

Chemical recognition of conspecifics in a neotropical lizard, *Liolaemus pacha* (Iguania: Liolaemidae): relation to visual displays, season and sex

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Abstract Chemical cues play an important role in sexual recognition in several lizard species. Here, we investigated whether the neotropical lizard, *Liolaemus pacha* (Iguania: Liolaemidae) can discriminate between chemical information obtained from males or females. In addition, we also considered the effect of season (reproductive vs. post-reproductive) and the sex of the tested individual. We experimentally tested scent discrimination, using a terrarium previously occupied by a male, a female, and an untreated terrarium as control as sources of different chemical scents. We counted the number of tongue flicks, a measure of chemical exploratory behavior, and the visual displays triggered by these scents for 10 min. Males performed significantly more tongue flicks when female scent was present than when male and control scents were present, indicating sexual recognition. However, females did not show a significant difference in those same conditions, indicating a lack of sexual recognition. For visual displays, males showed significantly higher rates to female and male scents than to control, whereas females did not show any difference. During the reproductive season, the number of tongue flicks and visual displays were higher than during the post-reproductive season. Our results suggest that for male *L. pacha*, chemical cues play an important role in mate recognition. We discuss the apparent lack of recognition in females. We suggest that the observed seasonal

behavioral differences might be associated with physiological changes related mainly to reproduction.

Keywords Lizards · Communication · Pheromones · Tongue flicks · Headbob displays · Argentina

Introduction

Communication is an important part of sexual selection, with sexual signals being critical for mate choice and, hence, reproduction. Mate choice requires the correct identification of the species, the recognition of mates to coordinate the sexual behavior (i.e., sexual recognition) and the individual mate assessment to increase reproductive success (Andersson 1994; Johansson and Jones 2007). In this context, chemical senses play an important role in sexual communication of many animals (Wyatt 2003). Squamate reptiles have a highly developed vomeronasal organ (Halpern 1992; Mason and Parker 2010). Using tongue flicks (TFs), reptiles collect chemical samples from the environment and deliver them to the vomeronasal organ (Mason 1992; Cooper 1994; Schwenk 1995). Several studies across different lizard taxa have shown that chemical cues are involved in sexual recognition (López et al. 1998; Cooper and Pérez-Mellado 2002), informing different aspects such as age (López et al. 2003; Martín and López 2013), body size (Carazo et al. 2007; Huyghe et al. 2012), familiarity (Bull et al. 2000; Font and Desfilis 2002), health condition (López et al. 2006), and reproductive state (Head et al. 2005).

Lizards of the genus *Liolaemus* (Iguania: Liolaemidae), with more than 250 species, offer a great potential to study communication from ecological and evolutionary perspectives (Abdala and Quinteros 2014). Nevertheless,

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information about communication is still scarce. Although it has been known that chemical signaling occurs in several *Liolaemus* species (e.g., Labra and Niemeyer 1999; Labra et al. 2001), and season modulates this recognition (Labra 2008), the possible role of chemical cues in sexual signaling in *L. pacha*, as well as in the majority of *Liolaemus* lizards, has not been studied.

Liolaemus pacha is a territorial lizard, males having larger home ranges than females (Halloy et al. 2013 and references therein). Males defend their territories by performing headbob displays, sometimes occurring together with other visual behaviors such as forelimb wave displays (Halloy 2012; Vicente and Halloy 2015). Because chemical scents triggered headbob displays in other *Liolaemus* species (e.g., *L. tenuis*, Labra 2008), indicating that some information from the scent is perceived by the receiver, we expected that visual displays of *L. pacha* are also triggered by the conspecific scents. On the other hand, because season was found to modulate chemical recognition in *Liolaemus* species (Labra 2008), we expected that chemical recognition is influenced by seasonal effects. Thus, as a first step toward investigating the role of chemical cues on sexual signaling in *L. pacha* lizards, our objectives were: (1) to determine if *L. pacha* distinguishes male and female scents from a control scent (i.e., sexual recognition), (2) to explore the visual responses (headbob and forelimb wave displays) triggered by chemical cues, (3) to evaluate if sexual recognition changes between seasons (reproductive vs. post-reproductive), and (4) to examine whether these responses are different between sexes.

Materials and methods

Study species

Liolaemus pacha is a small diurnal lizard found in the Tucuman province, northwestern Argentina (previously known as *L. quilmes*, Juárez Heredia et al. 2013). Males are more colorful than females, showing a pattern of yellow, reddish and light-blue spots, whereas females are brownish and cryptic (Juárez Heredia et al. 2013). It is an insectivorous and oviparous lizard (Ramírez-Pinilla 1992; Halloy et al. 2006). According to Ramírez-Pinilla (1992), the reproductive season occurs during the austral spring (October–December) followed by a post-reproductive season during the austral summer (January–March). Males emerge from hibernation in September, at the beginning of the austral spring and females appear 4–6 weeks later (Halloy and Robles 2003). Mating occurs in late October and early November, and newborns are observed in late December and January (Ramírez-Pinilla 1992).

Study area

We captured, by noosing, 9 males and 10 females during the reproductive season (16–20 October, 2013) and 10 males and 9 females during the post-reproductive season (13–17 January, 2014) in “Los Cardones” (26°40′1.5″S, 65°49′5.1″W, datum: WGS84; 2725 m), Tucumán province, northwestern Argentina. This site is located on the western slope of the Sierras Calchaquíes and corresponds to the phytogeographic region of Prepuna (Cabrera and Willink 1980). It is characterized by semi-arid climate, tall cacti (*Trichocereus terscheckii*), scattered shrubs, and large rocks.

Housing

Upon capture, the lizards were kept in individual cloth bags and were taken to the Animal Behavior Institute (Fundación Miguel Lillo, 3 h by car), where they were exposed to ambient temperatures (20–35 °C) and a natural photoperiod (13L:11D). Lizards were housed individually in plastic terraria (Exo-Terra Faunarium, 37 × 22 × 25 cm), covered with a plastic mesh. Because sun rays did not reach the terraria directly, UV-enriched fluorescent tubes (i.e., “daylight” tubes) were placed over the enclosures for 3 h each day. The terraria were located on shelves and were visually isolated from one another with cardboard. Each terrarium had a rock for basking and a shelter. For substrate, we used a synthetic leather fabric, which is easy to clean and change after each experiment. Water was permanently available and mealworms (*Tenebrio molitor*) were given every couple of days. Lizards were held in their enclosures for at least 5 days, without being disturbed, before testing started. This protocol follows methods presented in literature on *Liolaemus* (e.g., Labra and Niemeyer 1999), to allow the lizards to familiarize themselves with their new environment and ensure the deposition of chemical compounds. Once the experiments were over, all the lizards were taken back to Los Cardones and released where they had been captured.

Experimental design

To test the hypothesis of sexual recognition in *L. pacha*, we used a repeated-measures design in which each lizard was placed in random order in three experimental terraria (or scent treatments): a terrarium previously occupied by a male, a terrarium previously occupied by a female, and an untreated terrarium that served as control. All individuals were used as scent donors as well as subjects when assigned that role. The same observer (NSV) recorded each trial with a digital camcorder (Sony HDR-Cx290), placed at 50 cm from the terrarium, for 30 min. Based on

preliminary testing, we observed that lizards generally started tongue-flicking within the first 15 min. Thus, we filmed lizards for 30 min to ensure having 10 min-recordings post-first TF, since we were not viewing the recordings while running an experiment in order to not disturb the lizards. Before an experiment, the individual to be tested was removed from its enclosure and maintained in a cloth bag for 30 min. After that, the lizard was placed in a terrarium under a dark cover for 1 min to reduce stress produced by handling, after which the observer slowly removed the cover and started recording. When finished, the lizard was returned to its own enclosure and was kept undisturbed until the following day, when the next trial started. All trials took place between 10:00 and 17:00 h, during the lizards' usual activity period and when ambient temperature ranged from 28 to 33 °C.

Statistical analyses

In each trial, we counted the number of TFs and the number of visual displays (visual displays = head-bobs + forelimb wave displays, because of low numbers for the latter behavior). All frequencies were counted during the 10 min following the first TF (visual displays were not performed before the first TF). Values are reported as $\bar{X} \pm SE$.

To test the effect and the relative importance of scent treatment, sex, season, and the interaction between them (considered as fixed effects) on TFs, we performed generalized linear-mixed models (GLMMs, Zuur et al. 2009). The individual was considered as a random effect. Because our data, using a Poisson distribution, were overdispersed (e.g., variance bigger than the mean, Zuur et al. 2009), we changed our models to a binomial negative distribution with log-link function, using the glmmADMB package (Skaug et al. 2014). Models were evaluated with information-theoretic procedures, initially considering all possible combinations of predictor variables (Burnham and Anderson 2002). Akaike's information criterion, corrected for small sample size (AIC_c), was calculated for each

model (Burnham and Anderson 2002). Model comparisons were made with ΔAIC_c , which is the difference between the lowest AIC_c value (i.e., best of suitable models) and AIC_c from all other models. The AIC_c weight of a model (w_i) signifies the relative likelihood that the specific model is the best of the suite of all models. We evaluated the support for predictor variables summing w_i across all models that contained the parameter being considered (parameter likelihood, Burnham and Anderson 2002). Parameter estimates were calculated using model-averaged parameter estimates based on w_i from all candidate models. To supplement parameter-likelihood evidence of important effects, we calculated 95 % confidence interval limits (CL) of parameter estimates. Multiple comparisons between treatment levels were performed with the R package multcomp. These analyses were carried out using the software R (v. 3.2.0, R Core Team 2015).

Because visual displays were performed at low frequencies and GLMMs did not fit neither the Poisson nor negative binomial distributions, we used non-parametric statistics. Variation in visual displays considering the three different scents was analyzed with Friedman two-way analyses of variance, for each sex separately. Analyses and post hoc comparisons were performed with the agricolae package (Mendiburu 2015). All tests were two-tailed, and differences were considered significant at $p < 0.05$.

Results

The best model explaining the variation in the number of TFs included scent, sex, and season as explanatory variables ($w_i = 0.48$, Table 1), although there was considerable model uncertainty in relation to the interactions (Table 2). In males, only female scents triggered significantly more TFs (Fig. 1). In females, TFs were not significantly different among scent treatments, neither in reproductive nor in post-reproductive season (Tukey test $p > 0.05$).

In males, during the reproductive season, female scent elicited significantly more TFs than male scent (Tukey test

Table 1 Summary of model-selection results for models explaining variation in tongue flicks in relation to scent treatments (Sc), sex of the tested individual (Sx), season (Sn), and the interactions between them

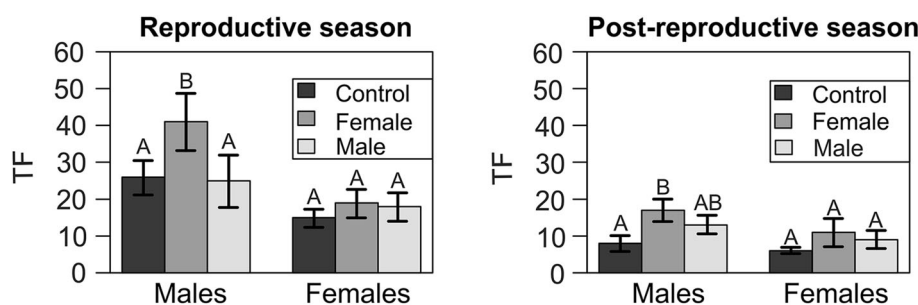
Response variable	Models	<i>K</i>	AIC _c	ΔAIC	<i>w_i</i>
Tongue flicks	Sc Sx Sn	7	818.08	0	0.48
	Sc Sx Sn Sc:Sn	9	820.13	2.04	0.17
	Sc Sx Sn Sc:Sx	9	820.49	2.40	0.14
	Sc Sx	6	821.08	2.99	0.11
	Sc Sx Sn Sc:Sn Sc:Sx	11	822.56	4.47	0.05
	Sc Sx Sc:Sn	8	823.01	4.92	0.04
	Null	3	839.24	21.15	0.00

k is the number of estimated parameters. Most important models are listed in decreasing order of importance, see "Materials and methods" for more details

Table 2 Parameter likelihood, estimates (\pm SE), 95 % confidence interval limits (CL) for explanatory variables describing variation in tongue flicks

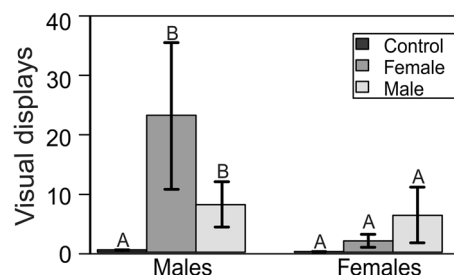
Response variable	Explanatory variable	Parameter likelihood	Parameter estimates \pm SE	CL	
				Lower	Upper
Tongue flicks	Intercept		2.65 \pm 0.18	2.28	3.02
	Scent (female)	0.99	0.38 \pm 0.16	0.08	0.69
	Scent (male)	0.99	0.16 \pm 0.15	-0.15	0.46
	Season (post-reproductive)	1.00	-0.78 \pm 0.21	-1.20	-0.35
	Sex (male)	0.85	0.40 \pm 0.19	-0.10	0.82
	Scent:season (female:post-reproductive)	0.26	0.29 \pm 0.23	0.03	0.77
	Scent:season (male:post-reproductive)	0.26	0.36 \pm 0.23	-0.16	0.75
	Scent:sex (female:male)	0.19	0.25 \pm 0.23	-0.20	0.70
	Scent:season (male:male)	0.19	-0.08 \pm 0.23	-0.54	0.37

Explanatory variables with CL excluding zero are in bold. See “Materials and methods” for details

Fig. 1 Mean number of tongue flicks against three types of scents (male, female, and control), considering sex of the tested individual and season. Standard error bars are shown. Means with the same letter are not significantly different ($p > 0.05$)

$z = -2.25$, $p = 0.05$) and control scent (Tukey test $z = 2.78$, $p = 0.01$; Fig. 1), but TFs elicited by male scent did not differ from the control (Tukey test $z = -0.47$, $p > 0.05$). During the post-reproductive season, female scent also elicited significantly more TFs in males than control scent (Tukey test $z = 3.13$, $p = 0.004$), but it did not trigger significantly more TFs than male scent (Tukey test $z = -0.90$, $p > 0.05$; Fig. 1). TFs produced by male scent did not differ from TFs produced by control scent (Tukey test $z = 1.84$, $p > 0.05$).

Visual displays were affected by season, showing a decrease during post-reproductive season (0.44 ± 0.18) compared with respect to reproductive season (6.44 ± 2.38). We only analyzed reproductive season for each sex, because visual displays during the post-reproductive season were rare or absent. During the reproductive season, males performed significantly more visual displays ($F = 6.75$; $p = 0.02$) to female (23.22 ± 12.49) and male scent (8.00 ± 4.01) than to control scent (0.44 ± 0.29 ; Fig. 2). On the other hand, females performed more visual displays to male scent (6.20 ± 4.81) than to female (1.90 ± 1.37) and control scents (0.10 ± 0.10). However, differences between the latter two scents were not significant ($F = 1.92$; $p > 0.05$; Fig. 2).

**Fig. 2** Mean number of visual displays flicks against three types of scents (male, female, and control) in males and females during the reproductive season. Standard error bars are shown. Means with the same letter are not significantly different ($p > 0.05$)

Discussion

Our result that male *L. pacha* emitted a higher number of TFs to a female scent than to a control stimulus indicates sexual recognition by males. This result agrees partly with previous studies made in other *Liolaemus* species (Labra and Niemeyer 1999; Labra et al. 2001), where the authors found sexual recognition only during reproductive season. Male *L. pacha* recognizes females in both seasons but with lower interest (i.e., lower TFs) in post-reproductive season.

The higher rate of TFs in males to female scent may be related to finding and recognizing potential mates as well as evaluating their reproductive state (Labra and Niemeyer 1999; Carazo et al. 2007; Scott et al. 2015). In the field, a courting male approaches a female by tongue-flicking the substrate near her, and when they are at close range, by contacting her cloacal region (NSV pers. obs.). Chemical cues probably inform the male on the reproductive status of the female, maximizing his reproductive success by recognizing receptive females, especially during reproductive season when a male overlaps his home-range with two or more females (Robles and Halloy 2009). Evaluating females before engaging in reproductive attempts may maximize male fitness benefits, helping to offset energetic and survival costs of mating by primarily focusing a male's efforts on high-value females (Thomas 2011; Swierk et al. 2013).

It is intriguing that females did not show recognition whereas males did. One possibility is that females can recognize scents with just a few TFs. There is considerable literature that states that the absence of discrimination does not exclude recognition, because recognition refers to an underlying internal neural process, which can occur with or without detectable behavioral discrimination (e.g., Sherman et al. 1997). Thus, an apparent lack of interest (i.e., low number of TFs) does not necessarily indicate a lack of discrimination, but rather a lizard may have recognized the conspecific scent but no further tongue-flicks are needed. If this is true, males also should potentially recognize scents with just a few TFs, and subsequent tongue-flicking may have another function, such as the localization of chemical sources (Cooper 1998). Another possibility is that females did not recognize chemical cues, suggesting that females may not use chemical cues for mate choice. Considering a previous study on this species by Robles and Halloy (2012) in which females did not choose males based on visual cues (e.g., body size, coloration and familiarity), females may need both chemical and visual signals to identify a male. Other lizard species also failed to show sexual recognition based on chemical cues alone (Font et al. 2012; Baird et al. 2015; Scott et al. 2015). In fact, female choice has rarely been demonstrated in territorial lizards (e.g., Olsson and Madsen 1995; Lailvaux and Irschick 2006). Thus, more studies are needed to determine whether females recognize males and if they do this by using both types of signals.

Only a few studies in *Liolaemus* have considered visual displays triggered by chemical cues (e.g., Labra 2008). For example, female *L. tenuis* show higher rates of visual displays when exposed to male feces. In *L. pacha*, the visual response triggered by chemical cues differed between sexes. Males responded significantly with visual displays when exposed to conspecific scents. Because male and female chemical stimuli were sufficient to trigger

visual responses in this lizard, we conclude that chemical scents play a major role in social interactions in *L. pacha*. Thus, *L. pacha* uses various sensory modalities to communicate with potential mates and rivals. Although not significant, female scent tended to elicit a higher visual response than male scent, suggesting more interest by males for female cues. Possibly, female scents induce males to invest more energy into courtship, when the likelihood of mating is very high (Swierk et al. 2013). On the other hand, because females showed neither different visual responses nor different number of TFs to conspecific scents, we suggest that females might need visual and chemical cues simultaneously to trigger responses.

During the reproductive season, the number of TFs and visual displays were higher than in the post-reproductive season in both sexes. These results are similar to those found in other studies (Labra and Niemeyer 1999; Labra et al. 2001; Halloy 2012). We suggest that the observed seasonal behavioral differences could be related to physiological changes that are related mainly to reproduction (e.g., Cooper and Pérez-Mellado 2002). Chemical cues recognition and the high number of visual displays exhibited by males of *L. pacha* could facilitate the establishment of their territories. Once formed, the detection of chemical cues and the performance of visual displays, such as headbobs, could also assist in the maintenance of territorial boundaries throughout the breeding season as well as in defending females (Baird et al. 2015). During the post-reproductive season, when no more mating occurs and other activities such as foraging and basking prevailed, chemosensory demands as conspecific recognition became less important, thus the overall number of TFs and visual displays may diminish.

To conclude, we found evidence that a male *L. pacha* recognizes females based on chemical cues, whereas females do not recognize males. Future studies will need to evaluate this apparent lack of recognition in females, among other questions, and evaluate the role of chemical cues in mate choice experiments.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval Animal care and experiments were conducted according to guidelines for the use of animals in research, published in Animal Behaviour (1991). All applicable international, national, and/or institutional guidelines for the care and use of animals were

followed. This article does not contain any studies with human participants performed by any of the authors.

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