Colour polymorphism and conspicuousness do not increase speciation rates in Lacertids

Thomas de Solan [1], Barry Sinervo [2,†], Philippe Geniez [3], Patrice David [1,4], Pierre-André Crochet[1,4, *]

Affiliations

[1] CEFE, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France

[2] Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, CA, United States of America

[3] CEFE, Univ Montpellier, CNRS, EPHE-PSL, IRD, Montpellier, France

† deceased author

[4] equal contributions

*Corresponding author

Correspondence: pierre-andre.crochet@cefe.cnrs.fr

Abstract

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

Key words: colouration, sexual selection, polymorphism, speciation, reptiles

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 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 lose 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 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).

However, other lines of arguments suggest that polymorphism could reduce speciation rates

and that the effect of polymorphism depend on mate choice within polymorphic populations. While

assortative mating by morph could indeed enhance speciation and promote shifts from ancestral

polymorphism to derived monomorphism through speciation (Jamie and Meier 2020), disassortative

mating by morph is likely to slow speciation and retain polymorphism through the speciation process

(Jamie and Meier 2020). As reported in *Heliconius numata* (Chouteau et al. 2017), disassortative

mate preferences based on color morph has the potential to hamper ecological specialization by

enhancing the homogenization of genomic backgrounds; ultimately preventing ecological speciation.

Last, we argue that 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 colour traits should be less likely to result in reproductive isolation compared to non-

polymorphic species. To sum up, the effect of colour polymorphism on speciation rate could depend

on mate choice within population, which casts doubt on the generality of the morphic speciation

hypothesis.

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 macroevolutionary 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 colourations, and

(ii) the Lacertini, that live mostly in temperate habitats in Europe and are more often colourful.

Among those three clades, many species present conspicuous colourations. Bright colourations 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 colour. Such polymorphism can be found

in both sexes when it occurs on ventral colouration, 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 colour polymorphism as several morphs differing in ventral colouration 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 colourations 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 colouration data obtained from literature and photographs of live specimens

for most species of the family Lacertidae (see "Data acquisition" for species excluded and source of

information) to address two questions: (i) what are the evolutionary histories of conspicuous

colourations and colour polymorphism in this family? (ii) Is there an effect of conspicuousness and

colour polymorphism on speciation rate? We hypothesized that brightly coloured 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 colourations on speciation. For

colour polymorphism, based on the morphic speciation hypothesis, we predicted that colour

polymorphism increases speciation rates in lacertids. During the course of our study, we became

aware of the publication of Brock et al. (2022) who had independently addressed the same question

using the same group of species but using different data and methods (see discussion). Although our

study started out as a completely independent work, unknowing that another group was addressing

the same subject, it is important to understand why we came to opposite conclusions to Brock et al.

(2022) and have devoted a section to address 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 colouration 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 colourations 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

colourations if, at least in males, (1) the ventral side, or a part of its ventral side (throat, belly), was

not white or grey, or (2) the flanks displayed several ocelli or spots that contrast with the rest of the

dorsal/flank areas and are of a different colour, or (3) the species displayed a specific colour 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 clearly distinct colours on the same body

region. We did not score colouration as polymorphic if the morphs were not clearly distinguished,

nor if the distinct morphs were associated with age or sex, or correspond to different parts of the

annual cycle (green dorsal coloration in males of many species of Lacertinae disappear outside

breeding season). Species where colouration varies geographically but not within populations were

not treated as polymorphic, even though it was sometimes difficult to determine if some variation in

colouration reported in the literature was geographically structured or not. Finally, a few species

display polymorphism on dorsal pattern that is not linked to conspicuous coloration (different types

of patterning of brown female dorsal coloration in *Podarcis* for example, see Ortega et al. 2014;

Ortega et al. 2015). Such polymorphism is rare and always occurs in species which also show

polymorphism for conspicuous ventral coloration; as a consequence, there is no species with

polymorphism but not conspicuous coloration in our data. Data on sexual colourations and

polymorphism are provided in Supplementary Table S1and some examples are provided in Figure S1.

174   We used the phylogeny provided by Garcia-Porta et al. (2019) as backbone phylogeny. We

175 subsequently added the 85 non-insular and non-parthenogenetic species that were not sampled by

176 Garcia-Porta. These species were added to the backbone tree using the function

177 add.species.to.genus from the phytools package (Revell 2012). For 17 species (listed in Table S1)

178 where the phylogenetic position was known from previous works, the species was added with its

179 sister taxa at a random divergence date. If no phylogenetic information was available, the species

180 was randomly located in its genus; this applied to 68 species in our phylogeny, of which only four

181 were treated as polymorphic (see Table S1). We repeated this operation one hundred times in order

182 to account for phylogenetic uncertainty generated by randomly added species in all analyses.

184 **Trait evolution and ancestral state reconstruction**

185 We investigated the evolutionary inertia for conspicuous colourations and polymorphism using the δ

186 values (Borges et al. 2019). This index is designed to measure phylogenetic signal in categorical traits,

187 with high δ value indicating high phylogenetic signal (i.e. strong phylogenetic constraint to trait

188 evolution). To test the significance of the observed δ, we compared with a Wilcoxon test the

189 distribution of the 100 observed δ, measured on the 100 phylogenetic trees, against a null

190 distribution obtained by measuring δ after randomization of the trait data among species

191 (phylogenetic signal = zero). In addition, we reconstructed the ancestral state of the colouration with

192 the make.simmap function from the phytools package (Revell 2012). This function simulates

193 stochastic character histories using the state of the character on the tips and a continuous-time

194 reversible Markov model. For this analysis, colouration was coded with three states: (1) no

195 conspicuous colouration, (2) presence of conspicuous colourations without polymorphism, (3)

196 presence of conspicuous colourations and polymorphism. Transition rates between states were

197 allowed to differ and we did not exclude transitions from (1) to (3) although no such transitions were

198 recovered by the model (see below). We repeated the ancestral state reconstruction (ASR) on the

199 100 phylogenetic trees, with 100 simulations for each analysis.

201 **Character associated diversification analysis**

202 We used several methods to compare the rates of speciation between species with and without

203 conspicuous colours, and between species with and without polymorphism. We excluded the species

204 lacking conspicuous colourations of the polymorphism analysis because there are no direct

205 evolutionary transitions from non-conspicuous to polymorphic, see results of the ASR). We however

206 tested the influence of this exclusion by repeating the polymorphism analysis with all the species.

207   First, we used the speciation/extinction analysis of BAMM (Rabosky 2014) to detect shifts in

208 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 colourations and colour

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

colourations 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 colourations and

performed the test.

Finally, we fitted State Dependent Diversification models (SDD) to test the influence of

conspicuous colourations and colour polymorphism on the diversification rates of Lacertid. For each

trait, we implemented four SDD models: two models measuring character dependent diversification,

plus the corresponding two null models estimating Character Independent Diversification (CID). The

first SDD 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 SDD 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.

Comparison with Brock et al. (2021)

Although our study and the study of Brock et al. (2021) were made on the same taxonomic groups,

our analysis reached an opposite conclusion to the study of Brock et al. (see below). We thus made

additional analyses to understand the origin of these differences. In order to explain the differences

of results between our study and Brock et al.'s (2021), we performed the four SDD models included

in main analysis, HiSSE, BiSSE, CID2 and CID4, as well as the STRAPPS and FiSSE analyses, while

changing the factors that changed between the two studies.

(i) Our analysis included more species than in Brock et al.'s analysis (294 vs 262), and we

excluded insular species, which was not done in Brock et al.'s analysis. We tested how this difference

of species sampling affected our results by repeating our analysis using only the species included by

Brock et al. (2021). For this analysis we used species coloration character states as coded in our

database and the R script as in our main analysis.

(ii) Our coding of character states differed from Brock et al. (2021)'s in some species. Among

the species we had in common, 10 species were coded as polymorphic in our dataset while they

were coded as monomorphic in Brock et al. dataset, and 7 species were coded as monomorphic in

our dataset while they were coded as polymorphic in Brock et al. dataset (see Table S2 for coloration

data of Brock et al., and the rational of our coding). We tested how these differences affected our

results by repeating the analysis with both the species and the character states used by Brock et al.

(2021). The R script used for this analysis was the same as for our main analysis.

(iii) Although we used the same R package (HiSSE; Beaulieu 2017), the HiSSE package was

recently updated, and our analysis was based a more recent version than Brock et al. (2021). As a

result, there are several differences in the R function between Brock et al.'s analysis and our analysis.

This results in differences of functions (the function specifically built for CID4 models was removed in

the recent version), but also in differences in the number of transition rates between states in SDD

models. We tested how differences in R script affected our results by re-running the original Brock et

al.'s analysis using their script, species and character states (hence repeating their analysis entirely

without changing anything).

All the analyses were made on the phylogenetic tree produced by Garcia-Porta et al. (2019),

which was used in both our main analysis and Brock et al. (2021). Brock et al. (2021) built a second

phylogeny on which they repeated all their analysis, without affecting their conclusion. We did not

used this phylogeny in the comparison because it was built with only five genes, while Garcia-Porta

et al.' phylogeny was built with one dataset of 324 anonymous nuclear loci and one dataset of 6269

protein-coding nuclear loci. In addition, some clades identified in Brock et al.' phylogeny were at odd

with previous results: for example, the Gallotiinae are nested within Lacertinae in Brock et al (2021),

while they are sister clades in Garcia-Porta et al. (2019), Arnold et al. (2007) and Kapli et al. (2011).

RESULTS

Conspicuous colourations were frequent in lacertids, as they were present in 63% of the species

analyzed (Figure 1). Colour polymorphism, on the other hand, was rarer and only concerns 13% of

the species analysed; it concerned the ventral region (throat and/or belly) in all polymorphic species

except for the four species of the genus *Tropidosaura* where we identified polymorphism in the

bright coloration of the lower flanks (see Tables S1, S2). 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 colourations and colour polymorphism

(Figure S2, 43 acquisitions vs 23 losses for colourations and 15 acquisitions vs 3 losses for

polymorphism). Transitions from dull-coloured to polymorphism, 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-colour state in lacertids. Finally, the ancestor of lacertids probably

displayed conspicuous colourations without being polymorphic (Figure S2).

Character associated diversification analysis

We wanted to test whether conspicuous colouration 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 coloured. Including inconspicuous species would confound the effects of

polymorphism per se and conspicuousness. When included, however, species lacking conspicuous

colourations 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 colourations

nor the presence of colour polymorphism affected speciation rates (p>0.5 for all tests across the 100

trees).

The DR statistic showed that inconspicuously and conspicuously coloured 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 coloured 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 colouration and polymorphism characters
are indicated at the tips. Tip branches are coloured 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 colouration 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 colour polymorphism on the diversification of species with conspicuous

colourations. 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 colouration,
and with and without colour polymorphism.

Figure 3. Frequency of the best fitting diversification models for the sexual colouration and colour
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.

Polymorphism analysis applied to all species, including those without sexual colorations

The results of STRAPP and FiSSE analysis were not affected by the inclusion of species without sexual
colorations. Both analyses indicated that speciation rates were independent of the presence of color
polymorphism (p>0.5 for all tests across the 100 trees).

When species without sexual colorations were included, SDD models indicated that color
polymorphism was probably independent of the rates of diversification. The HiSSE model was the
best-fitting model for only 2 trees, while CID2 and CID4 were the best fitting models for 44 and 54
trees respectively.

Comparison with Brock et al. (2021)

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 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 coding of character states (STRAPPS test: p=0.98; FiSSE test: $\lambda_0 =$

0.10, λ_1=0.13, p=0.88), or theirs (STRAPPS test: p=0.98; FiSSE test: λ_0 = 0.10, λ_1 = 0.14, p=0.98).

When we repeated our analysis with the same species as in Brock et al. (2021), the model

with the lowest AIC was still CID4, like in our main analysis (AIC and parameters values for all SDD

models in Table S3). This indicates that the inclusion of species not included in Brock et al. (2021) and

the exclusion of insular species in our analysis were not at the origin of the difference of results.

When we built the SDD models with the species and character states of Brock et al. (2021),

the results were opposite to what we previously found: the HiSSE model scored the lowest AIC, just

before CID4 model (AIC$_{HiSSE}$ = 1838, AIC$_{CID4}$ =1841; see Table S3 for the score of the other models). The

difference of SDD model's results between our study and Brock et al. study thus lies in in the way of

coding polymorphism.

When we used the R script, the species and the character states of Brock et al. (2021), we

also found that the HiSSE model scored the lowest AIC (AIC$_{HiSSE}$ = 1835), while the other SDD models

all had much higher AIC values (AIC$_{BiSSE}$ = 1862, AIC$_{CID4}$ =1901, AIC$_{CID4}$ =1913; parameters values in

Table S3). Note that, compared to the recent version of the R package on the same data, the AICs

obtained with the older version were lower for the state-dependent models (HISSE and BISSE) and

much higher for non-state dependent models (CID2 and CID4). Note also that the SDD models did not

perform properly in any analysis using Brock et al.'s data and character states, as 6 of the 8 estimated

parameters were at the boundary of the allowed interval in our HISSE model (all four extinction rates

and two transition rates are zero, see Table S3).

DISCUSSION

Our analyses suggested that neither the presence of conspicuous colourations nor colour

polymorphism increases the rates of speciation in Lacertids. We also showed that conspicuous

colourations and colour polymorphism are labile across taxonomy, and were gained and lost several

times during the diversification of Lacertids. The lack of effect of conspicuous colourations 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 colour 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), including one that used the same family as model (Brock et al. 2021).

Inconsistent results on Lacertids

The lack of effect of colour polymorphism on speciation rates contradicts the conclusions of

Brock et al. (2021) obtained on the same family Lacertidae. Although Brock et al. (2021) used a

different phylogeny, they also used the same phylogeny as us and this did not affect their conclusion.

We also excluded insular species and parthenogenetic species, because speciation mechanisms in

these species are unlikely to depend on polymorphism, unlike Brock et al. (2021). In addition, their

phylogeny only included species that were represented in the molecular dataset. While this avoided

placing species randomly within their genus, as we did (we checked that our results were robust to

the random position of species with no genetic data within their genus by repeating all analyses on

100 trees, see methods), this also resulted in removing a considerable fraction of the Lacertidae

species from their data. Worryingly, this fraction of species excluded from their analysis is biased

between the two main clades of Lacertidae (Table S1): their dataset lacks 17 species of Lacertini out

of 143 but 66 species of Eremiadini out of 203. Since polymorphic species are mostly Lacertini, it

seems dangerous to underrepresent the mostly non-polymorphic Eremiadini when comparing the

diversification rate of polymorphic and non-polymorphic species. If we wanted to maintain our

choice to include as many species as possible in the dataset, switching from Garcia-Porta et al's tree

to Brock et al's tree would only decrease the number of randomly added species from 68 to 57. Last,

Garcia-Porta et al's backbone is based on genomic data while Brock et al's tree, based on a small

amount of sequence data, has obtained some spurious relationships. Finally, when we tested how

this difference of species sampling affected our results by repeating our analysis using only the

species included by Brock et al. (2021) and using species coloration character states as coded in our

database, we found the same conclusion of no effect of polymorphism on diversification. We are

thus confident that our choice of using Garcia-Porta et al.'s (2019) phylogeny and including species

that have no genetic data available was the best methodological choice, but the use of different

phylogenies and different species did not cause the differences in the two studies.

Another possible reason is that our attributions of character states (polymorphic versus

nonpolymorphic) differed in some cases from Brock et al. (17 species highlighted in yellow in Table

S2), and indeed repeating our analysis with the species and character coding of Brock et al. (but using

our R script and phylogeny) suggested a possible influence of polymorphism on diversification, as the

best model this time was the HiSSE model. 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 colouration, while Brock et al. (2021) considered only throat colouration -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, colour 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).

One of the reasons for the different conclusions between our study and Brock et al. is thus

differences in species trait coding (see Table S2), partly resulting from differences in interpreting

available evidence, partly resulting from a restriction of polymorphism to the throat coloration in

Brock et al. 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

colouration, West-Eberhard 1986, and excluding geographical 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)

when we used Brock et al.'s data and character states with the new version of HiSSE. The same

problem was already apparent in Brock et al.'s original results (their Table 2, repeated here in Table

S3). Especially worrying is the fact that the net turnover parameters are not estimated (parameters

at boundary) for the two state classes (polymorphic and non-polymorphic) of the A class of the

hidden state. The higher diversification of polymorphic species is thus only supported in one of the

two classes of the hidden state using the new version of the R package HiSSE, which does not allow

to conclude on the impact of polymorphism on diversification rates according to Beaulieu and

O'Meara (2017). 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), and that Brock

et al. results are less robust when using their species and trait coding with the new version of HiSSE

suggests that the result of Brock et al (2021) might have been partly (mostly?) driven by a type-1

error.

In conclusion, the differences between the results of Brock et al. (2021) and our results

concerning the impact of colour polymorphism on diversification in Lacertidae originate partly from

Brock et al.'s choice to restrain colour polymorphism to throat colour polymorphism only and partly

from methodological issues associated with the R package HiSSE.

Conspicuous colorations, sexual selection and speciation in lizards

The lack of effect of conspicuous colourations 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 colourations 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 more research on
other taxonomic groups is needed. Finally, the occurrence of conspicuous colouration 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 colouration (Cooper and Pèrez-Mellado
2002; Khannoon et al 2011; Gabirot et al. 2013). It is thus possible that considering the presence of
conspicuous colourations, even when they are sexually dimorphic, is not sufficient to detect an effect
of sexual selection on speciation.
An additional explanation for the lack of correlation between conspicuous colourations /
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 colour assortative mating) while indirect

genetic results also suggest some possible assortative mating in *Podarcis melisellensis* (Huyghe et al.

2010).

One main limitation of our work lies in the data we used to score the colouration. Neither

photographs nor literature sources account for variation of ultraviolet (UV) colouration. Lacertids

frequently use UV colouration 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 colouration and polymorphism in our dataset. However, known UV signals in lizards are

always displayed on a patch with a visibly different colour 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 colouration in animals. A second methodological limitation may

stem from the strong geographical bias prevailing in the taxonomic information. 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 colourations and

colour polymorphism are present in the equatorial region. However, we can predict that undescribed

species are more abundant in the Eremiadini (where colour polymorphism is rare) than Lacertini

(where colour polymorphism is widespread, see Fig. 1 and Table S1), because taxonomic revisions for

many Lacertini have already been published and undescribed cryptic diversity remains higher now in

Eremiadini (pers. obs.). This should result in higher diversity and hence higher diversification rates for

Eremiadini than currently estimated, and hence further reinforce the lack of difference between

polymorphic and non-polymorphic species in terms of diversification rate.

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.

Conclusion

Our analyses suggest that the speciation of lacertids was not influenced by the presence of

conspicuous sexual colourations nor by colour 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 colouration

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.

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.

Acknowledgements

574   We thank all photographers who contributed to the amphibians and reptiles photo collection
575 managed by PG.

Data, scripts, code, and supplementary information availability

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

Conflict of interest disclosure

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

Funding

583 TdS benefited from a PhD grant from the CNRS. PAC and PD aknowledge recurrent funding from the CNRS
584 for this study.

References

Abalos J, Pérez i de Lanuza G, Carazo P, Font E (2016) The role of male colouration 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 colour 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 colour 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.

Arnold, E. N., O. Arribas, and S. Carranza. 2007. Systematics of the Palaearctic and Oriental lizard
tribe Lacertini (Squamata: Lacertidae: Lacertinae), with descriptions of eight new genera. *Zootaxa*,
1430,1–86.

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 colour 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) Colour 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 colouration 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 colour 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.

Kapli, P., N. Poulakakis, P. Lymberakis, and M. Mylonas. 2011. A re-analysis of the molecular
phylogeny of Lacertidae with currently available data. *Basic and Applied Herpetology,* **25**, 97–104.

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 colour
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
colouration 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 colouration 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 colouration, 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)
colouration 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, D. L., and E. E. Goldberg. 2015. Model Inadequacy and Mistaken Inferences of Trait-
Dependent Speciation. *Systematic Biolology*, **64**, 340–355.

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

819 rates across herbivorous mammals. *American Naturalist*, **187**, 468–480.

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

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

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

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

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

831