

A continental assessment of diurnality in frog calling behaviour

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Abstract Acoustic signalling is evolutionarily important, influencing sexual selection and serving as a premating isolation mechanism. There is a strong evolutionary basis for acoustic signalling to occur nocturnally across many terrestrial vertebrate groups including mammals, reptiles and amphibians. Within some of these groups, there is a general assumption that ‘most taxa are nocturnal’ in their acoustic signalling, and this is a particularly strong held view for most frogs. Here we challenge this well-accepted notion by quantifying diurnal calling behaviour in Australian frogs, leveraging a continental-wide citizen science dataset. Of 196 species present in the citizen science dataset, 140 (71%) were recorded at least once during the day. Of the most commonly observed species (i.e. species with at least 150 calls recorded in the database), there were surprisingly high rates of diurnal calling: 14 species had >25% of their calls recorded during the day. We also found that the relative rate of diurnal calling in frogs showed a strong phylogenetic signal, suggesting that the plasticity in calling behaviour as it relates to time of the day is strongly evolutionarily conserved. Our results highlight a suite of ecological and evolutionary questions that are worthy of further investigation.

Key words: acoustic signalling, anurans, behaviour, frog calling, phylogenetic signal.

INTRODUCTION

Virtually every animal species – through a range of morphological, behavioural and physiological characteristics – performs some form of signalling. Signalling is a fundamental component of the reproduction, fitness and personality of individuals (Rohwer & Rohwer 1978; Hammerschmidt & Todt 1995), and at population and species levels, signalling often serves as a premating isolation mechanism, dictating species boundaries and driving sexual selection (Otte 1974; Rendall *et al.* 2009; Emlen *et al.* 2012). Of all signals, acoustic signalling is arguably one of the most ubiquitous across terrestrial vertebrates (cf. visual signalling), including amphibians, mammals and reptiles (Chen & Wiens 2020), highlighting the importance of understanding the ecological and evolutionary consequences of acoustic signalling.

Many vertebrate classes and corresponding lineages have evolved to show predominantly nocturnal or diurnal behaviour patterns in order to optimise the relative costs and benefits of nocturnal or diurnal activity (e.g. balancing the perceived and realised predation risks throughout different times of the day;

Metcalf *et al.* 1998). Within mammals for example, diurnality has independently re-emerged in a variety of lineages (Smale *et al.* 2003). Even within a specific class (i.e. Aves), there can be diverging life history strategies, where some orders (e.g. Passeriformes) are predominantly diurnal and other orders (e.g. Strigiformes) are predominantly nocturnal. This differentiation of daily activity patterns can even be evident within a sympatric genus (e.g. jackals; Loveridge & Macdonald 2003). Such differentiation in activity patterns, across different taxonomic levels, likely results from niche separation (i.e. partitioning space and other resources in time based on activity or the efficiency of resource acquisition). Understanding the relationship between phylogenetic relatedness and diurnal and/or nocturnal activity is important for understanding how this life history strategy evolved among and within specific taxonomic groups.

The activity pattern of an organism (i.e. nocturnal or diurnal) should evolutionarily influence its form of signalling used. Indeed, acoustic communication evolved from nocturnal activity independently across vertebrate groups (Chen & Wiens 2020), probably reflecting an evolutionary response to maximise acoustic signalling when visual signalling is inadequate. However, acoustic signalling is likely to evolve in other cases when visual signalling is inadequate, for example in complex environments (e.g. dense forests) or over longer distances. Therefore, quantifying whether acoustic signalling is generally nocturnal or

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diurnal within and among species may provide a better understanding of how acoustic signalling evolved as a dominant form of signalling across vertebrates.

Several groups of animals are ancestrally nocturnal (Anderson & Wiens 2017; Chen & Wiens 2020), leading to present-day activity patterns that are predominantly nocturnal, that is, amphibians, gekkotan lizards, crocodylians and mammals. In many of these groups, species within them are simply assumed to be nocturnal, but very little data are available to support these assumptions. Frogs are one such example that are suggested to be generally nocturnal. For example, survey guidelines state that ‘most species [of frogs] are nocturnal and are more readily detected at night’ (Commonwealth of Australia 2010). Other texts state that ‘most species of adult anurans are completely or partly nocturnal’ (Rich & Longcore 2006, pg. 197); that ‘in many species of anuran amphibians (frogs and toads), adults are normally active only at night’ (Duellman & Trueb 1994); and ‘in general, anurans tend to be nocturnal’ (Rocha *et al.* 2015). Quantification of such behaviour has been historically limited, given a lack of available data and the relative cost of collecting detailed behaviour data. While frogs may be primarily nocturnal, diurnal activity may be absent, rare or even common in specific taxa.

Here we quantify the relative nocturnality or diurnality of calling behaviour in Australian frogs, leveraging a broad-scale empirical dataset of frog recordings that was collected by citizen scientists and validated by experts (Rowley *et al.* 2019; Rowley & Callaghan 2020). Specifically, we (i) quantified the number of species that called during the day, (ii) quantified the relative rates of diurnal calling by species to enable cross-species comparisons and (iii) tested for evolutionarily relatedness (i.e. phylogenetic signal) in the relative rates of diurnal calling across species.

METHODS

We used the FrogID citizen science dataset (Rowley *et al.* 2019) to quantify diurnal calling in frogs. FrogID – hosted by the Australian Museum – is a successful citizen science project throughout continental Australia, with more than 200 000 records of calling frogs. Participants use their smartphone and record calling frogs for 20–60s periods, and these records are then submitted to a central database where they are identified to species by expert reviewers. We used FrogID data from 11th November 2017 to 31 March 2020, contributed by 12 410 users. All records with a location accuracy of >3000 m were eliminated from analyses as these represent uncertain records potentially with far greater accuracy issues (Rowley *et al.* 2019). For more details on the FrogID dataset and methodological details (see Rowley *et al.* 2019; Rowley & Callaghan 2020).

For each record, we calculated the sunrise and sunset time by passing the record’s coordinates and date of occurrence to the ‘getSunlightTimes’ function from the *suncalc* package in R (Thieurmel & Elmarhraoui 2019). We then were able to delineate any record that was between sunrise and sunset using these times. In order to be conservative, however, we defined the diurnal period of the day as the period between 2 h past sunrise and 2 h before sunset. Our initial summary investigated all records in the FrogID dataset. But because many species are sampled relatively few times (Rowley & Callaghan 2020), in order to quantify the proportion of a species’ calls that were diurnal and nocturnal we only investigated species with at least 150 total records in the dataset.

We used a recently published global phylogenetic tree for amphibians (Jetz & Pyron 2018), trimmed to our relevant taxa, using the consensus tree fully sampled from 10 000 posterior trees including imputed taxa. The phylogenetic tree was downloaded from: <https://doi.org/10.5061/dryad.cc3n6j5>. We then tested for phylogenetic signal using the *phylosignal* package in R (Keck *et al.* 2016). All analyses were carried out in R statistical software (R Core Team 2020) and relied heavily on the tidyverse workflow (Wickham *et al.* 2019).

RESULTS

We used a total of 91 121 recordings from 68 112 unique latitude/longitude sites resulting in 164 270 records of 196 species of frogs. Across all recordings, there was a clear pattern where the majority of recordings (56%) were made between 19:00 and 22:00 (Fig. S1), suggesting that most citizen scientists sample during these hours for frogs. Of all recordings, 39% were recorded between official sunrise and sunset times based on that respective record’s location, whereas 61% were recorded between sunset and sunrise. Of all recordings, 19% were classified as diurnal (i.e. at least 2 h after sunrise and 2 h before sunset) whereas 81% of recordings were classified as nocturnal. Of all 196 species, 140 species (71%) were recorded at least once during the day (Table S1). Of the most-recorded species (i.e. 74 species with at least 150 records recorded in the dataset), the proportion of diurnal records varied considerably, ranging from 0 for *Cophixalus ornatus*, *Cylorana alboguttata*, *Cylorana novaehollandiae*, *Litoria xanthomera*, *Mixophyes coggeri* and *Uperoleia altissima* to 0.72 for *Crinia tasmaniensis* and 0.43 for *Geocrinia vitoriana* (Fig. 1). Of all 74 species considered, the mean proportion of diurnal calls was 0.12 ± 0.14 (Fig. 1; Fig. S2).

Out of the total 23 150 recordings classified as diurnal, 10 species made up 75% of these records, with the majority being *Crinia signifera* (27.6%), followed by *Limnodynastes peronii* (9.69%), *Crinia glauerti* (8.13%), *Limnodynastes tasmaniensis* (7.33%), *Limnodynastes dumerilii* (7.16%), *Litoria fallax* (4.20%), *Litoria adelaidensis* (3.14%), *Litoria moorei*

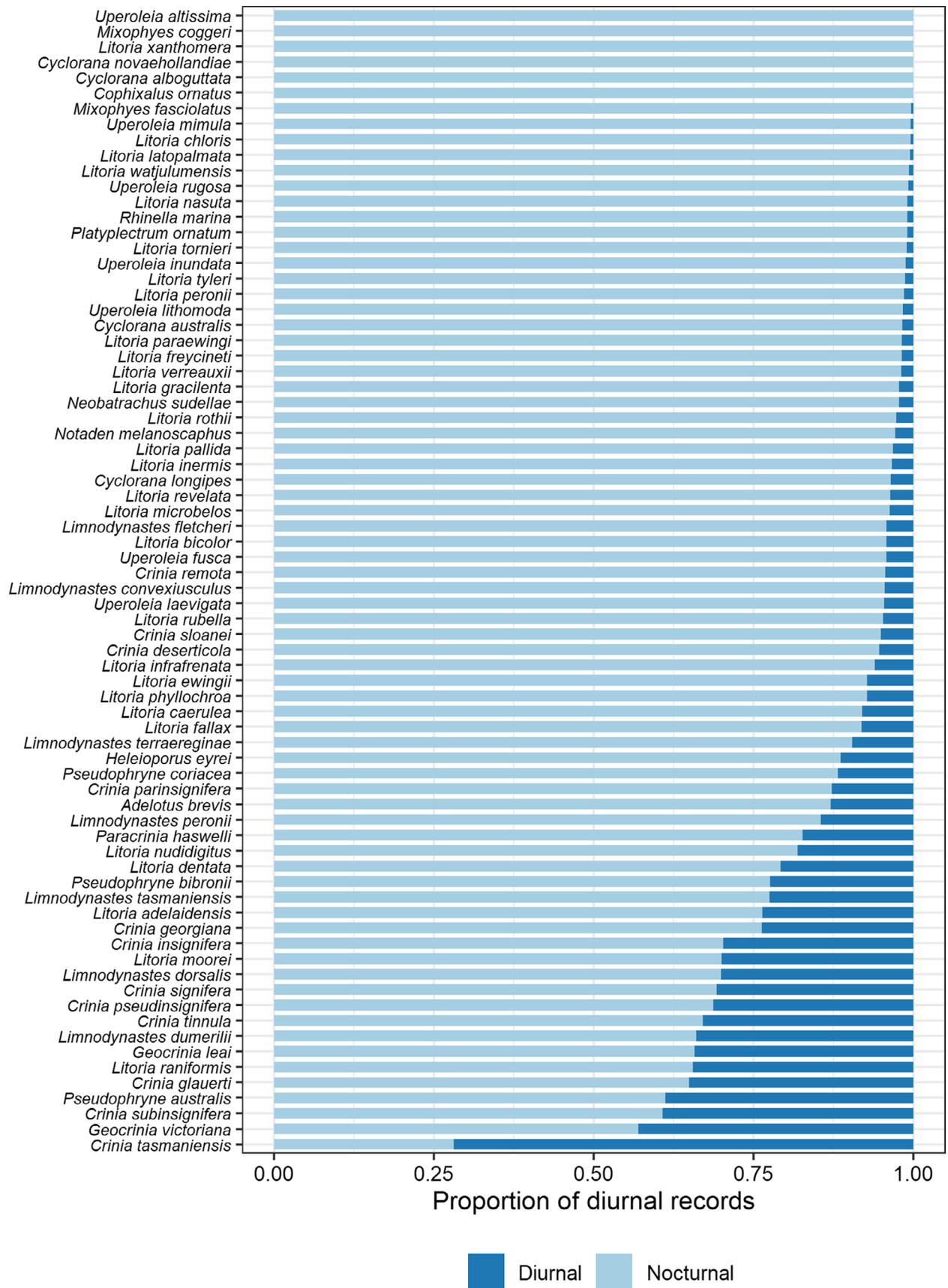


Fig. 1. The proportion of diurnal and nocturnal recordings for 74 species with a minimum of 150 total records.

(2.98%), *Crinia georgiana* (2.93%) and *Crinia parinsignifera* (2.66%); reflecting the overall commonness of these species in the dataset. The proportion of diurnal calling by a species showed a strong phylogenetic signal ($K^* = 0.382$, $P = 0.0001$), for all potential tests (Fig. 2; Table 1). Most diurnally calling frogs were in the family Myobatrachidae, and at the genus level, *Geocrinia* had the highest mean proportion of diurnal calls (0.39; $N = 2$ species), followed by *Crinia* (0.27; $N = 12$ species), and *Pseudophryne* (0.24; $N = 3$ species). However, not all genera in the family had a high proportion of diurnal calls, with frogs in the myobatrachid genus *Uperoleia* rarely recorded calling in the day (0.02; $N = 7$ species). The family Hylidae displayed little diurnal calling in

Table 1. Results of a phylogenetic signal analysis investigating whether there was phylogenetic signal in the species-specific rates of diurnal calling (i.e. the proportion of recorded calls which were diurnal)

	Cmean	I	K	K*	Lambda
Statistic	0.374	0.149	0.365	0.382	0.931
P-value	0.0001	0.0007	0.0008	0.0001	0.0001

both genera *Litoria* (0.07; $N = 29$) and *Cyclorana* (0.01; $N = 4$ species), except for the bell frogs (*Litoria rainformis* and *L. moorei*). Species in the family Limnodynastidae did not appear to be highly diurnal

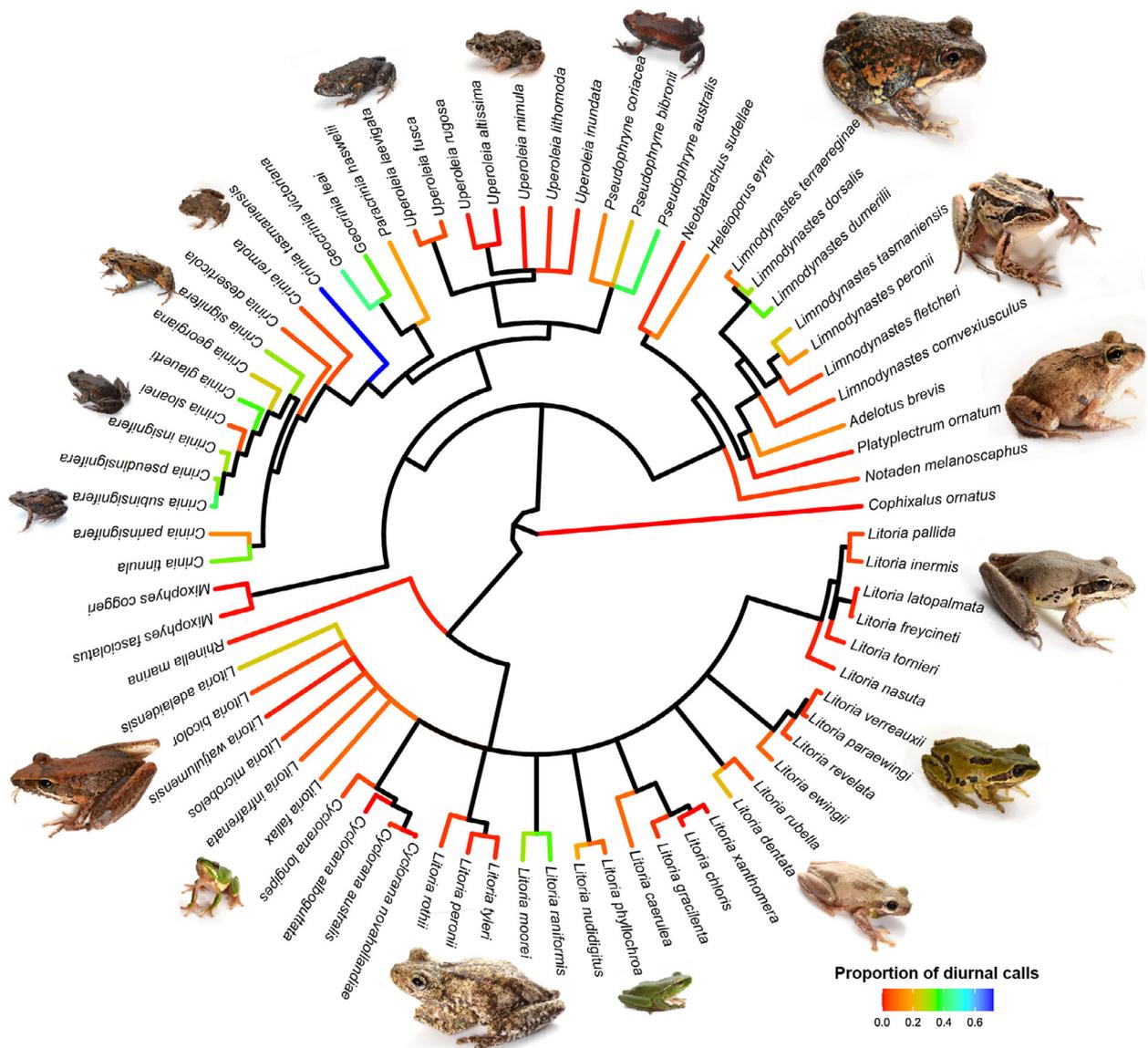


Fig. 2. Phylogenetic tree representing the proportion of diurnal calls for each of 74 species included in analysis (i.e. those with >150 records).

in their calling activity except for the banjo frogs (*L. dumerilii* and *Limnodynastes dorsalis*).

DISCUSSION

Macro-ecological comparisons of entire continental faunas are expensive and time-consuming. With the advent of citizen science (Jordan *et al.* 2015), there are increasingly available data to make continental-scale comparisons to deduce patterns in biogeography, species richness and relative abundance (Devictor *et al.* 2010; Kobori *et al.* 2015; Callaghan *et al.* 2020). We leveraged a continental-scale citizen science dataset to highlight a surprisingly high rate of diurnal calling behaviour across Australian frogs, despite a generally assumed pattern of nocturnality in frogs in general (Duellman & Trueb 1994; Rich & Longcore 2006, pg. 197; Rocha *et al.* 2015), and Australian frogs specifically (Commonwealth of Australia 2010). We found that most Australian frog species, 140 of the 196 species available in the dataset (including the introduced Cane Toad *Rhinella marina*), showed at least some evidence of diurnal calling, with at least one record of them calling during the day. For 14 species, a substantial proportion (>25%) of recordings of the species were during the day. Diurnal calling in frogs probably has an evolutionary, physiological, and/or ecological basis. We found a strong phylogenetic signal (Fig. 2), reinforcing the idea that diurnal behaviour is strongly evolutionarily conserved (Chen & Wiens 2020). For example, some closely related species (e.g. *Litoria peronii*, *Litoria tylerii* and *Litoria rothii*) all showed similar rates of diurnal calling behaviour. However, there was substantial divergence in the proportion of diurnal calling detected even within closely related species (e.g. *L. dumerilii* and *Limnodynastes terraereginae* or *C. parvinsignifera* and *Crinia timmula*; Fig. 1 and Table S1). This conforms with other taxa (e.g. mammals or birds) where there are diverging and converging behaviours of diurnality taxonomically. Yet more work is needed to understand the generality of these responses in frogs.

In frogs, drivers for interspecific differences in diurnality of calling may be related to a species' ability to withstand desiccation, influenced by physiological adaptations and their macrohabitat, and breeding microhabitat, or to avoid predation, either via toxins or crypsis. Indeed, the three species with the highest proportion of diurnal calls are small (<2 cm body length) frog species that call from secretive positions in wet or moist microhabitats. Other species with relatively high rates of diurnal calls are known to produce toxins (e.g. *Pseudophryne*; Smith *et al.* 2002) probably reducing their predation risk. Avoiding competition with conspecific males or other calling frog species via acoustic interference may also be a driver for diurnal

calling activity (e.g. Wagner 1989). Our findings open up a suite of research questions that should be further explored at smaller-scales, including how does frog calling diurnality differ (i) across habitat types, (ii) between urban and non-urban areas, (iii) across functional groups, (iv) with known predator abundances or anti-predator defenses, (v) with breeding strategies and (vi) across the breeding season (Mccallum & Mccallum 2018). All of these will fundamentally enhance our understanding of the ecological and evolutionary mechanisms promoting diurnality of calling behaviour in frogs.

In addition to the interesting ecological and evolutionary consequences of our results, we also highlight important implications for survey practices of frogs. Previously, there was one well-known group of diurnally active and calling frogs in Australia – the 'Day Frogs' (genus *Taudactylus*). Here we reveal for the first time the relatively high rate of diurnality in calling behaviour among many other species across genera and families. The recognition that calling diurnality of calling is so widespread in Australian frogs has implications for documenting species distributions and trends in Australian frogs, particularly important considering the large number of threatened frog species in Australia. Three of the top 10 species in terms of their proportion of diurnal calling are globally threatened species (*C. timmula*, *Pseudophryne australis*, *Litoria aurea*, IUCN 2020). Further, some species which have been rarely recorded in the dataset, such as *Cophixalus neglectus*, *Cophixalus saxatilis* and *Notaden weigeli*, were only recorded during the day with 1, 3 and 2 records respectively (Table S1). Although most frogs are probably more active at night, there is potential to increase sampling during the day as well.

While our findings were made possible via large-scale citizen science data, there are several associated biases with such citizen science data (Bird *et al.* 2014). First, citizen scientists from the FrogID project showed a distinct sampling bias within a day where most sampling (i.e. recordings) takes place during the evening hours (Fig. S1). This bias of observations towards the evening hours suggests that the prevalence and rate of diurnal calling behaviour is potentially conservative, given that the sampling may reflect the bias of assuming frogs are nocturnal. This temporal sampling bias within a day is likely to be systematic, influencing species in the same direction: observers are not preferentially sampling one species over another at a given time of day. This systematic bias highlights that the relative species-specific rates of diurnal calling are likely to be comparable across species (i.e. Fig. 2). FrogID records are generally biased towards areas of dense human population (Callaghan *et al.* 2020), potentially leading to taxonomic or other bias in our dataset (e.g. few arid-zone species, or small range-restricted species meet our criteria of 150 recordings in

FrogID). And therefore, more ‘urban species’ may be disproportionately represented in our dataset. Clearly, more dedicated sampling during the day – from both citizen scientists and experts – is necessary to fully understand the extent and prevalence of diurnal calling behaviour of frogs. However, the recent increase in passive acoustic monitoring devices (e.g. Smith *et al.* 2020) combined with machine learning for identifying frog species (e.g. Brodie *et al.* 2020), will potentially help to overcome biases associated with citizen science sampling in FrogID (e.g. a lack of null records) and current frog sampling protocols employed by experts (e.g. largely nocturnal), providing the necessary data to better understand diurnal calling behaviour of frogs in Australia.

We revealed widespread diurnal calling behaviour across a taxonomically, ecologically and geographically diverse frog fauna, with important implications for our understanding of evolutionary process and patterns, as well survey design. Previous investigations into the daily activity patterns of frogs has generally been limited to intensive field-work, usually at localised spatial extents (e.g. Woolbright & Stewart 1987; Runkle *et al.* 1994; Hodgkison & Hero 2001; Nelson *et al.* 2017; Mccallum & Mccallum 2018). As with other taxa (e.g. mammals, birds) there are clear divergences in the nocturnality and diurnality of behaviour patterns among species, highlighting that other factors are at play which promote niche separation and coexistence. Our results will help to better understand how and when acoustic signalling evolved within predominantly nocturnal taxa such as frogs. The scale of this study was made possible via citizen science data, and these data – combined with more local-scale behavioural studies – should serve as the basis for a suite of future studies investigating the prevalence and underlying mechanisms that promote diurnal calling in frogs, as well as how this relates to the broader evolution of diurnal and/or nocturnal behaviour.

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AUTHOR CONTRIBUTIONS

Corey Callaghan: Formal analysis (lead); methodology (lead); visualization (equal); writing-original draft (equal); writing-review & editing (equal). **Jodi**

Rowley: Conceptualization (lead); formal analysis (supporting); methodology (supporting); visualization (equal); writing-original draft (equal); writing-review & editing (equal).

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CONFLICT OF INTEREST

We declare no conflict of interest.

Data availability statement

All data cannot be made Open Access due to data sensitivity/privacy of the underlying recordings and localities of rare species, but a subset of these data (i.e. depending on geoprivacy concerns) are made available to researchers on an annual basis (Rowley & Callaghan 2020). Further data can be requested from the Australian Museum or the corresponding author.

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SUPPORTING INFORMATION

Additional supporting information may/can be found online in the supporting information tab for this article.

Fig. S1. The total submission patterns from all 91 121 unique FrogID submissions to the FrogID dataset.

Fig. S2. The distribution of number of species and the proportion of diurnal calls for those species.

Table S1. The number of diurnal calls, total number of recordings, and the percent of recordings that were diurnal for 140 species of Australian frogs.