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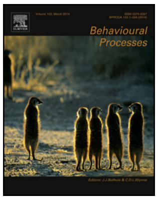

Dynamic sexual dichromatism produces a sex signal in an explosively breeding Neotropical toad: A model presentation experiment

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ABSTRACT

Many animals breed in large mating aggregations, where males must rapidly discriminate between prospective mates and rivals. Selection may favour features that facilitate rapid discrimination in these aggregations. The explosively breeding Neotropical Yellow Toad, *Incilius luetkenii*, exhibits a rapid and dramatic colour change; males change from a cryptic brown to a conspicuous lemon yellow for their brief breeding period. Females, in contrast, remain cryptic brown throughout the year. The function of this temporary, sex-specific colour change is unknown. We tested the hypothesis that yellow colouration displayed by male *I. luetkenii* facilitates sex recognition during both daytime and nighttime mating aggregations. We created yellow and brown model toads and presented them to males during a breeding event. Male *I. luetkenii* responded significantly more intensely to brown models compared to yellow models, approaching them and making more amplexus attempts on the brown versus yellow models. This strong pattern held true regardless of ambient light intensity, making this the first study to expose a dynamic colour signal that operates during both day and night. Our results indicate that male *I. luetkenii* use colouration to quickly discriminate between males and females during their brief, explosive mating aggregations. Our findings suggest that the rapid, dramatic colour change of male *I. luetkenii* facilitates sex recognition, which could provide a significant fitness advantage to males in the form of reduced energy expenditure and reduced risk of injury by other males. Dynamic dichromatism may provide similar fitness benefits in any organisms that mate in large, competitive aggregations.

1. Introduction

Many animals breed in dense mating aggregations comprising tens to thousands of individuals, including diverse insects (Antolin and Strand, 1992; Beani and Turillazzi, 1990), fish (Foote et al., 1997), anurans (Wells, 2007), snakes (Shine et al., 2005), birds (Ligon, 1999), and mammals (Orbach et al., 2014). Within these aggregations, males often engage in scramble competition polygyny, roaming to find and secure a breeding partner before their rivals do (Thornhill and Alcock, 1983). Scramble competition polygyny should select for attributes that allow animals to rapidly acquire mates (Thornhill and Alcock, 1983), such as high mobility and locomotion (Dickinson, 1992; Schwagmeyer, 1988), well-developed sensory organs (Andersson and Iwasa, 1996), and sexually dimorphic features (Able, 1999).

Sexual dichromatism is a common type of sexual dimorphism wherein females and males exhibit differences in colouration (Badyaev and Hill, 2003; Endler, 1984). Sexual dichromatism may arise from a combination of sexual selection for bright colouration in males and natural selection for cryptic colouration in females (Andersson, 1994). Bright male colouration should be favoured if it enhances a male's ability to repel rivals or attract mates (Andersson 1994). Sexual dichromatism has most commonly been studied in birds (e.g. Badyaev and Hill, 2003), fishes (e.g. Kodric-Brown, 1998), lizards (e.g. Macedonia et al., 2002), and butterflies (e.g. Allen et al., 2011). In these groups, bright male colouration has been shown to signal important information about males, including physiological condition (e.g. Thompson et al., 1997), dominance (e.g. Kodric-Brown, 1998), and fighting ability (e.g. Olsson, 1994). Sexual dichromatism has recently garnered attention in anurans (e.g. Bell and Zamudio, 2012; Doucet and Mennill, 2010; Maan and Cummings, 2009; Ries et al., 2008). Sexual dichromatism is relatively rare in anurans, having been documented in only 2% of species (Bell and Zamudio, 2012). Bell and Zamudio (2012) distinguish two classes of sexual dichromatism in anurans: ontogenetic dichromatism and dynamic dichromatism. Of the dichromatic

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species, ontogenetic dichromatism is more common than dynamic dichromatism (at least 92 species documented from 18 families and subfamilies exhibit ontogenetic dicromatism; Bell and Zamudio, 2012) and it occurs when females and males are permanently different in colour. Dynamic dichromatism is uncommon (31 species documented from 9 families and subfamilies; Bell and Zamudio, 2012), occurring when males experience a temporary change in colour, typically during the breeding season (e.g. the European moor frog, *Rana arvalis*; Ries et al., 2008).

Applying our knowledge of the mating tactics of species exhibiting sexual dichromatism may advance our understanding of the selective pressures favouring these colour differences. In animals that breed explosively (i.e. for a short duration when environmental conditions are favourable), differences in colouration between viable, opposite-sex mates and non-viable, same-sex mates should facilitate reproduction (Sztatecsny et al., 2012). Dynamic dichromatism, rather than ontogenetic dichromatism, may evolve when signals of sex are important for only an extremely brief period of an animal's life cycle (i.e. a brief breeding season), especially if the conspicuous colouration is costly to produce or maintain.

The Neotropical Yellow Toad, *Incilius* (*Bufo*) *luetkenii*, is an explosively breeding species that exhibits dramatic dynamic sexual dichromatism in a scramble competition mating system (Doucet and Mennill, 2010). Males rapidly shift from a cryptic brown to conspicuous lemon yellow at the onset of their very brief mating event, coincident with the first rain of the year in their dry forest habitat (Doucet and Mennill, 2010). After males enter amplexus, they quickly return to their cryptic colouration until females complete egg laying, and then disperse (Doucet and Mennill, 2010). With a short breeding season that lasts just one to three days, a rapid shift toward conspicuous colouration in males may facilitate quick discrimination between sexes while reducing risk of injury within these animals' large mating aggregations (Sztatecsny et al., 2012).

In this study, we tested the hypothesis that male *I. luetkenii* use conspicuous yellow colouration to discriminate between prospective female breeding partners and rival males. To test this hypothesis, we presented males with models of yellow toads simulating the colour of breeding males, and models of brown toads simulating the colour of non-breeding males and breeding females. If this short-lived colour dimorphism is important in sex discrimination, we predicted that males would approach the brown models more frequently than yellow models, and that males would attempt to mate with the brown models more frequently than the yellow models. Furthermore, *I. luetkenii* aggregate during both day and night at the onset of the rainy season, which may favour colour signals that are effective in both high- and low-light conditions. We therefore predicted discrimination between yellow and brown models would be highest during the day, but would still be present, albeit at lower levels, at night.

2. Methods

2.1. Study site and species

We conducted this experiment in Sector Santa Rosa of the Guanacaste Conservation Area, a UNESCO World Heritage Site in northwestern Costa Rica (10°40′ N, 85°30′ W). This site is dominated by Neotropical dry forest, where the climate is defined by little-to-no rain during the dry season from mid-November to mid-May, and abundant rain for the rest of the year (Campos and Fedigan, 2013). *I. luetkenii* is distributed across the Pacific lowlands from southern Mexico to central Costa Rica (Savage, 2002) and is common in Sector Santa Rosa (Doucet and Mennill, 2010). These toads are understood to emerge from underground hideaways and form breeding aggregations at the onset of the rainy season (Savage, 2002). We have found these aggregations to persist for the first 1–3 days following the first significant rain of the year at our study site. Annually, we witness hundreds of individuals aggregating in seasonally dry creek beds that have been filled by the first rain. The aggregations form during the evening of the first rain, peak in number the following morning, then decline but remain for up to two more days. Males scramble to enter amplexus with females when they arrive at the mating aggregation, and remain in amplexus throughout the morning. Egg laying occurs after most males have either entered amplexus or left the pond. Our observations suggest that the mating aggregations of *I. luetkenii* can be best understood as scramble competition polygyny, given that males do not hold resources and actively compete with rival males by engaging in searching and male–male displacement behaviour for incoming females at these sites (Wells, 2007).

Male *I. luetkenii* exhibit conspicuous yellow colouration during their short breeding events, whereas females are cryptic and dull in colour (Fig. 1a and e). Previous work has shown that males rapidly change back from yellow to brown following amplexus (Doucet and Mennill, 2010). In designing this experiment, we chose to present models to males rather than females, because some authors argue that females exhibit little choice in scramble competition polygyny (Rausch et al., 2014), a notion that matches our observations that females undergo intense harassment by many males as they approach the mating aggregation.

All work was approved by our university's animal care committee (Animal Care Permit #AUPP-13-16) and the government of Costa Rica (MINAE).

2.2. Model design

We created six yellow and six brown model toads from nontoxic modeling clay (Craftsmart Polymer Clay). We based the shape of the models on photographs taken at our study site in previous years. We used the 82 mm average snout-to-vent length of 81 males that we measured in 2013; this falls within the published size range of both males and females, though females are generally larger than males (77–99 mm for males, 73–107 mm for females; Savage, 2002). We baked the clay to harden it and used nontoxic acrylic paint to colour the models (Craftsmart Acrylic Paint). We painted brown models made from white clay (7:2:1 Golden Brown:Olive:Black; numbers refer to colour ratios, and colours refer to the respective Craftsmart Acrylic Paint name). We produced yellow models from yellow clay that did not require base paint. We used paint to highlight prominent features on both the brown and yellow models, including tympana (9:1 Olive:Black), parotid gland outlines (Black), eye outlines (Black), and throat (9:1 White:Beige). We glued plastic eyes into eye cavities of the models, using identical eyes for the yellow and brown models (model: ISPE-1, 10 mm, brown; glasseyesonline.com). We made all models resistant to water damage by coating the models with nontoxic sealer (Outdoor Mod Podge Waterproof Sealer). Yellow models were designed to simulate males in the breeding season whereas brown models were designed to simulate the colour of males outside of the breeding season, or females throughout the year. The only major difference between the yellow and brown models was the base colour (Fig. 1b and c).

2.3. Model presentation

We conducted a total of 114 trials by presenting pairs of yellow and brown models to live toads following the first significant rain of the year on 10 May 2014. The breeding event started in the evening of 10 May (*N* trials = 9) and persisted across 11 May (*N* = 64), and 12 May (*N* = 20), concluding in the afternoon of 13 May 2014 (*N* = 10). A