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Location of fruit using only airborne odor cues by a lizard

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Abstract

Although squamate reptiles are known to locate conspecifics by scent-trailing and to locate and identify prey by tongue-flicking substrates, an ability to locate food using only airborne cues has previously only been suspected based on observations that dead animals can be used as bait for Komodo dragons and that some nocturnal geckos aggregate on flowers. We conducted a simple field test of the ability of the omnivorous lizard *Podarcis lilfordi* to find fruit hidden under opaque cups. When a board having two identical cups spaced 1 m apart, one empty and the other hiding a freshly cut piece of apricot, was placed in the habitat, lizards first contacted the cup hiding fruit at well above chance frequency. Upon contact with a cup, lizards were significantly more likely to stay next to the cup, tongue-flick at high rates, climb the cup, and attempt to bite the cup if it hid a piece of apricot. The ability to follow a concentration gradient of airborne volatile chemicals to its source is very likely mediated by olfaction, but participation by or primacy of vomerolfaction cannot be excluded.

Keywords: Behavior; Olfaction; Vomerolfaction; Chemical senses; Squamata; Lacertidae; *Podarcis lilfordi*

1. Introduction

Among terrestrial vertebrates, the ability to locate odor sources is adaptive for finding food and conspecifics. This ability is well-developed in mammals and even in some birds. Squamate reptiles, the lizards and snakes, are widely known for following scent trails on surfaces [1,2]. For lizards, although many species have the ability to locate and identify prey using chemical cues sampled by tongue-flicking substrates [3,4], it has not been clear whether they can locate foods using only airborne chemicals. We show that at least one species of lizard can.

Knowledge about the ability of lizards to locate food using airborne chemical cues has languished for three reasons. First, the vast majority of studies of chemosensory discriminations in lizard feeding have focused on lingual sampling of chemicals by direct contact with substrates, discriminations likely to be mediated by vomerolfaction [5–7]. Second, the focus on such discriminations involving large, complex molecules [8] may have led investigators to ignore possible responses to volatile chemicals having small molecules. Nevertheless, the squamate olfactory system detects small molecules and even the vomeronasal system responds to some of them [9]. Finally, most lizards are insectivores [10] that might use olfactory cues to detect prey at close range, but are less likely than herbivores to be able to detect odorous plants from a greater distance.

On the other hand, airborne cues might be useful for locating certain foods, and field observations suggest that lizards may capitalize on the opportunity. Because carcasses are highly odorous, scavengers might locate them using airborne cues. Komodo dragons, *Varanus komodoensis*, appear to be drawn to carcasses of goats placed in the field as bait [11]. Airborne insect pheromones might also be used to locate prey, but this seems likely only for specialists on abundant, aggregated insects. Omnivorous and herbivorous lizards would appear to have the most widespread opportunity for location of food using airborne cues because many plants have evolved odors specifically to attract pollinators or dispersers. For omnivorous and herbivorous lizards, especially those that feed on flowers or odorous fruits, an ability to follow food odors to the source could be very beneficial. Field observations of nocturnal geckos in New

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Zealand aggregated on flowering plants suggest that they may be able to follow concentration gradients of airborne odorants from plants to their sources [12].

We studied the ability of the small (ca. 80 mm maximum snout-vent length), omnivorous lacertid lizard *Podarcis lilfordi* from Aire islet off the coast of Menorca, Balearic Islands, Spain to locate an odorous food. *P. lilfordi* actively forages for prey, but also eats plants, which form a substantial portion of its diet [13]. It eats some flowers, including pollen and nectar, but the bulk of its plant food consists of fruits [13]. We hypothesized that these lizards could locate fruit using airborne chemical cues for the reasons given above and because they are easily collected by using fruit as bait in opaque containers. They are drawn in large numbers by the odors of pear fruit and climb rocks placed against the container to locate the fruit, eventually jumping into the container.

2. Methods

To detect an ability to locate fruit using only airborne chemical cues, we placed plastic cups in the environment and observed the relative attraction of lizards to cups hiding fruit and empty control cups, as well as the behavior of lizards subsequent to arrival at the cups. The plastic cups were opaque, being dark brown in color. They were 45 mm tall, 37 mm in diameter at the smaller, closed end and 61 mm in diameter at the open end. Small holes were made in the cups above a lizard's line of sight. Two cups were inverted and placed one m apart on a wooden board (Fig. 1). One cup concealed a freshly cut piece of apricot; nothing was placed beneath the other cup.

In each trial, the board was placed in the open in an area where lizards were actively foraging, typically where the lizards could be heard or seen to be moving under clumps of vegetation downwind of the board. On 31 May 2000, we conducted 22 trials at 10:25–12:00 h in sunny conditions with a light breeze. The board was moved to new locations between trials to avoid repeated testing of the same individuals. The cups were in direct sunlight in 13 trials and in filtered sun in the others. Once a board had been positioned for a trial, we withdrew a minimum of 5 m and stood motionless until the conclusion of the trial. In each trial, we recorded which cup first attracted a lizard (actual touch) and the lizard's behaviours, including tongue-flicking, pushing and climbing the cup, and attempts to bite the cup.

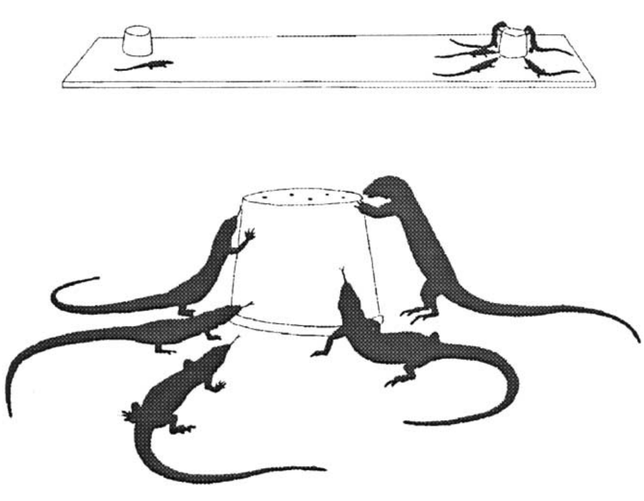

Fig. 1. Identical opaque cups were placed 1 m apart, equidistant from the ends of a board placed in the field where *P. lilfordi* foraged freely (upper drawing). The lower drawing shows lizards tongue-flicking and climbing a cup hiding a freshly cut piece of apricot.

The significance of the differences in the proportion of first lizards to contact empty cups and cups hiding fruit was assessed by a binomial test assuming equal probability for each type of cup [14]. A Fisher exact probability test [14] was made of the difference in tendency to quickly leave the cup or to remain by it, tongue-flicking the cup repeatedly, climbing it and attempting to bite it between first individuals that arrived at empty cups versus cups hiding fruit. The significance tests were two-tailed, with $\alpha = .05$.

3. Results

A lizard first touched the cup hiding fruit in 17 trials and the cup not hiding fruit in the other five trials. Lizards were attracted at significantly greater than chance frequency to the fruit (binomial $P = .008$). As the lizards approached, many could be seen tongue-flicking. They typically moved directly to the cup hiding fruit without meandering movements. In numerous instances, several lizards were simultaneously attracted to the cup hiding fruit (Fig. 1). After investigating the cup hiding fruit, some individuals examined the empty cup briefly before leaving the board.

The difference in behavior after arrival at a cup was even more striking. Sixteen of seventeen individuals remained with the cup that hid fruit, tongue-flicking repeatedly, pushing, climbing and attempting to bite the cup (Fig. 1). The other individual left the area quickly. The five individuals at cups not hiding fruit all left it quickly after no more than a few tongue-flicks. Individuals were significantly more likely to quickly leave empty cups and to remain with cups containing fruit, tongue-flicking frequently, climbing and biting the cups (Fisher $P < .0005$).

Although we did not record the numbers or behaviors of lizards other than the first individuals that arrived for each trial, multiple individuals were attracted frequently to cups hiding fruit, much more so than to empty cups. In the three instances that we did record, there were five, five and seven individuals simultaneously present at a cup hiding fruit. The behavior of latecomers to cups hiding fruit was similar to that of the first individuals to arrive, i.e., many of them tongue-flicked the cups repeatedly, and attempted to climb and/or bite the cups.

4. Discussion

The lizards clearly detected the odor of apricot and followed it to its source. Although we did not record the time between placement of the cups and arrival of a lizard, the response occurred rapidly, sometimes in well under 1 min and infrequently over 3 min. The ability to locate fruit using airborne odorants is clearly adaptive, and rapidity of response may be important in *P. lilfordi* due to strong intraspecific competition for food in the extraordinarily dense population on Aire [15].

The ability to discriminate between prey chemicals and control substances by lingually sampling chemicals from substrates appears to be universal in lizards that are insectivorous active foragers and to be absent in insectivorous ambush foragers [3,4,16]. Omnivorous lizards derived from actively foraging ancestors, such as *P. lilfordi* [3,17], additionally show strong tongue-flicking and biting responses to plant food chemicals [18,19], responses lacking in insectivores [20,21]. *P. lilfordi* and presumably some other omnivorous lizards are thus able to locate odorous plant foods from a distance and to discriminate between foods and nonfood by tongue-flicking substrates, which permits evaluation of potential food at hand and in some lizard taxa allows scent-trailing [22].

The chemical senses used by *P. lilfordi* to locate the fruit by responding to airborne odorants are unknown. Presumably, olfaction, vomerolfaction or a combination of them mediate the ability to follow a plume of airborne volatile chemicals to its source. Olfaction may well be important because this sense is responsive to volatile substances, and is well developed in many lizards, especially geckos and lacertids [23,24]. Olfactory cues often induce tongue-flicking for vomerolfactory sampling [25,26]. A role for vomerolfaction is also a distinct possibility. This sense mediates discriminations involving prey chemicals sampled by tongue-flicks contacting substrates [27]. Other tongue-flicks pass through a volume of air without contacting a substrate [28]. Such tongue-flicks might be important in sampling volatile chemicals for vomerolfaction and possibly gustation [9,29,30]. In garter snakes, the only squamates other than *P. lilfordi* known to be able to locate airborne food scents, vomerolfaction mediates the ability [30].

Further studies are needed to determine the range of lizard taxa capable of locating foods using airborne chemical cues, the types of foods located, and the sense(s) that mediate this ability. Because the only study available for snakes suggests the importance of vomerolfaction and the proposed mechanism is tropotaxis [31,32], we might expect the ability to be well developed only in lizards having the deeply forked tongues believed to be essential for tropotaxis. On the other hand, the observation that nocturnal gekkonid lizards aggregate on flowering plants, coupled with the absence of deep lingual forking and the presence of highly developed olfaction, suggests that olfaction might play an important role and that vomerolfactory tropotaxis may be absent or reduced in these lizards. Whatever the distribution of the ability and its sensory bases, the ability to locate plant foods by following concentration gradients of airborne chemicals affords at least one omnivorous lizard species and perhaps others a previously unknown flexibility in foraging behavior.

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