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Signal use by collared lizards, *Crotaphytus collaris*: the effects of familiarity and threat

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Abstract Many lizard species use lateral compressions of the body during agonistic encounters. I investigated the signal value of the frequency at which these displays are presented and how that rate is affected by familiarity and threat. The response of resident collared lizards (*Crotaphytus collaris*) to tethered strangers, neighbors on the correct boundary, and neighbors displaced to the opposite boundary, was recorded by counting the number of lateral displays directed at the intruder and the number of subsequent acts of escalated aggression. There was no relationship between size asymmetry of the opponent and the rate of lateral display or aggression, nor was there a relationship between body size and the rate of lateral display or aggression. However, there was a high positive correlation between lateral display rate and aggression, suggesting that the rate of lateral displays is a conventional signal of motivation to attack. The highest rates of display and aggression were directed toward displaced neighbors, somewhat less toward strangers, and the least toward neighbors at the correct boundary. The ratio of aggressive acts to lateral displays followed the same pattern, presumably because the perceived threat to the resident decreases in the same order. Taken together these data suggest that collared lizards are able to assess the threat of an opponent and signal motivation to respond aggressively towards that opponent.

Keywords Aggressive signals · *Crotaphytus collaris* · Lateral displays · Motivation · Threat displays

Introduction

Many species communicate during agonistic encounters with stereotyped threat displays (Huntingford and Turner 1987), which presumably advertise the quality of the sender to the receiver, allowing rapid assessment of the sender without costly physical escalation (Huntingford et al. 2000). Much of the research on the evolution of animal communication has focused on the use of signals in the form of vocalizations, body size, and weaponry (e.g., Davies and Halliday 1978; Hughes 1996; Bee et al. 1999) to advertise some aspect of the sender's resource holding potential (RHP) to potential mates or rivals. The difficulty in addressing the evolution of threat displays is determining how honesty is maintained by individuals with conflicting interests, despite the apparent incentive to exaggerate (Zahavi 1975; Zahavi and Zahavi 1997; Johnstone 1995). Recently, a major focus in the study of communication has been on the classification of signals and what the signal communicates to the receiver (e.g., Enquist and Leimar 1983; Enquist 1985; Vehrencamp 2000) by examining the cost imposed on the sender, whether it is a physiological constraint or the risk of retaliation from the receiver (Vehrencamp 2000).

Many fish (Zahavi 1981; Hurd 1997) and lizard (Carpenter and Ferguson 1977; Carpenter 1978; Brandt 2003) species communicate during agonistic encounters with lateral displays that involve stretching and lateral compression of the body. The display itself presumably signals body size to the rival since it cannot be a deceptive signal of body size. As long as all contestants stretch and enhance their apparent body size, senders cannot lie about their true body size with lateral displays because larger individuals will still appear relatively larger and smaller individuals will still appear relatively smaller (Zahavi 1981; Wagner 1992). However, the duration of lateral displays and the rate at which they are performed may signal some aspect of the sender's quality other than body size, such as fighting ability, stamina, or motivation to attack (Zahavi and Zahavi 1997). Zahavi and Zahavi (1997) predicted that the use of lateral displays likely

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signals to the receiver the motivation of the sender to attack. Motivation to fight varies temporally, and also with experience and familiarity, depending on the perceived threat (Jaeger 1981; Ydenberg et al. 1988; Temeles 1994), and would not be expected to be signaled by a badge, but instead by a graded behavioral signal (Olsson 1994; Vehrencamp 2000). Those species that display individual recognition may be more likely to evolve graded signals that communicate intention or motivation (Senar 1990) because knowledge of previous outcomes can be used as an asymmetry during opponent assessment, allowing for information transfer without physical attacks (van Rhijn and Vodegel 1980).

Territorial neighbors rely primarily on displays to convey information (i.e., the “dear enemy” phenomenon; Fisher 1954), but they will escalate to physical aggression if the perceived threat of the neighbor and the value of the contended resource is sufficient to outweigh the cost of the escalated encounter (Ydenberg et al. 1988; Temeles 1994; Husak and Fox 2003). Examining signal use and subsequent escalated aggression during encounters between rivals that vary in the degree of familiarity and threat may shed light upon the signal content of the displays used during the interactions. I staged interactions with collared lizards (*Crotaphytus collaris*), and varied familiarity and threat by examining the response of resident males to strangers, neighbors at the boundary at which they are normally encountered, and neighbors that have been displaced to the boundary opposite to where they are normally encountered. The latter interaction represents an encounter between rivals where the neighbor is “familiar” to the resident due to prior assessments, but now represents more of a threat to territory ownership because he may have lost his territory or is trying to expand his current territory to monopolize more females (Ydenberg et al. 1988; Husak and Fox 2003).

The collared lizard is a territorial, iguanian lizard whose use of lateral displays during conspecific interactions is well documented (e.g., Fitch 1956; Yedlin and Ferguson 1973), but the signal value of the display for this and other lizard species remains unclear. Collared lizards have also been shown to display the dear enemy phenomenon and individual recognition (Fox and Baird 1992; Husak and Fox 2003), making them a good species with which to test the signal content of lateral display use. It has also been discerned in collared lizards that when neighbors are displaced, residents do recognize the neighbor as displaced and not just as another stranger (Husak and Fox 2003).

The purpose of this investigation was to determine the signal value of the rate with which collared lizards give lateral displays. Theory predicts that escalation should increase as asymmetries in RHP decrease, that is, as individuals become closer matched and assessment becomes more difficult (Enquist and Leimar 1983, Olsson 1992, Molina-Borja et al. 1998). Therefore, I tested if the rate of lateral displaying is related to body size (and body size asymmetry between opponents). I also tested whether the rate of lateral displaying signals motivation to attack

by looking for a relationship between the rate of display and the rate of subsequent physical attacks on an opponent. I also examined the use of lateral displays during interactions where the familiarity and perceived threat of the opponents varied, and whether or not this variation affects what is communicated with the signal.

Methods

The study site was located at Sooner Lake in north-central Oklahoma on a substrate consisting of concrete-covered boulders that were imported to construct Sooner Lake dam. In May-June 1999 and 2000, lizards were captured by noosing and marked with toe-clips as well as with a unique pattern of coloured beads, attached with a short length of monofilament fishing line sewn through the base of the tail, for visual identification at a distance (after Fisher and Muth 1989). When first captured, I measured each lizard to the nearest 0.5 mm for snout-vent length (SVL). General methods were as described in Husak and Fox (2003). I created scale maps of the study site so that daily sightings could be used to determine home ranges. I walked the site daily, observed lizards with binoculars, and mapped their locations so that territories could be defined by the minimum convex polygon procedure (Stone and Baird 2002), using at least 20 sightings per lizard (the point at which territory size asymptotes for this population). Data were collected for all sightings and intrusions (see below) when the substrate temperature was 30–40°C, the optimal temperature range for collared lizards in central Oklahoma (Uzee 1990).

Once territory boundaries were defined, I conducted the following trials with 20 resident subjects, each against: (1) neighbor male at the familiar boundary, (2) neighbor male displaced to the opposite boundary, and (3) stranger male at the ‘familiar’ neighbor boundary (hereafter referred to as neighbor, displaced neighbor, and stranger, respectively). Thus, I conducted a total of 60 trials. I conducted intrusions so that the order of type of intrusion (e.g., neighbor, displaced neighbor, or stranger) was random and no lizard was used in more than one trial on a given day. Intrusions were spaced as far apart temporally as possible to eliminate any effects of order on the response of the lizards. The mean number of days between successive intrusions for a given resident lizard was 7 days (range 3–9 days). We conducted all intrusions during June 1999 and 2000 after territories had been established and while aggression was at its peak in central Oklahoma (Baird et al. 2001). We captured strangers from areas at least 2 km away from the study site to ensure that subject residents were not familiar with intruders. Neighbor or stranger adult males were introduced at the boundary of the territories of adult males by tethering them to a 4.5-m pole with approximately 8 cm of monofilament fishing line and placing them at the desired location on a large rock draped with a neutral-colored piece of carpet to avoid flight into otherwise accessible cracks and crevices. I conducted 10-min focal observations on each target resident during the encounter and counted the number of lateral displays, as well as the number of escalated aggressive acts after the first lateral displays. Escalated aggressive acts included: attacking, charging at the intruder and making contact; biting, including those with an immediate release and those where the bite was maintained for several seconds; fighting, physical combat that involves grappling and wrestling between the opponents; and superimpositions, resident places his body over the intruder’s. All trials were size-matched such that strangers matched, within 1 mm SVL, the size of the neighbor that was normally encountered at that boundary. However, since residents were paired with their neighbors (and strangers size-matched to the residents’ neighbors) and residents were not necessarily the same size as their natural neighbors (nor as the strangers matched in size with those neighbors), residents were not always size matched with intruders. Thus, there was some degree of body size asymmetry between residents and intruders. However, the maximum asymmetry between a resident and an intruder was only a 6.5% difference in

SVL. Strangers were returned to the exact point of capture after interactions.

Some interactions (12 of the 60) were stopped before 10 min due to the intensity of aggression, so I divided the number of lateral displays and the number of aggressive acts by the total time of the respective interaction. I terminated interactions when it was apparent that continued escalated aggression would result in severe injury to one of the lizards (e.g., when a lizard bit a lizard on the head and did not release after several seconds). The shortest interaction due to interruption was 246 s. I detected heterogeneity of variances, so I log-transformed data before analysis. In some interactions there were no displays or aggressive acts, so I added 1 to all counts. All data were then log-transformed. I calculated a size asymmetry index as the difference in SVL between resident and intruder. I used correlation analysis to test for significant relationships among variables measured during the three types of intrusions. I compared the number of lateral displays per minute and the number of aggressive acts per minute for each treatment using repeated measures ANOVA with resident as the repeated measure and intruder type (neighbor, displaced neighbor, or stranger) as the factor. Tukey's Honestly Significant Difference (HSD) multiple comparison tests (Kuehl 2000) were used to test for differences in resident responses between the different intruder types. I then compared the ratio of aggressive acts per minute to lateral displays per minute among the three treatments with repeated measures ANOVA and Tukey's multiple comparison tests. All statistics were conducted with SAS version 8 (PROC MIXED, SAS Institute 1999). Where appropriate, a sequential Bonferroni adjustment for multiple related tests was applied to confirm significance (Rice 1989).

Results

There was no significant relationship between the rate of display and body size asymmetry for any of the types of intrusions ($n=20$ for all; Neighbor: $r=0.078$, $P=0.743$; Displaced neighbor: $r=-0.263$, $P=0.262$; Stranger: $r=-0.407$, $P=0.075$), nor was there a significant relationship between the rate of aggression and body size asymmetry for any of the types of intrusions ($n=20$ for all; Neighbor: $r=0.098$, $P=0.681$; Displaced neighbor: $r=-0.264$, $P=0.261$; Stranger: $r=-0.427$, $P=0.061$). This was also true when the direction of the asymmetry was considered (e.g., asymmetry values were negative if the resident was smaller than the intruder). There was no significant correlation between the rate of display and the resident's SVL ($n=20$ for all) for intrusions involving neighbors at familiar boundaries ($r=0.101$, $P=0.671$). However, there was a significant inverse relationship between the rate of display and the resident's SVL for intrusions involving displaced neighbors ($r=-0.598$, $P=0.005$) and a negative correlation between the rate of display and the resident's SVL for intrusions involving strangers ($r=-0.472$, $P=0.036$, nonsignificant after Bonferroni adjustment). Similarly, there was no significant correlation between the rate of aggression and the resident's SVL ($n=20$ for all) for intrusions involving neighbors at familiar boundaries ($r=0.007$, $P=0.977$). However, there was a significant inverse relationship between the rate of aggression and the resident's SVL for intrusions involving displaced neighbors ($r=-0.538$, $P=0.014$) and a nonsignificant negative correlation between the rate of aggression and

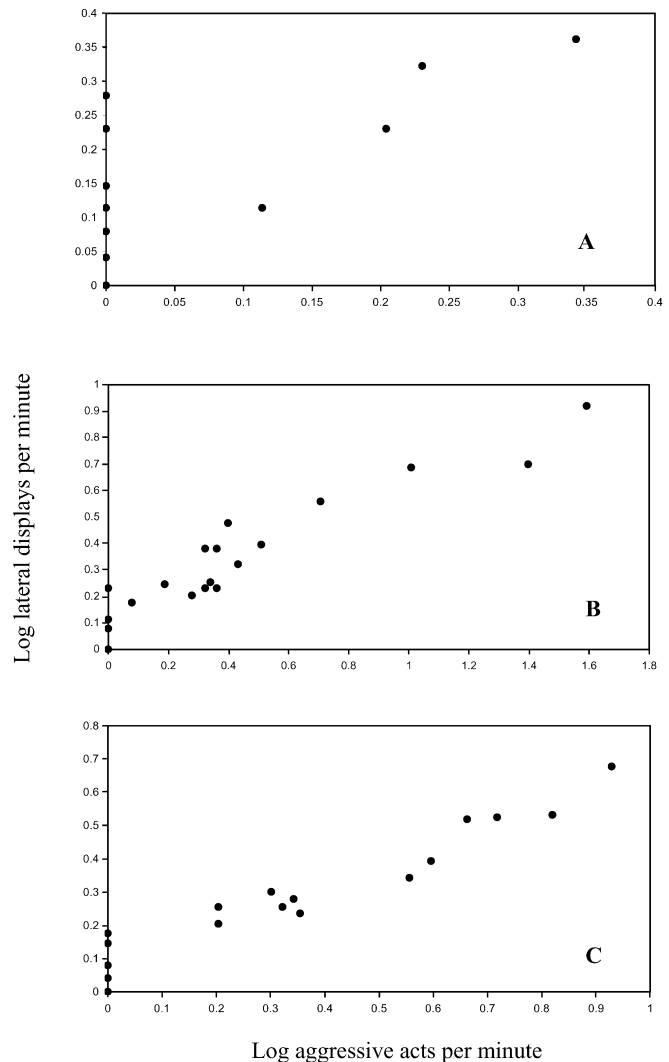


Fig. 1 Lateral displays per minute (log transformed) plotted against physically aggressive acts (log transformed) per minute for resident adult male collared lizards, *Crotaphytus collaris*, responding to **A** neighbors, **B** displaced neighbors, and **C** strangers size-matched to those neighbors

the resident's SVL for intrusions involving strangers ($r=-0.420$, $P=0.065$).

There was a significant positive correlation detected between the number of lateral displays per minute, and the number of aggressive acts per minute for all three types of intruders ($n=20$ for all; Neighbor: $r=0.725$, $P<0.001$; Displaced neighbor: $r=0.947$, $P<0.001$; Stranger: $r=0.961$, $P<0.001$; Fig. 1A–C).

There was a significant difference in the number of lateral displays per minute ($F_{2,41}=10.57$; $P=0.0002$), the number of aggressive acts per minute ($F_{2,42.5}=10.88$; $P=0.0002$), and the ratio of aggressive acts per minute to displays per minute ($F_{2,38}=8.86$; $P=0.0007$) directed toward the different intruder types (Table 1). Residents displayed more toward displaced neighbors (Tukey's HSD, $P=0.0001$) and strangers (Tukey's HSD, $P=0.017$) than toward neighbors (Table 1), but there was no

Table 1 Mean responses (± 1 SE) of adult male collared lizards, *Crotaphytus collaris*, to neighbors at the familiar boundary, neighbors displaced to the opposite boundary, and strangers size-matched to those neighbors

Intruder	Lateral displays per minute	Aggressive acts per minute	Ratio of aggression rate to lateral display rate
Neighbor	3.3 \pm 0.9	0.7 \pm 0.4	0.09 \pm 0.04
Displaced neighbor	15.3 \pm 3.9	21.8 \pm 10.4	0.70 \pm 0.10
Stranger	10.4 \pm 2.2	8.2 \pm 2.4	0.50 \pm 0.18

significant difference in the rate of display between strangers and displaced neighbors (Tukey's HSD, $P=0.41$). Residents also directed more physically aggressive acts toward displaced neighbors (Tukey's HSD, $P<0.0001$) and strangers (Tukey's HSD, $P=0.017$) than toward neighbors (Table 1), but there was no significant difference in the rate of aggression between strangers and displaced neighbors (Tukey's HSD, $P=0.40$; Table 1). Similarly, the ratio of aggressive acts per minute to displays per minute was greater toward displaced neighbors (Tukey's HSD, $P=0.0005$) and strangers (Tukey's HSD, $P=0.025$) than toward neighbors (Table 1), but there was no significant difference in ratios between strangers and displaced neighbors (Tukey's HSD, $P=0.35$).

Discussion

Size differences between opponents are typically an important asymmetry during agonistic encounters (e.g., Maynard Smith and Parker 1976; Enquist and Leimar 1983; Olsson 1992). However, in this investigation, the unimportance of body size differences, at least in closely matched individuals, was supported by the fact that no relationship was found between either lateral display rate or escalated aggression and size asymmetry. Perhaps larger asymmetries such as the size difference between larger adults (105+ mm SVL) and those just reaching sexual maturity (75–80 mm SVL) would provide different results.

Signals have been shown in numerous taxa to communicate body size (e.g., Clutton-Brock and Albon 1979; Hughes 1996; Jenssen et al. 2000), but in this study I found no clear relationship between the rate of lateral displays and body size. Logically, lateral displays cannot be used as bluffs to increase the apparent size of the individual (as long as all individuals use them), nor can the rate of display be expected to communicate something that can be more easily communicated without repetitive motions (i.e., during the first lateral display). There was no relationship between display use and SVL for the neighbor interactions, but when threat increased an inverse relationship was detected. Perhaps smaller residents have more motivation because they are new territory holders and have more to lose than older individuals that have reproduced more, or perhaps the response is a reflection of the individual's inexperience with territory challenge by a rival.

The rate of lateral display appears to be used honestly by collared lizards to signal motivation to attack. Species

capable of individual recognition, such as collared lizards (Husak and Fox 2003), may be more likely to evolve signals that communicate intention or motivation during opponent assessment (Senar 1990) because knowledge of previous contests and outcomes can be used as an asymmetry during contests (van Rhijn and Vodegel 1980). The different signal classifications based on maintenance cost as proposed by Vehrencamp (2000) make some similar predictions, but using several lines of evidence, I can suggest potential signal classifications for collared lizard lateral displays. One possibility is that the rate of lateral display is a "vulnerability handicap," which is maintained by vulnerability to receiver attacks and signals willingness to take risks. This is unlikely since encounters in lizards do not often become intensely escalated (Baird et al. 2003). Brandt (2003) showed that the duration of lateral displays in the side-blotched lizard (*Uta stansburiana*) is a "quality handicap," which are signals maintained by production costs (e.g., Vehrencamp 2000; Marden and Rollins 1994) of endurance or stamina. The extended period of lateral compression of the body during displays compromises breathing, signaling endurance or stamina to display while handicapped (Brandt 2003). Further research is needed to test the hypothesis that collared lizard lateral displays are a quality handicap. Because of the likely respiratory cost of lateral compression, it is likely that the rate of lateral compression may be a "general handicap," which is maintained by production costs (Vehrencamp 2000). However, the possibility that the rate of lateral displays is a "conventional signal" maintained by receiver retaliation costs and signaling motivation, willingness to fight, or fighting ability (Vehrencamp 2000, 2001; Molles and Vehrencamp 2001) cannot be completely ruled out from these considerations alone.

Consideration of how the rate of display changed in interactions with intruders of differing threat and familiarity offers insight into what the rate of lateral display is conveying to rivals. The presumed cost of lateral compression combined with the increase in rate of lateral displays with increase in intruder threat is strong evidence for the "general handicap" signal classification, where motivation and the value of the resource is conveyed in the signal (Vehrencamp 2000). However, the information content of lateral displays likely varies depending on context and presentation. The lateral display itself, upon initial use, may serve merely as a signal of body size. Thus, the context of the lateral displays and how they are used may signal various attributes of the lizard's quality and motivation. More data need to be collected to test

how context may change the use and content of this signal.

Comparing the ratios of aggressive acts to lateral displays in each context revealed that lizards relied more on displays during interactions with neighbors at familiar boundaries than they did during interactions with strangers. However, the fact that residents relied much less on displays when a neighbor was displaced revealed the role of familiarity in assessment and subsequent signaling. The responses were as expected if one considers the threat imposed by each type of intruder (Ydenberg et al. 1988; Husak and Fox 2003). Neighbors rely primarily on displays during agonistic encounters, presumably because they have previously assessed each other during contests (Ydenberg et al. 1988). When faced with a stranger, on the other hand, displays must be backed up with aggression, and more displays must be accompanied by more aggressive acts for the signal to be maintained (Table 1). Since neighbors have repeatedly assessed each others' RHP, when threat increases, by a familiar neighbor displaced to the opposite boundary, a resident should respond more with escalated aggression and less so with ritualized displays since the cost to the resident of potentially losing a territory has presumably increased. However, even in this case, the rate of display still increased and predicted the subsequent physically aggressive response. This is most likely due to the fact that lizards may be exhausted at some times and well rested at others due to prior locomotor, displaying, and/or fighting activities. This makes some assessment necessary even between familiar individuals.

In summary, collared lizards appear to use the rate of lateral displays as a signal of motivation to attack, most likely as a "general handicap" signal. The results of this investigation reveal the complexity involved in communication between neighbor and stranger collared lizards. Use of lateral displays and subsequent aggression depends on the intruder and his perceived threat. Previously assessed asymmetries in RHP between neighbors, as well as the value of the resource to the resident, appear to be important during agonistic encounters as shown by the differential display use during the three types of interactions. Residents waste little effort on aggression toward neighbors, instead relying on displays to communicate information; however, residents waste little time on displays when neighbors become more of a threat. Between unfamiliar rivals there have been no prior assessments, threat is high, and so responses to strangers are intermediate between these two scenarios.

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