

1 **Poison frog social behaviour under global change:**  
2 **potential impacts and future challenges**

3  
4 Lia Schlippe Justicia<sup>a,1\*</sup>, Chloe A. Fouilloux<sup>b,2</sup> and Bibiana Rojas<sup>a,b,3\*</sup>

5  
6 <sup>a</sup>*Department of Interdisciplinary Life Sciences, Konrad Lorenz Institute of Ethology,*  
7 *University of Veterinary Medicine Vienna, Savoyenstraße 1, 1160, Vienna, Austria*

8 <sup>b</sup>*University of Jyväskylä, Department of Biology and Environmental Science, P.O. Box 35,*  
9 *40014, Jyväskylä, Finland*

10  
11 <sup>1</sup>ORCID: 0000-0002-4362-2139; <sup>2</sup>ORCID: 0000-0003-1265-5824;

12 <sup>3</sup>ORCID: 0000-0002-6715-7294

13  
14 \*Authors to whom correspondence should be addressed: lia.schlippe@vetmeduni.ac.at;  
15 bibiana.rojas@vetmeduni.ac.at

16  
17  
18  
19 **Acknowledgements**

20 BR is grateful to Matthieu Paquet, Mylene Mariette, Susana Varela, and Rita Covas for the  
21 invitation to participate in this special issue. We would like to thank Ria Sonnleitner for her  
22 insightful comments on the manuscript, and Mileidy Betancourth for sharing her thoughts  
23 on the potential impact of global change on poison frog territoriality.

27 Abstract

28

29 The current and cascading effects of global change challenge the interactions both between  
30 animals (i.e. social and sexual behaviour) and between them and the environment they  
31 inhabit. Amphibians are an ecologically diverse class with a wide range of social and sexual  
32 behaviours, making them a compelling model through which to understand the potential  
33 adaptations of animals faced with the effects of human-induced rapid environmental  
34 changes (HIREC). Poison frogs are a particularly interesting system, as they display diverse  
35 social behaviours that shape the way individuals interact with each other and with their  
36 environment, thus offering a tractable system to investigate how diverse, closely-related  
37 species may respond to the impacts of HIREC. Here, we discuss the potential impacts of  
38 global change on poison frog behaviour, and the future challenges this group may face in  
39 response to such change. We pay special attention to parental care and territoriality, which  
40 are emblematic of this clade, and consider how different species may flexibly respond and  
41 adapt to increasingly frequent and diverse anthropogenic stress. More specifically, we  
42 hypothesise that some parents may increase care (i.e. clutch attendance, distance travelled  
43 for tadpole transport) in HIREC scenarios, and that species with more generalist oviposition  
44 and tadpole deposition behaviours may fare more positively than their less flexible  
45 counterparts; we predict that the latter may either face increased competition for resources  
46 limited by HIREC or will be forced to adapt and expand their natural preferences. Likewise,  
47 we hypothesise that human-driven habitat alteration will disrupt the acoustic and visual  
48 communication systems due to increased noise pollution and/or changes in the surrounding  
49 light environment. We highlight the need for more empirical research combining behavioural  
50 ecology and conservation to better predict species' vulnerability to global change and  
51 efficiently focus conservation efforts.

52

53

54

55 Keywords

56 HIREC; communication; behavioural plasticity; parental care; territoriality; tadpoles

57

58

59

60

61

62

## 63 Introduction

64 Environmental changes, including shifting continents and ice ages, have been shown to  
65 prompt diverse responses in organisms across a wide range of taxa (Ricklefs and Schluter  
66 1993; Rosenzweig 1995) throughout evolutionary time. However, the unprecedented scale  
67 and pace of recent and current human-induced rapid environmental changes (HIREC),  
68 such as habitat destruction/fragmentation (Pimm and Raven 2000), climate change  
69 (Parmesan and Yohe 2003), and exposure to novel biotic (e.g. exotic species, pathogens  
70 and parasites: Lockwood et al. 2013) and abiotic (e.g. environmental pollutants: Rohr et al.  
71 2006) stressors, represent new challenges for many species which have not experienced  
72 such rapid changes in their evolutionary past (Palumbi 2001). The impact of HIREC on the  
73 natural world is colossal (Wake and Vredenburg 2008; Cowie et al. 2022), affecting the  
74 availability of important resources (i.e. food, shelter; Fahrig 2003), altering conspecific and  
75 heterospecific interactions (Tuomainen and Candolin 2011; Candolin and Wong 2012), and  
76 ultimately threatening many species and populations (Pimm and Raven 2000; Wake and  
77 Vredenburg 2008; Cowie et al. 2022).

78 For many animals, survival and reproduction in rapidly changing environments are  
79 expected to be shaped by the plasticity of their behavioural responses (Hendry et al. 2008;  
80 Sih et al. 2011; Sih 2013; Wong and Candolin 2015). Sometimes behavioural changes may  
81 be enough for an individual to adapt to new conditions or can provide additional time for  
82 genetic adaptation to occur (Pigliucci 2001). For example, great tits (*Parus major*) in urban  
83 environments have learnt to adjust their song frequency to avoid interference from city noise  
84 (Slabbekoorn and Peet 2003), while northern quolls (*Dasyurus hallucatus*) in Australia have  
85 learnt to avoid eating highly-toxic invasive cane toads (*Rhinella marina*) (Kelly and Phillips  
86 2017). However, species can also show maladaptive responses in HIREC scenarios, such  
87 as sea turtle hatchlings following artificial light instead of natural cues (Tuxbury and Salmon,  
88 2005), or aquatic insects ovipositing on asphalt or glass that resemble the surface of water  
89 (Kriska et al. 1998; Kriska et al. 2008), causing serious population declines (Tuomainen  
90 and Candolin 2011; Robertson et al. 2013). In other cases, behavioural changes can  
91 determine which individuals will survive and reproduce under novel conditions, acting as a  
92 driving force in evolutionary processes (West-Eberhard 2003; Crispo 2007; Tuomainen and  
93 Candolin 2011). Thus, changes in behaviour will directly influence how species evolve  
94 under HIREC.

95 While individual behavioural responses will affect population dynamics on a local  
96 scale, the effect of HIREC on sociality and inter-species interactions has far-reaching  
97 ecological implications for broader community dynamics. Environmental changes can

98 directly and indirectly influence the way in which individuals interact, not only with other  
99 species (e.g. predators and prey, hosts and parasites), but also with each other (Candolin  
100 and Wong 2012). Social interactions, ranging from choosing a mate to providing offspring  
101 with care, can be affected by HIREC in multiple ways (Croft et al. 2008). For example, ship  
102 noise reduces the ability of Lusitanian toadfish (*Halobatrachus didactylus*) to detect  
103 conspecific acoustic signals, essential for mate attraction (Vasconcelos et al. 2007), while  
104 water turbidity reduces male-male competition in three-spined stickleback (*Gasterosteus*  
105 *aculeatus*), compromising the honesty of agonistic signals, which are relevant indicators of  
106 parenting ability (Wong et al. 2007). Similarly, human disturbance can directly reduce the  
107 nest attendance of bearded vultures (*Gypaetus barbatus*), increasing the probability of  
108 breeding failure (Arroyo and Razin 2006).

109         Social interactions have a critical effect on individual fitness (Allee et al. 1949) and,  
110 consequently, on population dynamics. Parental care, for example, is known to enhance  
111 the offspring's fitness by increasing their survival, growth and/or quality, and, ultimately,  
112 their lifetime reproductive success (Royle et al. 2012). Despite the obvious benefits for the  
113 offspring, parental care comes at a cost to the caregiver in the form of energy expenditure,  
114 loss of mating opportunities, and increased predation risk while tending to their young  
115 (Alonso-Alvarez et al. 2012). Thus, an individual's investment in parental care depends on  
116 the value of their existing offspring in relation to future reproductive opportunities (Alonso-  
117 Alvarez et al. 2012; Royle et al. 2012). Under changing environmental conditions, both the  
118 energetic costs of care for the parents and the fitness benefits for the young could be  
119 altered, influencing population recruitment success (Alonso-Alvarez et al. 2012; Ratikainen  
120 et al. 2018). In the face of low resource availability, parents can, for instance, reduce their  
121 current offspring investment with the expectation of better reproductive opportunities in the  
122 future (Winkler 1987). This decline in care quality, in turn, can alter various offspring  
123 behaviours during adulthood, including aggressiveness and boldness (Armstrong 2019),  
124 cognition (Bredy et al. 2004) and F1's parental behaviour (Gromov 2009). Research  
125 conducted in songbirds, for example, has shown that nutritional stress during early  
126 development stages (when songbirds depend on their parents for food), negatively affects  
127 brain development and male song quality in adulthood (Nowicki et al. 2002). In rodents,  
128 offspring who are groomed less frequently during early postnatal periods exhibit lower  
129 spatial learning and memory in adulthood (Liu et al. 2000; Bredy et al. 2004). Decreased  
130 investment in the face of challenging environmental conditions is not the rule, however, as  
131 some parents appear to increase their workload in the face of sub-optimal conditions  
132 (Vincze et al. 2017). Ultimately, the adaptability of parental behaviour/cooperation appears

133 to be the most accurate predictor of species successfully overcoming the varied pressures  
134 of global change in the wild (Vincze et al. 2017).

135 Although behavioural responses to global change largely differ between species,  
136 amphibians are excellent models to study them due to their broad range of social  
137 behaviours and their wide distribution across latitudes and climates, being found in all  
138 continents except Antarctica. Furthermore, their key position in trophic webs, their role as  
139 sentinel species and bioindicators of ecosystem health thanks to their sensitivity to  
140 environmental changes, and their dramatic decline around the globe (Hopkins 2007), make  
141 them a useful system to study the impact of human disturbances. In fact, amphibians are  
142 considered the most threatened vertebrate class on the planet (Stuart et al. 2004; Wake  
143 and Vredenburg 2008; Nori et al. 2015; IUCN 2020; Cordier et al. 2021), primarily due to  
144 habitat fragmentation/destruction, and the spread of a pathogenic fungus (Daszak et al.  
145 2003; Pounds et al. 2006; Cordier et al. 2021).

146 One of the most emblematic and well-studied groups of amphibians showing  
147 complex and diverse social behaviours are Neotropical poison frogs (Dendrobatoidea).  
148 Distributed from Nicaragua in Central America to Bolivia in South America, poison frogs  
149 generally inhabit tropical rainforests (Summers and Tumulty 2014), often in areas that are  
150 under severe degradation, and exhibit a large diversity in mating systems, parental care  
151 strategies, and communication modalities (reviewed in Summers and Tumulty 2014). Males  
152 generally defend long-term territories from conspecifics through so-called advertisement  
153 calls and, if necessary, physical combat (Fig.1A; Pröhl 2005). Defending these territories is  
154 often crucial to male reproductive success, as courtship, mating, and oviposition take place  
155 therein (Pröhl 2005). In most species, males perform parental care, which consists of clutch  
156 attendance and larval transport (Fig. 1B) from terrestrial oviposition sites (e.g. leaf litter,  
157 leaves on bushes) to water bodies such as streams, temporary ponds, or small pools of  
158 water formed in plant structures (i.e., phytotelmata) (Summers and Tumulty 2014).  
159 Tadpoles are confined in these water bodies until completing metamorphosis (Weygoldt  
160 1987; Lehtinen et al. 2004; Summers and McKeon 2004; Schulte et al. 2020). While  
161 uniparental male care is the basal reproductive strategy in poison frogs (Weygoldt 1987;  
162 Carvajal-Castro et al. 2021), multiple lineages have evolved biparental or exclusive female  
163 care, where females transport tadpoles (Fig. 1C) and feed them with unfertilized trophic  
164 eggs (Summers et al. 1999a). The transition to female or biparental care has been  
165 suggested to be the result of using small phytotelmata with scarce food resources (Brown  
166 et al. 2010; Carvajal-Castro et al. 2021), and biparental care has been proposed as the  
167 precursor of monogamy (Tumulty et al. 2014). It is precisely the interaction between the

168 diverse sexual and social systems of poison frogs, combined with the pressing effects of  
169 HIREC, what makes this family a relevant model through which to test and understand the  
170 impacts of global change.

171



172

173 **Fig 1 Poison frogs and their unique social behaviours may be impacted by global change** A)  
174 Males of *Dendrobates tinctorius* engaged in physical combat, where often one male pushes, kicks,  
175 and gets on top of the other trying to press them against the substrate; B) Male *Ameerega hahneli*  
176 transporting his tadpoles (pointed at by the arrow) to a body of water; C) Tadpole (pointed at by the  
177 arrow) transport is done by females in *Oophaga granulifera*; D) Habitat disturbance can alter the way  
178 in which colours are perceived by con- and heterospecifics, as shown in *O. pumilio*, and thus affect  
179 communication systems; E) Males of *D. tinctorius* are in charge of clutch (pointed at by the arrow)  
180 attendance; F) Climate change can increase the risk of tadpole death (agonising tadpoles pointed at  
181 by the arrow) by desiccation of nurseries; G) *Ranitomeya ventrimaculata* parents (pointed at by the  
182 dashed arrows) lay clutches (pointed at by the solid arrow) in bromeliads occupied by a large tadpole  
183 in periods of low rainfall to increase the survival probabilities of the tadpole therein; H) *O. lehmanni*

184 is highly threatened due to illegal pet trade activities. Males are thought to be more likely to be found  
185 by collectors because of their vocalisations (see the inflated vocal sac pointed by the arrow); I)  
186 *Andinobates bombetes* adjusts their calling behaviour to avoid interference caused by traffic noise.  
187 Photo credits: Bibiana Rojas (A, B, C, E, F, G); Justin P. Lawrence (D); Mileidy Betancourth (H);  
188 Fernando Vargas (I).

189

190 Although global change is expected to influence social behaviours in several ways,  
191 surprisingly little is known about how these effects take place in wild populations of poison  
192 frogs. Importantly, further research combining animal behaviour and conservation biology  
193 (Caro 1999) is necessary to identify species-specific relevant HIREC and to understand  
194 how they may adapt (or not) their behaviours accordingly. Only by doing so, we may be  
195 able to evaluate populations' vulnerability to global change, develop predictive models and  
196 focus conservation efforts (Schroeder et al. 2011). Here, we illustrate key points about the  
197 potential impacts of, and responses to, HIREC using Neotropical poison frogs' social  
198 behaviours as a model system. We specifically focus on territoriality and parental care  
199 behaviours, as they could be of special importance due to their capacity of buffering  
200 offspring against HIREC. Using this information as a baseline, we identify knowledge gaps  
201 and formulate new testable hypotheses to assess (1) the nature and magnitude of HIREC  
202 impact on wild populations of poison frogs, and (2) potential parental care and aggression  
203 responses to these HIREC.

204

## 205 Impacts of global change on poison frogs

206 Poison frogs depend on a wide variety of microhabitats across development. Leaf litter and  
207 phytotelmata, for example, serve as primary breeding sites, shelter, and nurseries for  
208 poison frogs; in addition to being defendable resources for territorial species, they provide  
209 more stable temperature and humidity conditions than open areas with little canopy  
210 (Duellman and Trueb 1994). The dependence on suitable microhabitats together with the  
211 obligate use of small water bodies for reproduction or development make many Neotropical  
212 frogs particularly vulnerable to HIREC (Donnelly and Crump 1998; Touchon and Warkentin  
213 2009).

### 214 **Habitat loss and climate change**

215 Many tropical regions are being subject to unprecedented rates of habitat loss (Lewis et al.  
216 2015; Taubert et al. 2018). Over the last decade, deforestation patterns in the Amazonian

217 rainforest have switched from localised large forest clearings to geographically spread  
218 small-scale deforestation events driven by land use change (i.e. agricultural expansion,  
219 pasture) and exploitation (i.e. mining, logging activities) (Grau and Aide 2008; Hugo 2008;  
220 Kalamandeen et al. 2018). Small-scale deforestation pressures are expected to affect more  
221 remote areas and populations. This type of deforestation is also recognised as one of the  
222 main causes of more frequent and intense anomalies in the Amazonian hydrological cycle,  
223 such as extreme weather events (i.e. El Niño Southern Oscillation, hereafter El Niño) and  
224 dry spells during the rainy season (Lovejoy and Nobre 2018), which may be further  
225 exacerbated by global warming (Jiménez-Muñoz et al. 2016). Both the loss of habitat and  
226 more frequent climatic anomalies can affect poison frogs in multiple ways throughout their  
227 life stages, potentially leading to different behavioural responses and adaptations.

### 228 *Disruption in communication systems*

229 Habitat alteration through small-scale deforestation can directly affect conspecific  
230 communication in two different ways. First, because human-made gaps are known to have  
231 increased radiation and higher temperatures than other areas of the forest (Vitt et al. 1998),  
232 male calling behaviour can become unsustainable over long periods of time. This is  
233 because, in degraded conditions, males would be more exposed and thus could incur  
234 higher evaporative water loss and potential overheating. These physiological stressors  
235 entail behavioural consequences as, in the mid-to-long term, males would be unable to  
236 devote as much time to attract females and advertise territory ownership. Second,  
237 variations in the forest's light environment can make an animal's appearance change too  
238 (Endler 1993), which has been proven crucial in the courtship behaviour of some lekking  
239 bird species (Théry and Endler 2001). The detectability of the variable colour patterns found  
240 in *D. tinctorius*, likewise, has been shown to differ depending on whether they are seen  
241 under an open or closed canopy (Rojas et al. 2014). While this has been studied mostly in  
242 the context of predator-prey interactions, such differences in detectability in response to the  
243 surrounding light environment could be particularly relevant for species in which colour  
244 patterns play a role in mate choice (e.g., *O. pumilio*: Summers et al. 1999b; Maan and  
245 Cummings 2008; Yang et al. 2019) or underlie differences in other behavioural patterns  
246 such as boldness or aggressiveness (e.g., *O. pumilio*: Rudh et al. 2013; Pröhl and  
247 Ostrowski 2011; Crothers and Cummings 2015; *O. granulifera*: Willink et al. 2013; 2014).  
248 Importantly, human-driven habitat disturbance may not only affect the light environment but  
249 also the structure of the forest floor, which can alter detectability and visual contrast, thus  
250 causing potential interference in communication between conspecifics (Barnett et al. 2021).

### 251 *Increased care and aggression under HIREC: a parent's perspective*

252 Reduced vegetation cover and longer dry spells could result in higher egg mortality as a  
253 result of dehydration, especially for amphibian species with non-aquatic eggs (Touchon and  
254 Warkentin 2009). For example, Delia et al. (2013), found that offspring of the glass frog  
255 *Hyalinobatrachium fleischmanni*, a species with parental care, had higher mortality rates in  
256 years of low rainfall. Similar situations could arise in poison frogs due to the high  
257 susceptibility of their terrestrial clutches to evaporative water loss; in *Allobates*  
258 *paleovarzensis*, for instance, only 8.6% of the clutches survived until the transporting stage  
259 following an El Niño event compared to ~70% survival during a standard season (Rocha et  
260 al. 2021).

261         There are several behaviours that may help adult poison frogs reduce the  
262 vulnerability of their eggs to HIREC. On the one hand, choosing suitable oviposition sites is  
263 particularly important if larvae are unable to leave these sites when conditions become  
264 unfavourable. For example, in the tree frog *Dendropsophus ebraccatus*, a unique species  
265 which can flexibly choose between aquatic and non-aquatic deposition sites, changes in  
266 rainfall patterns since 1972 have altered oviposition-site selection (Touchon 2012).  
267 Although egg mortality was generally higher in aquatic sites due to greater predation risk,  
268 altered rainfall patterns driven by climate change increased clutch dehydration risk, shifting  
269 the optimal site choice by parents from terrestrial to aquatic habitats over the span of only  
270 40 years. *D. ebraccatus* clearly provides an excellent system to measure the success of  
271 the adaptive decision-making by parents; however, whether or not poison frogs are as  
272 flexible in their use of oviposition and tadpole deposition sites requires further research. For  
273 terrestrially-breeding frogs, buffering the negative effects of HIREC could largely depend  
274 on the parents' capacity to select for specific microhabitats with favourable structures.  
275 *Dendrobates tinctorius*, for example, is a terrestrial-breeding frog with clutch attendance  
276 (Fig. 1D) and uniquely flexible deposition choices compared to other species that also use  
277 ephemeral pools as nurseries. *D. tinctorius* fathers transport tadpoles to diverse pools that  
278 range enormously across vertical (0 m - >20 m), physical (19 mL - 270 L), and chemical  
279 (pH = 3 - 7) gradients (Fouilloux et al. 2021). We hypothesise that, when faced with the  
280 pressures of HIREC, species that can access (and tolerate) a wider variety of nurseries will  
281 fare better than those with narrower options. Flexible species may also benefit in modulating  
282 care investment based on climatic conditions, where when desiccation risk is high parents  
283 spend additional effort accessing especially deep/stable nurseries compared to potentially  
284 more relaxed, "riskier" choices throughout a consistently rainy season. Further, we predict  
285 sites with denser canopy cover as well as abundant leaf litter and vegetal structures (e.g.  
286 fallen branches and hollow trunks) to provide more stable microclimate conditions for  
287 successful egg development. Nevertheless, different microhabitats may be weighed

288 differently depending on species-specific biological and life-history requirements.  
289 Therefore, a better understanding of microhabitat use of species both in undisturbed and  
290 disturbed areas is essential to implement effective conservation efforts.

291         On the other hand, to compensate for adverse environmental conditions, parents  
292 may adjust intensity and frequency of clutch attendance to guarantee offspring survival (see  
293 examples in invertebrates (Dick et al. 1998), fish (Green and McCormick 2005), reptiles  
294 (Stahlschmidt and DeNardo 2010), and birds (Vincze et al. 2017)). Males of *H. fleischmanni*,  
295 for example, increase both the frequency and time spent on egg care in response to a  
296 reduction in relative humidity (Delia et al. 2013). One of the most common ways anurans  
297 provide egg attendance is by placing their body over the eggs to reduce evaporative water  
298 loss or directly moistening the eggs through physical contact with the ventral integument  
299 (Wells 2010). Although this behaviour has been suggested for some poison frogs (Souza  
300 et al. 2017), it is not ubiquitous across the family (Rocha et al. 2021). Furthermore, some  
301 amphibians can increase the amount of glycoprotein-rich jelly cores, jelly layers or matrices  
302 surrounding the clutches, which protect embryos from dehydration and predators (Delia et  
303 al. 2020). So far, little research has focused on the potential egg attendance plasticity that  
304 poison frogs may present under environmental stress. Considering that egg attendance  
305 conflicts with other fitness-related activities, such as foraging and mating (e.g. Delia et al.  
306 2013), investigating the trade-offs of parental decisions under environmental changes is  
307 essential to predict population dynamics. Thereby, if the costs of maintaining the current  
308 clutch surpass their fitness benefits, we would predict individuals to reduce their parental  
309 care effort or even abandon clutches completely as seen in other species (e.g. Bustnes and  
310 Erikstad 1991; Suski and Ridgway 2007; Öberg et al. 2015).

311         It is noteworthy that in territorial species, such as most dendrobatid frogs (Pröhl  
312 2005), the trade-off between defending territories and attending multiple clutches  
313 simultaneously may become magnified under habitat loss. Habitat loss and fragmentation  
314 can limit species movement as well as the availability of resources and suitable territories  
315 (Fahrig 2003). In the resulting smaller and densely packed habitat patches, aggression  
316 rates between highly territorial individuals may increase due to higher number of encounters  
317 and more competition for limited resources and territories (Fisher et al. 2021). In male tree  
318 lizards (*Urosaurus ornatus*), for instance, aggressive interactions between individuals are  
319 more frequent in resource-limited burned sites than in resource-rich habitats (Lattanzio and  
320 Miles 2014). More energy spent on territorial defence could translate into a reduced ability  
321 to attract further mates or attend multiple clutches, directly influencing mating systems. This  
322 conflict between aggression and direct care of offspring has been found in multiple animals

323 (e.g. Lissåker and Kvarnemo 2006; DeAngelis et al. 2020). Importantly, filial cannibalism  
324 occurs in some dendrobatid frogs, both in adult males when taking over a new territory (e.g.  
325 *Allobates femoralis*: Ringler et al. 2017) and in females to decrease parental investment of  
326 a mate in unrelated clutches (e.g. *Dendrobates auratus*: Summers 1989). Thus, we predict  
327 that higher densities and lower resource availability could also lead to more territorial  
328 intrusions by males, more competition among females, and, as a result, an increase in filial  
329 cannibalism events.

330 Finally, because egg attendance and territorial defence may become more  
331 energetically demanding under harsh environmental conditions, we hypothesise that  
332 alternative care strategies such as plastic biparental care and monogamy could become  
333 favoured over evolutionary time. This is the case in the Atlantic labrid fish *Symphodus tinca*,  
334 who changes from no parental care to uniparental care when temperature and predators  
335 increase during the breeding season (Van den Berghe 1990), or in plovers (*Charadrius*  
336 spp.), where temperature stochasticity increased males parental cooperation during  
337 incubation (Vincze et al. 2017). Given that some poison frogs can show parental flexibility  
338 and a parent can take over tadpole transport when the other parent goes missing (for more  
339 details see next section), we encourage future studies to investigate whether flexibility can  
340 be found in other parental care behaviours such as egg attendance.

#### 341 *Consequences on larval survival and possible evolutionary trajectories under HIREC*

342 The alteration of forest habitats for different human land-uses, as well as changes in climate  
343 patterns can also affect poison frogs during larval and adult stages by modifying the  
344 availability and quality of important resources and microhabitats. For example, by clearing  
345 primary forest and reducing the canopy cover, the ground becomes more exposed to solar  
346 radiation, which increases near-ground temperature and, in turn, phytotelmata desiccation  
347 risk (del Pliego et al. 2016; Rivera-Ordóñez et al. 2019). This is especially concerning given  
348 that the depletion of some resources (e.g. bromeliad phytotelmata) has been related to  
349 serious population declines in some poison frog species (Pröhl 2002; Vargas-Salinas and  
350 Amézquita 2013; Meza-Joya et al. 2015).

351 Phytotelmata, used in multiple poison frog species to deposit their tadpoles  
352 (Weygoldt 1987; Summers and McKeon 2004; Lehtinen et al. 2004; Schulte et al. 2020;  
353 Fouilloux et al. 2021), can naturally vary in water volume, nutrient composition, food  
354 sources, stability as well as the risk of competition and predation (Lehtinen et al. 2004).  
355 Consequently, parents have to assess all these different ecological factors, which can be  
356 highly unstable and vary in space and time (Rudolf and Rödel 2005; Schulte and Lötters

357 2013), and adapt their deposition strategy according to this information (Webb et al. 1999;  
358 Schulte and Lötters 2013). The selection of suitable rearing sites will play a key role in the  
359 successful development and survival of their offspring (Refsnider and Janzen 2010), and  
360 thus will have direct effects on the population recruitment for multiple species. However,  
361 HIREC might further exacerbate the instability and availability of good-quality phytotelmata,  
362 imposing multiple novel costs on parental care and territoriality. Importantly, nursery  
363 desiccation is already considered one of the most common abiotic causes of tadpole  
364 mortality (Fig. 1E), even in tropical rainforests where annual rainfall is abundant (Murphy  
365 2003a; Rudolf and Rödel 2005; BR, pers. observ.).

366 Some authors have suggested plastic feeding behaviour as one possible  
367 mechanism to deal with phytotelmata desiccation. According to this hypothesis, some  
368 poison frog species would switch from avoiding tadpole/egg deposition in pools already  
369 containing conspecifics (to minimise predation: Caldwell and Araújo 1998; Summers 1999)  
370 to systematically deposit them with conspecifics which can be a form of food resource. For  
371 example, in *Ranitomeya ventrimaculata*, clutches are laid more often in bromeliad axils  
372 where there is already a tadpole towards the end of the rainy season (Fig. 1F) (Poelman  
373 and Dicke 2007). This way, parents are thought to accelerate their older offspring's  
374 development and increase their chance to reach metamorphosis before temporary pools  
375 dry out, which can happen within days. Likewise, older tadpoles of the species *Ranitomeya*  
376 *variabilis* may feed on younger siblings when resources are low (Brown et al. 2009).  
377 However, although cannibalising conspecific tadpoles provides higher nutritional value than  
378 other prey for some amphibian species (e.g. Crump 1990), the direct benefits of cannibalism  
379 through enhanced growth rates in poison frogs have not been disentangled from the  
380 benefits of eating 'just' another (i.e., heterospecific) tadpole. Instead, tadpole cannibalism  
381 is thought to be the result of indiscriminate predatory behaviour to eliminate potential  
382 competitors (Caldwell and Araújo 1998; Summers and McKeon 2004). Further, weaker  
383 avoidance or even active choice of pools with conspecific tadpoles at the end of the rainy  
384 season could also be the result of less suitable sites available or parents using tadpole  
385 presence as a cue for pool quality and persistence, as is the case in *Dendrobates tinctorius*  
386 (Rojas 2014). This last idea is further supported by a study on *Edalorhina perezii*  
387 (Leptodactylidae), which also loses their sensitivity to invertebrate predators late in the rainy  
388 season (Murphy 2003b).

389 A reduction in the number of suitable nurseries could also lead to the convergence  
390 of site choice by multiple parents (potentially from multiple species), increasing overall larval  
391 density in pools. Therefore, we predict that under HIREC, competition between tadpoles

392 from the same or different species could become stronger, potentially benefitting certain  
393 species over others by exploiting alternative food supplies (i.e. feeding on other tadpoles of  
394 either the same (cannibalism) or different species). Cannibalism can have major  
395 consequences at the population level for some species, eliminating large proportions of  
396 offspring or entire cohorts in extreme cases (Polis 1981). That is the case in *Ranitomeya*  
397 (formerly *Dendrobates*) *ventrimaculata*, where only one tadpole survives in most pools  
398 regardless of the number of tadpoles deposited therein (Summers 1999).

399 We hypothesise that a reduction in the number of suitable phytotelmata available in  
400 a territory will force parents to transport their tadpoles longer distances until deposition sites,  
401 increasing direct and indirect associated costs. For example, transporting individuals might  
402 directly increase their mortality risk by presumably spending more time exposed to potential  
403 predators (Rojas and Endler 2013; Pašukonis et al. 2019), as well as indirectly reduce their  
404 fitness by investing less time and energy on territorial defence and mating opportunities  
405 (Pašukonis et al. 2019). From the larvae point of view, in dendrobatid species where adults  
406 transport tadpoles singly into phytotelmata, travelling longer distances would mean leaving  
407 siblings unattended for longer periods of time and, thus, increasing their probability of dying  
408 from desiccation, predation or fungal infection. All these costs may, in turn, become  
409 accentuated in human-disturbed habitats, where different microclimatic conditions,  
410 vegetation cover, and assemblages of predators pose new threats and increased stress  
411 (Knowlton and Graham 2010). One possible behavioural response that might be favoured  
412 to reduce the costs of transporting tadpoles longer distances could be to transport as many  
413 tadpoles as possible at the same time. Ringler et al. (2013) found a significantly positive  
414 correlation between the distance of *Allobates femoralis* males to their home territories  
415 during tadpole transport and the number of tadpoles on their back, suggesting that the  
416 number of tadpoles that parents decide to take up at once is influenced by the distance to  
417 suitable water bodies. This would mean that at least some species of poison frogs may be  
418 capable of adjusting their behaviour depending on the availability of tadpole deposition sites  
419 and buffer to some degree their reduction due to HIREC. Another response to deal with  
420 increased parental costs (i.e. longer transporting distances) that could be favoured over  
421 evolutionary time is the appearance of female parental care plasticity in otherwise  
422 uniparental male care systems. Because most female poison frogs do not defend territories  
423 (Pröhl 2005), they might gain considerable fitness benefits by flexibly taking over parental  
424 duties and increase the survival chances of the clutches in which they have already invested  
425 significant time and energy. Female parental care plasticity has been previously reported  
426 in some poison frogs (e.g. *Allobates femoralis*, *Dendrobates tinctorius*, *Anomaloglossus*  
427 *beebei*) where, in absence of the male caregiver, females show compensatory parental

428 care behaviour by transporting tadpoles both under laboratory (Ringler et al. 2015; Fischer  
429 and O'connell 2020) and natural conditions (Ringler et al. 2013; Rojas and Pašukonis 2019;  
430 Pettitt 2012). However, this plasticity has not been found in other close species like  
431 *Allobates paleovarzensis* (Rocha et al. 2021).

432 Finally, human-transformed habitats may also affect parents' orientation capacity by  
433 attenuating their familiarity with sensory cues. For example, in *Oophaga pumilio*, orientation  
434 depends both on the distance and the habitat type (forests or pastures) (Nowakowski et al.  
435 2013). Thus, given than males often select tadpole deposition sites outside of their  
436 territories or core areas (Ringler et al. 2013; Pašukonis et al. 2019), parents' ability to find  
437 good rearing sites in the first place, or to return to selected phytotelmata in the case of  
438 tadpole feeding species, could be impaired. To date, very little work has explored the  
439 manner(s) in which land-use changes influence movement behaviour in poison frogs.  
440 However, it is reasonable to predict that they could have great impacts not only on parental  
441 decisions and territorial defence, but also on population dispersal and gene flow. This is,  
442 therefore, a subject that merits further investigation.

443

#### 444 **Pet trade, infectious diseases and pollution**

445 In the Amazonian and Chocó rainforests, the fast development of large- and small-scale  
446 agriculture, urbanisation, and mining activities (Fig. 2), especially of gold mining  
447 (Kalamandeen et al. 2018; Palacios-Torres et al. 2018), are not only modifying habitats but  
448 also polluting the environment (Folchi 2001; Piscoya Arbañil 2012; Gamarra Torres et al.  
449 2018). Furthermore, processes like globalisation, accidental or deliberate introduction of  
450 exotic species, and, especially pet trade in the case of poison frogs, are increasing the  
451 transmission of and susceptibility to pathogens and parasites in previously isolated  
452 populations (e.g. Fecchio et al. 2021; Santos et al. 2021).



453

454 **Fig 2 Illegal mining** Small-scale deforestation due to illegal mining activities is threatening  
455 the habitat of many species of poison frogs in the Amazon and the Chocó regions, two of  
456 Earth's biodiversity hotspots. Here, illegal mining activity in French Guiana (Photo: Jerémy  
457 Lemaire)

458

459         Illegal pet trade is recognised as one of the major threats for dendrobatid poison  
460 frogs (Gorzula 1996; Gaucher and MacCulloch 2010; Nijman and Shepherd 2010; Brown  
461 et al. 2011; Betancourth-Cundar et al. 2020), as hobbyists are often after exotic colour  
462 variants, which can reach exorbitant prices in the market. This practice has been notably  
463 increasing in South America with the popularisation of the internet (Máximo et al. 2021),  
464 placing increased risks to the anurans of this region. Besides obvious long-term  
465 consequences such as decreased genetic diversity, the extirpation of individuals from  
466 natural populations is thought to affect the two sexes differently, with males being at a  
467 higher risk of being detected due to the conspicuousness of their vocalisations (Fig. 1H)  
468 (Betancourth-Cundar et al. 2020), which they use to fend rivals off and to attract females.  
469 This can obviously alter the care provided to offspring, particularly in species in which  
470 parental-care duties are predominantly performed by males, but it can also result in  
471 population declines as the populations end up being heavily female-biased (Betancourth-  
472 Cundar et al. 2020). Globalisation and amphibian pet trade are also widely recognised as

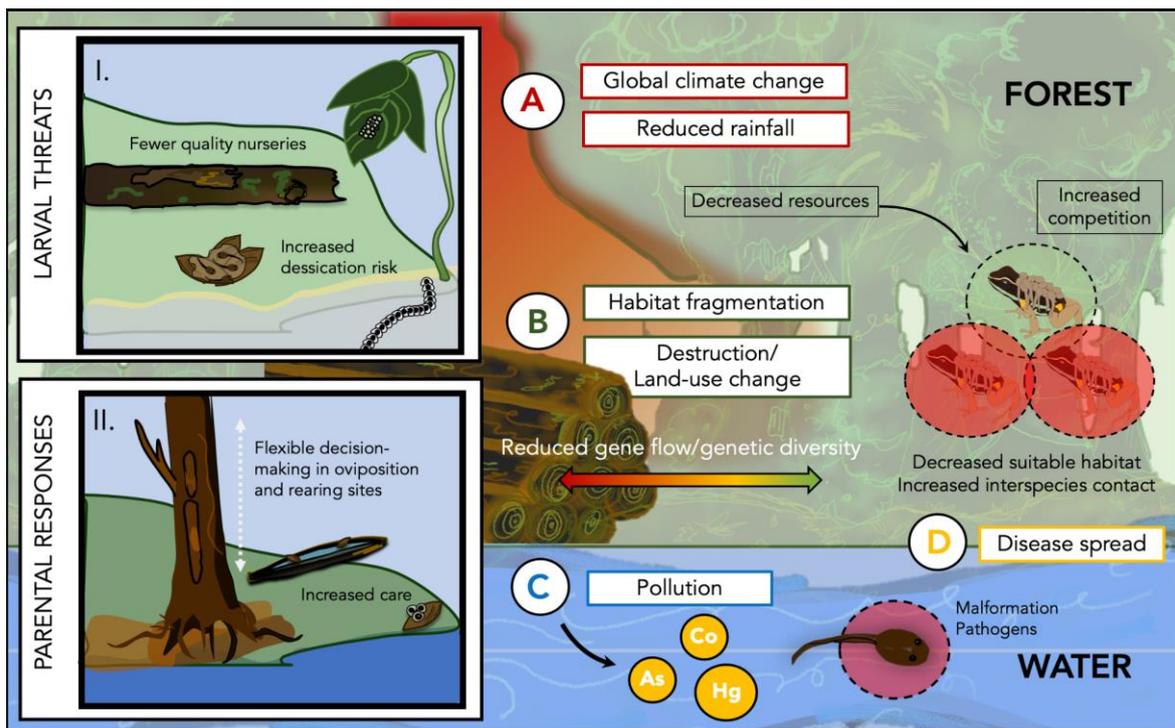
473 one of the main drivers of the global spread of amphibian pathogens such as the chytrid  
474 fungus *Batrachochytrium dendrobatidis* (hereafter *Bd*) (Fisher and Garner 2007), one of the  
475 most dramatic examples of newly-emerged pathogens, which causes the infectious disease  
476 chytridiomycosis. Therefore, it is not surprising that *Bd* has recently been detected in  
477 dendrobatid species in the wild.

478 *Bd* is known to be responsible for the mass mortalities of many amphibian  
479 populations and some species extinctions worldwide (Daszak et al. 2003; Lips et al. 2005;  
480 Pounds et al. 2006). Indeed, *Bd* prevalence in Dendrobatidae was recently found to be  
481 higher than in Bufonidae and Hylidae in an Amazonian population (Courtois et al. 2015).  
482 While the impact of *Bd* on poison frog populations is still poorly known, in other species it  
483 can inhibit the immune response (Fites et al. 2013), impact their body condition and growth  
484 (Parris and Cornelius 2004), reduce their locomotion and foraging performance (Chatfield  
485 et al. 2013; Venesky et al. 2009), and even change their advertisement calls (An and  
486 Waldman 2016). Moreover, because *Bd* zoospores are aquatic, species more dependent  
487 on water are expected to be the most impacted due to prolonged periods of time exposed  
488 to *Bd* zoospores (Bielby et al. 2008). Thus, in the scenario proposed above, where global  
489 change may cause higher densities of tadpoles sharing rearing sites, *Bd* transmission within  
490 and between species could exponentially increase. Likewise, we predict energetically costly  
491 activities such as parental care and territory defence to also be affected, because infected  
492 individuals may have to relocate energy from reproduction, calling or parental care into  
493 immunity. This means that infected individuals may be less able to defend their territories  
494 or perform parental care, which would indirectly cause higher offspring mortality rates.  
495 Given the importance of social behaviours on population dynamics, further research  
496 investigating the impacts of *Bd* on such behaviours is required.

497 In addition, chemical pollutants derived from agriculture (e.g. herbicides, pesticides)  
498 and mining activities (e.g. metals and metalloids: Hg, Cu, Co, Zn, As, etc.) can impair  
499 individuals' defensed and further increase their susceptibility to pathogens and diseases  
500 (Christin et al. 2003). Similarly, when found in low concentrations they can delay growth  
501 and metamorphosis (Carey and Bryant 1995), cause malformations (Unrine et al. 2004;  
502 Ferrante and Fearnside 2020), alter fertility and fecundity (Adams et al. 2021), or even  
503 cause sex-reversals (Nemesházi et al. 2020) often causing devastating consequences for  
504 amphibian populations (Brühl et al. 2013). Increasing evidence demonstrates effects on a  
505 wide range of amphibian behaviours, such as reduced rates of activity (e.g. swimming,  
506 feeding, breeding) or ability of tadpoles to escape predation (Shuman-Goodier and Propper  
507 2016; Sievers et al. 2019). In two-lined salamanders (*Eurycea bislineata*), for instance,

508 exposure to sublethal concentrations of mercury reduced their motivation to feed (Burke et al. 2010) whereas it impaired swimming performance in American toad (*Bufo americanus*)  
 509 larvae (Bergeron et al. 2011). Although chemical contaminants have also been reported to  
 510 alter multiple social behaviours such as territorial behaviour in other taxa (e.g. vom Saal et al. 1995; Bell 2001), to our knowledge no study has addressed this possibility in  
 511 amphibians. Given the strong detrimental effects of pollutants to egg and tadpole survival  
 512 and development, we would expect selection to favour individuals capable of recognising  
 513 and avoiding oviposition and rearing sites based on chemical pollutant concentrations. As  
 514 far as we are aware, however, this ability has been investigated in some anurans but not in  
 515 poison frogs. For example, adults of the grey treefrog (*Hyla versicolor*) avoided ponds for  
 516 oviposition if contaminated with the glyphosate pesticide Roundup (Takahashi 2007).  
 517  
 518

519



520

521 **Figure 3 Conceptual overview.** The main driving forces of HIREC (A, B, C, D) interact across  
 522 habitats implicating cascading effects on the social behaviours of amphibians. Throughout the tropics  
 523 these disturbances will impact a large diversity of species with consequences detectable at every  
 524 life stage. (I.) We predict that HIREC will particularly threaten juveniles and larvae, where less  
 525 consistent rainfall and higher temperatures will limit the availability and diversity of larval nurseries  
 526 and increase the desiccation probability of clutches. (II.) In response to these threats, we hypothesise  
 527 that parents will both increase care and the flexibility in deposition choices.

528

529 Social behaviours can also be impacted by an important, yet often underestimated,  
530 form of anthropogenically-driven pollution, noise pollution. For acoustically communicating  
531 species, as is the case of most anuran species, anthropogenic background noise can mask  
532 vocalisations and thus disrupt key species-specific communication (Simmons and Narins  
533 2018). For instance, masking of acoustic signals could inhibit males' calling activity (Sun  
534 and Narins 2005), reduce females' ability to localise male's advertisement calls (Caldwell  
535 and Bee 2014), or change female's mate choice, potentially selecting for less fit males  
536 (Barrass 1985) or males with lower-quality of parental care (Pettitt et al. 2020). Masked  
537 male calls may not only attract fewer females, but also make territorial calls less audible,  
538 affecting male territorial defence by reducing their ability to detect and discriminate against  
539 conspecific intruders, as shown in birds (Kleist et al. 2016). This, in turn, may translate into  
540 more conspecific intrusions, aggressive encounters and increased filial cannibalism rates.  
541 To cope with anthropogenic noise, some species can modify their call characteristics to  
542 contrast acoustically with the noise pollution. For example, Cauca poison frogs,  
543 *Andinobates bombetes*, (Fig. 11) vocalise in moments of low background noise and call less  
544 when noise is higher (Vargas-Salinas and Amézquita 2013; Jiménez-Vargas and Vargas-  
545 Salinas 2021), while Bloody Bay poison frogs (*Mannophryne olmonae*) increase higher  
546 frequency calls and decrease inter-pulse intervals (Clemmens 2014). However, because  
547 changes in calling characteristics could potentially be opposed to female mate preferences,  
548 future research should investigate if such responses could become maladaptive.

## 549 Conclusions

550 1. HIREC have great impacts on the way organisms interact among them and with their  
551 environment, imposing new threats for multiple species. Behaviour is often the first  
552 response to environmental changes, and its plasticity can determine how organisms adapt  
553 (or not) to HIREC. Social behaviour responses, in particular, are of especial importance  
554 given their role in population dynamics (i.e. reproductive success, offspring survival, etc.).  
555 Thus, by combining animal behaviour and conservation issues we can improve our  
556 understanding and predictions of how susceptible different species and populations are to  
557 HIREC.

558 2. Due to their diverse and complex social behaviours, as well as their occurrence in often  
559 degraded habitats, poison frogs are an interesting group to study the potential impacts of  
560 and social responses to HIREC (see Fig. 3 for a summary).

561 3. To compensate for negative HIREC impacts, we predict individuals to increase parental  
562 care costs by spending more time attending clutches and transporting tadpoles to further

563 and fewer nursery sites. Furthermore, we hypothesise higher species-specific aggression  
564 rates both in adults and tadpoles, as well as more frequent filial cannibalistic events due to  
565 limited resources/territories and anthropogenic noise. Finally, altered environmental  
566 conditions derived from small-scale deforestation (i.e. higher radiation, increased  
567 temperature, changes in ambient light) or increased noise pollution may disrupt important  
568 conspecific communication processes by reducing the calling capacity of males or by  
569 modifying mate detectability, courtship and choice.

570 4. Here, we have examined the impact of different anthropogenic stressors in poison frogs  
571 individually. However, the reality is usually more complex, with individuals having to cope  
572 with multiple HIREC acting simultaneously. Even more complicated, these novel  
573 anthropogenic stressors can interact with each other or with natural stressors, causing  
574 negative synergistic effects. For example, while tadpoles managed to cope with predator-  
575 induced stress and low concentrations of pesticides separately, when exposed to both at  
576 the same time they showed substantial mortality (Relyea and Mills 2001). All these potential  
577 interactions make predictions harder.

578

579

580 Funding and Conflict of interests

581 The authors declare no competing interests.

582 BR acknowledges funding from the Academy of Finland (No. 345974) and startup funds from the  
583 University of Veterinary Medicine Vienna.

584 Contributions

585 BR conceived the paper; LS-J wrote the first draft, CF designed the figure. All the authors discussed  
586 the ideas, contributed to the following drafts, and approved the final version of the manuscript.

587

588 References

589 ~~590~~ James, E., Leeb, C., & Brühl, C. A. (2021). Pesticide exposure affects reproductive capacity of common  
590 toads (*Bufo bufo*) in a viticultural landscape. *Ecotoxicology*, 30(2), 213-223.  
591 <https://doi.org/10.1007/s10646-020-02335-9>

592 ~~593~~ Lee, W. C., Park, O., Emerson, A. E., Park, T., & Schmidt, K. P. (1949). Principles of animal ecology.

593 ~~594~~ Bonso-Alvarez, C., Velando, A., Royle, N. J., Smiseth, P. T., & Kölliker, M. (2012). The evolution of  
594 parental care. *The evolution of parental care. 1st ed Oxford (UK): Oxford University Press.*  
595 <https://doi.org/10.1002/ajhb.22473>

596 ~~597~~ O, D., & Waldman, B. (2016). Enhanced call effort in Japanese tree frogs infected by amphibian chytrid  
597 fungus. *Biology letters*, 12(3), 20160018. <https://doi.org/10.1098/rsbl.2016.0018>

598 ~~599~~ Armstrong, T. A. (2019). *The influence of maternal care duration on offspring phenotypes in African  
599 cichlids* (Doctoral dissertation, University of Glasgow). <https://doi.org/10.5525/gla.thesis.76736>

600 ~~601~~ Royo, B., & Razin, M. (2006). Effect of human activities on bearded vulture behaviour and breeding  
601 success in the French Pyrenees. *Biological Conservation*, 128(2), 276-284.  
602 <https://doi.org/10.1016/j.biocon.2005.09.035>

603 ~~604~~ Barnett, J. B., Varela, B. J., Jennings, B. J., Lesbarrères, D., Pruitt, J. N., & Green, D. M. (2021). Habitat  
604 disturbance alters color contrast and the detectability of cryptic and aposematic frogs. *Behavioral  
605 Ecology*, 32(5), 814-825. <https://doi.org/10.1093/beheco/arab032>

606 ~~607~~ Arras, A. N. (1985). The effects of highway traffic noise on the phonotactic and associated reproductive  
607 behavior of selected anurans. (Doctoral dissertation, Vanderbilt University).

608 ~~609~~ Hill, A. M. (2001). Effects of an endocrine disrupter on courtship and aggressive behaviour of male three-  
609 spined stickleback, *Gasterosteus aculeatus*. *Animal Behaviour*, 62(4), 775-780.  
610 <https://doi.org/10.1006/anbe.2001.1824>

611 ~~612~~ Bergeron, C. M., Hopkins, W. A., Todd, B. D., Hepner, M. J., & Unrine, J. M. (2011). Interactive effects of  
612 maternal and dietary mercury exposure have latent and lethal consequences for amphibian larvae.  
613 *Environmental science & technology*, 45(8), 3781-3787. <https://doi.org/10.1021/es104210a>

614 ~~615~~ Betancourth-Cundar, M., Palacios-Rodríguez, P., Mejía-Vargas, D., Paz, A., & Amézquita, A. (2020).  
615 Genetic differentiation and overexploitation history of the critically endangered Lehmann's Poison

- 616 Frog: *Oophaga lehmanni*. *Conservation Genetics*, 21(3), 453-465. [https://doi.org/10.1007/s10592-](https://doi.org/10.1007/s10592-020-01262-w)  
617 [020-01262-w](https://doi.org/10.1007/s10592-020-01262-w)
- 618 Bedy, T. W., Lee, A. W., Meaney, M. J., & Brown, R. E. (2004). Effect of neonatal handling and paternal  
619 care on offspring cognitive development in the monogamous California mouse (*Peromyscus*  
620 *californicus*). *Hormones and Behavior*, 46(1), 30-38. <https://doi.org/10.1016/j.yhbeh.2003.09.017>
- 621 Town, J. L., Morales, V., & Summers, K. (2009). Tactical reproductive parasitism via larval cannibalism  
622 in Peruvian poison frogs. *Biology Letters*, 5(2), 148-151. <https://doi.org/10.1098/rsbl.2008.0591>
- 623 Town, J. L., Morales, V., & Summers, K. (2010). A key ecological trait drove the evolution of biparental  
624 care and monogamy in an amphibian. *American Naturalist*, 175(4), 436-446.  
625 <https://doi.org/10.1086/650727>
- 626 Town, J. L., Twomey, E., Amezcuita, A., De Souza, M. B., Caldwell, J. P., et al. (2011). A taxonomic  
627 revision of the Neotropical poison frog genus *Ranitomeya* (Amphibia: Dendrobatidae). *Zootaxa*,  
628 3083(1), 1-120. <https://doi.org/10.1055/sos-SD-201-00174>
- 629 ühl, C. A., Schmidt, T., Pieper, S., & Alscher, A. (2013). Terrestrial pesticide exposure of amphibians:  
630 An underestimated cause of global decline?. *Scientific reports*, 3(1), 1-4.  
631 <https://doi.org/10.1038/srep01135>
- 632 Burke, J. N., Bergeron, C. M., Todd, B. D., & Hopkins, W. A. (2010). Effects of mercury on behavior and  
633 performance of northern two-lined salamanders (*Eurycea bislineata*). *Environmental Pollution*,  
634 158(12), 3546-3551. <https://doi.org/10.1016/j.envpol.2010.08.017>
- 635 Stnes, J. O., & Erikstad, K. E. (1991). Parental care in the common eider (*Somateria mollissima*):  
636 factors affecting abandonment and adoption of young. *Canadian Journal of Zoology*, 69(6), 1538-  
637 1545. <https://doi.org/10.1139/z91-216>
- 638 andolin, U., & Wong, B. B. (Eds.). (2012). *Behavioural responses to a changing world: mechanisms and*  
639 *consequences*. Oxford University Press.
- 640 Caldwell, J. P., & de Araújo, M. C. (1998). Cannibalistic interactions resulting from indiscriminate  
641 predatory behavior in tadpoles of poison frogs (Anura: Dendrobatidae) 1. *Biotropica*, 30(1), 92-103.  
642 <https://doi.org/10.1111/j.1744-7429.1998.tb00372.x>
- 643 Caldwell, M. S., & Bee, M. A. (2014). Spatial hearing in Cope's gray treefrog: I. Open and closed loop  
644 experiments on sound localization in the presence and absence of noise. *Journal of Comparative*  
645 *Physiology A*, 200(4), 265-284. <https://doi.org/10.1007/s00359-014-0882-6>
- 646 rey, C., & Bryant, C. J. (1995). Possible interrelations among environmental toxicants, amphibian  
647 development, and decline of amphibian populations. *Environmental health perspectives*, 103(suppl  
648 4), 13-17. <https://doi.org/10.1289/ehp.103-1519280>
- 649 ro, T. (1999). The behaviour–conservation interface. *Trends in ecology & evolution*, 14(9), 366-369.  
650 [https://doi.org/10.1016/S0169-5347\(99\)01663-8](https://doi.org/10.1016/S0169-5347(99)01663-8)
- 651 arvajal-Castro, J. D., Vargás-Salinas, F., Casas-Cardona, S., Rojas, B., & Santos, J. C. (2021).  
652 Aposematism facilitates the diversification of parental care strategies in poison frogs. *Scientific*  
653 *reports*, 11(1), 1-15. <https://doi.org/10.1038/s41598-021-97206-6>
- 654 Hatfield, M. W., Brannelly, L. A., Robak, M. J., Freeborn, L., Lailvaux, S. P., & Richards-Zawacki, C. L.  
655 (2013). Fitness consequences of infection by *Batrachochytrium dendrobatidis* in northern leopard  
656 frogs (*Lithobates pipiens*). *EcoHealth*, 10(1), 90-98. <https://doi.org/10.1007/s10393-013-0833-7>
- 657 hristin, M. S., Gendron, A. D., Brousseau, P., Ménard, L., Marcogliese, D. J., Cyr, D., ... & Fournier, M.  
658 (2003). Effects of agricultural pesticides on the immune system of *Rana pipiens* and on its  
659 resistance to parasitic infection. *Environmental Toxicology and Chemistry: An International Journal*,  
660 22(5), 1127-1133. <https://doi.org/10.1002/etc.5620220522>

- 661 Lemmens, C. G. (2014). A Not-So-Silent Spring: The Impacts of Traffic Noise on Call Features of The  
662 Bloody Bay Poison Frog (*Mannophryne olmonae*).
- 663 Bordier, J. M., Aquilar, R., Lescano, J. N., Leynaud, G. C., Bonino, A., Miloch, D., ... & Nori, J. (2021). A  
664 global assessment of amphibian and reptile responses to land-use changes. *Biological*  
665 *Conservation*, 253, 108863. <https://doi.org/10.1016/j.biocon.2020.108863>
- 666 Bourtois, E. A., Gaucher, P., Chave, J., & Schmeller, D. S. (2015). Widespread occurrence of Bd in  
667 French Guiana, South America. *PLoS one*, 10(4), e0125128.  
668 <https://doi.org/10.1371/journal.pone.0125128>
- 669 Bowie, R. H., Bouchet, P., & Fontaine, B. (2022). The Sixth Mass Extinction: fact, fiction or speculation?.  
670 *Biological Reviews*. <https://doi.org/10.1111/brv.12816>
- 671 Trispo, E. (2007). The Baldwin effect and genetic assimilation: revisiting two mechanisms of evolutionary  
672 change mediated by phenotypic plasticity. *Evolution: International Journal of Organic Evolution*,  
673 61(11), 2469-2479. <https://doi.org/10.1111/j.1558-5646.2007.00203.x>
- 674 Hoff, D. P., James, R., & Krause, J. (2008). *Exploring animal social networks*. Princeton University  
675 Press. <https://doi.org/10.1515/9781400837762>
- 676 Bothers, L. R. and M. E. Cummings (2015). A multifunctional warning signal behaves as an agonistic  
677 status signal in a poison frog. *Behav. Ecol.* 26: 560–568. <https://doi.org/10.1093/beheco/aru231>
- 678 Rump, M. L. (1990). Possible enhancement of growth in tadpoles through cannibalism. *Copeia*, 1990(2),  
679 560-564. <https://doi.org/10.2307/1446361>
- 680 Kaszak, P., Cunningham, A. A., & Hyatt, A. D. (2003). Infectious disease and amphibian population  
681 declines. *Diversity and Distributions*, 9(2), 141-150. <https://doi.org/10.1046/j.1472-4642.2003.00016.x>
- 682 [4642.2003.00016.x](https://doi.org/10.1046/j.1472-4642.2003.00016.x)
- 683 Angelis, R., Dodd, L., & Rhodes, J. (2020). Nonapeptides mediate trade-offs in parental care strategy.  
684 *Hormones and behavior*, 121, 104717. <https://doi.org/10.1016/j.yhbeh.2020.104717>
- 685 Alia, J. R., Ramírez-Bautista, A., & Summers, K. (2013). Parents adjust care in response to weather  
686 conditions and egg dehydration in a Neotropical glassfrog. *Behavioral Ecology and Sociobiology*,  
687 67(4), 557-569. <https://doi.org/10.1007/s00265-013-1475-z>
- 688 Alia, J., Bravo-Valencia, L., & Warkentin, K. M. (2020). The evolution of extended parental care in  
689 glassfrogs: Do egg-clutch phenotypes mediate coevolution between the sexes?. *Ecological*  
690 *Monographs*, 90(3), e01411. <https://doi.org/10.1002/ecm.1411>
- 691 Pliego, P. G., Scheffers, B. R., Basham, E. W., Woodcock, P., Wheeler, C., Gilroy, J. J., ... &  
692 Edwards, D. P. (2016). Thermally buffered microhabitats recovery in tropical secondary forests  
693 following land abandonment. *Biological Conservation*, 201, 385-395.  
694 <https://doi.org/10.1016/j.biocon.2016.07.038>
- 695 Eck, J. T., Faloon, S. E., & Elwood, R. W. (1998). Active brood care in an amphipod: influences of  
696 embryonic development, temperature and oxygen. *Animal Behaviour*, 56(3), 663-672.  
697 <https://doi.org/10.1006/anbe.1998.0797>
- 698 O'Connell, M. A., & Crump, M. L. (1998). Potential effects of climate change on two neotropical amphibian  
699 assemblages. *Climatic change*, 39(2), 541-561. [https://doi.org/10.1007/978-94-017-2730-3\\_20](https://doi.org/10.1007/978-94-017-2730-3_20)
- 700 Duellman, W. E., & Trueb, L. (1994). *Biology of amphibians*. JHU press.
- 701 Ehler, J. A. (1993). The color of light in forests and its implications. *Ecological monographs*, 63(1), 1-27.  
702 <https://doi.org/10.2307/2937121>

- 703 Ahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual review of ecology, evolution,*  
704 *and systematics*, 34(1), 487-515. <https://doi.org/10.1146/annurev.ecolsys.34.011802.132419>
- 705 ecchio, A., de Faria, I. P., Bell, J. A., Nunes, R., Weckstein, J. D., & Lima, M. R. (2021). Mining  
706 increases the prevalence of avian haemosporidian parasites in Northeast Amazonia. *Parasitology*  
707 *Research*, 120(2), 605-613. <https://doi.org/10.1007/s00436-020-06986-9>
- 708 rrrante, L., & Fearnside, P. M. (2020). Evidence of mutagenic and lethal effects of herbicides on  
709 Amazonian frogs. *Acta Amazonica*, 50, 363-366. <https://doi.org/10.1590/1809-4392202000562>
- 710 cher, E. K., & O'Connell, L. A. (2020). Hormonal and neural correlates of care in active versus  
711 observing poison frog parents. *Hormones and behavior*, 120, 104696.  
712 <https://doi.org/10.1016/j.yhbeh.2020.104696>
- 713 her, D. N., Kilgour, R. J., Siracusa, E. R., Foote, J. R., Hobson, E. A., Montiglio, P. O., ... & Wice, E.  
714 W. (2021). Anticipated effects of abiotic environmental change on intraspecific social interactions.  
715 *Biological Reviews*, 96(6), 2661-2693. <https://doi.org/10.1111/brv.12772>
- 716 her, M. C., & Garner, T. W. (2007). The relationship between the emergence of *Batrachochytrium*  
717 dendrobatidis, the international trade in amphibians and introduced amphibian species. *Fungal*  
718 *Biology Reviews*, 21(1), 2-9. <https://doi.org/10.1016/j.fbr.2007.02.002>
- 719 es, J. S., Ramsey, J. P., Holden, W. M., Collier, S. P., Sutherland, D. M., Reinert, L. K., ... & Rollins-  
720 Smith, L. A. (2013). The invasive chytrid fungus of amphibians paralyzes lymphocyte responses.  
721 *Science*, 342(6156), 366-369. <https://doi.org/10.1126/science.1243316>
- 722 lchi, M. (2001). Conflictos de contenido ambiental y ecologismo de los pobres: no siempre pobres, ni  
723 siempre ecologistas. *Ecología política*, (22), 79-100.
- 724 uilloux, C. A., Serrano Rojas, S. J., Carvajal-Castro, J. D., Valkonen, J. K., Gaucher, P., Fischer, M. T.,  
725 ... & Rojas, B. (2021). Pool choice in a vertical landscape: Tadpole-rearing site flexibility in  
726 phytotelm-breeding frogs. *Ecology and Evolution*. <https://doi.org/10.1002/ece3.7741>
- 727 amarra Torres, O. A., Barrena Gurbillón, M. A., Barboza Castillo, E., Rascón Barrios, J., Corroto, F., &  
728 Taramona Ruiz, L. A. (2018). Fuentes de contaminación estacionales en la cuenca del río  
729 Utcubamba, región Amazonas, Perú. *Arnaldoa*, 25(1), 179-194.  
730 <http://dx.doi.org/http://doi.org/10.22497/arnaldoa.251.25111>
- 731 aucher P, MacCulloch R. 2010. *Dendrobates tinctorius*. *The IUCN Red List of Threatened Species*  
732 2010:e.T55204A11265402 [https://dx.doi.org/10.2305/IUCN.UK.2010-](https://dx.doi.org/10.2305/IUCN.UK.2010-2.RLTS.T55204A11265402.en)  
733 [2.RLTS.T55204A11265402.en](https://dx.doi.org/10.2305/IUCN.UK.2010-2.RLTS.T55204A11265402.en)
- 734 ruzula, S. (1996). The trade in dendrobatid frogs from 1987 to 1993. *Herpetological Review*, 27(3), 116-  
735 122.
- 736 au, H. R., & Aide, M. (2008). Globalization and land-use transitions in Latin America. *Ecology and*  
737 *society*, 13(2).
- 738 een, B. S., & McCormick, M. I. (2005). O2 replenishment to fish nests: males adjust brood care to  
739 ambient conditions and brood development. *Behavioral Ecology*, 16(2), 389-397.  
740 <https://doi.org/10.1093/beheco/ari007>
- 741 romov, V. S. (2009). Interactions of partners in family pairs, care of the offspring, and the role of tactile  
742 stimulation in formation of parental behavior of the Mongolian gerbil (*Meriones unguiculatus*) under  
743 laboratory conditions. *Biology bulletin*, 36(5), 479-488.  
744 <https://doi.org/10.1134/S1062359009050082>

- 745 Endry, A. P., Farrugia, T. J., & Kinnison, M. T. (2008). Human influences on rates of phenotypic change  
746 in wild animal populations. *Molecular ecology*, 17(1), 20-29. [https://doi.org/10.1111/j.1365-  
747 294X.2007.03428.x](https://doi.org/10.1111/j.1365-294X.2007.03428.x)
- 748 Hopkins, W. A. (2007). Amphibians as models for studying environmental change. *ILAR journal*, 48(3),  
749 270-277. <https://doi.org/10.1093/ilar.48.3.270>
- 750 Ingo, G. (2008). Trends in land degradation in South America. In *Management of natural and  
751 environmental resources for sustainable agricultural development. World Meteorological  
752 Organization, Workshop Proceedings. Portland, Oregon.*
- 753 IUCN (2020). The IUCN Red List of Threatened species. *International Union for Conservation of Nature  
754 and Natural Resources.*
- 755 Ménez-Muñoz, J. C., Mattar, C., Barichivich, J., Santamaría-Artigas, A., Takahashi, K., Malhi, Y., ... &  
756 Van Der Schrier, G. (2016). Record-breaking warming and extreme drought in the Amazon  
757 rainforest during the course of El Niño 2015–2016. *Scientific reports*, 6(1), 1-7.  
758 <https://doi.org/10.1038/srep33130>
- 759 Ménez-Vargas, G. M., & Vargas-Salinas, F. (2021). Does anthropogenic noise promote advertisement  
760 call adjustments in the rubi poison frog *Andinobates bombetes*?. *Behaviour*, 1(aop), 1-19.  
761 <https://doi.org/10.1163/1568539X-bja10080>
- 762 Lamandeen, M., Gloor, E., Mitchard, E., Quincey, D., Ziv, G., Spracklen, D., ... & Galbraith, D. (2018).  
763 Pervasive rise of small-scale deforestation in Amazonia. *Scientific reports*, 8(1), 1-10.  
764 <https://doi.org/10.1038/s41598-018-19358-2>
- 765 Kelly, E., & Phillips, B. L. (2017). Get smart: native mammal develops toad-smart behavior in response to  
766 a toxic invader. *Behavioral Ecology*, 28(3), 854-858. <https://doi.org/10.1093/beheco/axx045>
- 767 Geist, N. J., Guralnick, R. P., Cruz, A., & Francis, C. D. (2016). Anthropogenic noise weakens territorial  
768 response to intruder's songs. *Ecosphere*, 7(3), e01259. <https://doi.org/10.1002/ecs2.1259>
- 769 Howlton, J. L., & Graham, C. H. (2010). Using behavioral landscape ecology to predict species'  
770 responses to land-use and climate change. *Biological Conservation*, 143(6), 1342-1354.  
771 <https://doi.org/10.1016/j.biocon.2010.03.011>
- 772 Ziska, G., Horváth, G., & Andrikovics, S. (1998). Why do mayflies lay their eggs en masse on dry asphalt  
773 roads? Water-imitating polarized light reflected from asphalt attracts Ephemeroptera. *The Journal  
774 of Experimental Biology*, 201(15), 2273-2286. <https://doi.org/10.1242/jeb.201.15.2273>
- 775 Ziska, G., Malik, P., Szivák, I., & Horváth, G. (2008). Glass buildings on river banks as “polarized light  
776 traps” for mass-swarming polarotactic caddis flies. *Naturwissenschaften*, 95(5), 461-467.  
777 <https://doi.org/10.1007/s00114-008-0345-4>
- 778 Attanzio, M. S., & Miles, D. B. (2014). Ecological divergence among colour morphs mediated by  
779 changes in spatial network structure associated with disturbance. *Journal of Animal Ecology*, 83(6),  
780 1490-1500. <https://doi.org/10.1111/1365-2656.12252>
- 781 Hightinen, R. M., Lannoo, M. J., & Wassersug, R. J. (2004). Phytotelm-breeding anurans: past, present  
782 and future research. *Miscellaneous Publications, Museum of Zoology, University of Michigan*, 193,  
783 1-9.
- 784 Lewis, S. L., Edwards, D. P., & Galbraith, D. (2015). Increasing human dominance of tropical forests.  
785 *Science*, 349(6250), 827-832. <https://doi.org/10.1126/science.aaa9932>
- 786 Paus, K. R., Burrowes, P. A., Mendelson III, J. R., & Parra-Olea, G. (2005). Amphibian population declines  
787 in Latin America: a synthesis 1. *Biotropica: The Journal of Biology and Conservation*, 37(2), 222-  
788 226. <https://doi.org/10.1111/j.1744-7429.2005.00029.x>

- 788 sáker, M., & Kvarnemo, C. (2006). Ventilation or nest defense—parental care trade-offs in a fish with  
790 male care. *Behavioral Ecology and Sociobiology*, 60(6), 864-873. [https://doi.org/10.1007/s00265-](https://doi.org/10.1007/s00265-006-0230-0)  
791 [006-0230-0](https://doi.org/10.1007/s00265-006-0230-0)
- 792 u, D., Diorio, J., Day, J. C., Francis, D. D., & Meaney, M. J. (2000). Maternal care, hippocampal  
793 synaptogenesis and cognitive development in rats. *Nature neuroscience*, 3(8), 799-806.  
794 <https://doi.org/10.1038/77702>
- 795 ckwod, J. L., Hoopes, M. F., & Marchetti, M. P. (2013). *Invasion ecology*. John Wiley & Sons.
- 796 vejoy, T. E., & Nobre, C. (2018). Amazon tipping point. *Science Advances*, 4(2), eaat2340.  
797 <https://doi.org/10.1126/sciadv.aat2340>
- 798 aan, M. E., & Cummings, M. E. (2008). Female preferences for aposematic signal components in a  
799 polymorphic poison frog. *Evolution: International Journal of Organic Evolution*, 62(9), 2334-2345.  
800 <https://doi.org/10.1111/j.1558-5646.2008.00454.x>
- 801 áximo, I. M., Brandao, R. A., Ruggeri, J., & Toledo, L. F. (2021). Amphibian illegal pet trade and a  
802 possible new case of an invasive exotic species in Brazil. *Herpetological Conservation and*  
803 *Biology*, 16(2), 303-312. <https://doi.org/10.1186/1471-2156-14-70>.
- 804 eza-Joya, F. L., Ramos-Pallares, E., & Hernández-Jaimes, C. (2015). Use of an agroecosystem by the  
805 threatened dart poison frog *Andinobates virolinensis* (Dendrobatidae). *Herpetological Review*,  
806 46(2), 171-176.
- 807 urphy, P. J. (2003a). Does reproductive site choice in a neotropical frog mirror variable risks facing  
808 offspring?. *Ecological Monographs*, 73(1), 45-67. [https://doi.org/10.1890/0012-](https://doi.org/10.1890/0012-9615(2003)073[0045:DRSCIA]2.0.CO;2)  
809 [9615\(2003\)073\[0045:DRSCIA\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2003)073[0045:DRSCIA]2.0.CO;2)
- 810 urphy, P. J. (2003b). Context-dependent reproductive site choice in a Neotropical frog. *Behavioral*  
811 *Ecology*, 14(5), 626-633. <https://doi.org/10.1093/beheco/arg042>
- 812 emesházi, E., Gál, Z., Ujhegyi, N., Verebélyi, V., Mikó, Z., Üveges, B., ... & Bókony, V. (2020). Novel  
813 genetic sex markers reveal high frequency of sex reversal in wild populations of the agile frog  
814 (*Rana dalmatina*) associated with anthropogenic land use. *Molecular Ecology*, 29(19), 3607-3621.  
815 <https://doi.org/10.1111/mec.15596>
- 816 man, V., & Shepherd, C. R. (2010). The role of Asia in the global trade in CITES II-listed poison arrow  
817 frogs: hopping from Kazakhstan to Lebanon to Thailand and beyond. *Biodiversity and*  
818 *conservation*, 19(7), 1963-1970. <https://doi.org/10.1007/s10531-010-9814-0>
- 819 ri, J., Lemes, P., Urbina-Cardona, N., Baldo, D., Lescano, J., & Loyola, R. (2015). Amphibian  
820 conservation, land-use changes and protected areas: A global overview. *Biological Conservation*,  
821 191, 367-374. <https://doi.org/10.1016/j.biocon.2015.07.028>
- 822 wakowski, A. J., Otero Jiménez, B., Allen, M., Diaz-Escobar, M., & Donnelly, M. A. (2013). Landscape  
823 resistance to movement of the poison frog, *Oophaga pumilio*, in the lowlands of northeastern Costa  
824 Rica. *Animal Conservation*, 16(2), 188-197. <https://doi.org/10.1111/j.1469-1795.2012.00585.x>
- 825 wicki, S., Searcy, W. A., & Peters, S. (2002). Brain development, song learning and mate choice in  
826 birds: a review and experimental test of the "nutritional stress hypothesis". *Journal of Comparative*  
827 *Physiology A*, 188(11), 1003-1014. <https://doi.org/10.1007/s00359-002-0361-3>
- 828 berg, M., Arit, D., Pärt, T., Laugen, A. T., Eggers, S., & Low, M. (2015). Rainfall during parental care  
829 reduces reproductive and survival components of fitness in a passerine bird. *Ecology and*  
830 *Evolution*, 5(2), 345-356. <https://doi.org/10.1002/ece3.1345>
- 831 alacios-Torres, Y., Caballero-Gallardo, K., & Olivero-Verbel, J. (2018). Mercury pollution by gold mining  
832 in a global biodiversity hotspot, the Choco biogeographic region, Colombia. *Chemosphere*, 193,  
833 421-430. <https://doi.org/10.1016/j.chemosphere.2017.10.160>

- 834 Parnesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across  
835 natural systems. *nature*, 421(6918), 37-42. <https://doi.org/10.1038/nature01286>
- 836 Harris, M. J., & Cornelius, T. O. (2004). Fungal pathogen causes competitive and developmental stress in  
837 larval amphibian communities. *Ecology*, 85(12), 3385-3395. <https://doi.org/10.1890/04-0383>
- 838 Šukonis, A., Loretto, M. C., & Rojas, B. (2019). How far do tadpoles travel in the rainforest? Parent-  
839 assisted dispersal in poison frogs. *Evolutionary Ecology*, 33(4), 613-623.  
840 <https://doi.org/10.1007/s10682-019-09994-z>
- 841 Pettitt, B. A. (2012). *Paternal effort in relation to acoustically mediated mate choice in a Neotropical frog*.  
842 University of Minnesota.
- 843 Pettitt, B. A., Bourne, G. R., & Bee, M. A. (2020). Females prefer the calls of better fathers in a  
844 Neotropical frog with biparental care. *Behavioral Ecology*, 31(1), 152-163.  
845 <https://doi.org/10.1093/beheco/arz172>
- 846 Gliucci, M. (2001). *Phenotypic plasticity: beyond nature and nurture*. JHU Press.
- 847 Imm, S. L., & Raven, P. (2000). Extinction by numbers. *Nature*, 403(6772), 843-845.  
848 <https://doi.org/10.1038/35002708>
- 849 Escoya Arbañil, J. A. (2012). Minería y contaminación ambiental en Piura.  
850 <https://doi.org/10.33017/RevECIPeru2011.0053/>
- 851 Belman, E. H., & Dicke, M. (2007). Offering offspring as food to cannibals: oviposition strategies of  
852 Amazonian poison frogs (*Dendrobates ventrimaculatus*). *Evolutionary Ecology*, 21(2), 215-227.  
853 <https://doi.org/10.1007/s10682-006-9000-8>
- 854 Polis, G. A. (1981). The evolution and dynamics of intraspecific predation. *Annual Review of Ecology and*  
855 *Systematics*, 12(1), 225-251. <https://doi.org/10.1146/annurev.es.12.110181.001301>
- 856 Pounds, J. A., Bustamante, M. R., Coloma, L. A., Consuegra, J. A., Fogden, M. P., Foster, P. N., ... &  
857 Young, B. E. (2006). Widespread amphibian extinctions from epidemic disease driven by global  
858 warming. *Nature*, 439(7073), 161-167. <https://doi.org/10.1038/nature04246>
- 859 Köhl, H. (2002). Population differences in female resource abundance, adult sex ratio, and male mating  
860 success in *Dendrobates pumilio*. *Behavioral Ecology*, 13(2), 175-181.  
861 <https://doi.org/10.1093/beheco/13.2.175>
- 862 Köhl, H. (2005). Territorial behavior in dendrobatid frogs. *Journal of herpetology*, 39(3), 354-365.  
863 <https://doi.org/10.1670/162-04A.1>
- 864 Köhl, H., and Ostrowski, T. (2011). Behavioural elements reflect phenotypic colour divergence in a  
865 poison frog. *Evol. Biol.* 25, 993–1015. <https://doi.org/10.1007/s10682-010-9455-5>
- 866atikainen, I. I., Haaland, T. R., & Wright, J. (2018). Differential allocation of parental investment and the  
867 trade-off between size and number of offspring. *Proceedings of the Royal Society B*, 285(1884),  
868 20181074. <https://doi.org/10.1098/rspb.2018.1074>
- 869 Efsnyder, J. M., & Janzen, F. J. (2010). Putting eggs in one basket: ecological and evolutionary  
870 hypotheses for variation in oviposition-site choice. *Annual Review of Ecology, Evolution, and*  
871 *Systematics*, 41, 39-57. <https://doi.org/10.1146/annurev-ecolsys-102209-144712>
- 872 Elyea, R. A., & Mills, N. (2001). Predator-induced stress makes the pesticide carbaryl more deadly to  
873 gray treefrog tadpoles (*Hyla versicolor*). *Proceedings of the National Academy of Sciences*, 98(5),  
874 2491-2496. <https://doi.org/10.1073/pnas.031076198>

- 875 Scklefs, R. E., & Schluter, D. (Eds.). (1993). *Species diversity in ecological communities: historical and*  
876 *geographical perspectives* (Vol. 7). Chicago: University of Chicago Press.  
877 <https://doi.org/10.1046/j.1420-9101.1994.7050635.x>
- 878 Ringle, E., Pašukonis, A., Hödl, W., & Ringle, M. (2013). Tadpole transport logistics in a Neotropical  
879 poison frog: indications for strategic planning and adaptive plasticity in anuran parental care.  
880 *Frontiers in Zoology*, 10(1), 1-10. <https://doi.org/10.1186/1742-9994-10-67>
- 881 Ringle, E., Pašukonis, A., Fitch, W. T., Huber, L., Hödl, W., & Ringle, M. (2015). Flexible compensation  
882 of uniparental care: female poison frogs take over when males disappear. *Behavioral Ecology*,  
883 26(4), 1219-1225. <https://doi.org/10.1093/beheco/arv069>
- 884 Ringle, E., Beck, K. B., Weinlein, S., Huber, L., & Ringle, M. (2017). Adopt, ignore, or kill? Male poison  
885 frogs adjust parental decisions according to their territorial status. *Scientific Reports*, 7(1), 1-6.  
886 <https://doi.org/10.1038/srep43544>
- 887 Vera-Ordóñez, J. M., Justin Nowakowski, A., Manansala, A., Thompson, M. E., & Todd, B. D. (2019).  
888 Thermal niche variation among individuals of the poison frog, *Oophaga pumilio*, in forest and  
889 converted habitats. *Biotropica*, 51(5), 747-756. <https://doi.org/10.1111/btp.12691>
- 890 Robertson, B. A., Rehg, J. S., & Sih, A. (2013). Ecological novelty and the emergence of evolutionary  
891 traps. *Trends in ecology & evolution*, 28(9), 552-560. <https://doi.org/10.1016/j.tree.2013.04.004>
- 892 Rocha, S., Lima, A. P., & Kaefer, I. L. (2021). Key roles of paternal care and climate on offspring survival  
893 of an Amazonian poison frog. *Anais da Academia Brasileira de Ciências*, 93.  
894 <https://doi.org/10.1590/0001-376520212021006>
- 895 Ehr, J. R., Kerby, J. L., & Sih, A. (2006). Community ecology as a framework for predicting contaminant  
896 effects. *Trends in Ecology & Evolution*, 21(11), 606-613. <https://doi.org/10.1016/j.tree.2006.07.002>
- 897 Rojas, B. (2014). Strange parental decisions: fathers of the dyeing poison frog deposit their tadpoles in  
898 pools occupied by large cannibals. *Behavioral Ecology and Sociobiology*, 68(4), 551-559.  
899 <https://doi.org/10.1007/s00265-013-1670-y>
- 900 Rojas, B., & Endler, J. A. (2013). Sexual dimorphism and intra-populational colour pattern variation in the  
901 aposematic frog *Dendrobates tinctorius*. *Evolutionary Ecology*, 27(4), 739-753.  
902 <https://doi.org/10.1007/s10682-013-9640-4>
- 903 Rojas, B., & Pašukonis, A. (2019). From habitat use to social behavior: natural history of a voiceless  
904 poison frog, *Dendrobates tinctorius*. *PeerJ*, 7, e7648. <https://doi.org/10.7717/peerj.7648>
- 905 Rojas, B., Rautiala, P., & Mappes, J. (2014). Differential detectability of polymorphic warning signals  
906 under varying light environments. *Behavioural processes*, 109, 164-172.  
907 <https://doi.org/10.1016/j.beproc.2014.08.014>
- 908 Boyle, N.J., Smiseth, P.T. & Kölliker, M. (2012) *The evolution of parental care*. Oxford University Press,  
909 Oxford. <https://doi.org/10.1093/acprof:oso/9780199692576.001.0001>
- 910 Ud, A., Breed, M. F., and Qvarnström, A. (2012). Does aggression and explorative behaviour decrease  
911 with lost warning coloration? *Biol. J. Linn. Soc.* 108, 116–126. <https://doi.org/10.1111/j.1095-8312.2012.02006.x>
- 913 Rold, V. H., & Rödel, M. O. (2005). Oviposition site selection in a complex and variable environment:  
914 the role of habitat quality and conspecific cues. *Oecologia*, 142(2), 316-325.  
915 <https://doi.org/10.1007/s00442-004-1668-2>
- 916 Santos, W. S., Gurgel-Gonçalves, R., Garcez, L. M., & Abad-Franch, F. (2021). Deforestation effects on  
917 *Attalea* palms and their resident *Rhodnius*, vectors of Chagas disease, in eastern Amazonia. *PLoS*  
918 *one*, 16(5), e0252071. <https://doi.org/10.1371/journal.pone.0252071>

- 919 Schroeder, J., Nakagawa, S., & Hinsch, M. (2011). Behavioural ecology is not an endangered discipline.  
920 *Trends in ecology & evolution*, 26(7), 320-321. <https://doi.org/10.1016/j.tree.2011.03.013>
- 921 Schulte, L. M., & Lötters, S. (2013). The power of the seasons: rainfall triggers parental care in poison  
922 frogs. *Evolutionary Ecology*, 27(4), 711-723. <https://doi.org/10.1007/s10682-013-9637-z>
- 923 Schulte, L. M., Ringler, E., Rojas, B., & Stynoski, J. L. (2020). Developments in amphibian parental care  
924 research: History, present advances, and future perspectives. *Herpetological Monographs*, 34(1),  
925 71-97. <https://doi.org/10.1655/HERPMONOGRAPHS-D-19-00002.1>
- 926 Human-Goodier, M. E., & Propper, C. R. (2016). A meta-analysis synthesizing the effects of pesticides  
927 on swim speed and activity of aquatic vertebrates. *Science of the Total Environment*, 565, 758-  
928 766. <https://doi.org/10.1016/j.scitotenv.2016.04.205>
- 929 Levers, M., Hale, R., Parris, K. M., Melvin, S. D., Lanctot, C. M., & Swearer, S. E. (2019). Contaminant-  
930 induced behavioural changes in amphibians: A meta-analysis. *Science of the Total Environment*,  
931 693, 133570. <https://doi.org/10.1016/j.scitotenv.2019.07.376>
- 932 Sih, A. (2013). Understanding variation in behavioural responses to human-induced rapid environmental  
933 change: a conceptual overview. *Animal Behaviour*, 85(5), 1077-1088.  
934 <https://doi.org/10.1016/j.anbehav.2013.02.017>
- 935 Sih, A., Ferrari, M. C., & Harris, D. J. (2011). Evolution and behavioural responses to human-induced  
936 rapid environmental change. *Evolutionary applications*, 4(2), 367-387.  
937 <https://doi.org/10.1111/j.1752-4571.2010.00166.x>
- 938 Simmons, A. M., & Narins, P. M. (2018). Effects of anthropogenic noise on amphibians and reptiles. In  
939 *Effects of anthropogenic noise on animals* (pp. 179-208). Springer, New York, NY.  
940 [https://doi.org/10.1007/978-1-4939-8574-6\\_7](https://doi.org/10.1007/978-1-4939-8574-6_7)
- 941 Labbekoorn, H., & Peet, M. (2003). Birds sing at a higher pitch in urban noise. *Nature*, 424(6946), 267-  
942 267. <https://doi.org/10.1038/424267a>
- 943 Souza, J. R., Kaefer, I. L., & Lima, A. P. (2017). The peculiar breeding biology of the Amazonian frog  
944 *Allobates subfolionidificans* (Aromobatidae). *Anais da Academia Brasileira de Ciências*, 89, 885-  
945 893. <https://doi.org/10.1590/0001-37652017201602>
- 946 Bahlschmidt, Z., & DeNardo, D. F. (2010). Parental behavior in pythons is responsive to both the hydric  
947 and thermal dynamics of the nest. *Journal of Experimental Biology*, 213(10), 1691-1696.  
948 <https://doi.org/10.1242/jeb.041095>
- 949 Stuart, S. N., Chanson, J. S., Cox, N. A., Young, B. E., Rodrigues, A. S., Fischman, D. L., & Waller, R. W.  
950 (2004). Status and trends of amphibian declines and extinctions worldwide. *Science*, 306(5702),  
951 1783-1786. <https://doi.org/10.1126/science.1103538>
- 952 Summers, K. (1989). Sexual selection and intra-female competition in the green poison-dart frog,  
953 *Dendrobates auratus*. *Animal behaviour*, 37, 797-805. [https://doi.org/10.1016/0003-3472\(89\)90064-X](https://doi.org/10.1016/0003-3472(89)90064-X)
- 954 [https://doi.org/10.1016/0003-3472\(89\)90064-X](https://doi.org/10.1016/0003-3472(89)90064-X)
- 955 Summers, K. (1999). The effects of cannibalism on Amazonian poison frog egg and tadpole deposition  
956 and survivorship in *Heliconia* axil pools. *Oecologia*, 119(4), 557-564.  
957 <https://doi.org/10.1007/s004420050819>
- 958 Summers, K., Symula, R., Clough, M., & Cronin, T. (1999b). Visual mate choice in poison frogs.  
959 *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 266(1434), 2141-2145.  
960 <https://doi.org/10.1098/rspb.1999.0900>
- 961 Summers, K., Weigt, L. A., Boag, P., & Bermingham, E. (1999a). The evolution of female parental care in  
962 poison frogs of the genus *Dendrobates*: evidence from mitochondrial DNA sequences.  
963 *Herpetologica*, 254-270.

- 964 Summers, K., & McKeon, C. S. (2004). The evolutionary ecology of phytotelmata use in Neotropical  
965 poison frogs. *Miscellaneous Publications, Museum of Zoology, University of Michigan*, 193, 55-73.
- 966 Summers, K., & Tumulty, J. (2014). Parental care, sexual selection, and mating systems in neotropical  
967 poison frogs. In *Sexual selection* (pp. 289-320). Academic Press. <https://doi.org/10.1016/B978-0-968-12-416028-6.00011-6>
- 969 Sun, J. W., & Narins, P. M. (2005). Anthropogenic sounds differentially affect amphibian call rate.  
970 *Biological conservation*, 121(3), 419-427. <https://doi.org/10.1016/j.biocon.2004.05.017>
- 971 Luski, C. D., & Ridgway, M. S. (2007). Climate and body size influence nest survival in a fish with  
972 parental care. *Journal of Animal Ecology*, 730-739. <https://doi.org/10.1111/j.1365-2656.2007.01242.x>
- 974 Akahashi, M. (2007). Oviposition site selection: pesticide avoidance by gray treefrogs. *Environmental  
975 Toxicology and Chemistry: An International Journal*, 26(7), 1476-1480. <https://doi.org/10.1897/06-976-511R.1>
- 977 Aubert, F., Fischer, R., Groeneveld, J., Lehmann, S., Müller, M. S., et al. (2018). Global patterns of  
978 tropical forest fragmentation. *Nature*, 554(7693), 519-522. <https://doi.org/10.1038/nature25508>
- 979 Déry, M., & Endler, J. A. (2001). Habitat selection, ambient light and colour patterns in some lek-  
980 displaying birds. In *Nouragues* (pp. 161-166). Springer, Dordrecht. [https://doi.org/10.1007/978-94-981-015-9821-7\\_14](https://doi.org/10.1007/978-94-981-015-9821-7_14)
- 982 Duchon, J. C. (2012). A treefrog with reproductive mode plasticity reveals a changing balance of  
983 selection for nonaquatic egg laying. *The American Naturalist*, 180(6), 733-743.  
984 <https://doi.org/10.1086/668079>
- 985 Duchon, J. C., & Warkentin, K. M. (2009). Negative synergism of rainfall patterns and predators affects  
986 frog egg survival. *Journal of Animal Ecology*, 78(4), 715-723. [https://doi.org/10.1111/j.1365-2656.2009.01548.x](https://doi.org/10.1111/j.1365-987-2656.2009.01548.x)
- 988 Romainen, U., & Candolin, U. (2011). Behavioural responses to human-induced environmental change.  
989 *Biological Reviews*, 86(3), 640-657. <https://doi.org/10.1111/j.1469-185X.2010.00164.x>
- 990 Tumulty, J., Morales, V., & Summers, K. (2014). The biparental care hypothesis for the evolution of  
991 monogamy: experimental evidence in an amphibian. *Behavioral Ecology*, 25(2), 262-270.  
992 <https://doi.org/10.1093/beheco/art116>
- 993 Axbury, S. M., & Salmon, M. (2005). Competitive interactions between artificial lighting and natural cues  
994 during seafinding by hatchling marine turtles. *Biological Conservation*, 121(2), 311-316.  
995 <https://doi.org/10.1016/j.biocon.2004.04.022>
- 996 Pirine, J. M., Jaqoe, C. H., Hopkins, W. A., & Brant, H. A. (2004). Adverse effects of ecologically relevant  
997 dietary mercury exposure in southern leopard frog (*Rana sphenoccephala*) larvae. *Environmental  
998 Toxicology and Chemistry: An International Journal*, 23(12), 2964-2970. [https://doi.org/10.1897/03-696.1](https://doi.org/10.1897/03-999-696.1)
- 1000 van den Berghe, E. P. (1990). Parental care evolution in a labrid fish: *Symphodus tinca*.
- 1001 Vargas-Salinas, F., & Amézquita, A. (2013). Traffic noise correlates with calling time but not spatial  
1002 distribution in the threatened poison frog *Andinobates bombetes*. *Behaviour*, 150(6), 569-584.  
1003 <https://doi.org/10.1163/1568539X-00003068>
- 1004 Asconcelos, R. O., Amorim, M. C. P., & Ladich, F. (2007). Effects of ship noise on the detectability of  
1005 communication signals in the Lusitanian toadfish. *Journal of Experimental Biology*, 210(12), 2104-  
1006 2112. <https://doi.org/10.1242/jeb.004317>

1007 Venesky, M. D., Parris, M. J., & Storfer, A. (2009). Impacts of *Batrachochytrium dendrobatidis* infection  
1008 on tadpole foraging performance. *EcoHealth*, 6(4), 565-575. [https://doi.org/10.1007/s10393-009-](https://doi.org/10.1007/s10393-009-0272-7)  
1009 [0272-7](https://doi.org/10.1007/s10393-009-0272-7)

1010 Incze, O., Kosztolányi, A., Barta, Z., Küpper, C., Alrashidi, M., Amat, J. A., ... & Székely, T. (2017).  
1011 Parental cooperation in a changing climate: fluctuating environments predict shifts in care division.  
1012 *Global Ecology and Biogeography*, 26(3), 347-358. <https://doi.org/10.1111/geb.12540>

1013 Att, L. J., Avila-Pires, T. C., Caldwell, J. P., & Oliveira, V. R. (1998). The impact of individual tree  
1014 harvesting on thermal environments of lizards in Amazonian rain forest. *Conservation Biology*,  
1015 12(3), 654-664. <https://doi.org/10.1111/j.1523-1739.1998.96407.x>

1016 M Saal, F. S., Nagel, S. C., Palanza, P., Boechler, M., Parmigiani, S., & Welshons, W. V. (1995).  
1017 Estrogenic pesticides: binding relative to estradiol in MCF-7 cells and effects of exposure during  
1018 fetal life on subsequent territorial behaviour in male mice. *Toxicology Letters*, 77(1-3), 343-350.  
1019 [https://doi.org/10.1016/0378-4274\(95\)03316-5](https://doi.org/10.1016/0378-4274(95)03316-5)

1020 Wake, D. B., & Vredenburg, V. T. (2008). Are we in the midst of the sixth mass extinction? A view from  
1021 the world of amphibians. *Proceedings of the National Academy of Sciences*, 105(Supplement 1),  
1022 11466-11473. <https://doi.org/10.1073/pnas.0801921105>

1023 Webb, J.N., Houston, A.I., McNamara, J.M., Székely, T. (1999). Multiple patterns of parental care. *Anim*  
1024 *Behav* 58:983–993 <https://doi.org/10.1006/anie.1999.1215>

1025 Wells, K. D. (2010). The ecology and behavior of amphibians. University of Chicago Press.  
1026 <https://doi.org/10.7208/9780226893334>

1027 West-Eberhard, M. J. (2003). *Developmental plasticity and evolution*. Oxford University Press.

1028 Heygoldt, P. (1987). Evolution of parental care in dart poison frogs (Amphibia: Anura: Dendrobatidae).  
1029 *Journal of Zoological Systematics and Evolutionary Research*, 25(1), 51-67.  
1030 <https://doi.org/10.1111/j.1439-0469.1987.tb00913.x>

1031 Willink, B., Brenes-Mora, E., Bolaños, F. and Pröhl, H. (2013). Not everything is black and white: color  
1032 and behavioral variation reveal a continuum between cryptic and aposematic strategies in a  
1033 polymorphic poison frog. *Evolution* 67(10): 2783-2794. <https://doi.org/10.1111/evo.12153>

1034 Willink, B., Bolaños, F., and Pröhl, H. (2014). Conspicuous displays in cryptic males of a polytypic poison-  
1035 dart frog. *Behav. Ecol. Sociobiol.* 68, 249–261. <https://doi.org/10.1007/s00265-013-1640-4>

1036 Inkler, D. W. (1987). A general model for parental care. *The American Naturalist*, 130(4), 526-543.  
1037 <https://doi.org/10.1086/284729>

1038 Song, B., & Candolin, U. (2015). Behavioral responses to changing environments. *Behavioral Ecology*,  
1039 26(3), 665-673. <https://doi.org/10.1093/beheco/aru183>

1040 Song, B. B., Candolin, U., & Lindström, K. (2007). Environmental deterioration compromises socially  
1041 enforced signals of male quality in three-spined sticklebacks. *The American Naturalist*, 170(2),  
1042 184-189. <https://doi.org/10.1086/519398>

1043 Song, Y., Blomenkamp, S., Dugas, M. B., Richards-Zawacki, C. L., & Pröhl, H. (2019). Mate choice  
1044 versus mate preference: inferences about color-assortative mating differ between field and lab  
1045 assays of poison frog behavior. *American Naturalist*, 193(4), 598-607.  
1046 <https://doi.org/10.1086/702249>

1047