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**Author(s):** Schlippe Justicia, Lia; Fouilloux, Chloe A.; Rojas, Bibiana

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# Poison frog social behaviour under global change: potential impacts and future challenges

Lia Schlippe Justicia<sup>1</sup> · Chloe A. Fouilloux<sup>2</sup> · Bibiana Rojas<sup>1,2</sup>

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## Abstract

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

**Keywords** HIREC · Communication · Behavioural plasticity · Parental care · Territoriality · Tadpoles

## Introduction

Environmental changes, including shifting continents and climatic fluctuations, have been shown to prompt diverse responses in organisms across a wide range of taxa (Ricklefs and Schluter 1993; Rosenzweig 1995) throughout evolutionary time. However, the unprecedented scale and pace

of recent and current human-induced rapid environmental changes (HIREC), such as habitat destruction/fragmentation (Pimm and Raven 2000), climate change (Parmesan and Yohe 2003), and exposure to novel biotic (e.g. exotic species, pathogens, and parasites: Lockwood et al. 2013) and abiotic (e.g. environmental pollutants: Rohr et al. 2006) stressors, represent new challenges for many species which have not experienced such rapid changes in their evolutionary past (Palumbi 2001). The impact of HIREC on the natural world is colossal (Wake and Vredenburg 2008; Cowie et al. 2022), affecting the availability of important resources (i.e. food and shelter; Fahrig 2003), altering conspecific and heterospecific interactions (Tuomainen and Candolin 2011; Candolin and Wong 2012), and ultimately threatening many species and populations (Pimm and Raven 2000; Wake and Vredenburg 2008; Cowie et al. 2022).

For many animals, survival and reproduction in rapidly changing environments are expected to be shaped by the

✉ Lia Schlippe Justicia  
lia.schlippe@vetmeduni.ac.at

✉ Bibiana Rojas  
bibiana.rojas@vetmeduni.ac.at

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

<sup>2</sup> Department of Biology and Environmental Science, University of Jyväskylä, P.O. Box 35, 40014 Jyväskylä, Finland

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

While individual behavioural responses will affect population dynamics on a local scale, the effect of HIREC on sociality and interspecific interactions has far-reaching ecological implications for broader community dynamics. Environmental changes can directly and indirectly influence the way in which individuals interact, not only with other species (e.g. predators and prey, hosts and parasites) but also with each other (Candolin and Wong 2012). Social interactions, ranging from choosing a mate to providing offspring with care, can be affected by HIREC in multiple ways (Croft et al. 2008). For example, ship noise reduces the ability of Lusitanian toadfish (*Halobatrachus didactylus*) to detect conspecific acoustic signals, essential for mate attraction (Vasconcelos et al. 2007), while water turbidity reduces male-male competition in three-spined stickleback (*Gasterosteus aculeatus*), compromising the honesty of agonistic signals, which are relevant indicators of parenting ability (Wong et al. 2007). Similarly, human disturbance can directly reduce the nest attendance of bearded vultures (*Gypaetus barbatus*), increasing the probability of breeding failure (Arroyo and Razin 2006).

Social interactions have a critical effect on individual fitness (Allee et al. 1949) and, consequently, on population dynamics. Parental care, for example, is known to enhance the offspring's fitness by increasing their survival, growth and/or quality, and, ultimately, their lifetime reproductive success (Royle et al. 2012). Despite the obvious benefits for the offspring, parental care comes at a cost to the caregiver in the form of energy expenditure, loss of mating opportunities, and increased predation risk while tending their young

(Alonso-Alvarez et al. 2012). Thus, an individual's investment in parental care depends on the value of their existing offspring in relation to future reproductive opportunities (Alonso-Alvarez et al. 2012; Royle et al. 2012). Under changing environmental conditions, both the energetic costs of care for the parents and the fitness benefits for the young could be altered, influencing population recruitment (Alonso-Alvarez et al. 2012; Ratikainen et al. 2018). In the face of low resource availability, parents can, for instance, reduce their current investment into offspring with the expectation of better reproductive opportunities in the future (Winkler 1987). This decline in care quality, in turn, can cause long-term changes in the behaviour of the offspring, including aggressiveness and boldness (Armstrong 2019), cognition (Bredy et al. 2004), and F1's parental behaviour (Gromov 2009). Research conducted in songbirds, for example, has shown that nutritional stress during early development stages (when songbirds depend on their parents for food), negatively affects brain development and male song quality in adulthood (Nowicki et al. 2002). In rodents, offspring who are groomed less frequently during early postnatal periods exhibit lower spatial learning and memory in adulthood (Liu et al. 2000; Bredy et al. 2004). Decreased investment in the face of challenging environmental conditions is not the rule, however, as some parents appear to increase their workload in the face of sub-optimal conditions (Vincze et al. 2017). Ultimately, the adaptability of parental behaviour/cooperation appears to be the most accurate predictor of species successfully overcoming the varied pressures of global change in the wild (Vincze et al. 2017).

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

One of the most emblematic and well-studied groups of amphibians showing complex and diverse social behaviours are Neotropical poison frogs (Dendrobatidae) and their closest relatives (Aromobatidae), altogether referred to as the superfamily Dendrobatoidea (Cope 1865; Grant et al. 2006) and hereon referred to as 'poison frogs' for simplicity. Distributed from Nicaragua in Central America to Bolivia

in South America, poison frogs generally inhabit tropical rainforests (Summers and Tumulty 2014), often in areas that are under severe degradation, and exhibit a large diversity in mating systems, parental care strategies, and communication modalities (reviewed in Summers and Tumulty 2014). Males generally defend long-term territories from conspecifics through so-called advertisement calls and, if necessary,

physical combat (Fig. 1A; Pröhl 2005). Defending these territories is often crucial to male reproductive success, as courtship, mating, and oviposition take place therein (Pröhl 2005). In most species, males perform parental care, which consists of clutch attendance and larval transport (Fig. 1B) from terrestrial oviposition sites (e.g. leaf litter and leaves on bushes) to water bodies such as streams, temporary



**Fig. 1** Poison frogs and their unique social behaviours may be impacted by global change. **A** Males of *Dendrobates tinctorius* engaged in physical combat, where often one male pushes, kicks, and gets on top of the other trying to press them against the substrate; **B** male *Ameerega hahneli* transporting his tadpoles (pointed at by the arrow) to a body of water; **C** tadpole (pointed at by the arrow) transport is done by females in *Oophaga granulifera*; **D** habitat disturbance can alter the way in which colours are perceived by con- and heterospecifics, as shown in *O. pumilio*, and thus affect communication systems; **E** males of *D. tinctorius* are in charge of clutch (pointed at by the arrow) attendance; **F** climate change can increase the risk of tadpole death (agonising tadpoles

pointed at by the arrows) by desiccation of nurseries; **G** *Ranitomeya ventrimaculata* parents (pointed at by the dashed arrows) lay clutches (pointed at by the solid arrow) in bromeliads occupied by a large tadpole in periods of low rainfall to increase the survival probabilities of the tadpole therein; **H** *O. lehmanni* is highly threatened due to illegal pet trade activities. Males are thought to be more likely to be found by collectors because of their vocalisations (see the inflated vocal sac pointed by the arrow); **I** *Andinobates bombetes* adjusts their calling behaviour to avoid interference caused by traffic noise. Photo credits: Bibiana Rojas (**A, B, C, E, F, G**); Justin P. Lawrence (**D**); Mileidy Betancourth (**H**); Fernando Vargas (**I**)

ponds, or small pools of water formed in plant structures (i.e. phytotelmata) (Summers and Tumulty 2014). Tadpoles are confined in these water bodies until completing metamorphosis (Weygoldt 1987; Lehtinen et al. 2004; Summers and McKeon 2004; Schulte et al. 2020). While uniparental male care is the basal reproductive strategy in poison frogs (Weygoldt 1987; Carvajal-Castro et al. 2021), multiple lineages have evolved biparental or exclusive female care, where females transport tadpoles (Fig. 1C) and feed them with unfertilised trophic eggs (Summers et al. 1999a). The transition to female or biparental care has been suggested to be the result of using small phytotelmata with scarce food resources (Brown et al. 2010; Carvajal-Castro et al. 2021), and biparental care has been proposed as the precursor of monogamy (Brown et al. 2008, 2010; Summers and Tumulty 2014; Tumulty et al. 2014). It is precisely the interaction between the diverse sexual and social systems of poison frogs, combined with the pressing effects of HIREC, that makes this group a relevant model through which to test and understand the impacts of global change.

Although global change is expected to influence social behaviours in several ways, surprisingly little is known about how these effects take place in wild populations of poison frogs. Moreover, most studies analyse environmental stressors independently, often underseeing potential interactions and synergic effects. For example, while tadpoles manage to cope with predator-induced stress and low concentrations of pesticides separately, when exposed to both at the same time they show substantial mortality (Relyea and Mills 2001). Further research combining animal behaviour and conservation biology (Caro 1999) is necessary to identify species-specific relevant HIREC and to understand how they may adapt (or not) their behaviours accordingly. Only by doing so, we may be able to evaluate populations' vulnerability to global change, develop predictive models and focus conservation efforts (Schroeder et al. 2011). Here, we illustrate key points about the potential impacts of, and responses to, HIREC using Neotropical poison frogs' social behaviours as a model system. We specifically focus on territoriality and parental care behaviours, as they could be of special importance due to their capacity to buffering offspring against HIREC. Using this information as a baseline, we identify knowledge gaps and formulate new testable hypotheses to assess (1) the nature and magnitude of HIREC impact on wild populations of poison frogs, and (2) potential parental care and aggression responses to these HIREC.

## Impacts of global change on poison frogs

Poison frogs depend on a wide variety of microhabitats in different life stages. Leaf litter and phytotelmata, for example, serve as primary breeding sites, shelters, and nurseries for poison frogs; in addition to being defendable resources

for territorial species, they provide more stable temperature and humidity conditions than open areas with little canopy (Duellman and Trueb 1994). The dependence on suitable microhabitats together with the obligate use of small water bodies for reproduction or development make many Neotropical frogs particularly vulnerable to HIREC (Donnelly and Crump 1998; Touchon and Warkentin 2009).

## Habitat loss and climate change

Many tropical regions are subject to unprecedented rates of habitat loss (Lewis et al. 2015; Taubert et al. 2018). Over the last decade, deforestation patterns in the Amazonian rainforest have switched from localised large forest clearings to geographically spread small-scale deforestation events driven by agricultural intensification, land-use change, and natural resource exploitation (i.e. mining and logging activities) (Grau and Aide 2008; Hugo 2008; Kalamandeen et al. 2018). Small-scale deforestation pressures are expected to affect more remote areas and populations. This type of deforestation is also recognised as one of the main causes of more frequent and intense anomalies in the Amazonian hydrological cycle, such as extreme weather events (i.e. El Niño Southern Oscillation, hereafter El Niño) and dry spells during the rainy season (Lovejoy and Nobre 2018), which may be further exacerbated by global warming (Jiménez-Muñoz et al. 2016). Both the loss of habitat and more frequent climatic anomalies can affect poison frogs in multiple ways throughout their life stages, potentially leading to different behavioural responses and adaptations.

## Disruption in communication systems

Habitat alteration through small-scale deforestation can directly affect conspecific communication in two different ways. First, because human-made gaps are known to have increased radiation and higher temperatures than other areas of the forest (Vitt et al. 1998), male calling behaviour can become unsustainable over long periods of time. This is because, in degraded conditions, males would be more exposed and thus could incur higher evaporative water loss and potential overheating. These physiological stressors entail behavioural consequences as, in the mid-to-long term, males would be unable to devote as much time to attract females and advertise territory ownership. Second, variations in the forest's light environment can make an animal's appearance change too (Endler 1993), which has been proven crucial in the courtship behaviour of some lekking bird species (Théry and Endler 2001). The detectability of the variable colour patterns found in *D. tinctorius*, likewise, has been shown to differ depending on whether they are seen under an open or closed canopy (Rojas et al. 2014). While this has been studied mostly in the context of predator-prey

interactions, such differences in detectability in response to the surrounding light environment could be particularly relevant for species in which colour patterns play a role in mate choice (e.g. *O. pumilio*: Summers et al. 1999b; Maan and Cummings 2008; Yang et al. 2019) or underlie differences in other behavioural patterns such as boldness or aggressiveness (e.g. *O. pumilio*: Rudh et al. 2013; Pröhl and Ostrowski 2011; Crothers and Cummings 2015; *O. granulifera*: Willink et al. 2013, 2014). Importantly, human-driven habitat disturbance may not only affect the light environment but also the structure of the forest floor, which can alter detectability and visual contrast, thus causing potential interference in communication between conspecifics (Barnett et al. 2021). Furthermore, because poison frog colouration is partly based on carotenoid pigments acquired through the diet (Twomey et al. 2020), changes in the prey community availability driven by habitat disturbances could also alter the colouration of individuals. In fact, several studies have shown that a diet rich in carotenoids can indeed produce changes in colouration (Brenes-Soto and Dierenfeld 2014; Umbers et al. 2016; Stückler et al. 2022) and increase the reproductive success of captive frogs (Ogilvy et al. 2012; Dugas et al. 2013). Thus, changes in prey availability could affect the intake of carotenoids or their precursors and, in turn, affect intraspecific communication, particularly in species where colouration plays an important role in mate selection, as mentioned above.

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

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

There are several behaviours that may help adult poison frogs reduce the vulnerability of their eggs to HIREC. On the one hand, choosing suitable oviposition sites is particularly important if larvae are unable to leave these sites when conditions become unfavourable. For example, in the tree frog *Dendropsophus ebraccatus*, a unique species which can flexibly choose between aquatic and nonaquatic deposition sites, changes in rainfall patterns since 1972 have altered oviposition-site selection (Touchon 2012). Although egg

mortality was generally higher in aquatic sites due to greater predation risk, altered rainfall patterns driven by climate change increased clutch dehydration risk, shifting the optimal site choice by parents from terrestrial to aquatic habitats over the span of only 40 years. *D. ebraccatus* clearly provides an excellent system to measure the success of the adaptive decision-making by parents; however, whether or not poison frogs are as flexible in their use of oviposition and tadpole deposition sites requires further research. For terrestrially-breeding frogs, buffering the negative effects of HIREC could largely depend on the parents' capacity to select specific microhabitats with favourable structures. *Dendrobates tinctorius*, for example, is a terrestrial-breeding frog with clutch attendance (Fig. 1D) and uniquely flexible deposition choices compared to other species that also use ephemeral pools as nurseries. *D. tinctorius* fathers transport tadpoles to diverse pools that range enormously in their vertical position (0–>20 m), size (19 mL to –270 L), and chemical composition (pH=3 to –7) (Fouilloux et al. 2021). We hypothesise that, when faced with the pressures of HIREC, species that can access (and tolerate) a wider variety of nurseries will fare better than those with narrower options. Species with flexible behaviour may also benefit from modulating care investment based on climatic conditions, e.g. when desiccation risk is high parents spend additional effort accessing especially deep/stable nurseries compared to potentially more relaxed, “riskier” choices throughout a consistently rainy season. Furthermore, we predict sites with denser canopy cover as well as abundant leaf litter and vegetal structures (e.g. fallen branches and hollow trunks) to provide more stable microclimate conditions for successful egg development. Nevertheless, different microhabitats may be weighed differently depending on species-specific biological and life-history requirements. Therefore, a better understanding of the microhabitat use of species both in undisturbed and disturbed areas is essential to implement effective conservation efforts.

On the other hand, to compensate for adverse environmental conditions, parents may adjust the intensity and frequency of clutch attendance to guarantee offspring survival (see examples in invertebrates (Dick et al. 1998), fish (Green and McCormick 2005), reptiles (Stahlschmidt and DeNardo 2010), and birds (Vincze et al. 2017)). Males of *H. fleischmanni*, for example, increase both the frequency and time spent on egg care in response to a reduction in relative humidity (Delia et al. 2013). One of the most common ways anurans provides egg attendance is by placing their body over the eggs to reduce evaporative water loss or directly moistening the eggs through physical contact with the ventral integument (Wells 2010). Although this behaviour has been suggested for some poison frogs (Souza et al. 2017), it is not ubiquitous across the family (Rocha et al. 2021). Furthermore, some amphibians can increase

the amount of glycoprotein-rich jelly cores, jelly layers, or matrices surrounding the clutches, which protect embryos from dehydration and predators (Delia et al. 2020). So far, little research has focused on the potential egg attendance plasticity that poison frogs may present under environmental stress. Considering that egg attendance conflicts with other fitness-related activities, such as foraging and mating (e.g. Delia et al. 2013), investigating the trade-offs of parental decisions under environmental changes is essential to predict population dynamics. Therefore, if the costs of maintaining the current clutch surpass their fitness benefits, we would predict individuals to reduce their parental care effort or even abandon clutches completely, as seen in other taxa (e.g. birds: Bustnes and Erikstad 1991; Öberg et al. 2015; fish: Suski and Ridgway 2007).

It is noteworthy that in territorial species, such as most dendrobatid frogs (Pröhl 2005), the trade-off between defending territories and attending multiple clutches simultaneously may become magnified under habitat loss. Habitat loss and fragmentation can modify species movement as well as the availability of resources and suitable territories (Fahrig 2003), which can alter the carrying capacity of the area in different ways. Firstly, habitat fragmentation could reduce population density if edge effects are negative (e.g. increased predation pressure), or if the fragmented habitat is not able to sustain larger populations (Mullu 2016). Given that the costs of mate search in females depend on the number of suitable mates available, a lower population density could detract energy and time from tadpole care in species with female egg-feeding and tadpole transport. By contrast, the remaining patches of habitat could also increase population density by concentrating the surviving individuals from the disturbed habitat (Mullu 2016). In the resulting smaller and densely packed habitat patches, aggression rates between highly territorial individuals may increase due to a higher number of encounters and more competition for limited resources and territories (Fisher et al. 2021). In male tree lizards (*Urosaurus ornatus*), for instance, aggressive interactions between individuals are more frequent in resource-limited burned sites than in resource-rich habitats (Lattanzio and Miles 2014). More energy spent on territorial defence could translate into a reduced ability to attract further mates or attend multiple clutches, directly influencing mating systems. This conflict between aggression and direct care of offspring has been found in multiple animals (e.g. Lissåker and Kvarnemo 2006; DeAngelis et al. 2020). Importantly, filial cannibalism occurs in some dendrobatid frogs, both in adult males when taking over a new territory (e.g. *Allobates femoralis*: Ringler et al. 2017) and in females to decrease parental investment of a mate in unrelated clutches (e.g. *Dendrobates auratus*: Summers 1989). Thus, we predict that higher densities and lower resource availability could also lead to more territorial intrusions by

males, more competition among females, and, as a result, an increase in filial cannibalism events.

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

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

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

Phytotelmata are used in multiple poison frog species to deposit their tadpoles (Weygoldt 1987; Summers and McKeon 2004; Lehtinen et al. 2004; Rojas 2014, 2015; Schulte et al. 2020; Fouilloux et al. 2021), can naturally vary in water volume, nutrient composition, food sources, stability as well as the risk of competition and predation (Lehtinen et al. 2004). Consequently, parents have to assess all these different ecological factors, which can be highly unstable and vary in space and time (Rudolf and Rödel 2005; Schulte and Lötters 2013), and adapt their deposition strategy according to this information (Webb et al. 1999; Schulte and Lötters 2013). Furthermore, the size of these breeding pools has been associated with the evolution of different parental care strategies (e.g. trophic egg feeding and biparental care evolved in species using smaller pools; Brown et al. 2010). The selection of suitable rearing sites will play a key role in the successful development and survival of their offspring (Refsnider and

Janzen 2010), and thus will have direct effects on the population recruitment for multiple species. However, HIREC might further exacerbate the instability and availability of good-quality phytotelmata, imposing multiple novel costs on parental care and territoriality. Because these stressors could be especially pronounced in small phytotelmata, species with parental care strategies such as egg feeding could be particularly affected. Importantly, nursery desiccation is already considered one of the most common abiotic causes of tadpole mortality (Fig. 1E), even in tropical rainforests where annual rainfall is very high (Murphy 2003; Rudolf and Rödel 2005; BR, CF pers. observ.).

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

A reduction in the number of suitable nurseries could also lead to the convergence of site choice by multiple parents, potentially from multiple species that in "normal" conditions would select for smaller/more unstable pool types (e.g. bromeliads). Consequently, we predict that under HIREC the overall larval density in pools will increase, and competition between tadpoles from the same or different species could become stronger, potentially benefitting certain species over

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

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

2015; Fischer and O'Connell 2020) and natural conditions (Ringler et al. 2013; Rojas and Pašukonis 2019; Pettitt 2012). However, this plasticity has not been found in other close species like *Allobates paleovarzensis* (Rocha et al. 2021).

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

### Pet trade, infectious diseases, and pollution

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

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

(Betancourth-Cundar et al. 2020). The global amphibian pet trade is also widely recognised as one of the main drivers of the worldwide spread of amphibian pathogens such as the chytrid fungus *Batrachochytrium dendrobatidis* (hereafter Bd) (Fisher and Garner 2007), one of the most dramatic examples of newly-emerged pathogens, which causes the infectious disease chytridiomycosis. Therefore, it is not surprising that Bd has recently been detected in dendrobatid species in the wild.

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

In addition, chemical pollutants derived from agriculture (e.g. herbicides and pesticides) and mining activities (e.g. metals and metalloids: Hg, Cu, Co, Zn, and As) can impair individuals' immune defences and further increase their susceptibility to pathogens and diseases (Christin et al. 2003). Similarly, when found in low concentrations, they can delay growth and metamorphosis (Carey and Bryant 1995), cause malformations (Unrine et al. 2004; Ferrante and Fearnside 2020), alter fertility and fecundity (Adams et al. 2021), or even cause sex-reversals (Nemesházi et al. 2020), often leading to devastating consequences for amphibian populations (Brühl et al. 2013). Increasing evidence demonstrates effects on a wide range of amphibian behaviours, such as reduced rates of activity (e.g. swimming, feeding, and breeding) or ability of tadpoles to escape predation (Shuman-Goodier

**Fig. 2** Illegal mining. Small-scale deforestation due to illegal mining activities is threatening the habitat of many species of poison frogs in the Amazon and the Chocó regions, two of Earth's biodiversity hotspots. Here, illegal mining activity in Nouragues Natural Reserve, French Guiana. Photos: A) Bernard Gissinger; B) Alexandre David



and Propper 2016; Sievers et al. 2019). In two-lined salamanders (*Eurycea bislineata*), for instance, exposure to sub-lethal concentrations of mercury reduced their motivation to feed (Burke et al. 2010), whereas it impaired swimming performance in American toad (*Anaxyrus* [formerly *Bufo*] *americanus*) larvae (Bergeron et al. 2011). Although chemical contaminants have also been reported to 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 amphibians. Given the strong detrimental effects of pollutants on egg and tadpole survival and development, we would expect selection

to favour individuals capable of recognising and avoiding egg-laying and rearing sites based on chemical pollutant concentrations. As far as we are aware, however, this ability has been investigated in some anurans but not in poison frogs. For example, adults of the grey treefrog (*Hyla versicolor*) avoided ponds for oviposition if contaminated with the glyphosate pesticide Roundup (Takahashi 2007).

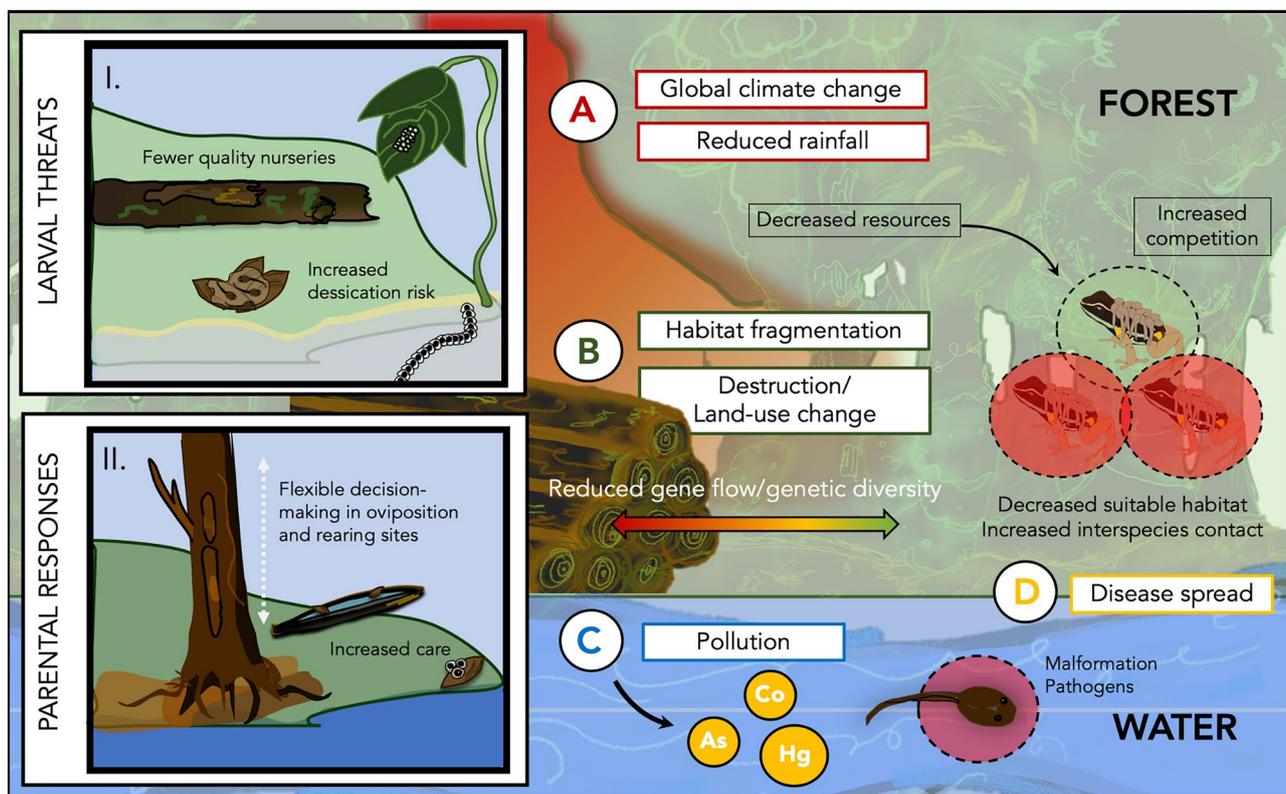
Social behaviours can also be impacted by an important, yet often underestimated, the form of anthropogenically driven pollution, noise pollution. For acoustically communicating species, as is the case of most anuran species, anthropogenic background noise can mask vocalisations and

thus disrupt key species-specific communication (Simmons and Narins 2018). For instance, masking of acoustic signals could inhibit males' calling activity (Sun and Narins 2005), reduce females' ability to localise male's advertisement calls (Caldwell and Bee 2014), or change female's mate choice, potentially selecting for less fit males (Barrass 1985) or males with lower quality of parental care (Pettitt et al. 2020). Masked male calls may not only attract fewer females but also make territorial calls less audible, affecting male territorial defence by reducing their ability to detect and discriminate against conspecific intruders, as shown in birds (Kleist et al. 2016). This, in turn, may translate into more conspecific intrusions, aggressive encounters, and increased filial cannibalism rates. To cope with anthropogenic noise, some species can modify their call characteristics to contrast acoustically with noise pollution. For example, Cauca poison frogs, *Andinobates bombetes* (Fig. 1I), vocalise in moments of low background noise and call less when noise is higher (Vargas-Salinas and Amézquita 2013; Jiménez-Vargas and Vargas-Salinas 2021), while Bloody Bay poison frogs (*Mannophryne olmonae*) increase higher frequency

calls and decrease inter-pulse intervals (Clemmens 2014). However, because changes in calling characteristics could potentially be opposed to female mate preferences, future research should investigate if such responses could become maladaptive.

## Conclusions

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



**Fig. 3** Conceptual overview. The main driving forces of HIREC (**A** climate change, **B** habitat fragmentation, **C** chemical pollution, and **D** novel pathogens and diseases) interact across habitats implicating cascading effects on the social behaviours of amphibians. Throughout the tropics, these disturbances will impact a large diversity of species with consequences detectable at every life stage. (I) We predict

that HIREC will particularly threaten juveniles and larvae, where less consistent rainfall and higher temperatures will limit the availability and diversity of larval nurseries and increase the desiccation probability of clutches. (II) In response to these threats, we hypothesise that parents will both increase care and the flexibility in deposition choices

2. Due to their diverse and complex social behaviours, as well as their occurrence in often degraded habitats, poison frogs are an interesting group to study the potential impacts of and social responses to HIREC (see Fig. 3 for a summary).
3. To compensate for negative HIREC impacts, we predict individuals to increase parental care efforts by spending more time attending clutches and transporting tadpoles to further and fewer nursery sites. However, this increase in parental costs will only be sustained to the point that it does not outweigh individual fitness. Furthermore, we hypothesise higher species-specific aggression rates both in adults and tadpoles, as well as more frequent filial cannibalistic events due to limited resources/territories and anthropogenic noise. Finally, altered environmental conditions derived from small-scale deforestation (i.e. higher radiation, increased temperature, and changes in ambient light) or increased noise pollution may disrupt important conspecific communication processes by reducing the calling capacity of males or by modifying mate detectability, courtship, and choice.
4. Here, we have examined the impact of different anthropogenic stressors on poison frogs individually. However, the reality is usually more complex, with multiple HIREC and natural stressors acting and interacting simultaneously in unexpected ways. All these factors make predictions harder to formulate.

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## Declarations

**Conflict of interest** The authors declare no competing interests.

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