Relationships between chemosensory behaviour and foraging mode within lacertid lizards

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Summary

We assess associations between chemosensory capacity and foraging mode within lacertid lizards. Species of Lacertidae differ considerably in indices of foraging mode, and therefore seem well suited to test the adaptive nature of a coupling between foraging and sensory ecology. We observed tongue-flick (TF) rates of members from eight species in the field and in experimental conditions with no prey stimuli, with chemical stimuli, with visual stimuli and with both chemical and visual stimuli. All species increased TF rates in response to both purely visual and purely chemical prey cues, and the increase was most pronounced when both types of stimuli were offered simultaneously. Absolute TF rates in experimental conditions differed considerably among species, and species means obtained in experimental situations correlated closely with those observed in the field. Species that spend a relatively large amount of their time budget actively searching for food tend to use their vomeronasal system more frequently. Although all species in our study retained the capacity of recognizing prey chemicals, our data corroborate the idea of a functional link between an active foraging style and the usage of chemical information.

Keywords: lizard, Lacertidae, senses, tongue-flicking, foraging.

Introduction

The ability to perceive changes in the environment is of extreme importance to the survival and reproductive success of many animals. Therefore, it can be expected that natural selection will favour the evolution of sensory systems

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that function best in the specific context in which they are used (e.g., Mollon & Regan, 1999; Kimchi & Terkel, 2001; Hagelin, 2004). On the other hand, the set of sensory systems at its disposal may also limit an animal's behavioural options. These considerations lead to the expectation of co-evolution between sensory abilities and behavioural strategies. While such an association seems obvious at a wide taxonomical level, few studies have explored the issue at lower levels (i.e., within a family of species). Therefore, it is unclear how fast sensory systems change with changing behavioural contexts.

Broad comparative analyses involving members of different lizard families revealed a strong association between foraging mode and the development of the vomeronasal apparatus and prey chemical discrimination abilities (Schwenk, 1993; Cooper, 1994, 1997). Sit-and-wait foragers, that sit at a certain site and wait until a prey approaches, primarily use vision to scan the environment, show low rates of tongue-flicking and generally show poor prey chemical recognition capacities (Cooper & Van Wyk, 1994; Cooper, 1995). In contrast, active foraging lizards (species that move through the habitat in search for food items) typically exhibit high tongue-flick (TF) rates and use both visual and chemical cues to detect prey (Nicoletto, 1985b). These animals apparently have good chemosensory prey recognition capacities and some are even capable of locating prey using chemical cues only (Auffenberg, 1984; Cooper, 1995, 1997).

Foraging strategy is conserved in most lizard families, with all member species showing comparable movement intensities (Cooper, 1994). In some families however, there seems to be substantial variation in foraging behaviour, notably in Gekkonidae (Cooper, 1995), Scincidae (Castanzo & Bauer, 1993; Cooper & Whiting, 2000) and Lacertidae (Huey & Pianka, 1981; Cooper & Whiting, 1999). These families make excellent study systems to investigate the association between foraging strategy and the relative use of the visual and chemoreceptive senses (Cooper & Habegger, 2000). Active foraging is considered plesiomorphic in Lacertidae (Perry, 1999; Huey & Pianka, 2006), but some species display activity levels that mean sit-and-waiting most of their time of activity (Huey & Pianka, 1981; Cooper & Whiting, 1999).

In this study, we compare TF rates of lizards belonging to eight lacertid species in different experimental situations (with and without visual and chemical cues of prey) and correlate differences in responses to their foraging strategy. We predict that species with a more active style of foraging will exhibit higher TF rates, especially in the presence of cues of potential prey items.

Material and methods

Animals

We captured specimens of six species of lizards during spring by noose at different localities in Europe: *Lacerta vivipara* (Kalmthout, Belgium), *Podarcis muralis* (Melreux, Belgium), *Psammodromus algirus*, *Psammodromus hispanicus*, *Acanthodactylus erythrurus* (Alicante, Spain), and *Podarcis peloponnesiaca* (Stymfalía, Greece). These animals were put back in their biotope in autumn. Specimens of two additional species, *Acanthodactylus aureus* and *Takydromus sexlineatus*, were obtained from the pet trade. Only adult animals were used in this study, with females only if not gravid. All animals were transferred to the laboratory at the University of Antwerp, Belgium. Outside experimentation, lizards were housed in glass terrariums (1.0 × 0.3 m, length × width) with a sandy substrate, different types of hiding places (flat rocks, branches, dry leaves) and a drinking bowl. Species were kept separate, with no more than 4 animals per terrarium. Light bulbs (100 W) were suspended 25 cm above the sandy surface and provided light and heat for 10 h per day, thus allowing lizards to obtain their preferred body temperatures. Food (live crickets, *Acheta domesticus*) was provided twice a week. All lizards readily ate the crickets. On occasions, lizards received additional invertebrate prey, obtained by sweeping a nearby field with a net. The week prior to the experiments, no food was offered to the lizards in order to stimulate their foraging propensities. All experiments took place within a month after housing the lizards in the laboratory.

Experimental set-up

Four 0.5 × 0.5 m glass terrariums were used in the experiments. They all contained a thin layer of sand, covered with moss. During the experiments, a 100-W light bulb was set alight above the terrariums, assuring that the lizards were active near optimal body temperatures. The back and side walls of the terrariums were covered with white paper to reduce disturbance. Lizards were observed through a one-way mirror, placed against the front side of the terrariums. With the lights in the observation room out and the bulb above the terrarium on, lizards were unable to see the observer.

One terrarium (CONTROL) contained only sand and mosses. The second terrarium (CHEMO) contained chemical cues of prey only. The chemical cues were deposited by live crickets (*A. domesticus*), which were allowed to run freely in the terrarium throughout a whole week prior to the observations. The morning of the behavioural tests, all crickets were removed from the terrarium (this required poking around in the moss layer, so we also prodded the moss in the other cages). The third terrarium (VISUAL) contained no prey chemical cues, but at the start of the observations, a transparent plastic container holding three live crickets was introduced into it by a pulley system. As soon as the lizard had noticed the crickets (lizards typically approached the container and pressed or even banged their snout against it), the container was removed and the counting of TFs started. The last experimental situation (VISUAL+CHEMO) was identical to the third, but in this case the terrarium was labelled with chemical prey cues (procedure as in CHEMO).

At the beginning of an experiment, an individual lizard was introduced into a test terrarium and allowed to habituate for 5 min. This habituation period seemed necessary, because most lizards will generally raise their TF rates when confronted with a novel environment (Aragón et al., 2001). Even typical sit-and-wait foragers have been shown to exhibit this increase (Simon et al., 1981, Cooper et al., 1994), which is probably indicative of general explorative behaviour and is not foraging-related. Preliminary observations showed that after 5 min, TF rates in the CONTROL treatment return to normal levels, compared to the behaviour in the housing terrariums. After this initial period, TFs were counted over a period of ten minutes (CONTROL, CHEMO) or for a period of three minutes following a clear response to the visual cues (VISUAL, VISUAL+CHEMO). The order in which the animals were subjected to the different situations was assigned randomly.

Field observations

Indices of foraging behaviour (Percent Time Moving, PTM and Movements Per Minute, MPM) were determined in the field as part of a larger study on foraging styles in lacertid lizards and details will be reported elsewhere. First proposed by Pianka et al. (1979), PTM and MPM are now routinely used to quantify foraging style in lizards, with higher values indicating a more active search for prey (Huey & Pianka, 1981; Perry et al., 1990; Perry, 1999, 2006). We used a PSION Workabout MX (Psion Teklogix), on which was installed a chronometer, to record movements. We observed lizards from a safe distance, with binoculars if necessary. We retained only observations from active, undisturbed adult animals for analysis, excluding sessions that contained movements clearly resulting from intraspecific interactions, predator attacks or disturbance by the observer. All observations were performed in favourable weather conditions, and no extensive basking bouts were observed. Observations on individual lizards in principle lasted for 10 min, but occasionally a session had to be interrupted because the animal disappeared from sight. Observations that lasted less than 3 min were excluded from analysis. It should be noted that our methodology does not allow discriminating foraging bouts from movements in other contexts (e.g., thermoregulatory shuttling, patrolling, general exploring). However, since we observed lizards in their familiar environment, and at the peak of their activity during favourable weather conditions, and disregarded any sessions with obvious disturbance, we are confident that our PTM and MPM measurements primarily reflect foraging style.

At the same time, we counted the number of TFs exhibited by the focal animal (‘Field TF rates’). Probably the resulting field TF rates are an underestimation, because sometimes vegetation or perspective of the observer prevented accurate observation, but they may indicate the relative importance of tongue-flicking in the natural behaviour of the species used in the experiments. As for movement behaviour, TFs may serve other functions than prey detection. Field TF rates thus reflect the general propensity of the species to obtain information by use of the vomeronasal apparatus.

Statistical analysis

TF rates were square-root transformed to improve normality (Shapiro-Wilk’s $W > 0.97$ in all experimental conditions after transformation). To test for differences in transformed TF rates, we used repeated measures analysis of variance, with treatment (CONTROL, VISUAL, ODOUR, VISUAL+ODOUR) as the within-subjects factor and species and sex as between-subjects factors. Box’s test of equality of covariance matrices and Mauchly’s test of sphericity indicated no significant departures from the asymmetry assumptions, so we based the hypothesis tests on univariate (averaged F-test) analyses. The analysis showed no effect of sex on TF rates, and none of the interaction effects involving sex proved significant. We therefore decided to pool data for both sexes in subsequent analyses.

Besides establishing the significance of the overall among-treatments difference, we were interested in the following pair-wise comparisons: CHEMO:CONTROL (can lizards detect the former presence of crickets through chemoreception?); VISUAL:CONTROL (does a visual stimulus of potential prey elicit increased tongue-flicking?); VISUAL+CHEMO: VISUAL and VISUAL+CHEMO:CHEMO (does a combination of stimuli further increase TF rates?). We used Tukey-Kramer a posteriori tests to evaluate these questions, respecting the repeated nature of our data set.

To test for associations between (1) field and laboratory-measured TF rates and (2) TF rates and foraging behaviour indices (PTM, MPM), we used conventional Pearson correlations and phylogenetic regression with independent contrasts (Felsenstein, 1985; Harvey & Pagel, 1991; Garland et al., 1992, 1993).

The latter approach requires information on the phylogenetic relationships among the study species. We used two alternative topologies, provided by Fu (2000). The first hypothesis (tree A) places *T. sexlineatus* outside the Eurasian group and at the base of the Lacertinae (Figure 2A in Fu, 2000); the second (tree B) considers *T. sexlineatus* a close relative of *L. vivipara* (Figure 2B in Fu, 2000), which is in line with earlier morphological studies (e.g., Arnold, 1989). Because there is little reliable information available on the divergence times within Lacertidae (James Harris, personal communication), we set all branch lengths to unity. The actual length of the branches usually does not have substantial effects on the results of phylogenetic analyses (Díaz-Uriarte & Garland, 1998). We checked that correlations between the absolute values of the standardised independent contrasts and their standard deviations were non-significant before performing phylogenetic regressions (see Garland et al., 1992). All regressions of independent contrasts were forced through the origin (Garland et al., 1992).

Observed field TF rate of *P. hispanicus* may be an underestimation of the real TF rate to a larger extent than for the other species in the study because the very small size of these lizards makes such detailed observations particularly difficult. We therefore repeated correlations that involved field TF rates after excluding the data for *P. hispanicus*.

All conventional statistics were performed in SPSS 12.0 for Windows. Phylogenetic analyses were carried out using the PDAP module (Midford et al., 2002) implemented in the Mesquite system (version 1.06, Maddison & Madisson, 2005).

Results

PTM, MPM, field TF rate, number of individuals used in the experiments and the TF rates in the experiments are presented in Table 1. The species we used in this study cover the range of mostly sit-and-waiting (*A. aureus*) to moderately active foragers (*L. vivipara*). Tongue flick rates differed among experimental situations ($F_{3,225} = 81.67$, $p < 0.001$) and among species ($F_{7,75} = 22.47$, $p < 0.001$). Because there was no significant species*treatment effect ($F_{21,225} = 1.12$, $p = 0.32$), we pooled the data for all species in the following analyses. A-posteriori tests revealed significant differences in TF rates between the CONTROL and VISUAL conditions ($p < 0.0001$) and between the CONTROL and CHEMO conditions ($p = 0.0023$), the treatments with prey cues showing higher TF rates than the CONTROL condition. The VISUAL+CHEMO condition showed a significantly higher tongue flick rate than the VISUAL ($p < 0.0001$) and the CHEMO treatment ($p < 0.0001$).

Species means of TF rates observed in the laboratory (CONTROL) and in the field correlate significantly, whether *P. hispanicus* is included in or excluded from the analysis (Pearson correlation, Table 2). A paired t-test comparing absolute TF rates in the field with those observed in the CONTROL situation reveals no significant difference (Paired t-test: $t_7 = 1.59$, $p = 0.16$), but this could be due to the underestimated field data for *P. hispanicus*; excluding this species suggests slightly higher TF rates in the field (Paired t-test: $t_6 = 2.43$, $p = 0.05$). Compared to the average (across all treatments) TF rates in the laboratory, field TF rates are somewhat lower (Paired t-test with *P. hispanicus* included: $t_7 = 3.97$, $p = 0.005$; without *P. hispanicus*: $t_6 = 3.51$, $p = 0.01$). Field TF rates tend to be higher in more actively foraging species, but conventional Pearson correlation coefficients were not significant at the 0.05 level (Table 2). When *P. hispanicus* is removed from the analysis, the association between field TF rates and PTM (but not MPM) becomes statistically significant (Table 2). Regression of independent contrasts yields similar results (Table 2), except that the independent contrasts of MPM and field TF rates correlate significantly as well when *P. hispanicus* is excluded.

Table 1. Mean (X ± SE) number of tongue-flicks per minute observed in the four experimental situations (VISUAL = cricket shown visually; CHEMO = situation with chemical cues; VISUAL+CHEMO = situation with both visual and chemical prey cues; CONTROL = situation without prey cues) and in the field (TFfield), and foraging behaviour indices (PTM, Percent Time Moving; MPM, Movements Per Minute) for eight species of lacertid lizards. N_e = number of lizards used in the experiments; N_f = number of individuals observed in the field.

Species	N_e	CONTROL	VISUAL	CHEMO	VISUAL+CHEMO	N_f	TFfield	PTM	MPM
Acanthodactylus aureus	13	2.1 ± 0.3	4.7 ± 0.5	2.3 ± 0.3	5.4 ± 0.6	30	2.22	6.68 ± 1.10	2.41 ± 0.34
Acanthodactylus erythrurus	10	2.6 ± 0.5	5.0 ± 0.7	2.9 ± 0.4	5.8 ± 0.9	27	4.01	16.26 ± 2.16	3.16 ± 0.34
Lacerta vivipara	9	4.3 ± 0.6	6.1 ± 0.9	6.4 ± 0.8	11.4 ± 1.3	21	7.26	33.20 ± 3.46	4.20 ± 0.40
Psammodromus algirus	10	4.2 ± 0.6	8.2 ± 0.8	6.1 ± 0.6	10.0 ± 0.8	43	5.27	20.68 ± 2.54	2.95 ± 0.33
Psammodromus hispanicus	10	3.6 ± 0.5	6.5 ± 0.8	3.7 ± 0.5	7.7 ± 1.00	6	2.34	25.99 ± 7.34	4.71 ± 1.34
Podarcis muralis	16	4.6 ± 0.5	8.3 ± 0.7	6.7 ± 0.5	11.7 ± 0.7	47	5.94	20.54 ± 1.68	3.05 ± 0.25
Podarcis peloponnesiaca	7	4.2 ± 0.5	7.1 ± 1.0	6.4 ± 0.6	9.8 ± 1.4	73	4.55	12.35 ± 1.20	2.10 ± 0.17
Takydromus sexlineatus	8	3.3 ± 0.5	4.8 ± 0.7	4.4 ± 0.6	8.7 ± 0.8	37	3.06	13.80 ± 2.27	1.60 ± 0.21

Table 2. Relationships between TF rates in the field (TFfield), TF rates observed in the CONTROL laboratory situation and two foraging indices (MPM and PTM). Shown are Pearson correlations of tip values and phylogenetic correlations (Felsenstein's independent contrasts) using two phylogenetic hypotheses. All analyses were run with and without *Psammodromus hispanicus*. N_s = number of species; N_c = number of contrasts.

	Pearson correlaties			Phylogenetic correlations using tree A			Phylogenetic correlations using tree B		
	N_s	r	p	N_c	r	p	N_c	r	p
Analyses including *P. hispanicus*									
TFfield vs CONTROL	8	0.86	0.006	6	0.74	0.036	6	0.79	0.02
TFfield vs PTM	8	0.55	0.16	6	0.53	0.18	6	0.67	0.06
TFfield vs MPM	8	0.19	0.65	6	0.1	0.8	6	0.37	0.36
Analyses excluding *P. hispanicus*									
TFfield vs CONTROL	7	0.89	0.007	5	0.76	0.04	5	0.82	0.024
TFfield vs PTM	7	0.86	0.014	5	0.94	0.001	5	0.96	0.001
TFfield vs MPM	7	0.61	0.15	5	0.85	0.014	5	0.93	0.002

Discussion

It has long been recognized that in squamate reptiles, chemosensory prey detection is associated with an active foraging style (reviews in Cooper, 1994; Halpern, 1992). Several authors have speculated on the adaptive nature of this relationship (Evans, 1961; Regal, 1978; Huey & Pianka, 1981), and it seems intuitively logical that lizards hunting actively for hidden prey should benefit from well-developed chemosensory abilities, especially when foraging in structurally complex environments with limited vista. However, since the variation in both foraging strategies and chemosensory structures has a strong phylogenetic component (Schwenk, 1993; Cooper, 1994), it has proven difficult to refute the alternative hypothesis: that the association between chemosensory abilities and foraging mode is an example of phylogenetic inertia. Especially when foraging mode (active versus sit-and-wait) and chemosensory capacity (ability versus inability to recognize prey) are expressed on a qualitative basis, there are just too few phylogenetically independent transitions to build a case on (Cooper, 1994). Here we took a different approach and correlated quantitative measures of foraging behaviour (PTM, MPM) and chemosensation (TF rates) within a single family of lizards. Our results demonstrate considerable interspecific variation in the use of the vomeronasal apparatus. They also suggest co-adaptation between foraging style and TF rates. At the same time, we found no evidence for the loss of chemoreceptive abilities in species that are closer to the ambush-extreme of the foraging behaviour continuum. It seems that all species have retained the capacity to recognize chemical prey cues; some just make more use of this ability.

The patterns in TF rates in the different experimental conditions basically correspond with the results of Nicoletto (1985a) for a scincid species (*Scincella lateralis*), classified as an active forager (Cooper & Hartdegen, 1999). Confronted with the prey stimuli in the experiments, all species adopt what could be called active foraging behaviour (explicitly investigating the environment for prey by use of the chemical senses). Even *A. aureus*, that sits still during most of its activity period, searches in that situation actively and with plenty tongue-flicking for prey after its detection but subsequent disappearance.

The differences in mean TF rate exhibited in the CONTROL and the CHEMO cages, respectively, indicate that all species studied were able to detect chemicals left behind by *A. domesticus* crickets. This is not strict evidence that all lizards recognized the chemicals as cues from potential prey (Dial & Schwenk, 1996). Lacertid lizards are known to increase TF rates in a variety of circumstances, e.g. when confronted with novel environments (Thoen et al., 1986) or with cues from conspecifics (e.g., López & Martin, 2001; Cooper & Perez-Mellado, 2002) or predators (e.g., Thoen et al., 1986; Van Damme & Quick, 2001; Amo et al., 2005). Still, lizards in our CHEMO treatment did not show any of the behaviours that are characteristic for lacertids when confronted with potential sources of stress (e.g., tail vibrations, ‘slow-motion’-behaviour, foot shakes, fast running bouts, see Verbeek, 1972; Thoen et al., 1986), suggesting that they were interested in, but not afraid of the (source of the) chemical cues.

The pronounced increase in TF rates in the VISUAL situation, compared to the CONTROL situation, demonstrates that lizards of all species studied will use their chemosensory capacities to retrieve prey items with which they lost visual contact. This behaviour bears resemblance to the ‘strike-induced chemosensory searching’ observed in many snakes (e.g., Chiszar et al., 1982; O’Connell et al., 1985; Cooper et al., 1989) and lizards (Cooper, 1991, 1992, 1993), further adding to the hypothesis that chemosensory searching following contact with a prey is an ancestral trait, retained in different squamate lineages (Cooper, 1989; Burghardt & Chmura, 1993; Cooper & Alberts, 1993). That all lizards approached interestedly and often attacked the prey even in the absence of chemical stimuli, suggests that lacertid lizards have at least two sensory systems that can, even independently, recognize prey items.

The highest TF rates were observed in the VISUAL+CHEMO treatment, indicating that chemical and visual stimuli act synergistically in eliciting TF rates and searching behaviour. A similar additive effect of olfactory and visual cues on foraging intensity has been described in other animals (e.g., lizards: Nicoletto, 1985a, b; fish: Kolkovski et al., 1997; and insects: Blackmer & Canas, 2005; Raguso & Willis, 2005). Possibly, the combined presence of different cues is an indication for the lizard that the prey must be near and encourages it to continue searching. A synergistic effect of cues from different sensory realms is also important in anti-predatory behaviour, where different signals are used to make a better assessment of risk (the 'threat sensitivity hypothesis', Helfman, 1989; see, e.g., Hartman & Abrahams, 2000; Amo et al., 2006). Similarly, a growing body of evidence suggests that animals use multiple signals in mate choice (e.g., Candolin, 2003; Hamilton & Sullivan, 2005). Overall, and not surprisingly, animals seem to integrate signals detected by different sensory systems when making decisions.

The strong correlation between field and laboratory TF rates lends support to the idea that TF rates in experimental situations at least qualitatively reflect TF rates in natural conditions (an assumption that has rarely been tested). That absolute TF rates in the field are somewhat above those observed in the CONTROL situation in the lab may indicate the presence of chemical cues in the field. That field TF rates are low compared to averaged experimental TF rates suggests that the cues were not as intense in the field as in the lab. However, comparisons of absolute TF rates are hampered by difficulties with observing animals in the field (which probably result in underestimated TF rates) and possible differences in the hunger status of the focal animals.

Tongue flick rates observed in the lab and in the field differed considerably among species. Although we (and many others before us) use TF rate here as a bio-assay for the degree of chemosensory excitation, it is not entirely sure that lizards that tongue-flick more also obtain a better picture of their chemical environment. On the contrary, one could argue that a lizard with extreme chemosensory powers would be able to acquire all necessary olfactory information in a single TF. However, this line of reasoning seems unlikely in our situation where the prey remained hidden. Still, future studies should try to establish correlations between TF rates and foraging performance (ability to actually find hidden prey) to confirm the usefulness of TF rates as indicators of chemoreceptive abilities. Assuming that TF rate does reflect chemosensory excitation, the differences among species can be explained in many ways. It is unlikely that the variation merely originates from differential reactions to captivity or experimentation, since remarkably parallel differences were observed in the field. It has been argued that the structural complexity of the environment should affect the sensory biology of animals (the 'sensory drive hypothesis', e.g., Ord et al., 2002; Bloch & Irschick, 2006). For instance, species living in highly cluttered areas should rely more on chemical or auditory stimuli than on visual cues. The species used in our study differ widely in microhabitat use, and those living in more open habitats (*A. aureus*, *A. erythrurus*) exhibited lower TF rates than those living in densely vegetated areas (e.g., *L. vivipara*). However, in the absence of quantitative information on the degree of visual obstruction in the respective environments, we cannot adequately test the sensory drive hypothesis.

A non-mutually exclusive hypothesis is that foraging mode affects TF rates. Actively foraging lizards looking for concealed prey should benefit more from good chemosensory capacities than ambush predators, and not only because it will help in discovering hidden prey items; actively hunting lizards must venture more frequently into unfamiliar parts of their home range, and being able to pick up chemical cues from lurking predators or conspecifics seems also very valuable in such a context (Anderson, 1993; Cooper, 1994). In contrast, high TF rates may actually be non-adaptive in ambush hunting, because the rapid movements of the tongue may give away the lizard's hide to the approaching prey, or even to predators (Cooper, 1998). Our results corroborate this idea at least partially. Field TF rates correlate with the percent of time spent moving (PTM), one of the most used indices of foraging activity, and our phylogenetically informed analyses suggest that this is not merely the result of historical contingency. Because the statistical significance of the correlation somewhat depends on the phylogenetic hypothesis used, and the inclusion/exclusion of one doubtful data point (*P. hispanicus*), we feel that future studies should expand this data set. Especially the addition of data from lacertid species exhibiting more extreme types of foraging behaviour (e.g., *Meroles* spp., Cooper & Whiting, 1999; *Nucras* *intertexta*, Pianka et al., 1979) would be of interest. More extreme sit-and-waiting species than *A. aureus*, with activity levels more resembling those of typical iguana ambushers (PTM < 1), might for example not react or react differently on the prey stimuli as presented in the experiments.

Despite the differences in absolute TF rates, all species studied here reacted similarly to the test situations. Hence, even if the sit-and-wait species in the study make use of their chemoreceptive senses less often, this has not resulted in the complete loss of this faculty. Perhaps it is merely the behavioural component (number of protrusions of the tongue per unit time) and not the morphological/physiological machinery (structure tongue, size of Jacobson's organ, abundance of the chemoreceptor cells in the epithelium) that has co-evolved with foraging mode. This would be in line with the idea that lacertids, of different foraging modes, make use of their chemical senses to gather information on variety of sources, not only food. It is possible that sit-and-wait species have retained chemoreceptive prey recognition abilities because they require the chemosensory equipment in other contexts (anti-predatory behaviour, intraspecific communication, species recognition). Future studies could address this question by comparing morphological and physiological correlates of chemoreceptive abilities (Schwenk, 1994; Cooper, 1997; Herrel et al., 2005) and by correlating TF rates in different contexts across species with different foraging styles. This would help understanding to what extent chemoreception and foraging mode have co-evolved in lacertids, and to what extent this affects the way in which other information is detected and processed.

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