

**Research article**

<https://doi.org/10.26496/bjz.2019.31>

## **Evolution of animal chemical communication: Insights from non-model species and phylogenetic comparative methods**

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**Abstract.** Chemical communication is probably the oldest, most ubiquitous form of information exchange in the natural world, spanning all three domains of life. While excellent sociobiological and behavioral ecological research has been conducted on the form and function of chemical signals in animals, we still know remarkably little on their evolution. Besides, much of our understanding of chemical signal diversity is restricted to insects, since studies on chemical communication in vertebrates are relatively scarce. In this review, I introduce the key concepts of animal communication and expand on the past, present, and future of research in chemical communication. When doing so, I highlight the current gaps in our knowledge on the evolution of the chemical communication system in animals, whilst emphasizing the heavy research bias towards lepidopterans. Here, I detail the benefits of using phylogenetic comparative methods to identify the motors and brakes that guide the evolution of chemical signals and chemical sensory systems. Moreover, I point out that focusing on non-model species in chemical ecology, specifically lizards, can provide valuable insights into how vertebrate chemical signals evolve, and how biological systems responsible for sending and receiving signals co-evolve with signal design. Lastly, I present a case study on lacertid lizards, demonstrating the possibilities of the phylogenetic comparative approach and the use of non-model species to study the evolution of animal chemical communication systems.

**Keywords.** Chemical signals, lizards, phylogenetic comparative methods, pheromones.

BAECKENS S. (2019). Evolution of animal chemical communication: Insights from non-model species and phylogenetic comparative methods. *Belgian Journal of Zoology* 149 (1): 63–93.  
<https://doi.org/10.26496/bjz.2019.31>

### **Animal communication**

From the time of DARWIN (1859, 1871), through the classic work of TINBERGEN (1953) and VON FRISCH (1967), to the extant greats such as WILSON (1965), animal communication has been a subject of profound interest to biologists. Whilst the study of animal signals began in earnest with Darwin's publication entitled *The Expression of the Emotions in Man and Animals* (DARWIN 1872), the phenomenon of animal communication has not gone unnoticed by early naturalists such as Aristotle and Pliny the Elder (reviewed by FÖGEN 2014). Undoubtedly, it is the immense variety of birdsongs, frog calls, coral reef fish colours and extravagant displays of peacock spiders that have lured the attention of many scientists and laymen alike. Yet, despite decades of excellent and thorough research, genuine mystery still surrounds the evolution of animal signals and the origins of signal diversity.

## Evolution of animal communication

A *signal* can be defined as any structure that alters the behaviour or physiological status of other organisms, which evolved because of that effect, and which is effective because the receiver's response has also evolved, and whereby typically (but not always) both sender and receiver benefit from the information exchange (MAYNARD-SMITH & HARPER 2003). According to the principles of Darwinian evolution, signals are selected for in such a way that they maximize the sender's fitness benefits, and this through their effect on the behaviour or physiology of receivers. Simultaneously, receivers use the same signals to try to increase their own fitness (JOHNSTONE 2000). *Communication* is stated as the act of sending and receiving signals.

Studying signal evolution, it is useful to make the distinction between the *content* of a signal, and its *design* (GUILFORD & DAWKINS 1991, 1993). The content is what is being communicated, or the information on which the receiver makes a decision. For example, animals may transmit (true or false) information to others about mate quality, ability to fight or escape predators, reproductive and social status, and access to resources (BRADBURY & VEHCAMP 1998). The design (or physical structure) of a signal allows the information to be effectively picked up and processed by the receiving animal (GUILFORD & DAWKINS 1993). ARNOLD's (1983) adaptation paradigm on the link between variation in morphology, performance and fitness can easily be applied to signals, whereby design is equivalent to morphology and efficacy is equivalent to performance. In his seminal paper, Arnold suggested splitting the adaptation process into two components: a performance and a fitness gradient. Whereas the performance gradient measures the effect of variation in design on variation in performance, the fitness gradient measures the effect of variation in performance on fitness. Thus, in order to explain the origin of the diversity in animal signal design, it is important to firstly understand the 'performance gradient' by studying the relationship between variation in signal design and variation in signal efficacy, since those design features (with a genetic basis) that increase the efficacy of a signal component are expected to be selected upon. Still, most research on the evolution of animal communication has focused on signal content, while the functional design of signals has received far less attention (but see ESPMARK *et al.* 2000 and APPS *et al.* 2015).

Signal efficacy is affected by two main factors: (1) the environmental conditions under which the signal is emitted, transmitted and detected, and (2) the response properties of the sensory system of the receiver (ENDLER & BASOLO 1998). The first step after signal production is the transmission of the signal through the medium, which can be air, water, vegetation or ground. Selection may favour signals that experience less attenuation, blocking, absorption, reflection, refraction and other distorting effects of the transmission medium. Signals are expected to evolve in order to minimize the effects of background noise and interfering signals from other species (ALBERTS 1992; ENDLER 1993; HUGHES *et al.* 2012; Fig. 1). Selection may also work indirectly to minimize environmental effects by favouring signalling behaviour during times and places at which detrimental factors are minimized. Once the signal reaches the receiver, it has to be picked up and processed. The sensitivity of the receptor system, together with the receiver's receptor condition (physiological state) and attentive status may influence how signals are processed, and whether and how the receiver will act upon a signal (ENDLER 1992, 1993). The receptor design is expected to evolve in order to 'optimally' detect and analyse the emitted signals of the sender (MAYNARD-SMITH & HARPER 2003).

When considering communication as the sole driving force of the evolution of animals' emitting and sensory systems, we can expect strong correlated evolution between the signal and receptor design of animals. This is, however, not always the case as other forces are likely to influence the evolution of either side of the communication channel as well, and not necessarily in the same direction. This might bias or constrain the co-evolution of an 'optimized' signal-receptor system. For example, many animals use their sensory system, not only in the context of communication, but also for spatial orientation and to locate prey and predators (LEMASTER & MASON 2001; SCHNITZLER *et al.* 2003). It seems unlikely that a

single type of sensory system can optimize all the different functions. Rather, a particular receptor design is expected to represent a compromise, reflecting the relative ecological relevance of each function. Another potential selective force influencing signal design diversity that might disrupt the evolution of an ‘optimized’ signal-receptor system, is *eavesdropping*, which is the interception (and use of information) of signals intended for another individual (PEAKE 2005; Fig. 1). Eavesdroppers or ‘emitter exploiters’ are typically (but not exclusively) heterospecifics, such as predators or signal-homing parasites, that acquire information about others by actively heeding to their signalling interactions, usually to the cost of the signaller, but also to the receiver (HUGHES *et al.* 2012). While eavesdropping animals only benefit from strategies maximizing signal interception, selection favours the design of signals and receptors that minimize the signal reception by exploiters (ENDLER 1993). Therefore, when studying signal evolution, it is necessary to integrate the complete communication system, from the emitting to the receiving end, as this enables researchers to identify the different selective forces (and their respective importance) at play.

Thus, in order to explain the variation in animal signals, scholars should shed light on the ecological drivers and constraints that impact the evolution of animal signal design. This can be achieved (1) by examining the functional design of animal signals and the relationship between signal design and signalling environment, and (2) by assessing the diversity in receptor design, and the ecological factors influencing its variation.

Natural selection favours the design of signals that work efficiently (ENDLER 1992; BOUGHMAN 2002), whereas sexual selection favours signals that convey a maximum amount of information and that are good predictors of offspring fitness (POMIANKOWSKI 1988; GRAFEN 1990; STEIGER *et al.* 2011; CHEN *et al.* 2012; CLUTTON-BROCK & HUCHARD 2013). Whilst animals only benefit from efficiently conveying information on their offspring fitness, natural and sexual selective forces do not necessarily drive the design of signals in the same direction. For example, a carotenoid-based orange colour may indicate

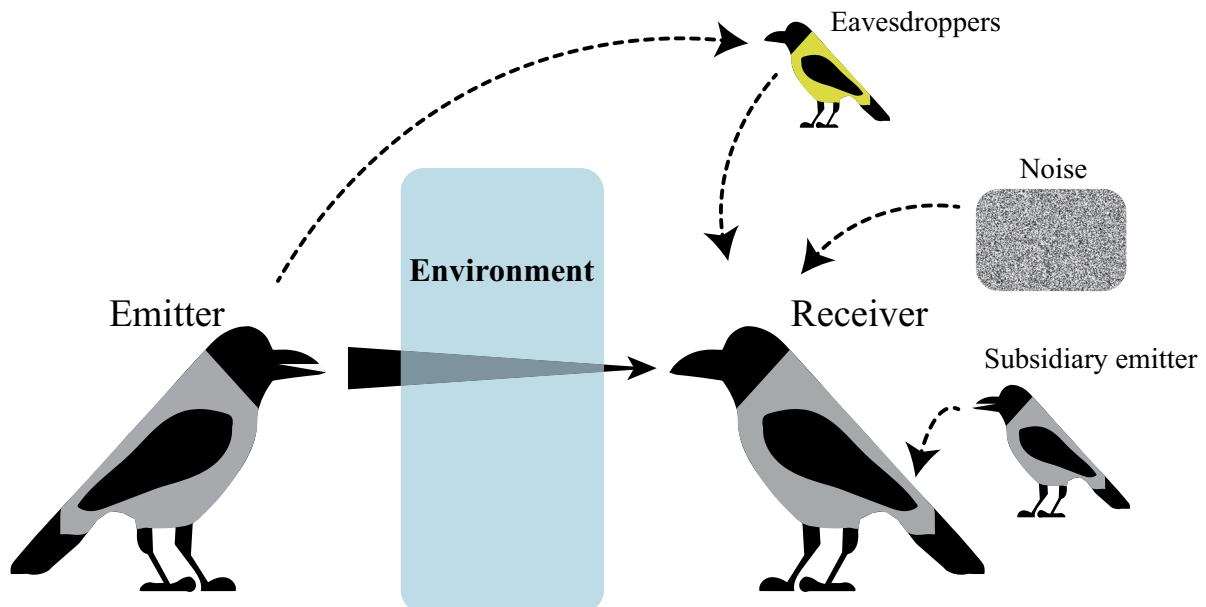


Fig. 1 – Schematic illustration of the components that affect the evolution of animal signal design. Efficacy-based selection favours those signalling features that maximize signal efficacy in a certain environment, that is: features that minimize environmental absorption, distortion, and interference, and minimize the effects of background noise, eavesdroppers, and signals from others (after ENDLER 1993).

feeding success in a bird, but visual environmental conditions and spectral sensitivity may favour the use of the colour blue (ENDLER 1992).

Of course, not all components of signals are necessarily adaptive, as traits can be (phylo)genetically constrained or simply spandrels of San Marco (GOULD & LEWONTIN 1979). Evidently, it is the interplay between selective and stochastic processes that shapes signal design divergence.

### Chemical communication

Animals exploit a wide variety of modalities to communicate with one another, with the visual, auditory, and chemical communication systems being the most common modes of information exchange in the animal kingdom. The visually-oriented birds of paradise (Paradisaeidae), for instance, exhibit extraordinary ornamental plumage and sophisticated, often bizarre, display behaviours to signal their quality to conspecifics (SCHOLLES 2008), and the highly venomous coral snakes (*Micrurus fulvius*) use their skin colouration as a warning signal towards predators (KIKUCHI & PFENNING 2010). Some animals rely on their auditory system; grasshoppers and frogs produce complex calls and croaks to advertise their superiority (RYAN & RAND 1995; RONACHER *et al.* 2008), wolves howl to signal territory (HARRINGTON & MECH 1979), and rattlesnakes rattle their tail to signal danger (SWAISGOOD *et al.* 1999). Many insects typically use their chemical communication system, with ants laying pheromone trails to guide nest mates to resources (WILSON 1965; REGNIER & WILSON 1971), and male moths exploiting chemical signals to attract conspecific females (RAINA *et al.* 1989). A small number of animals utilize seismic (vibratory) signals to search for prey (e.g., golden mole, *Eremitalpa granti*; MASON & NARINS 2002), to indicate threat (e.g., elephants, Elephantidae; O'CONNEL-RODWELL 2007) or during courtship (e.g., jumping spiders, Salticidae; ELIAS *et al.* 2003). While it is not unusual that a species exploits more than one signalling modality (multimodal communication; ROWE & GUILFORD 1996; PARTAN & MARLER 1999) in order to enhance the efficacy of a message (redundant-message hypothesis; JOHNSTONE 2000; ROWE 1999) or to convey several different messages (multiple-message hypothesis; HEBETS & PAPAJ 2005), the majority of animal groups focus on a subset of modalities.

Most theoretical and empirical investigations of the evolution of animal signals have focused on visual and auditory communication. By contrast, evolutionary studies of chemical signals are less common, perhaps reflecting our own sensory biases or the increased technical complexity associated with analysing chemical signals (SYMONDS & ELGAR 2008). Some authors have even argued that chemical communication is “the last frontier in the study of animal behaviour” (MOULTON 1968; HUNT *et al.* 2012). With the recent improvements in methods of chemical analysis (SCHULZ 2005), it is becoming increasingly clear that chemical signals are at play in multiple contexts in a wide variety of organisms, and that the diversity in chemical signal design is vast (MÜLLER-SCHWARZE & SILVERSTEIN 1980; MÜLLER-SCHWARZE 2006; WELDON *et al.* 2008; WYATT 2010).

Chemical signals have several advantages over signals in other modalities. They work in darkness, around obstacles, and can be still operative in the absence of the signaller. Chemical signals can also cover large distances or last for long periods of time, ranging from days to months (MACDONALD *et al.* 1990; MÜLLER-SCHWARZE 2006). Chemical communication is probably the oldest and, possibly, the most ubiquitous form of information exchange in the natural world (WYATT 2014), and has been reported in bacteria (TAGA & BASSLER 2003), fungi (BÖLKER & KAHMANN 1993), plants (BALUŠKA 2009), and almost all animal groups: insects (WILSON 1965; REGNIER & LAW 1968), molluscs (SUSSWEIN & NAGLE 2004), crustaceans (BREITHAUP & THIEL 2011), spiders (TRABALON 2012), fish (SOLOMON 1977), amphibians (WOODLEY 2010), reptiles (MASON & PARKER 2010), birds (CARO *et al.* 2015), and mammals (EISENBERG & KLEIMAN 1972), including humans (COMFORT 1971). In the words of EISNER & BERENBAUM (2002): “The vocabulary of living things is overwhelmingly chemical in nature”.

The origin of research on chemical communication dates to the second half of the 19<sup>th</sup> century, when chemical ecologists, such as the Belgian Léo Errera and German Ernst Stahl, discovered that plant secondary metabolites play an important role in plant-insect interactions and suggested that plant chemical diversity evolved under the pressure of herbivory (FRAENKEL 1959; HARTMANN 2008). During the late 1950s, evolutionary entomologists dominated the field of chemical ecology, with E.O. Wilson taking the lead, concentrating on the role of pheromones in the social behaviour of insects (e.g., BARTH 1965; WILSON 1965). Chemical ecology became a well-established discipline by the end of the second millennium, with the rise of journals such as *Journal of Chemical Ecology*, *Chemoecology*, *Chemical Communications* and *Chemical Senses*. Currently, the proper analytical tools for studying natural products chemistry are available and affordable, permitting comprehensive taxon-wide research on the evolution of chemical signal diversity and design. Some might say that the sudden expansion of knowledge on the evolutionary biology of chemical communication is a direct consequence of the recent breakthroughs by molecular biologists (EISNER & BERENBAUM 2002).

### Definitions

Research on chemical signals brings together scientists from various fields with many different areas of expertise, from behavioural ecologists, through organic chemists, to neuroscientists, all bringing their own gobbledygook and concepts. Hence it is important to define a few terms that are often applied in the context of chemical communication at the outset. Here, I follow the classifications proposed by WYATT (2014).

A chemical involved in the chemical interaction between organisms is called a *semiochemical*. Some of the semiochemicals emitted by animals are *chemical cues* that are used as a guide to future action, but have not evolved for this purpose; only the receiver's response is evolved. Carbon dioxide in exhaled breath, for example, can be exploited as a cue by blood-sucking mosquitoes as a way of finding a host (GILLIES 1980). Semiochemicals that have evolved as signals for within-species communication are considered *pheromones* when these are individual molecules causing a specific reaction to the receiver, or *signature mixtures* when these are variable chemical mixtures containing a subset of the molecules in an animal's chemical profile. Semiochemicals acting between individuals from different species are called *allelochemicals* and can be further divided depending on the costs and benefits to the emitter and the receiver: *allomones* when the emitter benefits, but not the receiver; *kairomones* when the receiver benefits, but not the emitter; *synomones* when both the emitter and the receiver benefit.

### Emitting system

Animal chemical signals (and cues) come from a bewildering variety of sources. Metabolites originating from *excretions*, such as urine and faeces, provide the energetically least expensive semiochemicals, and are used by many animals (LUCAS 1944). Male-male aggression in mice, for example, is triggered by a urinary mixture of 2-sec-butyl-4,5-dihydrothiazole and 3,4-hydro-exo-brevicommin (HARVEY *et al.* 1989), and faeces of the red fox (*Vulpes vulpes*) contain trimethylthiazoline, which alarms prey species (VERNET-MAURY 1980). However, most chemically-oriented animals have evolved a variety of specialised exocrine glands that produce *secretions*, which in turn carry chemical signals. The exocrine apparatus of social insects is well developed, with an impressive total of 105 different secretion glands, which clearly reflects the abundant use and importance of pheromonal communication in social insects (BILLEN 2006). The diversity of secretion glands in vertebrates is vast too, with each group having its own specialized gland system (MACDONALD *et al.* 1990; MÜLLER-SCHWARZE 2006). For example, most fish – not all – are equipped with caudal glands at the tail base (WEITZMAN & FINK 1985), whereas many amphibians have three different types of glands in their cloacal area: cloacal, pelvic, and abdominal glands (KIKUYAMA *et al.* 1995). The most developed gland in birds is the uropygial gland, which primarily serves to waterproof their plumage, but also plays a role in intraspecific communication and as repellent for intruders (GABIROT *et al.* 2016). Turtles and tortoises possess Rathke's glands, although

their role in producing chemical signals is still little explored (but see BRANN & FADOOL 2006; IBÁÑEZ *et al.* 2014). Most snakes have paired scent glands that open into the cloaca, and some (e.g., *Natrix* and *Macropisthodon*) have ‘nucho-dorsal’ glands under the skin of the dorsal neck area (MADISON 1977), whereas many lizards are equipped with epidermal glands in their cloacal region (MAYERL *et al.* 2015). The most diverse collection of glands among vertebrates can probably be found in mammals, which encompasses ventral, tarsal, subauricular, metatarsal and axillary glands (MYKYTOWICZ & GOODRICH 1974; EBLING 1988).

### Chemical compounds

Chemical signals and cues may involve a wide variety of molecules, from volatiles to non-volatiles, encompassing all major chemical classes such as proteins, peptides, hydrocarbons, steroids, carboxylic acids, aldehydes, ketones, esters, phenols and ketals (BLOMQUEST & BAGNÈRES 2010; APPS *et al.* 2015; WYATT 2015). A signal may consist of a single type of molecule, for instance cis-9-tetradecen-1-ol acetate, which is identified as the sex pheromone in the southern armyworm moth *Prodenia eridania* (JACOBSON *et al.* 1970), or cis-7,8-epoxy-2-methyloctadecane, which is a sex pheromone emitted by the gypsy moth *Porthetria dispar* (BIERL *et al.* 1970). However, many, probably most, chemical signals are not single compounds, but consist of a species-specific combination of molecules, sometimes even in a precise ratio. The combination *is* the signal. For example, the female sex pheromone of the Canadian red-sided garter snakes (*Thamnophis sirtalis parietalis*) consists of a homologous series of long-chain saturated and Z-monounsaturated methyl ketones (MASON *et al.* 1989), and the axolotl *Ambystoma mexicanum* emits multiple glycosylated sodefrin precursor-like factor proteins during courtship (MAEX *et al.* 2016). The sex pheromone of the oak leaf roller (*Archips semiferanus*) is identified as a specific blend (67:33 ratio) of trans-11- and cis-11-tetradecenyl acetates (MILLER *et al.* 1976).

### Receiving system

From the slender antennae of the silk moth to the sizable nose of the saiga antelope, the sensory systems with which animals pick up chemical cues and signals from the environment vary dramatically among species. Yet, at the cellular level, chemosensation in all animals involves the same sequence of actions: (1) chemosensory receptors are exposed to the outside world in the membrane of chemosensory cells; (2) the arrival of a semiochemical, (3) which is converted into a signal by binding to a chemosensory receptor protein; (4) and finally, the signal is projected to a specific region in the brain via axons of the receptor neurons (HILDEBRAND & SHEPHERD 1997; KRIEGER & BREER 1999; KAUPP 2010).

The chief chemosensory systems (or organs) of terrestrial vertebrates are the *main olfactory system* and *accessory olfactory system* or *vomerinasal system* (ALLISON 1952; EISTHEN 1997; MÜLLER-SCHWARZE 2006). Both systems are located in the nasal region, and, although structurally distinct, their general organization is very similar: both possess specialized sensory epithelia for chemical uptake and neurone bundles for information transduction, and both project information to a specific area (bulb) in the brain for information processing (MORALES & BACIGALUPO 1996). The main olfactory epithelium of amniotes is located in the nasal cavity, and is solely capable of detecting airborne volatile compounds; an action referred to as *olfaction* (or ‘smelling’ by lay). The vomerinasal organ, first described by Ludvig Jacobson in 1811 (TROTIER & DØVING 1998), occurs in amphibians, mammals, reptiles, and embryonic birds. In snakes and lizards (Squamata) the vomerinasal organ is often well developed and capable of detecting volatile and non-volatile chemicals (SCHWENK 1993, 1995; COOPER 1995a, 1997a), sometimes referred to as *vomerolfaction* (COOPER & BURGHARDT 1990). Squamate vomerolfaction is mediated by *tongue-flicking* behaviour in which the tongue samples substrate-bound or air-born chemicals in the environment and delivers them to the vomerinasal organs above the roof of the mouth (FILORAMO & SCHWENK 2009). Unlike the main olfactory system, the vomerinasal system of squamates depends on the active, or voluntary, stimulation of the chemosensory organs by chemicals collected by the tongue (DAGHFOUS *et al.* 2012). Functionally, the main olfactory and vomerinasal system have different

roles in the execution of several species-typical behaviours (HALPERN 1987). Excellent reviews and monographs describe and discuss the anatomy, function and evolution of chemoreception systems in invertebrate and vertebrates in great detail (see e.g., BOSSERT & WILSON 1963; EISENBERG & KLEIMAN 1972; KEVERNE 1999; KRIEGER & BREER 1999; EISTHEN & WYATT 2006; KAUPP 2010).

## Studying the evolution of chemical communication

### Research approach

Explaining the baffling diversity in animal phenotypes is one of the major challenges of evolutionary biology. While experimental evolutionary studies can explain the process of trait divergence on a small (intraspecific) scale (e.g., LAPIEDRA *et al.* 2018; BARRETT *et al.* 2019), only comparative biology may elucidate trait evolution on a macroevolutionary scale (CLUTTON-BROCK & HARVEY 1979; LOSOS & MILES 1994). In the absence of detailed time series, in which evolution of a trait can be traced directly through time, comparing current patterns of variation among species provides the best possible clues about a trait's evolutionary history, and the factors that may have driven or constrained its evolution (HARVEY & PAGEL 1991). For the last thirty years, *comparative biology* has become widely appreciated and acknowledged as fundamental in studying evolution and adaption (HARVEY & PURVIS 1991; GARLAND *et al.* 1992; MILES 1993; LOSOS & MILES 1994; SIH & GLEESON 1995). The philosophy of comparative biology, however, is not novel, and can be easily traced back to Darwin and his famed 'Tree of Life' sketch (BARRETT *et al.* 1987). This particular domain in science lies particularly strongly at the heart of some:

*“The old-guard Feyeraabend-esque naysayers who cling to the desperate belief that science is just the province of who can shout loudest, and most effectively corrupt and coerce others, all in pursuit of their favourite myths, should take stock of the field of comparative biology: combative, and yes, often petty and self-serving, it has in these past 25 years or so produced a steady, even if sometimes stumbling, triumph of the scientific method applied to this particular outpost of the field of evolution.”*

— MARK PAGEL (2014)

The *comparative method* is basically an analytical approach that studies species in a historical framework with the aim to elucidate the mechanism at the origin of their diversity. Species are typically the 'unit' of study in comparative research, but populations can be the focus as well (e.g., DRIESSENS *et al.* 2017). The main goal of comparative research is to investigate the adaptive significance of organismal traits by linking ecological variation with phenotypic trait variation. When comparative analyses indicate that species that inhabit similar environments resemble each other in a certain phenotypic trait, it is plausible to assume that this particular trait is an adaption to the environment: a product of evolution by natural selection. Of course, convergent evolution is not the only reason why species can have a similar appearance; common descent can lead to similarity between species' phenotypes too (CHEVERUD *et al.* 1985; HUELSENBECK *et al.* 2000; GOOLSBY 2015). It was already evident and recognized from the time of Darwin that patterns of interspecific variation cannot be interpreted without taking into account the underlying common descent of species. Remarkably, the application of this simple truth only became reality in the 1980s with the development of the statistical tools to do so; an uprising triggered by FELSENSTEIN's influential work on independent contrast (1985). Statistically, the effect of phylogeny on trait variation can be regarded as a confounding factor that violates assumptions about non-independence of the unit of analysis, and that potentially introduces spurious correlations across traits (FELSENSTEIN 1985, 2004). Now, with modern phylogenetic tools, comparative biologists can go well beyond 'statistically controlling for phylogeny' and can treat the evolutionary history of species as an interesting phenomenon on its own. Examining the biological diversity in the light of the phylogeny opens up horizons to explore, for instance, the correlated evolution of traits (e.g., DIAZ-URIARTE & GARLAND 1996), phylogenetic signals in interspecific data (e.g., REVELL *et al.* 2008), ancestral states

(e.g., HUELSENBECK & BOLLBACK 2001; PAGEL *et al.* 2004), mode of trait evolution (e.g., O'MEARA 2012, O'MEARA *et al.* 2015), and rates of speciation/extinction and diversification (e.g., NEE *et al.* 1994; MADDISON *et al.* 2007). The use of *phylogenetic comparative methods* has become extremely popular over recent years (Fig. 2), with statistical improvements to the existing methods being published almost weekly (COOPER *et al.* 2016). Hand in hand with the wealth of open-access genetic information (e.g., GenBank®) and reliable phylogenies of numerous animal groups, even at low taxonomic level, the field of comparative biology is blossoming as never before (BENSON *et al.* 2009; SAYERS *et al.* 2009). For further resources and guidance, I encourage scholars new to the field to turn to some of the seminal work of Luke Harmon (e.g., HARMON 2018), the online blog of Liam Revell (<http://blog.phytools.org>), and the book '*Concepts and Practice*' by GARAMSZEGI (2014).

Phylogenetic comparative methods have also found their way into the field of animal communication. An excellent study by GARAMSZEGI *et al.* (2005), for example, compares the song repertoire of 39 passerine bird species with their respective brain size, and establishes that species with highly complex songs tend to have large intersexual differences in brain size. Another comparative analysis, now on the visual display behaviour of 53 anole lizard species, shows that lizards' display duration is linked with their level of sexual size dimorphism, and that the amount of environmental light in which displays are performed affects the display complexity of a lizard (ORD & MARTINS 2006). In an attempt to unravel the factors influencing the diversity of advertisement calls in dart-poison frogs (Dendrobatidae), ERDTMANN & AMÉZQUITA (2009) show that variation in call traits cannot be explained by ecological variation, but find species' calls to be highly phylogenetically informative; meaning that, a strong relationship exists between how closely related species are and how similar they are in any feature of the advertisement call – an outcome only made possible by the use of phylogenetic comparative tools. Surprisingly, multi-species comparisons of the design of chemical signals are almost entirely lacking. This is probably due to the combination of only very recent developments in chemical analytical and statistical comparative tools, and the time researchers need to assemble a large-scale multi-species chemical dataset. A recent study by WEBER and colleagues (2016) on perfume signalling in orchid bees (*Euglossa*) is one of the first studies on the macroevolution of chemical signal design in animals, and the factors influencing design diversity. Based on the chemical composition of the chemical signals of 65 *Euglossa* species,

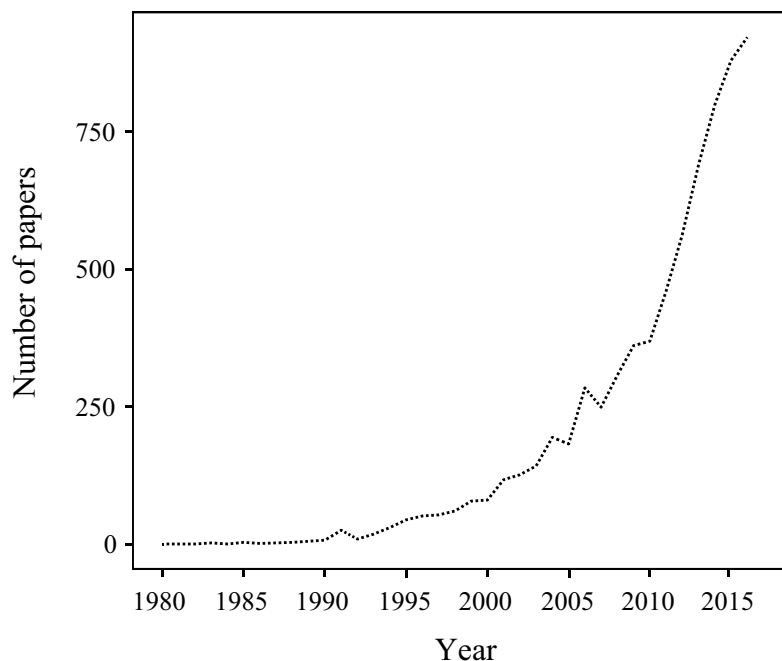


Fig. 2 – The number of papers containing the phrase 'phylogenetic comparative' published each year from 1980 to 2016. Data obtained from COOPER *et al.* 2016.



WEBER *et al.* (2016) suggest that the evolution of species-specific signal design in *Euglossa* is rapid, is impacted by sympatric *Euglossa* species, and may be a function of both a burst of chemical signal divergence early in speciation and subsequent reproductive character displacement.

The sensory system has also been subjected to phylogenetic comparative analyses. Excellent studies have been published on the evolution of vertebrate eyesight (e.g., BOWMAKER 2008; FERNANDEZ & MORRIS 2007; SIMÕES *et al.* 2015, 2016) and hearing (DOOLING & FAY 2000; BOHN *et al.* 2006), and on the main olfactory and vomeronasal system too (EISTHEN 1997). Research has focussed on several aspects of the latter two sensory systems: size of the bulbs in the brain (e.g., GITTLEMAN 1991; BARTON *et al.* 1995), size of the organs themselves (e.g., SCHLUESSEL *et al.* 2008), structure and type of receptor cells in the epithelia (e.g., EISTHEN 1992; COOPER 1997b), and morphology of the chemical sampling devices (e.g., SCHWENK 1994a, 1994b; COOPER 1995a).

Tests on the hypothesis that the design of the signal receiving system of animals is evolved to ‘optimally’ detect and process the emitted signals, have been limited to within-species analyses or comparisons of two species. For example, VOGT & RIDDIFORD (1981) showed that both the morphological and biochemical design of the antennae of male silk moths (*Antheraea polyphemus*) are maximally tweaked to the sex pheromone [11,12-H]trans-6,cis-11-hexadecadienyl acetate emitted by conspecific females, which enables long-distance detection (up to 4.5 km). Evidence for co-adaptation between signal and receptor design was also found in the Tungara frog (*Physalaemus pustulosus*), where the low frequency mating call of male frogs is exactly tuned to stimulate the inner ear receptor organ of females of the same species (RYAN *et al.* 1990). Although valuable, studies focussing on one species lack the wider insight that can be gained from multi-species comparative studies. The few studies that opted for a broad taxon-wide comparative approach examined correlated evolution between signal and sensory design in the hearing sensitivity and social calls of bats, frogs and katydids (WILCZYNSKI *et al.* 2001; BOHN *et al.* 2006; MONTEALEGRE-Z 2009). To my knowledge, no study to date has examined this hypothesis for the chemical communication system (but see case study on page 75).

## Lizards as study model

### From an evolutionary point of view

Lizards have starred in many research branches of evolutionary biology, and have proven excellent models for studying locomotion performance (e.g., VAN DAMME *et al.* 1997; IRSCHICK & LOSOS 1998; VAN DAMME & VANHOODYDONCK 2001), feeding mechanics (e.g., AERTS *et al.* 1997; HERREL *et al.* 2001, 2007a), life-history patterns (e.g., SHINE 1980; BAUWENS 1999; MESQUITA *et al.* 2016a, 2016b), thermal physiology (e.g., VAN DAMME *et al.* 1990; SCHEERS & VAN DAMME 2002; VERWAJEN & VAN DAMME 2007a; HERREL *et al.* 2007b), developmental (in)stability (e.g., VERVUST *et al.* 2008; LAZIĆ *et al.* 2015), island evolution (e.g., MEIRI 2007; PAFILIS *et al.* 2009; VERVUST *et al.* 2009; NOVOSOLOV *et al.* 2016) and foraging behaviour (e.g., HUEY & PIANKA 1981; PERRY 1999; VITT *et al.* 2003; COOPER 2005). Some lizard taxa have played a pioneering role in our current understanding on the powers of natural selection, such as the genus *Anolis* on adaptive radiation (LOSOS *et al.* 1998; LOSOS & RICKLEFS 2009).

Students of animal communication have also repeatedly used lizards as model organisms. This is hardly surprising as the diversity and complexity of the signals and displays exploited by lizards is vast. Understandably, the majority of studies on lizard communication focus on the visual and chemical communication systems, since lizards rely more strongly on those two modalities for everyday activities. Nevertheless, some lizards produce sounds (WEVER *et al.* 1963), although this is predominantly restricted to Gekkota (but see LABRA *et al.* 2013; BAECKENS *et al.* 2019), as they are unique among lizards in having laryngeal specializations for vocalization and well-developed auditory sensitivity (reviewed by FRANKENBERG & WERNER 1991). Research on the visual modality of lizards has broadened our knowledge on the evolution of colour polymorphism (e.g., SINERVO & LIVELY (1996)

on *Uta stansburiana*; HUYGHE *et al.* (2007) on *Podarcis melisellensis*), Batesian mimicry (e.g., HUEY & PIANKA (1977) on *Heliobolus lugubris*), colour crypsis (e.g., STUART-FOX *et al.* 2008 on *Bradypodion taeniabronchum*), and visual signal design and efficacy (e.g., NICHOLSON *et al.* 2007; DRIESSENS *et al.* 2017 on *Anolis*), to name a few. In contrast to the number of studies on visual communication in lizards, the literature on lizard chemical communication is relatively meagre, although it is a major factor in the life of many lizard species. However, in recent years, the discipline of chemical communication in reptiles has been growing (MASON & PARKER 2010; MARTÍN & LÓPEZ 2014).

Within vertebrates, lizards are a promising clade to study the evolution of chemical communication, and for various reasons. Consider four. Firstly, lizards use chemical cues and signals during a variety of activities, such as prey detection or foraging, predator detection, species and individual recognition, mate choice, and territoriality (reviewed by MASON 1992; MASON & PARKER 2010). Secondly, aside from the faeces, cloacal secretions, and skin lipids that contain socially relevant chemical stimuli (MASON & PARKER 2010), many lizards possess specialized glands in the dermis of their inner thighs, which produce waxy secretions involved in chemical signalling (reviewed by COLE 1966; MAYERL *et al.* 2015). Thirdly, the chemoreception system of many lizards is highly sophisticated, comprising of a well-developed olfactory and vomeronasal system for chemical processing, and a forked tongue for chemical sampling (SCHWENK 1993, 1995; COOPER 1995a, 1996; Fig. 3). Both sensory systems are, furthermore, functionally interrelated (HALPERN & MARTÍNEZ-MARCOS 2003), with (volatile) scent stimuli being first received through the nares and processed by the olfactory organs, which in turn triggers tongue-flick-mediated vomerolfaction (HALPERN 1992; COOPER 1994; SCHWENK 1995). Fourthly, the interspecific variation in chemical signal design, investment in chemical signalling, development of the chemoreception system, and overall reliance on chemical communication, appears considerably large (SCHWENK 1995; COOPER 1997a, 1997b; VITT & PIANKA 2005; MARTÍN & LÓPEZ 2014). In spite of that, lizards are still underrepresented in the field of chemical ecology, where the literature is heavily biased towards insects. A literature search by SYMONDS & ELGAR in 2008 revealed that 79% of the studies on pheromone diversity have focussed on insects, while less than 1% examined lizards. The exceptional research interest for insect pheromones is most likely the result of its economic value as an application in pest management, rather than its biological value to understand the evolution of chemical communication.

Nevertheless, the chemosensory system of lizards has received some attention in the past, with the lingual system being the main focus due to its significance in the evolutionary history of squamates (Fig. 4). The central role of the tongue is nicely illustrated by the fact that families of lizards and snakes

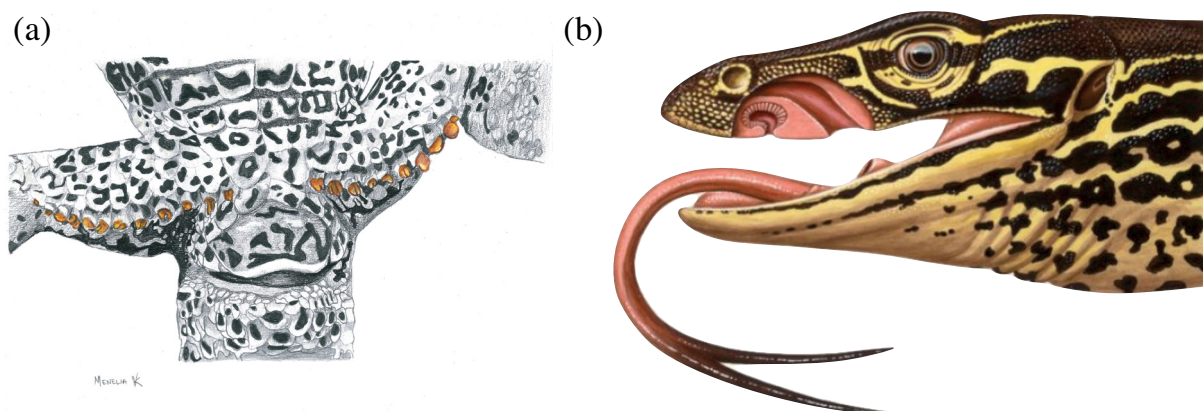


Fig. 3 – An illustration of the chemosignalling and chemoreception systems of lizards, with respectively (a) two rows of femoral pores on the inner thighs of a male lacertid (illustration made by Menelia Vasilopoulou-Kampitsi) and (b) a tongue-flicking varanid showing its olfactory and vomerolfactory system on a lateral section.

have traditionally been attributed to either the more ‘primitive’ ‘Iguania’ (a group with fleshy tongues used in prey capture, a sit-and-wait foraging strategy, and relatively limited chemoreceptive abilities) or the ‘derived’ ‘Scleroglossa’ (that use their jaws to capture food, have a forked tongue for vomerolfaction, and forage actively). Whether the ‘Iguanian’ characteristics are truly ancestral, and the ‘Scleroglossan’ ones derived, is a matter of debate (LOSOS *et al.* 2012), but, at least at the family level, there is strong evidence for correlated evolution between squamates’ mode of foraging and the degree of development of their vomeronasal-lingual system (SCHWENK 1994a, 1994b, 1995; COOPER 1995a, 1995b, 1997a). Of course, the strict and conservative separation of ‘chemically-oriented’ ‘Scleroglossa’ (comprising all Gekkota, Lacertoidea, Scincoidea and Anguimorpha) and ‘visually-oriented’ ‘Iguania’ seems flawed in the sense that many ‘scleroglossans’ also have excellent eyesight (PÉREZ I DE LANUZA & FONT 2014; MARTIN *et al.* 2015) and frequently use visual displays (COOPER *et al.* 2003; FONT *et al.* 2012b), while many ‘iguanians’ also use chemical cues to discriminate among prey items (COOPER & LEMOS-ESPINAL 2001) and in intraspecific communication (SIMON *et al.* 1981; DUVAL 1979; BAECKENS *et al.* 2016).

While the chemosensory system of lizards has been the topic of several studies in the past, comparative research on the chemosignalling system and chemical signal design in lizards is almost completely lacking (but see PINCHEIRA-DONOSO *et al.* 2008 and see case study on page 75). Besides, the recent molecular phylogeny of squamates proposed by ZHENG & WIENS in 2016, which is fundamentally discordant with the morphology-based phylogeny suggested by GAUTHIER *et al.* (2012), partially tackles the insights gained from earlier studies on the evolution of squamate chemoreception in the 1990s by ‘tongue-specialists’ K. Schwenk and W.E. Cooper, Jr. In addition, while Schwenk’s and Cooper’s research provided us with excellent data on squamates’ tongue morphology and use, none of the studies has explored this at a lower taxa level, e.g., within a family. Therefore, it is unclear how sensory systems change on relatively small evolutionary time scales. Clearly, this calls for comprehensive research on the evolution of lizard chemical communication, integrating all aspects of communication (emitting system,

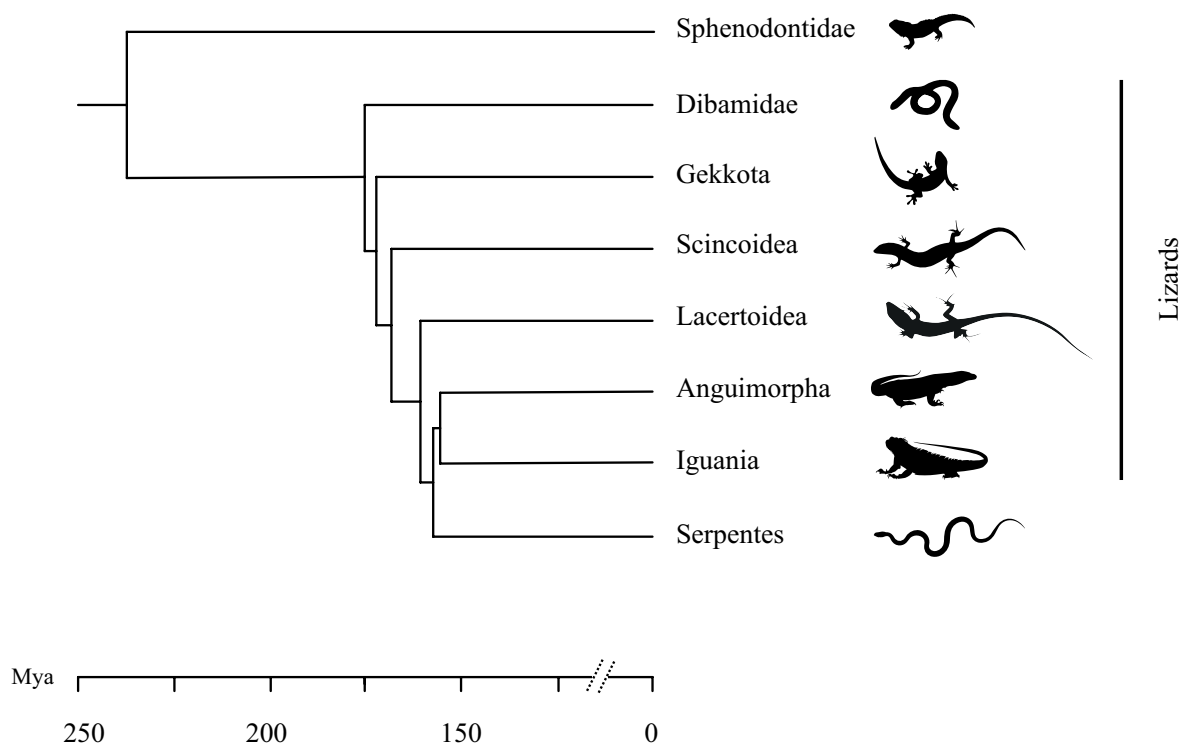


Fig. 4 – Time-calibrated lepidosaurian phylogeny presenting Sphenodontidae and all squamate infraorders. Note that ‘lizards’ are a paraphyletic taxonomic group. Molecular phylogeny based on ZHENG & WIENS (2016). ‘Mya’ = million years ago.

signal design, receiving system), by taking a phylogenetic interspecific comparative approach while concentrating on one specific lizard family.

The family Lacertidae constitutes an excellent group of lizards for studying the evolution of chemical communication. Lacertids rely intensely on chemical cues for predator avoidance (e.g., VAN DAMME & QUICK 2001; AMO *et al.* 2004a, 2004b, 2004c; MARTÍN *et al.* 2015a), prey detection (e.g., COOPER & PÉREZ-MELLADO 2002b; VERWAIJEN & VAN DAMME 2007b), and on chemical signals for many aspects of inter- and intraspecific communication (reviewed by MARTÍN & LÓPEZ 2014). All lacertid species (except one: *Meroles anchietae*) are equipped with follicular epidermal ('femoral') glands on their inner thighs, which produce a waxy cocktail of proteins and lipids that is actively, or passively, deposited on the substrate (MASON & PARKER 2010; DE VILLIERS *et al.* 2015; MANGIACOTTI *et al.* 2019). Recent analyses have revealed that these femoral gland secretions operate as chemical signals that are involved in a variety of social contexts, such as territory demarcation and assessment (ARAGÓN *et al.* 2001a; FONT *et al.* 2012a; MARTÍN & LÓPEZ 2012), male rival assessment (LÓPEZ & MARTÍN 2002; CARAZO *et al.* 2007; KHANNOON *et al.* 2011), female choice (CARAZO *et al.* 2011; KOPENA *et al.* 2011, 2014; GABIROT *et al.* 2013; MARTÍN & LÓPEZ 2013, 2015), assessment of female reproductive status (COOPER & PÉREZ-MELLADO 2002a), individual recognition (GABIROT *et al.* 2010a, 2010b), sex identification (KHANNOON *et al.* 2010) and species recognition (BARBOSA *et al.* 2006; GABIROT *et al.* 2010b).

Moreover, the biogeographic history and substantial ecological radiation of lacertids (ARNOLD 1989a, 1989b) may provide a valuable opportunity for researchers to examine the environmental factors driving the evolution of lizard chemical communication. Distributed over most parts of the Old World, more than 320 lacertid species, assigned to 42 genera, have successfully radiated into a wide array of habitats and climate regions; from subarctic tundra through temperate heathlands and forests, alpine meadows and Mediterranean maquis, steppe and gravel semi-deserts, and monsoonal rainforest to sandy dune systems in the desert (ARNOLD 1989a, 1989b; HARRIS *et al.* 2002). Within these habitats, lacertids utilize a great diversity of microhabitats and substrates, ranging from herby vegetation over stony undergrounds to shifting sands. Other species climb extensively in shrubs or trees (VANHOODYDONCK & VAN DAMME 1999; VANHOODYDONCK *et al.* 2009). Although most lacertids share the same general morphology and many aspects of their ecology (e.g., diurnal, heliothermic, oviparous; CASTILLA *et al.* 1999; VAN DAMME 1999; VITT & PIANKA 2007), they appear to differ in colouration and conspicuousness (PÉREZ I DE LANUZA & FONT 2010, 2015, 2016), sexual size dimorphism (PÉREZ I DE LANUZA *et al.* 2013), foraging mode (HUEY & PIANKA 1981, PERRY *et al.* 1990; PERRY 1999; VERWAIJEN & VAN DAMME 2007a, 2007b, 2008), anti-predator behaviour (VANHOODYDONCK & VAN DAMME 2003), and even some aspects of their diet. Although most lacertids have a predominantly arthropod-based diet, the relative contribution of different types of arthropods varies considerably among species (DÍAZ 1995; CARRETERO 2004; HERREL *et al.* 2004) and some species, especially (but not exclusively) island-dwellers consume large amounts of plant material (PÉREZ-MELLADO & TRAVESSET 1999; VAN DAMME 1999; HERREL *et al.* 2004). Although prey availability undoubtedly steers much of the interspecific variation in diet in lacertids, several species have been shown to prefer or avoid certain food items (see CARRETERO 2004 for a review).

### From a practical point of view

Most lacertid species are widespread and locally abundant, although some desert species may hold low-density populations (PIANKA 1971; pers. obs.). With the proper amount of speed, commitment, coordination and flair, lacertids are fairly easy to capture in the wild by hand or noose (i.e., a fishing rod and a tiny nylon snare to hurl around the lizard's neck, GARCÍA-MUÑOZ & SILLERO 2010). Alternative catching techniques have been used (e.g., sling shots, 'lizard grabber', 'whomping'; PIANKA 1994; WITZ 1996), but are now out-dated or considered unethical<sup>1</sup>. Generally, keeping lizards in captivity

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<sup>1</sup> Pianka (1994) on catching lizards in the Outback of Australia: "For much of my research, it is essential that I collect the animal for a permanent museum specimen, dead or alive, in any way possible, so I often shoot lizards with either a BB gun or .22-caliber dust shot."

does not pose any great difficulty and they appear to behave ‘naturally’ in experimental set-ups. In addition, lizards require relatively little food and space. These characteristics enable herpetologists to obtain valuable information on a large number of individuals in a reasonable short time span.

### Case study

Early investigations on a limited number of species revealed considerable differences in the chemical composition of the glandular secretions in lacertid lizards (MARTÍN & LÓPEZ 2014), and in several aspects of the chemical emitting and receiving system of lizards (SCHWENK 1993, 1995; COOPER 1995a, 1997a). Since only recently, the evolutionary processes causing this disparity were largely unknown.

From 2015 on, I started to quantify the diversity in the design of the lizard chemical communication system in order to examine the phylogenetic constraints and ecological drivers that influence the evolution of this diversity. I approached this question by integrating the three components of communication: emitting system → signal design → receiving system. Based on histological sections and literature data, I, first, documented variation in absence/presence of epidermal glands, gland size, and number of glands in lizard species. Phylogenetic comparative tests indicated a strong and significant phylogenetic signal in epidermal gland number among lacertids, with no effect of climate on interspecific variation in gland number. In contrast, substrate use did affect gland number with shrub-climbing species having fewer glands than species inhabiting other substrates (BAECKENS *et al.* 2015). Second, using gas chromatography-mass spectrometry (GC-MS), I established the existence of vast disparity in the chemical composition of the glandular secretion of 64 lacertid lizards, distributed over Africa, Asia and Europe (Fig. 5).

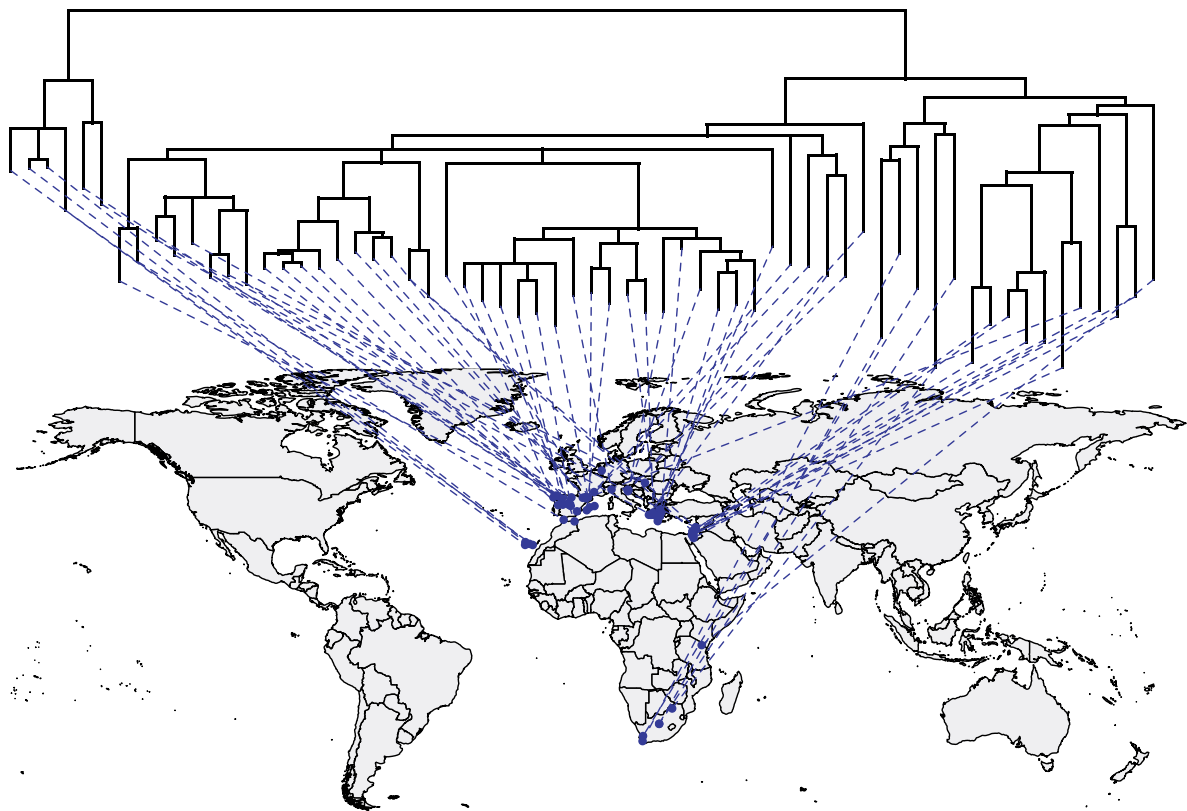


Fig. 5 – A projection of the lacertid phylogeny onto a geographic world map, in which the tops of the tree are connected to the catch-locations of the lizards on the map via dotted lines (data from BAECKENS *et al.* 2018a).

Comparative statistics showed that despite the strong phylogenetic signal in chemical signal design, variation in climatic conditions best explained the interspecific variation in signal design (BAECKENS *et al.* 2018a). Specifically, species living in hot, dry environments contained higher proportions of stable compounds of high molecular weight in their secretions (Fig. 6). Hot and dry conditions increase evaporation rate of chemicals, subsequently, decreasing the longevity of a signal. Stable and heavyweight compounds most likely experience reduced evaporation rates and counteract the rapid signal fade-out through evaporation, generating a highly persistent scent-mark. By contrast, species inhabiting wet, humid conditions produced highly aromatic secretions containing numerous different compounds of low molecular weight (Fig. 6). Such chemical mix probably creates a volatile-rich signal that can be used for long-distance airborne communication. Additional statistical analyses were unable to establish any correlative evidence for a link between interspecific variation in signal design and other biological drivers, such as dietary composition (BAECKENS *et al.* 2017a) and intensity of sexual selection (based on the degree of sexual size dimorphism; BAECKENS *et al.* 2018b).

Third, behavioural observations combined with data from previous work revealed considerable interspecific variation in the chemoreceptive behaviour of lizard species. Specifically, I provided evidence that foraging mode, not phylogenetic relatedness drives convergent evolution of similar levels of chemosensory investigation in lizards and snakes (BAECKENS *et al.* 2017b). The findings of this study showed that baseline tongue-flick rate (TFR) is higher in active than ambush foragers. Although baseline TFR appeared phylogenetically stable in some lizard taxa, this turned out to be a consequence of concordant stability of foraging mode: when foraging mode shifts within taxa, so does baseline TFR. In addition, I found that baseline TFR is a good predictor of prey chemical discriminatory ability, as I established a strong positive relationship between baseline TFR and TFR in response to prey. Fourth, I observed substantial differences in the vomerolfactory-lingual system of lacertid lizards on the basis of tongue measurement and micro-CT images of the vomeronasal organs. Although the results imply independent evolution of tongue and vomeronasal-organ form, I did find some evidence for co-variation between sampler and sensor, i.e., tongue forkedness was correlated with the thickness of the sensory epithelium of the vomeronasal-organ (BAECKENS *et al.* 2017c).

Overall, the findings of this research project showed that the design of the chemical communication system of lizards varies considerably among species, and appears to have evolved relatively quickly (BAECKENS *et al.* 2015; 2017a, 2017b, 2017c; 2018a, 2018b; GARCÍ-ROA *et al.* 2017). Searching for evolutionary patterns of variation, I found that comprehensive phylogenetic comparative analyses were unable to ascribe interspecific variation in the chemical signal design of lacertids to among-species

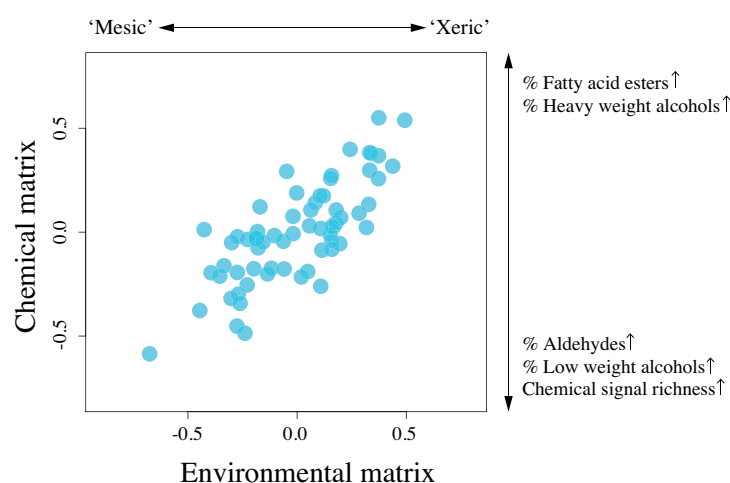


Fig. 6 – Scatterplot showing the significant relationship between the chemical composition of the glandular secretions of lacertid lizards and the environment they inhabit (modified from BAECKENS *et al.* 2018a). For details on the interpretation of the figure, see BAECKENS *et al.* 2018a.



differences in diet (BAECKENS *et al.* 2017a) or intensity of sexual selection (BAECKENS *et al.* 2018b). Conversely, I established convincing evidence for an important role of the climatic environment in explaining variation in the chemical signalling system of lacertids (BAECKENS *et al.* 2018a), which might result from differential selection on signal efficacy; the ability of signals to travel efficiently through the medium and to attract the attention of the receiver. These findings provide evidence for convergent evolution in the chemical signalling system of lacertid lizards; a result revealed by the use of a phylogenetic comparative approach.

Lizards rely on their chemoreception system to sample chemical signals from the surroundings for communication purposes, yet, some species also use their chemical senses to forage. The foraging mode of lizards strongly predicted interspecific variation in vomerolfactory behaviour (tongue-flick rate) (BAECKENS *et al.* 2017b), but not vomeronasal-lingual morphology (BAECKENS *et al.* 2017c). However, the latter was related with species degree of investment in chemical signalling, cautiously hinting for co-evolution between the signal emitting system and signal receiving system, hence the evolution of an ‘optimal’ communication system (BAECKENS *et al.* 2017c).

While this work has shed initial light on the macro-evolutionary processes moulding variation in the design of the chemical communication system of lacertid lizards, there are still numerous questions to be answered in further research studies. For instance, it would be worthwhile to examine the relationship between species’ investment in chemical signalling system (gland number, chemical signal design) and conspicuous body colouration to assess whether there is a trade-off between investments in signalling modalities. Moreover, comparative statistics can aid in examining the potential effect of eavesdropping predators on the evolution of the lizard chemical communication system. No studies have attempted to investigate the potential costs of the use of scent-marks in lizards with regards to chemical eavesdropping. Scholars could study whether high predatory environments (inhabited by chemically-oriented hunters, such as snakes) impact the evolution of the emitting system or signal design of lizards in any way. More advanced phylogenetically-informed statistics can test whether the evolution of certain features of the chemical signalling system have influenced diversification and speciation rate in lizards. Clearly, there has never been a better time than now to be a comparative chemical ecologist.

### Outlook

Traditionally, researchers have taken a sociobiological and behavioural ecological approach to study various aspects of chemical communication in a few focal animal species. Today, with the recent improvements in methods of chemical analysis and bio-imaging (SCHULZ 2005, EGGELING 2018), researchers can now also turn to the phylogenetic comparative method and perform large-scale among-species comparisons allowing macro-evolutionary studies of chemical communication. Insects have typically been the go-to subjects of study in the field, but researchers should be encouraged to examine non-model species, such as lizards, as they can provide excellent groups to investigate the drivers and constraints that guide the evolution of the systems responsible for sending out and receiving signals.

### Acknowledgments

The author thanks Raoul Van Damme, Peter Aerts, Katleen Huyghe, Panayiotis Pafilis, José Martín, and Stefan Van Dongen, as well as three anonymous reviewers for significantly improving drafts of this manuscript, Menelia Vasilopoulou-Kampitsi for the artwork, Josie Meaney for linguistic advice, and the *Royal Belgian Society for Zoology* for inviting me to write this review. This work was part of Simon Baeckens’ doctoral thesis at the University of Antwerp, which was made possible through financial support from the University of Antwerp. Simon Baeckens is currently a FWO postdoctoral fellow (12I8819N) at the Functional Morphology lab (University of Antwerp).

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Manuscript received: 10 February 2019

Manuscript accepted: 14 June 2019

Published on: 5 July 2019

Branch editor: Ellen Decaesstecker