Chemical signaling glands are unlinked to species diversification in lizards

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Abstract

Sexual selection has long been thought to increase species diversification. Sexually selected traits, such as sexual signals that contribute to reproductive isolation, were thought to promote diversification. However, studies exploring links between sexually selected traits and species diversification have thus far primarily focused on visual or acoustic signals. Many animals often employ chemical signals (i.e., pheromones) for sexual communications, but large-scale analyses on the role of chemical communications in driving species diversification have been missing. Here, for the first time, we investigate whether traits associated with chemical communications—the presence of follicular epidermal glands— promote diversification across 6,672 lizard species. In most analyses, we found no strong association between the presence of follicular epidermal glands and species diversification rates, either across all lizard species or at lower phylogenetic scales. Previous studies suggest that follicular gland secretions act as species recognition signals that prevent hybridization during speciation in lizards. However, we show that geographic range overlap was no different in sibling species pairs with and without follicular epidermal glands. Together, these results imply that either follicular epidermal glands do not primarily function in sexual communications or sexually selected traits in general (here chemical communication) have a limited effect on species diversification. In our additional analysis accounting for sex-specific differences in glands, we again found no detectable effect of follicular epidermal glands on species diversification rates. Thus, our study challenges the general role of sexually selected traits in broad-scale species diversification patterns.

Keywords: follicular epidermal glands, chemical communication, sexual selection, pheromones, femoral pores, speciation

Introduction

Sexual selection has been thought of as the "engine of speciation" since Darwin (Andersson, 1995; Darwin, 1871; Lande, 1981; West-Eberhard, 1983), but support for this idea remains contentious (Kraaijeveld et al., 2011). Longstanding theories predict that sexually selected traits, which often drastically differ between closely related species, may drive speciation via several mechanisms (Lande, 1981; Maan & Seehausen, 2011; Panhuis et al., 2001; Ritchie, 2007). Most commonly, sexually selected traits that are directly involved in assortative mating and/or reproductive isolation may promote speciation (Lande, 1981; Ritchie, 2007; West-Eberhard, 1983). For instance, signaling and sensory traits are often targets of sexual selection and are important in forming reproductive barriers during or after speciation (Panhuis et al., 2001; Ritchie, 2007; Schaefer & Ruxton, 2015). Several studies, albeit at low taxonomic scales (e.g., within families), have found that sexually selected signals, such as conspicuous colors in birds and mate calls in frogs, are indeed associated with a higher rate of speciation (Beltrán et al., 2021; Boul et al., 2007; Hoskin et al., 2005; Maia et al., 2013; Portik et al., 2019; Seddon et al., 2008; Uy et al., 2018; Wilkins et al., 2013, but see Miller et al., 2021). However, despite the prevalence of various sensory modalities in sexual communication (Wiens & Tuschhoff, 2020), comparative studies regarding the influence of sexual signals on species diversification rates (speciation minus extinction rates) have been focused on visual or acoustic signals.

Sexual communication based on chemical signals is widespread across the tree of life (Johansson & Jones, 2007; Symonds & Elgar, 2008; Wiens & Tuschhoff, 2020; Wyatt, 2003). Intraspecific chemical signals, that is, pheromones, serve in the exchange of information between individuals within a species, most commonly across sexes (Johansson & Jones, 2007; Symonds & Elgar, 2008). Depending on the nature of the receiver, intraspecific chemical signals can be under intersexual (e.g., mate attraction or mate choice; Johansson & Jones, 2007) and/or intrasexual selection (e.g., during male-male contests; Moore et al., 1997). Intersexual chemical signals (sex pheromones) are often involved in assortative mating and mate choice (Johansson & Jones, 2007; Teale et al., 1994), which has been implicated in the

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process of reproductive isolation and speciation (reviewed in Smadja & Butlin, 2009).

Traditionally, intersexual chemical signals have been thought to act as species recognition signals that may promote speciation by reinforcement (Bacquet et al., 2015; Phelan & Baker, 1987, reviewed in Smadja & Butlin, 2009). Furthermore, many studies have documented geographical variation in chemical signaling and mate preference within species (Darragh et al., 2020; Groot et al., 2009; Runemark et al., 2011; Smadja & Butlin, 2009). Such interpopulation differences in chemical signals might be a result of divergent selection on chemical signals posed by distinct environmental conditions for efficient signal transfer, that is, due to sensory drive (reviewed in Yohe & Brand, 2018; Wang et al., 2021) or a correlated response because of adaptation to different local selective environments (Runemark et al., 2011). Under both these conditions, chemical signals may act as potent isolation barriers and may eventually lead to speciation in allopatry (Boughman, 2001; Servedio & Boughman, 2017; Smadja & Butlin, 2009; Yohe & Brand, 2018). Alternatively, intersexual chemical signals may also limit speciation. For instance, chemical signals may mediate preferential mating among dissimilar genotypes (i.e., negative assortative mating), thereby preventing the formation of reproductive barriers and lowering the probability of speciation (Servedio & Bürger, 2014; Van den Berg et al., 1984). However, the mechanism by which intrasexual chemical signals promote speciation (assuming they do) remains unclear. One potential hypothesis could be the widespread use of chemical signals in male-male competition, for example, as agonistic signals (Grether et al., 2009; Widemo & Johansson, 2006), that might promote speciation by a range of mechanisms (see Tinghitella et al., 2018). In summary, there is substantial evidence that sexually selected chemical signals may be involved in the process of speciation (Smadja & Butlin, 2009).

In lizards (here defined as all squamates except snakes, see below), follicular epidermal glands that secrete semiochemicals through specialized pore-bearing scales (femoral and precloacal pores) have evolved independently several times (García-Roa et al., 2017a; Mayerl et al., 2015; Schwenk, 1995). The lipophilic and proteinaceous secretions by the follicular epidermal glands are considered the primary source of chemical signals in lizard communications (Alberts, 1990; Mangiacotti et al., 2021; Martín et al., 2014; Mason & Parker, 2010; Mayerl et al., 2015). The major functions of follicular gland secretions across lizard groups remain hotly contested (Baeckens et al., 2018b; MacGregor et al., 2017; Mayerl et al., 2015). However, numerous studies have shown the use of follicular epidermal gland secretions in a range of intersexual chemical communications such as mate attraction, female mate choice, and species recognition (Martín & López, 2000; López et al., 2002; López & Martín, 2005; Martín & López, 2006a; Johansson & Jones, 2007; Martín & Lopez, 2010; Thomas, 2011; Martín & López, 2012; Gabirot et al., 2013; Raya-García et al., 2020). Other studies showed gland secretions might be involved in different stages of male-male competition to gain access to mates (i.e., intrasexual selection), including rival assessment, territorial recognition, and demarcation (Alberts et al., 1992; Hews et al., 2011; López & Martín, 2002, 2011; Martín & López, 2007; Martín et al., 2007). Under both these selection scenarios, follicular gland-mediated chemical signaling may act as a potent isolation barrier (Servedio & Boughman, 2017;

Smadja & Butlin, 2009; Yohe & Brand, 2018). For instance, many closely related lizard species often differ drastically in their chemical compounds secreted via follicular epidermal glands (Baeckens et al., 2018b; Donihue et al., 2020; Kabir et al., 2020; Mangiacotti et al., 2021). Thus, these compounds have been presumed to enable species recognition (Barbosa et al., 2005; Gabirot et al., 2010a, 2010b; García-Roa et al., 2016a; Labra, 2011; Mangiacotti et al., 2021; Marshall et al., 2002; Martín & López, 2006b; Raya-García et al., 2020; Zozaya et al., 2019), suggesting potential involvement of these compounds in speciation by reinforcement in sympatry. Many studies have also shown geographic variation in follicular gland chemical signal composition and the number of glands (Baeckens et al., 2018a; Campos et al., 2020; Martín Rueda et al., 2015), and corresponding mate preference divergence in lizards (Khannoon et al., 2013; Raya-García et al., 2020; Runemark et al., 2011; Servedio & Boughman, 2017; Yohe & Brand, 2018). Such divergence in chemical composition is tightly linked to environmental factors (Baeckens et al., 2015, 2018a; Jara et al., 2018; Romero-Diaz et al., 2021), which might be a result of sensory drive and may lead to the formation of cryptic species in allopatry (Gabirot et al., 2012; Martín Rueda et al., 2015; Yohe & Brand, 2018; Zozaya et al., 2019). Overall, above evidence indicates that follicular gland-mediated chemical signaling in lizards may act as a reproductive barrier.

In general, factors influencing reproductive isolation (e.g., occurrence of sexual signals) among populations may affect species diversification (Sobel et al., 2010). Thus, follicular gland-mediated chemical communication may explain diversification rate differences across lizard lineages. This topic is of prime importance not only in understanding the macroevolutionary consequences of chemical communications in lizards but also for theories on sexually selected signaling strategies and speciation research. Understanding the role of sexual selection in governing species diversification has long been a major goal of evolutionary biology (Andersson, 1995; Darwin, 1871; Lande, 1981; West-Eberhard, 1983). Despite chemical signals being a universal form of sexual communication (Symonds & Elgar, 2008), to-date no large-scale study has tested its role in promoting diversification rates. Furthermore, comparative studies have found mixed support for the role of sexually selected traits in driving diversification rates (e.g., Chen & Wiens, 2020; Emberts & Wiens, 2021; Huang & Rabosky, 2014; Miller et al., 2021). An important question is whether only certain types of sexually selected traits affect diversification (e.g., chemical but not acoustic). Thus, understanding the importance of chemical signaling in diversification will shed light on the effect (or lack thereof) of sexual signaling strategies across different modes of communication strategies in general (Wiens & Tuschhoff, 2020). Finally, our macroevolutionary approach may also help settle the debate on the general role of chemical communication in lizard speciation (see García-Roa & Carazo, 2017; MacGregor et al., 2017).

Earlier investigations that examined the tempo and mode of follicular gland evolution within a phylogenetic framework showed heterogeneity in gland number and chemical secretion evolution among different lizard groups (García-Roa et al., 2017a, 2017b). However, it is currently unclear what the exact mechanism by which variation in gland number or location (femoral or precloacal) might be under selection related to either the type or amount of chemical secretions (Baeckens et al., 2015; Pincheira-Donoso et al., 2008), and potentially to speciation. More importantly, none of the previous studies have tested whether the occurrence of chemical signaling glands per se is related to lineage and species diversification rates. Here, we extensively tested whether the independent origins of the follicular epidermal gland are associated with increased species diversification rates in thousands of lizard species using three different statistical methods.

If follicular epidermal glands in lizards predominantly function as a sexual signal, we predicted that lineages with follicular epidermal glands would have a different diversification rate than those without follicular epidermal glands. We also performed additional analyses to understand the overall geographic mode of speciation that follicular gland chemical signals may aid in, assuming follicular gland secretions are involved in the formation of reproductive barriers. Specifically, if secretions from follicular epidermal glands are predominantly involved in species recognition, that is, act as a "species identity badge" for reinforcement, we predicted the follicular epidermal gland system would be more common in sympatry/parapatry than in allopatric sibling species (Symonds & Elgar, 2004).

Alternatively, if follicular epidermal glands are unrelated to diversification rates because (a) sexual signals drive diversifications only in some clades and not in other/in whole group (see Miller et al., 2021), (b) follicular epidermal glands' primary functions are unrelated to sexual signaling (e.g., MacGregor et al., 2017), or (c) sexually selected signals do not affect diversification rates (e.g., Chen & Wiens, 2020; Emberts & Wiens, 2021; Huang & Rabosky, 2014). To tease apart these alternative possibilities, we first tested the influence of follicular gland on diversification across different taxonomic time scales-for all lizard species, infraorders, and lizard families (Graham et al., 2018). We predicted that the effect of follicular gland occurrence on species diversification to be much stronger in shallower time scale (e.g., family) than in deep time scales (e.g., infraorder) as such shallow timescale effects on diversification, for other sexual traits (e.g., sexual dichromatism; Miller et al., 2021), were shown to be stronger in recent studies. To address the above alternative possibility (c), we repeated our analysis in one family of lizards (Liolaemidae; see Methods) using a data set with explicit information on sex-specific gland occurrence. In many Liolaemid species, glands are entirely absent in females-expected if follicular gland occurrence is a product of sexual selection. Therefore, we expect that sex-specific occurrence of follicular glands (i.e., only in males) to be unrelated to diversification rates if sexually selected traits generally have no effect on species diversification rates.

Methods

Data collection and phylogeny

We gathered data on the occurrence of follicular epidermal glands for 6,672 of 7,261 lizard species (~92%) valid as of the August 2021 version of the reptile database (Uetz et al., 2021). We obtained data for 4,461 species from a previous study (García-Roa et al., 2017a) and additional data for 2,211 species from primary literature source. For all species in our data set, we recorded the location of the specialized secretion pores: (a) femoral pores—present on both hind legs and (b) precloacal pores—present above the anterior border of the cloaca (see Supplementary Figure S1), and the mean

Some species show geographic variation in pore presence and pore size (e.g., Bezy, 1967). However, such geographic variation is not reported for most species. Therefore, we could not account for it in our study. Nevertheless, in cases where species show geographic variation in pore size or presence, we coded them as having follicular glands. Chemical communication in many reptiles is sometimes achieved via secreting organs other than the follicular epidermal glands. For instance, almost all skink species lack follicular epidermal glands and henceforth are coded as gland absence in our study. Nevertheless, some skinks employ chemical communication by other means (e.g., for intraspecific signaling via skin-derived chemical signals: Cooper & Vitt, 1986, fecal secretions: Fenner & Bull, 2011; see Discussion). However, since data on whether such chemical signaling is present in other species are not available for most species, coding species as chemically signaling or not risks a substantial amount of false negative data. Therefore, we solely focus on the association between follicular glands and species diversification (similar to, e.g., García-Roa et al., 2017a), and not all modes of chemical signaling.

In total, 2,773 of the 6,672 lizard species (41.56%) in our dataset had either femoral or precloacal pores (Supplementary Data). Some lizard species (e.g., many members of the family Anguidae) lack legs. Femoral pores cannot be present in such species. However, many legless lizards have precloacal pores (e.g., Pygopus and most amphisbaenians; Supplementary Data; Mayerl et al., 2015). Therefore, we did not omit legless lizards from our analysis. Snakes, a large monophyletic group nested within lizards, entirely lack follicular epidermal glands (i.e., both femoral and precloacal pores; Mason & Parker, 2010; Weldon et al., 2008). Hence, our analyses are focused only on lizards. However, we ran a sensitivity analysis that includes snakes (coded as having no follicular epidermal glands; see Supplementary Material, Supplementary Table S2, and Supplementary Figure S7) to test whether their inclusion might change our results.

In many lizard species, follicular glands are present only in males. However, sex-specific differences are not reported for most species, so we consider follicular epidermal gland presence if pores were observed in either of the sexes (García-Roa et al., 2017a). Nevertheless, to understand sex-specific follicular gland differences in explaining diversification rates (i.e., expected under sexual selection), we collected follicular gland data (i.e., the presence or absence of femoral and/or precloacal pores) separately for males and females in the family Liolaemidae for which data on follicular gland presence is frequently reported for both the sexes (295 of 333 species in this family). Sex-specific data for other families and infraorders are scarce (not available for >50% of species).

We used the Tonini et al. (2016) DNA-only (i.e., non-PAS-TIS) time-calibrated phylogenetic tree in our study because it contains more sampled species than the (Zheng & Wiens, 2016) tree. We could match data for 3,535 species in this tree of the 6,672 lizard species that had information on the presence or absence of follicular glands. We nevertheless used data for all 6,672 species to account for incomplete sampling in the diversification analyses (see below).

Diversification rates

We used three methods to infer the influence of follicular epidermal glands (a binary trait) on diversification rates. We focused on tip-level estimates of diversification rates and did not estimate speciation and extinction rates separately as they are difficult to accurately estimate using extant phylogeny (Bhaskar et al., 2020, Upham et al., 2021). All the analyses were carried out in the R statistical software version 4.2.0 (R Core Team, 2022).

State-dependent speciation and extinction

We used state-dependent diversification models to understand the influence of binary character (follicular gland) on diversification rates. The state-dependent speciation and extinction models are a class of birth-death models where diversification rates depend on evolving character traits (Maddison et al., 2007). We use two commonly used families of models: (a) the Binary State Speciation and Extinction (BiSSE; Maddison et al., 2007) and (b) the Hidden State Speciation and Extinction (HiSSE; Beaulieu & O'Meara, 2016). The main difference is that HiSSE accounts for an unknown "hidden trait" in addition to the trait of interest that may influence the diversification rate. The HiSSE framework is thus better than the BiSSE in accurately detecting trait association with rate shifts, as the BiSSE models are prone to high Type 1 errors (Rabosky & Goldberg, 2015). We had a total of 9 SSE models in our analysis (see below). State-dependent speciation and extinction (SSE) analyses were carried out using the hisse package (Beaulieu et al., 2022).

In the complex BiSSE model, (a) both diversification and transition rates are different for each observed state (i.e., presence or absence of follicular glands; *BiSSE full*). Under this model, the diversification is thus allowed to differ between the lineages with and without follicular epidermal glands. In the subsequent two models, (b) only diversification (*BiSSE equal trans*), or (c) transition rate (*BiSSE equal DR*), across the states are allowed to vary. In the simplest BiSSE model (d), both diversification and transition rates between the states are constrained to be the same (*BiSSE null*).

We also included three hidden state models in the comparisons. In the first two HiSSE models, the diversification rate was different for each of the four combinations of the two observed states (presence or absence of follicular epidermal glands) and two hidden states (A and B), that is, four parameters of turnover. These two models differed in the number of transition rates. In the most complex HiSSE model (HiSSE full), (e) included five parameters of transitions among states, involving a single transition rate among the observed hidden states $(0A \rightarrow 0B \text{ or } 1A \rightarrow 1B)$ but a different rate for each of the combinations of observed and hidden states (0A \rightarrow 1A, 1A \rightarrow 0A, 0B \rightarrow 1B, and 1B \rightarrow 0B). The simple HiSSE model (f) had three transition rates (*HiSSE simple*). This model included a single transition rate in each direction between follicular gland presence and absence (i.e., irrespective of hidden state) and a single transition rate parameter among the hidden state. In the third HiSSE model (g), the diversification rates are allowed to vary only between the hidden states and have a single transition rate parameter for both hidden and observed

states (*HiSSE null*). The last two null models included character-independent diversification rates under which the diversification rates are unlinked to character transitions. The first model (h) had four diversification rate parameters to resemble a BiSSE model (*CID-2*). The later model (i) included eight diversification rate parameters to resemble a HiSSE model (*CID-4*).

In all the SSE models, we incorporated sampling fractions for each state separately to account for incomplete taxon sampling. We specified state-specific sampling fraction by calculating the proportion of sampled species in the analysis for each state from the global dataset (6,672 species). In the global level analyses, we assigned a prior probability of follicular gland absence to be 1 in the root node based on previous evidence (García-Roa et al., 2017a; Mayerl et al., 2015). Relative fits of the model were determined using Akaike weights (AICw). Tip-level net diversification rates were obtained by a model averaging procedure using the AICw. In model averaging, we included models that contributed $\geq 5\%$ of the total AICw, following Caetano et al. (2018). Tip-level net diversification rates were compared between species with and without follicular glands using phylogenetic ANOVA (Garland et al., 1993) from the phytools package (Revell, 2012).

Structured rate permutations on phylogenies

To corroborate results from SSE models, we also conducted Bayesian Analysis of Macroevolutionary Mixtures (BAMM) analysis that estimates diversification rates independent of trait evolution (Rabosky, 2014). We used default BAMM settings with the number of iterations set to 100,000,000 and priors specified using the setBAMMpriors function from the BAMMtools package in R (Rabosky et al., 2022). To account for incomplete sampling, the sampling probability was set as the proportion of species included in the analysis (0.48; i.e., 3,535/7,262 lizard species). The MCMC (Markov chain Monte Carlo) output convergence was evaluated using the conda package (Plummer et al., 2006). We discarded the first 10% of the posterior samples as burn-in and ensured that all analyses had an effective sample size > 200. We then performed structured rate permutations on phylogenies (STRAPP) analysis to test for the influence of binary traits on diversification rates estimated by BAMM. In the STRAPP analysis, we performed 10,000 permutations of the BAMM rate shifts associated with each species under a null distribution of the Mann-Whitney U-test statistics using the traitDependentBAMM function. Diversification rates are estimated using time-constant and time-variable BAMM models in two separate runs.

Fast, intuitive state-dependent speciation-extinction

We also performed a nonparametric test (FiSSE) to understand the influence of follicular epidermal glands on speciation rates—fast, intuitive state-dependent speciation–extinction (FiSSE) analysis (Rabosky & Goldberg, 2017). Here, the speciation rate value was first calculated using the inverse of equal splits statistics (weighted sum of branch lengths between the tip and the tree's root) and compared between clades with and without follicular epidermal glands (Rabosky & Goldberg, 2017). For null comparisons, we simulated follicular epidermal glands 5,000 times using the empirical transition rate parameters and calculated the inverse equal-split statics for each simulation. The inverse of equal-split statistics estimated from the simulations is then compared against the empirical value (Rabosky & Goldberg, 2017).

Subclade-level analyses and sexual differences in follicular glands

To understand the phylogenetic scale-dependency of the follicular gland on diversification rates (Miller et al., 2021), we repeated SSE analyses focusing on shallower phylogenetic scales-infraorders and families. We followed the August 2021 version of the Reptile Database taxonomic scheme for family, and infraorder classification (Uetz et al., 2021). In these analyses, we used only families and infraorders with $\geq 10\%$ but $\leq 90\%$ of their species presenting follicular epidermal glands. We arrived at this threshold as SSE models have low power in detecting rate shifts when one character state is much rarer than another (<10%; Davis et al., 2013; Kodandaramaiah & Murali, 2018). Following this criterion, we repeated SSE analysis for three families (Agamidae, Gekkonidae, and Diplodactylidae) and two infraorders (Iguania and Gekkota). In some clade-level analyses, although we found support for the character-independent diversification model (e.g., Gekkonidae), the comparison of tip-level rates using phylogenetic ANOVA revealed significant differences. We consider such significant results are likely due to hidden trait effects on diversification (Beaulieu & O'Meara, 2016; Miller et al., 2021). Furthermore, for clades that received support for character-dependent model of diversification, we performed additional simulation analysis to understand whether these results were due to model inadequacy (see Supplementary Material; Caetano et al., 2018; Rabosky & Goldberg, 2015).

To account for sex-specific differences in the occurrence of follicular glands, we repeated our SSE analysis for the family Liolaemidae. We coded the presence or absence of follicular epidermal glands as a binary trait for males and females of each species separately. However, for the SSE analysis, we recoded the sex-specific data as the presence of follicular gland only when it was reported in males and not in both sexes. We did not perform a multicharacter SSE analysis (e.g., MuHiSSE; Herrera-Alsina et al., 2019) as only in 8.1% of species, both sexes lack follicular glands, and there are no species in which only females have glands. We did not perform BAMM for both sexual differences and subclade-level analyses as this approach has low power in detecting trait associations with rate shifts for smaller tree sizes (Kodandaramaiah & Murali, 2018; Moore et al., 2016; Rabosky & Huang, 2016).

Follicular epidermal gland and species range dynamics

To understand whether the follicular epidermal gland is more common in sympatry than allopatry, we tested for differences in the amount of range overlap between sister species pairs with (a) both species having follicular epidermal gland (presence-presence), (b) both species have no follicular epidermal gland (absence-absence), and (c) one of them having follicular epidermal gland (presence-absence). However, because there were only three sister pairs where only one has follicular epidermal glands, we did not include them in the statical comparisons.

Sister pairs were identified using the phylogeny of Tonini et al. (2016). We used the function *extract_sisters* from the *diverge* package to obtain sister pairs (Anderson & Weir, 2021). To ensure the identified sister pairs represent the true evolutionary relationships, only sister pairs in genera represented by more than 80% of species in the genus were retained (Jezkova & Wiens, 2018). Finally, the proportion of range overlap was calculated as the area of species with the smallest range divided by the area shared by both species. Species distribution maps were obtained from the updated version (GARD 1.7) of (Roll et al., 2017, available from Caetano et al., 2022). We employed the phylogenetic ANOVA for this analysis.

Results

Follicular epidermal gland and species diversification

The character-independent model (CID-4) received the best support out of the nine models in our SSE analysis (AICw: 0.999; Table 1), suggesting no association between the follicular gland and net diversification rates at the global level. Indeed, our comparison of the tip-level diversification rates from the best model shows no significant differences between lineages with and without follicular epidermal glands (mean $DR_{absence}$: 0.0934; $DR_{presence}$:0.0937; p = .284). Ancestral state estimates from the best model show follicular glands are present in most lineages of the infraorder Lacertoidea and have been repeatedly lost in the Gekkota and Iguania (Figure 1).

The BAMM analyses identified 33 and 42 shifts in net diversification rates under the time-constant and time-variable models, respectively (Supplementary Figures S2–S4). Irrespective of the model used, STRAPP analysis also found no significant effect of the follicular gland on net diversification rate (time-constant model: p = .884; time-variable model: p = .876). The nonparametric FiSSE analyses also corroborated BAMM and SSE analyses showing no effect of follicular glands on speciation rates ($\lambda_0 = 0.089$; $\lambda_1 = 0.090$; p = .929).

Subclade-level analyses and sexual differences in follicular glands

The subclade-level SSE analyses show support for the character-independent diversification models in four out of five clades (see all AICws in Table 2). In the family Diplodactylidae

Table 1. Summary of state-dependent speciation and extinctionhypotheses and associated model fits from diversification analyses forthe global data set.

Model	AIC	ΔΑΙC	AICw	
BiSSE full	28,353.763	758.851	< 0.001	
BiSSE equal trans	28,436.491	841.579	< 0.001	
BiSSE equal DR	28,355.464	760.552	< 0.001	
BiSSE null	28,438.861	843.948	< 0.001	
HiSSE full	27,818.028	223.115	< 0.001	
HiSSE simple	27,818.538	223.625	< 0.001	
HiSSE null	27,882.222	287.31	< 0.001	
CID-2	28,359.474	764.561	< 0.001	
CID-4	27,594.913	0	0.9999	

Note. AIC = Akaike information criterion; ΔAIC = the difference in Akaike scores between the best model and the current model; AICw = Akaike weights. See methods for a full abbreviation of models. Bold row represents the model with the highest AICw.

and in both Gekkota and Iguania, the tip-level diversification rates are not significantly different between lineages with and without follicular glands (all P > .05; Figure 2). Although the independent character model received the highest support in the Gekkonidae (Table 2), the model-averaged net diversification rates were significantly higher in lineages with follicular glands than without them (F =171.373; p = .003). Finally, we received some support for character-dependent diversification in the family Agamidae (HiSSE simple AICw: 0.519; Table 2). Model-averaged tip rates in the Agamidae showed the net diversification rates were significantly lower in lineages with follicular glands than in lineages without them (F = 195.903; p = .008; Figure 2). However, further simulation analyses confirmed that this is likely a result of the underlying tree structure rather than a true association (Supplementary Figure S5). The FiSSE analysis also showed no significant associations in none of the clades (Supplementary Table S1).

The analyses accounting for sex differences in the follicular gland in the Liolaemidae found equal support for character-dependant and -independent model of diversification rates in SSE analysis (HiSSE full and HiSSE null: AICw = 0.49; Table 3). The tip-level diversification rates however showed no significant association with follicular glands (Figure 3;



Figure 1. Follicular epidermal gland and species diversification in lizards. (A) Ancestral state reconstructed using parameter estimates from best-fit state-dependent speciation and extinction (SSE) model (gray—absence of follicular gland and green—presence of follicular gland); prevalence of follicular glands in three major infraorders are highlighted. (B) Box-violin plot showing the model-averaged tip-level diversification rates for lineages with follicular glands (presence) and no follicular glands (absence) from the SSE model. Boxplots show the medians, first and third quartiles, and outliers (black). *p*-value from phylogenetic ANOVA comparing the two groups is provided at the top.

Table 2: Summary of state-dependent speciation and extinction hypotheses and associated model fits from diversification analyses for the subcladelevel analysis.

	Iguania		Gekkota		Agamidae		Gekkonidae		Diplodactyloidae	
	AIC	AICw	AIC	AICw	AIC	AICw	AIC	AICw	AIC	AICw
BiSSE full	8,839.399	< 0.001	7,958.39	< 0.001	2086.065	0.001	4,753.57	< 0.001	823.708	0.006
BiSSE equal trans	8,884.982	< 0.001	7,985.71	< 0.001	2,094.971	< 0.001	4,761.33	< 0.001	823.465	0.007
BiSSE equal DR	8,857.258	< 0.001	7,998.128	< 0.001	2,089.753	< 0.001	4,780.774	< 0.001	821.708	0.016
BiSSE null	8,902.071	< 0.001	8,020.898	< 0.001	2,099.293	< 0.001	4,787.107	< 0.001	821.477	0.018
HiSSE full	8,710.067	< 0.001	7,867.771	0.002	2,075.961	0.16	4,709.305	0.081	821.599	0.017
HiSSE simple	8,689.806	0.141	7,870.672	< 0.001	2,073.608	0.519	4,708.406	0.127	817.814	0.11
HiSSE null	8,725.125	< 0.001	7,948.743	< 0.001	2,097.71	< 0.001	4,747.882	< 0.001	819.396	0.05
CID-2	8,728.599	< 0.001	7,893.123	< 0.001	2,086.378	0.001	4,785.369	< 0.001	825.708	0.002
CID-4	8,686.186	0.859	7,855.364	0.998	2,074.581	0.319	4,704.748	0.792	813.916	0.775

Note. AIC = Akaike information criterion. AICw = Akaike weights. See Methods for a full abbreviation of models. Bold row represents the model with the highest AICw.



Figure 2. Follicular epidermal gland and species diversification in lizards (subclade-level analyses). Box-violin plot showing the model-averaged tip-level diversification rates for lineages with follicular glands (presence) and no follicular glands (absence) from the state-dependent speciation and extinction model for (A) Iguania, (B) Gekkota, (C) Gekkonidae, (D) Agamidae, and (E) Diplodactylidae. Boxplots show the medians, first and third quartiles, and outliers (black). *p*-value from phylogenetic ANOVA comparing the two groups is provided at the top. CID-4 model received the highest support for Gekkonidae.

Table 3. Summary of state-dependent speciation and extinction

 hypotheses and associated model fits from diversification analyses for

 the family Liolaemidae.

Model	AIC	ΔΑΙC	AICw
BiSSE full	1,109.664	22.092	<0.001
BiSSE equal trans	1,108.016	20.444	< 0.001
BiSSE equal DR	1,118.956	31.384	< 0.001
BiSSE null	1,106.362	18.79	< 0.001
HiSSE full	1,087.578	0.006	0.49
HiSSE simple	1,094.178	6.606	0.018
HiSSE null	1,087.572	0	0.491
CID-2	1,101.977	14.406	< 0.001
CID-4	1,103.39	15.819	< 0.001

Note. AIC = Akaike information criterion; Δ AIC = difference in Akaike scores between the best model and current model; AICw = Akaike weights See Methods for a full abbreviation of models. Bold rows represents model with highest AICw.

p = .186), so does the FiSSE analysis ($\lambda_0 = 0.209$; $\lambda_1 = 0.248$; p = .4195).

Follicular epidermal gland system and species range dynamics

We identified a total of 250 sister species pairs, of which 81 pairs had follicular glands in both species and 166 species pairs had no follicular epidermal glands (and three had a mixed condition, see above). The distribution of proportion geographic range overlap between the sister pairs is right-skewed (median = 0.024), with most sibling species pairs not overlapping in their present geographic range (Supplementary



Figure 3. Follicular epidermal gland and species diversification in Liolaemidae. Box-violin plot showing the tip-level diversification rates for lineages with follicular glands (presence) and no follicular glands (absence) from the best-fit state-dependent speciation and extinction model. Boxplots show the medians, first and third quartiles, and outliers (black). *p*-value from phylogenetic ANOVA comparing the two groups is provided on top.

Figure S6). We found no significant difference in the amount of geographic range overlap between sister species pairs with and without follicular glands (Figure 4; p = .819).

Discussion

Sexual section has long been thought to be involved in the process of speciation, with most comparative studies focusing on visual and acoustic signals. In this study, we investigated



Figure 4. Follicular epidermal gland and geographic range dynamics. Box-violin plot showing the proportion of geographic range overlap between sister species pairs with both species pairs having follicular glands (presence–presence) and not having glands (absence–absence). Boxplots show the medians, first and third quartiles, and outliers (black). *p*-value from phylogenetic ANOVA comparing the two groups is provided at the top.

a key missing aspect, chemical signals-an alternative signaling strategy-that may affect diversification rates for the first time. Chemical signaling via follicular epidermal gland is highly prevalent in lizards (i.e., excluding snakes), with over 41% of currently recognized species having either femoral or precloacal pores (Figure 1A). Such widespread occurrence is expected if follicular glands have influenced the rate at which species diversify. However, contrary to our prediction, we found that diversification rates in lineages with and without follicular glands are similar in all lizards and across major families and infraorders. Furthermore, we also found that the degree of geographic range overlap between sister species or range size are unrelated to follicular glands. Our results suggest that follicular epidermal glands occurrence may not be involved in species diversification in lizards. In general, our study implies that sexually selected signaling strategiesbeyond acoustic and visual signaling-have minimal role on large-scale species diversification dynamics.

Our results add to a recent growing body of evidence that shows sexually selected traits (e.g., colors, songs, and weapons) have a limited role in governing large-scale diversification patterns (Chen & Wiens, 2020; Emberts & Wiens, 2021; Huang & Rabosky, 2014, Miller et al., 2021). The lack of relationship we found between the presence of follicular glands and diversification rates is puzzling as several studies found evidence for chemical signals in species recognition and assortative mating in lizards (Barbosa et al., 2005; Colosimo et al., 2020; Gabirot et al., 2010b, 2010a, 2012; Labra, 2011; López & Martín, 2002; Mangiacotti et al., 2021; Martín & López, 2006b; Zozaya et al., 2019). However, these studies did not test links between the presence of follicular glands and an increase in species diversification rates, but only on chemical composition. One possible explanation for this discrepancy is that the effects of sexual signaling traits on diversification are scale-dependent, as shown for other sexually selected traits (Kraaijeveld et al., 2011; Miller et al., 2021). For example, a recent comprehensive study found the rate of range expansion as a major driver of diversification in lizards and snakes compared to all other ecological and life-history

traits (did not include follicular glands; Li & Wiens, 2022). It may be that chemical signaling has an effect only within some lizard groups. However, when we repeated our analyses at much shallower phylogenetic scales (families and infraorders), we again failed to find support for this idea. Although the infraorder Iguania and Gekkonidae showed some weak effect in the SSE analysis, this is potentially due to other hidden trait effects on diversification-as the character-independent model received the best support (Beaulieu & O'Meara, 2016, Miller et al., 2021). Agamids showed a negative effect of follicular gland presence on diversification rate. However, simulation analysis suggested this is likely due to model inadequacy (Supplementary Materials; see also Rabosky & Goldberg, 2015). Given that we found consistent results across the three methods and our dataset covered almost all lizard species (92%), we think our results are less influenced by the limitations of the methods we employed or data coverage (Mynard et al., 2023).

There could be a range of explanations for why we did not find an association between diversification rates and chemical signaling glands in lizards. First, follicular glands majorly perform functions unrelated to mate choice or species recognition such that they need not necessarily be related to speciation. For instance, follicular glands may be under sexual selection in some species and not in others. In accordance with this view, studies have suggested the involvement of follicular epidermal glands in social communications (Baeckens & Whiting, 2021; Mason & Parker, 2010). Under this scenario, we do not expect follicular epidermal glands to be associated with diversification rates. A related critique could be that follicular glands are sometimes present in both sexes and therefore have not evolved under sexual selection. However, our analysis that considered the sex-specific differences in follicular glands in the family Liolaemidae also failed to reveal a significant effect of follicular gland on diversification (Figure 3 and Table 3). Follicular gland secretions are known to be involved in species recognition in some Liolaemus species (García-Roa et al., 2016b; Labra, 2011; Labra et al., 2001). We are therefore fairly confident in our conclusion that sexually mediated chemical signaling based on follicular glands has limited influence on diversification. Furthermore, follicular glands might be involved in the generation of reproductive barriers to prevent hybridization, but this may not be the main driver of the rate at which species diversify at the macroevolutionary scale. This argument is well supported by the fact that many lizard species tend to form hybrids (Jančúchová-Lásková et al., 2015), especially in lizards lineages that have follicular glands (e.g., in family Lacertiade: Jančúchová-Lásková et al., 2015 or lizard genus Liolaemus: Olave et al., 2018). We considered the occurrence of follicular glands (presence/absence) as a proxy for chemical signaling. Such an assumption does not account for differences in chemical gland secretion composition between species. Therefore, it is possible that diversity in gland secretion composition might be linked to diversification rates, while the occurrence of glands per se does not. Finally, follicular gland-based chemical signals may be primarily involved in male-male competition in lizards (e.g., Martín & López, 2007), but the general mechanism by which it affects diversification is less clear (reviewed in Tinghitella et al., 2018). It may be that traits that mediate male-male competition have no stronger effect on diversification at large scales (Emberts & Wiens, 2021).

Signaling traits could be under direct selection (i.e., divergent selection) in sympatry during the process of speciation or after secondary contact to maintain reproductive isolation and prevent hybridization (Schaefer & Ruxton, 2015; Symonds & Elgar, 2008; West-Eberhard, 1983). Although we did not directly test signal divergence (see, for instance, Mangiacotti et al., 2021), we predicted that follicular glands might be selected for in lizard lineages showing greater sympatry. Our analysis failed to recover an association between the amount of geographic range overlap among sister species pairs with follicular gland occurrence. Since most squamate species speciated allopatrically (Supplementary Figure S6; Jezkova & Wiens, 2018), reinforcement via signaling may be selected for in only a few species. Previous studies have shown divergent chemical signaling between closely related species (Gabirot et al., 2010b, 2012; García-Roa et al., 2016a; Labra, 2011; Raya-García et al., 2020) that seem to be modulated by environmental factors (Baeckens et al., 2015, 2018a; Jara et al., 2018; Romero-Diaz et al., 2021), but recent evidence indicates that involvement of such chemical signals in preventing hybridization is limited (MacGregor et al., 2017). Combined, our results imply that the follicular gland may play only a minor role in the evolution of reproductive isolation in most lizard species. Nevertheless, it is important to note that some species may use a combination of signaling modalities for reinforcement under some conditions (e.g., color and pheromones; Kabir et al., 2020). It is currently unclear if chemical signals may aid reproductive isolation in this context. Clearly, large-scale studies are essential to understand the additive effect of multiple signaling modalities on reproductive isolation and species diversification (Partan, 2013).

Many lizard species chemically communicate via secreting organs other than the follicular epidermal glands. For example, some lizards (e.g., in the genus Tropidurus) have melanistic patches in the ventral sides of their thighs and their cloacae that may secrete chemicals for communication (Bruinjé et al., 2020). Certain cordylid lizards possess, in addition to follicular epidermal glands, generational glands that might be used in marking territories (Mouton et al., 2014). Apart from this, some reptiles are also known to communicate chemically via fecal secretions (Moreira et al., 2008; Schwenk, 1995). For instance, many snakes use fecal secretions as a major mode of chemical signaling as they lack follicular epidermal glands (Ford, 1986), and many snakes and lizards also chemically communicate via skin-derived chemical signals (Shine et al., 2002, Whiting et al., 2009). We did not account for such alternative modes of chemical signaling as they are rarely reported. However, such chemical signaling may also act as a potent reproductive barrier. For example, Shine et al. (2002) found male-directed courtship behavior to be much stronger against skin secretions of conspecific but not heterospecific female sea snakes and that the skin secretions may act as an isolation barrier in sympatry. It is possible that these alternative chemical communications may affect diversification even when follicular glands do not. We acknowledge that our conclusions pertain strictly to follicular gland-based chemical signals in lizards. We also emphasize that chemical signaling may have a stronger effect on diversification in other groups, such as insects (e.g., Cama et al., 2022), which remains to be explored.

Overall, our study found little support for an association between the presence of chemical signaling follicular epidermal glands and species diversification rates in lizards in general and even after accounting for sex-specific differences. Recent evidence suggests follicular epidermal gland secretions may act as species recognition signals and enable cryptic speciation in some lizards (Mangiacotti et al., 2021; Zozaya et al., 2019). Our results imply that, in general, follicular epidermal glands (i.e., a proxy for chemical signaling that might be under sexual selection) do not appear to influence species diversification rates at the broader phylogenetic context. However, these results do not eliminate the possibility that diversification rates are influenced by specific types of chemical signaling traits (e.g., specific chemical compositions of gland secretions) or chemical-secreting organs other than the follicular epidermal glands in lizards. Our study adds to the longstanding debate on the role of sexually selected traits in governing large-scale diversification patterns (Chen & Wiens 2020; Emberts & Wiens, 2021; Huang & Rabosky, 2014; Kraaijeveld et al., 2011; Miller et al., 2021).

Supplementary material

Supplementary material is available online at Evolution.

Data availability

The data set and R codes supporting the results are made available in the figshare repository (private link: https://figshare.com/s/53e6ddf2836e8f42e6d2).

Ethical statement

None declared.

Author contributions

G.M. devised the study, performed the analyses, and led the writing. U.R. and S.M. advised on methodology and study design and contributed to the revision of the manuscript.

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