtained inserting an iron wire in the model to simulate a territorial posture with the anterior part of the body raised and showing throat colouration (Molina Borja, 1981).

Since difference in individual size has been proved to affect the outcome of male-male combats in *P. muralis* (Sacchi et al., 2009) and the lizards tested against the model did not always had the same size as the model (SVL = 67 mm, see Table A1 in Supplementary materials for lizard mean size), we performed a preliminary test to investigate the potential inhibitory effect of such a difference. Latency (i.e., the time between the insertion of the model in the terrarium and the first movement of the focal lizard) was used as a proxy for the potential inhibitory effect (the longer the latency, the larger the effect) and it was regressed against the signed difference between lizard and model size ($SVL_{lizard} - SVL_{model}$). The regression was not significant (one-way ANOVA: $F_{1,28} = 1.27$; P = 0.27), so we assumed that model size did not affect lizard aggressive response.

The videos were analysed in the platform BORIS (Behavioral Observation Research Interactive Software, Friard and Gamba, 2016, freely available at www.boris.unito.it). All the behaviours addressed to the stimulus were scored as follows: 1) no interest (i.e., walking across the terrarium without any interactions with the stimulus); 2) interest without aggression (i.e., observing or tongue-flicking towards the stimulus); 3) interest with overt aggression (i.e., biting against the stimulus).

Scores for the three treatments were compared using a Kruskal-Wallis test and Mann-Whitney tests were used as *post-hoc* tests. Analyses were performed under the R rel. 3.4.2 statistical environment (R Development Core Team, 2017) and, otherwise stated, reported values represent means and standard errors.

RESULTS

The higher aggression score (i.e., 3) was observed only for the mirror treatment, where 63.3% (19 out of 30) of males bit the stimulus. The highest score achieved by males in the other two treatments was 2, with 66.7% and 56.7% in control and silicone model treatments respectively. These differences were highly statistically significant (Kruskal-Wallis: $\chi^2 = 26.021$, d.f. = 2; P < 0.001). Mann-Whitney *post-hoc* tests showed that aggression scores did not differ between control and silicone models (P = 0.44); on the opposite, both comparisons involving
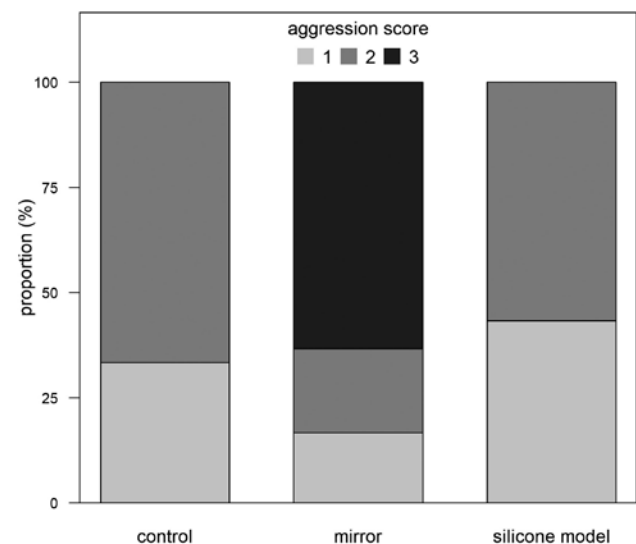

Fig. 1. Proportions of aggressive responses against the stimuli (control, plaster model, and mirror respectively) by common wall lizards (see methods for scoring details).

mirror were significant (P < 0.001 in both cases), being the score of the mirror treatment always higher than the other two (Fig. 1).

DISCUSSION

Our experiment demonstrated that visual stimuli are important releasers in triggering aggressive behaviours in the common wall lizard. It is often difficult to disentangle the effect of single key stimuli in a complex stimulus, but the approach used in this study allowed us to separate the effect of a simple cue, the shape of a lizard, by the composite effect of shape and motion. The result is not as trivial as it might seem, because some lizard species actively respond to simplified and motionless models by activating some territorial behaviours, demonstrating that they do not necessarily need more complex visual stimuli. This is true for some Agamidae, such as the tawny dragon lizard, *Ctenophorus decresii*, whose territorial behaviour has been intensively studied. Indeed, males of this polymorphic species engage in complex displays to defend territories and they use the same behavioural patterns also against models, responding differently even to throat colours (Yewers et al., 2016). Also cordylids, such as *Platysaurus minor* and *P. monotropis*, show overt aggression behaviours against models, demonstrating poor species recognition when models of different congenerics were proposed (Korner et al., 2000). All the above examples support the hypothesis that oversimplified visual stimuli can provoke an aggressive response in these taxa.

The common wall lizards were not interested in the presence of models within the enclosures and their only possible reaction was moving sometimes around and on the fake lizards and tongue-flicking at a certain distance. These behaviours were adopted even when the control stimulus (i.e., the white paper sheet) was inserted in the enclosure, so no conclusion can be inferred because they could be due to simple exploration activity. By contrast, the mirrored image always caused an alert posture, such as "freezing" in front of the mirror, repeated tongue-flicking or push-up displays, often culminating in overt aggression against the image with multiple bites or jumps. Numerous authors proved that mirrors are efficient stimuli able to release aggressive behaviours for many species belonging to different families (Agamidae, Phrynosomatidae, and Dactyloidae) (Korzan et al., 2000; Brandt, 2003; Farrell and Wilczynski, 2006; Norfolk et al., 2010; Osborne et al., 2012; Dunham and Wilczynski, 2014). Interestingly, in all these cases the species belong to visually-oriented lizard clades, making such a result expectable. On the opposite, to our knowledge this is

the first time that the same kind of visual stimulus (i.e., a mirrored image) releases aggressive behaviour in a lacertid lizard, which is thought to be more chemical- than visual-oriented (but see Garcia-Roa et al., 2017; Baeckens et al., 2018). One main objection to the reliability of our results could be the different smell between the proposed stimuli and a real lizard, but we chose to exclude chemical stimuli in our experiment to disentangle the effect of shape, movement, and chemical hints. Our results confirm the observations by other authors that aggression releasers often are not single visual stimuli, such as a still image, but the combination of different stimuli, such as shape and motion (Macedonia and Stamps, 1994; Yang et al., 2001; Ord et al., 2002; Yang and Wilczynski, 2002; Van Dyk and Evans, 2008; Frohnwieser et al., 2017).

Previous research on the role of motion patterns in the visual displays of anoles demonstrated that motion is fundamental to attract the attention of lizards, particularly when a specific motion pattern is exhibited (Fleishman, 1992). The response to motion patterns is used by many territorial species to signal their presence to intraspecific opponents. These lizards use dewlap extension to communicate with rivals and partners and this display is often accompanied by a stereotypical head-bobbing movement. A detailed study on signal efficacy showed that motion patterns that combined high acceleration with high velocity were particularly effective. Nonetheless, at a short distance, even a small-amplitude motion in the visual periphery can be perceived by a lizard, causing a shift of gaze so that the image falls on a high-resolution portion of the retina (Fleishman, 1992). Of course, lacertids and anoles do not share the same evolutionary history (Pyron et al., 2013), so a detailed study on visual acuity and efficacy of the formers would be hoped. Simple stimulus, such as shape, could be enough to trigger a territorial response in basal lizard clades, but not in modern lizards that use chemical stimuli as the main releaser in intraspecific communication. Previous studies on animal communication demonstrated that the sensory system of the receiver determines which signals can be detected and that, in majority of cases, sensory systems serve multiple purposes and must be capable of detecting many types of different stimuli, such as mates, food, habitat, and opponents (Fuller and Endler, 2018). Responding to all the stimuli could be extremely costly, so there is selection on sensory systems to efficiently capture relevant stimuli in the environment (Fleishman, 1992; Fuller and Endler, 2018). This could explain why motionless or slow-moving shapes do not elicit aggressive responses in the common wall lizard, whereas mirrored images do.

Further studies will be necessary to fully understand

the aggressive behaviour of the common wall lizard and the underlying releasing mechanisms, as well as to support the relationship between phylogeny, territoriality, and the complexity of visual stimuli. Nevertheless, we demonstrated that mirrored images are able to activate the aggressive response also in a lacertid lizard, which sets the stage for a wider and comparative study using other species and stimuli.

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SUPPLEMENTARY MATERIAL

Supplementary material associated with this article can be found at < http://www.unipv.it/webshi/appendix > Manuscript number 24651.

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