

How phylogeny and foraging ecology drive the level of chemosensory exploration in lizards and snakes

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Abstract

The chemical senses are crucial for squamates (lizards and snakes). The extent to which squamates utilize their chemosensory system, however, varies greatly among taxa and species' foraging strategies, and played an influential role in squamate evolution. In lizards, 'Scleroglossa' evolved a state where species use chemical cues to search for food (active foragers), whereas 'Iguania' retained the use of vision to hunt prey (ambush foragers). However, such strict dichotomy is flawed as shifts in foraging modes have occurred in all clades. Here, we attempted to disentangle effects of foraging ecology from phylogenetic trait conservatism as leading cause of the disparity in chemosensory investment among squamates. To do so, we used species' tongue-flick rate (TFR) in the absence of ecological relevant chemical stimuli as a proxy for its fundamental level of chemosensory investigation, that is baseline TFR. Based on literature data of nearly 100 species and using phylogenetic comparative methods, we tested whether and how foraging mode and diet affect baseline TFR. Our results show that baseline TFR is higher in active than ambush foragers. Although baseline TFRs appear phylogenetically stable in some lizard taxa, that is a consequence of concordant stability of foraging mode: when foraging mode shifts within taxa, so does baseline TFR. Also, baseline TFR is a good predictor of prey chemical discriminatory ability, as we established a strong positive relationship between baseline TFR and TFR in response to prey. Baseline TFR is unrelated to diet. Essentially, foraging mode, not phylogenetic relatedness, drives convergent evolution of similar levels of squamate chemosensory investigation.

Introduction

The chemical senses are critically important for many animals (Müller-Schwarze & Silverstein, 1980; Müller-Schwarze, 2006; Wyatt, 2014), and reptiles represent no exception (Mason & Parker, 2010; Martín & López, 2014). Squamate reptiles (lizards and snakes) rely strongly on their ability to perceive chemicals from the environment for a variety of social and ecological activities, such as mate assessment (e.g. Martín & López, 2000; Baeckens, 2017), predator avoidance (e.g. Van Damme *et al.*, 1995; Van Damme & Castilla, 1996) and

foraging (e.g. Cooper, 1997, 2008), and have evolved highly sophisticated vomerolfactory systems and tongues for chemical sampling (Schwenk, 1993, 1995; Cooper, 1995a, 1996).

Squamate vomerolfaction is mediated by 'tongue-flicking' (TF) behaviour in which the tongue samples substrate-bound or airborne chemicals in the environment and delivers them to the vomeronasal organs above the roof of the mouth (Filoramo & Schwenk, 2009). Unlike the (anatomically distinct) main olfactory system, the vomeronasal system depends on the active, or voluntary, stimulation of the chemosensory organs by chemicals collected by the tongue (Daghfous *et al.*, 2012).

Cooper (1995a,b, 1997, 2008) has argued that the degree to which squamates invest in such an active mode of tongue-flicking behaviour is strongly

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influenced by their ecology, such as mode of foraging or food preference. To illustrate, lizards are traditionally categorized as ambush foragers or active foragers (Huey & Pianka, 1981). Ambush or 'sit-and-wait' foragers wait immobile for prey to approach before they attack. Typically, ambush foragers rarely tongue-flick while at ambush posts, and do not use chemical cues to search for food (Cooper *et al.*, 1994a). In contrast, active foragers move through the habitat actively searching for prey, tongue-flicking frequently as they go, and locating and identifying food by the use of chemical cues (Evans, 1961). Besides foraging mode, diet also may impact squamate tongue-flicking behaviour. For instance, generalist predators of small animals are known to respond to chemical cues from a wide range of potential prey (Cooper, 2000a; Cooper & Pérez-Mellado, 2002), whereas food specialists generally only are able to chemically discriminate their food of interest from other food types, and usually, with high levels of elicited tongue-flick behaviour (Cooper & Arnett, 2003).

The extent to which squamates utilize their chemosensory systems also varies greatly among taxa, and has played an influential role in squamate evolution (Vitt *et al.*, 2003). Among lizards, for instance, the 'Scleroglossa' (Gekkota, Lacertoidea, Scincoidea and Anguimorpha) are labelled highly 'chemically-oriented', whereas the 'Iguania' are often regarded as marginally 'chemically-oriented', and rather 'visually-oriented' (Schwenk, 1993, 1994; Vidal & Hedges, 2009). Such partition accords well with the conventional view of squamate phylogenetic history, in which the tongue played a key role. Still, such strict separatism is clearly flawed in the sense that many 'chemically-oriented' lizard species also have excellent eyesight (Pérez I de Lanuza & Font, 2014; Martin *et al.*, 2015) and frequently use visual displays (Cooper *et al.*, 2003a; Font *et al.*, 2012), whereas some 'visually-oriented' iguanians also use chemical cues to discriminate among prey items (Cooper & Flowers, 2000; Cooper & Lemos-Espinal, 2001) and in intraspecific communication (Simon *et al.*, 1981; Duvall, 1979; Baeckens *et al.*, 2016).

Clearly, squamates show a high degree of interspecific variation in their level of chemosensory behaviour. Yet, an extensive comparative attempt to disentangle the effect of ecology from phylogenetic trait conservatism as cause of this disparity among squamates is still lacking – until now. Previous studies showed that responses to prey chemicals are strongly linked to foraging behaviour, but these analyses included small numbers of species. In this study, we map and quantify the variation in squamate chemosensory investigation and examine whether and how ecology and phylogeny contribute to this variation. Using phylogenetic comparative methods, we investigate the direction in which foraging mode and diet may have pushed squamate chemosensory evolution, while strictly accounting

for shared ancestry among species. As squamates tongue-flick to chemically investigate stimuli, we hypothesize that a species' fundamental tongue-flick rate in the absence of ecologically important chemical stimuli, that is the baseline tongue-flick rate, reflects the overall importance of chemosensory searching for that species. Therefore, we expected a higher baseline tongue-flick rate for active foragers that search for chemical cues as they move through the environment, than ambush foragers, which conventionally rely more on their vision to detect prey. In line, we predicted a positive relationship between baseline tongue-flick rates and the tongue-flick rates in response to food. Herbivory and omnivory are more likely to evolve in active than ambush foragers, but herbivores and omnivores both discriminate plant food chemical from other cues regardless of the foraging modes of their insectivorous/carnivorous ancestors (Cooper, 2002; Cooper & Vitt, 2002). Therefore, if inclusion of plants in the diet affects baseline tongue-flick rate, it might be expected to do so only in plant eaters derived from ambush foragers. On the other hand, plant eaters derived from ambush foragers might locate food sources visually and then increase their tongue-flick rates to evaluate them (Cooper, 2002; Cooper & Vitt, 2002). In that case, plant consumption would be unlikely to affect the baseline tongue-flick rate. Because the effect of plant consumption on tongue-flick rate is uncertain, we examine this relationship without prediction. Lastly, we predict that baseline tongue-flick rates are lower in Iguania than other lizards, as almost all iguanian families are ambush foragers (Perry, 1999; Cooper *et al.*, 2001a,b,c). Hence, we predict a strong association between squamate phylogeny and baseline tongue-flick rate, but only if the influence of foraging mode is ignored.

Materials and methods

Baseline tongue-flick rate

Data on tongue-flick rates of 94 lepidosaurian species (80 lizards, 13 snakes and one tuatara) belonging to 31 families were extracted from literature (Table 1). For every species, we documented the mean number of tongue-flicks (elicited in 1 min) in response to a cotton swab impregnated with deionized or distilled water. This tongue-flick frequency will hereinafter be referred to as 'baseline' tongue-flick rate. We consider this baseline rate as a suitable proxy for a species' primary or fundamental level of chemosensory investigation via lingual sampling for analysis by the vomeronasal system, and as such, we will use it in interspecific comparisons.

In the past, researchers have applied a range of experimental assays to test species' chemoreceptive abilities (see Van Damme *et al.*, 1995; Cooper, 1998a; LeMaster & Mason, 2001; Verwaijen & Van Damme,

Table 1 Baseline and prey tongue-flick rate, diet and foraging mode for 94 lepidosaurian species, assembled from available literature.

Species	Family	Baseline TF rate mean \pm SE (n)	Prey TF rate mean	Diet	Foraging mode	Reference(s)
<i>Acanthodactylus boskianus</i> *	Lacertidae	4.9 \pm 1.5 (18)	15.59	I-C	AC	Cooper (1999a)
<i>Acanthodactylus scutellatus</i> *	Lacertidae	3.5 \pm 0.9 (18)	14.9	I-C	SW	Cooper (1999a)
<i>Acanthosaura crucigera</i> *	Agamidae	0 \pm 0 (20)	0	I-C	SW	Cooper <i>et al.</i> (2001b)
<i>Ameiva ameiva</i> *	Teiidae	7.1 \pm 1.6 (15)	15.2	I-C	AC	Cooper <i>et al.</i> (2002a)
<i>Anolis carolinensis</i> †	Dactyloidae	1.42 \pm 1.24 (6)	0.67	I-C	SW	Cooper (1989)
<i>Anolis chamaeleonides</i> *	Dactyloidae	0 \pm 0 (11)	0	I-C	SW	Cooper <i>et al.</i> (2001b)
<i>Anolis smallwoodi</i> *	Dactyloidae	0 \pm 0 (14)	0	I-C	SW	Cooper <i>et al.</i> (2001b)
<i>Aspidoscelis marmorata</i> ‡	Teiidae	10.3 \pm 2.1 (22)	-	I-C	AC	Punzo (2008)
<i>Blanus cinereus</i> §	Blaniidae	3.9 \pm 0.5 (18)	5.4	I-C	AC	López & Salvador (1992)
<i>Calotes mystaceus</i> †	Agamidae	0 \pm 0 (2)	1	I-C	SW	Cooper (1989)
<i>Calotes versicolor</i> ¶	Agamidae	0 \pm 0 (18)	0	I-C	SW	Ammanna <i>et al.</i> (2014)
<i>Chondrodactylus turneri</i> *	Gekkonidae	0.4 \pm 0.3 (13)	5.2	I-C	SW	Cooper (1999b)
<i>Coleonyx brevis</i> §	Eublepharidae	8 (22)	-	I-C	AC	Dial & Schwenk (1996)
<i>Coleonyx variegatus</i> *	Eublepharidae	4.2 \pm 0.9 (18)	11.6	I-C	AC	Cooper (1998b)
<i>Coluber constrictor</i> *	Colubridae	2.1 \pm 0.6 (7)	-	I-C	AC	Cooper <i>et al.</i> (2000a)
<i>Coluber flagellum</i> ¶	Colubridae	23.5 \pm 6.6 (16)	-	I-C	AC	Cooper <i>et al.</i> (1990)
<i>Cordylus cordylus</i> *	Cordylidae	0.3 \pm 0.1 (6)	1.1	I-C	SW	Cooper & Van Wyk (1994)
<i>Coronella austriaca</i> *	Colubridae	7.1 \pm 1.7 (15)	-	I-C	SW	Amo <i>et al.</i> (2004)
<i>Correlophus ciliatus</i> *	Diplodactylidae	2 \pm 0 (1)	14	O	SW	Cooper (2000a)
<i>Corucia zebrata</i> *	Scincidae	17.6 \pm 3.6 (12)	16.8	H	-	Cooper (2000b)
<i>Corytophanes cristatus</i> *	Corytophanidae	0 \pm 0 (18)	0	I-C	SW	Cooper (1999b)
<i>Crotalus culminatus</i> †	Viperidae	11.7 \pm 0.4 (2)	-	I-C	SW	Chiszar & Radcliffe (1976)
<i>Crotalus enyo</i> ‡	Viperidae	16.3 \pm 1.2 (2)	-	I-C	SW	Chiszar & Radcliffe (1976)
<i>Crotaphytus collaris</i> *	Crotaphytidae	0.39 \pm 0.18 (18)	1.2	I-C	SW	Cooper <i>et al.</i> (1996)
<i>Dipsosaurus dorsalis</i> §	Iguanidae	1.00 \pm 0.37 (17)	4.33	H	-	Cooper & Alberts (1991)
<i>Elgaria coerulea</i> *	Anguidae	3 \pm 1.0 (7)	14.57	I-C	AC	Cooper (1990b)
<i>Elgaria multicarinata</i> *	Anguidae	3.27 \pm 0.63 (11)	21.18	I-C	AC	Cooper (1990b)
<i>Eublepharis macularius</i> †	Eublepharidae	5.2 \pm 1.6 (12)	17.7	I-C	AC	Cooper (1995c)
<i>Eugongylus albofasciolatus</i> *	Scincidae	13.4 \pm 3.6 (12)	13.4	I-C	AC	Cooper (2002)
<i>Eumeces schneideri</i> *	Scincidae	4.6 \pm 0.7 (20)	7.2	O	AC	Cooper <i>et al.</i> (2000b)
<i>Eutropis macularia</i> *	Scincidae	3.6 \pm 1.2 (16)	16.1	I-C	AC	Cooper & Habegger (2000a)
<i>Furcifer pardalis</i> *	Chamaeleonidae	0 \pm 0 (20)	0	I-C	SW	Cooper <i>et al.</i> (2001b)
<i>Gallotia caesaris</i> *	Lacertidae	3.2 \pm 0.7 (20)	17.3	O	-	Cooper & Pérez-Mellado (2001a)
<i>Gallotia simonyi</i> *	Lacertidae	1.1 \pm 0.4 (17)	14.2	O	-	Cooper & Pérez-Mellado (2001a)
<i>Gekko gecko</i> *	Gekkonidae	0 \pm 0 (20)	0.1	I-C	SW	Cooper & Habegger (2000b)
<i>Gerrhosaurus nigrolineatus</i> †	Gerrhosauridae	3.62 \pm 0.91 (8)	-	I-C	AC	Cooper & Trauth (1992); Cooper <i>et al.</i> (1994b)
<i>Goniurosaurus luyi</i> *	Eublepharidae	10.5 \pm 5.9 (13)	6.5	I-C	AC	Cooper & Habegger (2000b)
<i>Heloderma suspectum</i> *	Helodermatidae	18.2 \pm 7.4 (6)	64.8	I-C	AC	Cooper & Arnett (2001)
<i>Heterodon platirhinos</i> ¶	Dipsadidae	7.2 \pm 2.1 (9)	-	I-C	AC	Cooper & Secor (2007)
<i>Holcosus undulatus</i> *	Teiidae	4.7 \pm 1.9 (9)	17	I-C	AC	Cooper (1990c)
<i>Hypsiglena chlorophaea</i> *	Dipsadidae	8.5 \pm 4.9 (21)	-	I-C	AC	Weaver <i>et al.</i> (2012)
<i>Iberolacerta cyreni</i> ‡	Lacertidae	3 \pm 0.2 (16)	-	I-C	AC	López & Martín (2012)
<i>Iberolacerta monticola</i> †	Lacertidae	4.6 \pm 1.2 (32)	-	I-C	AC	Aragón <i>et al.</i> (2000)
<i>Lampropeltis getula</i> §	Colubridae	20.68 (13)	-	I-C	AC	Williams & Brisbin (1978)
<i>Lampropholis coggeri</i> †	Scincidae	6.7 \pm 3.8 (40)	-	I-C	AC	Scott <i>et al.</i> (2015)
<i>Laudakia stellio</i> *	Agamidae	0 \pm 0 (5)	0	I-C	SW	Herrel <i>et al.</i> (1998)
<i>Leiolepis belliana</i> *	Agamidae	3.1 \pm 0.3 (11)	7.1	O	SW	Cooper (2003b)
<i>Lepidophyma flavimaculatum</i> *	Xantusiidae	0 \pm 0 (7)	7.7	I-C	SW	Cooper (2000c)
<i>Mesaspis moreletii</i> *	Anguidae	5.1 \pm 1.7 (17)	5.8	I-C	AC	Cooper & Habegger (2000c)
<i>Opheodrys aestivus</i> *	Colubridae	1.7 \pm 0.3 (8)	-	I-C	AC	Cooper (2007b)
<i>Pantherophis guttatus</i> *	Colubridae	22 \pm 3.6 (9)	-	I-C	AC	Weldon <i>et al.</i> (1990)
<i>Phymaturus punae</i> *	Liolaemidae	1.0 \pm 0.3 (8)	5.2	H	-	Cooper <i>et al.</i> (2001c)
<i>Pituophis melanoleucus</i> *	Colubridae	10.6 \pm 3.2 (19)	-	I-C	AC	Smith <i>et al.</i> (2015)
<i>Platysaurus pungweensis</i> *	Cordylidae	1.4 \pm 0.6 (13)	0.7	I-C	SW	Cooper & Steele (1999)
<i>Plestiodon fasciatus</i> ‡	Scincidae	3.8 \pm 1.1 (9)	10.2	I-C	AC	Cooper <i>et al.</i> (2000b)

Table 1 (Continued)

Species	Family	Baseline TF rate mean \pm SE (n)	Prey TF rate mean	Diet	Foraging mode	Reference(s)
<i>Plestiodon inexpectatus</i> ¶	Scincidae	1.1 (7)	3.3	I-C	AC	Loop & Scoville (1972)
<i>Plestiodon laticeps</i> †	Scincidae	3.14 \pm 1.51 (6)	-	I-C	AC	Cooper & Garstka (1987)
<i>Podarcis hispanicus</i> *	Lacertidae	1.8 \pm 0.2 (5)	10.2	I-C	AC	Cooper (1990c)
<i>Podarcis lilfordi</i> *	Lacertidae	5.7 \pm 1.1 (20)	9.8	O	AC	Cooper & Pérez-Mellado (2001b)
<i>Podarcis muralis</i> *	Lacertidae	4.6 \pm 0.7 (16)	7.9	I-C	AC	Cooper et al. (2002b)
<i>Podarcis siculus</i> *	Lacertidae	1.7 \pm 0.4 (6)	5.2	O	AC	Cooper & Pérez-Mellado (2002)
<i>Pogona vitticeps</i> *	Agamidae	0.6 \pm 0.2 (10)	4.6	O	SW	Cooper (2000d)
<i>Psammmodromus algirus</i> ‡	Lacertidae	4.1 \pm 0.4 (14)	-	I-C	AC	Martín et al. (2007)
<i>Python regius</i> *	Pythonidae	20.6 \pm 4.3 (10)	-	I-C	AC	Cooper (1991)
<i>Rhacodactylus auriculatus</i> *	Diplodactylidae	5.8 \pm 5.1 (4)	41.5	O	SW	Cooper (2000a)
<i>Rhacodactylus leachianus</i> *	Diplodactylidae	2.1 \pm 1.0 (8)	13.9	O	SW	Cooper (2000a)
<i>Salvator rufescens</i> *	Teiidae	3.8 \pm 0.9 (6)	17.2	I-C	AC	Cooper (1990c)
<i>Sauromalus ater</i> *	Iguanidae	1.6 \pm 0.3 (15)	4.8	H	-	Cooper & Flowers (2000)
<i>Sceloporus malachiticus</i> †	Phrynosomatidae	0.2 \pm 0.13 (2)	2	I-C	SW	Cooper (1989)
<i>Sceloporus poinsettii</i> *	Phrynosomatidae	0 \pm 0 (20)	0.2	O	SW	Cooper et al. (2001c)
<i>Sceloporus undulatus</i> †	Phrynosomatidae	0 \pm 0 (12)	17	I-C	SW	Hews et al. (2011)
<i>Sceloporus variabilis</i> *	Phrynosomatidae	0 \pm 0 (19)	0	I-C	SW	Cooper et al. (2001c)
<i>Sceloporus virgatus</i> †	Phrynosomatidae	0 \pm 0 (11)	-	I-C	SW	Hews et al. (2011)
<i>Scincella lateralis</i> *	Scincidae	1.9 \pm 0.2 (12)	2.9	I-C	AC	Cooper & Hartdegen (2000)
<i>Scincus mitranus</i> ‡	Scincidae	4.2 \pm 1.4 (9)	9.8	O	AC	Cooper et al. (2000b)
<i>CooSphenodon punctatus</i> *	Sphenodontidae	0 \pm 0 (10)	-	I-C	SW	Cooper et al. (2001b)
<i>Takydromus septentrionalis</i> *	Lacertidae	5 \pm 1.1 (12)	7.1	I-C	AC	Cooper et al. (2003b)
<i>Takydromus sexlineatus</i> *	Lacertidae	3.7 \pm 0.7 (17)	4.4	I-C	AC	Cooper et al. (2000c)
<i>Teira perspicillata</i> *	Lacertidae	3.6 \pm 0.7 (20)	5.8	I-C	AC	Cooper & Pérez-Mellado (2002)
<i>Thamnophis sirtalis</i> *	Natricidae	6.4 (7)	-	I-C	AC	Cooper & Burghardt (1990); Burghardt et al. (1988)
<i>Thecadactylus rapicauda</i> †	Phyllodactylidae	0 \pm 0 (8)	-	I-C	SW	Cooper (1995c)
<i>Tiliqua rugosa</i> *	Scincidae	11.5 \pm 4.2 (8)	12.9	O	AC	Cooper (2000e)
<i>Tiliqua scincoides</i> *	Scincidae	6.4 \pm 1.9 (9)	4.6	O	AC	Cooper (2000e)
<i>Trachylepis quinquetaeniata</i> *	Scincidae	6.5 \pm 1.6 (10)	5.5	I-C	AC	Cooper et al. (2003b)
<i>Trachylepis striata</i> *	Scincidae	2.9 \pm 0.9 (21)	7.6	I-C	AC	Cooper (2000f)
<i>Trogonophis wiegmanni</i> §	Trogonophidae	4.6 \pm 0.7 (12)	18.37	I-C	AC	López et al. (2014)
<i>Tropidurus hispidus</i> §	Tropiduridae	0 \pm 0 (19)	17.2	I-C	SW	Cooper et al. (2001c)
<i>Tupinambis teguixin</i> §	Teiidae	12.84 \pm 13.05 (19)	36.15	I-C	AC	Yanosky et al. (1993)
<i>Uromastix acanthinura</i> *	Agamidae	0.2 \pm 0.18 (4)	1.2	H	-	Herrel et al. (1998)
<i>Uromastix aegyptius</i> *	Agamidae	5.6 \pm 2.6 (10)	9.5	H	-	Cooper & Al-Johany (2002)
<i>Uta stansburiana</i> *	Phrynosomatidae	0.3 \pm 0.1 (21)	0.4	I-C	SW	Cooper et al. (2001b)
<i>Varanus exanthematicus</i> ¶	Varanidae	10.6 \pm 1.8 (18)	28	I-C	AC	Cooper & Habegger (2001)
<i>Varanus gouldii</i> *	Varanidae	4.14 \pm 1.79 (7)	38	I-C	AC	Garrett & Card (1993)
<i>Xenosaurus platyceps</i> *	Xenosauridae	0.2 \pm 0.2 (8)	6.8	I-C	SW	Cooper et al. (1998)

I-C, insectivorous–carnivorous; O, omnivorous; H, herbivorous; SW, sit-and-wait foraging; AC, active foraging.

*Sex not specified.

†Males.

‡Females.

§Both sexes included.

¶Juveniles.

2007; Font et al., 2012; Huyghe et al., 2012). To amass reliable comparative data, we chose in this study to use tongue-flick records obtained via the cotton swab technique. This widely practised method has an experimental approach, provides rapid results and is highly repeatable and reproducible (Cooper, 1998a). Essentially, to start a cotton swab trial, a swab is moved to a position just anterior to the animal's snout and held there for a fixed interval during which the animal may

respond with differential lingual behaviour. Typically, the experimenter approaches the animal's cage carefully, so as not to elicit escape behaviour or inhibit tongue-flicking. Subsequently, the researcher positions the cotton tip of a 15- to 30-cm wooden applicator 1–3 cm anterior to the animal's snout and, starting with the first tongue-flick, records the number of tongue-flicks directed to the swab within 60 s. The total experiment usually comprises multiple trials. In each trial the swab

bears a stimulus belonging to one of several categories of experiment and control stimuli. Experimental stimuli can be, for example, chemicals obtained from prey (e.g. Cooper & Vitt, 1989), predators (e.g. Amo *et al.*, 2004) or conspecifics (e.g. Baeckens *et al.*, 2017). Eau-de-cologne is often used as a pungency control, and deionized or distilled water as an odourless control (Cooper *et al.*, 2003b). Because the biological relevance of the experimental stimuli varies among species, quantitative comparisons among them are useful for inferring the ability to detect and responsiveness to chemicals from prey, predators and conspecifics. In contrast, baseline tongue-flick rates – while squamates are at rest – provide valuable information on the relative frequency of lingual chemosensory sampling of a novel stimulus. As the tongue-flick rate towards the odourless control is almost invariably reported in cotton swab studies, it suits as an excellent comparative tool.

Ideally, a researcher scores a set of behaviours during a swab trail: number of tongue-flicks, latency to the first tongue-flick, frequency of biting and tongue-flick attack score (TFAS; Burghardt, 1967). The latter score is considered a composite measure that combines the number of tongue-flicks and biting attacks to give a single index of response strength to chemical stimuli (see Cooper & Burghardt, 1990 for further explanation). Unfortunately, only few researchers encompass all these variables in their studies. The number of tongue-flicks is typically most often reported, henceforth the main reason we chose to retain this variable from the literature. Thus, as mentioned earlier, we use a species' average tongue-flick rate (per minute) directed towards the odourless control swab for comparative purposes.

Prey tongue-flick rate

For a subset of species (69 lizards) from the assembled data set on baseline tongue-flick rates, we also searched the literature for mean number of tongue-flicks (elicited in 1 min) in response to the species' preferred prey (thus, e.g. crickets for insectivores, and plant material for herbivores). This 'prey' tongue-flick rate will be used to determine the relationship between lizard baseline and prey tongue-flick rate.

Diet and foraging mode

We searched the literature for data on diet and foraging modes of all 94 species used in this study. Each species was assigned to a diet class (insectivorous/carnivorous; herbivorous; omnivorous) and a foraging mode (active foragers; sit-and-wait foragers).

Diet

For the most part the dietary categories are as defined by Cooper & Vitt (2002). Diet categories are based on plant volume, mass or energetic content of digestive

tract contents, percentage of items found in stomachs and percentage of stomachs including items. The variables reported in the literature and thus diverse and no single variable have been measured for all or even most species. Cooper & Vitt (2002) attempted to capture the degree of squamate plant consumption by defining three categories based on the available data. The categories are necessarily arbitrary because they are based on multiple metrics and because there are no nonarbitrary criteria for the degrees of plant consumption required for omnivory and herbivory.

Insectivorous–carnivorous species consume <10% plant matter for any of the data types except occurrence, which was excluded because the latter may elevated even when the percentage volume of plant material is very low (Cooper & Vitt, 2002). Although arbitrary, the 10% criterion is useful because it excludes species that may incidentally ingest small amounts of plant matter. Omnivores are species that consume at least 10%, but <90% plant matter using any of the quantitative variables. Herbivores are species for which plant consumption is at least 90% (Cooper & Vitt, 2002).

Species in our study that were not included in Cooper & Vitt (2002) include snakes (none of which ingest plant matter except incidentally), seven omnivorous and one herbivorous lizard species. Sources of dietary data for these species are included in references in Table 1. The data are quantitative for the omnivorous *Pogona vitticeps* (20%) and the herbivorous *Phymaturus punae*, and qualitative, but convincing for the omnivorous *Correlophus ciliates*, *Eumeces schneideri*, *Gallotia caesaris*, *G. simonyi*, *Leiolepis belliana* and *Rhacodactylus leachianus*.

Foraging mode

Sit-and-wait predators remain motionless while waiting for prey to approach close enough to attack, whereas active foragers actively search for food while moving through the environment (Huey & Pianka, 1981). Some authors categorize herbivorous lizards as 'active foragers' by definition, as 'waiting for plants to pass by is an unviable evolutionary strategy' (Herrel, 2007), whereas most believe these herbivores cannot be characterized as true 'predators' as they do not hunt animal prey, and hence do not fit into the traditional active/sit-and-wait dichotomy (Cooper, 2007a). Active and sit-and-wait foraging modes as conceived by Huey & Pianka (1981) apply strictly to insectivorous–carnivorous lizards and to searches for animal prey by omnivores. We therefore exclude all herbivores from the analyses involving foraging mode.

Although the active and sit-and-wait foraging modes are widely accepted as shorthand descriptors of foraging styles, foraging behaviour of lizards is variable (Perry, 1999; Cooper *et al.*, 2001a; Perry, 2007). The two major variables used to quantify lizard foraging modes are number of movements per minute (MPM) and proportion of the time spent moving (PTM) (Pianka *et al.*,

1979). Values of both variables are higher in active than sit-and-wait foragers (Perry, 1999; Cooper, 2005b). Although continuous variation exists in both variables (Perry, 1999; Cooper, 2005a,b, 2007a; Vitt & Pianka, 2007), suggesting that the quantitative foraging variables are distributed along a spectrum, and analysis combining two variables completely separates lizard species into the two modes with no overlap (Cooper, 2005a). A rule of thumb completely separate clusters is that sit-and-wait foragers have $PTM < 0.10$ and active foragers have greater PTM . Using MPM alone, some overlap exists between modes.

We assigned species to foraging mode categories based on PTM values or clusters in Cooper (2005a) when possible, but obtained MPM and PTM values of only 17 of the 80 lizard species (see Supplementary Material). When these data were not available, we assigned foraging mode to species in families that consist entirely of active or entirely of sit-and-wait foragers (Cooper, 1994). We were thus able to assign foraging mode for all 80 species. Our main analyses were conducted using the categorical foraging modes. However, before performing these analyses, we conducted tests for the 17 species to ascertain whether MPM and PTM values truly are greater for active than sit-and-wait foragers. Indeed, active foragers moved more often (phyloANOVA on MPM , $F_{1,16} = 17.328$, $P = 0.001$) and spent more time moving (phyloANOVA on PTM , $F_{1,16} = 32.072$, $P = 0.001$) than sit-and-wait foragers. These results validate use of the dichotomous variable as a measure of foraging behaviour in this study. Because the categorical foraging modes are so clearly separated, the categorical analyses provides a clear indication of the relationship of foraging mode to baseline tongue-flick rate and the degree of increase in tongue-flick rate in response to prey chemical cues.

Statistical analyses

The Bayesian phylogenetic tree presented by Pyron *et al.* (2013) was assumed to represent the evolutionary relationships among the study species in our phylogenetic analyses. The tree was constructed on the basis of five mitochondrial and seven nuclear gene regions. We obtained our point estimate of the phylogeny by pruning Pyron's tree to include only the 94 species of this study. Data were analysed and figures drawn in R STUDIO, version 0.98.501 (R Core Team 2012; R Studio 2013). Probabilities lower than 0.05 were considered statistically significant. Prior to analyses, we randomly resolved tree polytomies by transforming all multichotomies into a series of dichotomies (function *multi2di* in package *ape*; Paradis *et al.*, 2004), as several phylogenetic R packages do not accept trees with polytomies. Tongue-flick rates were transformed (square root) to conform to the statistical expectations of the analyses (Shapiro–Wilk's test ≥ 0.95 , $P < 0.001$).

First, we used both traditional (i.e. nonphylogenetic) analyses of variance (ANOVA) to assess differences in baseline tongue-flick rate between snakes and lizards and among lizard infraorder taxa.

Second, the phylogenetic signal for baseline tongue-flick rate was calculated using Pagel's λ and Blomberg's K (function *phylosignal* in package *phytools*; Revell, 2012). Standard errors were incorporated in the analysis to account for within-species variation and measurement errors, as these are believed to affect the outcome considerably (Ives *et al.*, 2007). Phylogenetic signals for the discrete traits (i.e. diet and foraging mode) were estimated by Pagel's λ (function *fitDiscrete* in package *geiger*; Harmon *et al.*, 2008). Phylogenetic signal is recognized to be the tendency of related species to resemble one another, and Blomberg's K and Pagel's λ are two quantitative measures of this pattern (Pagel, 1999; Blomberg *et al.*, 2003). K values that are approximately or equal to 1 match the expected trait evolution under the Brownian motion (BM) and indicate an apparent phylogenetic signal; K values far under 1 and closer to zero indicate little or no phylogenetic signal associated with random trait evolution or convergence; K values >1 suggest stronger similarities among closely related species than expected under BM, and thus indicate a substantial degree of trait conservatism (Blomberg *et al.*, 2003). Pagel's λ is a scaling parameter that ranges from zero to 1. Lambda values of zero indicate no phylogenetic signal, whereas values of 1 indicate a strong phylogenetic signal, matching trait evolution, expected under BM (Pagel, 1999). As the two metrics differ in their approach to testing for a phylogenetic signal, and to allow interstudy comparisons, we use both to ensure accurate interpretation of patterns in squamates fundamental levels of chemosensory investigating using the lingual–vomeronasal system. To visualize the effect of evolutionary history on baseline tongue-flick rates, we estimated their maximum-likelihood ancestral states for all nodes and along the branches of the phylogenetic tree (function *contMap* in package *phytools*; Revell, 2013). Ancestral state estimates are solely used to visualize systematic differences at the tip and node level, and no conclusions are based on them.

Third, phylogenetic ANOVAs were used to test for differences in baseline tongue-flick rates among diets and foraging modes (function *phyloANOVA* in package *phytools*; Revell, 2012). The statistical exercise was performed twice: (i) including all 93 squamate species and (ii) solely including lizard species. These additional analyses disregarding snakes may reveal specific patterns within lizards that could be overlooked when solely focussing on the complete squamate data set. No tests were performed on the snake taxa separately, as they only comprised thirteen species, which is a too small sample size for phylogenetic comparative analyses (Blomberg *et al.*, 2003). The tuatara outgroup was excluded from all ANOVA tests.

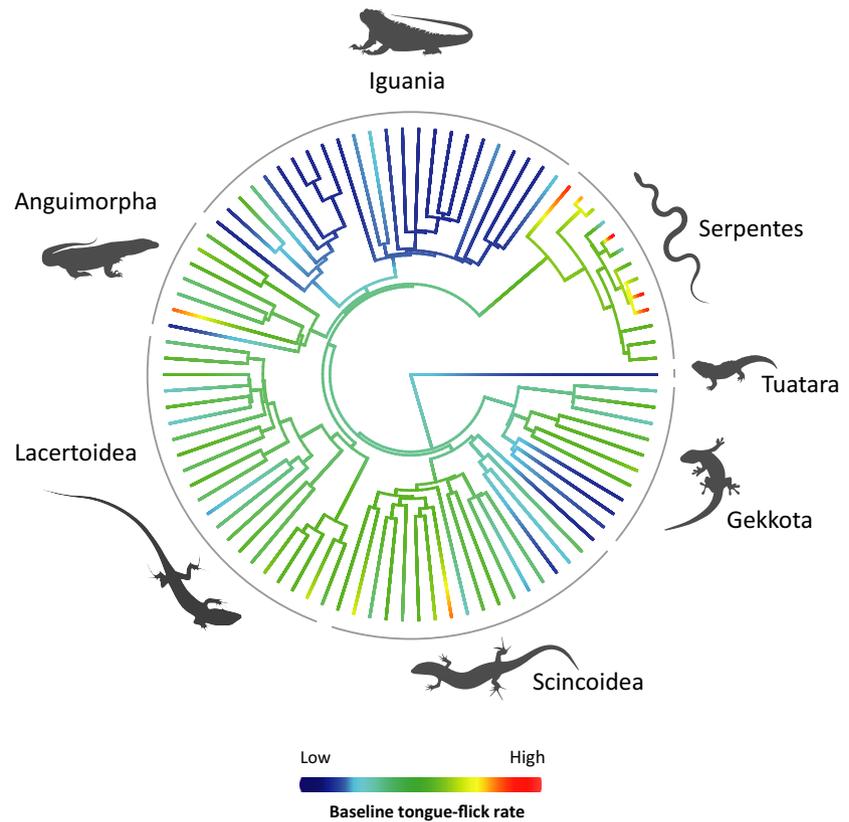


Fig. 1 Ancestral character estimation of baseline tongue-flick rate along the branches and nodes of the tree for 94 lepidosaurian species (lizards, snakes and the tuatara). The illustration succeeds in visualizing the phylogenetic conservative character of in the trait. Relationships based on the phylogeny proposed by Pyron *et al.* (2013). Illustration made in R (function *contMap* using *type = 'fan'*, in package *phytools*; Revell, 2013).

Lastly, to examine whether a species' fundamental level of chemosensory investigation is related to its level of investigation in response to food, we correlated baseline tongue-flick rates with prey tongue-flick rates, using a phylogenetic generalized least square regression (pGLS) analysis (function *pgls*; Freckleton *et al.*, 2002). Also, we examined whether diet and/or foraging mode had an effect on the difference in tongue-flick rate towards prey in comparison with their baseline rate. To do so, we firstly regressed prey tongue-flick rate against baseline rate and calculated phylogenetic residuals (function *'phyl.resid'*; Revell, 2009). Subsequently, we tested for differences in mean residual values among species with dissimilar diets and foraging modes.

Results

Baseline tongue-flick rate varied considerably among the 94 squamate species included in this study. They ranged between zero and nearly 21 tongue-flicks per minute (Fig. 1). The Eastern kingsnake *Lampropeltis getula* showed the maximum mean rate in the data set (20.68 times/min), but when focussing solely on the nonophidian squamates, the Gila monster *Heloderma suspectum* revealed the highest rate (18.20).

A traditional (nonphylogenetic) analysis of variance, established a strong significant difference in average baseline tongue-flick rate between snakes and lizards

(ANOVA; $F_{1,91} = 27.404$, $P < 0.001$). The average baseline tongue-flick rate of snakes (mean \pm SE: 12.18 ± 2.11) was much greater than that of lizards (3.64 ± 0.45), nearly three times greater (Fig. 2). The traditional

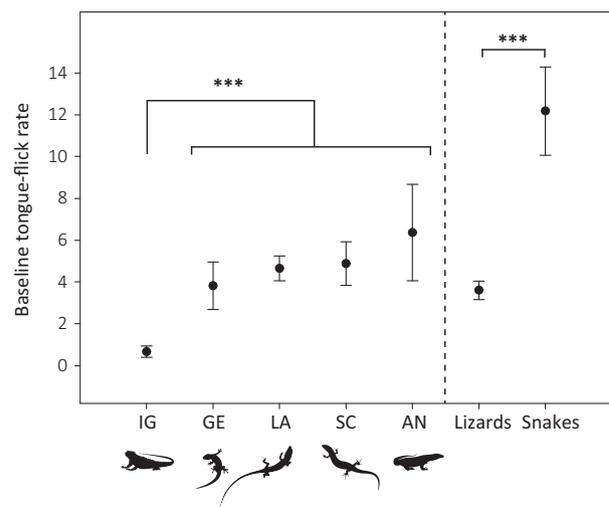


Fig. 2 Mean baseline tongue-flick rate (number of tongue-flicks in 60 s) for the different lizard infraorder, and for snakes and lizards separately. Error bars represent standard error of mean. IG, Iguania; GE, Gekkota; LA, Lacertoidea; SC, Scincoidea; AN, Anguimorpha. *** indicate level of statistical significance (i.e. $P < 0.001$).

Table 2 Descriptive statistics (mean, SEs, sample sizes) of baseline tongue-flick rates in the squamate species under study, where the tuatara outgroup is, thus, not included. Values are shown for all squamates, and for lizards and snakes separately.

	Squamates						Lizards						Snakes					
	Total	AC	SW	I-C	O	H	Total	AC	SW	I-C	O	H	Total	AC	SW	I-C	O	H
Mean	4.84	7.06	1.72	5.04	3.71	4.50	3.64	5.61	0.72	3.49	3.71	4.50	12.18	12.33	11.7	12.18	-	-
SE	0.57	0.76	0.63	0.67	0.80	2.73	0.45	0.55	0.25	0.50	0.80	2.73	2.11	2.69	2.66	2.11	-	-
<i>n</i>	93	52	33	73	14	6	80	42	30	60	14	6	13	10	3	13	-	-

AC, active foraging; SW, sit-and-wait foraging; I-C, insectivorous–carnivorous; O, omnivorous; H, herbivorous.

statistics established highly significant differences among some major infraorders of lizards (ANOVA; $F_{4,75} = 11.900$, $P < 0.001$), where Iguania (0.67 ± 0.27) exhibited a lower average baseline tongue-flick rate than Anguimorpha (6.36 ± 2.31 ; $P < 0.001$), Scincoidea (4.68 ± 1.04 ; $P < 0.001$), Lacertoidea (4.65 ± 0.59 ; $P < 0.001$) and Gekkota (3.82 ± 1.13 ; $P = 0.010$). Descriptive statistics of the baseline tongue-flick rates are provided in Table 2.

In general, all variables tested in this study showed strong phylogenetic signals, which were all statistically significant ($P < 0.001$). Baseline tongue-flick rate revealed a Pagel's λ of 0.811 and a Blomberg's K of 1.453, which implies that neighbouring taxa tend to resemble each other more – in their level of chemosensory investigation – than expected under Brownian motion of evolution (Fig. 3). The categorical variables diet and foraging mode exhibited Pagel's λ values of 0.966 and 0.999 respectively.

In an analysis accounting for the phylogenetic relationships, we found no effect of diet on baseline tongue-flick rate in squamates (phylANOVA, $F_{2,91} = 0.048$, $P = 0.969$). However, the overall effect of foraging mode was significant (phylANOVA, $F_{1,83} = 53.978$, $P = 0.001$), with active foragers exhibiting a higher tongue-flick rate than sit-and-wait predators (AC 7.06 ± 0.76 vs. SW 1.72 ± 0.63 ; $P = 0.001$). Comparable results arose when solely focussing on the lizard species from the data set; no effect of diet on tongue-flick rates (phylANOVA, $F_{2,77} = 0.433$, $P = 0.710$), but a significant effect of foraging mode (phylANOVA, $F_{1,70} = 88.749$, $P = 0.001$). The same was true when regressing (pGLS) baseline tongue-flick rate over MPM and PTM scores: species with a high baseline tongue-flick rate moved often (slope = 0.664, $P = 0.004$) and spent lots of time moving (slope = 0.681, $P < 0.001$; Supplementary Material).

Lastly, our results revealed that on average, a species' tongue-flick rate in response to prey items is approximately 1.6 times higher than its baseline tongue-flick rate. Moreover, baseline tongue-flick rate showed a highly positive relationship with prey tongue-flick rate ($r^2 = 0.462$, slope = 1.649, $P < 0.001$; Fig. 4). Whereas diet did not affect the difference in increase in tongue-flick rate (phylANOVA with residual values as

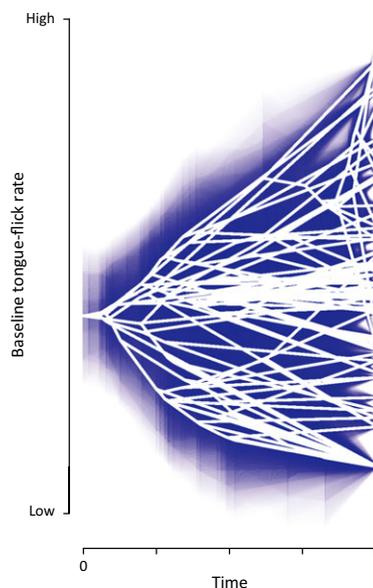


Fig. 3 A projection of the squamate phylogeny into a space defined by baseline tongue-flick rate (on *y*-axis) and time since the root (on *x*-axis). The vertical position of nodes and branches are computed via ancestral character estimation using likelihood. Uncertainty is shown via increasing transparency of the plotted blue lines around the points. Illustration made in R (function *fancyTree* using *type = 'phenogram95'*, in *phytools* package; Revell, 2013).

continuous variable, $F_{2,67} = 0.08$, $P = 0.842$), foraging mode did (phylANOVA, $F_{2,67} = 15.14$, $P = 0.001$). Thus, species with an active mode of foraging exhibited a higher increase in tongue-flick rate in contact with prey than sit-and-wait foragers did.

Discussion

Based on our data for nearly 100 squamate species, baseline rates of tongue-flicking are strongly related to phylogenetic groups, that is tend to be stable within such groups. However, this phylogenetic influence is a consequence of the stability of foraging modes within large taxa. This finding is similar to the phylogenetic clustering of prey chemical discrimination as measured

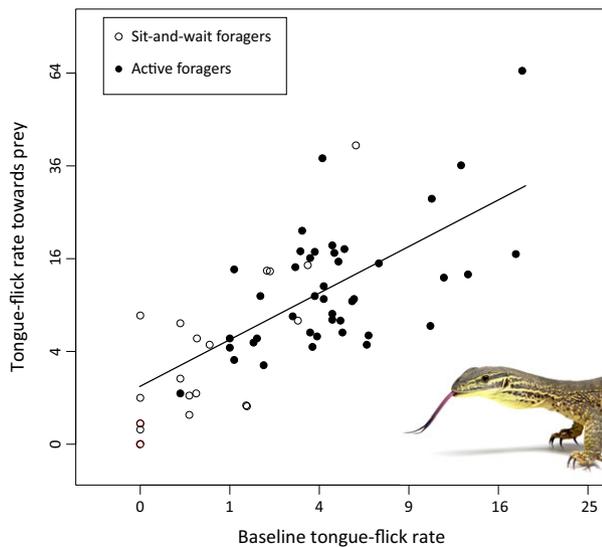


Fig. 4 Graph illustrating the interspecific relationship between baseline tongue-flick rate and tongue-flick rate elicited by prey, among 69 lizard species. Tongue-flick rate is the number of tongue-flicks in 60 s. A phylogenetic generalized least square regression analysis computed the solid regression line (function 'ppls'; Freckleton *et al.*, 2002). Note the square rooted scale on both axes.

by the ratio of baseline tongue-flick rate to tongue-flick rate and attack behaviour in response to prey chemical stimuli by diverse lizards (Cooper, 1995b, 1997). When the influence of foraging mode is taken into account, baseline tongue-flick rate is unrelated to the dietary categories we studied and is not affected by the degree of phylogenetic relationship. The latter finding is presumably a consequence of concordant shifts in baseline tongue-flick rate with shifts in foraging mode within phylogenetic groups, as occurs for prey chemical discrimination when foraging mode changes from its ancestral state (Cooper, 1994, 1997).

The above findings apply to traditionally defined lizards, which exclude snakes even though snakes are taxonomically speaking a subclade of lizards. We also found that snakes have higher baseline tongue-flick rates than lizards. This may be a consequence of increased reliance on chemosensory behaviour in ancestral snakes that is reflected in the more highly developed vomeronasal organ (Halpern, 1992), more elongated and more deeply forked tongues (Halpern, 1992; Schwenk, 1993, 1995; Cooper, 1995a, 1996), and more complex tongue-flicking movements than lizards (Gove, 1979), the latter permitting better chemical sampling from both air and substrates. Having such highly refined lingual–vomeronasal systems, snakes exhibit prey chemical discrimination regardless of foraging mode (Burghardt, 1967, 1970; Chiszar *et al.*, 1978, 1981; Cooper, 1991; Cooper *et al.*, 2000a). However, this result may also be an artefact of our data set

comprising solely 13 snake species. A detailed investigation of baseline tongue-flick rate by snakes in relation to foraging mode could be informative.

Tongue-flick rates vary widely among species and context, even within single lizard families (Cooper, 1994, 1995b, 1997; Verwajen & Van Damme, 2007). While moving through their environments, active foragers tongue-flick to gather chemical cues to the location and identity of prey, and to detect pheromones and the presence of predators (Burghardt, 1970; Mason, 1992; Cooper, 2007a). When they detect such chemical cues, they increase their tongue-flick rates to better assess the cues (e.g. pheromones: Cooper & Vitt, 1986, 1987; predator scent: Thoen *et al.*, 1986; Cooper, 1990a) and, in the case of prey or plant food scents, may bite the source even if it does not otherwise resemble food (Burghardt, 1967; Cooper & Burghardt, 1990; Cooper, 1998a). In contrast, ambush, or sit-and-wait, foragers have lower baseline tongue-flick rates than active foragers, and do not increase their tongue-flick rates significantly in response to food scent, although they do respond to both pheromones (Duvall, 1979) and predator stimuli (Downes & Shine, 1998).

As we strictly accounted for phylogenetic relatedness in our comparative statistics, differences between foraging modes cannot be assigned to shared ancestry. Foraging mode is a highly phylogenetically conservative trait among squamates, as indicated by the Pagel's λ of nearly 1. Our traditional statistics reveal that Iguania has a lower baseline tongue-flick rate than Scleroglossa. Although almost all iguanian families are ambush foragers (Perry, 1999; Cooper *et al.*, 2001a), foraging mode is more variable among scleroglossans (Perry, 2007; Reilly *et al.*, 2007). In Gekkota, for instance, gekkonids appear to be ambush foragers with some possible exceptions (Arnold, 1984; Werner *et al.*, 1997; Bauer, 2007), whereas many eublepharid geckos forage actively (Cooper, 1995b). Among major families of autarchoglossans, only the Cordylidae consists entirely of ambush foragers (Cooper *et al.*, 1997). The vast majority of species in the other autarchoglossan families are active foragers, but a few ambush foragers occur in Lacertidae and Scincidae (Cooper, 1994; Perry, 1999). Our data show that those scleroglossans that are ambush foragers also exhibit low baseline tongue-flick rates. As a consequence, the lower baseline tongue-flick rate of scleroglossan ambush foragers indicate that foraging mode, rather than phylogenetic relatedness, is responsible for a species' level of chemosensory investigation. Essentially, these results suggest foraging mode as a significant actor driving convergent evolution of similar levels of investment by tongue-flicking in squamates.

These shifts in chemosensory investigation are part of a larger trend in lizards for aspects of feeding ecology and behaviour that has had a profound impact on the

evolution of lizard extending over 100 million years and involving changes in methods of prey capture, morphological and physiological adaptations to enhance foraging skills in relation to methods of searching for and capturing prey, and to diet (Cooper, 1995b, 1997; Vitt *et al.*, 2003; Vitt & Pianka, 2005).

The degree to which tongue-flick rates increase in response to prey and predator scent and to pheromones varies greatly among taxa and types of stimuli. This increase and the ratio of tongue-flick rate when responding to prey chemicals to baseline tongue-flick rate are important clues to the chemosensory abilities of squamates, and permit experimental examination of abilities to discriminate among types of stimuli. Baseline tongue-flick rates, those in the absence of stimuli that may indicate the presence of risks and benefits, do not directly reveal anything about discriminatory capacities within species. Nevertheless, they provide an important window into the interspecific evolution of foraging behaviour, as indicated by the higher baseline rates of active foragers to search for cues as they move than ambush foragers, which are usually at rest when they visually detect approaching prey. For the latter, which maintain some degree of crypsis simply by remaining immobile (Vitt & Congdon, 1978; Vitt & Price, 1982), the movement of tongue-flicking is typically suppressed while they are at rest at ambush posts. Tongue-flicking then might reveal the lizard to predators or even their prey (Cooper, 1994, 1995b). Ambush foragers tongue-flick substrates most frequently when they first arrive at new site (Simon *et al.*, 1981; Cooper *et al.*, 1994a), but do not use chemical cues to select suitable ambush posts (Cooper, 2003a; Cooper & Whiting, 2003). Therefore, the major reason for the difference in baseline tongue-flick rate between active and ambush foragers is that active foragers search for prey using chemical cues sampled while they move and when evaluating a prey item at close range. In contrast, ambush foragers move infrequently (Perry, 1999; Cooper, 2005a, 2007a) and largely restrict tongue-flicking to a few seconds after arriving at a new position before resuming immobility.

Given the difference in baseline tongue-flick rates alone, one may predict foraging mode from the baseline tongue-flick rate of a particular species. Given the positive relationship between baseline tongue-flick rate and tongue-flick rate in response to prey chemical cues, baseline rates may also be used to predict the presence or absence of prey chemical discrimination, and even its apparent strength. Because our analyses were based on the categorical foraging mode variable, we encourage future research correlating tongue-flick variables to MPM and PTM using a larger data set.

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Supporting information

Additional Supporting Information may be found online in the supporting information tab for this article: **Table S1** Tongue-flick rate and foraging behaviour of 17 lizard species, assembled from the literature. **Figure S1** Graphs showing the relationship between (baseline and prey) tongue-flick rate, and two numerical parameters describing foraging behaviour (MPM, PTM) for active and sit-and-wait foragers.

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