

Chemical recognition in a snake–lizard predator–prey system

Antonieta Labra · Misque Hoare

Received: 26 February 2014 / Revised: 10 July 2014 / Accepted: 3 September 2014 / Published online: 17 September 2014
© Springer-Verlag Berlin Heidelberg and ISPA 2014

Abstract In a predator–prey interaction, the fitnesses of the predator and the prey depend on their abilities to recognize each other, a process that may involve different sensory modalities. Squamate reptiles are highly dependent on chemical senses for such recognition, and here we explored the ability of a generalist saurophagous snake, *Philodryas chamissonis*, to discriminate scents of two congeneric and sympatric lizard prey species, *Liolaemus nitidus* and *L. chiliensis*. A generalist saurophagous snake might just be sensitive to lizard scents in general, and if so, no discrimination between prey species is expected. However, these lizards use different substrates; *L. nitidus* basks on rocks, whereas *L. chiliensis* mainly basks on bushes and rarely on ground. The snake *P. chamissonis* basks on ground and rocks, and rarely on bushes. Therefore, if the rate of encounter affects the ability to recognize prey, we predict that *P. chamissonis* would show prey discrimination because scents of *L. chiliensis* may be encountered less frequently in its habitat. Results showed that the snake had a refined discrimination of lizard prey, reducing tongue flick rate and movements in response to scents from the common prey scents, *L. nitidus*. We also studied the ability of *L. chiliensis* to detect the snake and found that snake scents triggered a reduction in activity. The potential infrequent encounter between predator and prey may explain the asymmetric predator–prey recognition, as can be predicted from the “life-dinner” principle.

Keywords *Philodryas chamissonis* · *Liolaemus* · Saurophagous snake · Scents · Predator avoidance · Prey detection

Introduction

The fitnesses of predators and prey are intimately linked to their abilities to recognize each other; a predator needs to recognize its prey to be able to catch and eat it, while the prey needs to recognize the predator to maximize its possibilities to escape being detected and eaten (e.g., Davies et al. 2012). Animals use one or many sensory modalities to achieve this recognition (Bradbury and Vehrencamp 2011), and squamate reptiles are well known for their dependence on chemical senses for these assessments (Kats and Dill 1998; Mason and Parker 2010). For example, lizards exhibit antipredator behaviors in the presence of predator scents (Dial and Schwenk 1996; Amo et al. 2004b) and can discriminate between scents of species of a taxon (e.g., snakes) that pose different levels of threat, i.e., predators vs. non-predators (Dial and Schwenk 1996; Balderas-Valdivia and Ramírez-Bautista 2005; Durand et al. 2012). However, some species exhibit a generalized response to a predator taxon independent of the threat level imposed by the different species (Webb et al. 2009; Webb et al. 2010). This may be because a close phylogenetic relationship among the potential predators may determine similarities in their scent profiles (Balderas-Valdivia and Ramírez-Bautista 2005).

The ability of snakes to discriminate scents from different taxa of prey (e.g., mammals, amphibians, spiders, insects) has been extensively documented. This discrimination usually correlates with species feeding ecology (e.g., Burghardt 1967; Bevelander et al. 2006; Weaver et al. 2012), and generalist snakes show less precise discrimination (Greenbaum 2004). Prey chemical discrimination can also have an

A. Labra (✉) · M. Hoare
Instituto de Ciencias Biomédicas, Facultad de Medicina, Universidad de Chile, Santiago, Chile
e-mail: a.lillo@ibv.uio.no

A. Labra
Centre for Ecological and Evolutionary Synthesis (CEES),
Department of Biosciences, University of Oslo, Oslo, Norway

ontogenetic component due to constraints on the ability to catch and ingest different prey (e.g., Saviola et al. 2012; Saviola et al. 2013) or show geographic variation due to differences in the availability of the preferred prey (e.g., Arnold 1992; Cooper et al. 2000). Much less is known, however, about fine-tuned prey discrimination in snakes, i.e., ability to discriminate among prey of a taxon with similar scent profiles. Studies with the viper *Crotalus viridis viridis* showed that this species discriminated scents from diverse prey species of rodents and lizards, although from different genera (Saviola et al. 2012; Saviola et al. 2013). A finer discrimination was found in the colubrid *Coluber constrictor*, which distinguished between two congeneric lizard species, although one of them was allopatric to the snake (Cooper et al. 2000). Here we tested the ability of the colubrid snake *Philodryas chamissonis* (Dipsadidae) to discriminate chemical scents of two congeneric and sympatric lizard species.

Philodryas chamissonis is an endemic species from central Chile that consumes different tetrapod species, but mainly lizards (Greene and Jaksic 1992; Escobar and Vukasovic 2003; Sepulveda et al. 2006; Lobos et al. 2009; Muñoz-Leal et al. 2013). Therefore, *P. chamissonis* can be considered a generalist saurophagous snake, which would benefit from responding to any lizard scent. We tested its ability to discriminate scents of two sympatric *Liolaemus* (Liolaemidae) prey, *L. nitidus* and *L. chiliensis*, which share similarities in the chemical profiles in at least one pheromone source (Escobar et al. 2001), a condition that could make it hard for the predator to discriminate between them. However, these lizards are not syntopic; *L. nitidus*, as most *Liolaemus* species from central Chile, basks on rocks, whereas *L. chiliensis* basks on bush branches and secondarily on the ground below the bushes. The snake, *P. chamissonis*, basks on open ground and rocks (Mella 2005) and rarely on bushes, which suggests a low frequency of encounter with *L. chiliensis*. Furthermore, it may be hard for *P. chamissonis* to track scents deposited on bushes, which would result in that *L. chiliensis* scents may be rarely encountered. Here we test whether *P. chamissonis* acts as a generalist saurophagous snake showing not discrimination between the presumed rare and common prey or if its chemical recognition system has evolved to show a stronger response to the more commonly encountered prey under natural conditions.

The ability of some *Liolaemus* species to respond to *P. chamissonis* scents has been tested before, and in general, snake scents induce a reduction of activity, which presumably minimizes the possibility of being detected. In addition, species like *L. nitidus*, exhibit antipredator displays, such as tail movements (Labra and Niemeyer 2004; Troncoso-Palacios and Labra 2012), which may act to deflect the predator's attention to the autotomizable tail (Telemeco et al. 2011). However, the extent to which antipredator behaviors are exhibited is modulated by the actual predation risk experienced

under field conditions (Labra and Niemeyer 2004). Therefore, because *L. chiliensis* and *P. chamissonis* rarely bask in the same microhabitat, *L. chiliensis* might not perceive predation risk associated to the snake scents. However, even if the natural predation risk is low, *L. chiliensis* can be part of the snake's diet (Greene and Jaksic 1992), and it may expect that it keeps the ability to respond to *P. chamissonis* scents. Here, we also studied the response of *L. chiliensis* to the scents of this snake.

Materials and methods

During the spring–summer of 2010–2011, we captured ten adult males of *L. chiliensis* (mean snout–vent length (SVL) 74.51, standard deviation (SD) 9.42 mm) at Melipilla (33° 41' S 71° 13' W) and nine (not sexed) individuals of *P. chamissonis* (mean SVL 150.94, SD 23.13 cm) at different localities in central Chile, but far away (>200 km) from Melipilla. In addition, we collected four adult males of *L. nitidus* (mean SVL 80.12, SD 4.70 mm) at El Tabo (33° 29' S, 71° 37' W). Lizards and snakes were transported to the laboratory and placed in separate indoor vivaria with continuous ventilation and conditions mimicking those recorded in the field during normal hot days: 13:11 light–dark cycle with temperatures ranging between 12 and 33 °C provided by halogen lights. All reptiles were housed individually in plastic enclosures (44.5×32×25 cm) with a front window (10×5 cm) of plastic mesh, covered with hermetic lids partially replaced by a plastic mesh. Enclosures contained a pot for water, an inverted tile used for shelter and as a basking place, a wooden stick for use as a perch, and a 3-cm-deep sand layer on the floor. Water was provided ad libitum, and lizards were fed with mealworms dusted with vitamins (SERA reptimineral C) three times per week, whereas snakes were fed with newborn mice once a week. Reptiles were left undisturbed in their enclosures (except for the feeding) for at least 1 week before any trial, to allow habituation to the experimental enclosures and to release scents, because enclosures were used as substrate-borne scents. At the end of the experiments, all individuals were returned in healthy condition to their georeferenced collecting points.

General experimental design

We followed an established protocol (Labra and Niemeyer 2004; Troncoso-Palacios and Labra 2012). Briefly, the tested individual was removed from its enclosure and held in a cloth bag for 10 min on top of its own enclosure to reduce handling-associated stress (Labra 2011). Thereafter, the bag was moved to the experimental area where we opened it carefully, allowing the animal to move freely into the experimental enclosure. Once the animal was inside, the bag was removed

and the enclosure was covered with a sheet of glass (37 × 30 cm) that replaced the plastic lid during the trial. The glass was cleaned with ethanol (95 %) after each trial to remove any chemical traces of the tested individual, which may affect the behavior of the next tested individual. Reptiles were tested individually in a partially counterbalanced design in different treatments (enclosures), only once in each, unless we needed to repeat a treatment. Before using the enclosure of a scent-donor individual, the occupant was removed together with the water container, the stick, and the refuge. We filmed the behavior of the tested individual using a video camera Panasonic HDC-TM20 camcorder (Panasonic, Kadoma, Japan) installed 60 cm over the experimental enclosure. Because body temperature may affect antipredator behaviors (Amo et al. 2004b), at the end of each trial, we measured the cloacal temperature of the tested individual. If the temperatures were not close (± 2 °C) to the preferred body temperature of the species, the trial was discarded and repeated another day. This ensured that records were not biased due to differences in body temperatures. After the trial, the individuals (tested and scent-donor) were returned to their enclosures and kept undisturbed for at least 3 to 4 days before a new trial. Clean gloves were used for each trial to avoid cross contamination.

Specific design for *Philodryas chamissonis*

To standardize for hunger effects, snakes were unfed for 1 week prior to the experiments. Snakes were tested in enclosures of (1) *L. chiliensis*, (2) *L. nitidus*, or (3) odorless control, an unused enclosure with clean sand. The selected scent-donor weighted around 10 % of the snake's weight, which is within the range of reported prey/predator mass ratios for this snake (4 to 19 %; Greene and Jaksic 1992; Lobos et al. 2009). Using this protocol, we avoided exposing snakes to unattractive prey, i.e., too small or too big. Snakes were filmed for 5 min, and filming started as soon as the investigator was out of the visual range of the snake because snakes started to explore as soon as they were out of the bag. At the end of the trial, we checked that their cloacal temperatures were close to the species preferred value (~ 29 °C; Bozinovic and Rosenmann 1988).

Specific design for *Liolaemus chiliensis*

Lizards were tested in the enclosures of (1) conspecific, (2) own: the enclosure of the tested lizard, (3) snake, and (4) odorless control: an unused enclosure with clean sand. We investigated for the ability to discriminate conspecific and own scents to ensure that *L. chiliensis* can distinguish relevant scents from its own species, like several other *Liolaemus* species have been shown to do (Labra 2008). After we left the individual in the experimental enclosure, we recorded with

a stopwatch the latency to the first tongue flick (e.g., time elapsed from the lizard was introduced in the enclosure until its first tongue flick; minutes). Thereafter, the lizard behavior was filmed for 10 min. At the end of the trial, we checked that their cloacal temperatures were close to the species preferred value (~ 35 °C; Labra et al. 2009).

Reptile enclosures were used as substrate-borne scents as follows: those of *L. chiliensis* were used twice, once with a conspecific and the other with a snake. Most enclosures of *L. nitidus* were used twice, except one that needed to be used three times. Snake enclosures were used once, except for one that was used twice. To ensure that enclosures had the donor-scents required for each treatment, and not from a previously tested individual, the scent-donor was kept undisturbed (except for the feeding) in its enclosure for at least 4 days before use its enclosure. This was done even if it has been shown that 10 min is not long enough for lizards to leave traces that other individuals can detect (Labra and Niemeyer 1999). For those experiments in which snakes were tested, it is unlikely that they could leave a significant amount of scents in the 5 min of experimentation, considering that in experiments in which snake scents are collected, individuals are usually allowed to mark surfaces for at least 24 h (e.g., Webb et al. 2009; Durand et al. 2012). In addition, one important snake scent source is the malodorous secretions from the cloacal glands, which are released when snakes are disturbed (Mason and Parker 2010). During our experiments, snakes were treated carefully, and they never released these secretions while they were placed in or out the tested enclosure. Finally, although snakes also release volatile compounds (Shine and Mason 2012), it is unlikely that these would be detectable after more than 4 days.

Data analyses

From the videos, we determined the number of tongue flicks, i.e., number of times that the individual protruded and rapidly retracted the tongue, and the total motion time (seconds), i.e., the total time that the individual moved, including adjustments of body posture, head movements, and displacements of the body.

To determine the effects of the treatments (scents) upon latency to the first tongue flicks, number of tongue flicks, and motion time, we used a general linear model with repeated measurement, followed by post hoc Fisher LSD's test.

Results

Philodryas chamissonis: Scents significantly affected the number of tongue flicks ($F_{(2,14)}=4.75$; $p=0.024$) and the total

time in motion ($F_{(2,14)}=4.25$; $p=0.033$). Snakes tongue flicked (Fig. 1a) and moved less (Fig. 1b) in the presence of *L. nitidus* scents than in the presence of *L. chiliensis* scents and in the odorless control condition. No difference was found between the latter two treatments.

Liolaemus chiliensis: Latency to the first tongue flick was not affected by the type of scents ($F_{(3,27)}=0.99$; $p=0.41$), and its average value was $4.24 \pm (\text{SE}) 0.51$ min. Scents, however, did affect the number of tongue flicks ($F_{(3,27)}=4.21$; $p=0.014$); lizards tongue flicked more in the conspecific enclosure than in any other type of enclosure (Fig. 2a). The total motion time was also affected by the type of scents ($F_{(3,27)}=5.66$; $p=0.004$); lizards moved significantly less in enclosures with snake scents than with any other type of scents (Fig. 2b). The snake enclosure was the only treatment in which lizards ($n=4$) exhibited slow motion (very slow and stalking movements; Labra and Niemeyer 2004) and climbed the window fence ($n=4$). The latter, however, was observed once in the odorless control treatment.

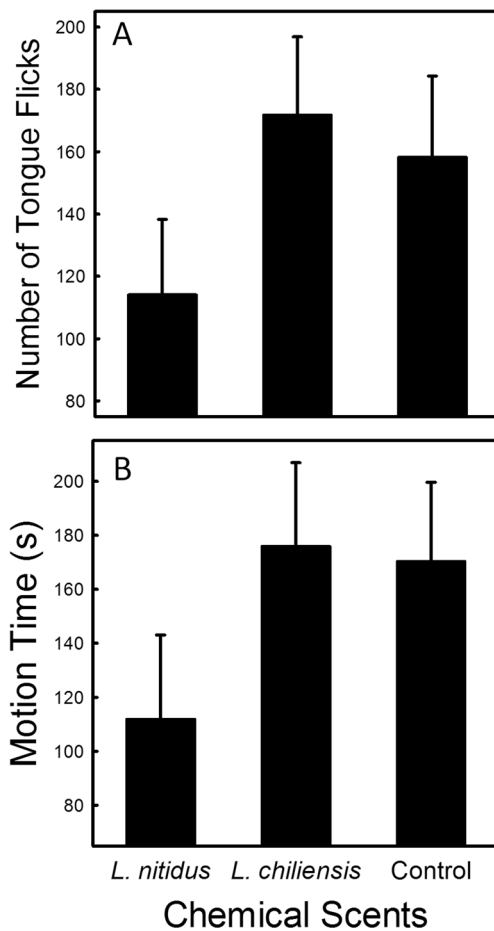


Fig. 1 Mean (+SE) response of *Philodryas chamissonis* to the three chemical stimuli: scents of *Liolaemus nitidus*, *Liolaemus chiliensis*, and an odorless control condition. **a** Number of tongue flicks. **b** Total motion time (seconds)

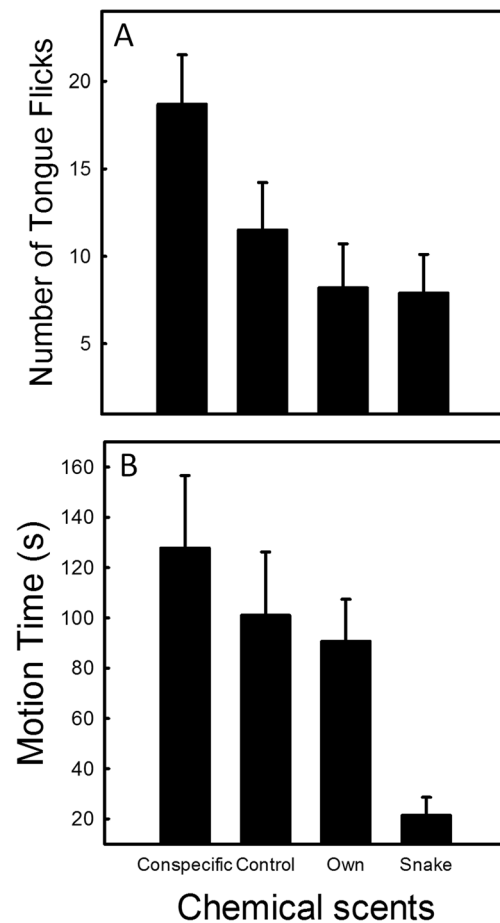


Fig. 2 Mean (+SE) response of *Liolaemus chiliensis* to four chemical stimuli: scents of a conspecific, own (from the tested individual), *Philodryas chamissonis*, and an odorless control condition. **a** Number of tongue flicks. **b** Total motion time (seconds)

Discussion

The saurophagous snake discriminated between congeneric lizard prey, showing less exploratory behavior (i.e., number of tongue flicks and motion time) in the presence of *L. nitidus* scents. This discrimination occurred even though the lizard species share some similarities in their scent profiles (Escobar et al. 2001). It is puzzling that *P. chamissonis* exhibits this fine-tuned response to lizard scents when it seems it would be advantageous to react to any lizard scent, and particularly to any *Liolaemus* scent (Escobar et al. 2001) because this genus is highly diverse and abundant in Chile (Vidal and Labra 2008). In fact, *P. chamissonis* can live in sympatry with up to seven *Liolaemus* species (Mella 2005). Possibly, *P. chamissonis* has an innate ability to react to lizard scents, which may be modulated by experience during ontogeny (Burghardt 1967; Clark 2004a), such as the rate of encounter with prey. Then, because *P. chamissonis* may encounter *L. chiliensis* at low frequency, the scents of this lizard may constitute a relatively novel stimulus for the snake. For

example, it has been argued that *Coluber constrictor* distinguished between two congeneric lizard species because one of these was allopatric, and its scents were novel (Cooper et al. 2000). The novelty of *L. chiliensis* scents is supported by the similar response that *P. chamissonis* had with these scents and the odorless control condition (i.e., more tongue flicks and movements). We doubt, however, that *P. chamissonis* cannot discriminate between these two novel conditions. Most probably, complementary behavioral tests may detect discrimination between these novel chemical environments, such as exposing snakes to scent-impregnated models that can be bitten (e.g., cotton swabs; Cooper et al. 2000).

Philodryas chamissonis is an ambush predator; when confronted with a prey, it usually remains motionless and attacks when the prey moves (personal observations). Thus, *P. chamissonis* may first detect the prey by chemical scents and then use visual information (movements) to attack it, as has been reported for other ambush forager snakes, which typically stop moving in the presence of prey scents (Clark 2004b; Du et al. 2009). Therefore, it is expected that *P. chamissonis* decreases its general activity when it detects scents of the common prey, *L. nitidus*. This result also indicates that the snake species not always exhibits less exploration in the presence of the less preferred prey (e.g., Burghardt 1967) or with novel stimuli (e.g., Amo et al. 2004a). The variation across species may reflect differences in the snake efficiency in chemical recognition (e.g., Mori and Hasegawa 1999) or in the strategy to get the information. Alternatively, how the prey scents are presented (cotton swab vs. substrate-borne scents) may determine the different responses to prey scents. Finally, because this is the first study on the ability of a *Philodryas* species to discriminate prey, it is unclear if congeneric species have a similar fine-tuned discrimination or if they would respond by reducing the exploration when confronted with the prey scents.

The lizard species studied here, *L. chiliensis*, recognized the snake scents, displaying a reduction of activity when confronted with these scents, a behavior that was not associated with a reduction in the display of tongue flicks, as in other *Liolaemus* species (Labra and Niemeyer 2004). By reducing their movements, prey increase the possibility of going undetected by a snake in the neighborhood, as judged by fresh scents (Labra and Niemeyer 2004; Troncoso-Palacios and Labra 2012). Because *P. chamissonis* usually attacks moving prey, remaining immobile increases the lizard's survival probabilities (Cooper et al. 2000; Downes 2002). Interestingly, snake scents triggered slow motion in *L. chiliensis*, a behavior that makes it hard to track the lizard (Downes and Adams 2001; Labra and Niemeyer 2004). Additionally, these scents triggered escape behaviors in the form of climbing the fence of the window (e.g. Cisterne et al. 2014).

A variety of antipredator displays are exhibited by lizards when they are confronted with snake scents (e.g., tail

movement, foot shake; Mori and Hasegawa 1999; Van Damme and Quick 2001), and in *Liolaemus* species, head bobs and tail movements have also been observed (Labra and Niemeyer 2004; Troncoso-Palacios and Labra 2012). *Liolaemus chiliensis* did not exhibit any of these displays, which may be a consequence of two not mutually exclusive factors. On one hand, *L. chiliensis* may perceive a low predation risk in snake scents because predator–prey encounters would occur relatively in a low frequency. Alternatively, the low exhibition of visual displays may reflect that this lizard inhabits bushes where visibility may be restricted. In fact, visual constraint has been proposed as a selective pressure involved in the evolution of distress calls in this species, which may act to warn conspecifics of predation risk in conditions where it is difficult to see the predator (Hoare and Labra 2013).

A previous study has indirectly shown the ability of *L. chiliensis* to discriminate conspecific scents; individuals were more reactive to acoustic stimuli when these were associated with conspecific scents than in an odorless control environment (Hoare and Labra 2013). Here, we confirm that *L. chiliensis* recognizes conspecifics, but we did not find clear evidence of chemical self-recognition (e.g., reduced tongue flicking confronted with their own scents, as compared to any other scent), like in all *Liolaemus* species tested before (Labra 2008; Aguilar et al. 2009; Troncoso-Palacios and Labra 2012). We doubt that *L. chiliensis* cannot discriminate between their own scents and an odorless control condition, and probably complementary behavioral tests will reveal discrimination between these two conditions, e.g., selection of retreat sites with own scent vs. odorless condition (Amo et al. 2004b). However, *L. chiliensis* seems to not have the same abilities of other *Liolaemus* species to discriminate scents, potentially a consequence of the microhabitat uses (bushes), where scents are not easily delivered and trailed.

In closing, we propose that the low overlap in the substrate used by *P. chamissonis* and *L. chiliensis*, at least during their basking activity, may cause in the snake to show less chemical recognition of this relatively uncommon prey. In addition, *P. chamissonis* typically coexists with several potential lizard prey species (Mella 2005), which may have led to a selective detection of familiar prey to avoid wasting time searching for difficult prey. Contrarily, it would be expected that the snake responded equally to scents of both lizard species. On the other hand, even if *L. chiliensis* may experience low predation by this snake, the safest strategy to keep the battle of life is to recognize snake scents and to display antipredator behaviors when exposed to these scents. We propose that in this system predator–prey, the “life-dinner” principle is working (Dawkins and Krebs 1979); if the prey fails, it loses its life. If the predator fails, it only loses a meal.

Acknowledgments The study was authorized by SAG (Resolution No. 7266) and by the Scientific Ethics Committee of the Faculty of Medicine, University of Chile. We thank K. Aguilera, F. Contreras, A. Martínez, B. Segura, G. Silva, F. Urra, A. Zapata, M. Penna, O. Acevedo and particularly to J. Constanzo, J. Lagos, F. Norambuena, and J. Troncoso-Palacios for their invaluable help in the field and laboratory. We are very grateful for the language improvements and important comments made by T.F. Hansen, and for the comments made by H. Díaz, C. Reyes-Olivares, F. Toledo and two anonymous reviewers, all of which improved significantly this manuscript. M. Hoare was supported by a fellowship from Fundación Guillermo Puelma (Universidad de Chile). Funds came from Fondecyt 1090251/1120181 (AL).

References

- Aguilar PM, Labra A, Niemeyer HM (2009) Self-chemical recognition in the lizard *Liolaemus fitzgeraldi*. *J Ethol* 27:181–184
- Amo L, López P, Martín J (2004a) Chemosensory recognition of its lizard prey by the ambush smooth snake, *Coronella austriaca*. *J Herpetol* 38:451–454
- Amo L, López P, Martín J (2004b) Thermal dependence of chemical assessment of predation risk affects the ability of wall lizards, *Podarcis muralis*, to avoid unsafe refuges. *Physiol Behav* 82:913–918
- Arnold SJ (1992) Behavioural variation in natural populations. VI. Prey responses by two species of garter snakes in three regions of sympatry. *Anim Behav* 44:705–719
- Balderas-Valdivia CJ, Ramírez-Bautista A (2005) Aversive behavior of beaded lizard, *Heloderma horridum*, to sympatric and allopatric predator snakes. *Southwest Nat* 50:24–31
- Bevelander G, Smith TL, Kardong KV (2006) Microhabitat and prey odor selection in the foraging pigmy rattlesnake. *Herpetologica* 62:47–55
- Bozinovic F, Rosenmann M (1988) Energetics and food requirements of the female snake *Philodryas chamissonis* during the breeding season. *Oecologia* 75:282–284
- Bradbury JW, Vehrencamp SL (2011) Principles of animal communication. Sinauer Associates, China
- Burghardt GM (1967) Chemical-cue preferences of inexperienced snakes: comparative aspects. *Science* 157:718–721
- Cisterne A, Vanderduys EP, Pike DA, Schwarzkopf L (2014) Wary invaders and clever natives: sympatric house geckos show disparate responses to predator scent. *Behav Ecol* 25:604–611
- Clark RW (2004a) Feeding experience modifies the assessment of ambush sites by the timber rattlesnake, a sit-and-wait predator. *Ethology* 110:471–483
- Clark RW (2004b) Timber rattlesnakes (*Crotalus horridus*) use chemical cues to select ambush sites. *J Chem Ecol* 30:607–617
- Cooper WE, Burghardt GM, Brown WS (2000) Behavioural responses by hatchling racers (*Coluber constrictor*) from two geographically distinct populations to chemical stimuli from potential prey and predators. *Amphibia-Reptilia* 21:103–115
- Davies NB, Krebs JR, West SA (2012) An introduction to behavioural ecology. Wiley-Blackwell, Oxford
- Dawkins R, Krebs JR (1979) Arms races between and within species. *P Roy Soc B-Biol Sc* 205:489–511
- Dial BE, Schwenk K (1996) Olfaction and predator detection in *Coleonyx brevis* (Squamata: Eublepharidae), with comments on the functional significance of buccal pulsing in geckos. *J Exp Zool* 276:415–424
- Downes SJ (2002) Does responsiveness to predator scents affect lizard survivorship? *Behav Ecol Sociobiol* 52:38–42
- Downes SJ, Adams M (2001) Geographic variation in antislake tactics: the evolution of scent-mediated behavior in a lizard. *Evolution* 55:605–615
- Du WU, Webb JK, Shine R (2009) Heat, sight and scent: multiple cues influence foraging site selection by an ambush-foraging snake *Hoplocephalus bungaroides* (Elapidae). *Curr Zool* 55:266–271
- Durand J, Legrand A, Tort M, Thiney A, Michniewicz RJ, Coulon A, Aubret F (2012) Effects of geographic isolation on anti-snakes responses in the wall lizard, *Podarcis muralis*. *Amphibia-Reptilia* 33:199–206
- Escobar MAH, Vukasovic MA (2003) Predation of *Philodryas chamissonis* (Serpentes: Colubridae) on chicks of *Aphrastura [Aphrastura] spinicauda* (Passeriformes: Furnariidae): an arboricolous snake? *Not Men Mus Nac Hist Nat (Santiago)* 352:18–20
- Escobar CA, Labra A, Niemeyer HM (2001) Chemical composition of precloacal secretions of *Liolaemus* lizards. *J Chem Ecol* 27:1677–1690
- Greenbaum E (2004) The influence of prey-scent stimuli on predatory behavior of the North American copperhead *Agkistrodon contortrix* (Serpentes: Viperidae). *Behav Ecol* 15:345–350
- Greene HW, Jaksic FM (1992) The feeding behavior and natural history of two Chilean snakes, *Philodryas chamissonis* and *Tachymenis chiliensis* (Colubridae). *Rev Chil Hist Nat* 65:485–493
- Hoare M, Labra A (2013) Searching for the audience of the weeping lizard's distress call. *Ethology* 119:860–868
- Kats LB, Dill LM (1998) The scent of death: chemosensory assessment of predation risk by prey animals. *Ecoscience* 5:361–394
- Labra A (2008) Multi-contextual use of chemosignals by *Liolaemus* lizards. In: Hurst JL, Beynon RJ, Roberts SC, Wyatt TD (eds) Chemical signals in vertebrates 11. SpringerLink, New York, pp 357–365
- Labra A (2011) Chemical stimuli and species recognition in *Liolaemus* lizards. *J Zool* 285:215–221
- Labra A, Niemeyer HM (1999) Intraspecific chemical recognition in the lizard *Liolaemus tenuis*. *J Chem Ecol* 25:1799–1811
- Labra A, Niemeyer HM (2004) Variability in the assessment of snake predation risk by *Liolaemus* lizards. *Ethology* 110:649–662
- Labra A, Pienaar J, Hansen TF (2009) Evolution of thermal physiology in *Liolaemus* lizards: adaptation, phylogenetic inertia, and niche tracking. *Am Nat* 174:204–220
- Lobos G, Escobar MAH, Thomson RF, Alzamora A (2009) *Philodryas chamissonis* (long-tailed snake) and *Liolaemus nitidus*. Predation determined by pit tag. *Herpetol Rev* 40:358
- Mason RT, Parker MR (2010) Social behavior and pheromonal communication in reptiles. *J Comp Physiol A* 196:729–749
- Mella JE (2005) Guía de campo Reptiles de Chile: Zona central. In Peñaloza AP, Novoa FF, Contreras M. Santiago, Chile, Centro de Ecología Aplicada Ltda, Pp xii+147
- Mori A, Hasegawa M (1999) Geographic difference in behavioral response of hatchling lizards (*Eumeces okadae*) to snake-predator chemicals. *Jpn J Herpetol* 18:45–56
- Muñoz-Leal S, Ardiles K, Figueroa RA, González-Acuña D (2013) *Philodryas chamissonis* (Reptilia: Squamata: Colubridae) preys on the arboreal marsupial *Dromiciops gliroides* (Mammalia: Microbiotheria: Microbiotheriidae). *Braz J Biol* 73:15–17
- Saviola AJ, Chiszar D, Mackessy SP (2012) Ontogenetic shift in response to prey-derived chemical cues in prairie rattlesnakes *Crotalus viridis viridis*. *Curr Zool* 58:549–555
- Saviola AJ, Chiszar D, Smith HM, Mackessy SP (2013) Chemosensory response in stunted prairie rattlesnakes *Crotalus viridis viridis*. *Curr Zool* 59:175–179

- Sepulveda M, Vidal MA, Farina JM (2006) *Microlophus atacamensis* (Atacama desert runner). Predation. *Herpetol Rev* 37:224–225
- Shine R, Mason RT (2012) An airborne sex pheromone in snakes. *Biol Lett* 8:183–185
- Telemeco RS, Baird TA, Shine R (2011) Tail waving in a lizard (*Bassiana duperreyi*) functions to deflect attacks rather than as a pursuit-deterrent signal. *Anim Behav* 82:369–375
- Troncoso-Palacios J, Labra A (2012) Is the exploratory behavior of *Liolaemus nitidus* modulated by sex? *Acta Herpetol* 7:69–80
- Van Damme R, Quick K (2001) Use of predator chemical cues by three species of lacertid lizards (*Lacerta bedriagae*, *Podarcis tiliguerta*, and *Podarcis sicula*). *J Herpetol* 35:27–36
- Vidal MA, Labra A (2008) *Herpetología de Chile*. Science, Santiago, Chile
- Weaver RE, Clark WH, McEwen DC (2012) Prey chemical discrimination by the desert Nightsnake (*Hypsiglena chlorophaea*): a comparison of invertebrate and vertebrate prey. *J Herpetol* 46: 523–526
- Webb JK, Du WG, Pike DA, Shine R (2009) Chemical cues from both dangerous and nondangerous snakes elicit antipredator behaviours from a nocturnal lizard. *Anim Behav* 77:1471–1478
- Webb JK, Pike DA, Shine R (2010) Olfactory recognition of predators by nocturnal lizards: safety outweighs thermal benefits. *Behav Ecol* 21: 72–77