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.

Trait evolution and ancestral state reconstruction

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

Character associated diversification analysis

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

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

Secondly, we inferred the speciation rates with the Diversification Rates statistic (DR statistic, Jetz et al. 2012). Despite its name, the DR statistic provides a better estimate of the rate of speciation than of net diversification (Title and Rabosky 2019). For a given species, the DR statistic is computed as a weighted average of the inverse branch lengths connecting the focal species to the root of the 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).

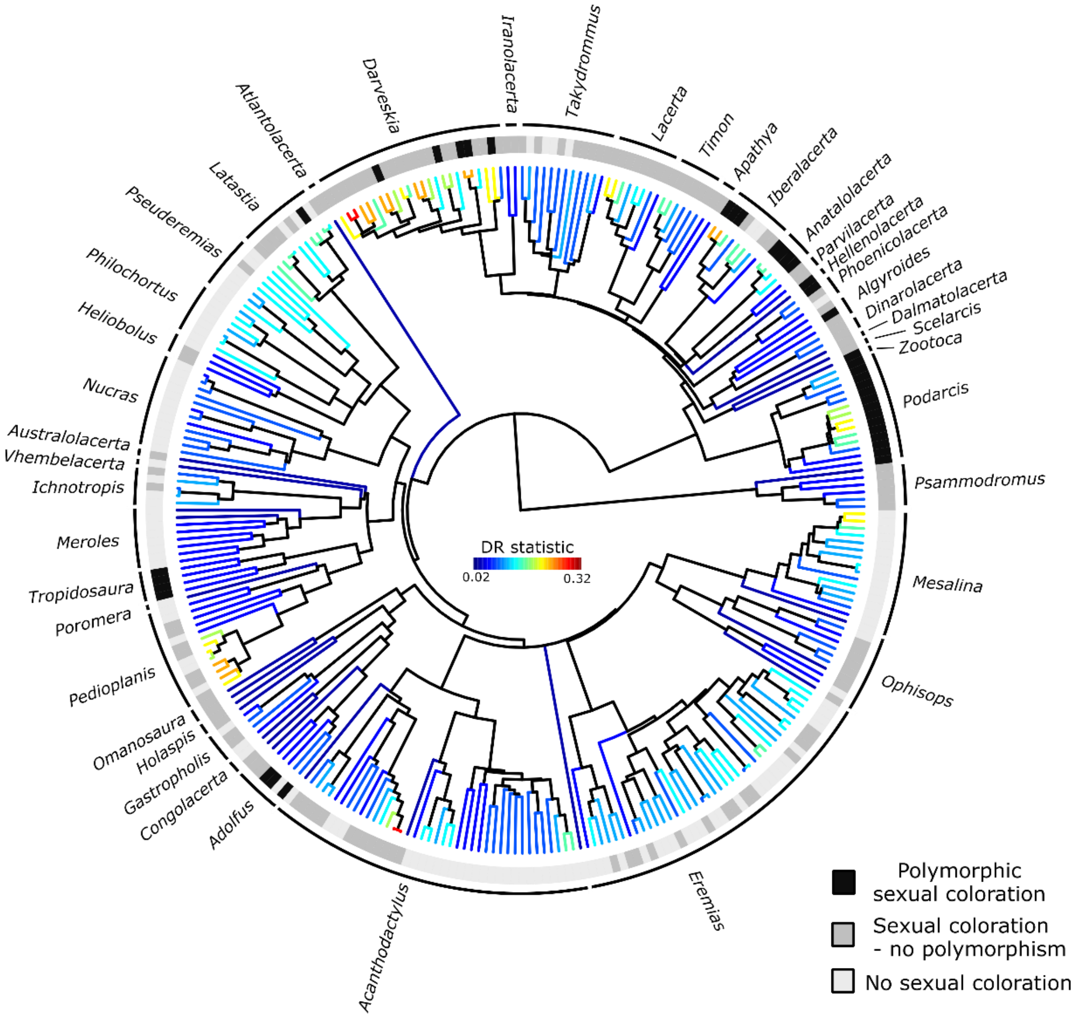

Figure 1. Phylogenetic relationships of the 295 Lacertids species included in the analysis. This tree was randomly chosen among the hundred trees produced for the analysis to account for phylogenetic uncertainty (see methods). States of sexual coloration and polymorphism characters are indicated at the 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).

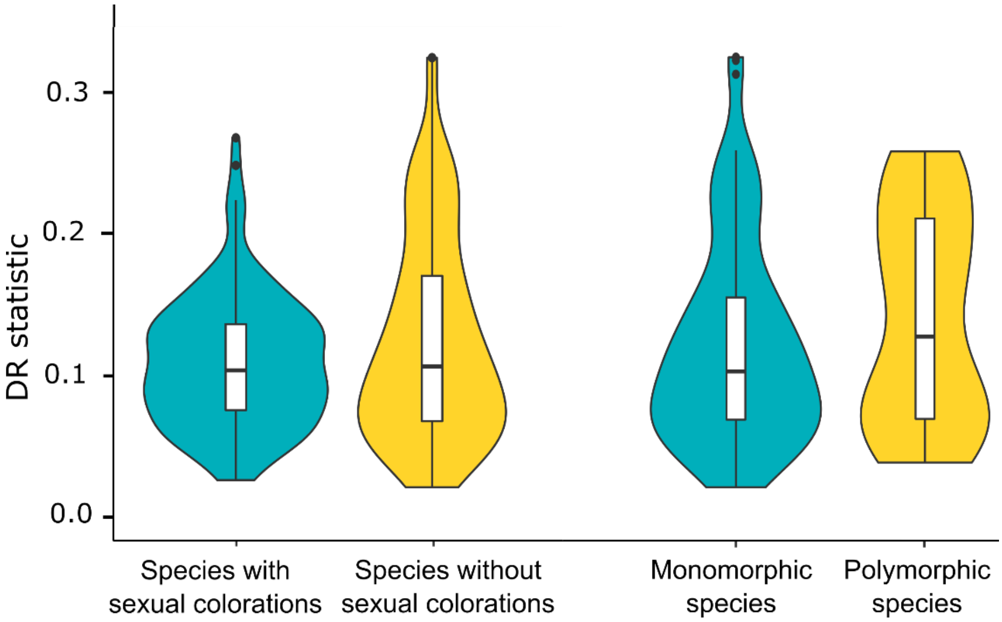

Figure 2. Violin plots of the DR statistic values for the species with and without sexual coloration, and with and without color polymorphism.

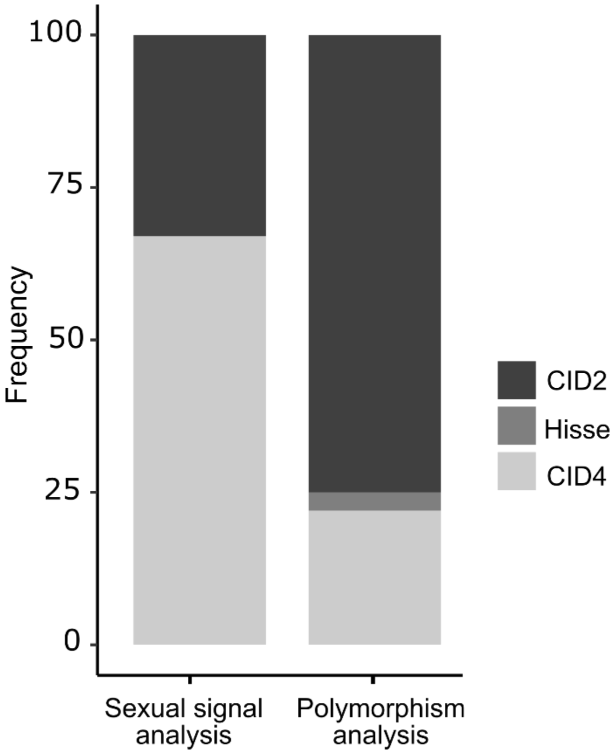

Figure 3. Frequency of the best fitting diversification models for the sexual coloration and color polymorphism analysis repeated across one hundred trees. Models with character dependent diversification (HISSE) were considered as best fitting when delta AICc > 2. BiSSE models were included in both analyses, 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

(Song and Bucheli 2010; Mejías et al. 2020). The few studies investigating this question found support for a positive correlation between speciation rates and evolutionary rates of sexual traits (Cardoso and Mota 2008; Gomes et al. 2016) but they were made on birds, and researches on other taxonomic groups are needed. Finally, the occurrence of conspicuous coloration might be a poor proxy of the intensity of sexual selection. In lacertids, mating choice and interspecific recognition are known to rely on pheromones as much as on coloration (Cooper and Pèrez-Mellado 2002; Khannoon et al 2011; Gabirot et al. 2013). It is thus possible that considering the presence of conspicuous colorations, even when they are sexually dimorphic, is not sufficient to detect an effect of sexual selection on speciation.

The lack of effect of color polymorphism on speciation rates contradicts the conclusions of Brock et al. (2021) obtained on the same taxonomic group. The first reason is that our attributions of character states (polymorphic versus nonpolymorphic) differed in some cases from theirs. We therefore re-checked our attributions in case of mismatches. Ten species considered monomorphic by Brock et al were considered polymorphic by us. Some of these reflect the fact that we coded polymorphism as the presence of discrete states on any conspicuous coloration, while Brock et al. (2021) considered only throat coloration -thus excluding four *Tropidosaura* species. For six other species we re-checked bibliographic references (see table S2) and confirmed mentions of polymorphism that had been apparently overlooked by Brock et al. 2021. Seven species were considered monomorphic by us and polymorphic by Brock et al. 2021. In four of these, color morphs do not co-occur within a population, but occur in allopatric populations or subspecies – which does not qualify as polymorphism *sensu stricto*. For the last three, we did not find any mention of polymorphism in the literature (and Brock et al. 2021 did not provide a reference). All in all, we believe that, although the status of each particular species can always been updated and discussed, our character states are more accurate and closer to the original definition of a polymorphic species and to the concept of morphic speciation (i.e. not focused only on throat coloration (West-Eberhard 1986) and excluding geographic races).

In addition, methodological issues can contribute to discrepancies in the results. The SDD methods have been criticized on the basis of high type-1 errors, i.e. they may detect differences in diversification rates even for neutral traits and are probably overparameterized as speciation and extinction can hardly be estimated independently (Rabosky and Goldberg 2015, 2017; Louca and Pennell 2020). This is illustrated by the fact that 6 of the 8 estimated parameters are at the boundary of the allowed interval in the HISSE model (all four extinction rates and two transition rates are zero, using Brock et al.'s data and character states) ; the same characteristic is present in Brock et al.'s original results (their Table 2) as well as in our run of their script with their data, character states and 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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