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Balearic lizards use chemical cues from a complex deceptive mimicry to capture attracted pollinators

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Abstract

Deceptive flowers from several plant species emit odors that mimic oviposition cues and attract female insects seeking for a laying site. *Helicodiceros muscivorus* is a species that emits an odor mimicking the foul smell of rotting meat and thereby attracts blowflies that usually oviposit on carcasses but are deceived into pollinating the plant. Thus, *H. muscivorus* is a striking case of pollination by brood-site deception. The Balearic lizard, *Podarcis lilfordi*, exhibits remarkable interactions with dead horse arum. Balearic lizards, which sometimes forage on carcasses, are attracted to blooming dead horse arum. We showed experimentally that *P. lilfordi* can detect chemical cues from carcasses on cotton swabs and exhibits elevated tongue-flick rates to carcass chemical cues compared to control stimuli. Lizards also detected and located hidden carcasses using only airborne chemical cues. The responses of lizards to chemical cues from the spadix of blooming dead horse arum were qualitatively and quantitatively similar to those to carcass odors. Therefore, the decay-like odor that attracts blowflies for the plant's benefit also attracts lizards. This attraction may initially have been somewhat favorable for lizards that eat blowflies, but slightly unfavorable for plants because the lizards ate some pollinators. We suggest that lizards attracted by odor may have learned later to use the plant for thermoregulation and then consume its fruits, making the association more positive for lizards and benefitted arum by seed dispersal.

KEYWORDS
behavior, deceptive mimicry, Lacertidae, olfaction, *Podarcis lilfordi*, vomerolfaction

1 | INTRODUCTION

Mimicry occurs in several organisms, including some flowering plants. Mimics can mimic signals or cues in several ecological contexts, including the attraction of pollinators (Dalziell & Welbergen, 2016). In deceptive systems, as found in some plant species, flowers signal the presence of a resource without providing it. These plants have thus evolved cues to cheat insects into the act of performing pollination (Urru, Stensmyr, & Hansson, 2011). Brood-site deception is a well-known system in plant species from different families. It is particularly common in Orchidaceae and Araceae (Ackerman, 1986;

Renner, 2006). Deceptive flowers are able to emit signals that trigger obligate innate responses of targeted insects (Stökl et al., 2010). In some cases, insects are duped with chemical mimicry. In this way, plant species signal the presence of a brood site (Atwood, 1985). Deceptive flowers can emit odors to mimic oviposition cues and attract female insects seeking for a site to lay eggs. This breeding site can be a carrion remain, as it is common in Araceae (Urru et al., 2011). The brood-site mimicking flowers attract mainly Diptera and Coleoptera (Endress, 1984).

Brood-site deceptive plant species can have a floral chamber that evolved to force pollinators to stay longer, as after an
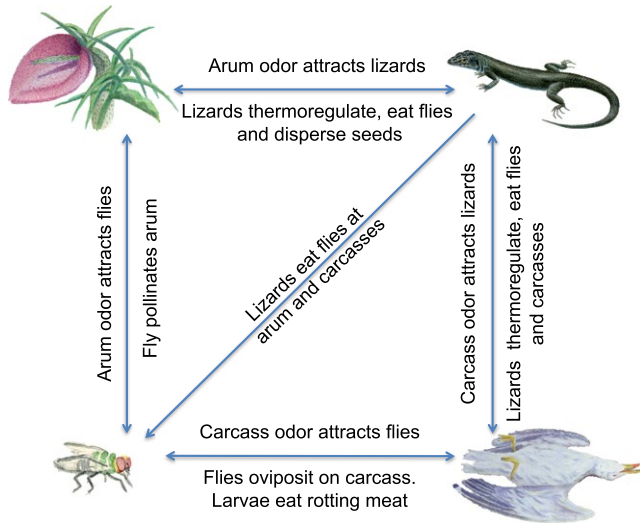
FIGURE 1 Dead horse arum employs deceptive mimicry by producing an odor that resembles the odor of rotting carcasses to attract blowflies that normally lay their eggs in carcasses to flowers. The blowflies pollinate dead horse arums without receiving any reward. Balearic lizards are attracted by odor to carcasses where they eat flies as well as rotting meat. Because the dead horse arum's odor is so similar to that of rotting meat, the lizards are attracted to blooming dead horse arum, where they eat flies. Presumably starting with this association between lizards and arum incidental to deceptive mimicry system, lizards expanded use of the plant for thermoregulation and as a food source. Consumption of fruits and passage of seeds contained in the fruits through the digestive tracts results in dispersal of seeds in feces. Thus, the Balearic lizard and the dead horse arum have developed a mutualism incidental the plant's deceptive mimicry. [Colour figure can be viewed at wileyonlinelibrary.com]

unrewarded visit they would quickly leave the plant without a successful pollination (Dafni, 1984). In Araceae, the trapping system is formed by a large modified leaf (the spathe) which holds an axis, the so-called spadix. The spadix bears female and male flowers. Inner waxy-smooth walls of floral chamber in combination with a ring of trichomes around the spadix act to block the exit/entrance to the chamber.

To attract pollinators, some fragrance-emitting glands called osmophores localized in the sterile part of the inflorescence produce a carrion or rotten meat odor (Stensmyr et al., 2002). In addition, brood-deceptive inflorescences can be thermogenic and can heat mimicking carrion, providing an energy reward to pollinators (Seymour, Gibernau, & Ito, 2003) and increasing volatilization of chemicals (Grant, Miller, Watling, & Robinson, 2008). Among chemical substances present in carrion odors produced by brood-site deceptive Araceae, some distinct oligosulfides are crucial cues to attract blowflies as they are used as key odors to locate carrion resources (Stensmyr et al., 2002).

The dead horse arum, *Helicodiceros muscivorus* Engler 1879 (Araceae, Aroideae), has evolved one of these complex deceptive pollination systems, imitating a vertebrate carcass by means of visual, olfactory, and thermal cues, attracting 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 that strongly attracts female blowflies.

The plant shows a large hairy pink or reddish spathe that looks like the surface of decaying meat. In addition, the upper sterile part of the floral spadix produces heat: The external surfaces of the plant, particularly the large spathe, can reach temperatures more than 10°C above air temperatures (Seymour et al., 2003). Thus, the imitation of a carcass with a warm and odorous surface is excellent. Attracted flies, coming from another arum where they became loaded with pollen, arrive at the plant and enter the floral chamber across a dark tubule that likely simulates a natural orifice in a carcass of a dead animal. Flies that enter are trapped in the floral chamber, where they transfer previously loaded pollen grains from another plant to receptive female flowers. Each individual arum blooms for no more than two days and, in some cases, only for a few hours (see more details in Pérez-Mellado, Cortázar, López-Vicente, Perera, & Sillero, 2000; Pérez-Mellado, Riera, Piccolo, & Potter, 2006; Pérez-Mellado, Riera, Hernández-Estévez, Piccolo, & Potter, 2007 and references therein).

The Balearic lizard, *Podarcis lilfordi*, is syntopic with dead horse arum on Aire Island, an islet off the coast of Menorca (Balearic Islands, Spain). On Aire Island, the Balearic lizard lives in an environment free of terrestrial predators. This lizard species exhibits a marked ecological release of its trophic niche, which is dramatically broader than the dietary niches of related mainland species (Pérez-Cembranos, León, & Pérez-Mellado, 2016; Pérez-Mellado, 1989; Pérez-Mellado & Corti, 1993). In fact, *P. lilfordi* is an omnivore that can detect a wide range of different prey types using olfaction and vomerolfaction (Cooper & Pérez-Mellado, 2001a, 2001b, 2002). Plant consumption is common among insular lizards (Pérez-Mellado & Traveset, 1999; Sáez & Traveset, 1995; Van Damme, 1999) and is linked with plant chemical discrimination. Thus, the Balearic lizard is able to identify both animal and plant foods using only chemical cues (Cooper & Pérez-Mellado, 2001a).

During the blooming period of dead horse arum in early spring, air temperatures on Aire Island are frequently cooler than the optimum temperatures for lizard activity (Ortega et al., 2014). Cool Balearic lizards use warm spathes of dead horse arums as thermoregulation sites where they warm, reaching their optimal body temperatures for activity faster than on any other substrate available in their natural habitat (Pérez-Mellado et al., in prep.). 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). The proportion of captured flies is relatively low in comparison with the total number of attracted flies. Consequently, such predation is likely to have a negligible effect on the pollination mechanism of the dead horse arum (Pérez-Mellado et al., 2000). There is a true mutualism between the Balearic lizard and the dead horse arum because, during the fruiting period, *P. lilfordi* is a legitimated seed disperser of *H. muscivorus*, enhancing seed germination (Pérez-Mellado et al., 2007).

In the context of the remarkable relationships among Balearic lizards, vertebrate carcasses, dead horse arum, and blowflies

(Figure 1), we investigated the ability of Balearic lizards to detect and locate carcasses and blooming dead horse arums. Many reptiles can use chemical cues to detect prey and other food items, as well as for mate recognition, other social behaviors, and detection of predators (Halpern, 1992). Actively foraging insectivorous–carnivorous lizards exhibit prey discrimination based on chemical cues sampled by tongue-flicking, whereas ambush foragers do not (Cooper, 1995, 1997). Omnivorous lizards detect chemical cues from animal prey, as well as from plant materials (Cooper, 2000). Chemoreception also plays an important role in carcass localization by alligators (Weldon et al., 1990, in Halpern, 1992), and the large lizard, *Varanus komodoensis*, appears to detect carrion using airborne chemical cues (Auffenberg, 1981), as can some snake species (Gillingham & Baker, 1981; Shivik & Clarck, 1997).

We investigated possible roles of chemical cues in the responses of Balearic lizards to chemical cues from bird carcasses and the spadix of dead horse arum. We assessed the similarity of responses by the lizards to chemical cues presented on a substrate to cues from the two sources and compared responses to each of them to control stimuli and insect prey stimuli to detect any responses. We also conducted field experiments on the ability of the lizards to locate hidden carcasses and spadices of dead horse arum using only airborne chemical cues. We discuss the findings in relation to the complex interactions among dead horse arum, blowflies, and Balearic lizards. Our underlying hypothesis was that chemosensory detection of blooming plants by Balearic lizards occurs as a response to the same chemical stimuli that allow lizards to detect the carcasses of mammals or birds, habitually consumed on Aire (Pérez-Cembranos et al., 2016).

2 | METHODS

2.1 | Study plants and animals

The dead horse arum is a plant of Tyrrhenian distribution; that is, it is present on Corsica, Sardinia, and the eastern part of the Balearic Islands, that is, Mallorca and Menorca islands.

Podarcis lilfordi (Squamata, Lacertidae) is a medium-sized lizard that inhabits the coastal islets of Menorca, Mallorca, and Cabrera archipelago (Pérez-Mellado, 1998). This lizard reaches high densities in Aire Island (Pérez-Mellado et al., 2008). Balearic lizards are active foragers that hunt insects and other invertebrates, but they also consume vegetal matter, carrion, conspecifics, or leftovers carried by tourists (Cooper, Pérez-Mellado, & Hawlena, 2014; Pérez-Cembranos et al., 2016; Pérez-Mellado & Corti, 1993). Lizards employed in laboratory trials were captured in Aire Island by noosing. Upon conclusion of the laboratory trials, the lizards were released at the same site of capture.

2.2 | Laboratory experiments

Prior to testing, lizards were individually housed for 1 day in translucent plastic terraria (40 × 26 × 26 cm) with a substrate of indoor–outdoor carpet, in a room with an ambient temperature of 25°C. Water was continuously available in a plastic petri dish. Light was provided by incandescent lamps. To reduce possible disturbances by investigators, the sides of the terraria were covered by brown paper.

Responses to chemical stimuli were assessed by presenting some chemicals on cotton swabs to the lizards and recording their tongue-flicking and biting behaviors (Cooper & Burghardt, 1990). We designed two different sets of trials. The first one was carried out using bird carrion and mealworms as sources of prey chemicals. In a second experiment, we employed mealworms as the source of prey chemicals and the spadix of dead horse arum plants. In both experiments, cologne (Mennen Skin Bracer, Spice Scent) was employed as a control to assess responses to a highly odorous, but biologically irrelevant stimulus. Providing some cautions, the cologne employed in this experiment is an excellent pungent control, because it lacks floral and fruit odors and was successfully used in several studies of reptiles chemical discrimination (Cooper, Pérez-Mellado, Vitt, & Budzynski, 2003 and references therein). Cologne was diluted to one part in three parts of distilled water to reduce possible aversive responses (Dial & Schwenk, 1996). In both experiments, we used distilled water as odorless control to assess the baseline tongue-flicking rate in the absence of detectable chemical cues added to swabs.

Stimuli for each trial were prepared by moistening the cotton swab of a 15-cm wooden applicator and, if necessary, adding other stimuli. Prey stimuli were prepared by firmly rolling the moistened swab on the outer surface of a mealworm or a piece of a bird carcass. Plant stimuli were obtained by firmly rolling the wet swab on the outer surface of a freshly cut spadix of *H. muscivorus* from its first day of odor production (Stensmyr et al., 2002). Lizards were tested in their individual terraria. A trial was initiated by slowly bringing a swab to a position 1–15 cm anterior to a lizard's snout. The trial began when the first tongue-flick was directed to the swab. If the lizard did not bite the swab, the observer recorded the number of tongue-flicks directed to the swab in 60 s. If the lizard bit the swab, the observer recorded the latency in seconds between the first tongue-flick and the bite, as well as the number of tongue-flicks prior to the bite.

In both experiments, we employed a randomized blocks design in which each individual was tested with all four stimuli. For the 20 adult lizards tested, we randomized the order of stimulus presentation to avoid potential bias. The minimum inter-trial interval was 30 min, and the maximum was 60 min.

2.3 | Field trials

The field study was conducted on Aire Island, off the coast of Menorca (Balearic Islands, Spain), in April of years 2005 and 2010. All field trials were conducted in sunny conditions during the morning hours of maximal lizard activity. To ascertain whether *P. lilfordi* detects and is attracted by the odors of rotting meat and the spadix of *H. muscivorus*, we used a method by which Cooper and Pérez-Mellado (2001b) showed that Balearic lizards can detect airborne

odors of fruit and use them to locate the fruit. We did two different experiments. In each of the two experiments, we inverted a single pair of black cups on open ground 1 m aside from each other. In the first experiment, one cup, acting as a control, was clean and empty; the other one hid rotting meat. We employed rotting meat from rabbit and bird carcasses found in Aire Island. In the second experiment, we presented one empty cup and the other cup hid a freshly cut spadix from a blooming dead horse arum on its first day of odor production (Pérez-Mellado et al., 2006). Cups had very small holes to let the odor to come out. After placing the cups, the observer moved at least 10 m away from the cups and stood immobile observing them.

The primary variables recorded were latency to approach and contact a cup and which cup was approached first. Additional behaviors were also recorded including whether the lizard pushed the cup, remained with the cup at least 10 s and whether lizards basked on the tops of cups. Only data for the first lizard to arrive were recorded, and only for the first cup it approached. Trials were discarded if no lizard approached either cup within 300 s. Pseudo-replications were avoided in the two experiments by placing the cups for each trial at a different location on the island. The high lizard density at Aire Island decreases the probability of pseudo-replications. In addition, we employed several cues to distinguish individual lizards, including body size, skin scars, different nuances, and the degree of tail regeneration.

We did two different experiments. However, the ideal situation would be to test lizards at the same time with cups covering meat and spadices and check for preferences of lizards to odors from spadix or meat. Unfortunately, we were unable to do both experiments at the same time because of the narrow temporal window to obtain in the field odorous spadices.

2.4 | Statistical analysis

We analyzed the number of tongue-flicks (tf), the proportion of lizards that bit the stimulus, and TFAS(R), the tongue-flick attack score for repeated measures designs (Cooper & Burghardt, 1990). TFAS(R) combines tongue-flicks, bites, and latency to bite, as an overall measure of response strength. Calculation of TFAS(R) depends on whether a lizard bites the cotton swab. If the lizard does not bite the swab, the TFAS(R) for that trial is the number of tongue-flicks in 60 s. If it bites, it is given by the sum of two terms: One term is the number of tongue-flicks, and the other term is calculated from latency to bite. The tongue-flick term is the maximum of tongue-flicks performed by the lizard in response to any of the stimuli in any single trial. Using the maximum number of tongue-flicks ensures that a bite is weighted more than any number of tongue-flicks. This seems to be the best strategy in studies of responses to food chemicals because bites reflect predation attempts. The second term in TFAS(R) is 60 minus latency to bite in seconds. Thus, term weights bites earlier in trials more heavily than those later in trials, because latency reflects the food identification (Cooper & Burghardt, 1990).

To analyze repeated measures, we employed a multilevel approach, where we test if our predictive model is better than a simple one-parameter mean model (Crawley, 2013). Thus, we began by specifying a baseline mixed-effects model with no fixed effects. That is, the fixed effect is just the overall mean value of the response variable. Then, we constructed our model of interest by including the fixed effect of stimuli and the random effect due to repeated measures. We assessed the significance of our model by comparing it with the baseline model. By comparing models, we asked whether stimuli, as predictors, are significantly better than the simple mean (baseline) model. To do it, models were compared with ANOVA. The post hoc analyses were carried out with Tukey contrasts (Pinheiro, Bates, DebRoy, & Sarkar, 2016). After the analysis of both laboratory experiments, we compared the number of tongue-flicks and TFAS, the tongue-flick attack score for independent groups (Cooper & Burghardt, 1990) from trials with carcass or spadix with ANOVA. Normality and homogeneity of variances were checked with Shapiro–Wilk and Fligner tests, respectively. Following the habitual procedure with this kind of experimental setup, we analyzed the four treatments of the two sets of experiments and then we applied a *post hoc* test of significance of pairwise comparisons.

The main effect of differences among stimuli in proportion of lizards biting swabs was tested by a Cochran Q test. Differences between pairs of stimuli were examined for significance using sign tests. Differences between the proportion of lizards biting the swabs with carcass odor and swabs with spadix odor were tested with Fisher's exact test.

In field experiments, the proportions of lizards that first contacted empty cups and cups hiding rotting meat or spadix of *H. muscivorus* were assessed by a binomial test assuming equal probability for each type of cup (Zar, 1996). A Fisher exact probability test (Zar, 1996) was conducted to determine the significance of the difference in the proportion of individuals that left (or remained by or climb) the empty cups and those covering a carcass or spadix. A Fisher test also was conducted to detect any difference in the proportion of males and females arriving at cups.

Significance tests were two-tailed with $\alpha = 0.05$ except where stated otherwise. All statistical analyses were carried out in the R environment (R Core Developmental Team, 2015), with the basic package and "psych" (Revelle, 2017), "nlme" (Pinheiro et al., 2016), and "ggplot2" (Wickham, 2009) packages.

3 | RESULTS

3.1 | Laboratory experiments

3.1.1 | Experiment with carcasses

All individuals tongue-flicked in all conditions (Table 1, Figure 2). The number of tongue-flicks differed among stimuli (maximum likelihood ratio, $\chi^2 = 15.76$, $p = .001$). More tongue-flicks were directed to swabs with carcass odor than to swabs with water (Tukey test, $p < .001$) or with cologne (Tukey, $p = .0059$). None of the remaining pairwise comparisons among stimuli were significant (Tukey, $p > .05$).

	Mealworms	Carcass	Cologne	Distilled water
Tongue-flicks (average ± SE)	9.8 ± 1.79	15.2 ± 3.13	6.55 ± 1.54	4.75 ± 1.09
Range	1–27	1–47	0–29	1–21
Individuals that bite	9	4	0	8

TABLE 1 Tongue-flicks and numbers of individuals that bit by 20 *Podarcis lilfordi* in response to chemical cues from mealworms, carrion, diluted cologne, and distilled water presented on cotton swabs in 60 s trials (*SE*, standard error)
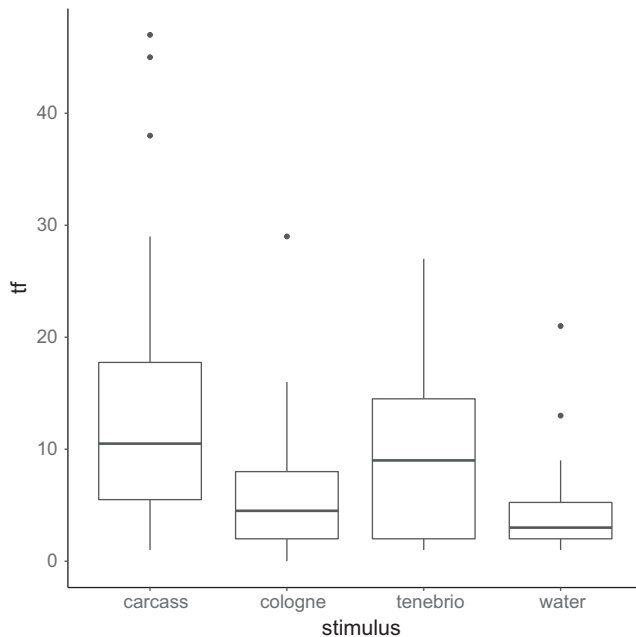

FIGURE 2 Boxplots of the first experiment of tongue-flick (tf) frequencies from *Podarcis lilfordi* of Aire Island in response to chemical stimuli from carcass, cologne, mealworms, and distilled water. Bottom and top of boxes are the first and third quartile, and the horizontal line inside the box is the median. The ends of whiskers represent the minimum and maximum values
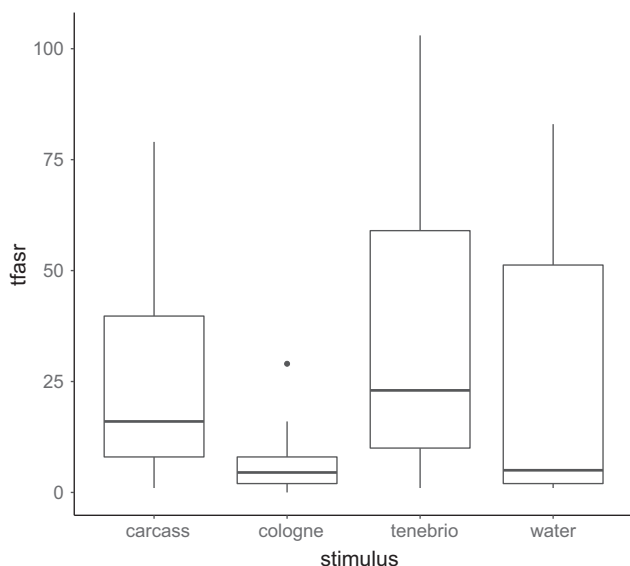

FIGURE 3 Boxplots of the first experiment of tongue-flick attack scores [TFAS(R)] from *Podarcis lilfordi* from Aire Island in response to chemical stimuli from carcass, cologne, mealworms, and distilled water

Less than half of the individuals bit swabs bearing mealworm chemicals (0.45) or water (0.40), and only 0.20 of lizards bit swabs bearing chemicals from carcass, whereas no lizard bit a swab bearing cologne (Table 1). The proportion of lizards that bit varied significantly among stimuli (Cochran *Q* test, *Q* = 12.96, *df* = 3, *p* = .0047). More lizards bit mealworm than cologne (sign test, *p* = .023) and water than cologne stimuli (sign test, *p* = .023). None of the remaining differences were significant (sign test, *p* > .05).

Mean TFAS(R) was greater for prey chemicals (mealworms) than for the other stimuli (Figure 3). Mean TFAS(R) differed among stimuli (χ^2 = 14.0879, *p* = .0028). Mean TFAS(R) was greater in response to mealworm than to cologne (Tukey, *p* < .001) and water than cologne (Tukey, *p* = .04). No other differences were significant (Tukey, *p* > .05 each).

3.1.2 | Experiment with spadix from *H. muscivorus*

Mean tongue-flicks differed among stimuli (χ^2 = 20.35, *p* < .001, Table 2 and Figure 4). Tongue-flicks directed to swabs bearing spadix odor were greater than those in response to mealworm (Tukey, *p* = .0059), water (Tukey, *p* < .001), and cologne swabs (Tukey, *p* = .025). No other differences were significant (Tukey, *p* > .05).

The proportion of lizards that bit differed among conditions (Cochran *Q* test, *Q* = 15, *df* = 3, *p* = .0018, Table 2). More lizards bit in response to mealworm than to spadix chemicals (sign test, *p* = .035) or water (sign test, *p* = .035). None of the remaining differences were significant (sign test, *p* > .05). No other differences were significant (Tukey, *p* > .05) using two-tailed tests, but the proportion that bit in response to mealworm stimuli was significantly greater than that for cologne under the one-tailed hypothesis that the lizards would attack prey stimuli more often than a control stimulus (sign test, *p* = .029).

TFAS(R) was greater for mealworm chemicals than for the other stimuli (Figure 5). TFAS(R) differed significantly among stimuli (χ^2 = 25.72, *p* < .0001). Responses were higher in the mealworm than in the water (Tukey, *p* < .0001), cologne (Tukey, *p* = .00022), and spadix conditions (Tukey, *p* < .0001).

3.2 | Comparisons of responses to carcass and spadix cues

Tongue-flicks directed to carcass and spadix stimuli were similar (one-way ANOVA, $F_{1,38}$ = 0.02, *p* = .89). The proportions of lizards that bit the swabs with carcass and with spadix odors were also similar (Fisher test, *p* = .66). Accordingly, no difference in TFAS was detected between the two stimuli ($F_{1,38}$ = 2.112, *p* = .154).

TABLE 2 Tongue-flicks and numbers of individuals that bit by 20 *Podarcis lilfordi* in response to chemical cues from mealworms, spadix from *Helicodiceros muscivorus*, diluted cologne, and distilled water presented on cotton swabs in 60 s trials (*SE*, standard error)

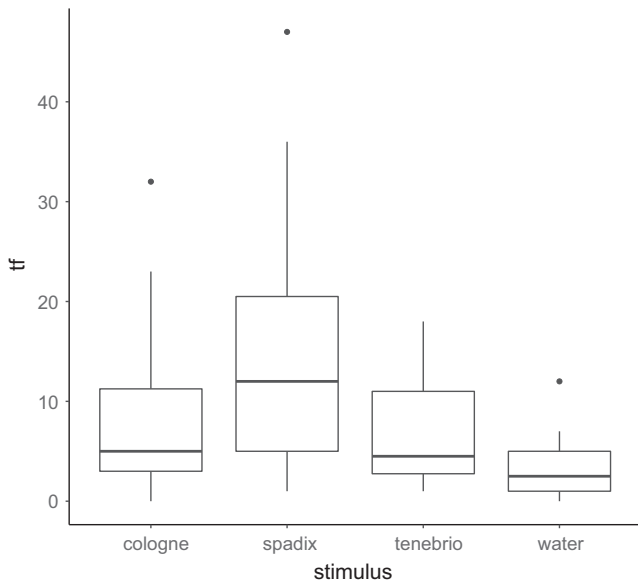|	Mealworms	Spadix	Cologne	Distilled water
Tongue-flicks (average ± *SE*)	6.95 ± 1.2	14.6 ± 2.9	8 ± 1.81	3.3 ± 0.67
Range	1–18	1–47	0–32	1–12
Individuals that bite	11	2	4	3

FIGURE 4 Boxplots of the second experiment of tongue-flick (tf) frequencies from *Podarcis lilfordi* from Aire Island in response to chemical stimuli from cologne, spadix from *Helicodiceros muscivorus*, mealworms, and distilled water
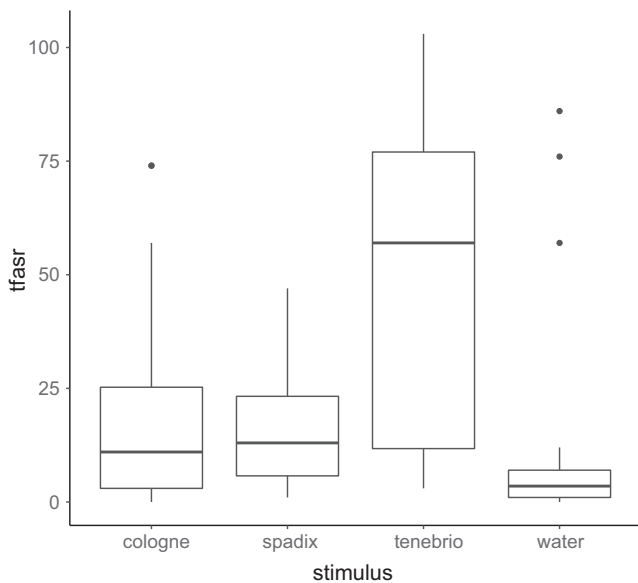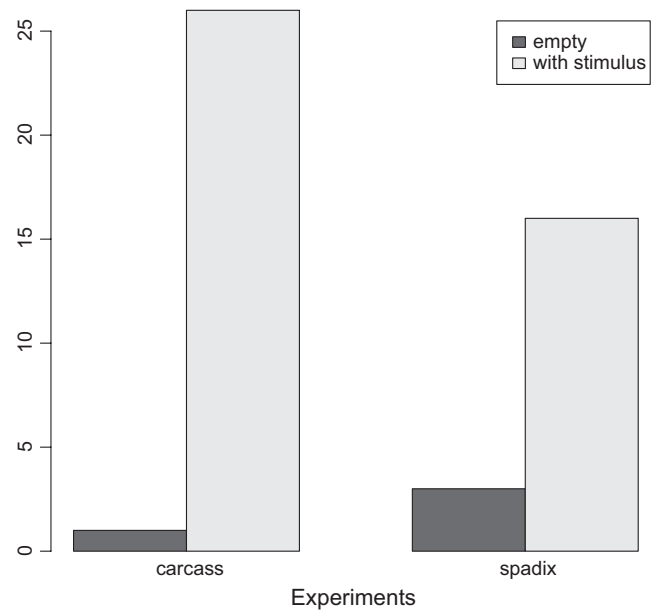

FIGURE 6 Proportions of Balearic lizards that arrived at empty cups or cups hiding an odor source

3.3 | Field experiments

3.3.1 | Experiment with carcasses

Lizards approached a cup containing a bird carcass in a higher proportion of trials than an empty cup (binomial test, $p < .001$; Figure 6). Twenty-two of 27 lizards that approached cups hiding carcasses stayed with the cups at least 10 s, and none of the three individuals that approached empty cups stayed with the cups more than 10 s. All lizards that stayed with cups that hid carcasses pushed the cups; none of the three that approached empty cups did so. Upon arrival, all lizards tongue-flicked cups, containing a carcass or not. Proportions of lizards that approached cups hiding carcasses did not differ between sexes (Fisher exact test, $p > .05$).

3.3.2 | Experiment with spadix of *H. muscivorus*

Lizards approached a cup containing a spadix in a higher proportion of trials than they approached an empty cup (binomial test, $p = .004$; Figure 6). Fourteen of 16 lizards that approached cups hiding spadix stayed with the cups at least 10 s, as did two of the three individuals that approached empty cups. Eleven of 14 (0.69) lizards that stayed with cups that hid spadix pushed the cups; neither of the two that

FIGURE 5 Boxplots of the second experiment of tongue-flick from attack scores [TFAS(R)] from *Podarcis lilfordi* from Aire Island in response to chemical stimuli from cologne, spadix from *Helicodiceros muscivorus*, mealworms, and distilled water

stayed with empty cups did so. This difference is not significant (Fisher exact test, $p = .083$). Proportions of lizards that approached to cups hiding spadix did not differ between sexes (Fisher exact test, $p = .26$). All lizards tongue-flicked cups upon arrival, containing a spadix or not.

3.4 | Arrival and staying at carcass vs. spadix

The number of individuals that approached the cups during the experiment with hidden carcasses was higher than the number of lizards approaching cups during the experiment with spadices (Fisher exact test, $p = .00032$). The proportion of individuals that approached a cup hiding an object did not differ significantly between the carcass and spadix experiments (Fisher exact test, $p = .66$). Among lizards that arrived at a cup hiding an object, the proportion that stayed for at least 10 s did not differ between the carcass and spadix experiments (Fisher exact test, $p = .70$). Latency until arrival at a cup was shorter for lizards that chose cups containing spadix (101.4 ± 21.4 s, range = 5–270 s, $n = 16$) than those that arrived at cups hiding carcasses (146.8 ± 17.48 s, range = 25–299 s, $n = 27$).

4 | DISCUSSION

Lizards from Aire Island are able to detect carcasses and blooming dead horse arums as a part of their foraging capacities. Both our field and laboratory results show that the Balearic lizard can detect chemical cues from rotting meat and its imitation by chemicals located in the spadix of *H. muscivorus*. Balearic lizards detect these chemical cues via vomerolfaction, as made clear by differential tongue-flick rates to cues on swab substrates. The ability to locate carcasses and the spadix of dead horse arum using only airborne chemical cues strongly suggests that this ability is supported by olfaction, although some squamates can use vomerolfaction to locate prey using airborne chemical cues. The ability of *P. lilfordi* to locate fruits by responding to airborne odorants was previously demonstrated (Cooper & Pérez-Mellado, 2001b).

Podarcis lilfordi exhibits a surprising array of individual foraging behaviors, probably maintained via observational learning that may differ among individuals. Lizards rapidly learned to use open spathes of *H. muscivorus* as perching sites for thermoregulation and sit-and-wait capture of flying prey. The behavior of the lizards, which are strongly attracted by conspecific foraging activities (Pérez-Cembranos & Pérez-Mellado, 2015), allows extremely rapid spread among individuals of incorporating novel food resources and foraging behaviors. This may explain the spread among lizards of foraging and basking behaviors on *H. muscivorus*.

We obtained a clear demonstration that Balearic lizards detected chemical cues from both carcasses and spadices of dead horse arum. For responses to mealworms, a common insect prey for lizards in Aire Island (Pérez-Cembranos et al., 2016), the greater number of tongue-flicks, higher values of tongue-flick attack scores and more frequent biting in response to mealworm stimuli than control stimuli

all provide evidence of detection. Lizards also responded better to chemical cues from the spadix of dead horse arum than to control stimuli, shown by the higher tongue-flick rate than for all other stimuli. Additional evidence from laboratory studies that Balearic lizards respond differentially to chemical cues from carcasses and spadices is that lizards bit more frequently and had higher tongue-flick attack scored when responding to mealworm cues than spadix cues. Although Balearic lizards responded more strongly to prey chemical cues from mealworms than to spadix cues, they responded almost identically to cues from carcasses and spadices. The numbers of tongue-flicks, bites, and the tongue-flick attack scores for these two stimuli are all statistically indistinguishable. Apparently, rotting meat is recognized as an edible item, but not as a prey item, because swabs soaked with odors of carcasses were rarely bitten, precluding high TFAS(R) scores.

Carrion flowers mimic the smell and appearance of rotting animal carcasses. These flowers evolved in several plant families and are particularly common in Araceae, with a large number of species with carrion flowers. *H. muscivorus* is a specialized carrion flower that emits scent dominated by oligosulfides and attracts mainly those flies that breed on carrion (Stensmyr et al., 2002; Urru et al., 2011). In Aire Island, lizards use this carrion flower as they use carcasses. That is, lizards have been observed frequently basking on dead rabbits and seagulls and capturing blowflies attracted by carrion during the last twenty years (Pérez-Cembranos et al., 2016). The use of carcasses is frequent in islands. Scavenging on seabird carcasses by the lacertid lizard *Teira dugesii* occurs frequently in the Selvagem Islands (Matias, Rebelo, Granadeiro, & Catry, 2009). Thus, it is not surprising that the confamilial Balearic lizard is able to detect and consume carrion on Aire Island and other locations (Pérez-Cembranos et al., 2016; Pérez-Mellado, 1989; Pérez-Mellado & Corti, 1993).

Because insular lizard and seagulls have coexisted for thousands of years in the Balearics (Pérez-Mellado, 2009), detection of carcasses by the lizards may have evolved long ago and represent a long-standing capacity. When the first dead horse arum seeds reached Aire Island, lizards were likely already able to detect blooming plants imitating rotting meat to which they are attracted by odor. The key for an easy detection of blooming dead horse arums is the degree of similarity between the odors of carcasses and blooming dead horse arum. It is of critical importance to dead horse arum's ability to attract blowflies for pollination and to the ability of Balearic lizards to locate the blooming plants. Linking electrophysiology and gas chromatography, Stensmyr et al. (2002) collected and analyzed odors of rotting meat and inflorescences of *H. muscivorus* chemically and observed electrophysiological responses to the odors by blowflies. Gas chromatography showed that the dead horse arum odor shares some key components with that of carrion. The foul smell is due to the presence of three specific oligosulfide components present in both carcasses and dead horse arum. Moreover, the responses triggered in flies by both the odors of carcasses and the dead horse arums were electrophysiologically indistinguishable (Stensmyr et al., 2002).

The probability of colonization by dead horse arum is higher at localities occupied by breeding colonies of seabird because abundant

organic matter and carrion attract blowflies and other potential pollinators (Boyce, 1994). We suggest that the Balearic lizard learned very early in their interactions with gulls how to exploit carcasses brought by gulls to colonies or even dead chicks and adult gulls. During cloudy Spring days on Aire Island, as well as on Dragonera Island off the southern coast of Mallorca (Balearic Islands), we observed lizards basking on seagull or rabbit carcasses for several minutes, taking advantage of the warm substrate of rotting bodies (V. Pérez-Mellado & A. Pérez-Cembranos, unpublished data). Thus, carcasses were exploited as a source of heat and as a foraging perch during suboptimal thermal periods during early spring.

Our results constitute the first experimental evidence that a lacertid lizard can use chemical cues to detect carcasses and decaying meat. Furthermore, we showed that this ability was employed to detect blooming dead horse arums that, in this way, attract not only blowflies, but also lizards. The amazing culmination of the story is that such attraction opened the door to a novel and complex interaction between the dead horse arum and the Balearic lizard, allowing lizards to use the plants as thermoregulation sites, as well as suitable perches for capturing blowflies, and even to detect and catch them inside floral tubules (Pérez-Mellado et al., 2007). Furthermore, the lizards and the plant have a strong mutual trophic dependence of the lizard and the plant during the fruiting period in June, which presumably account for the highest density of *H. muscivorus* ever recorded at any place in its geographic range (Pérez-Mellado et al., 2007 and unpublished data). We speculate that the intricate relationships among Balearic lizards, dead horse arum, and blowflies were initiated by attraction of lizards to dead horse arum by the odor resembling rotting meat.

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CONFLICT OF INTEREST

Authors declare they do not have any conflict of interest.

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