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.

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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
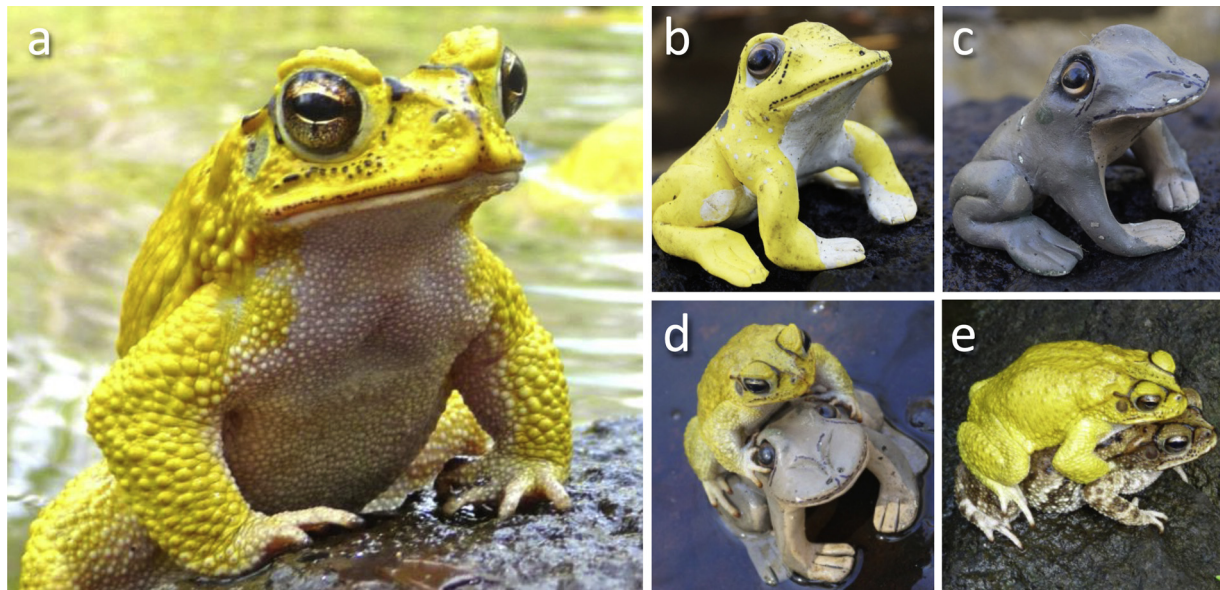
Fig. 1. Male Neotropical Yellow Toads, *Incilius luetkenii*, exhibit a conspicuous yellow colouration solely during their brief breeding event (a). We presented clay models of yellow toads (b) and brown toads (c) to males during their explosive mating aggregations. Males often responded by approaching and attempting amplexus with brown models (d), just as they do with live, brown females (e). (For interpretation of the references to colour in this figure legend and in the text, the reader is referred to the web version of this article.)

small number of trials were conducted during 31 May 2014 ($N = 11$), when a substantial rain that followed a 20-day dry period elicited an additional *I. luetkenii* mating event. Each trial consisted of the presentation of one brown and one yellow model for 5 min. Models were separated by 0.5 m and situated near the edge of three different ponds. We affixed fishing line to the bodies of the models and moved them in a lifelike manner, with short simulated hops up and down (as in Sztatecsny et al., 2012). If a model fell on its side or back and could not be moved upright using the fishing line, we paused the trial, placed the model upright, then resumed the trial. Upon trial completion, we moved the pair of models to a new location, at least 3 m from the preceding location, moving clockwise around the pond to avoid sampling the same toads repeatedly. Given that our subjects were unmarked, we cannot rule out that some individuals were sampled repeatedly. There were, however, hundreds of individuals at each of the three ponds and we moved systematically away from the subjects around the perimeter of the breeding aggregation. Because of this, we are confident that if any repeated sampling occurred it was very minimal. We used video cameras with infrared features to record each trial, allowing us to record across light and dark conditions (Bell & Howell DNV16HDZ digital video recorder).

2.4. Day versus night

We conducted this experiment during both daytime and nighttime hours, because *I. luetkenii* mate during both day and night, and because we were interested in documenting any changes in model preference as a function of ambient light intensity. We measured the intensity of light every 15 min throughout the breeding event to document changes in ambient light (EXTECH EasyView Digital Light Meter). Daytime trials ($N = 61$) were conducted between 05:25 h and 11:00 h and were defined by greater than 1.0 lux of ambient light intensity (Fig. 2). Nighttime trials ($N = 39$) were conducted between 23:30 h and 05:00 h and were defined by 1.0 lux or less of ambient light intensity (Fig. 2). During nighttime data collection, there was very little ambient light, with light from the moon and stars making it barely possible for us to make out the shapes

of animals on the ground. We minimized the use of artificial lights to conduct the experiment by avoiding the use of flashlights and relying on the infrared feature on our video cameras.

2.5. Evaluation of trials

We quantified the toads' responses to the model presentations based on video recordings using JWatcher software (v.1.0; Blumstein and Daniel, 2007). We evaluated four behaviours exhibited by male toads towards the models: number of physical contacts with each model, time in contact with each model, number of amplexus attempts with each model, and time in amplexus with each model. Amplexus attempts were scored when a male toad was on the model's back and had both arms around the sides of the model. Temporal measurements were calculated as the difference between the time of contact termination and the time of contact initiation.

2.6. Statistical analysis

Our data for all four behavioural responses were non-normal owing to a preponderance of values concentrated around zero. We used Wilcoxon signed-rank tests to compare the number of contacts, time in contact, number of amplexus attempts, and time in amplexus between yellow and brown models.

We were interested in determining whether there were differences in male colour preference for each behavioural measure in daytime versus nighttime trials. To analyze this, we split each response variable into responses to yellow models and responses to brown models (i.e. number of contacts with brown model, time in contact with brown model, number of amplexus attempts with brown model, time in amplexus with brown model, number of contacts with yellow model, time in contact with yellow model, number of amplexus attempts with yellow model, time in amplexus with yellow model). We then compared responses in the daytime versus the nighttime for each of those eight variables. We used Mann–Whitney U tests to compare the response measures between night and day.
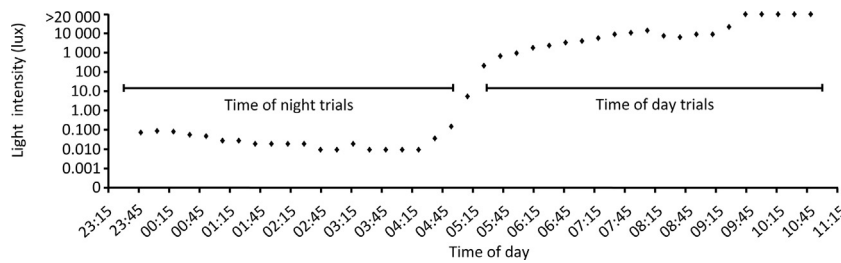
Fig. 2. Light intensity during nighttime trials and daytime trials of the model presentation experiment to Neotropical Yellow Toads, *Incilius luetkenii*.
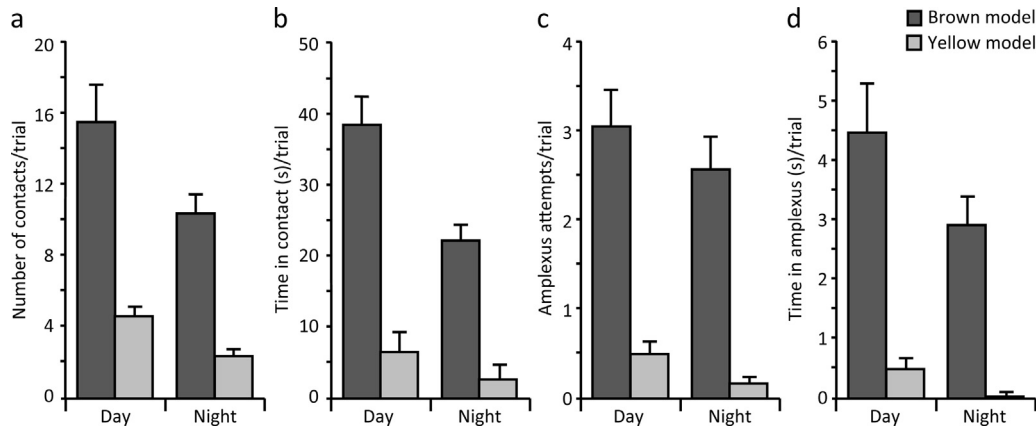

Fig. 3. Breeding male Neotropical Yellow Toads, *Incilius luetkenii*, respond significantly more intensely to brown models compared to yellow models for four behavioural measures: (a) number of contacts per trial, (b) time in contact per trial, (c) amplexus attempts per trial, and (d) time in amplexus per trial. We observed significantly higher response intensity during daytime trials compared to nighttime trials for 2 of 8 measures: number of contacts with the yellow model, and time in contact with the yellow model. Error bars represent standard error around the mean.

All statistical tests were conducted using SPSS (version 20; IBM, Chicago, IL, U.S.A.). All tests of significance were two-tailed, with a threshold of 0.05.

3. Results

Toads responded strongly to the presentation of the clay models, hopping towards at least one of the models in the majority of trials ($N = 100$ of 114 trials). We excluded fourteen trials from subsequent analysis because no toads responded to either the brown or yellow model.

3.1. Daytime trials

Male *I. luetkenii* responded significantly more intensely to brown models compared to yellow models across all behavioural measures during daytime trials (Fig. 3; Wilcoxon signed-ranks tests for number of contacts, time in contact, number of amplexus attempts, time in amplexus: all $Z > 5.2$, $N = 61$, $P < 0.001$).

3.2. Nighttime trials

As in the daytime trials, male *I. luetkenii* responded significantly more intensely to brown models across all behavioural measures (Fig. 3; Wilcoxon signed-ranks tests for number of contacts, time in contact, number of amplexus attempts, time in amplexus: $Z > 4.7$, $N = 39$, $P < 0.001$).

3.3. Day versus night

Male toads responded significantly more intensely to the models during the day versus night for two of eight trial response variables: number of contacts with the yellow model and time in

contact with the yellow model (Mann–Whitney U tests: number of contacts with yellow model: $U = 851$, $N1 = N2 = 100$, $P = 0.02$; time in contact with yellow model: $U = 830$, $N1 = N2 = 100$, $P = 0.01$). The six other measures were not significantly different (Mann–Whitney tests: $U > 930$, $N1 = N2 = 100$, $P > 0.05$).

4. Discussion

When presented with two model toads that differed only in base colouration, male *I. luetkenii* responded significantly more intensely to the brown female-like model compared to the yellow male-like model. Our results suggest that males use the conspicuous yellow colouration of other males as a signal of sex during the breeding period. Explosively breeding anurans that engage in scramble competition are expected to benefit from features that aid in rapid differentiation of mates versus rivals (Sztatecsny et al., 2012 Wells, 2007). Indeed, this phenomenon has been observed in a phylogenetically and geographically distant relative of *I. luetkenii*; the European moor frog (*R. arvalis*) also exhibits dynamic sexual dichromatism, with males shifting to a conspicuous blue colouration during the breeding season (Ries et al., 2008). When male *R. arvalis* were presented with differently coloured models, they also preferred to clasp brown models compared to blue models (Sztatecsny et al., 2012). In contrast with *R. arvalis*, however, *I. luetkenii* rapidly return to pre-nuptial colouration after mating (Doucet and Mennill, 2010). This difference opens potential for future work to explore further the function of these differences across dynamically dichromatic species. Our findings represent the second demonstration of the use of dynamic sexual dichromatism as a visual signal used by male anurans to quickly discriminate between mates and rivals, and the first demonstration that this pattern holds true both in daylight and during the night.

Our data suggest that the rapid, dramatic colour change of male *I. luetkenii* facilitates sex recognition, which could provide a significant fitness advantage to males. Turning a conspicuous yellow colour is likely costly for males, perhaps due to the increased predation risk of being yellow, or due to the increased energy expenditure of turning from brown to yellow. The net benefit of turning yellow must therefore outweigh the cost of remaining brown. Indeed, brown female *I. luetkenii* undergo intense aggressive harassment during the breeding season, with many males attempting amplexus on a single female (unlike in *Bufo pardalis*, Cherry, 1992). This intense aggression routinely results in female death; in all of the large aggregations we have observed in *I. luetkenii*, there has been at least one female floating dead in the middle of the mating aggregation with many males continuing to attempt amplexus. Given the high similarity in male and female colouration outside the breeding season (Doucet and Mennill, 2010; Savage, 2002), males might face significant risk of injury or death by other males if their sex was misidentified in the context of the breeding aggregation. Thus the yellow colouration of males might both facilitate the rapid identification of females and while also preventing the risk of injury by other males.

The conspicuous yellow colouration of male *I. luetkenii* during the breeding event may also be important to females. For example, females might prefer 'yellower' males, just as females prefer colourful males in other taxa (e.g. birds: Sætre et al., 1994 fish: Milinski and Bakker, 1990 insects: Kemp, 2007). Although we did not test this, female choice is likely constrained in *I. luetkenii* given their scramble mating system (Sullivan et al., 1995). In animals that engage in scramble competition polygyny, male mating success is closely tied to successful mate searching and winning overt male–male conflicts (e.g. thirteen-lined ground squirrels; Schwagmeyer and Woontner, 1986). Although males of some animal species do not engage in intrasexual struggles (Cherry, 1992), *I. luetkenii* males are intensely aggressive, which may limit active female mate choice. Indeed, Rausch et al. (2014) found that male *R. arvalis* nuptial colouration did not influence paternity success during scramble competition, and therefore was not a trait selected for by females. Females may still shape the outcome of successful amplexus based on other factors (e.g. female delay in oviposition; Eberhard, 1996), but females may have limited control over which males make contact with them and attempt amplexus with them.

Male toads could also use yellow colouration as a symbol of status; differences in yellow colour could signal fighting ability or condition. For example, in spadefoot toads (*Scaphiopus couchii*), male colouration is indicative of size and condition (Vásquez and Pfennig, 2007). The intensity of the yellow colouration in male *I. luetkenii* may be influenced by agonistic male–male interactions and may be similar to "badges" as signals of dominance in birds (Rohwer, 1982). Temporary colour change as a dominance signal has been observed in certain fishes (Kodric-Brown, 1998). For example, the intensity of temporary blue male nuptial colouration in pupfish (*Cyprinodon pecosensis*) is influenced by both intersexual and intrasexual selection. Male pupfish are most intensely blue when they possess a territory, engage in agonistic male–male interactions, and when there are gravid females present (Kodric-Brown, 1996). Future work with male *I. luetkenii* should evaluate whether variation in male yellow colouration reflects male fighting ability, dominance status, or some other aspect of male quality.

We compared male *I. luetkenii* responses to male and female models during the day and night, making this the first study of the function of dynamic colour signals across extremes in lighting environments. Males clearly preferred the brown models during both the bright light of day and the very dim light of night, although the toads seemed to be more responsive overall during the day for two response measures: number of contacts with the yellow model, and time in contact with the yellow model. Interestingly, the magnitude of the response to the yellow and brown models appears similar across light conditions, suggesting that male *I. luetkenii* were able to discriminate between the models equally well during both the day and the night. Our findings show that male *I. luetkenii* perceive and use this visual signal of sex during both day and night.

Our findings are consistent with the assumption that scramble competition polygyny selects for high-functioning sensory systems (Andersson and Iwasa, 1996) and that toads (*Bufo bufo*) possess good vision under low-light conditions (Aho et al., 1993). It is unclear whether male *I. luetkenii* are attending to the colour (chromatic signal) or brightness (achromatic signal) of male skin during the night. Nocturnal anurans have rod classes (Liebman and Entine, 1968), and attending to chromatic versus achromatic signals depends on whether the rod responses are summed or compared by the neural system (Gomez et al., 2010). Little is known about nocturnal colour vision in anurans; however, recent discoveries suggest colour vision in low-light conditions is not as rare as initially expected (Kelber and Roth, 2006). At least one anuran (*Hyla arborea*) is able to use colour signals during nighttime mating behaviour, with females preferring conspicuously coloured males (Gomez et al., 2009; Gomez et al., 2010). Males of 75% of the documented anuran species that exhibit dynamic colour changes during the breeding season tend to shift to become yellower than females (Bell and Zamudio, 2012). This disproportionate amount of yellow colouration in frog dynamic dichromatism may be selected for by the environment; shifts toward yellow skin colour may reflect the nocturnal forest visual light environment more efficiently, which has been documented as being yellow-green dominated with a peak flux of 560 nm (Veilleux and Cummings, 2012). Yellow colouration in animals is also relatively bright, and as such could effectively reflect the small amount of light available at night, even if the animals rely only on the achromatic versus the chromatic part of the signal. More work is needed to understand the roles of scotopic and photopic vision in low-light situations, and the particular importance of the yellow colouration in *I. luetkenii* and similar anuran species.

Few anuran species have been shown to exhibit dynamic sexual dichromatism, and fewer still in such a dramatic fashion as *I. luekenii*. The short, explosive breeding season of *I. luekenii* results in costly mate-recognition challenges. Our findings suggest that the dynamic shift toward conspicuous yellow colouration by males serves to overcome these challenges by facilitating rapid discrimination between potential mates and rivals. This is the first documentation of this phenomenon in toads, and the first documented tropical anuran to exhibit a dynamic and conspicuous visual signal of sex recognition. Our data also reveal that males successfully use the conspicuous yellow colouration during both daytime and nighttime breeding, suggesting that males may have effective low-light vision. Sex-specific signals are common in nature, and often appear to be a byproduct of stronger sexual selection on one sex (Andersson, 1994). Our findings suggest that in species with competitive mating aggregations, divergence in colouration between the sexes may be under direct selection to facilitate sex identification and prevent costly mistakes in sex recognition. A dynamic form of this dichromatism should be favoured when the cost of remaining conspicuously coloured is high.

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