

Chemoreception and the Assessment of Fighting Abilities in the Lizard *Liolaemus monticola*

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Abstract

When an individual faces the risk of a conflict, its ability to make 'correct' decisions is crucial to its fitness. Research on decision making has focused mainly on visual and acoustic signals, while chemical signals have received much less attention, despite their relevance for many species. Chemosignals can be detected in the absence of the signaller and, in the context of fighting risk, this property confers the advantage that the receiver can avoid agonistic interactions or, if they are unavoidable, that it can prepare itself for the conflict. I studied the behaviour of males of the lizard *Liolaemus monticola* in the laboratory when they were confronted with chemosignals of a potential opponent. During this 'pre-confrontation' stage, I tested the following predictions: (1) lizards can derive precise information from chemosignals of conspecifics, and use this to respond with precision to the perceived risk and (2) the best predictor of the receiver behaviour, and therefore the best predictor of the risk involved in the fight, is the relative fighting ability of opponents. As a measure of fighting ability, I used body size. 'Intruders' were placed in the terrarium of unfamiliar 'residents' during the absence of the latter, and their behaviours were recorded. Simple regressions were performed between the different behavioural variables and with the body sizes of intruder and resident, and with the relative difference in body sizes of opponents. The latter was the best predictor of intruder behaviour: it was negatively correlated with behaviours associated with activity (i.e. motion time), chemoexploration (i.e. number of tongue flicks) and behaviours associated with social interactions (i.e. head bobs). These results suggest that males can process information from chemosignals and decisions made during the 'pre-confrontation' stage are based on the assessment of the relative fighting abilities (i.e. relative body size) of opponents.

Introduction

The fitness of animals is strongly dependent on their abilities to make 'correct' decisions (i.e. where to bask and when to forage). The major underlying assumption of this decision-making process is that animals use information conveyed by different signals to weigh the costs and benefits of an action, and maximize the net benefits (for a review see

Dukas 1998; Krebs & Davies 1998; Shettleworth 1998). Both theoretical (Parker 1974; Enquist & Leimar 1983) and empirical evidence (Gosling et al. 1996a; Hazlett 1996) indicate that animals facing the risk of a fight make decisions based on the assessment of the relative fighting abilities of their opponents. In making these decisions, animals are crucially dependent upon information conveyed by signals directly related to fighting ability, such as

body size, strength, weaponry and age (Krebs & Davies 1998).

Lately, the parameters involved in the assessment of an opponent's fighting abilities have been investigated in a variety of taxa (e.g. spiders, Bridge et al. 2000; shore crabs, Sneddon et al. 2000; penguins, Renison et al. 2002; lizards, Baird & Sloan 2003; fishes, Moretz 2003; baboons, Fischer et al. 2004; paper wasps, Tibbetts & Dale 2004). The major insights have come almost entirely from studies of visual and acoustic signals, probably because these signals can be easily recorded, measured, simulated and manipulated (e.g. Tibbetts & Dale 2004). In contrast, although chemosignals play a significant role in intraspecific communication in many different taxa (e.g. Wyatt 2003), their role in decision making under fighting risk remains less explored. However, the available evidence indicates that chemosignals provide valuable information about potential opponents, and that pheromones (conspecific chemosignals) from individuals of higher competitive ability have stronger aversive properties than those of inferior individuals (Jones & Nowell 1989; Hurst 1993; Gosling et al. 1996a,b). In addition, aggression can be reduced if the chemosignals of the potential opponent are recognized as familiar (López & Martín 2002).

Research on decision making in the context of fights has been centred at the stage of direct interaction or confrontation between opponents (see Taylor & Elwood 2003; Morrell et al. 2005). However, chemosignals are unique among social signals in that they can be released in the absence of the receiver and be detected in the absence of the signaller (Gosling & Roberts 2001). Therefore, decisions can be made without direct interactions of opponents, and are particularly well suited to avoid costly agonistic interactions. Alternatively, if such interactions are unavoidable or 'desirable' (i.e. can secure a better-quality resource), information will allow receivers to prepare themselves for the conflict. Particularly so, if these are honest signals of the owner's characteristics (e.g. Gosling & Roberts 2001; Zala et al. 2004). Thus, animals can save energy by responding with precision to the requirements of the conflict. In this context, we may expect that receivers would be good at extracting information from chemosignals, and that their responses during the 'pre-confrontation' stage would be graded functions of the difference between their own fighting abilities and those of their opponents.

In lizards, chemosignals play an important role in intraspecific communication (Font 1996). In *Liola-*

emus, scent-ownership recognition is a widespread phenomenon; individuals of different species can discriminate between their own chemosignals and those from conspecifics of the same sex or potential sexual competitors (Labra & Niemeyer 1999; Labra et al. 2001a,b, 2002). These signals are probably released passively as animals drag the cloaca area along the substrate; faeces and pre-cloacal pores have pheromonal properties (Labra et al. 2002). The chemosignals delivered by potential competitors typically trigger an increase in behavioural displays, such as head bobs and tail waving (Labra & Niemeyer 2004). In addition, the presence and relative concentration of compounds of pheromonal secretions vary among conspecific males, which suggests that pheromones convey information about the individual's identity (Labra et al. 2001b). All together, data suggest that *Liolaemus* lizards use chemosignals to convey and assess individual information and that this facilitates decision making.

I studied the behavioural response of males of *Liolaemus monticola* confronted with chemosignals of an unknown potential opponent. This species was selected because it is territorial and aggressive (Fox & Shipman 2003), so that we expect that individuals would obtain significant benefits from assessing the characteristics of a potential opponent during a 'pre-confrontational' stage. I tested the following predictions: (1) lizards can derive accurate information from the chemosignals of conspecifics, and use this to respond precisely to the perceived risk involved in the fight and (2) the best predictor of receiver behaviour, that is the best predictor of the risk involved in the fight, is the relative fighting ability of opponents. As an indirect measurement of fighting ability, I used body size, an honest signal of fighting abilities in different taxa (e.g. Morris et al. 1995; Bridge et al. 2000), including lizards (Baird & Sloan 2003). I recorded the behaviour of 'intruder' males in the territory bearing the chemosignals of an absent 'resident' male.

Methods

Animals and Their Maintenance

Males of *L. monticola* were collected in Lampa (30 km northwest of Santiago, Chile) during the breeding season (spring). At Universidad de Chile, animals were placed in an indoor vivarium under a glass roof. They therefore had access to sunlight at a natural photoperiod and were able to exhibit their normal basking behaviour. The vivarium was

equipped with halogen lamps that maintained temperatures similar to those of a typical summer day (12–36°C). Lizards were housed individually in plastic enclosures (37 × 30 × 15 cm) covered with a plastic mesh. Enclosures had a small window in the front (10 × 5 cm) covered with a plastic mesh that admitted more light. Each enclosure contained 3 cm of sand on the floor, a bowl for water and a rock for shelter and basking. Water was supplied *ad libitum*, and food (mealworms) was provided every other day, dusted with vitamins once per week.

Experimental Design

Animals remained in their enclosures for 2 wk to habituate and to release pheromones. Resident individuals [snout-vent length (SVL) range 44.0–67.5 mm; $n = 5$] were assigned randomly to intruders (SVL range 45.6–65.4 mm; $n = 23$). The absolute body-size difference (SVL of intruder minus SVL of resident) ranged between –18.1 and +18.3 mm. Intruders were tested only once unless they did not respond, in which case the trial was repeated later (three occasions).

The resident was removed from its enclosure just before each trial. I also removed the rock and the bowl to reduce the availability of visual signals that might bias the results, even though rocks may have had a higher concentration of chemosignals. The intruder to be tested was removed from its enclosure, and placed in a cloth bag for 10 min; thereafter, the bag was opened, allowing the intruder to move freely into the resident's enclosure, simulating a territory invasion. During recordings, the enclosure's top was replaced by a glass covering, previously cleaned with alcohol.

Based on the knowledge of behaviour typically exhibited under aggressive scenarios, i.e. animal confronted with chemosignals of competitors (Labra & Niemeyer 2004) or directly with competitors (Trigoso-Venarino et al. 2002; Fox & Shipman 2003), I recorded the following variables:

1. *Latency to the first tongue flick*. Seconds elapsed between placement of the intruder in the resident's enclosure and the occurrence of the first tongue flick.

Thereafter, lizards were digitally videotaped for 10 min, and the number of the following behaviours were recorded later.

2. *Tongue flicks*. Protrusions and rapid retractions of the tongue. This is considered a measure of chemical exploration (Font 1996).

3. *Head bobs*. Up and down movements of the head.

4. *Tail waving*. Rapid movement from side to side of the entire tail or its posterior portion.

5. *Forelimb waving*. Movement of one or both forelimbs in a circular trajectory (Halloy & Castillo 2002).

6. *Face rub*. Rubbing of the face against the substrate.

7. *Digging*. Digging of a shallow hole in the sand with forelegs or hindlegs.

8. *Mouth gaping*. Open the mouth completely and the head is elevated such that the palate is perpendicular to the substrate. After some seconds, the mouth is closed accompanied by eye intrusion.

Durations (s) of the following behaviours were determined with a stopwatch.

9. *Motion time*. Total time during which the lizard moved, including adjustments of body posture, lateral head movements (scanning) and displacements of the body's centre of gravity; movements associated with the behaviours previously described were not included in this category.

10. *Latency to the first head bob*. Time elapsed from first tongue flick to first head bob. At the end of each trial, both resident and intruder were returned to their original enclosures.

Lizards were maintained in good condition during the entire experimental period and at the end of the study they were returned to the capture site.

Statistics

Simple regressions, using general linear/non-linear model (StatSoft, Inc. 2003), were calculated between the recorded behaviours and the three body measurements: resident's SVL, intruder's SVL and the relative body-size asymmetry, $\ln(\text{SVL}_{\text{intruder}}/\text{SVL}_{\text{resident}})$. Tail and forelimb waving, face rub, mouth gaping and digging occurred very infrequently, so their occurrence was combined with head bobs occurrence into a variable called 'display diversity'. This allowed determining variability in the diversity of behaviours displayed. Two variables, the number of head bobs and latency to the first head bob, were square root transformed to achieve normality.

Results

The variation of all behaviours was significantly related to the resident's SVL, whereas only the variation of motion time was significantly related to the intruder's SVL (Table 1). The relative body-size asymmetry, however, was the best predictor of all the intruder behaviours with the exception of those

Table 1: Simple regressions between behavioural responses of intruder males of *Liolaemus monticola* in the enclosures of potential opponents (residents) and resident snout-vent length (SVL), intruder SVL and relative body size asymmetry $\ln(\text{SVL}_{\text{intruder}}/\text{SVL}_{\text{resident}})$

Intruders' behaviours	Intruder SVL				Resident SVL				Relative body size			
	R ²	b	F _(1,21)	p	R ²	b	F _(1,21)	p	R ²	b	F _(1,21)	p
Latency to first tongue flick (s)	0.05	-53.8	1.04	0.320	0.19	73.2	4.90	0.038	0.22	-353.3	5.98	0.023
Number of tongue flicks	0.12	-12.2	2.97	0.100	0.34	13.7	10.86	0.003	0.42	-67.8	15.29	0.001
Motion time (s)	0.29	-76.3	8.49	0.008	0.18	40.0	4.47	0.046	0.40	-271.0	13.96	0.001
Number of head bobs ^a	0.03	0.6	0.70	0.412	0.47	1.5	18.35	0.0003	0.19	-4.3	4.83	0.039
'Displays diversity'	0.15	-0.7	3.78	0.070	0.23	0.6	6.43	0.019	0.34	-3.2	10.97	0.003
Latency to first head bob (s) ^a	0.00	-0.3	0.01	0.930	0.46	-7.4	17.84	0.004	0.27	25.3	7.90	0.010

^aBased on square root-transformed data.

related to head bobs. For head bob-related variables, the resident's SVL was the best predictor (Table 1). The relationships of the relative body-size asymmetry to latency to the first tongue flick and the number of tongue flicks are shown in Fig. 1a, b, respectively.

Eight individuals displayed behaviours other than head bobs, and two of them performed more than one behaviour. The displays were as follows: four males waved the tail, four gaped, two face rubbed, one forelimb waved and one dug.

Discussion

Scent marks in territories advertise potential costs to receivers, and may intimidate intruders. Moreover, invasion of a territory is a risky act of aggression because it invites retaliation. Observations of *L. monticola* behaviour in these simulated territory invasions suggest that intruders are able to perceive and use chemosignals to assess the body size of a resident male in its absence. Moreover, body size may be used as an honest signal of fighting ability because intruders responded according to the resident's SVL. Particularly evident were the head bob displays, a primary source of information during agonistic interactions (Trigoso-Venarito et al. 2002). The parameters used by males of *L. monticola* to assess body size and fighting ability from a complex blend of chemosignals remain largely unknown. However, knowing that in mammals the presence or concentration of volatile compounds of excretions with pheromonal properties is determined by age (Ma et al. 1999) and social status (Brown 1995; Miller et al. 1998), and that some of these compounds are mediated by androgens (Novotny et al. 1985), one might speculate that similar mechanisms operate in *L. monticola*.

Decisions made during the 'pre-confrontation' stage were not strongly related to intruder characteristics per se. The relative body-size asymmetry was a better predictor than the resident characteristics

alone (with the exception of head-bob variables). Intruders showed a gradual response (i.e. adjusted their behavioural responses) to the relative body-size asymmetry. This suggests an ability to process chemosensory information in a precise way. Therefore, decision making is based on a comparison of the intrinsic fighting abilities of the receiver and the signaller, as it is during the confrontational stage of a fight (Parker 1974; López & Martín 2001). Therefore, if males of *L. monticola* are forced to interact, the level of aggression displayed should be a function of their relative fighting characteristics. Because *Liolaemus* do have scent-ownership recognition (Labra & Niemeyer 1999; Labra et al. 2001a,b, 2002), the mechanism mediating the intruder's responses is probably self-referential phenotype matching (see Gosling & Roberts 2001).

In squamates, volatile compounds detected by olfaction presumably activate chemical exploration by the vomeronasal organ, mediated by tongue flicks (Cowles & Phelan 1958). Results with *L. monticola* support this proposal. The fact that latency to the first tongue flick correlated with the resident's SVL indicates that intruders may perceive volatile compounds by olfaction, which gives enough information about the resident's characteristics to decide when to begin the exploration. The balance between intruder and resident characteristics (relative body-size asymmetry), however, was a better predictor of the start of this exploratory behaviour; smaller intruders delayed exploration by showing longer latency to the first tongue flick. When they started exploring, however, the smaller intruders explored more, both chemically (higher number of tongue flicks) and behaviourally (longer motion time). Under natural conditions, increased exploration may involve an active search for places to hide or escape (see Petrulis et al. 2004) because the best strategy for smaller intruders is to avoid conflicts, as they have a higher probability of losing a confrontation

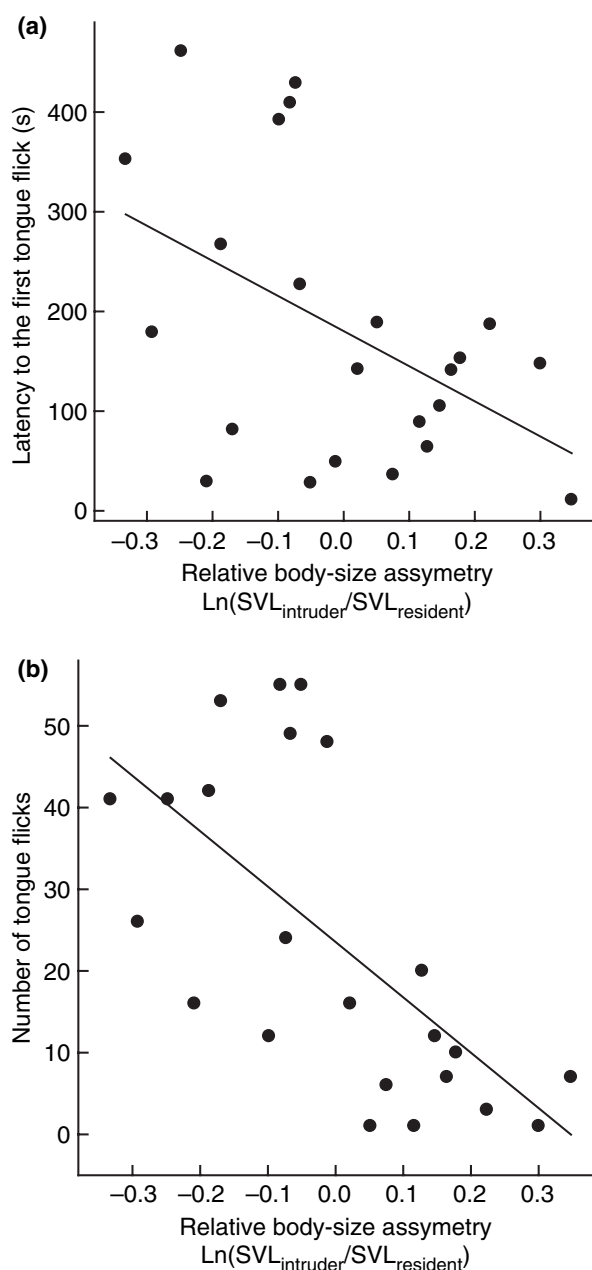


Fig. 1: Relationship between the relative body-size asymmetry $\ln(SVL_{\text{intruder}}/SVL_{\text{resident}})$ and two behaviours displayed by intruder males of *Liolaemus monticola* in the enclosures of unknown males. (a) Latency to the first tongue flick and (b) number of tongue flicks

(e.g. Baird & Sloan 2003). On the other hand, increased exploration is risky, as movements can attract the attention of an opponent. Interestingly, smaller intruders displayed head bobs sooner (i.e. shorter latency to the first head bob), made more head bobs and showed a higher 'displays diversity', some of which are directly associated with aggressive confrontations, i.e. tail waving directs potential

attacks by an opponent to a less important body part (Cooper 2001). Smaller intruders may possibly try to signal that they are good fighters while they are exploring. In contrast, intruders larger than residents, which probably are better fighters (e.g. Haenel et al. 2003), may not consider the resident a threat, and therefore need not investigate so intensely, or even demonstrate that they are good fighters. Such intruders moved less and showed fewer tongue flicks, less 'display diversity' and head bobs. In short, they did not waste energy. These observations add new antecedents to the relative recent attempts at understanding the paradox of why smaller individuals show more aggression and display the 'Napoleon strategy' (Just & Morris 2003; Moretz 2003; Jenssen et al. 2005; Morrell et al. 2005).

As in other species, body size is probably positively correlated with territory size in *L. monticola* (e.g. Haenel et al. 2003). If so, larger individuals with larger territories will not require proportionally greater energy to defend them against intruders because most of the intruders do not represent a threat. Thus, the ability to release chemosignals conveying information about fighting abilities may constitute an important means to reduce the daily energetic costs of territory maintenance.

This study suggests that chemosignals in a 'pre-confrontation' stage may confer significant advantages to signaller and receiver. Because many species are able to detect pheromones from conspecifics (Wyatt 2003), assessment of precise information conveyed by chemosignals, with the concomitant potential for precise modulation of response, may be more widespread among animals than previously thought. This ability may have been overlooked because many studies consider discrimination between only two alternatives (i.e. larger vs. smaller).

Finally, the results shed some light on a common problem in studies of chemical discrimination in squamates, namely, the high data dispersion. This dispersion could arise from the precise comparison that each receiver makes between its own characteristics, internal states or needs and those of the signaller. This will only be resolved when we have better information about the precise compounds that trigger particular behavioural responses, so that experimenters can control and manipulate the information conveyed by chemosignals (e.g. Novotny et al. 1985).

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