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Hemipenes eversion behavior: a new form of communication in two *Liolaemus* lizards (Iguania: Liolaemidae)

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Abstract: Males of several animals have intromittent organs and may use these in a communicative context during sexual or intrasexual interactions. In some lizards, hemipenes eversion behavior have been observed, and the aim of this study is to find out whether this behavior is functionally significant under a communicative approach. Here, we investigated the eversion of hemipenes in the Light Blue Lizard (*Liolaemus coeruleus* Cei and Ortiz-Zapata, 1983) and in the Valley Lizard (*Liolaemus quilmes* Etheridge, 1993) by filming the response of male focal lizards in different experimental settings: (*i*) an agonistic context, i.e., with a conspecific male, (*ii*) a sexual context, i.e., with a conspecific female, and (*iii*) a control treatment, i.e., without a treatment lizard. In both species, focal lizards showed this behavior only in an agonistic context, with interspecific differences as follows. *Liolaemus coeruleus* has longer times until eversion and dragging of hemipenes; however, it has shorter time of eversion and exposition of the hemipenes. *Liolaemus quilmes* has the opposite pattern compared with *L. coeruleus*. These indicate that eversion of the hemipenes can act as a visual display and as a signal of aggressive behavior towards conspecific rival males. The present study offers a new behavioral perspective on the use of masculine genitalia in lizards.

Key words: Squamata, visual displays, *Liolaemus coeruleus*, *Liolaemus quilmes*, male genitalia.

Résumé : Les mâles de plusieurs espèces d'animaux ont des organes d'intromission qu'ils peuvent utiliser dans un contexte de communication durant des interactions sexuelles ou intrasexuelles. Chez certains lézards, un comportement d'éversion des hémipénis a été observé, l'objectif de l'étude est de déterminer si ce comportement est important sur le plan fonctionnel dans une approche de communication. Nous avons examiné l'éversion des hémipénis chez *Liolaemus coeruleus* Cei et Ortiz-Zapata, 1983 et *Liolaemus quilmes* Etheridge, 1993 en filmant la réaction de lézards mâles dans les contextes expérimentaux suivants : (*i*) un contexte agoniste, soit avec un mâle conspécifique, (*ii*) un contexte sexuel, avec une femelle conspécifique et (*iii*) un contexte témoin, sans autre lézard. Chez les deux espèces, les lézards examinés présentaient ce comportement seulement dans le contexte agoniste, mais il y avait des différences entre les deux espèces. Chez *L. coeruleus*, l'intervalle avant l'éversion et le traînage des hémipénis était plus long, mais la durée de l'éversion et de l'exposition des hémipénis était plus courte, alors que chez *L. quilmes*, c'était le contraire. Ces résultats indiquent que l'éversion des hémipénis peut jouer un rôle de signal visuel et être un signe d'un comportement agressif envers des mâles rivaux de la même espèce. L'étude offre une nouvelle perspective comportementale sur l'utilisation des organes génitaux mâles chez les lézards. [Traduit par la Rédaction]

Mots-clés : squamates, signaux visuels, *Liolaemus coeruleus*, *Liolaemus quilmes*, organes génitaux mâles.

Introduction

In many groups of animals, males use intromittent organs to transfer their sperm during copulation (Smith 1984). The evolution of these organs is generally believed to be driven by selective factors related to sexual selection, ecology, and female genitalia morphology (Langerhans et al. 2016), which result in high morphological variety (de Souza et al. 2014). Male intromittent organs can be used as a communicative signal, mainly during courtship, as occurs in some insects (e.g., flies, beetles, wasps), fish (e.g., guppy), and different placental (e.g., monkeys, elephants, cavy, rodents, shrews) and marsupial (e.g., wallabies) mammals (Eisenberg et al. 1971; LaFollette 1971; West-Eberhard 1984; Stralendorff 1986; Eberhard 1990; Brooks and Caithness 1995; Maestripieri 2005; Ottway et al. 2005; Briceño et al. 2010). Furthermore, in mammals, the erect penis may send signals indicating a subordinate status (e.g., Rozenfeld and Rasmont 1991; East et al. 1993; Kutsukake and Castles 2004; Liebal et al. 2004) or, conversely, a dominant status (e.g., Ploog and MacLean 1963; LaFollette 1971; Rozenfeld and Rasmont 1991) among males.

Considering reptiles, males of the order Squamata have notably complex masculine genitalia called hemipenes (e.g., Arnold 1986a; Böhme and Ziegler 2009; Lee et al. 2015). They are formed by two eversible, sac-like structures that are frequently covered with different ornamentations such as calyces, papillae, flounces, and spines (Dowling and Duellman 1978). Until now, research on lizard hemipenes has focused mainly on their reproductive function (e.g., Conner and Crews 1980; Arnold 1986b) and their morphological characteristics (e.g., Böhme and Ziegler 2009; Quipildor et al. 2018). Although behavioral aspects have been given much less attention, there are some studies that explore copulation behavior (e.g., Tokarz 1989; Shine et al. 2000; Moreira and Birkhead 2004). Another interesting behavioral approach was made by in den Bosch (2001), who mentioned that during the breeding season, lacertid lizards shed their genital skin and deposit hemipenial blobs while everting and dragging their hemipenes.

Liolaemus Wiegmann, 1834 is a highly diverse genus of South American lizards with more than 260 species (Uetz et al. 2018). It is divided into two groups: the Chilean group or *Liolaemus* sensu

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Table 1. Summary of results when the conspecific male treatment was applied to Light Blue Lizards (*Liolaemus coeruleus*) showing the presence and absence of the hemipenes eversion behavior (HEB; *n* = 10), the number of times that a lizard defecates, the number of tongue flicks made by focal and treatment lizards, the main visual displays made by focal and treatment lizards, and snout–vent lengths of focal and treatment lizards.

HEB	Defecation	No. of tongue flicks		Main visual displays		Snout–vent length (mm)	
		Focal	Treatment	Focal	Treatment	Focal	Treatment
Presence	1	1	41	Head-bob, forelimbs	Closing eye	56.91	58.47
Presence	1	5	14	Head-bob, forelimbs	Closing eye	58.47	59.65
Presence	1	5	0	Head-bob, forelimbs, push-up	Closing eye	59.65	60.7
Absence	0	4	6	Forelimbs	Head-bob, forelimbs, moves	60.7	60.85
Presence	1	6	18	Head-bob, forelimbs	Closing eye, forelimbs, escape	60.85	60.99
Absence	2	4	1	Head-bob, forelimbs	Head-bob, forelimbs, moves	60.99	62.81
Absence	0	1	3	Head-bob, forelimbs	Forelimbs, charges, closing eye	62.81	62.91
Absence	1	3	2	Push-up, forelimbs	Head-bob, forelimbs, moves	62.91	63.49
Absence	1	2	0	Head-bob, forelimbs	Closing eye, escape	63.49	66.06
Absence	0	0	4	Head-bob, forelimbs, push-up	Head-bob, forelimbs, moves	66.06	63.49

stricto and the Argentinean group or *Eulaemus* Girard, 1858 (Laurent 1983). Accounting for the possibility of interspecific differences, we studied two *Liolaemus* species: the Light Blue Lizard (*Liolaemus coeruleus* Cei and Ortiz-Zapata, 1983) (Cei and Ortiz-Zapata 1983) belonging to the Chilean group and the Valley Lizard (*Liolaemus quilmes* Etheridge, 1993) (Etheridge 1993) belonging to the Argentinean group. Ruiz-Monachesi (2018) noted that *L. coeruleus* and *L. quilmes* males have a particular hemipenes eversion behavior (similar to in den Bosch 2001), which potentially may be used as a visual display (Ruiz-Monachesi 2018). This is an uncommon behavior in these lizards, which perform mainly other visual displays such as head-bob movement and forelimb waves (Halloy 1996, 2012; Halloy and Castillo 2002; Martins et al. 2004; Labra et al. 2007; Vicente and Halloy 2015; Ruiz-Monachesi 2018; Vicente 2018). However, Ruiz-Monachesi (2018) did not determine whether the social context affects this behavior. Conversely to in den Bosch (2001), Ruiz-Monachesi's (2018) observations were not carried out during the breeding season and lizards did not deposit hemipenial blobs nor did they change their genital skin. Based on Ruiz-Monachesi's (2018) observations, we ask whether this behavior could be a visual communication mechanism and, for the first time, give a detailed description of its function in *Liolaemus* lizards. Additionally, we examined whether the behavior is influenced by different social contexts, such as agonistic (i.e., in the presence of a conspecific male) or sexual (i.e., in the presence of a conspecific female) encounters. We expected to observe hemipenes eversion in sexual contexts, given that hemipenes have a reproductive function.

In *Liolaemus*, the precloacal pores are a source of chemical secretions (Valdecantos et al. 2014) with pheromonal properties (Labra et al. 2005; Valdecantos and Labra 2017). In other lizard genera, it was proposed that the absence of pheromonal pores might be associated with an increased use of visual displays (e.g., Lacertidae and Phrynosomatidae; Hews and Benard 2001; Baeckens et al. 2015). Based on lizards of the Chilean group having less precloacal pores than those of the Argentinean group (Laurent 1983; Jara et al. 2018), Martins et al. (2004) hypothesized that the former depended more on visual communication, whereas the latter might use the chemical modality more. *Liolaemus quilmes* males have a mean of 5.8 precloacal pores (Etheridge 1993), whereas *L. coeruleus* males lack these pores entirely (Cei and Ortiz-Zapata 1983). Thus, we expect that *L. coeruleus* to rely more heavily on visual displays (such as exposing their hemipenes longer) than *L. quilmes*. Additionally, as the number of tongue flicks is considered a proxy for chemical exploration (Font and Desfilis 2002; Baeckens et al. 2017a), we expect that *L. coeruleus* to make fewer tongue flicks than *L. quilmes*.

Materials and methods

We collected 20 *L. coeruleus* adults (10 males and 10 females) near Alumine, Neuquén (route 13 between Kilka and Primeros Pinos, Argentina: 38°54′14.70″S, 70°43′59.50″W; datum WGS84) in November 2015. Additionally, 15 *L. quilmes* specimens (9 males and 6 females) were collected near Rio Seco, Cafayate, Salta, Argentina (26°07′22.9″S, 65°58′06.1″W; datum WGS84) in November 2016. Both species were sampled during the post-hibernation season. Lizards were captured by hand (*L. coeruleus*) or using a loop (*L. quilmes*) and kept in individual cloth bags until their arrival at the laboratory. They were then placed in individual plastic enclosures (36 cm × 27 cm × 19 cm) covered with a plastic mesh lid. Enclosures contained 3 cm of sandy substrate, a rock to be used as shelter and basking place, and a small bowl with water ad libitum. Lizards were kept in an isolated room with a summer photoperiod of 13 h light : 11 h dark using halogen lamps, which maintained a mean ambient temperature of 30 ± 2 °C during the light phase. Every other day we fed each lizard two yellow mealworm (*Tenebrio molitor* Linnaeus, 1758) larvae that were dusted with vitamins. Prior to the experiments, lizards remained undisturbed in their enclosures for 1 week, allowing them acclimatize to the experimental conditions.

Appropriate actions were taken to minimize stressing the lizards. The study was conducted in accordance with international standards on animal welfare and is compliant with national regulations and the Argentinian Comité Nacional de Ética en la Ciencia y la Tecnología (Expediente No. 5344/99, Resolución 1047). At the end of all experiments, lizards were sacrificed with a pericardic Pentothal injection following a standard protocol (Scrocchi and Kretzschmar 1996). Lizards were fixed in 10% formol and conserved in 70% ethanol for their use in systematic studies and their final deposition in the herpetological collection of the Instituto de Bio y Geociencias del NOA (IBIGEO). These procedures were approved by the IBIGEO committee for the ethical use of animals and take into account animal welfare regulations. Animals were collected according to permit No. 4351-0026/2014 (*L. coeruleus*) and permit No. 815/13 (*L. quilmes*).

Experimental design

We filmed the behavioral response of a male focal lizard placed in sight of a treatment lizard of similar size, i.e., with a minimal snout–vent length difference between focal and treatment lizards (maximum difference of 2.57 mm; Tables 1 and 2), to avoid a possible effect of body size (e.g., Labra 2006). Each lizard performed three trials: (1) in an agonistic context, with a male individual; (2) in a sexual context, with a conspecific female; (3) in a control treatment, without a treatment lizard. We used a glass enclosure for the experiments equipped with clean (i.e., without

Table 2. Summary of results when the conspecific male treatment was applied to Valley Lizards (*Liolaemus quilmes*) showing the presence and absence of the hemipenes eversion behavior (HEB; *n* = 9), the number of times that a lizard defecates, the number of tongue flicks made by focal and treatment lizards, the main visual displays made by focal and treatment lizards, and snout–vent lengths of focal and treatment lizards.

		No. of tongue flicks		Main visual displays		Snout–vent length (mm)	
HEB	Defecation	Focal	Treatment	Focal	Treatment	Focal	Treatment
Presence	1	24	0	Head-bob, push-up, forelimbs, moves, mouth	Immobile, tail waving	49.6	50.33
Absence	0	2	4	Head-bob, forelimbs	Head-bob, forelimbs, moves	50.33	50.63
Absence	2	11	3	Head-bob, forelimbs, moves	Head-bob, moves, tail waving	50.63	51.02
Absence	0	3	7	Head-bob, push-up, moves	Forelimbs, moves	51.02	51.7
Absence	1	9	7	Moves	Head-bob	51.7	51.02
Presence	2	4	2	Moves	Moves	53	53.6
Absence	1	19	2	Push-up	Closing eye	53.6	53
Absence	0	7	8	Push-up, forelimbs	Head-bob, push-up, forelimbs	55.83	56.47
Presence	1	27	2	Head-bob, moves	Closing eye, moves	56.47	55.83

chemical scents) sandy substrate and divided by a transparent glass sheet into two equally sized 30 cm long sectors (Fig. 1). Before each trial, focal and treatment lizards were removed from their enclosures and held in an individual cloth bag for 10 min to minimize handling stress (e.g., Labra 2011). The experiment started with the introduction of the treatment lizard into one side of the experimental glass enclosure (60 cm long × 20 cm wide × 30 cm high). Then, the cloth bag with the focal lizard was opened to allow the animal to move freely into the opposite sector of the glass enclosure (30 cm long). Once the focal lizard entered the glass enclosure and we were out of its visual field, we registered the time of latency to the first movement with a digital stopwatch. Latency time is defined here as the time that passes from the moment the lizard enters the glass enclosure until it sees the treatment lizard and begins to move. After latency time, we videotaped the behavior of the focal lizard for 10 min using two digital video cameras (Sony DCR-SR67 and JVC GZ-EX210BU) installed at 40 and 20 cm in frontal and lateral views, respectively (Fig. 1). We saved the digital videos for further analyses, which were performed with VLC Media Player version 2.2.1. All focal lizards responded with certain latency, but if latency time exceeded 7 min, then the trial was canceled and repeated on a different day. After every trial, we verified that focal and treatment lizards were healthy before returning them to their enclosures where they remained undisturbed for at least 3 days before a new trial. To avoid cross-contamination, we changed gloves, cleaned glass enclosures with 96% ethanol, and discarded the experimental substrate after every trial. Each one of these trials was randomized until each individual completed all trials.
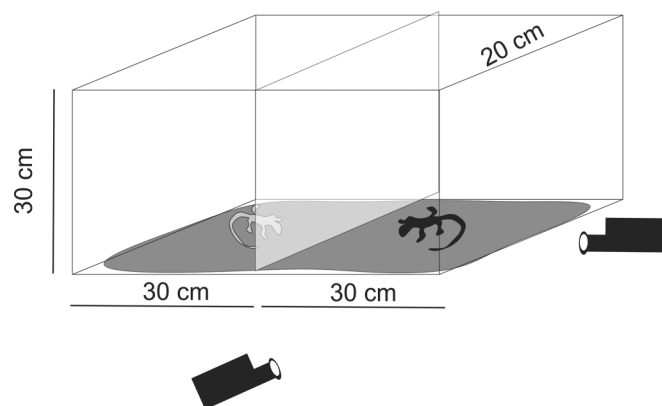
From the videos, we recorded the behaviors mentioned in Tables 1 and 2 and we analyzed the following variables only in those videos where the hemipenes eversion behavior was present:

(1) Time of the first defecation (s): time elapsed between the first movement to the lizard's first defecation;
(2) Time until the eversion (s): time between the lizard's first defecation and the eversion of the hemipenes;
(3) Duration of the eversion (s): total time in which the hemipenes are everted but not dragged;
(4) Duration of dragging (s): total time in which the hemipenes and cloaca are dragged through the substrate; and
(5) Number of tongue flicks: an index of chemical exploration (Font and Desfilis 2002) that considers the times that the lizard protrudes and rapidly retracts its tongue, regardless of whether the tongue touches the substrate, wall, or if it is waved in the air (e.g., Labra 2006).

Statistical analyses

Because our first objective was to test for differences between treatments, and not between species, we analyzed data from both species jointly (*n* = 19). From video analyses, we observed that those
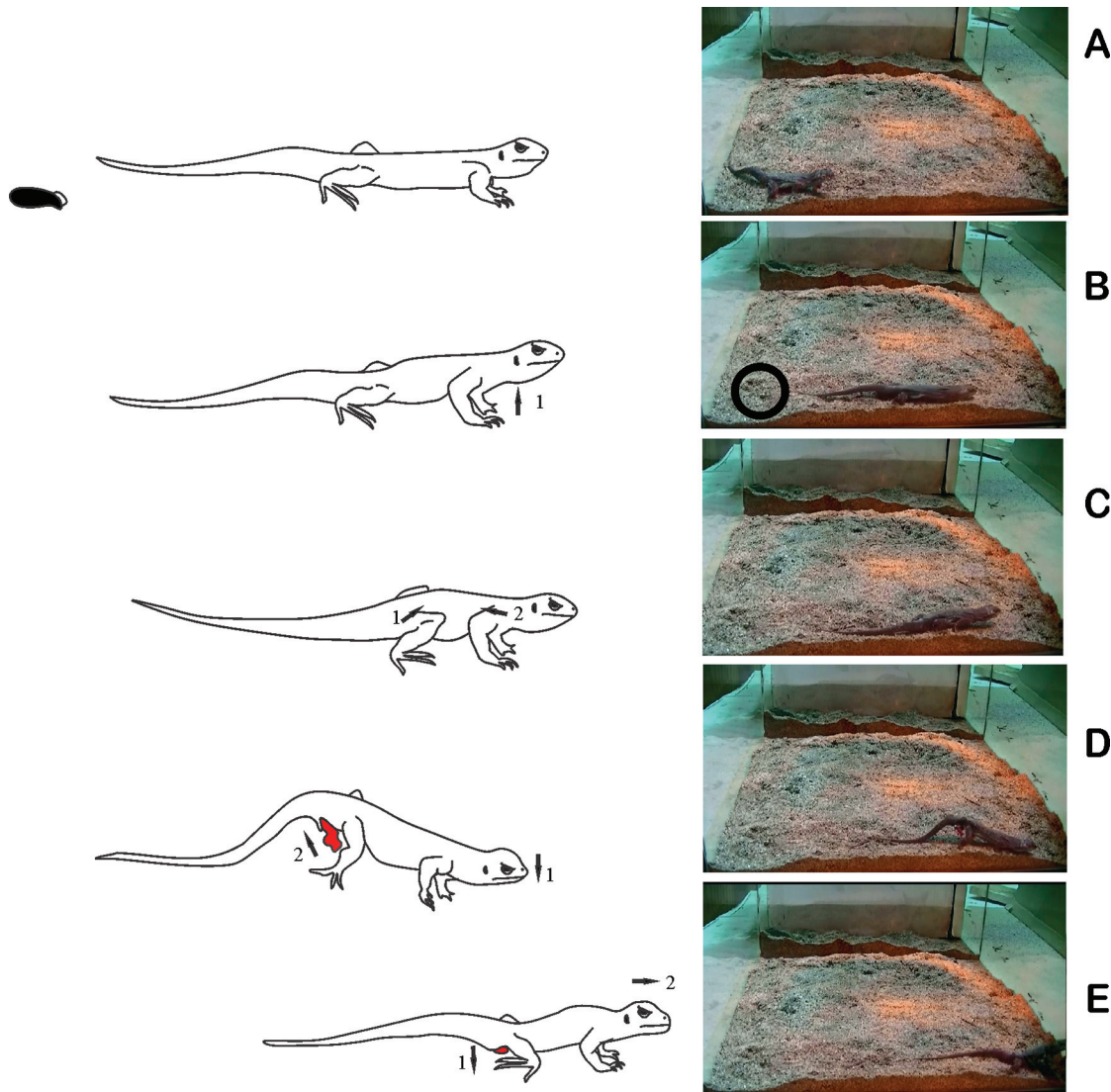
Fig. 1. Representative drawing of the experimental design used to film the behavioral response of *Liolaemus* lizards showing the glass enclosure divided by a transparent glass sheet, the focal (black) and treatment (grey) lizards, and the two digital video cameras installed at 40 cm and 20 cm in frontal and lateral views, respectively.

animals that everted their hemipenes only did so once. For this reason, we used Cochran's *Q* test because our response variable only had two possible outcomes (0 = absence of this behavior; 1 = presence of behavior). On the other hand, interspecific differences (*L. coeruleus* vs. *L. quilmes*) were analyzed only for those individuals that presented this behavior (*n* = 7). As neither response variables nor transformed response variables fulfilled assumptions of normality and homoscedasticity, we used a Mann–Whitney *U* test with species as the grouping factor. Data analysis was performed using STATISTICA version 7.0.

To analyze the number of tongue flicks (*n* = 19) as a response variable, we used the following predictor variables: species (*L. coeruleus*, *L. quilmes*), condition (focal, treatment), and hemipenes behavior (presence, absence). We performed generalized linear mixed models (GLMMS) using R (R Core Team 2015). The species, condition, and hemipenes behavior were fixed effects, whereas the individual identity of the subject lizard was considered a random effect. Because our data are over dispersed (Zuur et al. 2009), our models had a binomial negative distribution. Because of this, we implemented a binomial negative distribution with a log-link function using the glmmADMB package (Skaug et al. 2014). We explored all possible models and chose the best-fitting model, which had the lowest value for Akaike's information criterion corrected for small sample size (AIC$_c$) and the highest Akaike weight (*w$_i$*) (Burnham and Anderson 2004). Analyses were followed by post hoc Fisher's least significant difference (LSD) tests performed with the agricolae package (Mendiburu 2015).

Fig. 2. Drawing (left) and filmed sequence (right) showing the hemipenes eversion behavior in *Liolaemus* lizards: (A) defecation and beginning of the behavior; (B) lifting of anterior extreme; (C) lifting of posterior extreme; (D) hemipenes eversion; (E) dragging. Internal numbers indicate the sequence order and black arrows show the direction of movements. Right and left represent anterior and posterior extremes, respectively. The black circle in B indicates feces. Color version online.

Results

Description of hemipenes eversion behavior

After the first visual contact, hemipenes eversion behavior can be divided into five phases, which were always performed in the same manner by all individuals regardless of the species: (1) the lizard defecates, moves, and remains immobile with its body, head, and limbs (anterior and posterior) pressed against the substrate (Fig. 2A); (2) the lizard elevates its torso and head (movement 1, Fig. 2B), semi-flexes its anterior limbs, and holds this position for approximately 1 s; (3) posterior limbs lift and semi-flex forward (movement 1, Fig. 2C), while the anterior limbs move toward the posterior extreme (movement 2, Fig. 2C); (4) head and anterior limbs move rapidly downward (movement 1, Fig. 2D), while the posterior limbs and back lift pointing backward (movement 2, Fig. 2D) and the hemipenes evert; (5) back and cloaca move downward (movement 1, Fig. 2E) and the lizard advances, dragging its hemipenes and cloaca on the sandy substrate (movement 2, Fig. 2E).
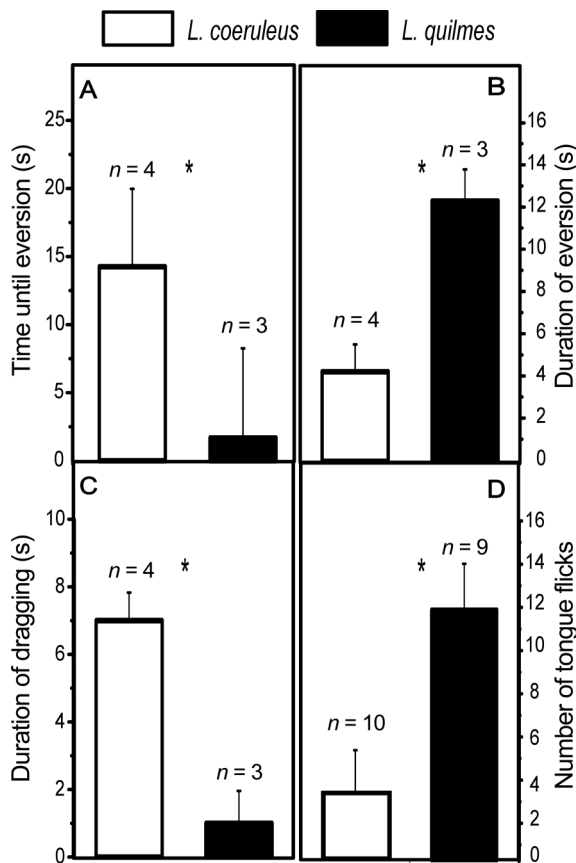
Social context experiments

Overall, seven focal lizards everted their hemipenes. Four of 10 (40%) *L. coeruleus* males (Table 1) and 3 of 9 (33.33%) *L. quilmes* males (Table 2) displayed this behavior. Moreover, the full sequence was visual contact, defecation, hemipenes eversion, and dragging (see Supplementary Videos S1 and S2).[1] The treatment analysis showed significant differences among them (Cochran's Q test, $Q_{[2]} = 14$, $P = 0.0032$, $n = 19$). The behavior was only observed in the agonistic treatment in seven individuals of both species (*L. coeruleus*: $n = 4$; *L. quilmes*: $n = 3$). Neither the control nor the sexual context triggered hemipenes eversion. The Mann–Whitney U test (see Table 3) in these seven individuals revealed species-specific differences in all variables except for the time of first

[1]Supplementary videos are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2018-0195.

Table 3. Results of the Mann–Whitney U test for males that presented hemipenes eversion behaviour when the conspecific male treatment was applied.

| Variable | *L. coeruleus* ($n = 4$) | *L. quilmes* ($n = 3$) | Mann–Whitney U test | |
			Z	P
Time of first defecation (s)	402±77.5	406±89	−0.35	0.72
Time until eversion (s)	14.25±5.72	1.66±6.6	**2.12**	**0.033**
Duration of eversion (s)	4.25±1.29	12.33±1.5	**1.18**	**0.025**
Duration of dragging (s)	7.00±0.83	1.00±0.96	**2.21**	**<0.001**

Note: Response variables (reported as mean ± SE) are time of first defecation, time until eversion, duration of eversion, and duration of dragging. The grouping variable is species (Light Blue Lizards (*Liolaemus coeruleus*) and Valley Lizards (*Liolaemus quilmes*)). Significant results ($P < 0.05$) are set in boldface type.

Fig. 3. Main differences between Light Blue Lizards (*Liolaemus coeruleus*) and Valley Lizards (*Liolaemus quilmes*) observed in an agonistic context: (A) time until eversion; (B) duration of eversion; (C) duration of dragging; (D) number of tongue flicks. Bars are mean + SE. Asterisks indicate statistically significant differences ($P < 0.05$) and n is sample size.

Table 4. Eleven possible generalized linear mixed models (GLMMS) generated when testing the relationship between the number of tongue flicks (TF) and the factors COND (condition: focal or treatment), HB (hemipenes behavior: present or absent), and SP (Light Blue Lizards, *Liolaemus coeruleus*: $n = 10$; Valley Lizards, *Liolaemus quilmes*: $n = 9$) when the conspecific male treatment was applied.

No.	Model	LogLik	AIC$_c$	w_i
1	TF ~ COND	−114.65	237.30	0.044
2	TF ~ HB	−114.00	235.99	0.086
3	TF ~ SP	−113.89	235.77	0.096
4	TF ~ COND + HB	−113.83	237.65	0.037
5	TF ~ COND + SP	−113.85	237.70	0.036
6	TF ~ HB + SP	−113.42	236.83	0.056
7	TF ~ COND + HB + SP	−112.98	237.96	0.032
8	TF ~ COND × HB	−113.83	237.65	0.037
9	**TF ~ COND × SP**	**−110.59**	**233.17**	**0.352**
10	TF ~ HB × SP	−112.17	236.34	0.072
11	TF ~ COND × HB × SP	−109.45	234.90	0.149

Note: LogLik, log-likelihood; AIC$_c$, Akaike's information criterion corrected for small sample size; w_i, Akaike weight. The best model is in boldface type (i.e., model No. 9) and has the lowest AIC$_c$ value and the highest w_i value.

whereas the treatment lizards did not differ (*L. coeruleus*: $Z = 0.9$, $P = 0.25$; *L. quilmes*: $Z = 0.4$, $P = 0.54$). Under focal condition, *L. coeruleus* made less tongue flicks than *L. quilmes* (*L. coeruleus*: $3.10 ± 2.07$ tongue flicks (mean ± SE) versus *L. quilmes*: $11.78 ± 2.20$ tongue flicks; Fig. 3D).

Discussion

The male intromittent organs in several animals have a sexual function, which have been explored mainly from a copulatory perspective (Smith 1984; Langerhans et al. 2016). However, there are numerous examples in nature of their use in intersexual communication (e.g., West-Eberhard 1984; Maestripieri 2005; Briceño et al. 2010) and (or) intrasexual communication (e.g., Ploog and MacLean 1963; LaFollette 1971; Rozenfeld and Rasmont 1991). In Squamata, there are no studies that tackle the communicative function of hemipenes. However Bohme (1983) suggested that the Tree Runner (*Plica plica* (Linnaeus, 1758)) lizard might use its hemipenes as a visual signaler during courtship, but there are no previous mentions of possible agonistic communicative function for hemipenes in Squamata. Here, we described the hemipenes eversion behavior in *Liolaemus* lizards in the absence of a sexual context (Figs. 2A–2E). Our experiments suggest that the presence of a conspecific male can induce this behavior (Supplementary Video S1 and S2).[1] Therefore, we hypothesize that it is used as an aggressive display among *Liolaemus* lizard males. Additionally, we observed differences between *L. coeruleus* and *L. quilmes* (Figs. 3A–3D). We suppose that this behavior has evolved under a complex communication context.

Contrary to our expectations, hemipenes eversion did not occur in sexual situations, i.e., the presence of a female did not trigger males to display their hemipenes. This is surprising but could be explained by the fact that we conducted the study shortly after the

defecation (Table 3, Figs. 3A–3C). Time until eversion was longer in *L. coeruleus* than in *L. quilmes* (Fig. 3A); conversely, *L. quilmes* showed a longer duration of eversion than *L. coeruleus* (Table 3, Fig. 3B). Finally, the duration of dragging was longer in *L. coeruleus* than in *L. quilmes* (Fig. 3C).

Regarding the number of tongue flicks made in an agonistic context and its relationship with the factors species (SP), condition (COND), and hemipenes behavior (HB), a total of 11 models were generated (Table 4). Based on AIC$_c$ values and Akaike weights, only one model was most informative: TF ~ COND × SP (Table 4). This model also was significant ($P = 0.001$). The factors COND and SP were not significant (COND: $F_{[1,34]} = 0.04$, $P = 0.86$; SP: $F_{[1,34]} = 0.19$, $P = 0.16$); however, COND × SP were significantly different ($F_{[1,34]} = 7.23$, $P = 0.001$). Post hoc analyses showed that *L. coeruleus* focal lizards differed from *L. quilmes* focal lizards ($Z = 2.9$, $P = 0.017$),

hibernation season and the lizards might prioritize other necessities, e.g., foraging activities and territorial defense, over reproduction.

Similar to the previously mentioned observations of hemipenes eversions in lacertid lizards (in den Bosch 2001), we saw that *Liolaemus* lizards defecated, everted their hemipenes, and dragged their hemipenes on the substrate. However, we did not observe the deposition of hemipenial blobs with viscous fluids, nor did we find any shed skin as described by in den Bosch (2001). It is possible that the dragging of hemipenes might serve to leave chemical signals and scents related to territorial marking, which is associated with a space defense behavior (Alberts 1992), because the presence of proctodeal glands (Burkholder and Tanner 1974; Valdecantos et al. 2015) possibly implies that chemical secretion occurs during this behavior as we shall discuss below.

As hemipenes eversion only occurred in an agonistic context, always after defecation by the focal lizard and frequently followed by an appeasing behavior by the receptor lizard, such as closing eyes, tongue flicking, or tail waving (Supplementary Video S2[1]; see Fox and Shipman 2003), we hypothesize that it is a form of aggressive behavior between two males. Here, we also observed other visual displays by both species, such as head-bobs, charges, forelimb waves, that accompany the hemipenes eversion behavior (Tables 1 and 2; Supplementary Video S2[1]). In concordance with our hypotheses, these latter behaviors are known to be used as signs of aggressiveness in other lizards (e.g., Ord 2001; Wilczynski et al. 2015; Peters et al. 2016). Interestingly, similar behaviors have been reported in some mammals, which also drag their penis and their anogenital region (Rozenfeld and Rasmont 1991; Ottway et al. 2005) during agonistic interactions. For example, bank vole (*Clethrionomys glareolus* (Schreber, 1780) = *Myodes glareolus* (Schreber, 1780)) males drag their penis to indicate dominance through chemical and visual signals (Rozenfeld and Rasmont 1991). It is possible that this behavior has a double communicative function (i.e., visual and chemical) because the prepuce in some mammals contain chemical glands (e.g., Clapperton et al. 1987). Furthermore, males of bank vole and other mammals such as elephants defecate prior to showing their penis (Eisenberg et al. 1971; Rozenfeld and Rasmont 1991) as we have observed in both *Liolaemus* species. This may indicate that feces are an important component of this agonistic behavior in different taxa.

We found several significant differences between *L. coeruleus* and *L. quilmes*, as the former lacks precloacal pores (Cei and Ortiz-Zapata 1983), which was thought to indicate a lower ability to use scents (Hews and Benard 2001). Therefore, we assumed that *L. coeruleus* would invest more in visual signals than *L. quilmes*. Contrary to this assumption, *L. coeruleus* males invested less time in the visual display of their hemipenes than *L. quilmes* males (Fig. 3B). Furthermore, *L. coeruleus* had a longer dragging phase than *L. quilmes* (Fig. 3C). On another hand, in concordance with our initial assumption, *L. coeruleus* showed a lower number of tongue flicks than *L. quilmes* (Fig. 3D). This is interesting because tongue flicks can be considered a proxy for chemical exploration (Baeckens et al. 2017a); therefore, *L. coeruleus* may present a greater investment in chemical signaling (dragging), but a smaller investment in chemical exploration (tongue flicks). Although *L. coeruleus* males lack precloacal pores, they do bear proctodeal glands (Valdecantos et al. 2015), which is similar to other lizards (e.g., Sagebrush Lizard (*Sceloporus graciosus* Baird and Girard, 1852): Burkholder and Tanner 1974), and possibly uses them during hemipenial dragging. In this case, a longer duration of dragging may help to increase chemical scents. On the other hand, *L. quilmes*, a species with precloacal pores (Etheridge 1993) that are used to facilitate chemical depositions (Baeckens et al. 2017b), everts its hemipenes more quickly (Fig. 2A) and spends more time showing them (Fig. 3B) compared with *L. coeruleus*. However, *L. quilmes* presents a heavier investment in chemical exploration (Fig. 3D), which indicates that it may use hemipenes eversion as a visual signal rather than a chemical signal (Fig. 3C). Thus, *L. quilmes* may present a smaller investment in chemical signaling (dragging), but a greater investment in chemical exploration (tongue flicks). One possibility is that males use this behavior to counterbalance their chemical morphological shortcomings (more or less chemical glands and tongue flicks). Future research is needed to test whether the hemipenes dragging behavior leaves a chemical trail by analyzing the response of both lizards (tongue flicks) to stimulus offered on a cotton swab with hemipenes scents and (or) to observe the behavior of lizards in an arena with these scents. Another possibility is that these interspecific differences are a consequence of a phylogenetic effect because both lizards represent the two main clades in the genus *Liolaemus* (Laurent 1983). *Liolaemus coeruleus* belongs to the Chilean group (Cei and Ortiz-Zapata 1983) and *L. quilmes* belongs to the Argentinean group (Etheridge 1993). Future research with a more extensive taxon sampling is needed to test whether this behavior is present in different groups of both clades and whether they present significant differences. Regardless, our results showed that this behavior is present in species that represent the two main clades of *Liolaemus*, which may suggest that it is present in other species of this genus.

If we consider the possibility of a double communicative function for this behavior, then it must be analyzed in the context of multi-modal communication (Bakker and Traniello 2013). Multi-modal communication implies that two or more different sensory modalities act together to send and receive information during communication (Bro-Jørgensen 2010). The hemipenes eversion behavior in *Liolaemus* may involve two sensorial modalities, i.e., a chemical one and a visual one. The eversion of hemipenes, as well as the feces, may act as visual signals, whereas the feces and hemipenial secretions may serve as chemical signals (in den Bosch 2001; Labra et al. 2002). Some studies of *Liolaemus* lizards suggest that chemical and visual modalities are positively associated (Thompson 2002; Martins et al. 2004; Labra et al. 2007; Vicente and Halloy 2017). Hence, if an individual is able to use both sensory modalities of the eversion behavior, then its message would be reinforced (Partan and Marler 2005).

In summary, we report for the first time the hemipenes eversion behavior in *Liolaemus* lizards. Our experiments showed that the presence of a conspecific male can induce hemipenes eversion. We hypothesize that this behavior may be an aggressive display among *Liolaemus* lizard males. On the other hand, we observed that *L. coeruleus* spent more time in the dragging phase (potential scent marking) and made fewer tongue flicks (less chemical exploration), whereas *L. quilmes* spent more time showing its hemipenes (visual signaling) and made more tongue flicks (less chemical exploration). In both species, this behavior seems to counterbalance their main form of communication, i.e., the presence of precloacal pores accompanies potentially more visual signaling, whereas the opposite is true in the absence of precloacal pores. We consider this to be an example of complex communication and hypothesize that the hemipenes eversion behavior could be used as chemical and visual (multi-modal) communications with a territorial function. The present study may be a starting point for the study of the male genitalia in lizards as a communication tool. Finally, as we had a small sample size, a more thorough research with a larger sample size is necessary to determine how general and common is this particular behavior in lizards.

Acknowledgements

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