

Short Note

Effects of sensory mode in prey discrimination and predatory behaviour of rock lizards

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Abstract. An essential part of foraging ecology is to understand the processes of detection, recognition and discrimination of prey, as well as the sensorial modalities involved. Often, predators do not rely on a single sensory system but on multiple interacting senses. Specifically, lizards mainly use vision and vomerolfaction for prey pursuit. Here, we used an experimental approach to study how the Carpetan rock lizard, *Iberolacerta cyreni*, responds to different types of stimuli (chemical, visual, or both combined) from two prey species. The number of individuals approaching the prey and the number of attacks differed between treatments, however, we did not find differences in latency time, number of individuals attacking the prey or number of tongue flicks. Our results suggested that visual cues combined with chemical stimuli enhanced detection of both prey species and that prey discrimination occurred posteriorly and independently of using any or both types of stimuli.

Keywords: foraging, *Iberolacerta cyreni*, predation, stimulus control.

Many predators show food preferences, selecting or avoiding certain food types independently of their availability in the environment (Brown, 2009). These preferences can be associated with different aspects such as the nutritive value of the prey, the age and sex of the predator, and/or the previous experience of the predator with a prey (Desfilis and Font, 2002; Eberhart and Ruby, 2019). In this sense, it is important to understand the mechanisms and sensory modes involved in prey detection, recognition and, ultimately, discrimination between preferred against less preferred prey.

Predators may rely on a single sensory mode to recognize prey or use multiple senses that interact with each other. For example, some crocodiles use mechanosensory cues to detect prey (Grap et al., 2020). Rattlesnakes (*Crotalus* spp.) rely on both visual and thermal

cues for prey recognition, while natricine and garter snakes (*Thamnophis* spp.) rely on chemical and/or visual stimuli (Chiszar et al., 1981; Burghardt and Denny, 1983). In lizards, several studies demonstrate that Iguanian species depend exclusively on the vision for prey recognition, while species from other families (Scincidae, Lacertidae, Anguidae and Teiidae) use both chemical and visual cues (reviewed in Cooper, 1995). Using chemical senses, lizards may sample by tongue-flicking different volatile and non-volatile compounds from the environment, being afterwards the vomeronasal system the responsible for obtaining information from these compounds (Cooper, 1990; Graves, 1993). Visually, lizards employ different types of prey cues, such as colouration (Askew et al., 1970; Civantos et al., 2004), shape and size (Loop, 1974; Eberhat and Ruby, 2019) and movement (Burghardt, 1964; Askew et al., 1970; Civantos et al., 2004; Ammann et al., 2014).

Nonetheless, most of the research about perception of prey cues by lizards have been focused on either: i) discrimination between prey-related cues against other types of stimuli not

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associated with prey (Cooper and Sherbrooke, 2009; Ammann et al., 2014) or ii) prey detection of a single prey type using a single sensory mode (Burghardt, 1964; Askew et al., 1970; Eberhart and Ruby, 2019), or multiple sensory modes (Desfilis et al., 2003). However, few studies have compared detection, recognition, and discrimination between different prey types using multiple sensory modes (but see Hasegawa and Taniguchi, 1996).

Here, we designed a laboratory experiment to explore the sensory modes (visual and chemical) that Carpetan rock lizards, *Iberolacerta cyreni*, may use to detect and to discriminate between two prey types that are either naturally selected (larvae of Coleoptera) or avoided (adults of Dictyoptera) in the diet (see Pérez-Mellado et al., 1991). The use of sensory modes in the predatory behaviour of lizards is related to phylogeny and foraging tactics, being active foragers more likely to use visual and chemical cues together (Cooper, 1995). Thus, as Carpetan rock lizards can use both active and sit-and-wait foraging strategies (Martín and Salvador, 1993), we predicted this species to use both visual and chemical stimuli in predatory behaviour. However, different sensory modes might be used in different ways. We hypothesized that visual stimuli might enhance detection of prey, such that, when only chemical cues were available, lizards would detect prey less effectively. However, for recognition and discrimination between different prey types, either visual or chemical stimuli alone might be enough.

During May-June 2018, we collected by noosing 14 adult male Carpetan rock lizards (*I. cyreni*) in an area of 3 km² around “Puerto de Navacerrada” (Sierra de Guadarrama, Madrid, Spain). Lizards were transported to “El Ventorrillo” MNCN-CSIC field station, 5 km from the capture site, where they were kept in individual terraria (71 × 46 × 37 cm length × width × height; see fig. 1C) for at least three weeks as acclimatization period. Shelter and water were provided *ad libitum*. Before the experiments, we fed lizards mealworm larvae (*Tenebrio molitor*)

and adult cockroaches (*Blaptica dubia*) on alternate days (i.e. one day mealworms, one day cockroaches). We fed lizards at least six days each prey species to ensure that lizards had experienced previously the two prey types that we used in the experiments. Based on the diet selection patterns observed in the field (Pérez-Mellado et al., 1991), we considered mealworms as the preferred prey and cockroaches as the less preferred prey. Furthermore, we observed that cockroaches were eaten less often than mealworms (data not shown). The last four days before the tests, lizards fasted (Cooper, 1990).

Trials were conducted in the home terraria of each lizard during 23-25th July, between 12 and 18 h (GMT), the period of greatest activity of these lizards (Martín, 2015). We used a repeated-measures factorial design to test each individual with either Chemical stimulus (Ch), Visual stimulus (V) or Combined (chemical + visual) stimuli (Co) (see below) of each of the two types of live prey: *T. molitor* (T) or *B. dubia* (B) (fig. 1A). Lizards were tested twice per day and trials were counterbalanced. The water container and the shelter were removed 30 min before the tests.

In each test, we presented the prey stimuli in vessels consisting of a transparent plastic cup (top diameter = 74 mm, bottom diameter = 54 mm, height = 115 mm) completely covered with adhesive tape, and a filter paper (140 mm²) fixed underneath. Visual cues arose from the plastic cup that contained one of the two types of prey inside. Chemical stimuli were presented on the filter paper, which had been left for 30 min before the tests in a box containing live individuals of one of the two prey types. In treatments with visual stimuli alone, we used an identical clean filter paper. At the beginning of the trial, the vessel was gently placed in the centre of the lizard’s terrarium.

We recorded the trials with a videocamera (Logitech B525) placed above the terraria (n = 84 videos of 15 min) and afterwards we analysed the recordings to measure the following

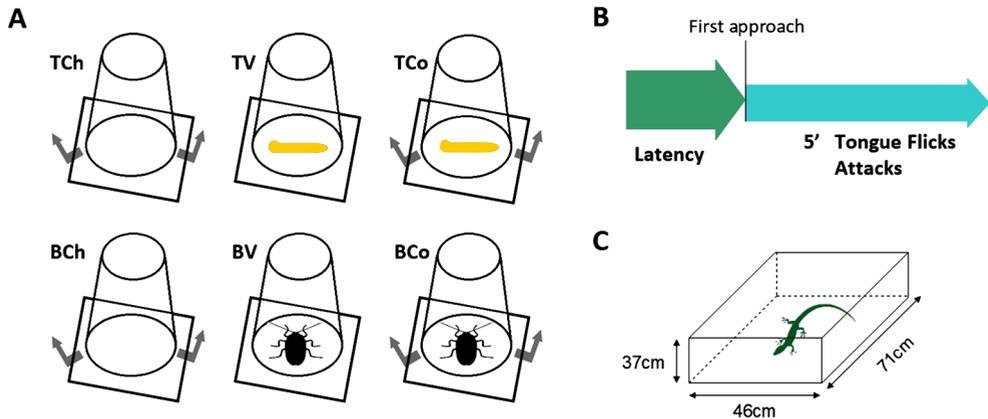


Figure 1. Procedures of the experiments. A: Treatments originated for the 3 by 2 factorial design. TCh = *Tenebrio* Chemical stimulus, TV = *Tenebrio* Visual stimulus, TCo = *Tenebrio* Combined stimulus, BCh = *Blaptica* Chemical stimulus, BV = *Blaptica* Visual stimulus, BCo = *Blaptica* Combined stimulus. B: Variables analyzed. C: Measurements of the terraria.

variables: a) the ‘number of individuals that approached the vessel’, b) ‘latency’ as the time since the vessel was placed in the terrarium until the lizard approached the vessel for the first time, c) the ‘number of individuals that attacked the vessel’, d) the ‘number of tongue-flicks’ (TFs) directed to the vessel for 5 min after the first approach and e) the ‘number of attacks’ to the vessel for 5 min after the first approach (fig. 1B). We assumed that latency time and the number of approaching lizards might be related to the ability to detect prey. We considered that the stimulus was recognized as a prey only if the lizard attacked the vessel, and we used the number of TFs and attacks as proxies of discrimination. If the lizard did not approach the vessel after 5 min, latency was ranked as the maximum time (5 min each), while the rest of the values were noted as 0.

We modelled the data using generalized mixed models for repeated measures. Prey type (*Blaptica* vs *Tenebrio*) and type of stimulus (Chemical, Visual or Combined) were added as fixed factors while the individual was included as a random factor. We fitted the models using a negative binomial distribution for latency times, TFs, and attacks, and a binomial distribution for the number of individuals approaching and attacking the vessel.

We selected the model with the lowest Akaike value corrected for small sample sizes (AICc), assessed the significance of all mixed models using the Likelihood-ratio test (LRT) as the omnibus test, and conducted likelihood-ratio chi-square tests to estimate the significance of fixed factors and its interaction. We made *Post-hoc* analyses using Z Test Holm-Bonferroni adjustments. Only those individuals ($n = 10$) that responded to the prey stimuli in more than three trials were included in the analysis.

The results of the GMM are summarized in table 1. Concerning the number of individuals that approached the vessel, only the type of stimulus had a significant effect (Likelihood-ratio chi-square test: $\chi^2 = 8.80$, $P = 0.012$) (fig. 2A). *Post-hoc* analyses showed that more lizards approached to the vessel with both stimuli combined (TCo, BCo) than with chemical stimulus alone (TCh, BCh) (Z-Test Holm-Bonferroni adjust: $Z = 2.71$; $P = 0.020$), but we did not find significant differences between combined (TCo, BCo) and visual stimuli alone (TV, BV) ($Z = 0.89$; $P = 0.38$). There were no significant differences between visual stimuli alone (TV, BV) and chemical stimuli alone (TCh, BCh) ($Z = 2.19$; $P = 0.058$).

In the model of latency time, only the type of stimulus was significant ($\chi^2 = 6.35$, $P = 0.042$) (fig. 2B). Latency was significantly

Table 1. Results of the GMM performed. Highlighted, the model selected. Likelihood ratio test (LRT) comparisons were made between the null model and the model selected using the lowest AICc value.

Variable	Model	Fixed factors	AICc value	LRT	
				χ^2	<i>p</i> -value
Individuals approaching	Null	–	75.74	–	–
	1	Prey	77.22	–	–
	2	Stimulus	69.02	11.23	<0.01
	3	Prey*Stimulus	73.18	–	–
Latency	Null	–	728.27	–	–
	1	Prey	730.25	–	–
	2	Stimulus	726.36	6.39	0.041
	3	Prey*Stimulus	733.31	–	–
Individuals attacking	Null	–	79.02	–	–
	1	Prey	80.52	–	–
	2	Stimulus	75.77	7.77	0.021
	3	Prey*Stimulus	82.06	–	–
Tongue flicks	Null	–	461.07	–	–
	1	Prey	463.37	–	–
	2	Stimulus	460.28	5.48	0.065
	3	Prey*Stimulus	465.10	–	–
Attacks	Null	–	368.91	–	–
	1	Prey	351.48	–	–
	2	Stimulus	328.54	–	–
	3	Prey*Stimulus	315.07	68.24	<0.01

lower for combined stimuli (TCo, BCo) than for chemical stimuli alone (TCh, BCh) ($Z = 2.51$; $P < 0.036$). There were no significant differences between combined (TCo, BCo) and visual (TV, BV) stimuli, nor between visual (TV, CV) and chemical stimuli (TCh, BCh) ($Z < 1.50$; $P > 0.20$ in both cases).

Concerning the number of individuals that attacked the vessel, the type of stimulus was close to significance but did not reach it ($\chi^2 = 5.69$, $P = 0.058$) (fig. 2C). Similarly, none model was explicative for TFs (see table 1; fig. 2D).

Both the type of prey and the type of stimulus and its interaction were significant for the number of attacks made ($\chi^2 > 100$, $P < 0.001$ for prey, stimulus and Interaction prey \times stimulus) (fig. 2E). *Tenebrio* larvae were attacked significantly more times than *Blattica* cockroaches independently of the type of stimulus presented ($Z > 60.00$; $P < 0.001$ in all cases). For *Tenebrio* larvae, the number of attacks was significantly greater in combined (TCo) than in chemical (TCh) or visual alone

(TV) tests ($Z > 65.00$; $P < 0.001$ in both cases). Visual stimuli alone (TV) elicited significantly more attacks than chemical stimuli alone (TCh) ($Z = 85.73$; $P < 0.001$). The *Blattica*, combined stimuli (BCo) elicited significantly more attacks than chemical (BCh) or visual alone (BV) ($Z > 65.00$; $P < 0.001$ in both cases), and visual stimuli (BV) elicited significantly more attacks than chemical ones (BCh) ($Z = 189.87$; $P < 0.001$). We also observed that, independently of prey type, a hundred per cent of the attacks ($n = 27$) were directed towards the filter paper in the chemical stimuli trials (TCh, BCh), while the cup glass received the total of the attacks ($n = 335$) when any type of visual cue was available (TV, TCo, BV, BCo).

Differences in both the number of individuals approaching the vessel and latency times indicated that visual cues combined with chemical stimuli enhance detection of prey rather than when chemical cues were alone. Similarly, experienced *Podarcis hispanica* lizards also showed differences in latencies between

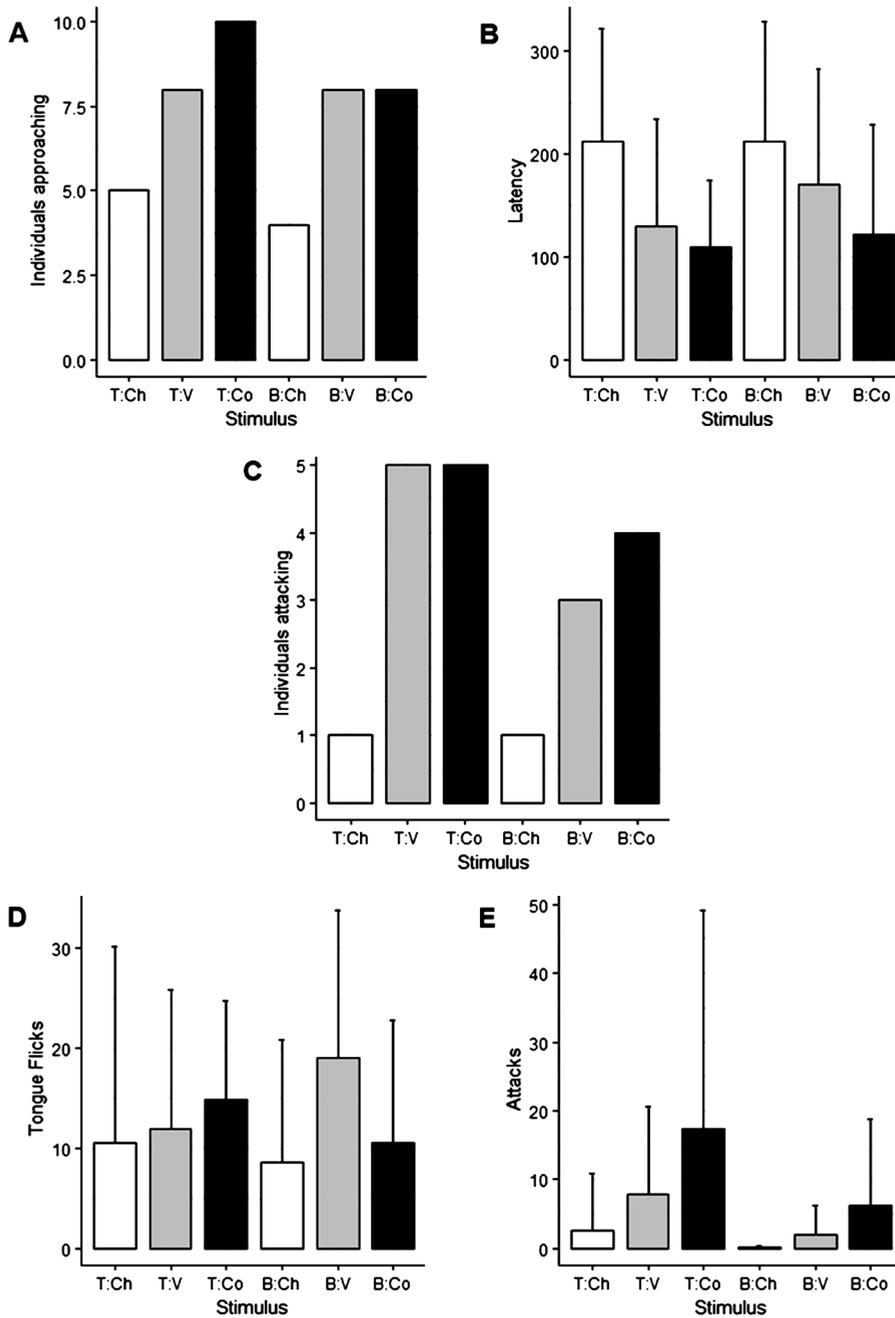


Figure 2. A: Number of Individuals approaching to the vessel according to different stimuli and prey; B: Mean (\pm s) of Latency in seconds according to different stimuli and prey; C: Number of Individuals attacking the vessel according to different stimuli and prey; D: Mean (\pm s) of Tongue Flicks according to different stimuli and prey; E: Mean (\pm s) of Attacks according to different stimuli and prey. TCh = *Tenebrio* Chemical, TV = *Tenebrio* Visual; TCo = *Tenebrio* Combined; BCh = *Blattica* Chemical, BV = *Blattica* Visual; BCo = *Blattica* Combined. Groups with the same letter do not differ significantly between each other.

combined visual and chemical stimuli and visual or chemical stimuli alone, indicating that both stimuli combined improved prey detection by this lizard (Desfilis et al., 2003). Nevertheless, Nicoletto (1985) did not find variation in latencies in *Scincella lateralis* skinks related to the type of stimuli presented. The ability or inability to detect prey related to sensory mode between these three species of lizards could be due to differences in the foraging tactics employed by each species (Cooper, 1995).

We did not find differences in detection between the two prey species independently of the type of stimuli. In this regard, our results suggest that preferences of *Tenebrio* over *Blaptica* may not be caused by detection impediments. However, other studies demonstrate that the background characteristics are relevant in the selection between similar-coloured prey (Askew et al., 1970). In our experiment, the background was the same for both prey types in all the trials, but colouration differs between prey types, thus, crypsis may also vary, and consequently, our results should be taken cautiously.

We did not find differences in the number of individuals attacking *Blaptica* and *Tenebrio* neither in relationship with the type of stimulus presented. Therefore, rock lizards might be able to recognize both prey types equally. In the same way, our results suggest that both visual and chemical stimuli alone make prey recognition possible in *I. cyreni* as it also occurs in other lizards (Cooper and Vitt, 1989; Cooper, 1990, 1991).

We did not find differences in the number of TFs between prey or stimulus, which was probably due to the low TF rates observed in all the trials. Some authors postulate that the absence of TFs could be explained by “learned laziness”: terraria might accumulate compounds of prey, making chemical cues an inadequate predictor of the presence of prey and, thus, lizards would learn not to use them for food pursuit (Desfilis et al., 2003). However, chemicals’ concentration may differ between what is accumulated in

the terrarium and the prey itself. Therefore, we expected TFs to be effective independently of chemical residuals in the environment. In this sense, familiarization with prey plus the size of the terrarium, which may affect the chemical gradient, may be more plausible explanations for the low rate of TFs observed. Alternatively, the lack of significance in both the number of individuals attacking the vessel or the TFs could be due to a small sample size in our experiment.

The number of attacks was dependent of the type of stimulus and the prey species. Visual stimuli always elicited more attacks than chemical stimuli alone, but combining chemical and visual cues had an additive effect on the number of attacks released. Desfilis et al. (2003) obtained similar results with experienced *P. hispanica*, but in the more distantly related *S. lateralis*, chemical stimuli do not seem to have such a synergistic effect (Nicoletto, 1985). We also observed that lizards attacked the filter paper when chemical cues were presented alone, while lizards attacked the plastic cup when visual stimuli were present. Lizards seemed to react to odour cues in the filter paper as if it was the prey, similarly to the attacks to cotton swabs bearing chemical stimuli observed in other studies (Cooper and Vitt, 1989; Cooper, 1990, 1991). Therefore, the presence of visual cues may enhance the accuracy of lizards’ predatory behaviour in nature. Alternatively, attacks directed to the paper might occur because lizards may be searching for potential prey hidden under the filter paper, as in the natural environment, prey may be hidden under the leaf litter.

Tenebrio larvae were attacked more frequently than *Blaptica* in all trials, indicating preferences for *Tenebrio* over *Blaptica*. These variations were produced with every type of stimuli suggesting that *I. cyreni* is able to discriminate between the two prey by both chemical and visual cues together or alone. According to Hasegawa and Taniguchi (1996), *Eumeces okadae* skinks were able to avoid undesirable prey by using both visual and chemical

cues. However, our results are based on predatory effort, i.e. number of attacks, instead of the absence of response to prey (Hasegawa and Taniguchi, 1996). Thus, we can confirm that discrimination between prey in our experiment is not related to difficulties in prey detection or recognition but on foraging decisions (i.e. attacking or not attacking) after prey recognition had occurred.

Taken together, our results reveal that rock lizards are able to detect, recognize prey and discriminate between types of prey by using both chemical and visual cues combined or alone. Importantly, joining of visual and chemical stimuli enhances detection and discrimination of prey. These results are relevant for increasing the knowledge of natural foraging behaviour in this species and its extension to other reptiles.

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References

- Ammanna, V.H.F., Saidapur, S.K., Shanbhag, B.A. (2014): Prey detection in juveniles of an agamid lizard, *Calotes versicolor* (Daudin, 1802) (Reptilia: Squamata). *Ital. J. Zool.* **81**: 155-159.
- Askew, H.R., Musimeci, M., Sloane, L., Stephan, L. (1970): Effects of prey movement and background on predatory behavior of chameleons. *Psychon. Sci.* **20**: 171.
- Brown, J.S. (2009): Foraging behaviour. In: *The Princeton Guide to Ecology*, p. 51-58. Levin, S.A., Carpenter, S.R., Godfray, H.G.J., Eds, Princeton University Press, Princeton, NJ, USA.
- Burghardt, G. (1964): Effects of prey size and movement on the feeding behavior of the lizards *Anolis carolinensis* and *Eumeces fasciatus*. *Copeia* **1964**: 576-578.
- Burghardt, G., Denny, D. (1983): Effects of prey movement and prey odor on feeding in garter snakes. *Z. Tierpsychol.* **62**: 329-347.
- Chiszar, D., Taylor, S.V., Radcliffe, C.W., Smith, H.M., O'Connell, B. (1981): Effects of chemical and visual stimuli upon chemosensory searching by garter snakes and rattlesnakes. *J. Herpetol.* **15**: 415-423.
- Civantos, E., Ahnesjö, J., Forsman, A., Martín, J., López, P. (2004): Indirect effects of prey coloration on predation risk: pygmy grasshoppers versus lizards. *Evol. Ecol. Res.* **6**: 201-213.
- Cooper, W.E. (1981): Visual guidance of predatory attack by a scincid lizard, *Eumeces laticeps*. *Anim. Behav.* **29**: 1127-1136.
- Cooper, W.E. (1990): Prey odor detection by teiid and lacertid lizards and the relationship of prey odor detection to foraging mode in lizard families. *Copeia* **1990**: 237-242.
- Cooper, W.E. (1991): Responses to prey chemicals by a lacertid lizard, *Podarcis muralis*: prey chemical discrimination and poststrike elevation in tongue-flick rate. *J. Chem. Ecol.* **17**: 849-863.
- Cooper, W.E. (1995): Foraging mode, prey chemical discrimination, and phylogeny in lizards. *Anim. Behav.* **50**: 973-985.
- Cooper, W.E., Vitt, L.J. (1989): Prey odor discrimination by the broad-headed skink (*Eumeces laticeps*). *J. Exp. Zool.* **249**: 11-16.
- Cooper, W.E., Sherbrooke, W.C. (2009): Prey chemical discrimination by tongue flicking is absent in the Texas horned lizard, *Phrynosoma cornutum*. *J. Herpetol.* **43**: 688-692.
- Desfilis, E., Font, E. (2002): Efectos de la experiencia sobre el comportamiento depredador de los reptiles. *Rev. Esp. Herpetol.*: 79-94.
- Desfilis, E., Font, E., Guillén-Salazar, F. (2003): Stimulus control of predatory behavior by the Iberian wall lizard (*Podarcis hispanica*, Sauria, Lacertidae): effects of familiarity with prey. *J. Comp. Psychol.* **117**: 309-316.
- Eberhart, K.S., Ruby, D.E. (2019): Prey selection by an ambush predator, *Sceloporus undulatus*. *J. Herpetol.* **53**: 32-38.
- Grap, N.J., Machts, T., Essert, S., Bleckmann, H. (2020): Stimulus discrimination and surface wave source localization in crocodylians. *Zoology* **139**: 125743.
- Graves, B.M. (1993): Chemical delivery to the vomeronasal organs and functional domain of squamate chemoreception. *Brain Behav. Evol.* **41**: 198-202.
- Hasegawa, M., Taniguchi, Y. (1996): Behavioral discrimination of prey with various defense mechanisms by the lizard *Eumeces okadae*. *J. Ethol.* **14**: 89-97.
- Loop, M.S. (1974): The effect of relative prey size on the ingestion behavior of the Bengal monitor, *Varanus bengalensis* (Sauria: Varanidae). *Herpetologica* **30**: 123-127.
- Martín, J. (2015): Lagartija carpetana – *Iberolacerta cyreni*. In: *Enciclopedia Virtual de los Vertebrados Españoles*. Salvador, A., Marco, A., Eds, Museo Nacional de Ciencias Naturales, Madrid. <http://www.vertebradosibericos.org> [Consulta: 20/01/2020].
- Martín, J., Salvador, A. (1993): Tail loss and foraging tactics of the Iberian rock-lizard, *Lacerta monticola*. *Oikos* **66**: 318-324.
- Nicoletto, P.F. (1985): The relative roles of vision and olfaction in prey detection by the ground skink, *Scincella lateralis*. *J. Herpetol.* **19**: 411-415.

Pérez-Mellado, V., Bauwens, D., Gil, M., Guerrero, F., Lizana, M., Ciudad, M.J. (1991): Diet composition and prey selection in the lizard *Lacerta monticola*. *Can. J. Zool.* **69**: 1728-1735.

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