Color polymorphism and conspicuousness do not increase speciation rates in Lacertids

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Abstract

Conspicuous body colors and color polymorphism have been hypothesized to increase rates of speciation. Conspicuous colors are evolutionary labile, and often involved in intraspecific sexual signaling and thus may provide a raw material from which reproductive isolation can easily evolve, while polymorphism could favor rapid evolution of new lineages through morphic speciation. Here, we investigated the influence of the presence/absence of conspicuous colorations, and of color polymorphism on the speciation of Lacertids. We used several state-dependent diversification models, and showed that, regardless of the methods, conspicuous colorations and color polymorphism were not related to species speciation. While the lack of correlation between conspicuous colorations and speciation rates is in line with most of the literature testing this hypothesis, the results for color polymorphism contradict previous studies, and question the generality of the morphic speciation hypothesis.

Key words: coloration**,** sexual selection, polymorphism, speciation, reptile

INTRODUCTION

Species diversification is not a constant process across time and taxonomic groups (Rabosky et al. 2007; Diaz et al. 2019). Within cephalopods for example, the Octopus order contains hundreds of species, while the much older order Nautilida only contains three species (Lindgren et al. 2004). Numerous studies have tried to explain these variations in diversification rates by investigating the links between ecology, life history traits or phenotype and extinction or speciation rates (Cardillo et al. 2003; Arbuckle and Speed 2015; Cooney and Thomas 2020). Among the traits investigated, those under sexual selection (sexual traits) have attracted a lot of attention because divergence in sexual traits can generate reproductive isolation between parapatric (Boul et al. 2007) or allopatric lineages (Price 1998; Panhuis et al. 2001) and strengthen reproductive barriers during secondary contact (Svedin et al. 2008), hence increasing speciation rates. However, sexual selection may also impose a burden on population viability and hence to increase extinction rates (Houle and Kondrashov 2002; Doherty et al. 2003; Kokko and Brooks 2003). The outcome of these opposing processes is difficult to predict and, until now, studies linking sexual selection and diversification rates have produced mixed results (Barraclough et al. 1995; Seehausen 2000; Kraaijeveld et al. 2011; Huang and Rabosky 2014; Cooney et al. 2017).

Another trait long suspected to increase the rates of speciation is polymorphism, here defined as the co-occurrence of as several discrete, heritable morphs co-occurring within populations. Polymorphic species have been suggested to have higher speciation rates, based on two lines of reasoning resting mainly on indirect or theoretical arguments.

The first line of reasoning is that polymorphism may increase the rate of speciation if morphs are associated to different ecological niches (i.e. ecomorphs). The presence of alternative ecomorphs within the same population widens the ecological niche of the species. This may in turn facilitate range expansion through an increase of colonization abilities and the persistence of populations in variable environments (Forsman et al. 2008; Takahashi and Noriyuki 2019), two factors that are known to increase speciation rates (Kennedy et al. 2017). Specialized ecomorphs have been observed in several species, but it is not yet clear whether they occur in lacertids. (Kusche et al. 2015; Lattanzio and Miles 2016; Whitney et al. 2018, Scali et al. 2016).

The second line of reasoning rests on the “morphic speciation” scenario (West-Eberhard 1986). According to this scenario, a polymorphic population can loses a morph during the colonization of a new environment or area, resulting in a rapid phenotypic divergence of the remaining morph(s) and ultimately in a reproductive isolation from the ancestral population (Corl et al. 2010*a*). The rapid phenotypic divergence after the loss of one morph may occur through (i) the cessation of gene flow from the missing morph, which used to continuously reintroduce maladapted alleles into the other morphs’ genetic backgrounds, preventing them from reaching their phenotypic

optima (character release, West-Eberhard 1986); (ii) a change in the fitness landscape, as optimal trait combinations for one morph may change when another morph disappears from the population. For example, loss of a morph can drastically change the predation pressure acting on the remaining morphs (Bond 2007) if predation generates frequency dependent selection (Olendorf et al. 2006). Similarly, competition among morphs can generate frequency-dependent selection in polymorphic species (Sinervo and Lively 1996).

While several authors have promoted the morphic speciation hypothesis, an intuitive argument suggests that polymorphism could have opposite effects on speciation depending on mate choice within polymorphic populations: assortative mating by morph can enhance speciation (and promote shifts from ancestral polymorphism to derived monomorphism through speciation, Jamie and Meier 2020). However, disassortative mating by morph is likely to slow speciation (and maintain polymorphism through the speciation process, Jamie and Meier 2020; Chouteau et al. 2017), while random mating relative to morph should promote less stringent mate choice in polymorphic species than in monomorphic species, as preferences span a larger spectrum of phenotypic space than in monomorphic species. In such cases (random or disassortative mating), the changes in color traits should be less likely to result in reproductive isolation compared to non-polymorphic species.

In spite of the theoretical interest generated by the “morphic speciation” hypothesis, this hypothesis has been examined empirically by only four studies until now. First, two studies investigated the effect of polymorphism on population divergence at small evolutionary scales (within a species complex in lizards, Corl et al. 2010*b*, 2012). They found that polymorphic populations were often ancestral, and that populations that lost a morph after colonizing a new environment showed reproductive incompatibilities with the ancestral population and rapid phenotypic changes. At macroevolutionnary scale, two studies found that polymorphism increased speciation rates in birds and in lacertid lizards (Hugall and Stuart-Fox 2012; Brock et al. 2021). Taken together, these findings support the hypothesis of increased speciation rates in polymorphic species.

The lacertid lizards (family Lacertidae) is a group of Squamata containing more than 300 species distributed across Europe, Africa and Asia. This family is split in two main clades, the Gallotiinae, which contains only a few and often insular species, and the Lacertinae, which contains most of the lacertids species. The Lacertinae are divided between (i) the tribe Eremiadini, that lives mainly in xeric habitats in North African and the Middle East and often display dull colorations, and (ii) the Lacertini, that live mostly in temperate habitats in Europe and are more often colorful. Among those three clades, many species present conspicuous colorations. Bright colorations are found in both sexes on the throat and the belly, and are known to influence female mate choice and male-males contests (Abalos et al. 2016; Badiane et al. 2020). In some species, males also display blue or green ocelli on their flanks, or conspicuous outer ventral scales, that serve as indicators of the male

quality during males intrasexual competition (Pérez i De Lanuza et al. 2014; Names et al. 2019). Furthermore, several lacertids present a polymorphism of color. Such polymorphism can be found in both sexes when it occurs on ventral coloration, but is restricted to males when it occurs on the flank. In the genus *Podarcis*, the Common Wall Lizard *P. muralis* has become a model species for the study of color polymorphism as several morphs differing in ventral coloration coexist in both sexes in most populations (Galeotti et al. 2013). These morphs may be related to different breeding strategies and life history traits (Calsbeek et al. 2010; Galeotti et al. 2013; but see Abalos et al. 2020) and they have a simple genetic determinism in *P. muralis* and in six other congeneric species, being controlled by two small regulatory genomic regions (SPR and BCO2, Andrade et al. 2019). Overall, the presence of specialized morphs and the variability of sexual colorations make the family Lacertidae an ideal model to investigate the impact of sexual selection on speciation rates and the hypothesis of morphic speciation.

Here, we use the coloration data of all the species of this family, to address two questions: (i) what are the evolutionary histories of conspicuous colorations and color polymorphism in this family? (ii) Is there an effect of conspicuousness and color polymorphism on species speciation? We hypothesized that brightly colored species undergo higher intensity of sexual selection than dull ones. However, because several previous studies failed to find a link between sexual selection proxies and speciation rates (Huang and Rabosky 2014; Cooney et al. 2017), we did not expect an effect of conspicuous colorations on speciation. For color polymorphism, based on the morphic speciation hypothesis, we predicted that color polymorphism increases speciation rates in lacertids. During the course of our study, we became aware of the publication of Brock et al. (2021) who had independently addressed the same question using the same group of species but using different data and methods (see discussion). Because our study leads to opposite conclusions, we think It is important to publish our results, and we have devoted a section of our study to adress the reasons that might explain this discrepancy.

MATERIAL AND METHODS

Data acquisition

We follow the taxonomy and species list of lacertids from the Reptile Database (Uetz et al. 2020). We removed from this list several categories of species that are expected to have speciation modes differing from the rest of the species and driven by mechanisms presumably not be affected by the presence of polymorphism. We first removed the parthenogenetic species, as they arise by interspecific hybridization and result in unisexual clones providing “instant” reproductive isolation from their parent species (several species of the genus *Darevskia*, noted as “parthenogenetic” in

Table S1). We also removed strictly insular species (species noted as “insular” in Table S1). Although morphic speciation might have helped the divergence of some insular species, we believe that geographic isolation remains the primary factors in of the speciation process. Supporting this idea, no case of in situ (intra-island) speciation is known in insular lacertids. We also removed four species for which we could not find any accurate information on the coloration and five species with an uncertain taxonomic status (as judged by two of us, PAC and PG). Insularity was assessed using the distribution information available in the reptile-database website. After these steps, we retained 295 species for the speciation analysis. The final list of all species, including all species removed from the dataset, can be found in Supplementary Table S1.

We scored the presence of sexual colorations and polymorphism from multiple sources, such as scientific and naturalist papers and field guides, but also multiple photographs taken by the authors in the field (sources listed in Table S1). A species was considered as having conspicuous colorations if, at least in males, (1) the ventral side, or a part of its ventral side (throat, belly), was not white, or (2) the flanks displayed several ocelli or spots that contrast from the rest of dorsal/flank areas and are of a different color, or (3) the species displayed a specific color during the mating season. Furthermore, we considered a species as polymorphic if, within a population, individuals of a same sex and age-class exhibit several distinct sexual colors. We did not score coloration as polymorphic if the morphs were not clearly distinguished, nor if the distinct morphs were associated with age or sex. Species where coloration varies geographically but not within populations were not treated as polymorphic, even though it was sometimes difficult to determine if some variation in coloration reported in the literature was geographically structured or not. Finally, a few species displayed dorsal polymorphism with non-conspicuous colors (Ortega et al. 2014; Ortega et al. 2015; Gallozzi et al 2022). However, such polymorphism always occurs in species which also show conspicuous ventral polymorphism, so this factor should not influence our analysis. Data on sexual colorations and polymorphism are provided in Supplementary Table S1. It should be noted that there is no polymorphic species without conspicuous coloration in Lacertids.

We used the phylogeny provided by Garcia-Porta et al. (2019) as backbone phylogeny. We subsequently added the 85 non-insular and non-parthenogenetic species that were not sampled by Garcia-Porta. These species were added to the backbone tree using the function add.species.to.genus from the phytools package (Revell 2012). This function randomly inserts new species within a predefined genus. If the phylogenetic position was known from previous work, the species was added with its sister taxa at a random divergence date. If no phylogenetic information was available, it was randomly located in its genus. We repeated this operation one hundred times in order to account for phylogenetic uncertainty in all analyses.

174 **Trait evolution and ancestral state reconstruction**

175 We investigated the evolutionary inertia for conspicuous colorations and polymorphism using the δ
176 values (Borges et al. 2019). This index is designed to measure phylogenetic signal in categorical traits,
177 with high δ value indicating high phylogenetic signal (i.e. strong phylogenetic constraint to trait
178 evolution). To test the significance of the observed δ, we compared with a Wilcoxon test the
179 distribution of the 100 observed δ, measured on the 100 phylogenetic trees, against a null
180 distribution obtained by measuring δ after randomization of the trait data among species
181 (phylogenetic signal = zero). In addition, we reconstructed the ancestral state of the coloration with
182 the make.simmap function from the phytools package (Revell 2012). This function simulates
183 stochastic character histories using the state of the character on the tips and a continuous-time
184 reversible Markov model. For this analysis, coloration was coded with three states: (1) no
185 conspicuous coloration, (2) presence of conspicuous colorations without polymorphism, (3) presence
186 of conspicuous colorations and polymorphism. Transition rates between states were allowed to
187 differ and we did not exclude transitions from (1) to (3) although no such transitions were recovered
188 by the model (see below). We repeated the ancestral state reconstruction (ASR) on the 100
189 phylogenetic trees, with 100 simulations for each analysis.

190

191 **Character associated diversification analysis**

192 We used several methods to compare the rates of speciation between species with and without
193 conspicuous colors, and between species with and without polymorphism. We excluded the species
194 lacking conspicuous colorations of the polymorphism analysis because there are no direct
195 evolutionary transitions from non-conspicuous to polymorphic, see results of the ASR). We however
196 tested the influence of this exclusion by repeating the polymorphism analysis with all the species.

197 First, we used the speciation/extinction analysis of BAMM (Rabosky 2014) to detect shifts in
198 speciation rates along the trees. This analysis allows the speciation rates to vary in time and among
199 branches and does not consider character states. We then applied the STructured RAte Permutations
200 on Phylogenies analysis (STRAPP, Rabosky and Huang 2016) to test if the speciation rates measured
201 with BAMM were different between species with and without conspicuous colorations and color
202 polymorphism. STRAPP compares the Mann–Whitney U-test statistic measuring the relationship
203 between the binary character state and speciation rates against a null distribution.

204 Secondly, we inferred the speciation rates with the Diversification Rates statistic (DR statistic,
205 Jetz et al. 2012). Despite its name, the DR statistic provides a better estimate of the rate of speciation
206 than of net diversification (Title and Rabosky 2019). For a given species, the DR statistic is computed
207 as a weighted average of the inverse branch lengths connecting the focal species to the root of the
208 phylogeny. We then used a non-parametric test, FiSSE (Fast, intuitive State-dependent Speciation

Extinction analysis, Rabosky and Goldberg 2017), to investigate the effect of conspicuous colorations and polymorphism on speciation rates. For a given tree, this test first measures the difference of mean DR statistic between species with different character states, and then compares this difference to a null distribution. When testing for polymorphism effect, we first measured the DR statistic on the whole tree, then removed the species lacking conspicuous colorations and performed the test.

Finally, we fitted State Dependent Diversification models (SDD) to test the influence of conspicuous colorations and color polymorphism on the diversification rates of Lacertid. For each trait, we implemented four models: two models measuring character dependent diversification, plus the corresponding two null models estimating Character Independent Diversification (CID). The first character dependent model we fitted was a Binary-State Speciation and Extinction model (BiSSE, Maddison et al. 2007). This model estimates one rate of speciation and extinction for each character state. The second character dependent model was the Hidden State Speciation and Extinction model (HiSSE; Beaulieu and O'Meara 2016). This model includes hidden states, which allows the diversification rates to vary within each state (e.g. polymorphic species can have two different diversification rates). We also fitted two Character Independent Diversification models: CID-2 and CID-4, which were the null models corresponding respectively to BiSSE and Hisse: (Beaulieu and O'Meara 2016). They respectively have the same number of parameters than BiSSE and HiSSE models, but differ in having their diversification parameters independent of the observed character state (i.e. diversification parameter set equal for the observed state and different for the hidden states). It should be noted that the diversification rates estimated by SDD and CID models are not time dependent, and only vary depending on characters states (unlike speciation/extinction analysis of BAMM; Rabosky 2014). We selected the best-fit model among these four models based on the Akaike Information Criterion corrected for sample size (AICc, models were preferred when delta AICc > 2). All the models were made using the R package hisse (Beaulieu 2017).

To account for phylogenetic uncertainty, we fitted the four SDD models, as well as STRAPPS and FiSSE analysis for each trait and phylogenetic tree. For SDD models, we assessed the best-fitting model each time.

Although our study and the study of Brock et al. (2021) were made on the same taxonomic groups, the results of our analysis contradict the results presented in Brock et al. (see below). We thus made additional analysis to investigate the origin of these differences (Supplementary Methods). We also repeated the STRAPPS and FiSSE analysis with (i) our coloration data and the species included in Brock et al. (2021), and (ii) the coloration data and species of Brock et al. (2021).

RESULTS

Conspicuous colorations were frequent in lacertids, as they were present in 63% of the species analyzed (Figure 1). Color polymorphism, on the other hand, was rarer and only concerns 13% of the species analyzed. Polymorphism was unequally distributed in lacertids: the subfamily Lacertini includes more than half of the polymorphic species while it only contained 100 species out of the 295 species of Lacertidae and within the Lacertini, all mainland species of the genus *Podarcis* were polymorphic species (see Table S1). Both traits showed high phylogenetic conservatism (median δ across phylogenies = 6.39, W=10e5, $p<0.001$ and median δ =75.7, W=10e5, $p<0.001$ respectively). The ancestral state reconstruction suggested more acquisitions than losses in the evolution of both conspicuous colorations and color polymorphism (Figure S1, 43 acquisitions vs 23 losses for colorations and 15 acquisitions vs 3 losses for polymorphism). Transitions from dull-colored to polymorphis, and the reverse, were very rare (0.04 and 1.1 on average across all trees respectively), indicating that, the polymorphic state evolves from a monomorphic conspicuous-color state in lacertids. Finally, the ancestor of lacertids probably displayed conspicuous colorations without being polymorphic (Figure S1).

Character associated diversification analysis

We wanted to test whether conspicuous coloration on the one hand, and polymorphism on the other hand, influence speciation rates. As explained above, to test for the effect of polymorphism, we excluded inconspicuous species, as the ancestral state of polymorphic lineages is always conspicuously colored. Including inconspicuous species would confound the effects of polymorphism per se and conspicuousness. When included, however, species lacking conspicuous colorations had a minor impact on the results, and did not change the overall conclusion (see Supplementary Methods).

The BAMM analysis detected a shift of speciation rates only in 21 trees out of the hundred trees. In addition, the STRAPP tests indicated that neither the presence of conspicuous colorations nor the presence of color polymorphism affected speciation rates ($p>0.5$ for all tests across the 100 trees).

The DR statistic showed that inconspicuously and conspicuously colored species had similar speciation rates (average λ_0 across trees = 0.11±0.04 and average λ_1 across trees = 0.13±0.07 respectively, non-significant: $p>0.5$ for all FiSSE tests, Figure 1 and 2). Similarly, there was no difference in DR statistic between species conspicuously colored monomorphic and polymorphic species (average λ_0 across trees = 0.12±0.07 and average λ_1 across trees = 0.14±0.07 respectively, non-significant: $p>0.5$ for all FiSSE tests, Figure 1 and 2).

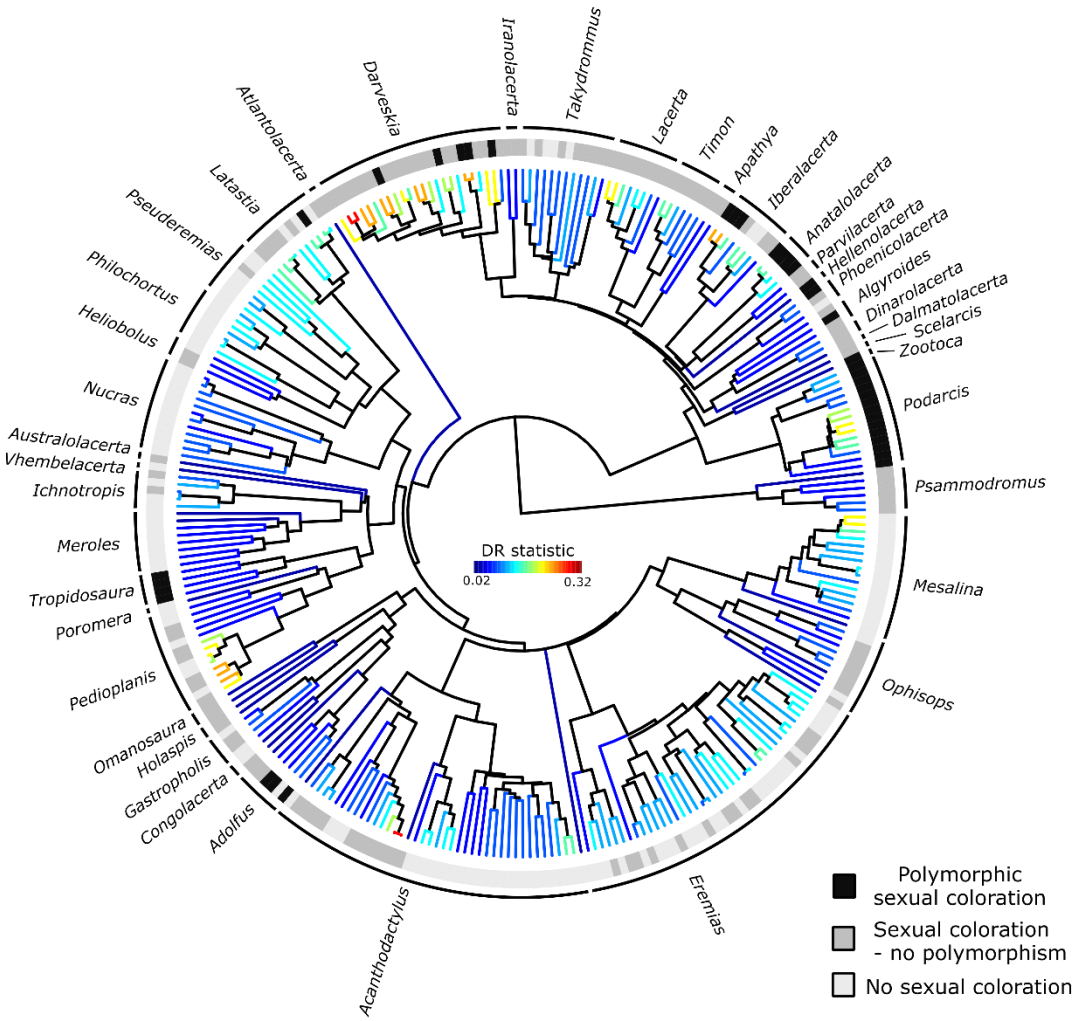

Figure 1. Phylogenetic relationships of the 295 Lacertids species included in the analysis. This tree was randomly chosen among the hundred trees produced for the analysis to account for phylogenetic uncertainty (see methods). States of sexual coloration and polymorphism characters are indicated at the tips. Tip branches are colored according to the mean DR statistic measured across all trees (an estimate of the branch-specific speciation rate).

Last, the best fitting State Dependent Diversification (SDD) models for the evolution of conspicuous coloration were models where diversification parameters are independent of the observed character state (CID 2 or CID 4) for all the trees (Figure 3). Similarly, we found a low support for an influence of color polymorphism on the diversification of species with conspicuous colorations. CID 2 and CID 4 were the best fitting models for 75 and 22 trees respectively, while HiSSE was the best fitting model for 3 trees only (Figure 3).

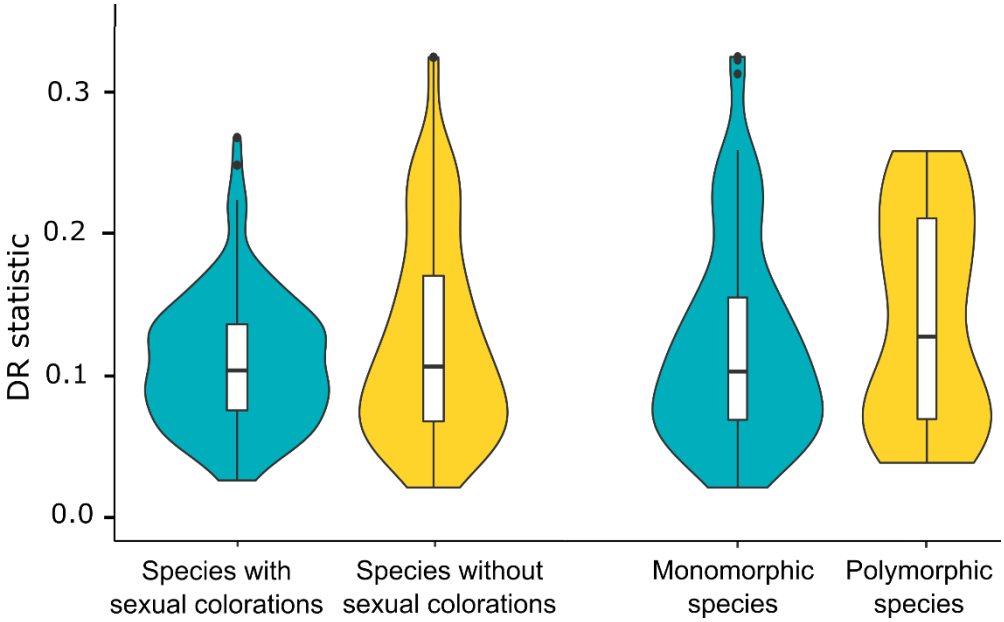

Figure 2. Violin plots of the DR statistic values for the species with and without sexual coloration, and with and without color polymorphism.

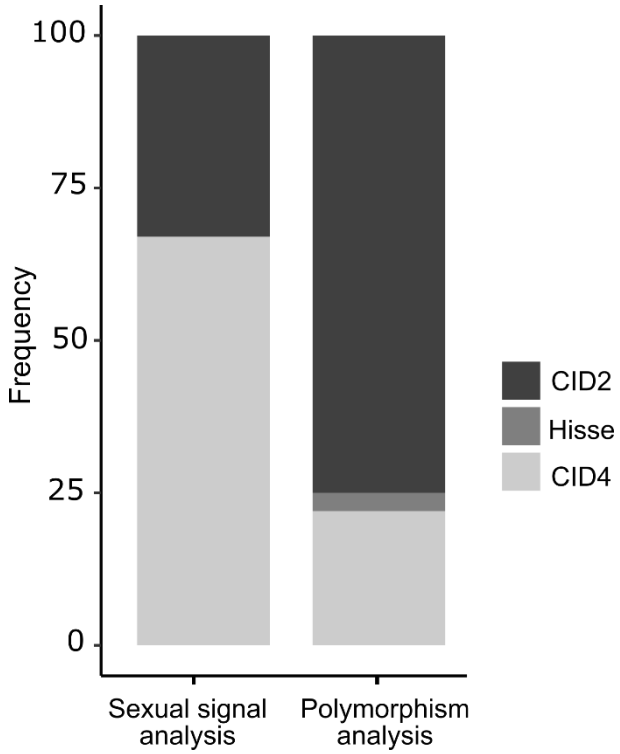

Figure 3. Frequency of the best fitting diversification models for the sexual coloration and color polymorphism analysis repeated across one hundred trees. Models with character dependent diversification (HISSE) were considered as best fitting when delta AICc > 2. BiSSE models were included in both analyses, but never had the lowest AICc.

The comparison with Brock et al.'s (2021) analysis indicated that the differences of results between our SDD models and theirs stem from differences in character states, i.e. in the species considered to be polymorphic *versus* not (for more details see Supplementary Results and Table S2), as well as from the use of an old version of the package encoding SDD models in Brock et al (2021). However, this difference of results only applied to SDD models. Unlike SDD models, the non-parametric FiSSE and STAPPS analysis never detected an effect of polymorphism on speciation in the set of species studied by Brock et al., whether we used our estimates of character states (STRAPPS test: p=0.98; FiSSE test: $\lambda_0 = 0.10$, $\lambda_1=0.13$, p=0.88), or theirs (STRAPPS test: p=0.98; FiSSE test: $\lambda_0 = 0.10$, $\lambda_1 = 0.14$, p=0.98).

DISCUSSION

Our analyses suggested that neither the presence of conspicuous colorations nor color polymorphism increases the rates of speciation in Lacertids. We also showed that conspicuous colorations and color polymorphism are labile across taxonomy, and were gained and lost several times during the diversification of Lacertids. The lack of effect of conspicuous colorations on speciation is in agreement with several previous studies (Huang and Rabosky 2014; Gomes et al. 2016; Cooney et al. 2017). However, our results for color polymorphism is in contradiction with the two studies that tested the morphic speciation hypothesis at multispecies level (Hugall and Stuart-Fox 2012; Brock et al. 2021).

The absence of effect of conspicuous colorations on speciation rates at the scale of a family contrasts with the accumulation of evidence showing an influence of sexual selection on pre-zygotic (Boughman 2001; Masta and Maddison 2002; Boul et al. 2007) and post-zygotic isolation (Vamosi and Schluter 1999; Naisbit et al. 2001) at short time scales. Yet, there is not necessarily a link between processes acting at short time scales and diversification rates observed at large phylogenetic scales. This decoupling could arise because different processes influence the creation of new species and their persistence over time. For instance, some authors found that sexual selection increases the risk of extinction in birds (McLain et al. 1995; Doherty et al. 2003; but see Cooney et al. 2017 for opposite results). However, SDD models were found to be unable to accurately measure both speciation and extinction rates (Beaulieu and O'Meara 2016; Louca and Pennell 2020), and this hypothesis is thus difficult to test using current comparative methods. The lack of correlation between speciation rates and the presence of sexual colorations could also come from the fact that speciation does not increase with the intensity of sexual selection but rather with the evolutionary rates of sexual traits (Cardoso and Mota 2008). These two features are not necessarily correlated, as a trait may be at the same time very conserved across species and under strong sexual selection

338 (Song and Bucheli 2010; Mejías et al. 2020). The few studies investigating this question found
339 support for a positive correlation between speciation rates and evolutionary rates of sexual traits
340 (Cardoso and Mota 2008; Gomes et al. 2016) but they were made on birds, and researches on other
341 taxonomic groups are needed. Finally, the occurrence of conspicuous coloration might be a poor
342 proxy of the intensity of sexual selection. In lacertids, mating choice and interspecific recognition are
343 known to rely on pheromones as much as on coloration (Cooper and Pèrez-Mellado 2002; Khannoon
344 et al 2011; Gabirot et al. 2013). It is thus possible that considering the presence of conspicuous
345 colorations, even when they are sexually dimorphic, is not sufficient to detect an effect of sexual
346 selection on speciation.
347 The lack of effect of color polymorphism on speciation rates contradicts the conclusions of
348 Brock et al. (2021) obtained on the same taxonomic group. The first reason is that our attributions of
349 character states (polymorphic versus nonpolymorphic) differed in some cases from theirs. We
350 therefore re-checked our attributions in case of mismatches. Ten species considered monomorphic
351 by Brock et al were considered polymorphic by us. Some of these reflect the fact that we coded
352 polymorphism as the presence of discrete states on any conspicuous coloration, while Brock et al.
353 (2021) considered only throat coloration -thus excluding four *Tropidosaura* species. For six other
354 species we re-checked bibliographic references (see table S2) and confirmed mentions of
355 polymorphism that had been apparently overlooked by Brock et al. 2021. Seven species were
356 considered monomorphic by us and polymorphic by Brock et al. 2021. In four of these, color morphs
357 do not co-occur within a population, but occur in allopatric populations or subspecies – which does
358 not qualify as polymorphism *sensu stricto*. For the last three, we did not find any mention of
359 polymorphism in the literature (and Brock et al. 2021 did not provide a reference). All in all, we
360 believe that, although the status of each particular species can always been updated and discussed,
361 our character states are more accurate and closer to the original definition of a polymorphic species
362 and to the concept of morphic speciation (i.e. not focused only on throat coloration (West-Eberhard
363 1986) and excluding geographic races).
364 In addition, methodological issues can contribute to discrepancies in the results. The SDD
365 methods have been criticized on the basis of high type-1 errors, i.e. they may detect differences in
366 diversification rates even for neutral traits and are probably overparameterized as speciation and
367 extinction can hardly be estimated independently (Rabosky and Goldberg 2015, 2017; Louca and
368 Pennell 2020). This is illustrated by the fact that 6 of the 8 estimated parameters are at the boundary
369 of the allowed interval in the HISSE model (all four extinction rates and two transition rates are zero,
370 using Brock et al.'s data and character states) ; the same characteristic is present in Brock et al.'s
371 original results (their Table 2) as well as in our run of their script with their data, character states and
372 package version (our Table S3). FiSSE and STRAPP have been developed to avoid this kind of

drawbacks and provide a more robust, and nonparametric, way of testing character-dependent speciation rates (Rabosky and Huang 2016; Rabosky and Goldberg 2017). The fact that these methods do not recover an effect of polymorphism, whatever the data and character states used (ours or Brock et al's) suggests that the result of Brock et al (2021) is likely a type-1 error.

An additional explanation for the lack of correlation between conspicuous colorations / polymorphism and speciation rates could be the limited role that pre-zygotic isolation has in lacertids diversification. The influence of sexual selection and polymorphism on species speciation occurs mainly at the pre-zygotic stage (West-Eberhard 1986; Coyne and Orr 1989; Gray and Cade 2000; Ritchie 2007). However, the influence of this stage in lacertids speciation is unclear: some species are partially able to recognize each other using pheromones (Barbosa et al. 2006; Gabirot et al. 2012), but interspecific courting seems to be frequent (Martín and López 2006; Galoyan et al. 2019), suggesting that post-zygotic isolation also play a strong role in the speciation process (Carretero 2008; Pinho et al. 2009). On the other hand, the groups in which an effect of sexual selection and polymorphism was reported are taxa where the pre-zygotic isolation is determinant for speciation (e.g birds, Barraclough et al. 1995; Brambilla et al. 2008). This may explain why, depending on the groups, sexual trait and polymorphism sometimes correlate with speciation rates and sometimes do not. We also lack data on the effect of morphs on mate choice in Lacertidae, as we only found some information on mate choice relative to morphs in *Podarcis muralis* (Pérez i de Lanuza et al. 2013; Sacchi et al. 2015, 2018, who found mixed support for color assortative mating) while indirect genetic results also suggest some possible assortative mating in *Podarcis melisellensis* (Huyghe et al. 2010).

We also wish to stress a previously neglected inherent difficulty with the detection of the morphic speciation model through comparative methods in empirical datasets. The diversification analyses used by us or by Brock et al. (2021) test for differences in diversification rates associated with the presence of polymorphism. Yet, the morphic species model predict that "polymorphic lineages should be ancestral and monomorphic lineages should be derived" (Corl et al. 2010b), as morphic speciation generates monomorphic species from polymorphic species. The signature of the morphic speciation model in phylogenies should thus be an excess of monomorphic species sister to a polymorphic species, not an increased diversification rate in clades where all species are polymorphic. This creates an overlooked paradox: detecting an increased net diversification rate in clades where most species are polymorphic would actually run against the predictions of the morphic species model, unless one assumes that some lineages have an inherent tendency to regain the polymorphic state quickly after it is lost – an assumption without clear support in the data.

A large variety of factors, besides those examined in this study, may explain the variations of speciation rates observed within groups (for instance diet, Tran 2016; habitat specialization Liedtke

et al. 2016 or reproduction mode, Lynch 2009). In lacertids, the two most diverse genera (*Acanthodactylus* and *Eremias*, representing 22% of all the Lacertid species) live in arid areas of the Middle East or North Africa. Similarly, an increase of lizard diversity in arid areas have been reported in biogeographic studies (Powney et al. 2010; Lewin et al. 2016). As such, this pattern suggests that hot and arid conditions play a strong role in the radiation of lacertids. Yet, the factors at the origin of these radiations are still unclear. Adaptive radiation seems unlikely, as most lacertids species living in arid areas seem to show similar ecological niches as inferred from distribution patterns: most arid regions of the Middle East or North Africa are inhabited by a maximum of 3-4 species of *Acanthodactylus* (large bodied) and 3-4 species of *Mesalina* (small bodied) segregated by habitat preferences within genus (e.g. Haas 1951; Blanc 1980; Werner 1982; Schleich et al. 1996; Nouira and Blanc 2003; Rifai et al. 2003; Baha El Din 2007), and most species diversity in the genera correspond with changes in these species between regions. However, such pattern could be the result of the strong relation between the environment and ecological and life history traits of lizards (e.g. increase in activity time and fecundity with temperature; Adolph and Porter 1993) that may have facilitated speciation in arid areas (discussed in Powney et al. 2010). Nevertheless, currently no studies properly tested this possible link, and this hypothesis is yet to be confirmed.

One main limitation of our work lies in the data we used to score the coloration. Neither photographs nor literature sources account for variation of ultraviolet (UV) coloration. Lacertids frequently use UV coloration for mate choice or to signal their fighting capacity (Olsson et al. 2011; Pérez i de Lanuza et al. 2014). Thus, in principle, we could have underestimated the frequency of conspicuous coloration and polymorphism in our dataset. However, known UV signals in lizards are always displayed on a patch with a visibly different color than the rest of the body (blue throat or green ocelli for instance), so it is unlikely that this issue affects our detection of conspicuousness, although it may have done so for polymorphism. As far as we know, there is currently no example of polymorphism limited only to UV coloration in animals. A second methodological limitation may stem from the strong geographical bias prevailing in the taxonomic researches. In the last twenty years, an intensive work unraveled the phylogeny of the lacertids of the northern hemisphere, allowing the description of numerous species. On the other hand, almost no taxonomic studies based on genetic data have been made on lacertids of the equatorial region. The diversity of species living in this region is thus probably strongly underestimated. It is difficult to predict in which ways this issue may influence our results, because species with and without conspicuous colorations and color polymorphism are present in the equatorial region.

Our analysis revealed that the speciation of lacertids was not influenced by the presence of conspicuous colorations nor by color polymorphism. These results support the idea of a decoupling of the effect of sexual selection on species diversification between short time scale (i.e. effects on

pre- and post-zygotic isolation) and large time scale (i.e. effects on rates of extinction/speciation). They also call into question the generality of the morphic speciation hypothesis, which is currently supported by only two large scale study (Hugall and Stuart-Fox 2012; Brock et al. 2021). The fact that prezygotic isolation does not appear to be determinant for the speciation in lacertids may explain this lack of effect of polymorphism and conspicuous coloration that we found. In the future, it would be interesting to test this hypothesis by investigating other taxa in which speciation is mainly driven by post-zygotic isolation.

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Data, scripts, code, and supplementary information availability

Data and scripts are available online: DOI: 10.5281/zenodo.7619485 (https://zenodo.org/record/7619485)

Conflict of interest disclosure

The authors declare that they comply with the PCI rule of having no financial conflicts of interest in relation to the content of the article.

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References

Abalos J, Pérez i de Lanuza G, Carazo P, Font E (2016) The role of male coloration in the outcome of staged contests in the European common wall lizard (*Podarcis muralis*). *Behaviour,* **153**, 607–631.

Abalos J, Pérez i de Lanuza G, Bartolomé A, Liehrmann O, Laakkonen H, Aubret F, Uller T, Carazo P, Font E (2020) No evidence for differential sociosexual behavior and space use in the color morphs of the European common wall lizard (*Podarcis muralis*). *Ecology and Evolution*, **10**, 10986–11005.

Adolph SC, Porter WP (1993) Temperature, activity, and lizard life histories. *American Naturalist*, **142**, 273–295.

Andrade P, Pinho C, Pérez i de Lanuza G, Afonso S, Brejcha J, Rubin C-J, Wallerman O, Pereira P, Sabatino SJ, Bellati A, Pellitteri-Rosa D, Bosakova Z, Bunikis I, Carretero M-A, Feiner N, Marsik P, Paupério F, Salvi D, Soler L, While GM, Uller T, Font E, Andersson L, Carneiro M (2019) Regulatory changes in pterin and carotenoid genes underlie balanced color polymorphisms in the wall lizard. *Proceedings of the National Academy of Sciences of the United States of America*, **116**, 5633–5642.

Arbuckle K, Speed MP (2015) Antipredator defenses predict diversification rates. *Proceedings of the National Academy of Sciences of the United States of America*, **112**, 13597–13602.

Badiane A, Martin M, Meylan S, Richard M, Decencière Ferrandière B, Le Galliard JF (2020) Male ultraviolet reflectance and female mating history influence female mate choice and male mating success in a polyandrous lizard. *Biological Journal of the Linnean Society*, **130**, 586–598.

Baha El Din SM (2007) A new lizard of the *Acanthodactylus scutellatus* group (Squamata: Lacertidae) from Egypt. *Zoology in the Middle East*, **40**, 5–18.

Barbosa D, Font E, Desfilis E, Carretero MA (2006) Chemically mediated species recognition in closely related *Podarcis* wall lizards. *Journal of Chemical Ecology*, **32**, 1587–1598.

Barraclough TG, Harvey PH, Nee S (1995) Sexual selection and taxonomic diversity in passerine birds. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **259**, 211–215.

Beaulieu JM (2017) Package 'hisse.' Available at https://cran.microsoft.com/snapshot/2017-09-17/web/packages/hisse/hisse.pdf

Beaulieu JM, O'Meara BC (2016) Detecting hidden diversification shifts in models of trait-dependent speciation and extinction. *Systematic biology*, **65**, 583–601.

Blanc CP (1980) Studies on the *Acanthodactylus* of Tunisia IV. Geographic distribution and habitats. *Journal of Herpetology*, **14**, 391–398.

Bond AB (2007) The evolution of color polymorphism: crypticity, searching images, and apostatic selection. *Annual Review of Ecology, Evolution, and Systematics*, **38**, 489–514.

Borges R, Machado JP, Gomes C, Rocha AP, Antunes A (2019) Measuring phylogenetic signal between categorical traits and phylogenies. *Bioinformatics*, **35**, 1862–1869.

Boughman JW (2001) Divergent sexual selection enhances reproductive isolation in sticklebacks. *Nature*, **411**, 944–948.

Boul KE, Chris Funk W, Darst CR, Cannatella DC, Ryan MJ (2007) Sexual selection drives speciation in an Amazonian frog. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 399–406.

Brambilla M, Janni O, Guidali F, Sorace A (2008) Song perception among incipient species as a mechanism for reproductive isolation. *Journal of Evolutionary Biology*, **21**, 651–657.

Brock KM, McTavish EJ, Edwards DL (2021) Color polymorphism is a driver of diversification in the

lizard family Lacertidae. *Systematic Biology*, **71**, 24–39.

Calsbeek B, Hasselquist D, Clobert J (2010) Multivariate phenotypes and the potential for alternative phenotypic optima in wall lizard (*Podarcis muralis*) ventral colour morphs. *Journal of Evolutionary Biology*, **23**, 1138–1147.

Cardillo M, Huxtable JS, Bromham L (2003) Geographic range size, life history and rates of diversification in Australian mammals. *Journal of Evolutionary Biology,* **16**, 282–288.

Cardoso GC, Mota PG (2008) Speciational evolution of coloration in the genus *Carduelis*. *Evolution*, **62**, 753–762.

Carretero MA (2008) An integrated assessment of a group with complex systematics: the Iberomaghrebian lizard genus *Podarcis* (Squamata, Lacertidae). *Integrative Zoology*, **3**, 247–266.

Chouteau M, Llaurens V, Piron-Prunier F, Joron M (2017) Polymorphism at a mimicry supergene maintained by opposing frequency-dependent selection pressures. *Proceedings of the National Academy of Sciences*, **114**, 8325-8329.

Cooney CR, Thomas GH (2020) Heterogeneous relationships between rates of speciation and body size evolution across vertebrate clades. *Nature Ecology & Evolution*, **5**, 101–110.

Cooney CR, Tobias JA, Weir JT, Botero CA, Seddon N (2017) Sexual selection, speciation and constraints on geographical range overlap in birds. *Ecology Letters*, **20**, 863–871.

Cooper Jr WE, Pèrez-Mellado V (2002) Pheromonal discriminations of sex, reproductive condition, and species by the lacertid lizard *Podarcis hispanica*. *Journal of Experimental Zoology*, **292**, 523-527.

Corl A, Davis AR, Kuchta SR, Comendant T, Sinervo B (2010a) Alternative mating strategies and the evolution of sexual size dimorphism in the side-blotched lizard, *Uta stansburiana*: a population-level comparative analysis. *Evolution*, **64**, 79–96.

Corl A, Davis, AR, Kuchta SR, Sinervo B (2010b). Selective loss of polymorphic mating types is associated with rapid phenotypic evolution during morphic speciation. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 4254–4259.

Corl A, Lancaster LT, Sinervo B (2012). Rapid formation of reproductive isolation between two populations of side-blotched lizards, *Uta stansburiana*. *Copeia*, **2012**, 593–602.

Coyne JA, Orr HA (1989) Patterns of speciation in *Drosophila*. *Evolution*, **43**, 362–381.

Diaz LFH, Harmon LJ, Sugawara MTC, Miller ET, Pennell MW (2019) Macroevolutionary diversification rates show time dependency. *Proceedings of the National Academy of Sciences of the United States of America*, **116**, 7403–7408.

Doherty PF, Sorci G, Royle JA, Hines JE, Nichols JD, Boulinier T (2003) Sexual selection affects local extinction and turnover in bird communities. *Proceedings of the National Academy of Sciences of the United States of America*, **100**, 5858–5862.

Forsman A, Ahnesjö J, Caesar S, Karlsson M (2008) A model of ecological and evolutionary consequences of color polymorphism. *Ecology*, **89**, 34–40.

Gabirot M, López P, Martín J (2012) Differences in chemical sexual signals may promote reproductive isolation and cryptic speciation between Iberian Wall Lizard populations. *International Journal of Evolutionary Biology*, **2012**, 1–13.

Gabirot M, López P, Martín J (2013) Female mate choice based on pheromone content may inhibit reproductive isolation between distinct populations of Iberian wall lizards. *Current Zoology*, **59**, 210–220.

Galeotti P, Sacchi R, Pellitteri-Rosa D, Bellati A, Cocca W, Gentilli A, Scali S, Fasola M (2013) Colour polymorphism and alternative breeding strategies: effects of parent's colour morph on fitness traits in the Common Wall Lizard. *Evolutionary Biology*, **40**, 385–394.

Gallozzi F, Colangelo P, Senczuk G, Castiglia R (2022) Phylogeographic and bioclimatic determinants of the dorsal pattern polymorphism in the Italian Wall Lizard, *Podarcis siculus*. *Diversity*, **14**, 519.

Galoyan EA, Tsellarius EY, Arakelyan MS (2019) Friend-or-foe? Behavioural evidence suggests interspecific discrimination leading to low probability of hybridization in two coexisting rock lizard species (Lacertidae, *Darevskia*). *Behavioral Ecology and Sociobiology*, **73**, 1–10.

Garcia-Porta J, Irisarri I, Kirchner M, Rodríguez A, Kirchhof S, Brown JL, MacLeod A, Turner AP, Ahmadzadeh F, Albaladejo G, Crnobrnja-Isailovic J, De la Riva I, Fawzi A, Galán P, Göçmen B, Harris DJ, Jiménez-Robles O, Joger U, Jovanović Glavaš O, Karış M, Koziel G, Künzel S, Lyra M, Miles D, Nogales M, Oğuz MA, Pafilis P, Rancilhac L, Rodríguez N, Rodríguez Concepción B, Sanchez E, Salvi D, Slimani T, S'khifa A, Qashqaei AT, Žagar A, Lemmon A, Moriarty Lemmon E, Carretero MA, Carranza S, Philippe H, Sinervo B, Müller J, Vences M, Wollenberg Valero KC et al. 2019. Environmental temperatures shape thermal physiology as well as diversification and genome-wide substitution rates in lizards. *Nature Communications*, **10**, 1–12.

Gomes ACR, Sorenson MD, Cardoso GC (2016) Speciation is associated with changing ornamentation rather than stronger sexual selection. *Evolution*, **70**, 2823–2838.

Gray DA, Cade WH (2000) Sexual selection and speciation in field crickets. *Proceedings of the National Academy of Sciences of the United States of America*, **97**, 14449–14454.

Haas G (1951) Remarks on the status of the lizard *Eremias olivieri* Audouin. *Copeia*, **1951**, 274–276.

Houle D, Kondrashov AS (2002) Coevolution of costly mate choice and condition-dependent display of good genes. *Proceedings of the Royal Society B: Biological Sciences*, **269**, 97–104.

Huang H, Rabosky DL (2014) Sexual selection and diversification: reexamining the correlation between dichromatism and speciation rate in birds. *The American Naturalist*, **184**, E101–E114.

Hugall AF, Stuart-Fox D (2012) Accelerated speciation in colour-polymorphic birds. *Nature*, **485**, 631–634.

Huyghe K, Small M, Vanhooydonck B, Herrel A, Tadić Z, Van Damme R, Backeljau T (2010) Genetic divergence among sympatric colour morphs of the Dalmatian wall lizard (*Podarcis melisellensis*). *Genetica*, **138**, 387-393.

Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO (2012) The global diversity of birds in space and time. *Nature*, **491**, 444–448.

Kennedy JD, Borregaard MK, Jønsson KA, Holt B, Fjeldså J, Rahbek C (2017) Does the colonization of new biogeographic regions influence the diversification and accumulation of clade richness among the Corvides (Aves: Passeriformes)? *Evolution*, **71**, 38–50.

Khannoon ER, El-Gendy A, Hardege JD (2011) Scent marking pheromones in lizards: cholesterol and long chain alcohols elicit avoidance and aggression in male *Acanthodactylus boskianus* (Squamata: Lacertidae). *Chemoecology*, **21**, 143-149.

Kokko H, Brooks R (2003) Sexy to die for? Sexual selection and the risk of extinction on JSTOR. *Annales Zoologici Fennici*, **40**, 207–219.

Kraaijeveld K, Kraaijeveld-Smit FJL, Maan ME (2011) Sexual selection and speciation: The comparative evidence revisited. *Biological Reviews*, **86**, 367–377.

Kuhl H, Frankl-Vilches C, Bakker A, Mayr G, Nikolaus G, Boerno ST, Klages S, Timmermann B, Gahr M

(2021) An unbiased molecular approach using 3′-UTRs resolves the avian family-level Tree of Life. *Molecular Biology and Evolution*, **38**, 108–127.

Kusche H, Elmer KR, Meyer A (2015) Sympatric ecological divergence associated with a color polymorphism. *BMC Biology*, **13**, 82.

Lattanzio MS, Miles DB (2016) Trophic niche divergence among colour morphs that exhibit alternative mating tactics. *Royal Society Open Science*, **3**, 150531.

Lewin A, Feldman A, Bauer AM, Belmaker J, Broadley DG, Chirio L, Itescu Y, LeBreton M, Maza E, Meirte D, Nagy ZT, Novosolov M, Roll U, Tallowin O, Trape J-F, Vidan E, Meiri S (2016) Patterns of species richness, endemism and environmental gradients of African reptiles. *Journal of Biogeography*, **43**, 2380–2390.

Liedtke HC, Müller H, Rödel M-O, Menegon M, Gonwouo LN, Barej MF, Gvoždík V, Schmitz A, Channing A, Nagel P, Loader SP (2016) No ecological opportunity signal on a continental scale? Diversification and life-history evolution of African true toads (Anura: Bufonidae). *Evolution*, **70**, 1717–1733.

Lindgren AR, Giribet G, Nishiguchi MK (2004) A combined approach to the phylogeny of Cephalopoda (Mollusca). *Cladistics*, **20**, 454-486.

Louca S, Pennell MW (2020) Extant timetrees are consistent with a myriad of diversification histories. *Nature*, **580**, 502–505.

Lynch VJ (2009) Live-birth in vipers (Viperidae) is a key innovation and adaptation to global cooling during the Cenozoic. *Evolution*, **63**, 2457–2465.

Maddison WP, Midford PE, Otto SP (2007) Estimating a binary character's effect on speciation and extinction. *Systematic Biology*, **56**, 701–710.

Martín J, López P (2006) Pre-mating mechanisms favouring or precluding speciation in a species complex: chemical recognition and sexual selection between types in the lizard *Podarcis hispanica*. *Evolutionary Ecology Research*, **8**, 643–658.

Masta SE, Maddison WP (2002) Sexual selection driving diversification in jumping spiders. *Proceedings of the National Academy of Sciences of the United States of America*, **99**, 4442–4447.

McLain DK, Moulton MP, Redfearn TP (1995) Sexual selection and the risk of extinction of introduced birds on oceanic islands. *Oikos*, **74**, 27–34.

Mejías MA, Roncal J, Imfeld TS, Boisen S, Wilson DR (2020) Relationships of song structure to phylogenetic history, habitat, and morphology in the vireos, greenlets, and allies (Passeriformes: Vireonidae). *Evolution*, **74**, 2494–2511.

Naisbit RE, Jiggins CD, Mallet J (2001) Disruptive sexual selection against hybrids contributes to speciation between *Heliconius cydno* and *Heliconius melpomene*. *Proceedings of the Royal Society B: Biological Sciences*, **268**, 1849–1854.

Names G, Martin M, Badiane A, Le Galliard JF (2019) The relative importance of body size and UV coloration in influencing male-male competition in a lacertid lizard. *Behavioral Ecology and Sociobiology*, **73**, 1–14.

Nouira S, Blanc CP (2003) Distribution spatiale des Lacertidés (Sauria, Reptilia) en Tunisie ; caractéristiques des biotopes et rôle des facteurs écologiques. *Ecologia mediterranea*, **29**, 71–86.

Olendorf R, Rodd FH, Punzalan D, Houde AE, Hurt C, Reznick DN, Hughes KH (2006) Frequency-dependent survival in natural guppy populations. *Nature*, **441**, 633–636.

Olsson M, Andersson S, Wapstra E (2011) UV-deprived coloration reduces success in mate acquisition in male sand lizards (*Lacerta agilis*). *PLoS ONE*, **6**, e19360.

Ortega J, López P, Martín J (2014) Conspicuous blue tails, dorsal pattern morphs and escape behaviour in hatchling Iberian wall lizards (*Podarcis hispanicus*). *Biological Journal of the Linnean Society*, **113**, 1094-1106.

Ortega J, Pellitteri-Rosa D, López P, Martín J (2015) Dorsal pattern polymorphism in female Iberian wall lizards: differences in morphology, dorsal coloration, immune response, and reproductive investment. *Biological Journal of the Linnean Society*, **116**, 352-363.

Panhuis TM, Butlin R, Zuk M, Tregenza T (2001) Sexual selection and speciation. *Trends in Ecology & Evolution*, **16**, 364–371.

Pérez i de Lanuza G, Carazo P, Font E (2014) Colours of quality: Structural (but not pigment) coloration informs about male quality in a polychromatic lizard. *Animal Behaviour*, **90**, 73–81.

Pinho C, Kaliontzopoulou A, Carretero MA, Harris DJ, Ferrand N (2009) Genetic admixture between the Iberian endemic lizards *Podarcis bocagei* and *Podarcis carbonelli* : evidence for limited natural hybridization and a bimodal hybrid zone. *Journal of Zoological Systematics and Evolutionary Research*, **47**, 368–377.

Powney GD, Grenyer R, Orme CDL, Owens IPF, Meiri S (2010) Hot, dry and different: Australian lizard richness is unlike that of mammals, amphibians and birds. *Global Ecology and Biogeography*, **19**, 386–396.

Price T (1998) Sexual selection and natural selection in bird speciation. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, **353**, 251–260.

Rabosky DL (2014) Automatic detection of key innovations, rate shifts, and diversity-dependence on phylogenetic trees. *PLoS ONE*, **9**, e89543.

Rabosky DL, Donnellan SC, Talaba AL, Lovette IJ (2007) Exceptional among-lineage variation in diversification rates during the radiation of Australia's most diverse vertebrate clade. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 2915–2923.

Rabosky DL, Goldberg EE (2017) FiSSE: A simple nonparametric test for the effects of a binary character on lineage diversification rates. *Evolution*, **71**, 1432–1442.

Rabosky DL, Huang H (2016) A robust semi-parametric test for detecting trait-dependent diversification. *Systematic Biology*, **65**, 181–193.

Revell LJ (2012) Phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, **3**, 217–223.

Rifai L, Modrý D, Necas P, Amr ZS (2003) The occurrence of *Acanthodactylus hardyi* Haas, 1957 in the Hashemite Kingdom of Jordan and notes on its ecology. *Zoology in the Middle East*, **28**, 33–38.

Ritchie MG (2007) Sexual selection and speciation. *Annual Review of Ecology, Evolution, and Systematics*, **38**, 79–102.

Sacchi R, Ghitti M, Scali S, Mangiacotti M, Zuffi MAL, Sannolo M, Coladonato AJ, Pasquesi G, Bovo M, Pellitteri-Rosa D (2015) Common wall lizard females *Podarcis muralis* do not actively choose males based on their colour morph. *Ethology*, **121**, 1145–1153.

Sacchi R, Coladonato AJ, Ghitti M, Mangiacotti M, Scali S, Bovo M, Zuffi M (2018) Morph-specific assortative mating in common wall lizard females. *Current Zoology,* **64**, 449-453.

Scali S, Sacchi R, Mangiacotti M, Pupin F, Gentilli A, Zucchi C, Sannolo M, Pavesi M, Zuffi MAL (2016)

Does a polymorphic species have a ‘polymorphic’ diet? A case study from a lacertid lizard. *Biological Journal of the Linnean Society*, **117**, 492–502.

Schleich HH, Kaestle W, Kabisch K (1996) *Amphibians and reptiles of North Africa*, Koeltz, Konigstein.

Seehausen O (2000) Explosive speciation rates and unusual species richness in haplochromine cichlid fishes: Effects of sexual selection. *Advances in Ecological Research*, **31**, 237–274.

Sinervo B, Lively CM (1996) The rock-paper-scissors game and the evolution of alternative male strategies. *Nature*, **380**, 240–243.

Song H, Bucheli SR (2010) Comparison of phylogenetic signal between male genitalia and non-genital characters in insect systematics. *Cladistics*, **26**, 23–35.

Svedin N, Wiley C, Veen T, Gustafsson L, Qvarnström A (2008) Natural and sexual selection against hybrid flycatchers. *Proceedings of the Royal Society B: Biological Sciences*, **275**, 735–744.

Takahashi Y, Noriyuki S (2019) Colour polymorphism influences species’ range and extinction risk. *Biology Letters*, **15**, 20190228.

Title PO, Rabosky DL (2019) Tip rates, phylogenies and diversification: what are we estimating, and how good are the estimates? *Methods in Ecology and Evolution*, **10**, 821-834.

Tran, LAP (2016) Interaction between digestive strategy and niche specialization predicts speciation rates across herbivorous mammals. *American Naturalist*, **187**, 468–480.

Uetz P, Freed P, Hošek J (2020) *The Reptile Database*. http://www.reptile-database.org.

Vamosi SM, Schluter D (1999) Sexual selection against hybrids between sympatric stickleback species: evidence from a field experiment. *Evolution*, **53**, 874–879.

Werner YL (1982) Herpetofaunal survey of the Sinai Peninsula (1966-77), with emphasis on the Saharan sand community. In: *Herpetological communities: A symposium of the Society for the Study of Amphibians and Reptiles and the Herpetologists'League*, August 1977 (Ed. Scott, N.J., Jr.) Washington, US Fish and Wildlife Service, Wildlife Research Report 13, pp. 153-161.

West-Eberhard, MJ (1986) Alternative adaptations, speciation, and phylogeny. (A review). *Proceedings of the National Academy of Sciences of the United States of America*, **83**, 1388–1392.

Whitney JL, Donahue MJ, Karl SA (2018) Niche divergence along a fine-scale ecological gradient in sympatric color morphs of a coral reef fish. *Ecosphere*, **9**, e02015.