The Evolution of Lizard Chemical Signals Across Time, Space, and Contexts

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Abstract. Research on the evolution and diversity of animal signals has long been dominated by studies of visual and acoustic modalities, leaving chemical communication comparatively overlooked. Moreover, within the existing chemical signaling literature, research has been strongly skewed toward invertebrates—leaving chemical signaling in vertebrates, especially nonmammalian groups, relatively underexplored. In this chapter, I argue that lizards represent a particularly promising group for advancing our understanding of chemical signal evolution in vertebrates. I highlight major macro-evolutionary advances over the past decade, during which large-scale phylogenetic comparative studies have begun to uncover how ecological, social, and phylogenetic factors shape chemical signal diversity across lizard species. In contrast, micro-evolutionary research—investigating how chemical signals evolve within species across space and time—is lagging behind, not just in lizards, but across vertebrates more broadly. Encouragingly, recent longitudinal and experimental studies are beginning to demonstrate the power of this approach. I also draw attention to the largely untapped potential of studying chemical communication under major anthropogenic perturbations, which are increasingly exploited in evolutionary research but remain rarely applied to chemical signaling systems. These coming years are especially promising for scholars seeking to connect macro-evolutionary patterns with fine-scale, contemporary evolutionary processes—a critical next step in understanding the evolution of vertebrate chemical signaling.

Keywords: Chemical communication · Signal evolution · Lacertid lizards · Macroevolution · Microevolution · Anthropocene · Phylogenetic comparative methods

1 The Skewed Landscape of Animal Signal Research

The study of animal communication has captivated naturalists and scientists for centuries—from the early writings of Aristotle and Pliny the Elder (Fögen, 2014) to Darwin's seminal work on emotional expression (Ekman, 2009), and the landmark discoveries of Tinbergen (1953), von Frisch (1967), and Wilson (1975). Building on this rich legacy,

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the evolution and function of animal signals remain actively studied, driven in part by the sheer richness and complexity of signaling diversity across taxa. However, many aspects of animal communication remain unevenly explored. Much of our current understanding has been shaped by a strong emphasis on visual and acoustic modalities: signals that are conspicuous, easily detected and tracked, and intuitive to human observers. As a result, dominant theories of animal communication have largely emerged from systems where displays are seen or heard (e.g., Andersson, 1982; Caro, 1995; Sinervo & Lively, 1996; Zuk & Kolluru, 1998).

In contrast, chemical communication—though evolutionary ancient and taxonomically widespread—has received comparatively less attention (Müller-Schwarze & Mozzel, 1977; Wyatt, 2014). This neglect may stem from human sensory biases and the technical complexity associated with identifying and manipulating chemical signals. And even when chemical communication has been studied in detail, the focus remained overwhelmingly narrow. Research has centered largely on invertebrates, particularly insects (Fig. 1), driven by applied interests in pest control and biological management (Hartmann, 2008; Symonds & Elgar, 2008; Witzgall et al., 2010). As a fortunate byproduct, these applied studies have produced some of the most detailed fundamental knowledge of chemical signal structure and function (Yew & Chung, 2015). However, the insights they offer are often limited in their relevance to vertebrates, where signal production and reception operate under vastly different physiological and ecological constraints.

Although recent years have seen growing recognition of the importance of chemical signals in vertebrate biology (Apps et al., 2015; Müller-Schwarze, 2006), research efforts remain heavily skewed. Mammals have received disproportionate attention (Fig. 1)—likely due to their prominence in biomedical research (e.g., rodents) and broader trends in science where charismatic fauna (e.g., elephants) tend to attract more attention than less "appealing" taxa (Rosenthal et al., 2017; Troudet et al., 2017). Meanwhile, nonmammalian vertebrates remain markedly underrepresented in the chemical communication literature, despite many of these groups relying heavily on chemosensory cues (Müller-Schwarze, 2006). Among them, the neglect of squamate reptiles, notably lizards, is particularly striking. Their deep reliance on chemical information, actively sampled from the environment via specialized vomeronasal systems and, in many species, forked tongues, has been widely acknowledged for decades (Bissinger & Simon, 1979; Cooper, 1994; Schwenk, 1994, 1995). This trait is so central to their biology that it has even shaped how they are portrayed in mythology, folklore, and popular media (Le Busque & Litchfield, 2023; Morgan, 2008). Yet, their chemical signaling systems remain surprisingly understudied—especially when compared to the wealth of research on mammals and, overwhelmingly, on insects.

2 Lizards as Models for Studying Chemical Signal Evolution

Despite their historical neglect, lizards have increasingly emerged as a promising vertebrate group for studying the evolution of chemical communication, for several reasons.

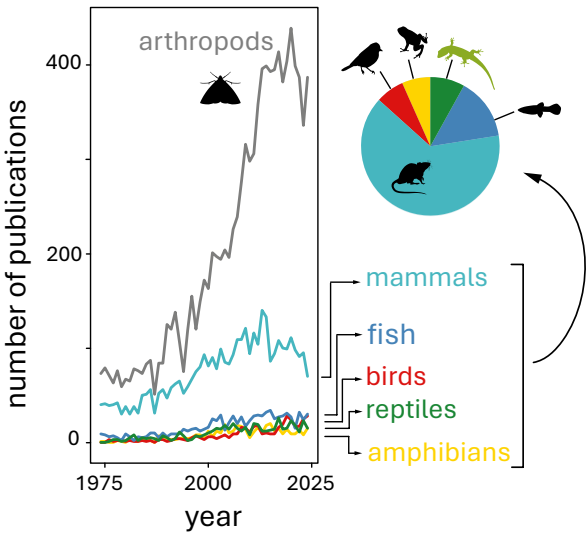


Fig. 1. Taxonomic bias in research on animal chemical signals. The graph shows the number of articles published on chemical signals over a 50-year period for all major vertebrate clades, alongside arthropods as a representative invertebrate group. A pie chart (top right) further illustrates the relative proportion of publications focused on each vertebrate group over this half-century of research. Two patterns emerge: first, studies on vertebrate chemical signaling are vastly outnumbered by those on arthropods—a group that itself represents only a portion of invertebrate diversity—highlighting a profound imbalance in research effort. Second, within vertebrates, chemical communication studies are overwhelmingly concentrated on mammals (64.1%), with far fewer publications addressing fishes (14.3%), reptiles (8.3%), birds (6.7%), and amphibians (6.6%). Data were obtained from a Scopus search (conducted on 03/04/2025), which queried peer-reviewed articles (excluding reviews) published between 1974 and 2024. Searches were restricted to title, abstract, and keywords using the terms (pheromone* OR "chemical signal*" OR "scent mark*" OR semiochemical* OR chemosignal*), in combination with taxon-specific scientific and common names† similar to Symonds and Elgar (2008). While this literature search was designed as a coarse, exploratory assessment to capture broad patterns in research focus rather than serve as an exhaustive bibliometric analysis, it nonetheless underscores a long-standing and persistent taxonomic bias in chemical communication research. †Search terms used for each group were as follows: reptiles = (reptilia OR reptile OR lepidosauria OR lepidosaur* OR testudines OR turtle* OR crocodilia* OR crocodil* OR squamata OR squamate* OR lizard* OR snake*); fishes = (fish OR fishes OR agnatha OR chondrichthyes OR osteichthyes); amphibians = (amphibia OR amphibian* OR anura* OR frog* OR caudata* OR salamander* OR gymnophiona OR caecilian*); mammals = (mammalia OR mammal* OR mice OR mouse OR rat OR rats); arthropods = (arthropoda OR arthropod* OR insect*).

First, many lizards possess specialized epidermal glands (e.g., femoral, precloacal, and generation glands), which are typically active in adult males and secrete waxy compounds onto environmental surfaces as scent marks during the reproductive season (Mayerl et al., 2015; Mouton et al., 2010). These secretions—chemically complex mixtures of lipophilic and proteinaceous compounds (Mangiacotti et al., 2023a, b)—can be detected by conspecifics and heterospecifics via tongue-flicking. Recent integrative research combining behavioral experiments, chemical analyses, and ecological data has revealed substantial diversity and specificity in these glandular secretions. Variations in composition and relative abundance of specific compounds can convey details about an individual's age, health, parasite load, hormonal state, immune condition, and even access to thermal resources. These chemical signals function not only in species, sex, and population recognition but also in mediating social interactions, including competitive and sexual encounters. This rapidly growing body of work has been extensively reviewed in recent years (e.g., Weldon et al., 2008; Mason & Parker, 2010; Font et al., 2012; Apps et al., 2015; Martín & López, 2015; Martín & López, 2024; Fleishman & Font, 2019). While epidermal gland secretions are generally considered the primary source of chemical signals in lizards, there is also evidence that other sources—such as feces, cloacal secretions, and skin lipids—may convey socially relevant chemical cues (Cooper & Vitt, 1984; Labra, 2008; Mason & Parker, 2010; Moreira et al., 2008).

Second, to efficiently collect and process complex chemical cues from the environment, many lizards have evolved a highly specialized chemosensory system: the vomeronasal-lingual system. This system consists of a tongue, sometimes highly forked to facilitate the detection of chemical gradients, which samples airborne and substrate-bound chemicals and delivers them to paired vomeronasal organs located in the roof of the mouth (Filoramo & Schwenk, 2009). Unlike in other vertebrates, the vomeronasal organs in squamates are anatomically and functionally independent from the main olfactory system (Graves, 1993; Keverne, 1999), enabling the precise detection and processing of a wide array of social signals and environmental cues.

Third, although all lizards share a broadly similar chemical communication system, there is considerable variation in the extent and specialization of both their signaling and receiving structures. While many lizards possess epidermal glands, others lack them altogether (Mayerl et al., 2015). In species with glands, these structures are typically active only in adult males; however, in some lineages, both sexes maintain functional glands (García-Roa et al., 2016; Martín et al., 2016). Moreover, gland size and number vary substantially across species, potentially reflecting differences in the degree of investment or reliance on chemical communication (Baeckens, 2017). Similarly, the morphology of the tongue and vomeronasal organs exhibits broad interspecific diversity (Baeckens et al., 2017a, 2017c; Cooper, 1996; Schwenk, 1993, 1994; Smith et al., 2008). In parallel, the composition of glandular secretions varies widely among species and populations—both in the specific compounds present and in their relative abundances (Martín & López, 2024; Mayerl et al., 2015). These layers of diversity offer a rich foundation for investigating the ecological and evolutionary forces shaping chemical communication.

Fourth, lizards have radiated across nearly all terrestrial ecosystems, except the coldest extremes, occupying a wide range of ecological niches and displaying remarkable phenotypic diversity (Huey et al., 2007; Roll et al., 2017). With over 7800 recognized

species, lizards are more species-rich than all mammals (currently ~6760 species; Burgin et al., 2018). Their well-resolved phylogenies (Tonini et al., 2016) make them especially well-suited for macro-evolutionary studies using phylogenetic comparative methods (Meiri, 2018). Lizards are also abundant and diverse on islands around the globe, where geographic isolation has promoted evolutionary divergence along unique ecological trajectories (Novosolov et al., 2013). These circumstances make them particularly valuable for investigating the ecological drivers of phenotypic evolution through island comparisons (Losos & Ricklefs, 2009).

Finally, from a practical perspective, lizards offer numerous experimental advantages. Many populations occur at high densities (Novosolov et al., 2016), have short generation times, and reach sexual maturity relatively quickly (Mancini et al., 2025), facilitating experimental designs both in the field and in controlled environments. This enables longitudinal and even multigenerational studies under seminatural or natural conditions.

In the sections that follow, I highlight recent research efforts that have capitalized on these advantageous traits to deepen our understanding of chemical signal evolution in lizards—across spatial and temporal scales, and a range of socio-ecological contexts.

3 Macro-evolutionary Patterns in Lizard Chemical Signaling

Some of the most extensive efforts to understand the evolution of chemical signaling in lizards have taken a macro-evolutionary, interspecific comparative approach. These studies examine traits of the chemical signaling system across species to detect covariation with ecological or social variables, aiming to infer the selective pressures and constraints that shape signal diversity. By identifying patterns of convergence, researchers can infer adaptive responses to similar environmental drivers or social pressures (Losos, 2011).

3.1 Abiotic Correlates and Efficacy-Based Selection

A major focus of these interspecific comparative studies has been to assess how environmental conditions shape chemical signal design, as predicted by efficacy-based selection theory (Endler, 1992, 1993; Guilford & Dawkins, 1991; Hebets & Papaj, 2005). This framework posits that signal traits that maximize transmission and reception are selectively favored, depending on the physical and sensory environment. In the context of chemical signaling, this involves understanding how abiotic factors (e.g., temperature, humidity, wind, and UV radiation) influence signal performance and drive evolutionary shifts across lizard lineages inhabiting different environments.

Harsh signaling environments—such as hot, windy, and high-UV habitats, where scent marks used for social communication degrade rapidly—can impose strong selective pressures on chemical communication systems (Alberts, 1992; Martín et al., 2024; Martín & López, 2013). One proposed response, the "within-channel compensation hypothesis," suggests that species may increase their investment in chemical signaling

by producing more secretion or modifying its composition for greater stability or longevity. Alternatively, the "between-channel compensation hypothesis" proposes that species may reduce reliance on chemical signaling and instead shift toward other modalities (e.g., visual signals) that perform more effectively under such environmental constraints (Alberts, 1992; Baeckens et al., 2015).

In lizards, comparative studies have tested these predictions by examining both the epidermal glands responsible for signal production and the chemical composition of the gland secretions. Early work focused on the presence and number of glands as a proxy for signal investment, owing to the relative ease of measuring this trait across museum specimens and field collections (Baeckens, 2017). More recently, researchers have also investigated the lipophilic and proteinic composition of glandular secretions (Mangiacotti, et al., 2023b), seeking to understand how variation in specific compound classes or ratios corresponds to environmental gradients. To date, most of this comparative work has focused on four major lizard groups—the South American *Liolaemus*, North American *Sceloporus*, Australian *Heteronotia* geckos, and, most prominently, the Old-World family Lacertidae—providing broad phylogenetic, geographic, and ecological coverage.

In *Liolaemus*, Escobar et al. (2001) were among the first to report environmental correlates of gland number. They proposed that harsh signaling environments—particularly those with high thermal variability or wind exposure—might favor increased glandular output to compensate for rapid signal degradation. However, later studies incorporating phylogenetic information and broader taxonomic sampling have added nuance. Overall, the phylogenetic signal tends to be strong, with gland number showing evolutionary conservatism within certain clades (García-Roa, Jara, et al., 2017c; Jara et al., 2018). In many cases, climatic factors explain only a small proportion of the variation in gland number, even within *Liolaemus* (Jara et al., 2018; Pincheira-Donoso et al., 2008).

In lacertids, no significant correlation between gland number and climate has been found (Baeckens, et al., 2015). Instead, gland number correlates more strongly with substrate use: species that climb shrubs or vertical structures tend to have fewer glands. Baeckens et al. (2015) argue that three-dimensional, shrubby microhabitats pose particular challenges for chemical signaling, as effective signal coverage across a vertically complex space would require large quantities of secretions. As such, selection may favor reduced investment in chemical signaling, potentially encouraging shifts toward more energetically efficient modalities better suited to these structurally complex habitats. This interpretation contrasts with the views by Escobar et al. (2001), which predicted increased glandular investment under comparable environmental constraints.

With the growing availability of techniques for processing large chemical datasets, researchers have increasingly shifted focus from gland number to the chemical composition of gland secretions. In a comparative study of 64 lacertid species, researchers found a strong association between climatic conditions and secretion composition (Baeckens, et al., 2018a). Lizards inhabiting xeric environments—dry and warm habitats—produced secretions dominated by high-molecular-weight alcohols and fatty acid esters, compounds linked to greater signal longevity under conditions of high evaporation and diffusion. Conversely, lizards from mesic environments—characterized by

high humidity, precipitation, wind, and solar radiation—exhibited greater chemical richness, with large proportions of aldehydes and low-molecular-weight alcohols. These volatile, highly aromatic compounds are thought to enhance signal detectability and facilitate airborne transmission, potentially supporting longer-range communication (Alberts, 1992; Apps et al., 2015; Weldon et al., 2008).

However, parallel studies on spiny lizards (*Sceloporus*) and geckos (*Heteronotia*) revealed contrasting patterns (Campos et al., 2020; Zozaya et al., 2022). In *Sceloporus* no relationship was found between chemical richness and climate, but a positive correlation emerged between aldehyde proportions and ambient temperature—a surprising result, given that aldehydes degrade rapidly under hot conditions. This contrasts with patterns observed in lacertids, where species from warmer environments tend to invest less in aldehydes, presumably to reduce signal degradation. Interestingly, *Sceloporus* species also showed very low levels of volatile unsaturated fatty acids—a metric not assessed in the lacertid dataset. In Australian *Heteronotia* geckos, patterns diverged yet again: secretion composition was associated with precipitation levels, but not with temperature—contrasting with both *Sceloporus* and lacertid results. One possible explanation is that these geckos are nocturnal and may not experience the extreme daytime heat affecting diurnal lizards, such as *Sceloporus* and lacertids. These conflicting findings underscore the need for broader, integrative analyses across lineages and environments.

Beyond investigating how species adjust chemical signal investment in response to abiotic constraints, several studies have more directly examined the between-channel compensation hypothesis (i.e., the idea that species may shift investment across sensory modalities when one channel is compromised; Baeckens et al., 2015). This line of inquiry asks whether limitations on one mode of signaling (e.g., chemical) lead to increased reliance on another (e.g., visual), or vice versa. In *Sceloporus* lizards, a series of studies has tested this hypothesis by evaluating trade-offs between chemical and visual signals. Although based on limited species samples and largely non-phylogenetic comparisons, these studies reveal a compelling trend: species lacking prominent abdominal color patches—a key visual display trait—tend to exhibit increased investment in chemical signaling (Hews & Benard, 2001; Hews et al., 2011; Martins et al., 2015, 2018; Pruett et al., 2016; Romero-Diaz et al., 2021). These findings support the idea that sensory investment is flexible, shifting in response to environmental and functional demands—a central tenet of efficacy-based signal evolution. Surprisingly, comparable analyses have yet to be conducted in lacertids, despite their marked interspecific variation in both chemical signaling and conspicuous coloration (Baeckens, 2019; Pérez i de Lanuza & Font, 2016). Examining whether similar modality trade-offs exist in this group—or in other colorful lineages—could offer key insights into the dynamics of multimodal signal evolution.

3.2 Socio-ecological Correlates and Content-Based Selection

A growing body of interspecific comparative research has explored predictions derived from content-based selection theory (Guilford & Dawkins, 1991; Hebets & Papaj, 2005). This framework posits that selection acts on the informational content of

signals—favoring traits that reliably convey fitness-relevant characteristics of the sender, such as condition, quality, and social status. In the context of chemical signaling, this involves examining how variation in signal composition reflects individual or species-level traits, including morphology, physiology, reproductive status, and behavior.

Content-based selection has historically been the most studied aspect of chemical signaling research—not only in lizards but across animals more broadly (Martín & López, 2024; Wyatt, 2014). Most of this research has focused on within-population variation, linking differences in chemical signals to individual quality metrics, such as body condition and parasite load (Martín & López, 2015, 2024). While these studies have been invaluable for understanding the information content of chemical signals, they offer limited insight into broader evolutionary forces shaping signal divergence across species. Nonetheless, the few macro-evolutionary studies that have been conducted suggest that interspecific variation in chemical signals may be driven by multiple ecological and social drivers (e.g., mate choice and intrasexual competition, social organization, dietary ecology, and species recognition), offering a promising yet underexplored avenue for understanding the evolution of lizard chemical communication.

One of the most obvious socio-ecological drivers of chemical signal evolution is the intensity and form of sexual selection. Across many lizard species, chemical signals display classic features of sexually selected traits: they are typically male-biased, emerge or intensify at sexual maturity, peak during the breeding season, and are often regulated by testosterone levels (Baeckens et al., 2017b; García-Roa, et al., 2017c; Mangiacotti et al., 2019; Martín et al., 2007). These patterns suggest that glandular secretions function as secondary sexual characters shaped by mate choice, male-male competition, or both. Behavioral evidence supports this view. Numerous studies have shown that chemical signals mediate female mate choice (e.g., Martín & López, 2000, 2006a, b, 2024; Olsson et al., 2003) and play a role in intrasexual competition and territory defense (e.g., López & Martín, 2002, 2011; Martín & López, 2007). Moreover, experimental work demonstrates that signal content is often condition-dependent, encoding information about health, hormonal status, immune competence, or competitive ability (Martín & López, 2015, 2024). Given this, it is plausible that variation in the strength of sexual selection across species drives divergence in chemical signal composition or investment. This hypothesis mirrors trends observed in other signaling modalities, where interspecific differences in sexual selection regimes explain significant variation in visual display, coloration, and song complexity (Chen et al., 2012; Garamszegi et al., 2005; Ord et al., 2001; Soma & Garamszegi, 2011). Recent comparative work supports this idea in lizards. In lacertids, species with greater sexual size dimorphism—a common proxy for sexual selection—showed increased expression of five distinct molecular weight regions in the proteinaceous fraction of their glandular secretions (Mangiacotti, et al., 2023c, 2023b). Interestingly, a parallel analysis of the lipid fraction found no such correlation (Baeckens, et al., 2018b), suggesting that lipids and proteins may convey different types of information.

Social organization represents another key axis along which chemical signaling systems may diversify. Just as sexual selection can shape signaling traits, so too can the demands of social living, which rely heavily on effective communication among conspecifics. It has been proposed that increased reliance on chemical signals for intraspe-

cific communication facilitates more efficient short-range interactions, thereby creating conditions favorable for transitions from solitary to group living. Some of the best support for this idea comes from insect societies, where increasing pheromone complexity has been linked to the evolution of sociality (Fischman et al., 2011; Van Oystaeyen et al., 2014). More recently, macro-evolutionary studies suggest that similar processes may operate in lizards. In this group, phylogenetic comparative studies have shown that the presence of epidermal glands is associated with an elevated evolutionary rate of transitions toward social groupings, including prolonged parent-offspring associations (Baeckens & Whiting, 2021). Such social structures evolved more readily in lineages with chemical signaling glands than in those without. This evidence suggests that chemical signaling may have helped create key selective conditions for the evolution of sociality in lizards—by facilitating kin recognition, supporting prolonged contact, and enhancing group cohesion (Baeckens & Whiting, 2021). While it is probable that efficient chemical communication indirectly fosters conditions conducive to social aggregation, the precise mechanisms linking chemical signaling to the emergence of sociality remain to be fully elucidated.

Diet has also been proposed as a potential driver of variation in chemical signaling, as differences in the intake of specific dietary compounds may influence the cues and signals synthesized or acquired by individuals or species (Symonds & Elgar, 2008). In lizards, dietary effects on chemical signals have been demonstrated experimentally at the individual level: supplementation with carotenoids and vitamin E has been shown to alter glandular secretion composition, increasing the proportion of α-tocopherol in treated individuals (García-Roa, Sáiz, et al., 2017a; Kopena et al., 2011, 2014). However, few studies have tackled this question from a macro-evolutionary perspective, and those that have found limited support for diet as a major driver of signal evolution in lizards. A broad comparative study in lacertids, for example, reported no correlation between diet breadth and chemical diversity or richness, nor between the intake of plants or ants and variation in the major chemical classes present in secretions (Baeckens, et al., 2017d). One exception was that species with an exclusive arthropod diet exhibited lower chemical signal richness, suggesting that incorporating plant material may allow for greater compound diversity, potentially by providing access to plant-derived compounds not found in animal prey (Baeckens, et al., 2017d). Overall, while diet may influence chemical signals within species or contribute to individual-level plasticity, it appears to be a relatively weak predictor of interspecific variation in the broad chemical profiles of lizard secretions.

Finally, species recognition, especially in zones of sympatry between closely related species, may drive signal divergence to avoid costly interspecific interactions. Coexistence in zones of sympatry can impose substantial fitness costs due to interspecific aggression, resource competition, or reproductive interference, including hybridization (Grether et al., 2017). These pressures may favor divergence in signaling traits involved in mate choice and competitive interactions (Ord & Stamps, 2009; Schaefer & Ruxton, 2015). In this context, chemical signals may play a key role in promoting pre-mating isolation and reducing the likelihood of costly heterospecific encounters (Smadja & Butlin, 2009). This appears to be the case in sympatric *Podarcis* lizards—a genus with well-documented instances of both current and historical hybridization (Yang et al., 2021). Recent work shows that sympatric *Podarcis* species exhibit greater

divergence in glandular secretions than closely related allopatric species (Mangiacotti, et al., 2021). This pattern is consistent with reproductive character displacement, in which signals diverge in sympatry to improve conspecific recognition during courtship or male-male contests (Grether et al., 2017; Pfennig & Pfennig, 2009). Similar patterns have been documented in Australian geckos, where sympatric species show more pronounced differences in chemical profiles than their allopatric counterparts, suggesting a convergent evolutionary response (Zozaya et al., 2019). By enhancing signal distinctiveness, chemical divergence likely improves species recognition, reinforcing reproductive isolation and contributing to the stable coexistence of closely related taxa.

4 Micro-evolutionary Patterns in Lizard Chemical Signaling

In the last 10 years, large-scale phylogenetic comparative analyses have taken crucial steps toward understanding the evolution of chemical signal diversity in lizards. These analyses have revealed important correlative patterns, linking signal traits to both abiotic and biotic factors across species. Yet to move beyond these broad associations and toward a more mechanistic understanding of signal evolution, it is valuable to examine how such patterns translate to finer evolutionary scales (Reznick & Ricklefs, 2009; Wright, 1982). Micro-evolutionary studies—focused on within-species signal evolution across space and time—allow for investigation into how chemical signal traits respond to selection pressures on ecological timescales. This approach also offers a valuable framework for experimentally testing hypotheses derived from macro-evolutionary analyses, by manipulating specific ecological or social factors thought to influence signal design. So far, most micro-evolutionary work in lizards has relied on among-population comparisons, with only a few studies taking longitudinal or experimental approaches. These early efforts have begun to uncover the role of plasticity, local adaptation, and natural selection in shaping chemical communication at fine evolutionary scales.

4.1 Among-Population Comparisons

Interpopulation comparisons represent the most common micro-evolutionary approach to studying chemical signaling in lizards. Yet, most studies to date have focused purely on reporting differences in gland number or secretion composition between two or more populations, and in some cases, paired these analyses with behavioral assays demonstrating that lizards can discriminate between populations based solely on scent (Escobar et al., 2003; Gabirot et al., 2008, 2010, 2012, 2013; García-Roa, Megía-Palma, et al., 2017b; Ibáñez et al., 2017; Iraeta et al., 2011; Khannoon et al., 2013; Martín et al., 2015; Martín & López, 2006a; Ortega et al., 2019). While such studies are valuable for revealing population-level divergence, their findings are much too often interpreted as evidence of local adaptation, despite lacking formal testing against environmental or socio-ecological gradients.

In a smaller number of cases, however, population-level differences in chemical signaling investment or composition have been rigorously tested against ecological predictors, with findings that echo the complexity observed at macro-evolutionary scales. For instance, Romero-Diaz et al. (2025) analyzed 55 populations of wall lizards (*Podarcis muralis*) across the Pyrenees, integrating detailed climatic and sociosexual variables. They found that investment in chemical signaling (as estimated by epidermal gland number) was elevated in populations with greater sexual size dimorphism, as well as in warmer environments with more vegetation complexity. These patterns suggest that chemical signaling investment may be shaped by both efficacy-based selection favoring greater investment under harsher environmental conditions and the local intensity of sexual selection.

Another important insight from among-population comparisons is that stochastic processes may also contribute to chemical signal divergence. These findings serve as a reminder that variation in chemical signal composition does not necessarily reflect adaptive evolution and caution against the temptation of adaptationist storytelling. In some cases, divergence may instead arise through neutral evolutionary change, especially in isolated populations or secondary contact zones. For instance, in the common wall lizard (*Podarcis muralis*), divergence in epidermal gland secretions between two lineages did not predict hybridization success, and introgression patterns closely resembled those of neutral genetic markers—suggesting that signal divergence may reflect drift rather than selection (MacGregor et al., 2017). In the Skyros wall lizard (*Podarcis gaigeae*), secretion composition varied most strongly among isolated islet populations and was positively correlated with neutral genetic divergence. Notably, mate preferences did not consistently align with chemical differences, pointing to a potential decoupling between signal evolution and sexual selection (Runemark et al., 2011). These cases illustrate that chemical signals and associated preferences can diverge under both stochastic and selective forces, complicating assumptions about their evolutionary drivers (Baeckens et al. 2026).

4.2 Longitudinal and Experimental Perspectives

While most micro-evolutionary studies have relied on spatial comparisons (i.e., allochronic study design), a smaller number have adopted temporal and experimental approaches (i.e., synchronic study design, sensu Hendry & Kinnison, 1999), offering valuable insight into how chemical signals shift over ecological timescales.

One particularly powerful example comes from an island introduction experiment with Aegean wall lizards (*Podarcis erhardii*) in the Greek Cyclades. Individuals from a predator-rich source population were translocated to five small, predator-free islets—environments lacking snakes or other terrestrial vertebrates (Fig. 2a; Donihue, et al., 2020a). This ecological release removed the need to limit conspicuous chemical signaling to avoid eavesdropping predators. Simultaneously, population densities increased fivefold within 4 years, intensifying intraspecific competition (Fig. 2b). Bite scar frequency nearly doubled in males compared to the source population, indicating elevated male-male aggression (Fig. 2c). In response to these rapid ecological changes—occurring over just four generations—males from the experimental islands developed richer

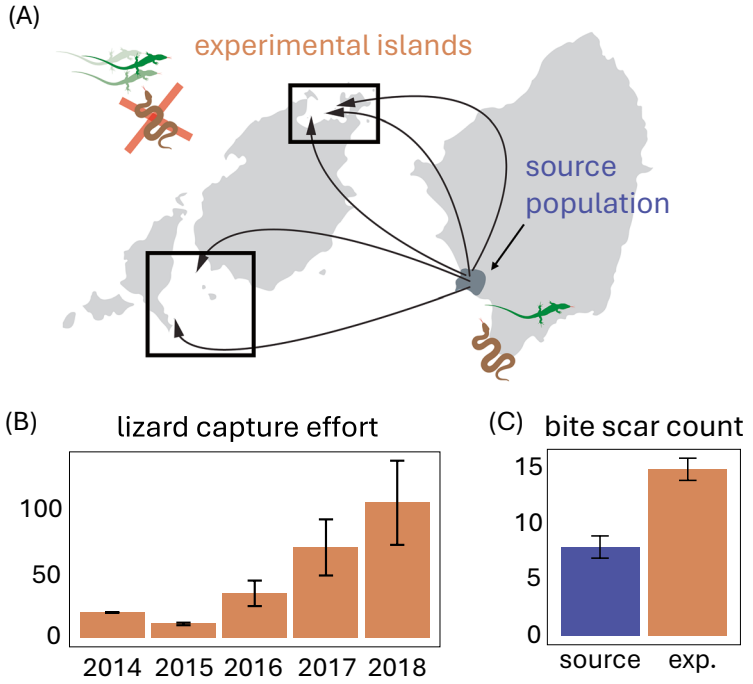


Fig. 2. Studying the speed and predictability of chemical signal divergence using an island introduction experiment. (**a**) Map of the Cycladic islands (Greece), showing the source population of *Podarcis erhardii* on the large island of Naxos and the 5 surrounding predator-free islets to which 20 lizards each were experimentally introduced in 2014 (arrows indicate translocation). (**b**) Mean annual lizard capture effort (± SE) pooled across all experimental islands from 2014 to 2018, illustrating the rapid increase in population densities following introduction. (**c**) Mean number of bite scars (± SE) recorded in 2018 from males in the source population and those on the experimental islands, highlighting elevated levels of intraspecific aggression in the predator-free experimental environments. (Data from Donihue, et al., 2020a; Baeckens, et al., 2025).

chemical secretions, with elevated levels of three lipids potentially linked to territoriality and mate attraction (Donihue, et al., 2020a). These shifts illustrate how signal design may evolve rapidly when selection pressures are relaxed on one front (i.e., predation) but heightened on another (i.e., social competition).

A follow-up longitudinal study on these same populations examined changes in scent marks from individually marked lizards over 2 consecutive years (Baeckens, et al., 2025). Across both individuals and populations, overall chemical composition shifted consistently in direction and magnitude. While the proportions of certain compounds (e.g., α-tocopherol) remained stable, others (e.g., oleic acid and octadecanoic acid) varied either over time or in a body size-dependent manner, highlighting the plasticity and complexity of individual chemical profiles. These findings provide rare empirical evidence that lizard chemical signals are dynamic traits, capable of respond-

ing to short-term ecological change. They also underscore the value of experimental and longitudinal approaches for linking specific environmental context to evolutionary shifts in communication systems.

5 Chemical Signal Evolution in the Anthropocene

We are living in an era in which human activities are reshaping ecosystems at unprecedented scales and rates (Barnosky et al., 2012; Ceballos et al., 2015). Understanding how, and how fast, animals respond to this rapidly changing world is essential for predicting population persistence and preventing extinctions (Shine & Baeckens, 2023; Stockwell et al., 2003). At the same time, such rapid anthropogenic changes offer an exceptional "natural laboratory" for studying evolution in action (Sarrazin & Lecomte, 2016).

Major anthropogenic perturbations, such as human-caused extreme climate events, biological invasions, and urbanization, are increasingly recognized as powerful evolutionary drivers (Baeckens & Donihue 2025; Grant et al., 2017; Johnson & Munshi-South, 2017; Moran & Alexander, 2014). Examples from across the animal kingdom show how such disturbances can lead to phenotypic change over short timescales: hurricanes have driven morphological evolution in anole lizards (Donihue, et al., 2020b); the introduction of cane toads in Australia has spurred evolutionary responses in both the invaders and native predators (Phillips et al., 2006; Shine, 2012), and urban environments have altered sexual signals such as frog croaks (Halfwerk et al., 2018), bird song (Slabbekoorn & Peet, 2003), and body coloration (Peneaux et al., 2021).

Yet despite the growing use of these perturbations as focal systems in evolutionary research, they have been rarely applied to the study of vertebrate chemical signaling—and remain almost entirely absent in lizard systems. This gap is striking, given that chemical signal production and efficacy are sensitive to environmental parameters that are commonly altered in human-dominated landscapes, such as temperature, pollution, and substrate structure. There is clear opportunity to explore how the urban heat island effects, soil contamination, or airborne pollutants influence chemical signal production and detectability; how invasive species reshape native signal-receiver dynamics, or how climate extremes (e.g., drought) disrupt the stability and persistence of chemical signals (Boullis et al., 2016; Groot & Zizzari, 2019). A recent study on sand lizards (*Lacerta agilis*) in Poland (Ibáñez et al., 2025) has begun to document shifts in chemical signal composition and diversity across urbanization gradients, but such efforts remain rare. Alarmingly little is known about how urbanization (delBarco-Trillo, 2026, this volume) and other anthropogenic pressures affect vertebrate chemical signaling more broadly. Expanding this research frontier is timely and necessary. Integrating chemical signaling into the broader framework of Anthropocene evolutionary biology will not only improve our understanding of how species respond to abrupt environmental change but may also help anticipate which traits or populations are most vulnerable in our rapidly changing world.

6 Outlook

Over the past decade, lizards have emerged as a promising system for studying the evolution of chemical communication. Macro-evolutionary studies have begun to reveal how climatic, ecological, and social factors shape signal diversity across species. Meanwhile, micro-evolutionary research, though still in its early stages, is uncovering how signals shift on ecological timescales.

Nonetheless, major gaps remain. Comparative work has focused heavily on a few clades, especially Old World lacertids, limiting broader generalizations. Expanding research across more lizard families and continents—while integrating multiple explanatory factors—will be crucial for developing a more comprehensive understanding of chemical signal evolution. Future studies should move beyond documenting simple correlations and instead model how traits and environments have coevolved across phylogenies (Cornwallis & Griffin, 2024).

Bridging broad evolutionary insights with behavioral function remains another critical challenge. While large-scale studies have mapped chemical diversity, the functional relevance of specific compounds remains largely unknown—although important progress is being made (Martín & López, 2024). Carefully designed behavioral assays, informed by both chemical profiling and comparative findings, will be key to understanding the information content and social utility of signals.

Perhaps most urgently, almost no work has addressed the heritability of lizard chemical signals—a prerequisite for understanding their evolutionary potential. Without estimates of genetic variance, we cannot distinguish evolutionary change from environmentally induced plasticity. Incorporating quantitative genetics and expanding genomic approaches should therefore be a major priority moving forward.

Finally, human-driven environmental change offers a powerful but underutilized opportunity to study chemical signal evolution in real time. Urbanization, biological invasions, and climate extremes are already reshaping habitats and social structures, creating novel selection pressures on communication systems.

By integrating macro- and micro-evolutionary approaches, behavioral validation, genetic foundations, and anthropogenic contexts, future work will not only expand our understanding of lizard chemical communication but also help position reptiles more centrally within the broader field of vertebrate signaling evolution. The future is bright for those eager to use lizards as a window to study the ecoevolutionary dynamics of chemical signals in vertebrates.

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