

1 **Research article**

2

3 **Title:** Parthenogenesis is self-destructive for scaled reptiles

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5 **SHORT RUNNING HEAD:** Parthenogenesis in Squamata

6

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20 Parthenogenesis is rare in nature. With 39 described true parthenogens, scaled reptiles  
21 (Squamata) are the only vertebrates that evolved this reproductive strategy. Parthenogenesis is  
22 ecologically advantageous in the short-term, but the young age and rarity of parthenogenetic  
23 species indicate it is less advantageous in the long-term. This suggests parthenogenesis is self-  
24 destructive: it arises often but is lost due to increased extinction rates, high rates of reversal or  
25 both. However, this role of parthenogenesis as a self-destructive trait remains unknown. We used  
26 a phylogeny of Squamata (5,388 species), tree metrics, null simulations and macroevolutionary  
27 scenarios of trait diversification to address the factors that best explain the rarity of  
28 parthenogenetic species. We show that parthenogenesis can be considered as self-destructive,  
29 with high extinction rates mainly responsible for its rarity in nature. Since these parthenogenetic  
30 species occur, this trait should be ecologically relevant in the short-term.

31

## 32 **Keywords**

33 Squamata, parthenogenetic, asexual, self-destruction, extinction.

34

## 35 **1. Background**

36 Asexual reproduction in vertebrates is rare. It occurs in squamates, fish, salamanders and frogs  
37 through gynogenesis, hybridogenesis, kleptogenesis and parthenogenesis [1]. While the former  
38 three mechanisms require male fertilization, in parthenogenesis the embryo develops from a  
39 female gamete alone. Particularly, true/constitutive parthenogenesis (i.e. sperm-independent  
40 asexual reproduction) is even rarer: it occurs solely in scaled reptiles (order Squamata; e.g. [1–  
41 4]) from the successful hybridization between genetically distant species [1,5,6]. The explanation  
42 for the macroevolutionary rarity of parthenogenesis in vertebrates remains elusive [1,4,7]. We

43 focus on parthenogenesis, although most aspects also apply to asexual vertebrates as we  
44 highlight below. Unless stated otherwise, we use 'asexual' for overall asexuality, 'parthenogen'  
45 for true/constitutive parthenogenesis and 'species' for each evolutionary unit in a phylogeny (i.e.  
46 evolutionary species concept [8]). Although the term 'species' has different meanings between  
47 reproductive modes, asexual species share some characteristics with sexual species (e.g. they  
48 evolve independently and each individual is more closely related to an individual of the same  
49 species than to individuals of a different species [9]).

50         The relatively young age and small number of parthenogenetic vertebrate species suggest  
51 that asexuality is evolutionarily disadvantageous on the long-term [10]. It rather functions as a  
52 short-term successful ecological strategy [4,11] (reviewed in [1]). No ancient species-rich clade  
53 of asexual species is known to occur in nature; only distantly related species [4,6]. This can  
54 result from clones' high extinction rates in the long-term due to low recombination—Muller's  
55 Ratchet [12]. The lack of DNA-repair meiotic mechanisms can also hinder asexual long-term  
56 viability [13] (however, asexual vertebrates can have functional meiosis [14,15]). Finally,  
57 asexual species' low genetic diversity [1,5] could hinder their adaptability to changing  
58 environments [16]. However, if clones' formation is fast enough, neutral replacement could take  
59 place before their long-term disadvantages [17,18].

60         In the short-term, asexuality can be ecologically successful. It can rapidly lead to  
61 population increases (i.e. no need for mating) and range expansions through the colonization of  
62 environments that are unsuitable for the parental species (i.e. geographic parthenogenesis) [1,5].  
63 When parthenogenetic populations colonize new and species poor environments, they expand  
64 their distribution of phenotypes and niche breadths (i.e. ecological release) [7]. Parthenogenetic  
65 lizards can even outcompete their sexual progenitors in some cases [19] and have greater aerobic

66 activity at low temperatures [20].

67         When a trait arises often but increases extinction rates, leading to short-lived and  
68 phylogenetically scattered species, it is self-destructive [21]. Self-destructive traits are also  
69 labile—frequently gained and lost, particularly when the rate of reversal (i.e. loss of the trait) is  
70 high [21]. Examples include salt tolerance (increased extinction rates or high trait reversal) [22]  
71 and selfing (high trait reversal) [23] in plants and colour polymorphism in birds (increased  
72 extinction rates) [24] (but see [21]). Asexuality could be considered a self-destructive trait [21];  
73 the phylogenetic ‘instability’ suggests either increased extinction rates, trait lability, or both.  
74 However, studies with invertebrates show no negative impact of asexuality on diversification  
75 rates [25,26]. Alternatively, the likelihood for asexual formation through hybridization could  
76 explain this ‘instability’ [5,27]. Successful hybridization relies on range overlap between  
77 parental species, while maintaining enough phylogenetic distance and genetic compatibility [27–  
78 30]. The role of asexuality as a self-destructive trait remains untested at the macroevolutionary  
79 level for vertebrates.

80         Squamates are a suitable system for studying the macroevolutionary dynamics of  
81 asexuality while focusing on parthenogenesis. There are 39 parthenogenetic squamates reported  
82 so far (e.g. [7]). We used four tree metrics, null simulations and alternative scenarios of trait  
83 evolution to test parthenogenesis as self-destructive trait in Squamata. First, we addressed if  
84 parthenogenetic species are younger than sexual species. Parthenogenetic species should be  
85 younger (1) if they arise frequently in nature but are relatively short-lived (higher extinction  
86 rates) and (2) given they generally originate from hybridization [1]. Second, we compared if the  
87 number of parthenogenetic species per origin of parthenogenesis is lower than expected. We  
88 expect each origin of parthenogenesis to give rise to fewer than expected parthenogenetic

89 species. Not only will parthenogenesis formation depend largely on the amount of range overlap  
90 and genetic diversity between hybridizing species [1]; in a scenario of self-destruction  
91 parthenogenetic species would frequently go extinct before possibly radiating. Together, these  
92 would hinder the accumulation of parthenogenetic species per origin of parthenogenesis. Third,  
93 we tested if parthenogenetic species are clustered or scattered. In a scenario of trait self-  
94 destruction, parthenogenetic species should be scattered throughout the phylogeny. Finally, we  
95 inferred the parameters responsible for the unstable macroevolutionary pattern of  
96 parthenogenesis under different scenarios. We expect that increased extinction rates will best-  
97 explain this pattern given the long-term limitations of parthenogenesis.

98

## 99 **2. Methods**

### 100 **2.1. Species data and phylogenies**

101 We identified 39 parthenogenetic species of Squamata from the literature (see electronic  
102 supplementary material 1, table S1). We used only species included in [31].

103 We used the posterior distribution of 10,000 phylogenies of Squamata with 9,754 species  
104 each [32]. We pruned all trees using ape v5.3 in R [33] to the species with molecular data in [32].  
105 The final set of phylogenies included 5,388 species. We calculated the 50% majority-rule  
106 consensus tree in MrBayes v3.2 [34]. The final tree included 23 out of 39 parthenogens (table  
107 S1). We examined the effects of 1) phylogenetic uncertainty using an alternative tree and 2)  
108 sampling bias by randomly allocating the state ‘parthenogen’ within each genus where the trait is  
109 known to occur (text S1-S2).

110

### 111 **2.2. Phylogenetic metrics**

112 We calculated four tree metrics for the consensus tree: Tip Age Rank Sum (TARS), Number of  
113 Tips per Origin (NoTO), Sum of Sister Clade Differences (SSCD), and Fritz & Purvis D statistic  
114 (FPD) [21,35]. We used phylometrics v0.01 in R [36] and tested for significance using the  
115 Wilcoxon rank-sum test for TARS, 1000 traits simulated under Brownian motion (BM) for  
116 NoTO and SSCD, and 1000 traits simulated under BM and 1000 random traits for FPD [21].  
117 When  $P_{\text{TARS}} < 0.05 / > 0.95$  parthenogenetic species have significantly shorter/longer tip lengths  
118 than sexual species. When  $P_{\text{NoTO}} < 0.05 / > 0.95$  each inferred origin of parthenogenesis (which is  
119 placed at the node for each independent parthenogenetic species or clade of parthenogenetic  
120 species) gives rise to fewer/more species than expected under a stochastic process. When  
121  $P_{\text{SSCD}} < 0.05 / > 0.95$  parthenogenetic species are more scattered/clustered than expected under a  
122 stochastic process. When absolute values of FPD are closer to 1 parthenogenetic species are  
123 randomly distributed throughout the phylogeny, while values closer to 0 indicate that the trait  
124 evolves as expected under BM.

125

### 126 **2.3. Macroevolutionary models**

127 We simulated different scenarios of trait evolution to test the parameters responsible for the  
128 macroevolutionary dynamics of parthenogenesis in squamates. The parameters include  
129 speciation rate for sexual ( $\lambda_0$ ) and parthenogenetic species ( $\lambda_1$ ), extinction rate for sexual ( $\mu_0$ ) and  
130 parthenogenetic species ( $\mu_1$ ), and rates of gain ( $q_{01}$ ) or reversal ( $q_{10}$ ). The initial values were 0.1,  
131 0.1, 0.03, 0.03, 0.01 and 0.01 (in units: per million years), respectively [21]. Since the method  
132 uses likelihood estimation, we repeated the analysis with these values both multiplied and  
133 divided by 5.

134 We simulated 9 scenarios for each set of initial parameters under different constraints: no

135 effect of parthenogenesis on speciation rates ( $\lambda_0=\lambda_1$ ) and/or extinction rates ( $\mu_0=\mu_1$ ), equal  
136 transition rates ( $q_{01}=q_{10}$ ) or no reversals ( $q_{10}=0$ ). The scenarios include: *a*) no constraints—  
137 parameters can be different between sexual and parthenogenetic species; *b*)  $\lambda_0=\lambda_1$ ,  $\mu_0=\mu_1$  and  
138  $q_{01}=q_{10}$ ; *c*)  $\lambda_0=\lambda_1$  and  $\mu_0=\mu_1$ ; *d*)  $\lambda_0=\lambda_1$  and  $q_{01}=q_{10}$ ; *e*)  $\mu_0=\mu_1$  and  $q_{01}=q_{10}$ ; *f*)  $\lambda_0=\lambda_1$ ; *g*)  $\mu_0=\mu_1$ ; *h*)  
139  $q_{01}=q_{10}$ ; and *i*)  $q_{10}=0$ . We fit each model using diversitree v0.9-13 in R (table 2; table S3-S4)  
140 [37].

141 To obtain a null distribution of tree metrics for the macroevolutionary scenarios, we used  
142 the parameters estimated in models *a-i* to simulate 100 trees with 5,388 species. We then  
143 estimated the tree metrics in the alternative scenarios. *P*-values indicate the proportion of  
144 simulated metric values that are lower than or equal to the observed metric values. Significance  
145 was considered if  $P\leq 0.01/P\geq 0.99$  after a Bonferroni correction [35]. Overall, we were interested  
146 in the relative role of each parameter and not in the specific fitted values of the rates. We tested  
147 for false discovery rates (model *b*) and power (models *a, c-i*) as the proportion of simulated  
148 metric values with  $P\leq 0.05$  for  $P_{\text{TARS}}$ ,  $P_{\text{NoTO}}$  and  $P_{\text{SSCD}}$ , or  $P>0.5$  for  $P_{\text{FPD}}$  (table S11-S13) [21].

149

### 150 **3. Results**

151 Parthenogenetic species are significantly younger than sexual species ( $P_{\text{TARS}}<0.001$ ; table 1).

152 The number of species that originate from parthenogenetic ancestors does not differ from those  
153 that originate from a trait evolving under BM ( $P_{\text{NoTO}}=0.278$ ). Species are not more scattered  
154 across the phylogeny than expected under BM ( $P_{\text{SSCD}}=0.103$ ) nor more randomly distributed  
155 (FPD=0.401). Results were consistent using an alternative phylogeny and to the impact of  
156 missing taxa (table S2).

157 Models *c-d, f, h-i* identify parthenogenesis as self-destructive either by higher extinction

158 rates compared to speciation ( $d, h-i$ ) or high rates of reversal ( $c, f$ ) (table 2). These models were  
159 not rejected (figure 1) and parameters suggest that parthenogenesis in squamates cannot be  
160 distinguished from a model where this state is frequently lost due to high extinction rates ( $d, h-i$ )  
161 or high rates of reversal ( $c, f$ ). Models  $a$  and  $g$  also have high rates of reversal, but the speciation  
162 rates are higher relative to extinction. Model  $e$  reflects a trait that increases/decreases speciation.  
163 Results were consistent using different initial parameters (table S3-S4) and alternative  
164 approaches (text S1-S2). We found low false discovery rates and high power to detect significant  
165 effects for each macroevolutionary scenario (table S11-S13).

166

#### 167 **4. Discussion**

168 Here we show that parthenogenesis in squamates can be considered a macroevolutionary self-  
169 destructive trait. Parthenogenetic species are significantly younger than sexual species. However,  
170 each origin of parthenogenesis does not give rise to fewer than expected parthenogenetic species.  
171 This could reflect some genera as *Darevskia* or *Aspidoscelis* that concentrate almost half of the  
172 described parthenogenetic squamates (~46%). Subsequent backcrosses could explain how each  
173 origin of parthenogenesis could give rise to more than one parthenogenetic species [5,38]. In  
174 fact, the uneven incidence of true parthenogens could explain that parthenogenesis is not as  
175 scattered in the phylogeny as expected. Only one species of Serpentes (i.e. *Indotyphlops*  
176 *braminus*) has been described as true parthenogenetic (figure 2). This suggests a higher tendency  
177 for lizards to produce parthenogenetic hybrids or biases towards the most studied clades [39].  
178 Null simulations should benefit from increased numbers of described parthenogenetic species  
179 and further motivate identifying asexual species in nature.

180 Results from the macroevolutionary scenarios also support parthenogenesis as self-



181 destructive. At first glance, results suggest that this trait increases extinction rates or rates of  
182 reversal. However, once asexuality is achieved, reversals to sexual reproduction would be very  
183 difficult [6,40] (but see [41]), particularly if the genes responsible for sexual traits (e.g.  
184 spermatogenesis, meiosis) degenerate [1,6]. This suggests that trait lability is not responsible for  
185 the ‘unstable’ pattern of parthenogenesis. We do not reject model *i* that identifies higher  
186 extinction rates in relation to speciation and null rates of reversal (figure 1). Thus, although high  
187 rates of reversal can also explain similar scenarios of trait evolution, the difficulty associated  
188 with reversal from asexuality indicates this should not be the case for parthenogenesis.  
189 Ultimately, parthenogenesis influences extinction rates (model *d*), even when coupled with a  
190 smaller effect on speciation rates (models *h-i*; table 2). While clonal diversity seems related to  
191 the balance between speciation and extinction [42], estimated extinction rates as high as  $10^{-1}$ ,  
192 exceeding speciation rates (table 2), suggest that parthenogenetic species would go extinct before  
193 possibly giving rise to additional parthenogenetic species. Note, however, that these speciation  
194 events are different from those in sexual species as they involve subsequent backcrosses [5,38].  
195 In practice, new parthenogenetic species would reflect new evolutionary units in the phylogeny.  
196 Whenever speciation rates for parthenogenetic species approaches extinction, the model was  
197 rejected (model *h*; table S4).

198         The low frequency of hybridization [5,27] does not seem to explain the  
199 macroevolutionary pattern we observe in squamates; we reject model *e* that indicates an effect of  
200 parthenogenesis solely on speciation (table 2). Besides, in models *h-i* (not rejected) speciation  
201 rates were higher for parthenogenetic species. This contradicts the idea of reduced origination  
202 events for parthenogenetic species compared to sexual species. Also, assuming that each  
203 parthenogenetic species originates only once underestimates the origination rate for asexuality.

204 Genotyping of *Darevskia armeniaca*, for example, suggests multiple interspecific origins  
205 between *D. valentini* and *D. mixta* [43] (but see [5]). Nevertheless, in models where the  
206 speciation rates were allowed to vary (models *a*, *e*, *g-i*), speciation rates for parthenogenetic  
207 species were always higher than speciation rates for sexual species. Models *a*, *e* and *g* were  
208 rejected. Models *h-i*—indicative of parthenogenesis self-destruction—were not rejected.  
209 Underestimation of parthenogens origination rates should have little impact on the results.

210 Neutral replacement of parthenogenetic species is an alternative explanation to the  
211 relative younger age of parthenogens. Before becoming extinct due to inherent ecological  
212 hindrances, parthenogenetic species could be younger from neutral replacement of existing  
213 clones [18,40,44]. Authors further argue that it is difficult to distinguish neutral replacement  
214 from increased extinction rates. In a scenario of clones' high turnover for each parthenogenetic  
215 species, we would expect the same outcome in our macroevolutionary models focused on the  
216 TARS metric (i.e. parthenogenetic species are younger than sexual species). Also, we would  
217 expect higher clone turnover to influence the number of parthenogenetic species per origin of  
218 parthenogenesis and the parthenogenetic species clustering. Specifically, if clones' neutral  
219 turnover continuously replaces older clones, this prevents them from aging. Subsequently, this  
220 would decrease the chance for new parthenogenetic species to establish and form species  
221 clusters. Importantly, authors focus on within-species level to distinguish processes occurring at  
222 the micro from the macroevolutionary level. Here we use a combination of macroevolutionary  
223 metrics that focus on interspecific age comparisons, origination events, species clustering, and  
224 simulations of alternative scenarios of trait evolution.

225 Asexuality is not a simple phenomenon. We used parthenogenetic species alone and  
226 simplified some aspects of hybridizing species. We considered parthenogens at the species-level

227 (but see [9]) and we did not account for backcrossing [5] or the complex reticulate topology in  
228 some genera [38]. By simplifying the models, we focused on the macroevolutionary dynamics of  
229 parthenogenesis in squamates rather than the microevolutionary mechanisms underlying  
230 parthenogenesis. Our results suggest that parthenogenesis could be self-destructive in the long-  
231 term, possibly explaining the ‘unstable’ pattern observed for parthenogenesis in Squamata.

232

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243

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371 **Table 1.** Estimates of four tree metrics on the consensus tree ( $n=5,388$ ). Significant values  
372 ( $P<0.05/P>0.95$  for TARS, NoTO and SSCD;  $FPD>0.5$ ) are boldfaced.

<b>Metric</b>	<b>Consensus tree</b>
Tip Age Rank Sum ( $P_{TARS}$ )	32576.0 ( <b>&lt;0.001</b> )
Number of Tips per Origin ( $P_{NoTO}$ )	1.278 (0.278)
Sum of Sister Clade Differences ( $P_{SSCD}$ )	35.376 (0.103)
Fritz & Purvis D statistic	0.401

373

374 **Table 2.** Parameter maximum likelihood estimates under macroevolutionary scenarios of trait  
375 evolution (*a-i*) using the starting parameters for the consensus tree ( $n=5,388$ ). Parameters include  
376 speciation rates for sexual/parthenogenetic species ( $\lambda_0/\lambda_1$ ), extinction rates for  
377 sexual/parthenogenetic species ( $\mu_0/\mu_1$ ) and rates of gain/reversal of parthenogenesis ( $q_{01}/q_{10}$ ).  
378 Rejected models are boldfaced (see figure 1).

<b>Macroevolutionary scenario</b>	$\lambda_0$	$\lambda_1$	$\mu_0$	$\mu_1$	$q_{01}$	$q_{10}$
<b>(a) No constraints</b>	0.048	0.27	$2.0 \times 10^{-8}$	$2.4 \times 10^{-6}$	$1.8 \times 10^{-3}$	0.30
<b>(b) <math>\lambda_0=\lambda_1, \mu_0=\mu_1, q_{01}=q_{10}</math></b>	0.059	0.059	$2.3 \times 10^{-5}$	$2.3 \times 10^{-5}$	$2.1 \times 10^{-4}$	$2.1 \times 10^{-4}$
<i>(c) <math>\lambda_0=\lambda_1, \mu_0=\mu_1</math></i>	0.059	0.059	$6.2 \times 10^{-7}$	$6.2 \times 10^{-7}$	$4.2 \times 10^{-4}$	0.13
<i>(d) <math>\lambda_0=\lambda_1, q_{01}=q_{10}</math></i>	0.059	0.059	$3.3 \times 10^{-5}$	0.27	$8.6 \times 10^{-4}$	$8.6 \times 10^{-4}$
<b>(e) <math>\mu_0=\mu_1, q_{01}=q_{10}</math></b>	0.059	0.085	$1.8 \times 10^{-9}$	$1.8 \times 10^{-9}$	$2.1 \times 10^{-4}$	$2.1 \times 10^{-4}$
<i>(f) <math>\lambda_0=\lambda_1</math></i>	0.059	0.059	$2.7 \times 10^{-6}$	$2.5 \times 10^{-5}$	$3.9 \times 10^{-4}$	0.13
<b>(g) <math>\mu_0=\mu_1</math></b>	0.048	0.27	$2.9 \times 10^{-6}$	$2.9 \times 10^{-6}$	$1.8 \times 10^{-3}$	0.30
<i>(h) <math>q_{01}=q_{10}</math></i>	0.059	0.24	$3.4 \times 10^{-7}$	0.49	$1.1 \times 10^{-3}$	$1.1 \times 10^{-3}$
<b>(i) <math>q_{10}=0</math></b>	0.059	0.13	$1.6 \times 10^{-7}$	0.46	$1.2 \times 10^{-3}$	0

379

380 **Figure 1.** Null distribution of four tree metrics for distinct macroevolutionary scenarios (*a-i*;  
381 coloured histograms) using the starting parameters for the consensus tree ( $n=5,388$ ). Dashed  
382 lines represent the observed metric value. Frequency (%) represents the proportion of simulated  
383 metric values that are lower than or equal to the observed. Significant values ( $P\leq 0.01/P\geq 0.99$ )  
384 are marked with an asterisk (\*).

385

386 **Figure 2.** Incidence of true/constitutive parthenogenesis in Squamata. The tree is drawn at the  
387 family-level, but all analyses were performed at the species-level ( $n=5,388$ ). Coloured edges/tip  
388 labels (solid purple) represent families that include parthenogenetic species. The barplot  
389 represents the number of parthenogenetic species per-family included (solid purple) and the  
390 number of described parthenogenetic species per-family (transparent purple). Vertical grey lines  
391 and silhouettes indicate the seven major clades.