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Barking up the wrong frog: global prevalence of misdirected amplexus in anuran amphibians

Shubham P. Soni[1,*,†], Vaishnavi Apte[2], Pranav Joshi[3], Vivek P. Cyriac[4,†]

[1]School of Arts and Sciences, Azim Premji University, Bengaluru 562125, India
[2]Nature Conservation Foundation, 1311, 'Amritha', Vijayanagar 1st Stage, Mysuru 570017, Karnataka, India
[3]Ecological Neuroscience Group, School of Natural Sciences, Macquarie University, Sydney, NSW 2109, Australia
[4]Centre for Ecological Sciences, Indian Institute of Science, CV Raman Road, Bengaluru 560012, Karnataka, India

[†]These authors contributed equally to this work.

[*]Corresponding author. 703 Mahavirdham, Devidayal Road, Mulund West, Mumbai, Maharashtra 400080, India. E-mail: sonishubhamp@gmail.com

ABSTRACT

Reproduction is an energy-expensive life process in many organisms, and accurate conspecific recognition is crucial to successful reproduction. Nonetheless, misdirected attempts at amplexus towards heterospecifics appear to be common in many anuran amphibians. Such reproductive interference can have significant ecological and evolutionary consequences, but its prevalence remains unknown. Here, we compile a global dataset of anuran misdirected amplexus and test how phylogenetic relatedness, ecological niche, breeding phenology, and geography influence the prevalence of anuran misdirected amplexus. We find misdirected amplexus to be significantly higher among more closely related heterospecific pairs than between random pairs, but still occurred between species of different families. Misdirected amplexus was also significantly more common in arboreal and terrestrial anurans, and among species pairs with similar body sizes or with similar microhabitat use. We also show that misdirected amplexus is significantly more common among explosive breeders compared with prolonged breeders and is more prevalent in temperate regions compared with the tropics. Overall, we show that misdirected amplexus among anuran amphibians is not a rare phenomenon and that its prevalence is influenced by evolutionary relatedness, microhabitat use, ecological similarity, and breeding phenology. These interactions have the potential to cause species decline, hence understanding them is crucial.

Keywords: interspecific amplexus; heterospecific mating; heterospecific amplexus; reproductive interference; niche overlap; breeding phenology; explosive breeding

INTRODUCTION

Reproduction is a fundamental aspect of every living organism. In sexually reproducing organisms, the existence of the species largely depends on successful mate recognition and reproduction (Ryan *et al.* 2003). Given that species also invest in other life processes, such as survival and growth (Chen *et al.* 2013), reproductive investment should be optimized by assessing the costs associated with resource allocation, survival, and fecundity (Williams 1966, Vitt *et al.* 2009). The energetic costs of reproduction specifically are threefold: (i) the production of eggs or sperm; (ii) investment towards secondary sexual characters; and (iii) investment towards reproductive behaviour (Wootton 1985). According to the 'costs of reproduction' hypothesis, reproductive strategies and life-history traits (e.g. reproductive age, clutch size) that maximize the sum of the present and future reproductive successes would evolve (Williams 1966, Stearns 1989, Harshman and Zera 2007, Bourne *et al.* 2023). Although several studies have found support for the 'costs of reproduction' hypothesis (Harshman and Zera 2007), there are several instances where species indulge in erroneous interactions. These sexual interactions between animal species that decrease the fitness of at least one of the species involved are known as reproductive interferences (Cothran 2015). Seven types of reproductive interference have been described: signal jamming, heterospecific rivalry, misdirected courtship, heterospecific mating attempts, erroneous female choice, heterospecific mating, and hybridization (Gröning and Hochkirch 2008). Such misdirected heterospecific interactions during the different stages of mate acquisition can lead to reproductive interference and can affect the fitness of individuals (McLain and

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Shure 1987, McLain and Pratt 1999, Thum 2007, Gröning and Hochkirch 2008, Maisonneuve *et al.* 2023). Although reproductive interference is widespread in many organisms (Gröning and Hochkirch 2008) and can affect the demography and structuring of ecological communities (Ting and Cutter 2018, Iritani and Noriyuki 2021), its ecological significance and prevalence in different groups remain understudied. Here, we aim to understand the prevalence of reproductive interferences through misdirected mating attempts in anuran amphibians.

Amphibians show a wide variety of reproductive strategies that range from aquatic egg laying to loss of larval stages or direct development to viviparity and parental care (Duellman and Trueb 1994). Based on combinations of reproductive traits, such as amplexus type, oviposition sites, clutch characteristics, development, and parental care, researchers have now identified >74 reproductive modes or strategies (Nunes-de-Almeida *et al.* 2021), making amphibian reproduction the most conspicuous feature of its biology (Duellman and Trueb 1994, Wells 2007). Amphibians are also one of the most vulnerable vertebrates to current climate change and other anthropogenic pressures (Carey and Alexander 2003), and many species are undergoing a drastic decline globally (Beebee and Griffiths 2005, Collins 2010, Luedtke *et al.* 2023). This has sparked interest in understanding how climate change, habitat alterations, and anthropogenic pressure can affect the breeding behaviour of anurans and influence their reproductive fitness. However, many species of amphibians frequently make mistakes in identifying conspecifics during mating attempts (Mollov *et al.* 2010, Serrano *et al.* 2022, Brischoux and Lorrain-Soligon 2023). Such interactions with heterospecifics can have ecological, evolutionary (Calabrese and Pfennig 2022, Chen *et al.* 2022), and behavioural (Schroeder and Podos 2023) implications that can lead to reproductive interference and also reduce fitness (Hettyey *et al.* 2014). Although misdirected amplexus is widespread and is known from >150 species of amphibians (Serrano *et al.* 2022), what drives the prevalence of such heterospecific interactions remains largely unexplored.

Here, we compile a dataset of published records of misdirected amplexus in amphibians and test specific hypotheses that drive the prevalence of such events. It has been shown that misdirected amplexus attempts are more frequent in a few amphibian families, such as Bufonidae, Ranidae, Hylidae, and Rhacophoridae (Serrano *et al.* 2022). Thus, we initially tested the prevalence of misdirected amplexus across different families. It has also been hypothesized that reproductive interference is more frequent among closely related species (Gröning and Hochkirch 2008). Given that the anatomies of species that produce sexual signals during mate acquisition are largely constrained by evolutionary relatedness (de Kort and ten Cate 2001), mistakes in recognizing such sexual signals are more likely among species that show low species divergence (de Kort and ten Cate 2001, Sosa-López *et al.* 2016). Thus, we tested the hypothesis that misdirected amplexus is more prevalent among closely related heterospecifics. Misdirected amplexus with heterospecifics can also occur when there is considerable overlap in mate recognition traits, such as body size, between species within the community (Okuzaki *et al.* 2010). Structurally complex environments can also affect the efficient transmission of mating signals (Goutte *et al.* 2018, Hardt and Benedict 2021), thereby increasing the chances of heterospecific mating owing to signal interference (Wollerman 1999, Gordon and Uetz 2012). Thus, we also tested the hypotheses that misdirected amplexus occurs among species with considerable overlap between species traits and microhabitats, and that misdirected amplexus would be more prevalent in structurally complex microhabitats, such as arboreal and terrestrial environments. Breeding phenology can also influence the chances of misdirected amplexus. Intense competition for mates in species with short bursts of synchronous breeding activity can lead to males amplecting heterospecific males or even inanimate objects (e.g. stones, shoes) (Pearl *et al.* 2005, Wells 2007). Thus, we tested whether misdirected amplexus was more frequent in explosively breeding species in comparison to prolonged breeders. We also tested whether misdirected amplexus was more common in temperate regions, where seasonal climatic changes restrict breeding activity to short periods, in comparison to tropical regions, which experience more stable climatic conditions.

MATERIALS AND METHODS

Data collection

We compiled a dataset of available published records on anuran misdirected amplexus through an exhaustive literature search. We used the software PUBLISH OR PERISH v.8, October 2021 (https://harzing.com/resources/publish-or-perish; Harzing 2007) to search for published articles indexed by 'Google Scholar' about misdirected amplexus in amphibians using specific keywords. The keywords included '(frog OR anura OR anuran) AND (interspecific OR intergeneric OR interfamilial OR homosexual OR cross OR erroneous OR unnatural OR unusual OR anomalous) AND (amplexus OR breeding OR mating OR fertilisation)'. Given that most observations of misdirected amplexus in amphibians were published in herpetological journals, we searched specifically for articles in 31 well-known herpetological journals using the same keywords (see Supporting Information, File S1). Articles that we found manually during random searches were added to this list. Additionally, we used the same keywords to search for images on social media and citizen science platforms, such as Facebook, Instagram, Wikimedia Commons, and iNaturalist (see Supporting Information, File S1). Social media and citizen science observations were included only when we could confirm the identity of the species, the locality, and when the observations were made in natural conditions and not in captivity. Species identities for such observations were confirmed based on references available on Amphibia-Web Database (https://amphibiaweb.org/) and Amphibians of the World v.6.2 (https://amphibiansoftheworld.amnh.org/). Data collection was carried out until December 2022.

Data classification

From each article in our list, we extracted the amplected species, i.e. the species that was on the bottom and mounted upon, and the amplectant species, i.e. the species that was on the top and mounted the other individual. We also noted the family of both the amplected and amplectant species, the geo-coordinates (if available), the zoogeographical zone, and the habitat in which the observation was made. For species wherein the exact coordinates were unavailable, we extracted the approximate latitude and longitude based on the broad location. We then classified these locations as tropical (between 23.5°S and 23.5°N) and temperate (outside the tropical belt) regions. The type of amplexus (i.e. inguinal, axillary, etc.) exhibited naturally by the amplectant and amplected species was noted following Carvajal-Castro *et al.* (2020). The type of amplexus generally seen in the amplectant and amplected species during conspecific mating was also noted using the paper by Carvajal-Castro *et al.* (2020) or other published literature. To this dataset, we added the data on misdirected amplexus compiled by Serrano *et al.* (2022) and removed any repeated observations to obtain our final dataset. In addition to these, we also collected body size data and microhabitat data that were available for both the amplected and amplectant species. The average body size (snout–vent length) data were obtained for males of each species from the amphibian traits database (Huang *et al.* 2023). Microhabitat use was classified as arboreal, terrestrial, aquatic, or burrowing, and was mostly obtained from the study by Moen and Wiens (2017) and the International Union for Conservation of Nature (IUCN) Red List of Threatened Species. In some cases, we also obtained microhabitat data from other published sources (see Supporting Information, File S1). Species that were classified as being semi-arboreal, semi-terrestrial, semi-aquatic, or semi-burrowing were grouped as arboreal, terrestrial, aquatic, or burrowing, respectively. We also classified the breeding phenology of the amplectant species as being either 'explosive' or 'prolonged' breeders following Wells (1977, 2007), Bell *et al.* (2017), and other published sources (see Supporting Information, File S1).

Statistical analyses

We performed all analyses in R v.3.6.0 (R Core Team 2019). To test whether misdirected amplexus is more prevalent in closely related species, we classified the taxonomic relatedness of the amplectant species with the amplected species as interspecific (within genus), intergeneric (between genera of the same family), interfamilial (between different families of the same order), interorder (between the three orders of amphibia), and non-amphibian (amplexus with other non-amphibian groups). We then used a χ^2 goodness-of-fit test to test for differences in the frequency of misdirected amplexus between groups against the null expectation and then carried out pairwise comparisons between groups using the R package RVAideMemoire v.0.9-69 (Hervé 2023). We also tested whether the phylogenetic distance between species pairs engaging in misdirected amplexus was more closely related to each other than random. To do this, we used a dated phylogeny that included each unique species pair from our dataset. We obtained this phylogeny by pruning out species from a large-scale dated amphibian tree generated by Portik *et al.* (2023) using the R package Phytools v.1.0-3 (Revell 2012). We extracted the phylogenetic variance–covariance matrix for our species pairs using the cophenetic.phylo function in the picante v.1.8.2 package (Kembel *et al.* 2010), then extracted the phylogenetic distance between each pair of species in our dataset using the extract.val function in phylin v.2.0.2 (Tarroso *et al.* 2015) and calculated the average observed pairwise distance. We then generated a null distribution of the mean pairwise distance by randomly shuffling the amplected species within each biogeographical zone using the R package permute v.0.9-7 (Simpson 2022) and generating 1000 new species pairs. We performed these block permutations within each biogeographical zone to produce a more conservative estimate of the null distribution. We compared the average observed pairwise distance with the null distribution of mean pairwise distance obtained from the block permutation of amplected species using a one-sample *t*-test.

To test whether misdirected amplexus is also more prevalent in sympatric species lacking niche segregation, we evaluated the overlap in body size, amplexus type, and microhabitat use. We first calculated the mean absolute difference in body size between amplected and amplectant species in our dataset. We then performed a 1000 block permutation of the body-size values of the amplected species within each biogeographical zone using the permute v.0.9-7 package (Simson 2022) and calculated the absolute difference in body size between species pairs to generate a null distribution of body-size differences. We then tested whether the absolute difference in body size was lower than the random null expectation using a one-sample *t*-test. Additionally, we tested the prevalence of misdirected amplexus in species occupying different microhabitats (arboreal, terrestrial, aquatic, or burrowing) using a χ^2 goodness-of-fit test, then performing pairwise comparisons using RVAideMemoire v.0.9-69 (Hervé 2023). We then scored each species pair in our dataset for microhabitat and amplexus type overlap and tested the prevalence of misdirected amplexus among species with and without microhabitat and amplexus type overlap using a χ^2 goodness-of-fit test. We also tested the prevalence of misdirected amplexus among species with explosive and prolonged breeding strategies and across climatic regimes, i.e. temperate vs. tropics, using a χ^2 goodness-of-fit test.

RESULTS

Our dataset included 482 observations, of which 392 (81.3%) observations were of misdirected amplexus between amphibians heterospecifics, 45 (9.3%) were incidences of necrophilia between conspecifics, three (0.62%) were misdirected amplexus between non-amphibian heterospecifics, and 42 (8.7%) were observations of misdirected amplexus with inanimate objects. Of these, we had 237 unique pairs of species involved in heterospecific amplexus involving 179 amplectant species and 181 amplected species. Misdirected amplexus was recorded in 19 frog families, but ~76% of the species belonged to four families: Bufonidae (23.2%), Ranidae (21.5%), Hylidae (19%), and Rhacophoridae (11.4%) (Fig. 1A).

The average cophenetic distance between heterospecific amplectic interactions was 186.75 and was significantly lower than the null distribution of average cophenetic distance obtained by random block permutation of amplected species ($t = 99.213$, d.f. = 1000, $P < .0001$; Fig. 1B). A χ^2 goodness-of-fit test on the number of misdirected amplexus indicated significant differences in the taxonomic relatedness of species interactions ($\chi^2 = 261.62$, d.f. = 4, $P < .0001$; Fig. 1C). About 40.5% of the observations of misdirected amplexus were intergeneric interactions within the same family and were significantly greater than all other interaction types ($P < .0001$) except for interfamilial interactions ($P = .36$), which accounted for

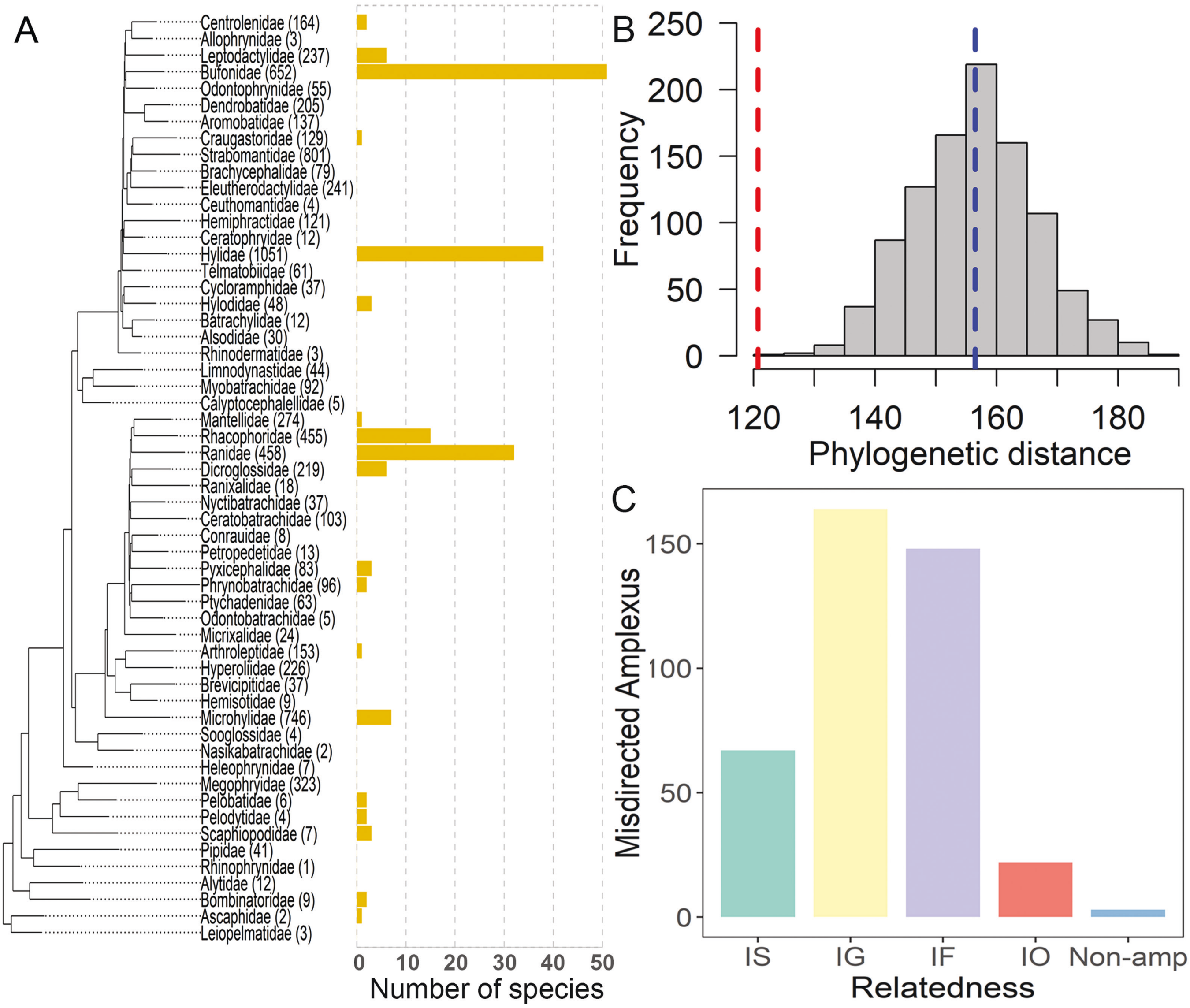

Figure 1. Phylogenetic distribution and relatedness among anuran species involved in misdirected amplexus. A, family-level phylogenetic tree of anurans adapted from Portik *et al.* (2023), with the number of species involved in misdirected amplexus. The numbers within parentheses represent the total number of species in each family. B, average pairwise phylogenetic distance between species pairs involved in misdirected amplexus (red vertical dashed line) compared with a random distribution of the mean phylogenetic distances. The blue vertical dashed line indicates the mean of the random distribution. C, frequency of misdirected amplexus observed across different levels of taxonomic organisation. Abbreviations: IF, interfamilial; IG, intergeneric; IO, interorder; IS, interspecific; Non-amp, with non-amphibian.

36.6% of the observations. Interspecific misdirected amplexus between species within the same genus accounted for 16.58% of the observations and was significantly greater than misdirected amplexus towards other amphibian orders ($P < .0001$) and other non-amphibians ($P < .0001$).

A one-sample *t*-test indicated that the mean absolute difference in body size was significantly lower compared with a null distribution of the mean body size differences obtained by random block permutation of amplected species ($t = 52.798$, d.f. = 1000, $P < .0001$; Fig. 2A). We also found significant differences in misdirected amplexus across microhabitat preferences ($\chi^2 = 35.374$, d.f. = 3, $P < .0001$; Fig. 2B). Misdirected amplexus was significantly more frequent in terrestrial (36.12%) and arboreal (36.12%) species compared with aquatic ($P = .009$) and burrowing species ($P < .0001$). Misdirected amplexus was also significantly more frequent in aquatic species (20%) compared with burrowing species (7.7%; $P = .007$). Instances of misdirected amplexus were also higher when there was an overlap in microhabitat preferences ($\chi^2 = 28.75$, d.f. = 1, $P < .0001$; Fig. 2C) and the amplexus type ($\chi^2 = 28.77$, d.f. = 1, $P < .0001$; Fig. 2D) of the amplectant and amplected species.

Comparing the prevalence of misdirected amplexus among breeding strategies, we found significantly greater instances of misdirected amplexus in explosive breeders compared with prolonged breeders ($\chi^2 = 24.961$, d.f. = 1, $P < .0001$; Fig. 3A) and in temperate regions compared with the tropics ($\chi^2 = 49.005$, d.f. = 1, $P < .0001$; Fig. 3B).

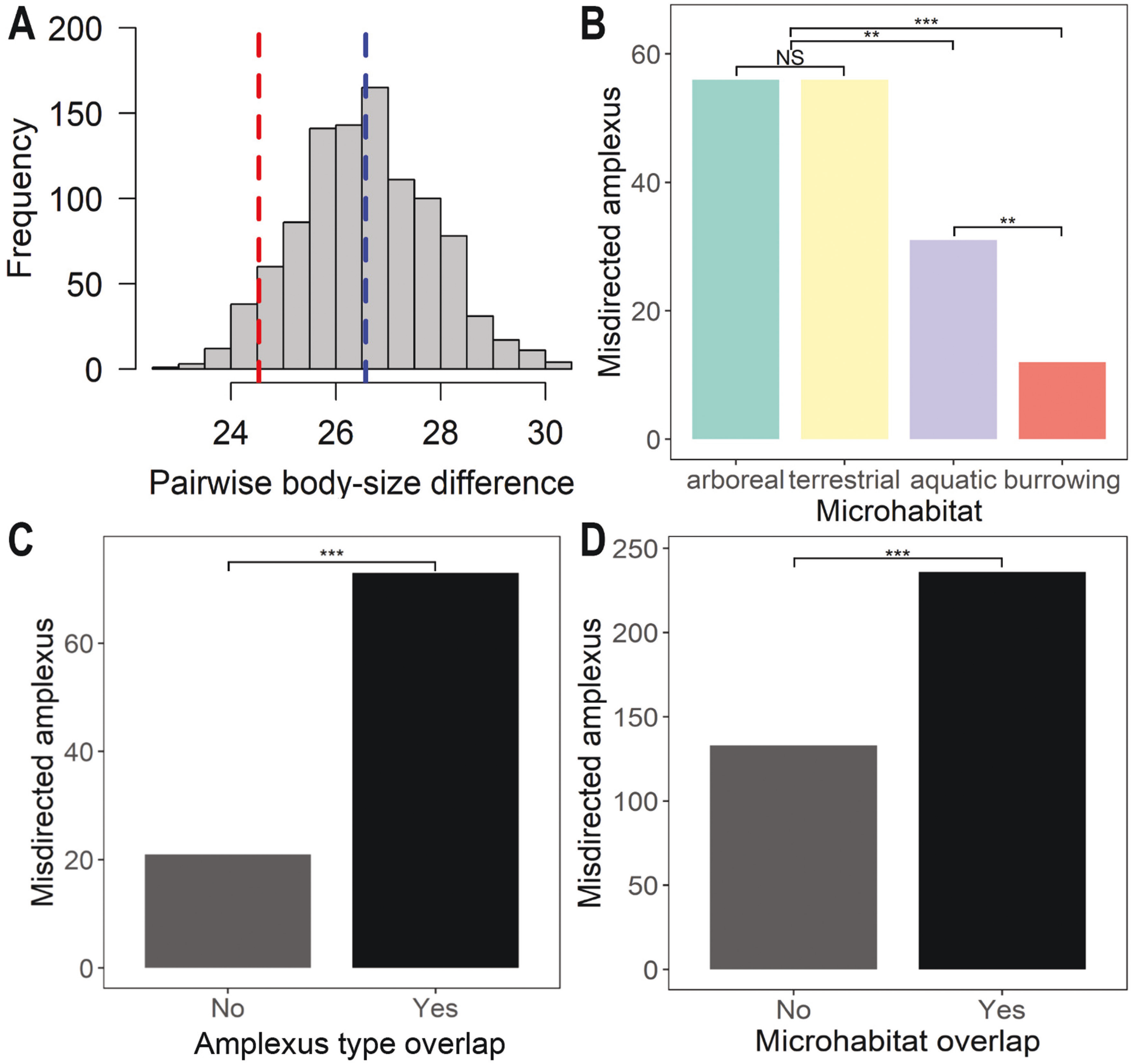

Figure 2. A, average difference in body size between species pairs involved in misdirected amplexus (red vertical dashed line) compared with a random distribution of body-size differences. The blue vertical dashed line indicates the mean of the random distribution. B, frequency of misdirected amplexus across different microhabitat usage. C, frequency of misdirected amplexus among species pairs with and without microhabitat overlap. D, frequency of misdirected amplexus among species pairs with and without similar types of amplexus. ****P* < .0001; ***P* < .01; NS, non-significant.

DISCUSSION

Our data, along with other recent studies, indicate that misdirected amplexus is not a rare phenomenon in anurans (Serrano *et al.* 2022, Brischoux and Lorrain-Soligon 2023). We collected 437 observations of true misdirected amplectic interactions (i.e. excluding instances of intraspecific necrophilia) spanning a period of about a century, from 1923 to 2023. Of the 437 records, there were 237 unique heterospecific amplectic interactions with 179 species involved in misdirected amplexus, suggesting that misdirected amplexus occurred more frequently (or was more frequently observed) in some species than in others. Misdirected amplectic interactions were unevenly distributed across the anuran tree and were primarily from four anuran families: Bufonidae, Hylidae, Ranidae, and Rhacophoridae.

Phylogenetic relatedness

Signals from closely related species are generally more similar to each other than to those of distantly related species, owing to common descent (Sosa-López *et al.* 2016). Thus, it is thought that reproductive interference is more likely among closely related sympatric species that show low levels of species divergence (Gröning and Hochkirch 2008, Kyogoku 2015). Several studies examining conspecific recognition among several groups have found that the ability to discriminate heterospecifics decreases

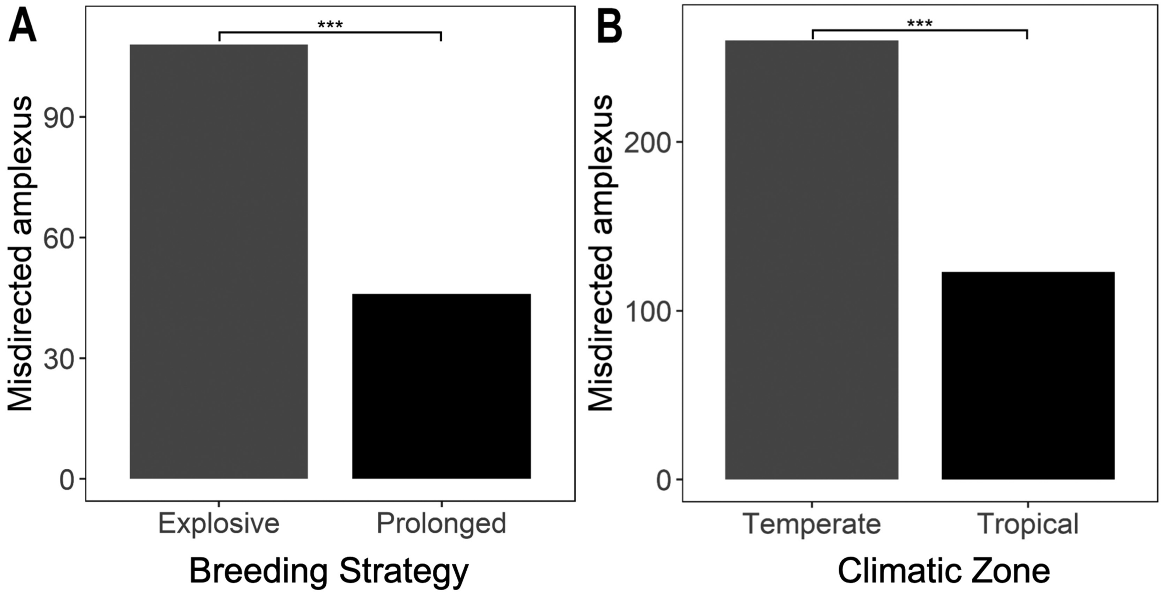

Figure 3. Frequency of misdirected amplexus between species with explosive and prolonged breeding strategies (A) and across geographical regions (B). ***$P < .0001$.

with evolutionary relatedness (de Kort and ten Cate 2001, Sosa-López *et al.* 2016). For instance, experiments have shown that in many species of birds and arthropods, males are unable to discriminate conspecifics from closely related heterospecifics, while discriminating distantly related heterospecifics (Verrell 1994, Clarke *et al.* 1996, de Kort and ten Cate 2001, Costa-Schmidt and Machado 2012, Saveer *et al.* 2014, Wolfenden *et al.* 2015, Wehi *et al.* 2017). Our results also indicated that the phylogenetic distance between species engaging in heterospecific amplectic interactions was significantly lower than random, lending support for the hypothesis that misdirected amplexus is greater among closely related heterospecifics.However, we also found that instances of intergeneric and interfamilial misdirected amplexus were significantly higher than misdirected amplectic events between species within genera. There were also some cases of misdirected amplexus with members of different amphibian orders, e.g. *Lithobates sphenocephalus* (order Anura) amplecting on *Ambystoma maculatum* (order Caudata).

Many amphibians use pheromones for intraspecific sexual signalling during the breeding season (Woodley 2010). Some of these sexual pheromones are highly conserved across species and could lead to mistaken conspecific recognition (Clarke *et al.* 1996, Saveer *et al.* 2014). For example, mating secretions (termed amplexins) produced in the nuptial glands of the frog *Rana temporaria* during the breeding season were structurally similar to the sexual pheromones associated with courtship behaviours in plethodontid salamanders (Willaert *et al.* 2013). Additionally, some courtship pheromones, such as the sodefrin-precursor-like factor (Herrboldt *et al.* 2021), which enhances female receptiveness in plethodontid salamanders (Houck *et al.* 2008), have now been shown to be expressed in many anurans (Janssenswillen *et al.* 2015, Bossuyt *et al.* 2019).

Although misdirected amplexus might not be random and is more prevalent among closely related species, the conserved nature of many chemical pheromones across amphibians could still lead to mistaken conspecific recognition (Rollmann *et al.* 2003) and misdirected amplexus among distantly related species.

Niche and microhabitat overlap

Habitat structure and composition can be a source for different levels of background noise and can significantly alter acoustic signals and affect effective communication (Forrest 1994, Boncoraglio and Saino 2007, Luther and Gentry 2013, Zaffaroni-Caorsi *et al.* 2023). Complex environments with dense vegetation cover can reflect sound, causing temporal signal distortions (Richards and Wiley 1980, Wells and Schwartz 1982, Forrest 1994, Blumenrath and Dabelsteen 2004). Such degradation or alteration of acoustic signals can lead to greater signal interference (Mathevon and Aubin 1997, Holland *et al.* 1998) and affect mating success (Gordon and Uetz 2012). Our analyses found that misdirected amplexus is more prevalent in arboreal and terrestrial species compared with aquatic and burrowing environments. Above-ground environments are structurally more complex than aquatic or burrowing environments (Gibert and Deharveng 2002, Grosberg *et al.* 2012), and thus, could lead to greater signal distortion and interference (Blumenrath and Dabelsteen 2004).

It has been suggested that the lack of sufficient niche segregation among sympatric species can lead to reproductive interference (Gröning and Hochkirch 2008). Our analyses showed that heterospecific reproductive interactions were more prevalent between species pairs that share similar ecological or reproductive traits. Heterospecific reproductive interactions were significantly more common in species with similar body sizes and that overlapped in their amplexus type and microhabitat use. Intense behavioural interference (including reproductive interference) between species generally leads to niche segregation (Grether *et al.* 2017) through character displacement (Laiolo 2012), niche partitioning (Friberg *et al.* 2013, García-Navas *et al.* 2023), or species exclusion that reduces interspecific competition (Kishi *et al.* 2009, Pastore *et al.* 2021) However, in some conditions, habitat filtering for similar traits might still allow ecologically similar species to coexist even with reproductive interferences (Ruokolainen and Hanski 2016).

Breeding phenology

Many species of frogs breed in large aggregations, often triggered by rainfall and lasting for very short periods (Wells 1977, Ulloa *et al.* 2019). Such explosive breeding strategies result in synchronous emergence of the species, which, consequently, reduces the size disparity among tadpoles, leading to reduced cannibalism in tadpoles and eggs (Petranka and Thomas 1995). However, large-scale emergence of a species in a short period can have cascading effects on the assembly and functioning of a species community (Fouquet *et al.* 2020; Getman-Pickering *et al.* 2023), leading to intense scramble competition for resources (Wells 2007). Such intense competition for mates, along with the inability to recognize conspecifics owing to acoustic interference, can lead to males amplecting heterospecifics (Pearl *et al.* 2005, Wells 2007). Our results also support this hypothesis, in that misdirected amplexus was significantly more common in explosive breeders compared with prolonged breeders. However, we still found that ~30% of the misdirected amplexus were in species that showed prolonged breeding. Such patterns could be because of the simplistic dichotomous definitions of explosive and prolonged breeders. In a more real sense, these two categories represent separate ends of a continuum, and a species population might lie anywhere on the gradient (Wells 2007). Many species have prolonged breeding seasons that are divided into short breeding bouts. For example, in the Costa Rican gliding tree frog, *Agalychnis spurrelli*, the breeding period is spread out across 4–5 months, but each breeding event lasts only 1 or 2 days, with a large number of individuals aggregating around ponds (Güell and Warkentin 2023). Breeding phenology can vary across populations of the same species (Cayuela *et al.* 2016) or vary temporally (Klaus and Lougheed 2013). For instance, in the North American frog *Rana boylii*, northern populations breed explosively, with breeding activity lasting only 1 week (Rombough and Hayes 2007), whereas the southern populations show prolonged breeding activity lasting for 6–7 weeks (Wheeler and Welsh 2008). Further studies on the prevalence of misdirected amplexus across populations varying in breeding phenology might provide a better understanding of the costs associated with these mating strategies. Breeding phenology of anurans also varies with latitude (Jørgensen *et al.* 1986). The tropics provide a more stable climate for breeding conditions to persist year round, whereas the breeding window in temperate zones is be shorter owing to high variability in climate (Janzen 1967, Deutsch *et al.* 2008, Gutiérrez-Pesquera *et al.* 2016, Shah *et al.* 2017). Such constrained breeding activity might lead to more species breeding explosively, resulting in scramble competition (Vitt *et al.* 2009) and a significantly greater prevalence of misdirected amplexus in the temperate zones than in the tropics.

Implications of misdirected amplexus

Studies have shown that reproductive interferences can potentially lead to population decline and community restructuring (Kyogoku and Wheatcroft 2020). Furthermore, climate change could alter anuran breeding strategies (Todd *et al.* 2010, Walpole *et al.* 2012, Klaus and Lougheed 2013, Forti *et al.* 2022) and increase negative heterospecific interactions (Parejo 2016, Canestrelli *et al.* 2017). The presence of invasive species could also lead to negative heterospecific reproductive interactions with native species (D'Amore *et al.* 2009). For instance, in island endemic species, invasive species can cause decreased reproductive success and chronic physiological stress in native species (Narayan *et al.* 2015), leading to population decline. Although we shed some insights into the factors affecting prevalence of misdirected amplexus in anurans, further studies exploring the ecological impacts of such maladaptive behaviours are crucial. Such studies are particularly important given the current amphibian crisis (Geyle *et al.* 2021, Lötters *et al.* 2023, Luedtke *et al.* 2023) and the need for informed conservation strategies (McCoy *et al.* 2021).

CONCLUSION

Misdirected amplexus in anurans amphibians is not a rare phenomenon. Its prevalence is influenced by multiple phylogenetic, ecological, and geographical factors. Although close phylogenetic relatedness influences the prevalence of misdirected amplexus, it can still be observed among distantly related species. Misdirected amplexus is also not random and is more common among frogs with explosive breeding strategies and among species with similar ecological traits. Geographical region also influences the prevalence of misdirected amplexus, with temperate zones showing higher prevalence compared with the tropics. Our study sheds some insights into the factors affecting the prevalence of misdirected amplexus in anurans. However, future studies on how these interactions are maintained within populations will be crucial to understand the ecological consequences of such negative heterospecific interactions.

SUPPLEMENTARY DATA

Supplementary data is available at *Biological Journal of the Linnean Society* online.

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AUTHOR CONTRIBUTIONS

S.S. and V.P.C. conceived the study; S.S., V.A., P.J., and V.P.C. collected the data; V.P.C. performed the analyses and made figures; S.S. and V.P.C. drafted and critically revised the manuscript.

CONFLICT OF INTEREST

None declared.

FUNDING

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DATA AVAILABILITY

Data underlying this study are available online as Supporting Information for this article at the *Biological Journal of the Linnean Society*.

REFERENCES

Beebee TJC, Griffiths RA. The amphibian decline crisis: a watershed for conservation biology? *Biological Conservation* 2005;**125**:271–85.

Bell RC, Webster GN, Whiting MJ. Breeding biology and the evolution of dynamic sexual dichromatism in frogs. *Journal of Evolutionary Biology* 2017;**30**:2104–15. https://doi.org/10.1111/jeb.13170

Blumenrath S, Dabelsteen T. Degradation of great tit (*Parus major*) song before and after foliation: implications for vocal communication in a deciduous forest. *Behaviour* 2004;**141**:935–58. https://doi.org/10.1163/1568539042360152

Boncoraglio G, Saino N. Habitat structure and the evolution of bird song: a meta-analysis of the evidence for the acoustic adaptation hypothesis. *Functional Ecology* 2007;**21**:134–42. https://doi.org/10.1111/j.1365-2435.2006.01207.x

Bossuyt F, Maex M, Treer D *et al.* Chemistry between salamanders: evolution of the SPF courtship pheromone system in Salamandridae. In: Buesching CD, ed. *Chemical Signals in Vertebrates 14*. Cham: Springer International, 2019, 205–20.

Bourne A, Ridley A, Cunningham S. Helpers don't help when it's hot in a cooperatively breeding bird, the southern pied babbler. *Behavioral Ecology* 2023;**34**:562–70.

Brischoux F, Lorrain-Soligon L. Anuran swingers: misdirected mating attempts occurred early during anuran diversification. *Biological Journal of the Linnean Society* 2023;**141**:529–36. https://doi.org/10.1093/biolinnean/blad108

Calabrese GM, Pfennig KS. Females alter their mate preferences depending on hybridization risk. *Biology Letters* 2022;**18**:20220310. https://doi.org/10.1098/rsbl.2022.0310

Canestrelli D, Bisconti R, Chiocchio A *et al.* Climate change promotes hybridisation between deeply divergent species. *PeerJ* 2017;**5**:e3072. https://doi.org/10.7717/peerj.3072

Carey C, Alexander MA. Climate change and amphibian declines: is there a link? *Diversity and Distributions* 2003;**9**:111–21. https://doi.org/10.1046/j.1472-4642.2003.00011.x

Carvajal-Castro JD, López-Aguirre Y, Ospina-L AM *et al.* Much more than a clasp: evolutionary patterns of amplexus diversity in anurans. *Biological Journal of the Linnean Society* 2020;**129**:652–63.

Cayuela H, Arsovski D, Thirion J-M *et al.* Contrasting patterns of environmental fluctuation contribute to divergent life histories among amphibian populations. *Ecology* 2016;**97**:980–91.

Chen C, Byrd CC, Pfennig KS. Male toads change their aggregation behaviour when hybridization is favoured. *Animal Behaviour* 2022;**190**:71–9. https://doi.org/10.1016/j.anbehav.2022.05.014

Chen W, Tang ZH, Fan XG *et al.* Maternal investment increases with altitude in a frog on the Tibetan Plateau. *Journal of Evolutionary Biology* 2013;**26**:2710–5.

Clarke CA, Cronin A, Francke W *et al.* Mating attempts between the scarlet tiger moth, *Callimorpha dominula* L., and the cinnabar moth, *Tyria jacobaeae* L. (Lepidoptera: Arctiidae), involve a common sex pheromone composition. *Experientia* 1996;**52**:636–8. https://doi.org/10.1007/bf01969746

Collins JP. Amphibian decline and extinction: what we know and what we need to learn. *Diseases of Aquatic Organisms* 2010;**92**:93–9. https://doi.org/10.3354/dao02307

Costa-Schmidt LE, Machado G. Reproductive interference between two sibling species of gift-giving spiders. *Animal Behaviour* 2012;**84**:1201–11. https://doi.org/10.1016/j.anbehav.2012.08.026

Cothran RD. The importance of reproductive interference in ecology and evolution: from organisms to communities. *Population Ecology* 2015;**57**:339–41. https://doi.org/10.1007/s10144-015-0488-z

D'Amore A, Kirby E, Hemingway V. Reproductive interference by an invasive species: an evolutionary trap? *Herpetological Conservation and Biology* 2009;**4**:325–30.

de Kort SR, ten Cate C. Response to interspecific vocalizations is affected by degree of phylogenetic relatedness in *Streptopelia* doves. *Animal Behaviour* 2001;**61**:239–47. https://doi.org/10.1006/anbe.2000.1552

Deutsch CA, Tewksbury JJ, Huey RB *et al.* Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences of the United States of America* 2008;**105**:6668–72. https://doi.org/10.1073/pnas.0709472105

Duellman WE, Trueb L. *Biology of Amphibians*. Baltimore: Johns Hopkins University Press, 1994.

Forrest TG. From sender to receiver: propagation and environmental effects on acoustic signals. *American Zoologist* 1994;**34**:644–54. https://doi.org/10.1093/icb/34.6.644

Forti LR, Hepp F, de Souza JM *et al.* Climate drives anuran breeding phenology in a continental perspective as revealed by citizen-collected data. *Diversity and Distributions* 2022;**28**:2094–109. https://doi.org/10.1111/ddi.13610

Fouquet A, Tilly T, Pašukonis A *et al.* Simulated chorus attracts conspecific and heterospecific Amazonian explosive breeding frogs. *Biotropica* 2020;**53**:63–73. https://doi.org/10.1111/btp.12845

Friberg M, Leimar O, Wiklund C. Heterospecific courtship, minority effects and niche separation between cryptic butterfly species. *Journal of Evolutionary Biology* 2013;**26**:971–9. https://doi.org/10.1111/jeb.12106

García-Navas V, Feliu N, Blumstein DT. Changes in the acoustic structure of Australian bird communities along a habitat complexity gradient. *Behavioral Ecology* 2023;**34**:930–40. https://doi.org/10.1093/beheco/arad060

Getman-Pickering ZL, Soltis GJ, Shamash S *et al.* Periodical cicadas disrupt trophic dynamics through community-level shifts in avian foraging. *Science* 2023;**382**:320–4. https://doi.org/10.1126/science.adi7426

Geyle H, Hoskin C, Bower D *et al.* Red hot frogs: identifying the Australian frogs most at risk of extinction. *Pacific Conservation Biology* 2021;**28**:211–23.

Gibert J, Deharveng L. Subterranean ecosystems: a truncated functional biodiversity: this article emphasizes the truncated nature of subterranean biodiversity at both the bottom (no primary producers) and the top (very few strict predators) of food webs and discusses the implications of this truncation both from functional and evolutionary perspectives. *BioScience* 2002;**52**:473–81. https://doi.org/10.1641/0006-3568(2002)052[0473:seatfb]2.0.co;2

Gordon SD, Uetz GW. Environmental interference: impact of acoustic noise on seismic communication and mating success. *Behavioral Ecology* 2012;**23**:707–14. https://doi.org/10.1093/beheco/ars016

Goutte S, Dubois A, Howard SD *et al.* How the environment shapes animal signals: a test of the acoustic adaptation hypothesis in frogs. *Journal of Evolutionary Biology* 2018;**31**:148–58. https://doi.org/10.1111/jeb.13210

Grether GF, Peiman KS, Tobias JA *et al.* Causes and consequences of behavioral interference between species. *Trends in Ecology & Evolution* 2017;**32**:760–72. https://doi.org/10.1016/j.tree.2017.07.004

Gröning J, Hochkirch A. Reproductive interference between animal species. *The Quarterly Review of Biology* 2008;**83**:257–82. https://doi.org/10.1086/590510

Grosberg RK, Vermeij GJ, Wainwright PC. Biodiversity in water and on land. *Current Biology: CB* 2012;**22**:R900–3. https://doi.org/10.1016/j.cub.2012.09.050

Güell BA, Warkentin KM. Phenology and environmental determinants of explosive breeding in gliding treefrogs: diel timing of rainfall matters. *Behavioral Ecology* 2023;**34**:1023–35. https://doi.org/10.1093/beheco/arad072

Gutiérrez-Pesquera LM, Tejedo M, Olalla-Tárraga MA *et al.* Testing the climate variability hypothesis in thermal tolerance limits of tropical and temperate tadpoles. *Journal of Biogeography* 2016;**43**:1166–78.

Hardt B, Benedict L. Can you hear me now? A review of signal transmission and experimental evidence for the acoustic adaptation hypothesis. *Bioacoustics* 2021;**30**:716–42. https://doi.org/10.1080/09524622.2020.1858448

Harshman LG, Zera AJ. The cost of reproduction: the devil in the details. *Trends in Ecology & Evolution* 2007;**22**:80–6. https://doi.org/10.1016/j.tree.2006.10.008

Harzing AW. *Harzing's Publish or Perish*. 2007. https://harzing.com/resources/publish-or-perish (December 2022, date last accessed).

Herrboldt M, Steffen M, McGouran C *et al*. Pheromone gene diversification and the evolution of courtship glands in plethodontid salamanders. *Journal of Molecular Evolution* 2021;**89**:576–87.

Hervé M. RVAideMemoire: testing and plotting procedures for biostatistics. R package version 0.9-83-7, 2023. https://doi.org/10.32614/CRAN.package.RVAideMemoire (December 2022, date last accessed).

Hettyey A, Vagi B, Kovács T *et al*. Reproductive interference between *Rana dalmatina* and *Rana temporaria* affects reproductive success in natural populations. *Oecologia* 2014;**176**:457–64.

Holland J, Dabelsteen T, Pedersen S *et al*. Degradation of wren *Troglodytes troglodytes* song: implications for information transfer and ranging. *Journal of the Acoustical Society of America* 1998;**103**:2154–66.

Houck LD, Watts RA, Mead LM *et al*. A candidate vertebrate pheromone, SPF, increases female receptivity in a salamander. In: Hurst JL, Beynon RJ, Roberts SC *et al*., eds. *Chemical Signals in Vertebrates 11*. New York: Springer, 2008, 213–21.

Huang N, Sun X, Song Y *et al*. Amphibian traits database: a global database on morphological traits of amphibians. *Global Ecology and Biogeography* 2023;**32**:633–41. https://doi.org/10.1111/geb.13656

Iritani R, Noriyuki S. Reproductive interference hampers species coexistence despite conspecific sperm precedence. *Ecology and Evolution* 2021;**11**:1957–69. https://doi.org/10.1002/ece3.7166

Janssenswillen S, Vandebergh W, Treer D *et al*. Origin and diversification of a salamander sex pheromone system. *Molecular Biology and Evolution* 2015;**32**:472–80. https://doi.org/10.1093/molbev/msu316

Janzen DH. Why mountain passes are higher in the tropics. *The American Naturalist* 1967;**101**:233–49. https://doi.org/10.1086/282487

Jørgensen CB, Shakuntala K, Vijayakumar S *et al*. Body size, reproduction and growth in a tropical toad, *Bufo melanostictus*, with a comparison of ovarian cycles in tropical and temperate zone anurans. *Oikos* 1986;**46**:379–89. https://doi.org/10.2307/3565838

Kembel SW, Cowan PD, Helmus MR *et al*. Picante: R tools for integrating phylogenies and ecology. *Bioinformatics (Oxford, England)* 2010;**26**:1463–4. https://doi.org/10.1093/bioinformatics/btq166

Kishi S, Nishida T, Tsubaki Y. Reproductive interference determines persistence and exclusion in species interactions. *The Journal of Animal Ecology* 2009;**78**:1043–9. https://doi.org/10.1111/j.1365-2656.2009.01560.x

Klaus SP, Lougheed SC. Changes in breeding phenology of eastern Ontario frogs over four decades. *Ecology and Evolution* 2013;**3**:835–45. https://doi.org/10.1002/ece3.501

Kyogoku D. Reproductive interference: ecological and evolutionary consequences of interspecific promiscuity. *Population Ecology* 2015;**57**:253–60. https://doi.org/10.1007/s10144-015-0486-1

Kyogoku D, Wheatcroft D. Heterospecific mating interactions as an interface between ecology and evolution. *Journal of Evolutionary Biology* 2020;**33**:1330–44. https://doi.org/10.1111/jeb.13687

Laiolo P. Interspecific interactions drive cultural co-evolution and acoustic convergence in syntopic species. *The Journal of Animal Ecology* 2012;**81**:594–604. https://doi.org/10.1111/j.1365-2656.2011.01946.x

Lötters S, Plewnia A, Catenazzi A *et al*. Ongoing harlequin toad declines suggest the amphibian extinction crisis is still an emergency. *Communications Earth & Environment* 2023;**4**:412.

Luedtke JA, Chanson J, Neam K *et al*. Ongoing declines for the world's amphibians in the face of emerging threats. *Nature* 2023;**622**:308–14. https://doi.org/10.1038/s41586-023-06578-4

Luther D, Gentry K. Sources of background noise and their influence on vertebrate acoustic communication. *Behaviour* 2013;**150**:1045–68. https://doi.org/10.1163/1568539x-00003054

Maisonneuve L, Elias M, Smadi C *et al*. The limits of evolutionary convergence in sympatry: reproductive interference and historical constraints leading to local diversity in warning traits. *The American Naturalist* 2023;**201**:E110–26. https://doi.org/10.1086/723625

Mathevon N, Aubin T. Reaction to conspecific degraded song by the wren *Troglodytes troglodytes*: territorial response and choice of song post. *Behavioural Processes* 1997;**39**:77–84. https://doi.org/10.1016/s0376-6357(96)00046-0

McCoy ED, Delis PR, Mushinsky HR. The importance of determining species sensitivity to environmental change: a tree frog example. *Ecosphere* 2021;**12**:e03526.

McLain DK, Pratt AE. Nestedness of coral reef fish across a set of fringing reefs. *Oikos* 1999;**85**:53–67. https://doi.org/10.2307/3546791

McLain D, Shure D. Pseudocompetition: interspecific displacement of insect species through misdirected courtship. *Oikos* 1987;**49**:291–6.

Moen DS, Wiens JJ. Microhabitat and climatic niche change explain patterns of diversification among frog families. *The American Naturalist* 2017;**190**:29–44. https://doi.org/10.1086/692065

Mollov I, Popgeorgiev G, Naumov B *et al*. Cases of abnormal amplexus in anurans (Amphibia: Anura) from Bulgaria and Greece. *Biharean Biologist* 2010;**4**:121–5.

Narayan EJ, Jessop TS, Hero JM. Invasive cane toad triggers chronic physiological stress and decreased reproductive success in an island endemic. *Functional Ecology* 2015;**29**:1435–44. https://doi.org/10.1111/1365-2435.12446

Nunes-de-Almeida CH, Haddad C, Toledo LF. A revised classification of the amphibian reproductive modes. *Salamandra* 2021;**57**:413–27.

Okuzaki Y, Takami Y, Sota T. Resource partitioning or reproductive isolation: the ecological role of body size differences among closely related species in sympatry. *The Journal of Animal Ecology* 2010;**79**:383–92. https://doi.org/10.1111/j.1365-2656.2009.01645.x

Parejo D. Informational mismatches: a neglected threat of climate change to interspecific interactions. *Frontiers in Ecology and Evolution* 2016;**4**:31. https://doi.org/10.3389/fevo.2016.00031

Pastore AI, Barabás G, Bimler MD *et al*. The evolution of niche overlap and competitive differences. *Nature Ecology and Evolution* 2021;**5**:330–7.

Pearl C, Hayes M, Haycock R *et al*. Observations of interspecific amplexus between western North American ranid frogs and the introduced American bullfrog (*Rana catesbeiana*) and an hypothesis concerning breeding interference. *The American Midland Naturalist* 2005;**154**:126–34.

Petranka JW, Thomas DAG. Explosive breeding reduces egg and tadpole cannibalism in the wood frog, *Rana sylvatica*. *Animal Behaviour* 1995;**50**:731–9.

Portik D, Streicher J, Wiens J. Frog phylogeny: a time-calibrated, species-level tree based on hundreds of loci and 5,242 species. *Molecular Phylogenetics and Evolution* 2023;**188**:107907.

R Core Team. *R: a Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing, 2019. http://www.R-project.org/

Revell L. phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* 2012;**3**:217–23.

Richards DG, Wiley RH. Reverberations and amplitude fluctuations in the propagation of sound in a forest: implications for animal communication. *The American Naturalist* 1980;**115**:381–99. https://doi.org/10.1086/283568

Rollmann SM, Houck LD, Feldhoff RC. Conspecific and heterospecific pheromone effects on female receptivity. *Animal Behaviour* 2003;**66**:857–61. https://doi.org/10.1006/anbe.2003.2290

Rombough CJ, Hayes MP. *Rana boylii* (foothill yellow legged frog) reproduction. *Herpetological Review* 2007;**38**:70–1.

Ruokolainen L, Hanski I. Stable coexistence of ecologically identical species: conspecific aggregation via reproductive interference. *The Journal of Animal Ecology* 2016;**85**:638–47. https://doi.org/10.1111/1365-2656.12490

Ryan MJ, Rand W, Hurd PL *et al*. Generalization in response to mate recognition signals. *The American Naturalist* 2003;**161**:380–94. https://doi.org/10.1086/367588

Saveer AM, Becher PG, Birgersson G *et al*. Mate recognition and reproductive isolation in the sibling species *Spodoptera littoralis* and *Spodoptera litura*. *Frontiers in Ecology and Evolution* 2014;**2**:18. https://doi.org/10.3389/fevo.2014.00018

Schroeder K, Podos J. Early exposure to songs of another subspecies enhances song discrimination in wild sparrow nestlings. *Animal Behaviour* 2023;**203**:123–32.

Serrano FC, Díaz-Ricaurte JC, Martins M. Finding love in a hopeless place: a global database of misdirected amplexus in anurans. *Ecology* 2022;**103**:e3737. https://doi.org/10.1002/ecy.3737

Shah AA, Gill BA, Encalada AC *et al.* Climate variability predicts thermal limits of aquatic insects across elevation and latitude. *Functional Ecology* 2017;**31**:2118–27. https://doi.org/10.1111/1365-2435.12906

Simpson GL. permute: functions for generating restricted permutations of data. Version 0.9-7, 2022. https://doi.org/10.32614/CRAN.package.permute (December 2022, date last accessed).

Sosa-López JR, Martínez Gómez JE, Mennill DJ. Divergence in mating signals correlates with genetic distance and behavioural responses to playback. *Journal of Evolutionary Biology* 2016;**29**:306–18. https://doi.org/10.1111/jeb.12782

Stearns SC. Trade-offs in life-history evolution. *Functional Ecology* 1989;**3**:259–68. https://doi.org/10.2307/2389364

Tarroso P, Velo-Antón G, Carvalho SB. PHYLIN: an R package for phylogeographic interpolation. *Molecular Ecology Resources* 2015;**15**:349–57. https://doi.org/10.1111/1755-0998.12312

Thum RA. Reproductive interference, priority effects and the maintenance of parapatry in *Skistodiaptomus* copepods. *Oikos* 2007;**116**:759–68.

Ting JJ, Cutter AD. Demographic consequences of reproductive interference in multi-species communities. *BMC Ecology* 2018;**18**:46. https://doi.org/10.1186/s12898-018-0201-0

Todd BD, Scott DE, Pechmann JHK *et al.* Climate change correlates with rapid delays and advancements in reproductive timing in an amphibian community. *Proceedings of the Royal Society B: Biological Sciences* 2010;**278**:2191–7. https://doi.org/10.1098/rspb.2010.1768

Ulloa JS, Aubin T, Llusia D *et al.* Explosive breeding in tropical anurans: environmental triggers, community composition and acoustic structure. *BMC Ecology* 2019;**19**:28. https://doi.org/10.1186/s12898-019-0243-y

Verrell PA. Is decreased frequency of mating among conspecifics a cost of sympatry in salamanders? *Evolution* 1994;**48**:921–5. https://doi.org/10.1111/j.1558-5646.1994.tb01373.x

Vitt LJ, Caldwell JP, Zug GR. *Herpetology*. Amsterdam: Elsevier/Academic Press, 2009.

Walpole AA, Bowman J, Tozer DC *et al.* Community-level response to climate change: shifts in anuran calling phenology. *Herpetological Conservation and Biology* 2012;**7**:249–57.

Wehi P, Monks A, Morgan-Richards M. Male tree weta are attracted to cuticular scent cues but do not discriminate according to sex or among two closely related species. *Ethology* 2017;**123**:825–34.

Wells KD. The social behaviour of anuran amphibians. *Animal Behaviour* 1977;**25**:666–93. https://doi.org/10.1016/0003-3472(77)90118-x

Wells KD. *The Ecology & Behavior of Amphibians*. Chicago: The University of Chicago Press, 2007.

Wells KD, Schwartz JJ. The effect of vegetation on the propagation of calls in the neotropical frog *Centrolenella fleischmanni*. *Herpetologica* 1982;**38**:449–55.

Wheeler C, Welsh H. Mating strategy and breeding patterns of the foothill yellow-legged frog (*Rana boylii*). *Herpetological Conservation and Biology* 2008;**3**:128–42.

Willaert B, Bossuyt F, Janssenswillen S *et al.* Frog nuptial pads secrete mating season-specific proteins related to salamander pheromones. *The Journal of Experimental Biology* 2013;**216**:4139–43. https://doi.org/10.1242/jeb.086363

Williams GC. Natural selection, the costs of reproduction, and a refinement of Lack's principle. *The American Naturalist* 1966;**100**:687–90. https://doi.org/10.1086/282461

Wolfenden A, Jones CG, Tatayah V *et al.* Endangered pink pigeons treat calls of the ubiquitous Madagascan turtle dove as conspecific. *Animal Behaviour* 2015;**99**:83–8. https://doi.org/10.1016/j.anbehav.2014.10.023

Wollerman L. Acoustic interference limits call detection in a neotropical frog *Hyla ebraccata*. *Animal Behaviour* 1999;**57**:529–36. https://doi.org/10.1006/anbe.1998.1013

Woodley SK. Pheromonal communication in amphibians. *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology* 2010;**196**:713–27. https://doi.org/10.1007/s00359-010-0540-6

Wootton RJ. Energetics of reproduction. In: Tytler P, Calow P, eds. *Fish Energetics: New Perspectives*. Dordrecht: Springer Netherlands, 1985, 231–54.

Zaffaroni-Caorsi V, Both C, Márquez R *et al.* Effects of anthropogenic noise on anuran amphibians. *Bioacoustics* 2023;**32**:90–120. https://doi.org/10.1080/09524622.2022.2070543