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Breeding biology and the evolution of dynamic sexual dichromatism in frogs

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Abstract

Dynamic sexual dichromatism is a temporary colour change between the sexes and has evolved independently in a wide range of anurans, many of which are explosive breeders wherein males physically compete for access to females. Behavioural studies in a few species indicate that dynamic dichromatism functions as a visual signal in large breeding aggregations; however, the prevalence of this trait and the social and environmental factors underlying its expression are poorly understood. We compiled a database of 178 anurans with dynamic dichromatism that include representatives from 15 families and subfamilies. Dynamic dichromatism is common in two of the three subfamilies of hylid treefrogs. Phylogenetic comparative analyses of 355 hylid species (of which 95 display dynamic dichromatism) reveal high transition rates between dynamic dichromatism, ontogenetic (permanent) dichromatism and monochromatism reflecting the high evolutionary lability of this trait. Correlated evolution in hylids between dynamic dichromatism and forming large breeding aggregations indicates that the evolution of large breeding aggregations precedes the evolution of dynamic dichromatism. Multivariate phylogenetic logistic regression recovers the interaction between biogeographic distribution and forming breeding aggregations as a significant predictor of dynamic dichromatism in hylids. Accounting for macroecological differences between temperate and tropical regions, such as seasonality and the availability of breeding sites, may improve our understanding of ecological contexts in which dynamic dichromatism is likely to arise in tropical lineages and why it is retained in some temperate species and lost in others.

Introduction

Sexual selection is a driving force in the evolution of conspicuous coloration and displays in animals (Darwin, 1871; Andersson, 1994; Andersson & Simmons, 2006). Whereas conspicuous displays or colour may increase the reproductive success of particular individuals, they can also be costly if the signaller is conspicuous to unintended receivers such as predators (Endler, 1980, 1983; Andersson, 1994; Ciccotto & Mendelson, 2016). Thus, animals have evolved numerous strategies to mediate trade-offs between natural and sexual selection with respect to signalling traits. For example, species with conspicuous displays typically delay trait expression until reproductive maturity or when the individual can bear the energetic investment involved in displaying a sexually selected trait (Zahavi, 1975; Booth, 1990). Likewise, some animals may largely conceal signalling traits, such as colour patches, feathers and scales, and selectively expose these traits to intended receivers (Endler, 1992; Vukusic *et al.*, 2002; Whiting *et al.*, 2003; Kemp & Macedonia, 2006; White *et al.*, 2015). Consequently, these brief displays attract the attention of intended receivers while enabling an

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organism to restrict the amount of time they are conspicuous to unintended receivers. When displays involve conspicuous coloration, another solution is dynamic colour change: the ability of an organism to switch a colour signal on and off over short periods of time using neurophysiological or hormonal control.

Cephalopods and chameleons are the banner organisms for dynamic colour change because of their ability to change colour over a time span of seconds to milliseconds (Hanlon *et al.*, 1999; Stuart-Fox & Moussalli, 2008, 2009; Allen *et al.*, 2013), but dynamic colour change is also common in anuran amphibians, fishes and other reptiles where hormonally regulated colour change typically occurs over the course of hours to days (Sumner, 1940; Cooper & Greenberg, 1992; Nilsson Sköld *et al.*, 2012; Kindermann *et al.*, 2013, 2014; Olsson *et al.*, 2013; Tang *et al.*, 2014). In many species with neurophysiologically mediated dynamic colour change, such as chameleons, conspicuous display coloration has evolved for social reasons via sexual selection and dynamic colour change allows animals to respond to a social or predatory cue by adjusting their signal according to a potential receiver's visual system (Stuart-Fox *et al.*, 2007, 2008; Stuart-Fox & Moussalli, 2008). By contrast, dynamic colour change in frogs is slower because it is hormonally mediated (but see Kindermann *et al.*, 2014) and is typically studied in the context of camouflage and thermoregulation (Camargo *et al.*, 1999; Tattersall *et al.*, 2006); however, studies in species with ephemeral colour differences between the sexes (dynamic sexual dichromatism) indicate that dynamic colour change in frogs may also evolve for social purposes via sexual selection (Wells, 1980; Ries *et al.*, 2008; Doucet & Mennill, 2010; Sztatecsny *et al.*, 2010, 2012; Rehberg-Besler *et al.*, 2015; Kindermann & Hero, 2016b).

Acoustic signals are clearly the dominant mode of communication in frogs, yet increasing evidence indicates that visual signals, such as arm waving and foot-flagging displays, play an important role in anuran communication, particularly in noisy environments (Lindquist & Hetherington, 1996; Haddad & Giaretta, 1999; Hödl & Amézquita, 2001; Hartmann *et al.*, 2004, 2005; Hirschmann & Hödl, 2006; Boeckle *et al.*, 2009; Reichert, 2012; Starnberger *et al.*, 2014). Many animals augment the conspicuousness of visual signals by enhancing the contrast between signals and the luminance, colour and/or pattern of signalling backgrounds (Bradbury & Vehrencamp, 1998), and frogs are no exception. For example, in diurnal *Staurois* frogs that engage in foot-flagging displays, foot webbing becomes brighter at sexual maturity and likely increases conspicuousness of territorial displays to potential male rivals (Stangel *et al.*, 2015). Furthermore, behavioural experiments in European treefrogs (*Hyla arborea*), squirrel treefrogs (*Hyla squirella*) and strawberry poison frogs (*Oophaga pumilio*) indicate that females prefer conspicuous males (Taylor *et al.*, 2007; Gomez *et al.*, 2009; Maan & Cummings, 2009), and in polymorphic red-eyed treefrogs (*Agalychnis callidryas*) and strawberry poison frogs, females mate assortatively with respect to colour pattern (Summers *et al.*, 1999; Jacobs *et al.*, 2016). Thus, luminance, colour and/or pattern are likely important components of species recognition and mate choice for many anurans, even in low-light conditions.

Dynamic sexual dichromatism is currently known from several dozen anuran species, but our present understanding of the physiological basis and function of this trait in frogs is limited (Bell & Zamudio, 2012; Rojas, 2016). Several anurans with dynamic dichromatism are explosive breeders in which males physically compete for access to females, such as the Asian bullfrog *Hoplobatrachus tigerinus* (Tabassum *et al.*, 2011) and Fleay's Barred-frog *Mixophyes fleayi* (Stratford *et al.*, 2010), suggesting that this trait functions as a visual signal in large breeding aggregations. Behavioural studies in two explosive breeding species with dynamic dichromatism (Fig. 1), the European moor frog (*Rana arvalis*) and the yellow toad (*Incilius luetkenii*), indicate that temporary divergence in coloration between the sexes prevents costly mistakes in sex recognition when males seek females in aggregations with male-biased operational sex ratios and scramble competition for mates (Doucet & Mennill, 2010; Sztatecsny *et al.*, 2012; Rehberg-Besler *et al.*, 2015). Similarly, in lek-breeding stony creek frogs (*Litoria wilcoxii*), yellow coloration in males during amplexus serves as an intrasexual signal that may diminish sperm competition or displacement by other males (Kindermann & Hero, 2016b). By contrast, male Trinidad poison frogs (*Mannophryne trinitatis*) turn black while calling and this colour change appears to play a role in dominance interactions in these highly territorial frogs (Wells, 1980). Finally, in sexually dichromatic spadefoot toads (*Scaphiopus couchii*), where dichromatism is ontogenetic (fixed), females may use carotenoid-based colour as an honest indicator of male quality in large breeding aggregations where acoustic signals are more difficult to assess (Vásquez & Pfennig, 2007). Thus, sexual dichromatism in frogs, and dynamic dichromatism in particular, may function as intrasexual (male–male competition) and/or intersexual (female choice) signals, particularly in species with explosive or lek-breeding systems.

Here, we update the global review of dynamic sexual dichromatism evolution and frequency in frogs by Bell & Zamudio (2012) and test the hypothesis that species with explosive or lek-breeding systems in the family Hylidae, a diverse and globally distributed radiation, are more likely to exhibit sexual dichromatism. Hylids are an ideal group for investigating trade-offs between natural and sexual selection with respect to signalling traits because they typically lack chemical defences and, like many frogs, rely on camouflage to avoid detection by visually oriented predators (Toledo & Haddad, 2009;

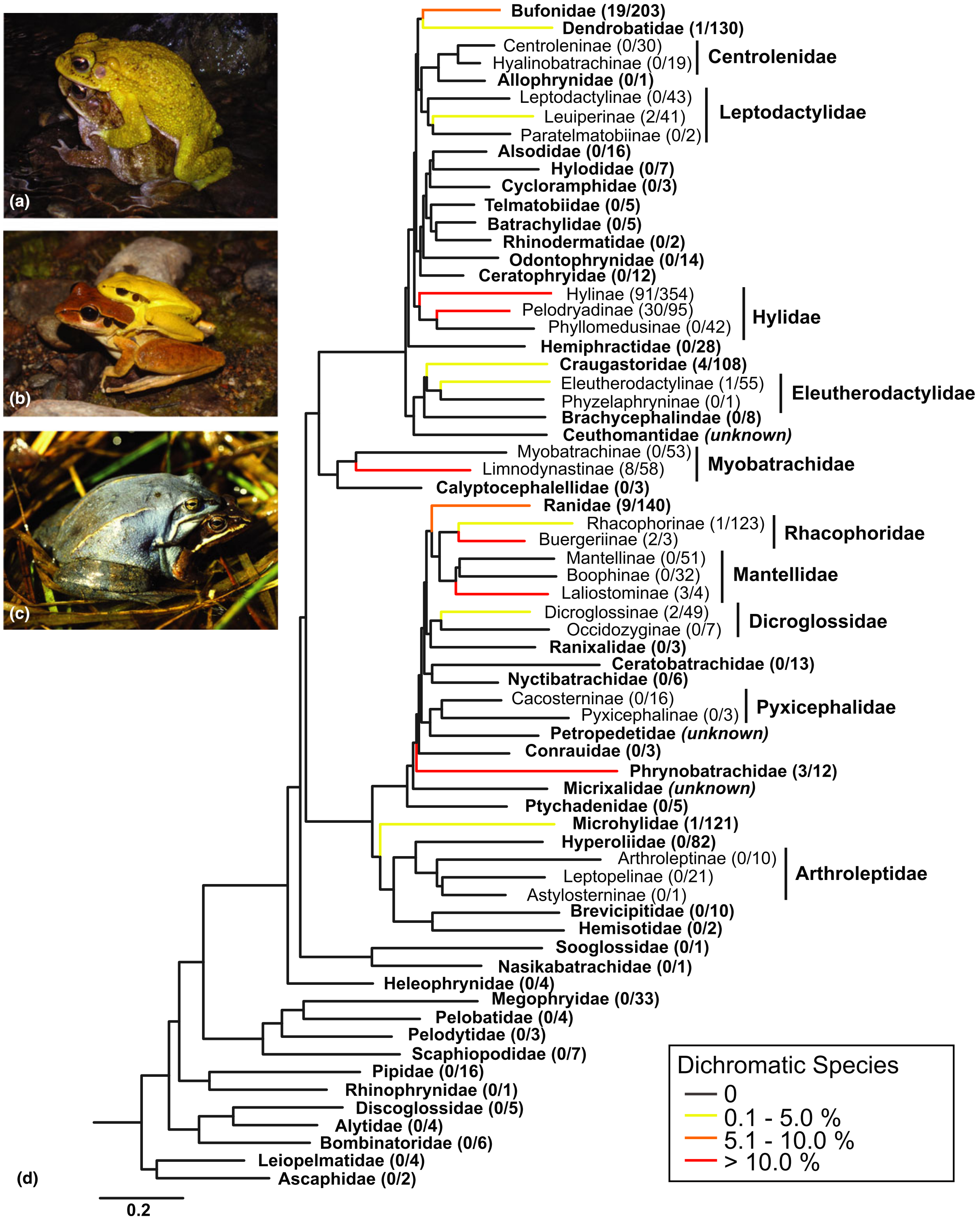

Fig. 1 Representative anurans exhibiting dynamic sexual dichromatism: (a) yellow toad *Incilius luetkenii*, photograph by Javier Sunyer; (b) stony creek frog *Litoria wilcoxii*, photograph by Matt Greenlees; (c) and European moor frog *Rana arvalis*, photograph by Lars Iversen; (d) phylogenetic distribution of dynamic sexual dichromatism. Families are shown in bold and subfamilies in regular print. Branches are coloured according to the percentage of species with dynamic sexual dichromatism. The proportion of dichromatic species over the total number of species evaluated is shown in parentheses for each tip. The phylogeny is modified from Pyron & Wiens (2011).

Wells, 2010; Rojas, 2016). Furthermore, sexual dichromatism is correlated with latitudinal variation in species richness, predation pressure and seasonality in other vertebrates (e.g. birds; Peterson, 1996; Badyaev & Hill, 2003; Friedman *et al.*, 2009; Simpson *et al.*, 2015; Dale *et al.*, 2015); therefore, we also investigated the relationship between dynamic dichromatism and species distribution (temperate or tropical) in hylids to assess whether broad macroecological factors may play a role in the prevalence and evolution of this trait.

Materials and methods

The distribution and diversity of dynamic sexual dichromatism in frogs

To establish the presence of dynamic sexual dichromatism in frogs, we searched the published scientific literature, consulted field guides, online databases (www.amphibiaweb.org and www.iucnredlist.org) and expert knowledge. Due to its ephemeral nature, dynamic sexual dichromatism is rarely reported in the literature; therefore, we established a set of criteria by which to identify dynamic dichromatism using colour photographs of live frogs (Fig. S1). Briefly, we scored species as dichromatic when images of breeding condition males (vocalizing, in amplexus, or engaging in breeding behaviour) showed a distinctly different dorsal coloration than females and nonbreeding males. All photographic evidence was assessed independently by two of the authors (RCB and GNW), and species in which dynamic dichromatism is suspected but unconfirmed were not included in subsequent analyses. Therefore, our scoring system was conservative and likely underestimated the prevalence of dynamic dichromatism. The final database includes 2146 species (of ~6700 described anuran species) for which we assessed the presence/absence of dynamic dichromatism (Table S1). For each species with dynamic sexual dichromatism, we also report the baseline and display colours and associated references (Table S2).

The evolution of sexual dichromatism in the family Hylidae

We gathered data from the literature on whether species form large breeding aggregations (explosive or lek-breeding species, as defined by Wells, 1977), and biogeographic distribution (temperate/tropical) for all hylid species for which we assessed the presence/absence of dynamic dichromatism (Table S3). With some exceptions, the breeding season in many hylid frogs is not as dramatically condensed as that of classic explosive breeders, such as arid-adapted bufonid and scaphiopodid frogs; however, following Wells (1977) we considered species in which individual populations have explosive breeding periods as 'explosive' (even if the breeding season of the species lasts for several months). Likewise, many hylids are lek-breeding species and we included these in the large breeding aggregation category. Species that do not form large breeding aggregations included prolonged breeders and those that breed in bromeliads. Species for which minimal information on physical appearance or general ecology is available were not included in subsequent analyses.

We generated a phylogeny with nucleotide sequence data from GenBank for all hylids for which we had phenotypic data. The resulting data set included two mitochondrial and four nuclear loci for 355 hylid frogs (approximately 37% of the currently recognized species in the family Hylidae; Table S3). We aligned sequences with Clustal X 2.0.10 (Larkin *et al.*, 2007), excluded any ambiguously aligned sites and used PartitionFinder 1.1.10 (Lanfear *et al.*, 2012) to establish the substitution models and partitioning scheme for the analysis (Table S4). We estimated the phylogeny using Bayesian phylogenetic analyses implemented in Beast 1.8.0 (Drummond *et al.*, 2012) with a speciation birth–death incomplete sampling tree prior and a lognormal relaxed clock that was unlinked across all markers. We enforced monophyly for the three subfamilies and 18 strongly supported monophyletic genera/lineages (bootstrap support >95 in Pyron & Wiens, 2011) and obtained posterior distributions from two independent Markov chain Monte Carlo (MCMC) simulations, each run for 350 million generations. We assessed parameter convergence using Tracer 1.5 (Rambaut *et al.*, 2013). The effective sample size (ESS) for each parameter was above 100, and simulations were repeated without sequence data to test the influence of priors on posterior distributions for all parameters. We combined tree files from replicate runs using LogCombiner and discarded the first 150 million trees as burn-in prior to summarizing the posterior distribution of trees using TreeAnnotator and generating a maximum clade credibility (MCC) tree. To account for phylogenetic uncertainty in the subsequent comparative analyses, we randomly selected 100 post-burn-in phylogenies from the posterior distribution and conducted analyses using both the MCC tree and the randomly selected subset of trees.

Both forms of sexual dichromatism (dynamic and ontogenetic) are present in the Hylidae. To reconstruct the evolutionary history of dynamic dichromatism, ontogenetic dichromatism and monochromatism across hylid frogs, we implemented stochastic character mapping (Bollback, 2006) on the MCC tree. This method calculates the conditional likelihood of each character state at each node and then samples the posterior distribution of states to simulate transitions between character states along each branch. Character state transitions are conditioned on a rate matrix and can occur at any point along a branch (i.e. they are not restricted to speciation events). We used the package phytools (Revell, 2012) implemented in R 3.1.1 to summarize the results of 100 simulated reconstructions on the MCC tree comparing the equal-rates, symmetrical-rates and all-rates-different models. We used a likelihood-ratio test to select the 'best' model and then reran the analysis across the set of 100 phylogenies to estimate transition rates between states.

To assess whether the evolution of dynamic dichromatism is correlated with biogeographic distribution or forming large breeding aggregations, we implemented BayesTraits v3, a reversible-jump MCMC method (Pagel & Meade, 2006) that visits dependent and independent models of binary character evolution in proportion to their posterior probability. Using a randomly selected set of 100 phylogenies, we ran MCMC analyses for independent and dependent models of character evolution for dynamic dichromatism (present or absent) with respect to biogeographic distribution (temperate or tropical) and breeding system (presence/absence of large breeding aggregations). Dynamic and ontogenetic dichromatism may have important differences in terms of evolutionary lability and function; thus, we did not include the seven species with ontogenetic (permanent) sexual dichromatism in correlated trait analyses. We were unable to assess the breeding system for one dichromatic and two monochromatic species; therefore, these character states were coded as missing data in analyses. We ran two independent Markov chains of 50 million generations each for independent and dependent models, with and without the covarion model (Tuffley & Steel, 1998), which allows traits to vary their rate of evolution within and between branches. We assessed convergence and verified that ESS values for all parameters were >200 with Tracer 1.5 and compared the relative performance of the different models via Bayes factors (BF). For traits with strong support for the dependent model of character evolution (BF > 5), we discarded the first 5 million generations as burn-in and calculated mean transition rates among character states. Finally, we implemented multivariate phylogenetic logistic regression in the R package phylolm (Paradis & Claude, 2002; Ives & Garland, 2010; Tung Ho & Ane, 2014) to examine the correlation structure among dynamic dichromatism, biogeographic distribution, breeding system and the interaction between biogeographic distribution and breeding system. We used the logistic_MPLE method, which maximizes the penalized likelihood of the logistic regression, ran 10 000 bootstrap replicates on the MCC tree, and used a likelihood-ratio test to select the 'best' model. These analyses did not include the three species for which we were unable to assess the breeding system.

Results

The distribution and diversity of dynamic sexual dichromatism in frogs

Our study considerably extends the previously documented prevalence of dynamic dichromatism (31 species from nine families and subfamilies; Bell & Zamudio, 2012) to include 178 species from 15 families and subfamilies (Fig. 1, Table S2). Of these combined records, 67 are documented in the peer-reviewed literature or are based on the authors' personal observations, whereas the remaining 111 are based on the criteria described in the methods (Table S2). This is still likely an underestimate of this ephemeral trait, and we provide a list of species in which dynamic dichromatism is suspected but unconfirmed to guide future research efforts (Table S2). The vast majority of the new records are from the family Hylidae, which is a predominantly arboreal group of frogs in which dynamic dichromatism appears to be quite common and occurs in both temperate and tropical species (Figs 1 and S2). We also documented high levels of dichromatism in the family Bufonidae, a diverse lineage of chemically defended species that inhabit a variety of habitats, and in the family Ranidae and subfamily Limnodynastinae (Myobatrachidae), which include predominantly stream-dwelling, leaf litter and semi-fossorial species.

Among the 178 anuran species that exhibit dynamic sexual dichromatism, this temporary colour change typically results in yellower coloration (165 species; Table S2). In a few cases, however, male coloration changes to black/darker shades relative to baseline colour (e.g. the dendrobatids *M. trinitatis* and *Rheobates palmatus*, and the ranids *Rana graeca, Rana sylvatica, Rana temporaria* and *Clinotarsus curtipes*), brighter green coloration (e.g. the phrynobatrachid *Phrynobatrachus natalensis*, and the hylids *Hypsiboas rufitelus* and *Itapohyla langsdorffii*) or vibrant blue coloration (e.g. *R. arvalis*). Mutual dynamic colour change occurs in at least one of these 178 species, the bufonid *Xanthophryne tigerinus*, in which both males and females exhibit display coloration that is yellower relative to baseline coloration (Table S2).

The evolution of sexual dichromatism in the family Hylidae

Within the diverse and widespread family Hylidae, dynamic dichromatism is present in two of the three subfamilies and 121 species of the 491 we assessed (Fig. 1; Table S2). Over 25% of species we assessed in the Hylinae and Pelodryadinae subfamilies are sexually dichromatic, and frogs in these subfamilies are found in diverse temperate and tropical habitats throughout the Americas, Europe and Asia (Hylinae), and Australia and Papua New Guinea (Pelodryadinae). By contrast, none of the Phyllomedusinae species are sexually dichromatic. This lineage of arboreal hylids is restricted to the neotropics, and most species have specialized reproductive modes, laying their eggs on leaves overhanging water or in tree hole cavities. Species in all three subfamilies form large breeding aggregations.

To examine transitions in dynamic dichromatism, ontogenetic dichromatism and monochromatism across hylids, we used stochastic trait mapping to reconstruct the timing and placement of changes on the hylid phylogeny. Our final data set of species for the analysis included 355 hylid species (seven with ontogenetic sexual dichromatism, 95 with dynamic sexual dichromatism and 253 sexually monochromatic species). We found the all-rates–different model was the best fit for mapping dichromatism on the hylid phylogeny (log-likelihood for equal-rates, symmetrical-rates and all-rates-different models was −285.884, −249.797 and −233.640, respectively; $\chi^2 = 32.3$, d.f. = 3, $P < 0.005$) and reconstructed monochromatism as the most likely ancestral state (Fig. S3). We found very high transition rates across the phylogeny (average of 205.6 changes between states across 10 000 simulations) demonstrating the high evolutionary lability of this trait. The vast majority of transitions occurred between dynamic dichromatism and monochromatism (Fig. 2), with roughly equivalent shifts from monochromatism to dynamic dichromatism (68.45) and reversals back to monochromatism (89.21). Transitions to ontogenetic dichromatism were less common and occurred more frequently from dynamic dichromatism (22.86) than from monochromatism (0.46), indicating that dynamic dichromatism may serve as an intermediate stage to ontogenetic dichromatism in this family (Fig. 2).

To test for potential selective mechanisms shaping the evolution of dynamic dichromatism in hylid frogs, we applied correlated trait evolution analyses between i) dynamic dichromatism and species distribution (temperate or tropical) and ii) dynamic dichromatism and large breeding aggregations (present/absent). We did not find evidence for concerted evolution between dynamic dichromatism and species distribution (Table 1). Although breeding aggregations in hylids are not typically considered ‘explosive’, more than half of the species in our data set form large breeding aggregations and more than one-third of those species exhibit dynamic dichromatism (Fig. 3). The dependent model diagram of evolutionary rates shows that transitions to dynamic dichromatism are much more likely among species that form large breeding aggregations than those that do not (q24 vs. q13; Fig. 3, Table S5). In addition, dichromatism is retained in a few lineages that do not form large breeding aggregations (q43; Fig. 3). Thus, we see concerted evolution of dynamic dichromatism and breeding biology in hylids with the evolution of large breeding aggregations preceding the evolution of dynamic dichromatism. Finally, in our multivariate phylogenetic logistic regression analyses we found that the interaction between species distribution and breeding aggregation was a significant predictor of dynamic dichromatism in hylids (likelihood-ratio test $\chi^2 = 5.4$, d.f. = 1, $P < 0.05$; Table 2). This result indicates that the association between dynamic dichromatism and breeding aggregation differs between temperate and tropical regions such that breeding aggregation is a strong predictor of dynamic dichromatism in tropical regions and not in temperate regions.

Discussion

Widespread diversity of dynamic sexual dichromatism in anurans

We identified dynamic sexual dichromatism in 178 frog species from 15 families and subfamilies in both temperate and tropical regions. Although this is a substantial increase from the initial review in Bell & Zamudio (2012), we assessed only ~30% of described frog diversity and were conservative in our assessments based on photographs; thus, we expect that the prevalence of

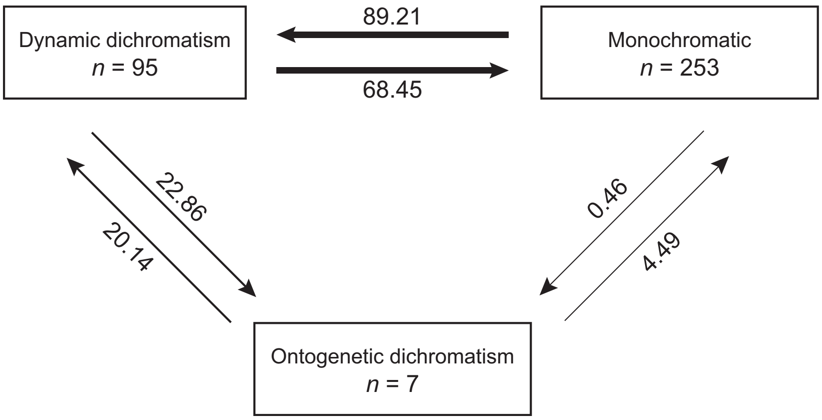

Fig. 2 Estimated transition rates between dynamic dichromatism, ontogenetic dichromatism and monochromatism in the Hylidae based on stochastic character mapping in phytools. The thickness of the arrows is proportional to the mean transition parameter estimate from 10 000 simulations across 100 phylogenies sampled from the posterior distribution of the phylogenetic analysis. Sample sizes included in the analysis are indicated for each character state.

Table 1 Transition rate models and associated marginal likelihood estimates from the stepping stone sampler for BayesTraits analyses. Bayes factors for each model compared to the model with strongest support (based on Bayes factors >5) are shown, with the best model indicated in bold.

	Dichromatism vs. Species distribution		Dichromatism vs. Breeding aggregation	
	Likelihood	Bayes factor	Likelihood	Bayes factor
Independent	−318.71	43.28	−433.87	74.08
Independent cv	**−297.07**	–	−415.91	38.16
Dependent	−321.79	−49.44	−413.79	33.92
Dependent cv	−296.43	1.28	**−396.83**	–

dynamic dichromatism in frogs is much greater than what we report here. The broad phylogenetic distribution of dynamic sexual dichromatism across the anuran tree of life suggests that this trait has evolved multiple times and that the underlying mechanisms and function of dynamic dichromatism may vary among lineages. In contrast to the initial review, our updated assessment of dynamic dichromatism includes at least one species, the Amboli toad *X. tigerinus*, in which both males and females are bright yellow during the breeding season (Biju *et al.*, 2009). Mutual dynamic colour change may also occur in a few other species including the microhylid *Cophixalus saxatilis* (Table S2). Bright coloration in female birds can reflect mutual mate choice (Hanssen *et al.*, 2006) or female territoriality and competition for limited resources (Heinsohn *et al.*, 2005; Murphy *et al.*, 2009). The Amboli toad thus presents an exciting opportunity to investigate whether similar mechanisms underlie mutual dynamic dichromatism in frogs.

Among frogs with dynamic sexual dichromatism, a temporary shift to yellow coloration is by far the most common display colour in both diurnal and nocturnal species (~95% of dichromatic species). The ability to discern colour differences is well documented in several diurnal anurans (Hailman & Jaeger, 1974; Sztatecsny *et al.*, 2012), but the extent of anuran colour discrimination in low-light conditions is unclear. Yellow coloration is typically brighter relative to background environments; therefore, in species that are active in low-light conditions, increased brightness of yellow frogs may serve as an effective achromatic signal. For example, males in the dynamically dichromatic yellow toads (*I. luetkenii*) distinguished between brown and yellow clay frog models in both daytime and night-time trials (Rehberg-Besler *et al.*, 2015), indicating that sexual differences in hue and/or luminance were

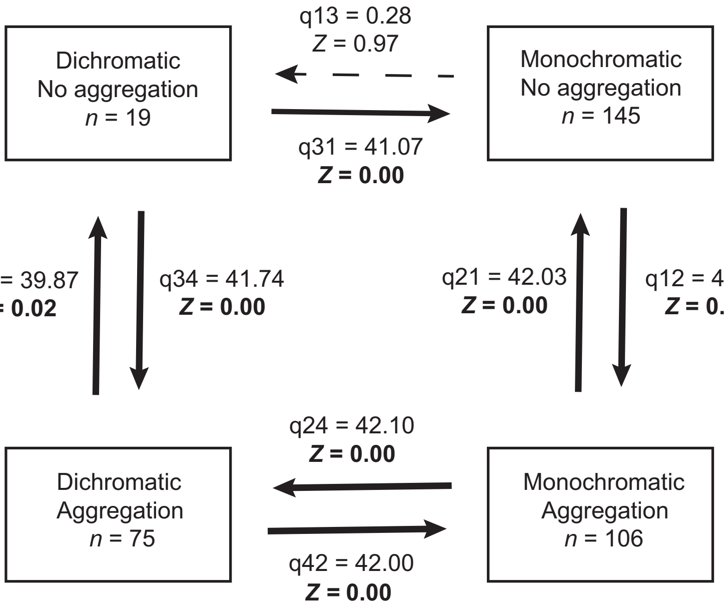

Fig. 3 Transition rates between discrete character states of dynamic dichromatism (present or absent) and large breeding aggregations (present or absent) across 348 species of hylid frogs taken from the posterior distribution of BayesTraits. The thickness of the arrow is proportional to the mean transition parameter estimate (*qij*) from the posterior distribution of BayesTraits, and *Z* indicates the frequency with which each was assigned to zero (*Z*) in the dependent model analysis. Probable transitions ($Z < 0.1$) are bolded, and improbable transitions ($Z \geq 0.20$) are represented by dashed arrows. Sample sizes (the number of species for each combination of traits) are indicated for each character state. We were unable to assess presence/absence of explosive breeding for one dichromatic and two monochromatic species; therefore, the sample sizes for these traits add up to 345 species.

Table 2 Summary of multivariate phylogenetic logistic regression analyses for the effects of large breeding aggregations (0 = absent, 1 = present) and distribution (0 = temperate, 1 = tropical) on dynamic dichromatism (0 = absent, 1 = present). Bolded predictors of dynamic dichromatism correspond to those significant at $P < 0.05$. Alpha is the phylogenetic correlation parameter estimate from phyloglm.

	Pen. Log-Likelihood	AIC	Breeding coefficient	Distribution coefficient	Breeding* Distribution coefficient	Alpha
Dichromatism ~ Breeding	−156.6	324.0	**1.722**	–	–	6.623
Dichromatism ~ Distribution	−192.1	395.2	–	0.641	–	11.489
Dichromatism ~ Breeding + Distribution	−150.7	315.4	**1.843**	0.829	–	3.799
Dichromatism ~ Breeding + Distribution + Breeding*Distribution	−148.0	313.3	0.672	−0.460	**1.353**	3.968

detectable in low-light conditions. The high prevalence of yellow coloration in dynamically dichromatic frogs may also reflect physiological limits as to which temporary colour changes are possible. Frog skin typically contains three pigment cell types: melanophores, which contain melanin; nonreflecting chromatophores, which contain pteridine or carotenoid pigments and are called xanthophores when they bestow yellow coloration and erythrophores when they bestow red coloration; and finally reflecting chromatophores called iridophores, which bestow bright and blue structural coloration (Bagnara, 1976). Histological studies in the dynamically dichromatic stony creek frogs (*L. wilcoxii*; Fig. 1) indicate that temporary changes to yellow coloration are accomplished by aggregating melanin within melanophores to reveal yellow xanthophores (Kindermann & Hero, 2016a), which may be a shared mechanism among frogs for displaying temporary yellow coloration. Thus, several nonmutually exclusive mechanisms may contribute to the high prevalence of yellow coloration in dynamically dichromatic anurans.

Trade-offs between natural and sexual selection with respect to signalling traits may partly explain why dynamic dichromatism is so common in hylid treefrogs. Hylids typically lack chemical defences and, like many frogs, rely on camouflage to avoid detection by visually oriented predators (Toledo & Haddad, 2009; Wells, 2010; Rojas, 2016). Thus, dynamic colour changes may serve as brief displays to attract the attention of intended receivers while enabling male frogs to restrict the amount of time they are conspicuous to unintended receivers. Anurans that are chemically defended, such as the bufonids and dendrobatids, exhibit conspicuous warning coloration year-round, indicating that increased visibility to predators is not costly in these species. Yet, several bufonids exhibit dynamic sexual dichromatism with males reverting to dull, baseline coloration after breeding (Table S1). Thus, the pervasiveness of dynamic dichromatism in both chemically defended and undefended species may reflect more universal benefits to remaining cryptic outside of the breeding season, or that maintaining bright coloration is energetically costly. Alternatively, changes in coloration may be linked to hormone fluctuation such that these colour changes are only possible during the breeding season. Although the role of hormones in mediating dynamic dichromatism in bufonids has not yet been characterized, laboratory experiments in rhacophorid and hylid treefrogs link increases in testosterone (*Buergeria robusta;* Tang *et al.*, 2014) or epinephrine (*L. wilcoxii*; Kindermann *et al.*, 2014) with dynamic yellow colour change. These distinct hormonal mechanisms, which are not necessarily linked with breeding activity in *L. wilcoxii,* may reflect differences in the adaptive (or possibly nonadaptive) role of dynamic colour change in different species.

The evolution of sexual dichromatism in hylid treefrogs

Within hylids, we found that transitions from dynamic dichromatism to ontogenetic dichromatism were much more frequent than those from monochromatism to ontogenetic dichromatism, suggesting that dynamic colour change may act as an evolutionarily intermediate state to ontogenetic colour change in this family. Furthermore, we found that the few hylids with ontogenetic dichromatism occur in tropical regions and do not necessarily form large breeding aggregations. Female choice is often cited as an evolutionary mechanism in sexually dichromatic vertebrates when males are the ‘brighter’ sex (Salthe, 1967; Andersson, 1982; Kodric-Brown & Brown, 1984; Wiens *et al.*, 1999; Cooper & Hosey, 2003; Todd & Davis, 2007; Caro, 2009) and is a more common component of courtship in frogs with prolonged breeding than in those with explosive breeding (Wells, 1977). Therefore, whereas behavioural studies and observations in dynamically dichromatic frogs indicate that temporary sexual colour differences serve as intrasexual signals (Wells, 1980; Sztatecsny *et al.*, 2012; Rehberg-Besler *et al.*, 2015), ontogenetic (permanent) colour differences, which are subject to natural and sexual selection year-round, may be more likely to serve as intersexual signals of mate quality (Vásquez & Pfennig, 2007; Maan & Cummings, 2009). Hylid genera with monochromatic, dynamically dichromatic and ontogenetically dichromatic species (*Scinax, Dendropsophus* and *Hypsiboas*) present an ideal opportunity to address these hypotheses with natural history observations of courtship behaviours (e.g. foot-flagging in *D. parviceps;* Hödl & Amézquita, 2001), mating system dynamics (e.g. male–male antagonistic interactions), controlled behavioural experiments (e.g. female mate choice and male sex recognition) and assessments of predation risk (e.g. clay model attack rates; Kindermann & Hero, 2016b).

Across hylids, we found concerted evolution of dynamic sexual dichromatism and large breeding aggregations, and that the evolution of forming breeding aggregations precedes the evolution of dynamic dichromatism. Behavioural experiments in the yellow toad (family Bufonidae) and European moor frog (family Ranidae) demonstrated that dynamic dichromatism serves to improve sex recognition in large breeding aggregations (Sztatecsny *et al.*, 2012; Rehberg-Besler *et al.*, 2015). Male–male scramble competition for mates and multiple amplexus are common in hylids that form large breeding aggregations; thus, behavioural sex-recognition experiments in hylids may reveal that dynamic dichromatism serves the same function in a third anuran family. The correlated trait analysis, however, also indicates that dynamic dichromatism is retained in hylid lineages that do not form large breeding aggregations. In hylids with prolonged breeding, dynamic dichromatism may serve in territorial or dominance interactions (e.g. *M. trinitatis;* Wells, 1980), as indicators of male quality (e.g. *S. couchii*; Vásquez & Pfennig, 2007), or functions that have not yet been explored in other anurans. For example, in the stony creek frog (*L. wilcoxii*), male dynamic colour change intensifies during amplexus, which may serve as a dominance signal to other males (Kindermann & Hero, 2016b) or alternatively may simply be a by-product of hormones released during amplexus to elicit sperm release (Kindermann *et al.*, 2014). Future studies of hylid mating behaviour, colour change physiology and visual systems will highlight the social environments that drive the evolution of sexual dichromatism in frogs and will contribute to our understanding of the trade-offs between natural and sexual selection with respect to signalling traits in animals.

Although most of the hylid species that exhibit dynamic dichromatism have tropical distributions, we did not find support for concerted evolution of dichromatism with respect to biogeographic distribution across the hylid phylogeny. Dynamic dichromatism is present in both tropical and temperate hylines and pelodryadines and absent in phyllomedusines (which are entirely tropical). Nonetheless, the multivariate phylogenetic logistic regression recovers the interaction between biogeographic distribution and forming breeding aggregations as a significant predictor of dynamic dichromatism in hylids. Specifically, breeding aggregation is a strong predictor of dynamic dichromatism in tropical regions and not in temperate regions. This pattern may be driven by a few predominantly temperate genera in the Hylinae (*Acris, Hyla* and *Pseudacris*), which occur in the Northern Hemisphere, and do not exhibit dynamic dichromatism even though a number of species form large breeding aggregations. Both Southern Hemisphere temperate species in the Hylinae that exhibit dynamic dichromatism belong to predominantly tropical genera, and one (*Scinax catharinae*) is an explosive breeder, whereas the other (*Hypsiboas leptolineatus*) is a pronged breeder in which males are territorial and engage in physical combat (Reinke & Deiques, 2010). By contrast, dynamic sexual dichromatism is common in both temperate and tropical pelodryadines, which occur throughout Australasia and include both explosive and prolonged breeders. Finally, phyllomedusines are an entirely tropical radiation in which many species form large breeding aggregations where visual signals, including colour pattern, are important aspects of intersexual communication (Jacobs *et al.*, 2016); yet, we did not find evidence of dynamic sexual dichromatism in this group. Amplexus and egg deposition in phyllomedusines are terrestrial (both occur on leaves overhanging water or in tree hole cavities; Zamudio *et al.*, 2016); therefore, scramble competition and mistakes in sex recognition may be less common in these species relative to frogs that deposit their eggs in shared aquatic habitats (i.e. ponds and streams). By contrast, most hylines and pelodryadines deposit their eggs in water, potentially creating more opportunities for mistakes in sex recognition or scramble competition to secure access to females when populations form large breeding aggregations (Wells, 1977). These differences in breeding biology and the biogeographic distribution of dynamic dichromatism among hylids indicate that macroecological differences between temperate and tropical regions, such as seasonality and the availability of breeding sites, may improve our understanding of ecological contexts in which dynamic dichromatism is likely to arise in tropical lineages and why it is retained in some temperate species and lost in others.

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Supporting information

Additional Supporting Information may be found online in the supporting information tab for this article:

Figure S1 Sample photographic criteria for assessing the presence of dynamic sexual dichromatism in the Australian hylid *Litoria revelata*.

Figure S2 Maximum clade credibility tree for 355 species of hylid frogs with traits (dynamic dichromatism, species distribution, and large breeding aggregation) indicated on the tips of the phylogeny.

Figure S3 Stochastic character mapping of dynamic dichromatism, ontogenetic dichromatism and monochromatism across 355 species of hylid frogs based on 100 SIMMAP simulations of character states on the MCC phylogeny implemented in phytools.

Table S1 List of anuran species assessed for the presence/absence of dynamic sexual dichromatism.

Table S2 Database of dynamic dichromatism for all families of frogs; male and female baseline colours; male and/or female display colour; evidence documenting dichromatism (D = documented in the literature, P = photographic, O = observed by authors); and associated references.

Table S3 GenBank accession numbers for two mitochondrial and four nuclear loci used to estimate the phylogeny of 355 hylid frogs in this study and trait values (dichromatism, geographic distribution, and breeding aggregation) for comparative analyses.

Table S4 Substitution models and partition schemes for Hylidae phylogenetic reconstruction.

Table S5 Median and upper/lower 95% HPD for correlated dynamic dichromatism and breeding aggregation transition rates from the posterior distribution of BAYES-TRAITS analysis.

Data S1 Full citations for references in Table S2 and references used to assess breeding biology in hylids.

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