

Short report

It sounds like food: Phonotaxis of a diurnal lizard

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ABSTRACT

Foraging diurnal lizards are well known for their use of visual and chemical cues to detect prey. We already showed that the Balearic lizard is able to detect prey using visual and chemical cues, even from airborne odors. In this study we carried out a field experiment to test if lizards can detect prey using acoustic cues. Our results show that *Podarcis lilfordi* is able to detect flies trapped inside opaque cups, only using acoustic cues. To our knowledge, this is the first known case of phonotaxis of a diurnal lizard. Thus, *P. lilfordi* can detect, from far away, current pollinators trapped inside floral chambers of the dead horse arum, *Helicodiceros muscivorus*. This is another behavioral trait displayed by the Balearic lizard during its complex interaction with the dead horse arum.

1. Introduction

Stimuli received by animals assume two forms: cues and signals. They may be transmitted and received using various sensory channels: tactile, visual, olfactory and acoustic (Bradbury and Vehrencamp, 2011). Several lizards have ears that can be advantageous, even in the absence of intraspecific audible communication (Breed and Moore, 2016 and references therein). Lizards are able to detect sounds covering a frequency range of hearing from 5 to 6 octaves, beginning at about 100 Hz (Manley, 1990). In fact, lacertid lizards were the subject of one of the first scientific attempts to behaviorally assess whether reptiles can hear (Berger, 1924 in Manley, 2000). Our knowledge about the ability of squamate reptiles to locate prey using auditory cues has received little attention, probably because a vast majority of lizards are visually or olfactory oriented vertebrates (Cooper and Burghardt, 1990).

The dead horse arum, *Helicodiceros muscivorus* Engler 1879 (Araceae, Aroideae), is a plant species that evolved an extraordinary deceptive pollination system, imitating a carcass of a mammal or bird by means of visual, olfactory, and thermal cues, that attract blowflies (Diptera, Calliphoridae), which are then employed as unrewarded pollinators (Angioy et al., 2004). During the blooming period, the plant produces an intense odor of decaying meat attracting female blowflies. Flies arrive at the plant and enter the floral chamber across a tubule that likely simulates a natural orifice of a dead animal. Flies that enter are trapped in the floral chamber where, due to their continuous attempts to escape, they transfer previously loaded pollen grains from another plant, to receptive female flowers.

The Balearic lizard, *Podarcis lilfordi* (Günther 1874), is syntopic with

dead horse arums on Aire Island (Balearic Islands, Spain). This lizard species exhibits a broad dietary niche in Aire (Pérez-Cembranos et al., 2016). Lizards are attracted by blooming warm spathes, using them as perching sites for thermoregulation. We already showed that *P. lilfordi* can detect chemical cues from carcasses, as well as chemicals from the spadix of *H. muscivorus* (Pérez-Cembranos et al., 2018). While at spathes, lizards are able to capture some of the arriving blowflies, as well as those trapped inside floral chambers (Pérez-Mellado et al., 2000, 2007). Moreover, there is a complex mutualism between the Balearic lizard and the dead horse arum because, during the fruiting period, *P. lilfordi* is the main seed disperser of *H. muscivorus* (Pérez-Mellado et al., 2007).

When trapped, blowflies produce an audible sound with their thoracic machinery (Esch and Wilson, 1967). This sound is similar to the sound produced during flight (Sueur et al., 2005), but clearly amplified by the floral chamber. During field work in Aire Islet, we observed lizards that appeared to turn, listen, and approach blooming spathes of *H. muscivorus*, where one or more flies were trapped (Fig. 1). Apparently, lizards were able to detect the sound from more than one or two meters away.

In squamate reptiles, we know only very few cases where auditory cues are employed to detect prey. In fact, there is only one experimental proof of a behavioral use of directional hearing in a lizard: the Turkish Gecko, *Hemidactylus turcicus*, is able to intercept calling crickets and also perform phonotaxis towards a speaker playing crickets songs (Sakaluk and Belwood, 1984). Even in Gekkonidae, the only lizards that clearly use strong vocalizations in intraspecific communication and as aggressive warning sounds (Marcellini, 1977; Werner et al., 1978), no

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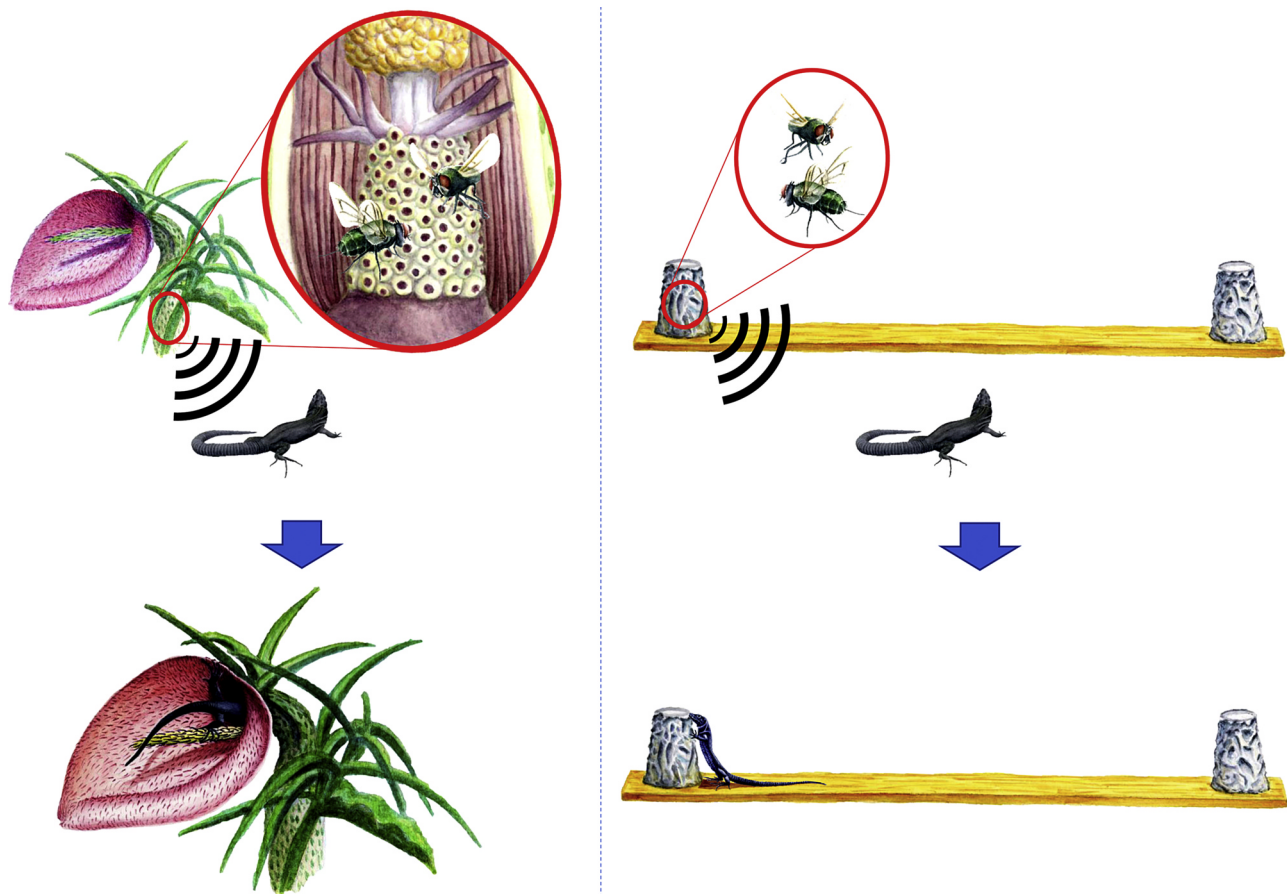


Fig. 1. Phonotaxis behavior of *Podarcis lilfordi*. Left, a lizard is attracted by the noise of flies trapped inside the floral chamber of *Helicodiceros muscivorus* and (below) the lizard enters to the chamber to capture flies. Right, the experimental setup with trapped flies inside one of the cups and (below) the exploratory behavior response made by the lizard towards the cup with flies.

phonotaxis to call playbacks have been shown so far. In summary, hearing using conditioned responses to sound have met with little success in squamate reptiles (Christensen-Dalsgaard, 2005).

In this study we want to test if the Balearic lizard can detect trapped flies using only auditory cues. Our prediction is that lizards are attracted to chambers with trapped flies, only oriented by the noise of flies.

2. Material and methods

2.1. Study animals

Podarcis lilfordi (Squamata, Lacertidae) is a medium-sized lizard that inhabits the coastal islets of Menorca (Pérez-Mellado, 1998). Balearic lizards are active foragers that hunt insects and other invertebrates, but they also consume vegetal matter, carrion and even conspecifics. The consumption of blowflies (Diptera) is intense during March and April, coinciding with the blooming period of the dead horse arum, particularly in the areas of Aire with highest density of *H. muscivorus* (Pérez-Cembranos et al., 2016).

2.2. Field experiments

Experiments were performed in Aire Islet, off the coast of Menorca (Balearic Islands) during May 2006, coinciding with the blooming period of the dead horse arum. We employed living blowflies from the species *Calliphora vicina*, one of the main pollinators of *H. muscivorus* (Stensmyr et al., 2002). Flies were captured by hand, just before experiments. We arranged an experimental setup with two plastic cups,

100 mm tall, 70 mm in diameter at the greater open end and 40 mm at smaller closed end. Cups were sealed with a layer of aluminum foil to avoid the use of visual and chemical cues by lizards. Two cups were placed 80 cm apart on a wooden smooth board. In each trial, one cup concealed 3–4 trapped living flies. Nothing was placed inside the other cup (Fig. 1). We employed three to four trapped flies instead of only one, to elicit the movement of flies inside the cup. We only consider a valid trial when we made sure that, prior to start the trial, flies were active and with an audible noise to the human ear.

In each trial, the board was placed in the open in an area where free-living lizards were actively foraging. We conducted 40 trials from 13:00 to 15:35 GMT in sunny conditions. To avoid pseudoreplications, the board was moved to new locations between trials. The cups were in direct sunlight in all trials. Once we had placed the board with the cups, we withdraw a minimum of 7 m and stood motionless until the end of the trial. In each trial we recorded which cup first attracted the first lizard approaching the board. We also recorded if the lizard, upon arrival, touched exploring the cup and if the lizard tongue-flicked towards the cup (Fig. 1).

Differences in the proportion of first lizards to approach empty cups or cups with trapped flies was tested with a binomial test, assuming equal probability for each type of cup (Crawley, 2013). The number of lizards exploring cups or doing tongue-flicks was compared with G-tests for males and females. All statistical analyses were carried out in the R environment (R Core Developmental Team, 2019), with the basic package and “RVAideMemoire” package (Hervé, 2019).

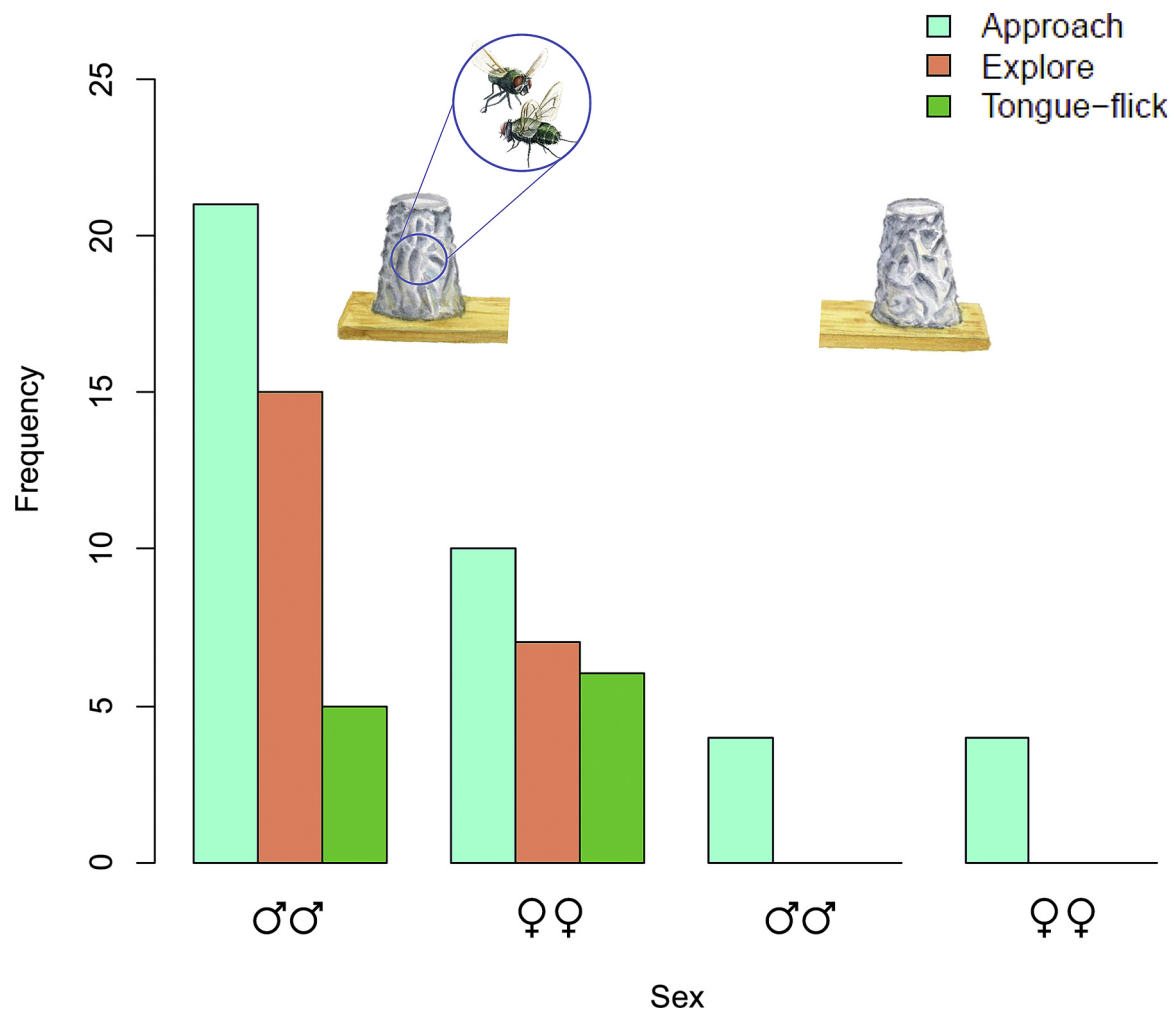


Fig. 2. Frequencies of male and female lizards approaching, exploring and tongue-flicking experimental cups with (left) or without (right) trapped flies.

3. Results

Immediately after the first sound of trapped flies came from a cup, lizards reacted turning their head to the direction of the cup with trapped flies and moved towards it from one to even three meters away. During this first approach, we never observed tongue-flickings of lizards. Thus, we can discard an orientation to the cup using chemical cues. Lizards approached the cups with trapped flies in 32 trials and the empty cups in the other eight trials. Thus, lizards were attracted at significantly greater than chance frequency to the trapped flies (binomial test, $p = 0.00018$, 95 % of confidence intervals: 0.64–0.91, probability of success: 0.80). From 39 trials where we were able to identify the sex of the first individual approaching, 21 males approached the cups with trapped flies and four males the empty cup (binomial test, $p = 0.00091$, 95 % confidence intervals: 0.64–0.95, probability of success: 0.84). In the case of adult females, we only observed 10 individuals approaching the cup with trapped flies and four approaching the empty cup (binomial test, $p = 0.179$). However, we did not detect significant differences between adult males and females in their response to trapped flies (G test, $G = 0.844$, $p = 0.3581$, Fig. 2).

Arriving to the cup, a different behavior of lizards was striking. No exploration or tongue-flicking were observed at empty cups, which were immediately abandoned. In cups with trapped flies, 15 males and seven females explored the cups, without significant differences between males and females (G test, $G = 0.0067$, $p = 0.935$). Only five males and six females, from those exploring cups, tongue-flicked them,

again without significant differences between sexes ($G = 3.811$, $p = 0.051$, Fig. 2).

We did not record the number and behaviors of lizards arriving after the first individuals to cups. However, as in the case of previous experiments with airborne odors (Cooper and Pérez-Mellado, 2001), multiple individuals were attracted to cups with trapped flies, much more than to empty cups.

4. Discussion

Lizards can hear well, mainly from < 1KHz to 10 KHz (Carr and Christensen-Dalsgaard, 2005). The ear of lizards is highly directional. The very simple turn of the head would direct the lizard to the sound source with a high precision (Christensen-Dalsgaard and Manley, 2005). However, there are very few data on sound localization in lizards, if we except the work of Sakaluk and Belwood (1984) with the Turkish Gecko, *H. turcicus* (see above). The scarce available information suggests that acute directionally hearing is likely to be a much more generally useful and advantageous feature of lizard ears (Christensen-Dalsgaard and Manley, 2005).

To our knowledge, this is the first experimental proof of phonotaxis in a diurnal lacertid lizard. Some lizards, as *Anolis sagrei*, are using auditory cues to assess predation risk or even to make a predator discrimination (Cantwell, 2016). But we do not have any experimental proof of the existence of phonotaxis to prey by diurnal lizards. In the case of *P. lilfordi*, the detection of noisy blowflies is incidental, because it is caused by the escape movements of flies from floral chambers of

dead horse arums or from our cups. This kind of phonotaxis to prey movements and sounds has been described in barn owls (*Tyto alba*, Payne, 1971), in the Indian false vampire bat (*Megaderma lyra*, Marimuthu and Neuweiler, 1987) and it is widespread in several taxa (see, for example, Page et al., 2008; Plep et al., 2008 and Rhebergen et al., 2015).

Even if we did not record the latency to respond to noise from flies, lizards moved towards the cups immediately after the first sound production by flies. According to our results, only adult lizards approached the cups during the trials, probably indicating that trapped flies were first detected by adult lizards, especially by males. This is the case of blooming spathes of *H. muscivorus*, frequently occupied, during the first day of opening, by trapped pollinators. In fact, open spathes are important foraging sites, mainly occupied by larger adult males of Aire lizard population (Pérez-Mellado et al., 2006).

Adult males were clearly more successful than adult females to approach cups with trapped flies, with non-significant differences between cups in the subset of trials corresponding to females. A first explanation for this result could be that it is the consequence of a smaller sample size of female trials. Because trials were performed in the field, with free-living lizards and during the peak of blooming for *H. muscivorus*, we do not know if females had a lower access to experimental setups, due to a higher local density of adult males (Pérez-Mellado et al., 2000 and Pérez-Mellado et al., 2006) or due to higher responsiveness of males to acoustic cues from trapped flies.

If the recognition of the noise from trapped flies as an acoustic cue from a prey is the product of a learning process (Pearce, 2008), adult males could have better opportunities than adult females and subadults to learn it, because of a higher probability to visit open spathes and capture trapped flies (Pérez-Mellado et al., 2006).

Further research is needed to establish the extent in the use of acoustic cues by the Balearic lizard, as well as the range of lizard taxa capable of locating noisy prey using acoustic cues.

CRedit authorship contribution statement

Ana Pérez-Cembranos: Methodology, Formal analysis, Writing - original draft, Writing - review & editing, Visualization. **Valentín Pérez-Mellado:** Conceptualization, Methodology, Formal analysis, Investigation, Writing - original draft, Writing - review & editing, Supervision, Funding acquisition.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.beproc.2020.104217>.

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