*Ichthyology & Herpetology* 113, No. 3, 2025, 517–526

# Dynamic Sexual Dichromatism Promotes Rapid Mate Recognition in an Explosive Breeding Toad

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**Many species reproduce by participating in explosive breeding events, where hundreds of individuals converge at specific locations for a short time period to mate. During these spectacular aggregations, many males must actively search and compete for a limited number of females. One idea is that sexual selection in explosive breeding species favors the evolution of communication strategies facilitating easy detection of males and females. As such, the emergence of dynamic sexual dichromatism, a reversible change of body coloration of one sex, might act as a visual signal promoting rapid mate recognition in dense breeding aggregations. We tested this idea in Asian Common Toads (*Duttaphrynus melanostictus*), an explosive breeder in which males quickly turn from brown to bright yellow for up to two days during mating. Thus, we first explored whether color differences of brown and yellow are sufficient to be perceived and distinguished by toads using a color vision model. In a set of behavioral experiments, we then tested the interactions of male toads with a yellow (resembling a breeding male) and a brown (resembling a female) 3D model toad to determine the functional significance of yellow male coloration during mating. Finally, we compared male body color, morphological parameters, and body condition of mated and non-mated males to investigate if these traits are influenced by securing a mate or female mate choice. Our results show that dynamic yellow coloration displayed by males can be easily discriminated against brown female conspecifics from a toad's point of view. During model experiments, males had twice as much physical contact with brown models and clasped them 40 times more often than yellow models. Coloration and several morphological traits did not differ between mated and non-mated males; hence, securing a mating partner was not influenced by variations in color or morphology. Our study supports the idea that dynamic sexual dichromatism repeatedly evolved as a visual signal mediating fast mate recognition in tropical and temperate anuran species solving a common problem in time-limited, dense breeding aggregations, by minimizing same-sex harassment and mismatch.**

IN scramble-competition mating systems, hundreds of individuals aggregate to breed during confined and ecologically preferable time windows. In these mating systems, mating partners are not exclusive, and therefore individuals compete for limited mating opportunities. Moreover, mating success primarily depends on the ability of males to rapidly and efficiently locate receptive females (Emlen and Oring, 1977; Thornhill and Alcock, 1983; Herberstein et al., 2017). Similarly, anuran amphibians (frogs and toads) form explosive breeding aggregations where sexually receptive individuals almost synchronously arrive at the breeding site and males competitively search and scramble for females during an extremely short spawning period (Wells, 2007; Vojar et al., 2015). Environments for explosive breeding can become even more intense when multiple species gather at the same time and place (Gottsberger and Gruber, 2004; Ulloa et al., 2019), potentially leading to acoustic-signal overlap of calling males, along with both biotic and abiotic background noise (e.g., rain), which confounds species and sex recognition (Gerhardt and Klump, 1988; Gerhardt and Bee, 2006). To avoid mismatch between conspecifics, one would expect that selection strongly favors behavioral strategies that facilitate rapid mate recognition and efficient mate acquisition. Yet, surprisingly few studies have explored these strategies, particularly in field settings during the height of activity in an explosive breeding event (but see Marco and Lizana, 2002; Sztatecsny et al., 2012; Yu and Sharma, 2012; Rehberg-Besler et al., 2015).

Many explosive breeders have evolved behavioral or communicative strategies to mediate sexual interactions (Wells, 2007; Yu and Sharma, 2012; Bell et al., 2017; Dittrich and Rödel, 2023). One approach to do this is through dynamic color change, which occurs when individuals rapidly (and reversibly) change their body color to communicate with conspecifics. Examples of rapid, dynamic color change can be found across the animal kingdom (Mäthger et al., 2009; Sköld et al., 2013; Ligon and McGraw, 2018), but relatively fewer species undergo dynamic sexual dichromatism, a color change of only one sex (Bell and Zamudio, 2012). Most anurans (frogs and toads) that fall into this latter category are in fact explosive breeders (Bell et al., 2017); however,

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Submitted: 18 November 2024. Accepted: 5 May 2025. Associate Editor: C. Bevier.

DOI: 10.1643/h2024105

very few studies explore how this mode of communication functions during such events. One of these studies looks at Moor Frogs, *Rana arvalis*, where males turn blue during their short reproductive season that lasts ≈1 week (Brehm, 1893). The color signal is thought to provide instant mate recognition and improve mating opportunities, but it does not appear to be related to common indices of body condition or other morphological traits (Sztatecsny et al., 2012), with the exception that mating success was positively related with blueness in small males (Hettyey et al., 2009). Another study in Neotropical Yellow Toads, *Incilius luetkenii*, shows that males turn bright yellow during breeding and suggests that bright coloration facilitates fast recognition of the opposite sex. The Neotropical Yellow Toads' color change fades when males amplex a female (Rehberg-Besler et al., 2015), and this might coincide with sperm release and egg-laying (Doucet and Mennill, 2009). Hence, it is possible that nuptial coloration is important while mate finding and may also be related to between-sex communication (Doucet and Mennill, 2009; Rehberg-Besler et al., 2015; Gardner et al., 2024). While this latter idea is intriguing, there is currently only very limited evidence that parameters of yellow coloration relate to male body condition (Hettyey et al., 2009; Shangi et al., 2022), and Gardner et al. (2021) found no evidence that females choose males based on body coloration (Gardner et al., 2021). Rather, in male-biased explosive breeding events, we see more often that females are chased and clasped immediately after their arrival, with some females dying in mating balls (Wells, 2007). Further studies are therefore needed to examine dynamic sexual dichromatism in field settings to better determine its functional significance in relation to both male–male and potential male–female interactions.

Here, we hypothesize that dynamic sexual dichromatism increases mating opportunities by facilitating rapid visual recognition of putative sexual partners. As such, this mechanism of visual signaling may have repeatedly evolved to mediate communication in explosive breeders because it represents an optimal signaling strategy to meet the environmental challenges posed by explosive breeding. Consistent with this view is work showing that dynamic sexual dichromatism is not likely an ancestral state in hylids, where this form of signaling is most common (Bell et al., 2017). As a step toward investigating this idea, we test our hypothesis by exploring the functional significance of dynamic sexual dichromatism in the Asian Common Toad, *Duttaphrynus melanostictus*, under natural conditions in Karnataka, India. The species is distributed throughout South and Southeast Asia, but observations of dynamic color changing populations are restricted to the Indian subcontinent, and they all form explosive mating aggregations (Fig. 1). Moreover, males in these populations change body coloration from an inconspicuous brown (that is like a female) to bright yellow during a brief two-day stint at the onset of the monsoon season (S. Stückler, K. V. Gururaja, G. Hegde, T. Wampula, and D. Preininger, pers. obs.). Our past work shows that stress hormones (catecholamines) mediate the production of bright yellow colorations in the Asian Common Toad (Stückler et al., 2022a); however, the functional significance of dynamic sexual dichromatism in males is still unknown.

To investigate if dynamic sexual dichromatism increases mating opportunities by facilitating rapid recognition of mating partners, we first explored whether color differences and similarities are sufficient to be easily perceived and distinguished by the toads. In a second step, we set up a model experiment, testing the behavioral response of male toads to different body colorations (a brown female and a yellow male) of realistic model toads. Considering the highly competitive breeding environment in Asian Common Toads, and the fact that females are amplected shortly after arriving at the breeding site, we predict that females have few options for choosing mates. Consequently, we expect that male colorations will not be associated with indices of traits that females might otherwise use to select a mating partner. Of course, we recognize that colorations may also provide cues to other males, and thus support forms of intrasexual signaling. To begin testing these ideas, we measured and compared coloration, morphology, and body condition between mated (in amplexus with a female) and non-mated males during an explosive breeding event. In support of the hypothesis that conspicuous male coloration facilitates instantaneous mate recognition, we expect to find no color variation between mated and non-mated males but differences in male response to the models.

## MATERIALS AND METHODS

***Study species and study site.***—The Asian Common Toad, *Duttaphrynus melanostictus*, inhabits moist places and breeds in stagnant water pools in South- and Southeast Asia (Ngo and Ngo, 2013). Maximum reproductive activity and development of oocytes in females coincides with the arrival of heavy rains and thereby differs throughout the Asian continent (Jørgensen et al., 1986). While toads exhibit dynamic sexual dichromatism (Fig. 1) and gather in explosive breeding events in most populations across the Indian subcontinent (e.g., Western Ghats), they breed throughout the year in other parts of Southeast Asia (Thailand, Java) with so far no evidence of sexual dynamic color change (Church, 1960; Jørgensen et al., 1986; Köhler et al., 2022).

We investigated dynamic color change during explosive breeding from 11–12 June 2023 (day 1 and 2) in a dry riverbed with rainwater-filled puddles, formed by heavy monsoon rains in the previous night, in Uttara Kannada, Karnataka, India (see supplementary material; see Data Accessibility). The breeding location consisted of three large, partly connected puddles of different sizes and water depths. The riverbed adjoined a 3–4 m high laterite wall on one side and a betel nut (*Areca catechu*) plantation on the other. Yellow males and brown females migrated from both sides to the breeding event.

***Visual model and color discrimination.***—First, we quantified whether conspecific males and females could detect spectral differences in body coloration among mated males (in amplexus), non-mated males (not in amplexus), and females (all in amplexus with a male) with a color vision model calculating the discriminability between different body colorations (using the R package PAVO; Maia et al., 2019). For this we randomly collected mated males ($n = 27$), non-mated males ($n = 27$), and females ($n = 27$) with a net from the breeding aggregation and immediately measured body coloration of flank, head, and vocal sac/throat with a

**Fig. 1.** Brown female and yellow male Asian Common Toad (*Duttaphrynus melanostictus*) in amplexus in their natural habitat in Karnataka, India.

spectrometer (JAZ series; Ocean Optics, Dunedin, USA) according a standardized protocol (Stückler et al., 2022a, 2022b, 2023). Spectral sensitivities are not available for the Asian Common Toad; therefore, we modeled the visual system of the toads using spectral sensitivities of Common Toads, *Bufo bufo* (function 'vismodel'; Yovanovich et al., 2017, 2019). We used standard daylight as the lighting condition ('D65'; Siddiqi et al., 2004; Green et al., 2019; Chaves-Acuña et al., 2020) and the longest photoreceptor (LWS cone) for achromatic vision (Siddiqi et al., 2004; Gödert et al., 2021).

We used a receptor-noise model calculating color differences (just-noticeable-differences, JNDs) with the function 'coldist' (Siddiqi et al., 2004; Chaves-Acuña et al., 2020), and calculated chromatic ($\mathrm{JND}_{(\mathrm{dS})}$) and achromatic ($\mathrm{JND}_{(\mathrm{dL})}$) contrasts comparing means of mated males against non-mated males and females. The threshold for discriminating between two colors is 1. Mean contrast values below 1 are indistinguishable, while JND values ranging from 1 to 3 signify poor detectability. Values above 3 indicate detectable contrasts (Vorobyev et al., 2001; Siddiqi et al., 2004; Igic et al., 2012; Chaves-Acuña et al., 2020). We set the photoreceptor proportion equally for the chromatic and achromatic calculations (Robertson et al., 2022) and the Weber fraction to 0.05 (Siddiqi et al., 2004).

***Model experiment.***—To experimentally test how male yellow coloration influences mate recognition, we used 3D model toads to observe live male responses to differing body colors in a natural explosive breeding aggregation. We created realistic toad models by casting a preserved Asian Common Toad from a specimen of the collection of the Natural History Museum Vienna. The cast was filled with polyurethane resin. The resulting object was scanned, adjusted to the size of an average male (5.5 cm SVL), and seven models were printed (3Dee GmbH & Co KG, Vienna; Fig. 2). We painted each model with non-toxic, water-based acrylic color paint (Daler-Rowney Ltd., Bracknell, United Kingdom). As reference we used spectral reflectance of yellow male and brown female coloration of the population kept in the Vienna Zoo (Stückler et al., 2022a; Stückler et al., unpubl. data; Fig. 2).

*Sensu* Sztatecsny et al. (2012), we presented a brown model resembling a female and a yellow model mimicking a breeding competitor to a group of male Asian Common Toads at the explosive breeding aggregation. The models were attached 70 cm apart from each other with a thin fishing line on the crossbar of a T-shaped wooden stick. The stick was 1.2 m long, allowing a distance of 1.5 m between experimenter and models as well as live toads. The experimenter lowered the models into the water and stood motionless for 2 min, so that the toads could recover from

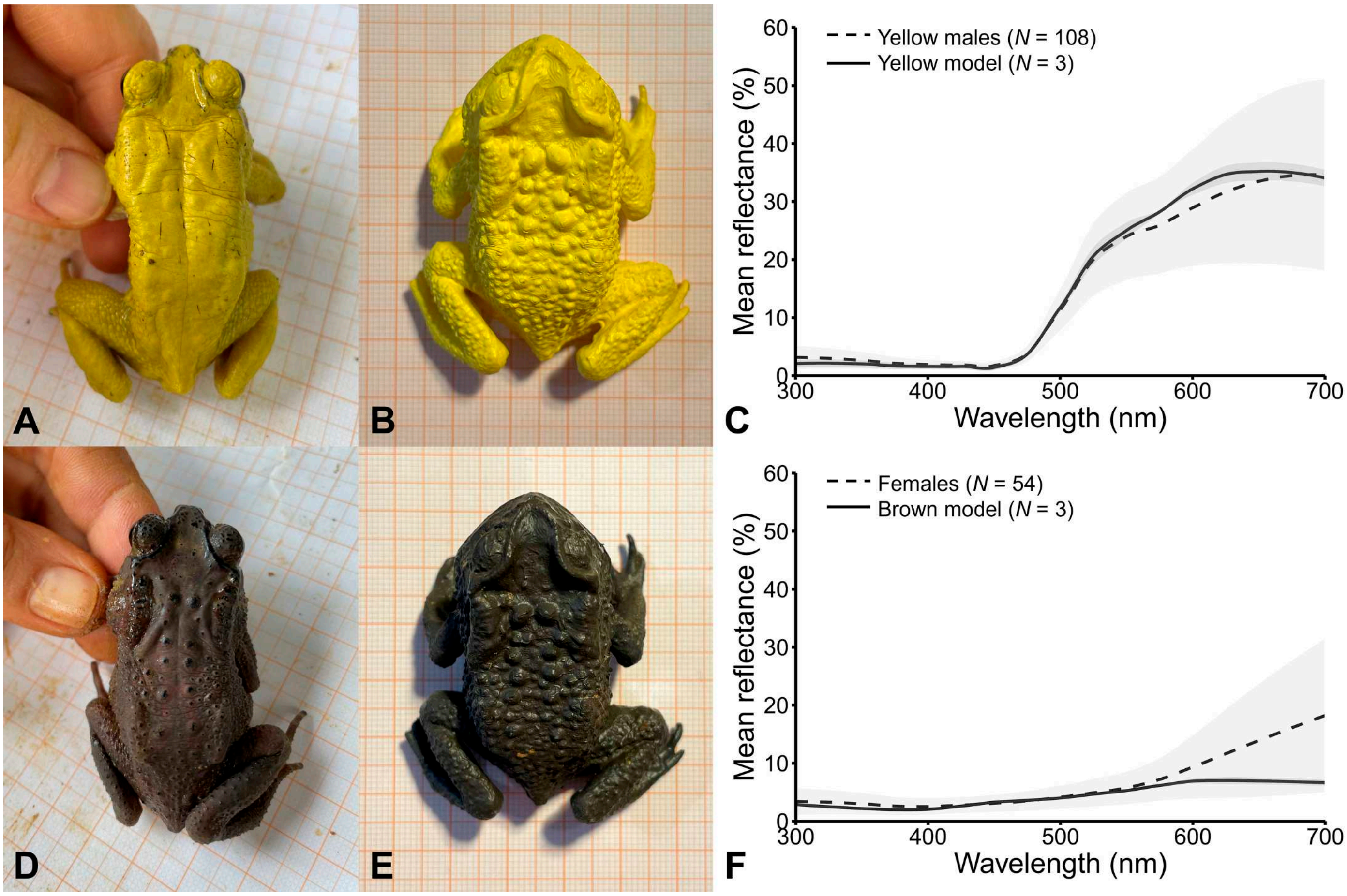

**Fig. 2.** Comparison of live and model Asian Common Toads (*Duttaphrynus melanostictus*): (A) a yellow male, (B) a yellow 3D model resembling a breeding male, (C) related reflectance measurements, (D) a female toad, (E) a brown 3D model resembling a female, (F) related reflectance measurements. The 3D model toads have an SVL of 5.5 cm.

human disturbance and resume natural behavior (habituation period). Then the experimenter moved the T-shaped stick with the model toads slightly up and down for 5 min to simulate activity (testing period). We video recorded each trial with a digital camera (Panasonic SDR-SW 21) on a tripod. We recorded 20 trials (= one male per video) on day 1 of the explosive breeding event during daylight. After each trial ended, we set up the next experiment 5 m away to avoid repeated testing of the same individuals. The videos were analyzed with the open-source video editor program Shotcut (version 17.10.02). Two blind observers recorded the number of active physical contact between male frogs with either the yellow or the brown model (i.e., pushing with snout and/or fore limbs) and the number and time(s) a male frog attempted to clasp (amplex) a model.

***Color and morphological measurements.***—To investigate the relationship of coloration and male body condition, we compared body coloration of flank, head, and vocal sac of mated ($n = 27$) and non-mated males ($n = 27$). Following color measurements, we obtained length and width of nuptial pad, forearm width and length, upper arm width and length, chest width, snout–vent length (SVL), snout–urostyle length (SUL), and weight of the same males. To calculate male body condition, we used the scaled mass index (SMI) derived from SVL and mass of males with a standard coefficient (Peig and Green, 2009; Liao, 2018; Landler et al., 2023). We calculated condition as SMI = m * $(L_0/L)^b$, in which m is the mass of the individual, $L_0$ the mean of SVL, and L the SVL of the individual. The coefficient b is calculated using a linear regression of the natural logarithm of body mass (as dependent variable) and the natural logarithm of SVL (as independent variable), following Landler et al. (2023). The coefficient (slope of the standard major axis) for our study population was 3.5079.

We analyzed the reflectance spectra in RStudio with the package PAVO (Maia et al., 2019). With the function ‘procspec,’ we applied LOESS smoothing of the reflectance spectra (opt = “smooth,” span = 0.35), and set all negative values to zero (fixneg = “zero”; Malpica et al., 2022; Webster et al., 2023). We analyzed brightness (mean brightness, calculated as the average reflectance over the range of 300–700 nm), hue (wavelength of maximum reflectance), and yellow chroma (calculated as the proportion of total reflectance in the 550–625 nm range), the essential attributes to describe and compare male breeding colorations (Delhey et al., 2003; Stückler et al., 2022a; supplementary information; see Data Accessibility). Spectral analyses were performed in RStudio with the package PAVO, function ‘procspec’ and ‘summary.rspec’ (mean brightness: “B2”; hue: “H1”; yellow chroma: “S1Y”).

***Statistical analysis.***—Upon substantial interrater reliability agreement for video analysis (Kappa = 0.706, $P < 0.001$;

Landis and Koch, 1977), we analyzed the number of physical contacts and amplexus attempts per video (5 min experimental period) using Wilcoxon signed rank tests.

To compare color measurements (flank, head, and vocal sac), morphology (length and width of nuptial pad, forearm width and length, upper arm width and length, chest width, SVL, and SUL), and SMI between mated and non-mated males, we first tested all parameters for homogeneity by using Levene's test and Shapiro-Wilk normality test to test for normal distribution. If the parameters were normally distributed, we used a two-sample t-test; otherwise, we used a Wilcoxon rank sum test. With Spearman correlations, we then compared color parameters of flank, head, and vocal sac with SMI to understand if male coloration provides a cue to male quality, regardless of whether they were in amplexus or not.

***Ethical statement and permits.***—All experiments reported in this article complied with the current laws of the country in which they were performed (India). The study was approved by the National Biodiversity Authority India (IN-KA97252580684335P). We followed the guidelines of the Association for the Study of Animal Behavior for animals in research (ASAB, 2024). Toads were handled carefully, and handling time was kept to a minimum (less than 5 min for color and morphological measurements). We did not collect any individual.

## RESULTS

***Description of the explosive breeding event.***—During five days and nights prior to the explosive breeding event, we observed four male Asian Common Toads that displayed partial to full yellow color change close to the eventual explosive breeding site. On these days, it rained on and off for periods of 10–30 min several times per day and night, with heavy continuous rainfall starting in the evening of 9 June 2023. The explosive breeding event lasted two days (≈30 hours), and activity started on the morning of 11 June 2023 (day 1) after heavy rainfall in the previous 36 hours, followed by a drop in temperature from 28°C to 24°C and an increase in relative humidity from 67% to 71% (compared to the mean temperature and mean relative humidity of the week before, Fig. 3). Mean temperature on day 1 was 24.2°C, and mean relative humidity was 70.8%. On day 2, mean temperature was 26.2°C and relative humidity was 70.9%. Sound pressure level of male chorus at the breeding site averaged 83.4 dBC (SE = 0.4, $n = 3$, distance 1 m; day 1, 1400 h). First spawn was observed around 1600 h of day 1. The operational sex ratio (OSR), counted in four randomly selected 1 $m^2$ plots, was 3.3:1 (males:females) on day 1. During the night, we observed less activity. The following morning, the breeding event continued with an OSR of 3.3:1, counting a total of 235 males and 71 females (all females were in amplexus with a male, leaving 164 single males). Thereafter, activity and individual number steadily decreased and ended in the early afternoon of day 2.

***Color vision model.***—We compared estimates of discriminability expressed as just-noticeable-differences (JNDs) between mated and non-mated males, looking specifically at the flanks, head, and vocal sac. Our results showed indistinguishable contrast for sufficient discrimination in both chromatic and achromatic conditions (flank: dS = 0.3, dL = 1.1; head: dS = 0.8, dL = 1.8; vocal sac: dS = 1.6, dL = 0.3). However, we found that contrast of yellow mated and non-mated males to brown colored females was much higher and clearly detectable (mated males: flank: dS = 21.3, dL = 26.1; head: dS = 17.4, dL = 22.6; vocal sac: dS = 7.4; dL = 2.9; non-mated males: flank: dS = 21.6, dL = 25; head: dS = 17.9, dL = 20.8; vocal sac: dS = 9.1, dL = 3.2) in chromatic and achromatic conditions.

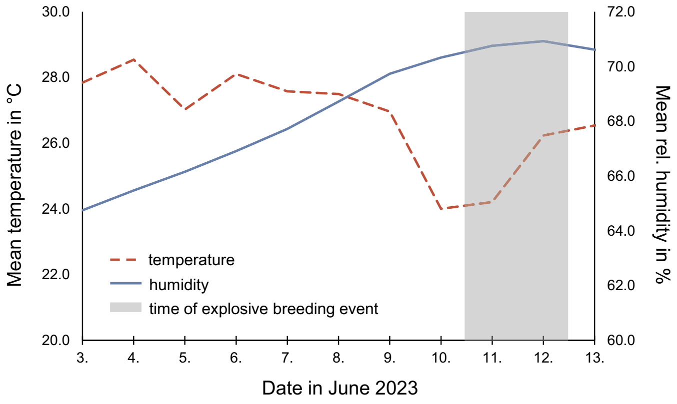

**Fig. 3.** Mean temperature (in °C, dashed red line) and mean relative humidity (in %, solid blue line) at our study site in Bare, India. The period of explosive breeding event of Asian Common Toads (*Duttaphrynus melanostictus*) is indicated in gray.

***Model experiment.***—Next, we tested the hypothesis that males use their bright yellow coloration to distinguish themselves from females during explosive breeding events. In support of this hypothesis, we found that male Asian Common Toads initiated significantly more physical contact (Wilcoxon signed-rank test; physical contact: z = –2.277, $n = 20$, $P < 0.05$) and amplexus attempts (Wilcoxon signed-rank test; amplexus: z = –4.514, $n = 20$, $P < 0.001$) with toad models that were brown, as opposed to toad models that were yellow (Fig. 4). Indeed, males made physical contact with brown models 133 times ($n = 20$ videos, mean/trial = 6.65), and they contacted yellow models 61 times ($n = 20$ videos, mean/trial = 3.05). Males attempted amplexus 86 times with brown models ($n = 20$, mean/trial = 4.3), whereas they attempted amplexus only 2 times with yellow models ($n = 20$, mean/trial = 0.1). In the total test period of 100 min, live males spent 225 seconds (3.75 min) in amplexus with brown models and only 5 seconds with yellow models.

***Comparison of mated and non-mated male traits.***—Finally, we tested whether mated and non-mated male toads showed any differences in brightness, hue, and yellow chroma of the flank, head, and vocal sac (Wilcoxon rank sum test, $P > 0.05$, $n = 27$/group, Fig. 5). We found no strong evidence of a relationship among any of these variables (Table 1); however, we did note a trend toward significance when it came to a positive association between yellow flank brightness and mated males.

Furthermore, we looked to see whether any of these color variables were linked to the length and width of nuptial pads, forearm width and length, upper arm width and length, and chest width. Yet, there was no evidence of any relationship (two-sample t-test, $P > 0.05$, $n = 27$/group, Table 1). We also found no relationship between brightness,

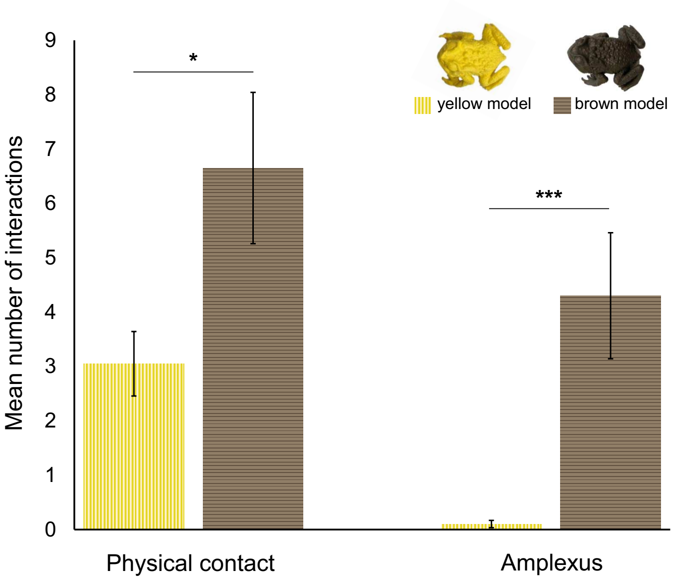

**Fig. 4.** Mean number of interactions (active physical contact or amplexus) of male Asian Common Toads (*Duttaphrynus melanostictus*) with a yellow model toad (resembling a male competitor) and a brown model toad (resembling a female) during an explosive breeding event in their natural habitat ($n$ = 20). Bars indicate standard error (SE) and asterisks significant differences of Wilcoxon signed-rank test: * $P < 0.05$; *** $P < 0.001$.

hue, and yellow chroma and SVL, SUL, weight, and body condition (SMI; Wilcoxon rank sum exact test: $P > 0.05$, $n$ = 27/group, Table 1). To this end, body condition of mated and non-mated male individuals did not explain yellow color parameters (brightness, hue, yellow chroma) of flank, head, and vocal sac (Spearman correlation, $P > 0.05$, $n$ = 54), regardless of whether they were in the amplexus or not. Consequently, males with higher SMI were not yellower or brighter or mating.

## DISCUSSION

Some populations of Asian Common Toads breed in highly competitive, explosive aggregations, where >200 males actively search for females. Our results show that the dynamic yellow coloration displayed by males during these mating events can be easily discriminated against brown female conspecifics. Males attempted to mate more often with brown model toads resembling females than with yellow models imitating males. Accordingly, we suggest that dynamic sexual dichromatism in the Asian Common Toad has evolved as a visual signal that mediates swift mate recognition in time-limited, dense breeding groups. Selection strongly favors the evolution of sensory and cognitive systems that help animals to find or secure a mate (Searcy and Nowicki, 2005), especially when mating is highly time constrained due to brief periods of favorable environmental conditions for mating and offspring survival (Sullivan, 1994). This is certainly the case for Asian Common Toads, which must quickly gather and breed immediately after the heavy rains at the onset of the summer monsoon, a period that is eventually followed by a prolonged dry period unfavorable for tadpole survival. A drastic color change therefore presumably facilitates rapid decision-making in the frenzy of explosive breeding.

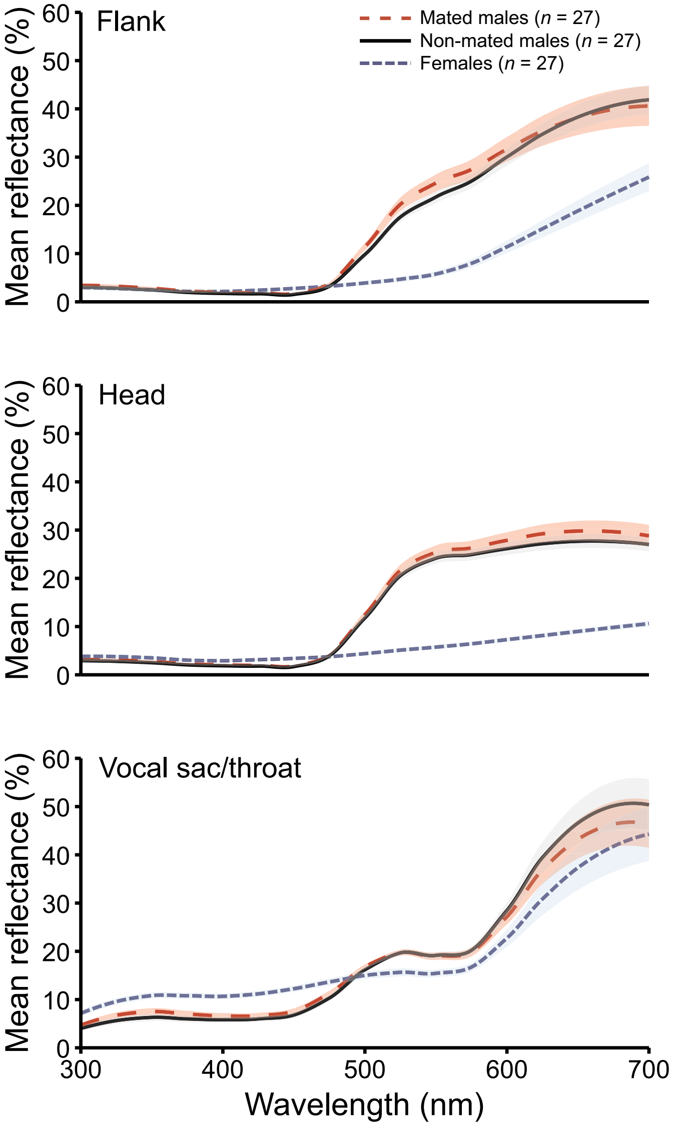

**Fig. 5.** Mean spectral reflectance (± SE) of flank, head, and vocal sac/throat of Asian Common Toads (*Duttaphrynus melanostictus*) mated males (loosely dashed red, $n$ = 27), non-mated males (solid black, $n$ = 27), and females (densely dashed blue, $n$ = 27) during explosive breeding in their natural habitat.

Our results are consistent with previous findings in two unrelated species, the Moor Frog (Sztatecsny et al., 2012) and the Neotropical Yellow Toad (Rehberg-Besler et al., 2015), demonstrating that dynamic sexual dichromatism acts as a visual signal to enable quick mate recognition in a way that likely reduces costly male–male mismatches. We hypothesize that this dynamic visual signal strategy is a repeatedly evolved solution to reduce same-sex harassment and quicker mate recognition in the context of explosive breeding for anuran amphibians, including both temperate and tropical species. Displaying conspicuous yellow or blue male coloration only transiently, and reversing them to a dull brown appearance after the explosive breeding event instead of permanent dichromatism, likely allows males to stay hidden from predators aside from the mating period. Hence, dynamic sexual dichromatism potentially serves

**Table 1.** Comparison of color measurements, morphological measurements, and body condition (SMI) of mated ($n = 27$) and non-mated males ($n = 27$), providing means and standard errors.

| Parameters | Mated males | Non-mated males | Z | P |
|---|---|---|---|---|
| Flank | | | | |
| Brightness | 14.79±0.86 | 13.86±0.61 | −1.8 | 0.07 |
| Chroma (in %) | 34.7±0.5 | 34.9±0.4 | −0.4 | 0.6 |
| Hue (nm) | 644±8.9 | 643±9.9 | −0.22 | 0.82 |
| Head | | | | |
| Brightness | 16.79±1.28 | 16.00±0.90 | −0.18 | 0.86 |
| Chroma (in %) | 33.3±0.5 | 32.8±0.4 | −1.06 | 0.29 |
| Hue (nm) | 681±6.1 | 691±2.5 | −0.59 | 0.55 |
| Vocal sac | | | | |
| Brightness | 19.28±1.11 | 19.66±1.20 | −0.44 | 0.66 |
| Chroma (in %) | 24.7±0.7 | 25.5±0.7 | −0.46 | 0.65 |
| Hue (nm) | 682±3.8 | 675± 7.1 | −0.44 | 0.66 |
| Morphology | | | | |
| SUL (mm) | 61.89±0.75 | 63.14±0.68 | −0.94 | 0.35 |
| SVL (mm) | 57.03±1.15 | 59.24±0.72 | −1.47 | 0.14 |
| Nuptial pad width (mm) | 1.74±0.07 | 1.75±0.06 | −0.09 | 0.93 |
| Nuptial pad length (mm) | 4.42±0.12 | 4.51±0.09 | −0.57 | 0.57 |
| Forearm width (mm) | 6.47±0.18 | 6.44±0.20 | −0.14 | 0.89 |
| Forearm length (mm) | 13.66±0.28 | 13.10±0.20 | −1.58 | 0.11 |
| Upper arm width (mm) | 6.12±0.19 | 6.25±0.17 | −0.49 | 0.63 |
| Upper arm length (mm) | 11.64±0.34 | 11.39±0.28 | −0.58 | 0.57 |
| Chest width (mm) | 21.25±0.40 | 21.73±0.30 | −0.94 | 0.35 |
| Weight (g) | 21.14±0.71 | 22.55±1.42 | −0.45 | 0.66 |
| Scaled mass index (SMI) | 22.24±0.98 | 21.73±1.20 | −0.45 | 0.66 |

conflicting demands of natural and sexual selection (predator avoidance and intrasexual competition) similar to sexual dimorphic signals on covert body parts of lizards, fish, and birds (Endler, 1983; Fuller and Berglund, 1996; Stuart-Fox and Ord, 2004; Dunn et al., 2015).

Previous studies and the current results clearly highlight that dynamic coloration might have evolved several times around the world under similar selection regimes (explosive mating conditions) to solve similar competitive problems (Sztatecsny et al., 2012; Rehberg-Besler et al., 2015). The question remains why evolution favored such functional adaptations in some explosive breeders, but not in others. Most aggregated breeders lack dynamic color change (Bell et al., 2017). High mating competition and fast mate recognition in monochromatic explosive breeding anurans might be regulated through other cues and/or signals, such as sexual size dimorphism or distinct release calls (Marco and Lizana, 2002; Yu and Sharma, 2012). Naturally, multiple solutions exist for a common problem; dynamic visual signals might provide only a further sensory adaptation for species where physiological mechanisms facilitate such adaptations, acting pre-emptively as opposed to the other strategies.

Our findings are also interesting to consider from a physiological perspective, particularly if dynamic sexual dichromatism is in fact a convergent trait among frogs. We previously showed that the yellow coloration in Asian Common Toads is produced by catecholamines. Signal mediation by stress hormones, the intense competition, and the short period to reproduce led us to the suggestion that dynamic sexual dichromatism was initially a by-product of a stress response (Stückler et al., 2022a) triggered by environmental stimuli that prelude highly competitive and brief explosive breeding events. As such, catecholamines stimulated melatonin aggregations in the skin, enabling a bright yellow appearance (Wright and Lerner, 1960; Abe et al., 1969; Goldman and Hadley, 1969) that presumably benefited signaler and receiver. Since females remain brown, the sensory and cognitive search mechanism for brown phenotypes as mates is maintained. In this case, the dynamic color trait would impact competitor response by increasing the odds of mating and likewise being selected and transformed into a visual signal. Physiological prerequisites, underlying mechanisms, and adaptive pathways facilitating and triggering color change yet remain unknown for most species. Future studies exploring how bright yellow (but also the blue in Moor Frogs) is produced are needed to also understand the physiological and morphological pathways of dynamic color adaptations, which could be utterly different and still provide a functionally convergent visual signal (Hagman and Ord, 2016).

It remains in question if and what traits could provide a basis for females to choose a potentially fit male in explosive mating systems. Previous investigation in the Neotropical Yellow Toad demonstrate that female mate choice was not influenced by male breeding coloration (Gardner et al., 2021) and remains quite unlikely considering the strong male-biased OSR where several males attempt to clasp a female, leaving females little to no chance to participate in forms of pre-copulatory mate choice (Trauth et al., 2000; Dittrich and Rödel, 2023). An example for females to overcome these effects which might suppress their own fitness was observed in Moor Frogs, where females elevate reproductive success by engaging in polyandry (Sztatecsny et al., 2006; Rausch et al., 2014). However, there is no information on polyandry for our study species. Females were observed leaving the mating arena immediately after egg deposition, trying to hide in holes and being chased by males while doing so. Consistent with this view, we found no association between measures of yellow color and morphological indices of health and condition, which can provide a basis for females to assess a potential mate (McGraw and Ardia, 2003; Pike et al., 2010) and mating success. Similarly, amplectant males did not show any size or morphological differences (large forearms or nuptial pads, *sensu* Greene and Funk, 2009) that might have allowed them to secure a mate more easily independent of coloration. This result resembles past findings in a monochromatic Asian Common Toad population in northeast Thailand, where there were no differences in size (SVL), weight, or body conditions between amplecting and non-amplecting males (Köhler et al., 2022).

In conclusion, we argue that similar environmental selection pressures for breeding and strong intrasexual competition repeatedly favored conspicuous male color adaptations convergently used to mediate male decisions rather than those of females. The conspicuous visual signals might be more effective and efficient to avoid costs of male–male mismatch and attacks than signals that regulate those agonistic encounters after they occurred. Explosive breeding systems therefore provide an interesting study system to understand how selection acts on color traits and influences dynamic visual signal design.

## DATA ACCESSIBILITY

The dataset used for this study is available via Mendeley Data (DOI: 10.17632/9d65fzcc2t.1). Supplemental material is available at https://www.ichthyologyandherpetology.org/h2024105. Unless an alternative copyright or statement noting that a figure is reprinted from a previous source is noted in a figure caption, the published images and illustrations in this article are licensed by the American Society of Ichthyologists and Herpetologists for use if the use includes a citation to the original source (American Society of Ichthyologists and Herpetologists, the DOI of the *Ichthyology & Herpetology* article, and any individual image credits listed in the figure caption) in accordance with the Creative Commons Attribution CC BY License.

## AI STATEMENT

The authors declare that no AI-assisted technologies were used in the design and generation of this article and its figures.

## ACKNOWLEDGMENTS

We are very thankful to Gopal's family who welcomed us into their home during field work. We thank Marc Sztatecsny for advice and Walter Hödl for guidance. We thank the Vienna National History Museum for their help in creating the toad models and Stephan Burgstaller and Carolin Dittrich for providing the R script for calculating body condition. We thank the editor Terry Grande and one anonymous reviewer for useful comments on the manuscript. The study was financially supported by the Austrian Academy of Sciences (ÖAW, DOC 25701 to SS), the National Science Foundation (OISE-1952542 to MJF), the Vienna Zoo, and the Society of the Friends of the Vienna Zoo.

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