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Male nuptial display colour and vocalisation appear to signal independent information in the whirring tree frog

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Abstract

When different modes of communication are used in combination and for example convey visual and acoustic information, they form a multimodal signal. Frogs are best known for using acoustic communication, but many species also use visual or colour signals, some of which are dynamic, and may be combined with acoustic signals. In this context, the question of whether these two modes of communication reinforce the same message or offer different information is poorly understood. Male whirring tree frogs, *Litoria revelata*, use a multimodal signal during courtship, which combines a vocalisation and dynamic sexual dichromatism, with nuptial display colours shifting from brown or grey to bright yellow. Here, we examined the properties of the advertisement call and nuptial colour of vocalising male whirring tree frogs and tested whether the two signals were likely to reinforce each other or convey independent information. We found only weak associations between elements of male colouration and vocalisations, suggesting that advertisement calls and nuptial colour do not reinforce each other and that the signals may instead convey different information.

Significance statement

Dynamic nuptial colour and vocalisation in combination is a relatively common multimodal signal in frogs but is unstudied. We looked for relationships between properties of colour and vocalisation in an Australian tree frog to explore whether the two sensory modes formed backup signals or multiple messages. We did not find predictive relationships between nuptial colour and vocalisation, supporting the multiple messages hypothesis and suggesting that nuptial colour is not necessarily directed at females for the purposes of mate attraction, potentially differing from the assumed function of the vocalisation. Our study is also the first to formally characterise aspects of dynamic sexual dichromatism in the whirring tree frog (*Litoria revelata*) and the first to describe the advertisement call of this species in its southern distribution. Whilst we do not specifically address the function of dynamic sexual dichromatism in this species, our findings do not contradict the existing literature in respect to it being a male-male directed signal.

Keywords Dynamic sexual dichromatism · Multimodal signalling · Multiple messages · Amphibian

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Introduction

Multimodal signals, in which two or more sensory modes are used to encode information, are commonplace (Rowe and Guilford 1999; Endler and Day 2006; Martín and López 2010). Well-documented examples include tidbitting in male fowl (*Gallus gallus*) that perform distinctive vocalisations, with elaborate visual displays to attract mates (Stokes 1971; Smith and Evans 2008); sexual signalling in ocellated lizards (*Timon lepidus*) where vitamin E, in pheromones, is used with body colouration, to signal male quality (Martín and López 2010); and the combined use of pyrazine odours and conspicuous colours to signal toxicity amongst insects (Rowe and Guilford 1996; White and Umbers 2021). When more than one mode is used, signals may reinforce each other as redundant 'backup signals' or convey independent information through 'multiple messages' (Johnstone 1996; Mitoyen et al. 2019).

Backup signals are thought to evolve to ensure that receivers 'get the message' (Johnstone 1996), particularly in complex or noisy environments (Grafe and Wagner 2007; Smith and Evans 2008). They may be characterised by a correlation between the expression of signal components (Mitoyen et al. 2019) or between signals and the same trait (Moreno-Rueda et al. 2021), such as bill colour and feather colour correlating with fitness traits in female cardinals (Cardinalis cardinalis; Jawor et al. 2004). Conversely, the lack of any predictive relationship between signal components argues for independence in their content and, hence, favours a 'multiple messages' explanation (Partan and Marler 2005; Gomez et al. 2011). An absence of correlations between signal components does not exclude the possibility of redundancy, however, given signals can be uncorrelated, yet correlate with the same individual fitness trait (Jawor et al. 2004; Mitoyen et al. 2019; Moreno-Rueda et al. 2021).

In multimodal signals, a single mode in isolation may not convey all of the intended information. In many insects, for example, 'backup' signals using colour and olfaction may only be effective when used in combination (Rowe and Guilford 1996). Signals can also be directed at multiple receivers whilst serving different functions, such as in *Heliconius* butterflies, where colour is used in both mimicry and intraspecific communication (Bybee et al. 2012). However, the advantages of multimodal signals are not always clear and could potentially be costly to the signaller, as unintended receivers such as predators are more likely to detect the signal if it uses multiple sensory modes (Kulachi et al. 2008; White et al. 2022).

Examples of multimodal courtship signals are known from a number of frog species and usually comprise an acoustic signal as one of the communication modes (Taylor et al. 2007; Vásquez and Pfennig 2007; de Luna et al. 2010; Gomez et al. 2011). Male frogs vocalise both to attract females and to keep rival males at bay (Davies and Halliday 1978; Littlejohn and Harrison 1985; Radwan and Schneider 1988; Gerhardt 1994). Vocalisations often signal male quality to females, and females prefer calls with lower frequency, higher pulse rates, and longer duration (Ryan et al. 1992; Welch et al. 1998; Doty and Welch 2001; Witte et al. 2001; Taylor et al. 2007). In the Blanchard's cricket frog, Acris blanchardi, for example, the manipulation of call frequency and complexity alters male attractiveness to females. Conversely, it is the duration of calls which appears to signal a male's genetic quality in the grey tree frog, Dryophytes versicolor (Welch et al. 1998; Witte et al. 2001).

Stepping beyond acoustic communication, the role of visual cues and colour in frog sexual signalling is not well understood, although it likely plays a larger role than previously thought (Gomez et al. 2011; Bell and Zamudio 2012; Rojas 2017). Whilst best known for their use of auditory communication and specifically the loud breeding calls of males, many frogs also draw on chemical signals, conspicuous colours, and/or dynamic visual displays such as foot flagging (Hödl and Amézquita 2001; Byrne and Keogh 2007; Rojas 2017). For example, the torrent frog, Staurois guttatus, signals using foot flagging but also has blue foot webbing, which suggests the possibility of multiple messages (Grafe and Wanger 2007). In frogs, colour signals may play important roles in social interactions. In natterjack toads (Epidalea *calamita*), colour correlates with individual quality, likely conveying information to potential mates (Zamora-Camacho and Comas 2019), whilst in Mannophryne trinitatis female throat colour is used as a signal in territorial defence (Wells 1980; Greener et al. 2020).

Documented anuran multimodal signals most often consist of vocal and visual components, with the sensory modes either 'backing up' (Taylor et al. 2007; Vásquez and Pfennig 2007) or conveying additional information (de Luna et al. 2010; Gomez et al. 2011). For example, the Central American frog, Allobates femoralis, relies on multimodal signals to identify conspecific intruders using non-redundant visual elements in association with a vocalisation (de Luna et al. 2010). In this species, the multimodal signal consists of auditory and visual components, incorporating body size and movement (de Luna et al. 2010). Multimodal courtship signals used for mate signalling in the squirrel tree frog, Dryophytes squirellus, also use both auditory and visual cues where females prefer faster call pulse rates but also, when call properties are kept the same, they prefer vocalising males with large lateral stripes (Taylor et al. 2007). The European tree frog, Hyla arborea, also produces a multimodal courtship signal consisting of a vocalisation and a colour signal, with both subcomponents attractive to the female (Gomez et al. 2009). In this case, the visual component is male vocal sac colouration, which is not strongly correlated to any aspect of their vocalisation, and so suggests that the two signals convey different information about the individual (Gomez et al. 2011). Further, ontogenetic male colour and vocalisation form a reinforcing multimodal courtship signal in the spadefoot toad, Scaphiopus couchii, with both colour and call associated with male condition (Vásquez and Pfennig 2007). Generally, multimodal signals in frogs have not been widely investigated and the potential for multimodal signalling in most anurans, especially those with dynamic sexual dichromatism, remains unexplored.

Anuran colour signals, in particular dynamic sexual dichromatism, have received much recent attention (e.g. Sztatecsny et al. 2010, 2012; Bell and Zamudio 2012;

Rehberg-Besler et al. 2015; Kindermann and Hero 2016; Bell et al. 2017; Rojas 2017; Greener et al. 2020). The key finding to date is that dynamic sexual dichromatism functions in intrasexual signalling and is directed at males (Sztatecsny et al. 2012; Rehberg-Besler et al. 2015; Kindermann and Hero 2016). Examples of dynamic sexual dichromatism used in male-male signalling include the blue nuptial colour of *Rana arvalis* and the yellow nuptial colour of *Incilius luetkenii* and *Litoria wilcoxii*. In all three species, colour is a reliable signal of an individual's sex and facilitates mate recognition in large, male-biased breeding aggregations (Wells 2007; Sztatecsny et al. 2012; Rehberg-Besler et al. 2015; Kindermann and Hero 2016; Bell et al. 2017). The relationship between dynamic nuptial colour and vocal signals, however, has not yet been investigated in frogs.

At least 178 anuran species globally from 15 families and subfamilies are reported to have dynamic sexual dichromatism, where males typically display a distinctive nuptial colour pattern on the dorsum during courtship and amplexus, and frequently whilst vocalising (Bell and Zamudio 2012; Bell et al. 2017). Consequently, there is broad potential for multimodal signalling, by conveying information through both male dynamic nuptial colours and vocalisation. Here, we investigated whether colour and vocal signals are correlated and if the information being conveyed is potentially either the same (reinforcement) or different (multiple messages), in the sexually dichromatic Australian tree frog, Litoria revelata. If the multimodal signals are reinforcing, then we predicted a correlation between colour and components of the call. In contrast, a 'multiple messages' hypothesis predicts independence between colour and vocalisation and hence the absence of any predictive relationship amongst the components of each, although corroboration of independence requires testing of trait function. Further, in the context of dynamic sexual dichromatism, the presence or absence of correlations between signal traits provides opportunity to infer whether the male nuptial colour in L. revelata is potentially male or female directed.

Materials and methods

Study species

The whirring tree frog (*Litoria revelata*) (Ingram et al. 1982) occurs along the east coast of Australia, in the south, from Ourimbah, New South Wales, to the Atherton Tablelands, Queensland, in the north (Anstis 2002; Sanders 2021). *Litoria revelata* utilises a variety of permanent or ephemeral water bodies for breeding, favouring those with emergent or fringing vegetation, and is most commonly associated with permanent to semi-permanent still ponds and swamps or slow-flowing streams in rainforest, wet and dry sclerophyll forests, wallum heathland, or partially cleared land (Anstis 2017; Sanders 2021).

Males have dynamic sexual dichromatism during the breeding season (Fig. 1; Bell et al. 2017). During courtship, males change colour from a cryptic brown, grey, or red-brown baseline colour to a brilliant lemon yellow or vellow-brown which extends over much of their dorsum. This yellow display colour is dynamic and typically only maintained whilst vocalising and during amplexus (GNW pers. obs.). During the day, males revert to their baseline colour (GNW unpublished data). Females do not display the yellow dorsal colour of breeding males, nor do they appear to demonstrate a distinctive dynamic nuptial colour and feature the same range of dorsal colours as non-breeding males (Bell et al. 2017); commonly, a red-brown dorsum appears in females (Fig. 1; GNW pers. obs.). Both males and females feature similar concealed patches of yellow and red in the armpit, groin, and thighs.

Vocalisation and breeding span most of the year, with peak calling activity between late August and November and late February to June (Anstis 2017; Sanders 2021). The species is primarily nocturnal with males vocalising through most hours of the night, although calling wanes in the hours before sunrise (this study). Infrequently, calling may occur diurnally, usually during overcast and rainy conditions



Fig. 1 Dynamic sexual dichromatism in *Litoria revelata*: A male in display colour, B male in baseline colour and C female. All frogs photographed at the study site by Grant Webster

Little is known on the specifics of mate choice and mate acquisition in L. revelata, including female preferences. Males gather and call around breeding sites during periods of reproductive activity, which may last from days to months, whilst females appear to arrive at breeding sites intermittently over the breeding event (this study). Possible mechanisms of mate acquisition may include female choice and scramble competition (Andersson and Isawa 1996; Andersson and Simmons 2006; Wells 2007; Sztatecsny et al. 2012). The function of nuptial signals, including calls and male colour, has not been examined previously, although it is assumed that the role of the male advertisement call is to attract prospective mates, as is generally the case in most frog species (Ryan et al. 1992; Welch et al. 1998; Witte et al. 2001; Taylor et al. 2007; Köhler et al. 2017). In support of this, we observed an unamplected gravid female actively moving towards adjacently housed vocalising males.

Study area

We conducted fieldwork at Wallingat National Park on the coastal plain of the mid-north coast of New South Wales, Australia (- 32.342140°, 152.448448°), where *L. revelata* occurs in high density around two large artificial permanent ponds with fringing emergent vegetation amongst regrowth of wet sclerophyll forest (National Parks and Wildlife Service 2007). The surrounding forest consisted of the tree species *Eucalyptus acmenoides*, *E. grandis, E. microcorys, E. pilularis, E. propinqua and Syncarpia glomulifera* and understorey species *Acacia binervata, Allocasuarina torulosa, Glochidion ferdinandi* and *Livistona australis*. The vegetation surrounding the ponds mostly comprised *Gahnia* spp., *Lomandra longifolia* and *Schoenoplectiella mucronata*.

Frog collection, vocalisation, spectral reflectance and morphological data

We collected frogs between 6 September and 12 October 2012 by spotlighting calling males at night which were often found sitting exposed on vegetation around the ponds. It was not possible to record data blind because our study was conducted in the field and only used wild frogs. We recorded the vocalisation of solitary (single/ unpaired) male frogs (n = 45) using a Zoom H4N H4 recorder with Sennheiser ME66 condenser microphone and K6 power module. The microphone was pointed in the direction of the frog at ca. 1 m, recording up to six advertisement calls per individual. We measured skin surface temperature of all the male frogs using a Testo 830-T1 laser thermometer held ca. 1 cm from the frog. Temperature was recorded immediately after the frog was collected, before colour processing, as handling can easily alter temperature in ectotherms.

We measured the spectral reflectance of 46 vocalising male frogs using an Ocean Optics Jaz Spectrometer with a pulsed xenon (PX-2) light source. The probe angle was held at 90°, flush against the frog, with the light source 5 mm from the frog's skin, set by the probe holder. A 99% white (Labsphere) and dark, standard, were used as a reference before any readings were taken and they were remeasured between every frog processed. Spectral reflectance was measured over an area of 19.6 mm² on the centre of the flank of each frog, roughly in line with the midpoint of the dorsum. The flank was chosen as it is typically the section of the dorsal surface that most strongly displays the nuptial colour (GNW unpublished data). Spectral measurements were taken at the pond, immediately after temperature was recorded.

We measured snout-urostyle length (SUL) to the nearest 0.02 mm within 20 min of capture using a pair of Kincrome callipers for 51 vocalising male frogs. We did not measure mass because variable hydration levels can have significant effects on mass, particularly in small frogs, and this was logistically difficult to control for in the field. Each frog had its SUL measured once, following colour measurement. One toe (toe tip of the longest toe on the left foot) was clipped to avoid resampling the same individual. Frogs were then released at the site of capture. On some occasions, processed frogs were observed to resume vocalisation within a few minutes of release.

Spectral processing and visual modelling

We lightly LOESS (locally weighted) smoothed all reflectance spectra prior to analyses to minimise spurious noise and zeroed any slightly negative values. To estimate viewer-subjective measures of male flank hue, saturation (or 'chroma'), and luminance, we used a simple trichromatic colour space model of frog vision (Fig. 2; Goldsmith 1990). We drew on the visual phenotype of the dendrobatid *Oophaga pumilio* (as the nearest available relative with sufficient data), modelled using a vitamin A1 pigment template (Govardovskii et al. 2000), with peak cone sensitivities (λ_{max}) of 466, 488, and 560 nm (Siddiqi et al. 2004). These results are therefore somewhat

Fig. 2 Male *Litoria revelata* (N=46) flank spectral reflectance (left) and their locations in a trichromatic model of anuran vision (right), with lines and points coloured as they might appear to a human observer for illustrative purposes. On the trichromatic model vertices, the short (S), medium (M), and long (L)-wavelength receptors are labelled, whilst the achromatic centre is indicated by the grey dot



tentative, in light of currently unknown differences in colour perception between *L. revelata* and *O. pumilio*. We estimated receptor quantum catches as the integrated product of male flank reflectance, blue-sky irradiance, and the above cone absorbances. Following well-established and validated methods, male 'hue' was taken to be the angle between the colour locus, the achromatic centre, and the short-wavelength receptor vertex, 'saturation' the distance between the colour locus and the achromatic centre, and 'luminance' the summed response of all receptors (Goldsmith 1990; Renoult et al. 2017). All visual modelling and spectral processing was carried out using the packages 'pavo' (v2.1; Maia et al. 2019) and 'lightr' (Gruson et al. 2019) for R (v3.5.1).

Vocalisation processing

Litoria revelata makes two distinct vocalisations, the normal 'whirring' call associated with reproduction that fits the definition of an advertisement call according to Köhler et al. (2017) and occasionally a shorter 'whistle' call, the function of which is unknown, although it is probably an agonistic signal or territorial call likely directed at other males. As the 'whistle' call was infrequently produced relative to the 'whirring' call, and not every male was recorded making this call, only the 'whirring' call was analysed in this study.

We processed recorded vocalisations using Raven Pro 1.5 (Bioacoustics Research Program 2017). Calls were recorded and processed in WAV format at a sampling rate



Fig. 3 Advertisement call of *Litoria revelata* ('whirring' call) displayed as a waveform (above) of relative amplitude (kU) (y-axis) and corresponding audiospectrogram (below) of frequency in kilohertz (kHz) (y-axis) over time in seconds (s) (x-axes), depicting call properties used in the analysis. The grey bar under the x-axes = 1 s. This call

features 26 pulses (with a single pulse indicated) over a duration of ca. 5.3 s, with a peak frequency of ca. 4.5 kHz (indicated with arrow (F)), and the pulse rate is ca. 4.9 s⁻¹. The arrow (S) indicates the call of a second male in the background visible on the audiospectrogram

of 44.1 kHz with 16 bits per sample, and audiospectrograms were calculated using a fast-Fourier transformation (FFT) of 512 points, 50% overlap and 86.1 Hz grid spacing, and Hanning windows. From these recordings, we extracted the following: duration (time in seconds) (s)-time interval of the call; pulse number-the distinct number of pulses in the call; pulse rate (s^{-1}) —pulse number divided by duration; and peak (dominant) frequency measured in kilohertz (kHz)the call frequency most powerfully expressed (Fig. 3). We also identified the high and low frequencies (kHz) of each recorded vocalisation. We recorded 1-6 calls from each frog and calculated an average value for all vocalisation properties for each individual. Calls were recorded from 45 individuals although only 44 recordings were used in the analysis as one was excluded as temperature was not recorded.

Data analysis

We constructed generalised linear models (GLMs) to separately examine the relationship between four properties of male calls-duration, pulse number, pulse rate, and peak frequency-and measures of colouration, body size, and temperature. In all global models, we included male flank hue, saturation, and luminance (as estimated above) as main effects, along with skin surface temperature and snout-urostyle length (SUL), since body temperature and body size are known to influence frog vocalisations (Keddy-Hector et al. 1992; Wong et al. 2004). All response variables were modelled using Gaussian errors and Identity link functions, and model assumptions were affirmed via inspection of residual plots. Following the estimation of these models, we used a restricted maximum-likelihood (REML) based information-theoretic approach (Burnham and Anderson 2002) to examine a subset of models for each call property. These models were comprised of all possible combinations of the above fixed-effect terms, with the proviso that body size and body temperature should be included as main effects in all subset models ('null' models were thus comprised of an intercept, male body size, and temperature). We used the R package 'stats' for global GLM construction and 'MuMIn' (Barton and Barton 2015) for model selection and averaging.

To further explore the relationships between properties of call and measures of colouration, we generated a correlation matrix that included all traits of interest, as well as male body size (SUL) and skin temperature. This allowed us to examine whether signals were correlated to the same trait (i.e. traits that were possibly suggestive of male fitness or quality) within an individual, in this case SUL and temperature. As vocalisation and nuptial colour potentially convey information on fitness (Davies and Halliday 1978; Gerhardt 1994; Zamora-Camacho and Comas 2019), correlations could be expected between the signals or between common individual traits, if the signals are likely reinforcing (Johnstone 1996; Mitoyen et al. 2019; Moreno-Rueda et al. 2021).

Results

Morphology, colour and vocalisation

Summary statistics for frog morphology, flank colour and vocalisation are presented in Table 1.

Vocal versus visual signals

We found minimal support for any relationship between features of male vocal and visual signals. The most parsimonious models of male call properties (duration, pulse number, pulse rate, and peak frequency) all included the 'null' model of male body temperature and size (Table 2), with only weak contributions from measures of flank colouration. Call duration and pulse number included positive, albeit extremely weak, contributions of flank saturation in the second-best model (with ca. 1.5-2 times the support for null models based on model weights; Table 3), whilst the second-best model of pulse rate included a likely negative contribution of male hue, although this too was minor (ca. 1.8 times the weight for the null model; Table 3). The leading models of peak call frequency included positive contributions of hue and saturation, suggesting that males that call with a higher peak frequency also tend to be 'yellower', although only slightly (ca. twice the weight of null model alone; Table 3). As expected, male body size and

Table 1 Means $(\pm SE)$ and ranges for SUL, skin surface temperature, spectral and vocal properties

| Variable | n | Mean | SE | Range | |
|-----------------------|----|-------|------|--------------|--|
| SUL (mm) | 51 | 28.91 | 0.22 | 24.84-31.80 | |
| Temperature (°C) | 45 | 16.49 | 0.39 | 11.50-22.50 | |
| Spectral properties | | | | | |
| Saturation | 46 | 0.16 | 0.04 | 0.082-0.231 | |
| Hue (°) | 46 | -0.75 | 0.01 | -0.79 - 0.69 | |
| Luminance | 46 | 0.66 | 0.13 | 0.37-0.98 | |
| Vocal properties | | | | | |
| Duration (s) | 45 | 6.00 | 0.23 | 3.40-10.54 | |
| Pulse number | 45 | 28.87 | 0.98 | 15.00-45.66 | |
| Pulse rate (s^{-1}) | 45 | 4.88 | 0.08 | 3.76-6.03 | |
| Peak frequency (kHz) | 45 | 4.55 | 0.03 | 3.96-5.00 | |
| High frequency (kHz) | 45 | 16.90 | 0.27 | 13.87-20.21 | |
| Low frequency (kHz) | 45 | 1.71 | 0.06 | 0.95-2.81 | |

| Table 2 A model-selection table detailing only the most | Response | Model | df | LL | AICc | Δ AICc | W |
|---|----------------|------------------------|----|----------|--------|---------------|------|
| parsimonious candidate models | Call duration | | | | | | |
| (as suggested by Δ AICc < 2) for the relationship between | | temp + SUL | 4 | -74.65 | 158.30 | 0.00 | 0.36 |
| male call properties and one | | temp + SUL + sat | 5 | -74.03 | 159.70 | 1.33 | 0.19 |
| or more linear combinations | Pulse number | | | | | | |
| of male body temperature | | temp + SUL | 4 | -140.37 | 289.80 | 0.00 | 0.32 |
| (temp), snout-urostyle length (SUL), flank-colour saturation | | temp + SUL + sat | 5 | - 139.50 | 290.60 | 0.84 | 0.20 |
| (sat), hue (hue), and luminance | Pulse rate | | | | | | |
| (bright). Estimate of the | | temp + SUL | 4 | -17.25 | 43.60 | 0.00 | 0.39 |
| log-likelihood (LL), adjusted | | temp + SUL + hue | 5 | -16.60 | 44.80 | 1.27 | 0.21 |
| Akaike information criterion | Peak frequency | | | | | | |
| to the leading model (Δ AICc). | | temp + SUL + hue | 5 | 11.79 | -12.0 | 0.00 | 0.31 |
| and relative weights (<i>w</i>) are | | temp + SUL | 4 | 10.13 | -11.2 | 0.75 | 0.21 |
| provided for each model | | temp + SUL + hue + sat | 6 | 12.27 | -10.2 | 1.77 | 0.13 |
| | | | | | | | |

Table 3 Model-averaged parameter estimates and adjusted standard errors for the most parsimonious models of male call properties (Δ AICc < 2; Table 2), along with their overall fit

| Response | Parameter | Est | SE | R^2 |
|----------------|-------------|-------|-------|-------|
| Call duration | Intercept | 5.27 | 4.90 | 0.19 |
| | Temperature | -0.23 | 0.09 | |
| | SUL | 0.15 | 0.15 | |
| | Saturation | 1.99 | 4.33 | |
| Pulse number | Intercept | 6.36 | 22.14 | 0.07 |
| | Temperature | -0.26 | 0.41 | |
| | SUL | 0.86 | 0.68 | |
| | Saturation | 12.65 | 22.96 | |
| Pulse rate | Intercept | 1.29 | 2.58 | 0.55 |
| | Temperature | 0.16 | 0.02 | |
| | SUL | -0.01 | 0.04 | |
| | Hue | -1.48 | 3.08 | |
| Peak frequency | Intercept | 8.13 | 1.86 | 0.32 |
| | Temperature | 0.02 | 0.01 | |
| | SUL | -0.07 | 0.20 | |
| | Hue | 2.46 | 2.39 | |
| | Saturation | 0.14 | 4.34 | |

temperature were predictive of several call properties. We found particularly strong associations between temperature and pulse rate, with warmer males voicing more pulses, and size and peak frequency, with larger males calling with a lower peak frequency (Table 3).

Additionally, no aspects of vocalisation or nuptial colour were significantly mutually correlated with either male body size (SUL) or skin surface temperature (see Supplementary Information). One limitation is that we could not control for frog skin temperature varying according to ambient air temperature, so this variable is not reliably informative of male quality in this context.

Discussion

According to animal signalling theory, two or more sensory modes are thought to increase the likelihood of detection by a receiver whilst reinforcing the same information (backup signals) or conveying different information as multiple messages. Correlations between signal traits support reinforcement (Johnstone 1996; Rowe and Guilford 1996; Taylor et al. 2007; Vásquez and Pfennig 2007; Smith and Evans 2008; de Luna et al. 2010; Gomez et al. 2011). Moreover, reinforcement can also be supported by correlations between signal traits and the same measures indicative of quality within an individual (Jawor et al. 2004), even in the absence of correlations between signal traits themselves (Moreno-Rueda et al. 2021). Here, we examined the visual and acoustic traits of a multimodal courtship signal in the frog Litoria revelata and found that components of flank colour (hue, saturation, and luminance) were not predictive of call properties (duration, pulse number, pulse rate, and peak frequency). Furthermore, males with higher peak call frequency were only very slightly more yellow (hue, saturation). All aspects of nuptial colour and call properties were also mutually uncorrelated to snout-urostyle length and skin temperature of the signal bearer. Together, these results provide no direct evidence for any association between the expression of acoustic and colour signals in male L. revelata, which is consistent with the 'multiple messages' hypothesis that the two modes likely signal independent information and inferably play different roles in communication.

Male L. revelata are yellow when they vocalise during the breeding season. Consequently, they use multimodal signalling, but whether the information conveyed is directed at males, females, or both is unresolved, although presently anuran dynamic nuptial colour is only known to be directed at males and indicates sex (Sztatecsny et al. 2012; Rehberg-Besler et al. 2015; Kindermann and Hero 2016). For example, vocal signals may have the dual function of attracting a female whilst also keeping male rivals at bay such as in the Victorian smooth froglet (*Geocrinia victoriana*; Littlejohn and Harrison 1985). In the case of *G. victoriana* however, the advertisement call is biphasic (Webster and Bool 2022), where the female-directed, and male-directed, call components are incorporated into a single vocalisation (Littlejohn and Harrison 1985), unlike the monophasic advertisement call of *L. revelata*.

Furthermore, colour may be an important signal at close range and convey different information to male and female receivers. Our finding is similar to signalling in the European tree frog, Hyla arborea, and the dendrobatid, Allobates femoralis, where visual and auditory subcomponents of courtship and territorial signals do not reinforce each other (de Luna et al. 2010; Gomez et al. 2011); however, it seemingly contrasts with findings from the squirrel tree frog, Dryophytes squirellus, where vocal and visual cues likely function as backup signals, as both are important in mate attraction (Taylor et al. 2007). It also contrasts with Couch's spadefoot toad, Scaphiopus couchii, where vocal and colour cues form redundant backup signals (Vásquez and Pfennig 2007). In both the European and squirrel tree frogs, and S. couchii, the visual components are directed at female receivers (Taylor et al. 2007; Vásquez and Pfennig 2007; Gomez et al. 2009), although the visual signals in these examples differ from the dynamic sexual dichromatism of L. revelata, so whether colour in this case would also be directed at females is not clear.

Duration, pulse rate and peak frequency are aspects of frog calls that are attractive to females, with females preferring lower frequencies and faster and longer calls (Ryan et al. 1992; Doty and Welch 2001; Witte et al. 2001; Taylor et al. 2007). In L. revelata, larger male body size was, expectedly, strongly associated with call frequency, resulting in lower frequency vocalisations. Presently however it is not known what function call traits play in mate choice in this species. Peak frequency in frogs is influenced by body size, with larger frogs vocalising at lower frequencies (Keddy-Hector et al. 1992), and in the toad *Bufo bufo*, it is a reliable signal of male quality that is used by conspecific males to settle disputes (Davies and Halliday 1978). We did not find any substantive relationship between the degree to which males were yellow and any aspect of their call. Intuitively, it is unlikely that aspects of male colour are conveying information primarily directed at females for the purpose of mate attraction, given the lack of correlations between colour and vocal traits normally attractive to females, and considering the known function of anuran dynamic sexual dichromatism (e.g. Sztatecsny et al. 2012). However, without testing for trait function, particularly nuptial colour, this is at best a preliminary conclusion. Further, additional examination of correlations between colour and vocal signals, and individual fitness traits, would add clarification to the likely purpose of this multimodal signal in *L. revelata* (and more broadly in anurans with dynamic sexual dichromatism) and the intended receiver or receivers.

Dynamic sexual dichromatism in frogs is believed to function as a signal indicating sex to other males, rather than to females (Sztatecsny et al. 2012; Rehberg-Besler et al. 2015; Kindermann and Hero 2016). Whilst our findings cannot directly support this hypothesis, given that we found no correlation between call and colour traits, and we did not test for trait function, they do not necessarily contradict it. A correlation between call and colour would suggest that dynamic sexual dichromatism in L. revelata is possibly a reinforcing backup signal and hence more likely directed at females for the purposes of mate attraction, rather than at males for the purpose of sex recognition. Male colour regularly advertises quality to females in anurans such as Scaphiopus couchii (Vásquez and Pfennig 2007) and inferably natterjack toads (Zamora-Camacho and Comas 2019), and other vertebrates more generally (e.g. bowerbirds, Endler and Day 2006; guppies, Kodric-Brown 1985; and three-spined sticklebacks, Rowland et al. 1995). However, colour can also advertise competitive or fighting ability in frogs including female Mannophryne trinitatis (Wells 1980; Greener et al. 2020) and male ability in a range of taxa such as Augrabies flat lizards (Platysaurus broadleyi; Whiting et al. 2006) and dragonflies (Libellula luctuosa; Moore 1990).

Irrespective of whether sexually selected dynamic colour in L. revelata (and other anurans) is directed at males, females, or both, it is possible that the nuptial colour also conveys information on male quality. Ontogenetic sexual dichromatism indicates quality in the neotropical frog Mannophryne trinitatis, a species known to defend individual territories (Greener et al. 2020). If nuptial display colour is indicative of male quality and this information is received by rival males in a breeding aggregation, the signal could help regulate social structure, preventing combat and associated energy expenditure, similar to the function of vocal signals in Bufo bufo (Davies and Halliday 1978). As dynamic sexual dichromatism in frogs is associated with large (and generally noisy) breeding aggregations (Bell et al. 2017), it would be beneficial to both sexes for male colour to indicate individual quality, to rivals, potential mates, or both.

We did not investigate whether aspects of colour are correlated with the 'whistle' call in *L. revelata*, which is anecdotally a probable territorial or agonistic signal and therefore likely directed at rival males. When several vocalising male *L. revelata* displaying nuptial colour were housed together, the 'whistle' call became the dominant vocalisation, whilst intensity of yellow nuptial colour visually increased (GNW unpublished data). If nuptial colour is primarily directed at males, it may form part of a backup signal with the 'whistle' call, rather than the female-directed courtship 'whirring' call. It is worth noting that direct conflict between male *L. revelata* was never observed over the course of this study, during which frogs were present in high-density breeding aggregations, in close proximity around breeding sites, and even when a female was once observed being amplected simultaneously by two males.

In summary, it is clear that nuptial colour in L. revelata is apparently unlikely to reinforce the information conveyed in the female-directed advertisement call, although this should be confirmed in future studies that examine trait function and additional correlations with other measures of individual quality, such as body mass. This suggests to us that multimodal signalling in L. revelata goes beyond mate attraction and likely also conveys other information, potentially male competitive ability to rival males. However, we cannot exclude the possibility that some other aspect of quality, or that similar, or even the same information is conveyed to females (e.g. immunocompetence), through male nuptial colour. As an additional caveat, without experimental manipulation similar to that conducted on Allobates femoralis (de Luna et al. 2010), Dryophytes squirellus (Taylor et al. 2007), Rana arvalis (Sztatecsny et al. 2012), Incilius luetkenii (Rehberg-Besler et al. 2015) and Litoria wilcoxii (Kindermann and Hero 2016), it is difficult to establish the function of the male nuptial colour in L. revelata.

Our study helps address a significant gap in data on multimodal signalling in frogs. To the best of our knowledge, our study is the first to test for a relationship between vocal and dynamic colour signals in any frog species. Consequently, these findings provide important insight into the nature of multimodal signalling in frogs. The lack of a significant relationship between vocal and colour traits is intriguing because it invites the possibility that males are signalling different information about quality. Future studies that address the nature of what that information represents will be hugely valuable. This could be investigated by experimentally testing for colour trait function independent of vocalisation; establishing whether the mechanism of the colour change is hormonal, similar to other sexually dichromatic anurans including Litoria wilcoxii (Kindermann et al. 2013) and Buergeria robusta (Tang et al. 2014); or exploring whether nuptial colour correlates with individual fitness traits of male frogs or their offspring.

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Data availability The dataset used in the analysis is accessible online via OSF: https://osf.io/b4xa8/?view_only=a4b14047326f44648d86 a6cef799d792.

Declarations

Ethics approval This research was carried out under NSW OEH scientific licence SL100887 and with Macquarie University animal ethics approval (ARA 2012–011).

Conflict of interest The authors declare no competing interests.

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