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Anthropogenic habitat modification alters calling phenology of frogs

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Abstract

Anthropogenic habitat modification significantly challenges biodiversity. With its intensification, understanding species' capacity to adapt is critical for conservation planning. However, little is known about whether and how different species are responding, particularly among frogs. We used a continental-scale citizen science dataset of >226,000 audio recordings of 42 Australian frog species to investigate how calling—a proxy for breeding—phenology varied along an anthropogenic modification gradient. Calling started earlier and breeding seasons lengthened with increasing modification intensity. Breeding seasons averaged 22.9 ± 8.25 days (standard error) longer in the most modified compared to the least modified regions, suggesting that frog breeding activity was sensitive to habitat modification. We also examined whether calls varied along a modification gradient by analysing the temporal and spectral properties of advertisement calls from a subset of 441 audio recordings of three broadly distributed frog species. There was no appreciable effect of anthropogenic habitat modification on any of the measured call variables, although there was high variability. With continued habitat modification, species may shift towards earlier and longer breeding seasons, with largely unknown ecological consequences in terms of proximate and ultimate fitness.

KEYWORDS
advertisement call, Australian frogs, bioacoustics, breeding season, citizen science, urbanization, vocal communication

1 | INTRODUCTION

Biodiversity is under tremendous pressure in the Anthropocene (Johnson et al., 2017; Sullivan et al., 2017). Habitat loss (e.g. deforestation) and fragmentation have undoubtedly driven species declines and extinctions (Dirzo et al., 2014; Young et al., 2016), but even subtle changes in temperature, resource availability, noise or light pollution caused by human modification can contribute to declines (Alberti, 2015; Hamer & McDonnell, 2008; Imhoff et al., 2010;

Perry et al., 2008; Shannon et al., 2016). Species either need to adapt with anthropogenic environmental changes or continue to decline.

Some species have successfully adjusted their behaviours to cope with novel selection pressures (Lowry et al., 2013; Merckx et al., 2021; Sih et al., 2011). These include changing active hours or nesting locations to avoid humans and novel predators (Tagg et al., 2013), and taking advantage of new food sources (e.g. crops, human-provided food) or habitats (e.g. artificial wetlands; Ditchkoff et al., 2006; Sih et al., 2011). Some organisms have had life-history

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changes, including altered breeding regimes, to align with changes in resource availability (Fleischer et al., 2003; Møller, 2009). Where reproduction is pushed into unfavourable periods, suitable breeding sites, mating opportunities, fecundity, and parent and offspring quality and survival can decline (Both et al., 2006; Dawson, 2008; Mayor et al., 2017). Differences in temperature, rainfall, food availability and light disturbance between urban and non-urban environments can influence reproductive timing (Beck & Heinsohn, 2006; Deviche & Davies, 2014), driving, for example, earlier and longer mating and breeding in urban areas compared to rural areas (Hart et al., 2018; Møller et al., 2015). This may benefit some species where increasing courtship and mating opportunities improve breeding success and fecundity (Halupka et al., 2021; Pröhl, 2003; Souza et al., 2021; Tarwater & Arcese, 2018). However, it is unclear how widespread phenological adjustments are among taxa inhabiting anthropogenically modified environments and what the implications are for species' persistence.

For acoustically communicating species, communication (e.g. vocalizations) and signal detection may also be compromised in anthropogenically modified landscapes, with fitness consequences that compound the effects of habitat loss and degradation (Bee & Swanson, 2007; Francis & Barber, 2013; Laiolo, 2010). Traffic and urban noise can directly interfere with signal propagation (Cunnington & Fahrig, 2010); buildings and artificial structures can promote signal scattering, potentially lowering signal efficiency (Rabin & Greene, 2002; Slabbekoorn et al., 2007); and pollution can indirectly affect vocal activity and complexity (Gorissen et al., 2005). Furthermore, artificial lighting can alter biological rhythms and predation risk, affecting the timing and amount of calling (Baker & Richardson, 2006; Dominoni & Partecke, 2015; Fuller et al., 2007; Hall, 2016). As male advertisement calls drive sexual selection for many species, particular calling behaviour may be better adapted to maintain reproductive success (Cunnington & Fahrig, 2010; Neelon & Höbel, 2019). Many components of calls are under behavioural and physiological control, including call duration, repetition rate, dominant frequency and signal timing (Bee et al., 2000; Bosch & De la Riva, 2004; Byrne, 2008; Neelon & Höbel, 2019). Adjustments to these (e.g. calling louder, at higher dominant frequency, or at a different time of day) can reflect adaptions to evolutionary novel (e.g. noisy or high light pollution) environments (Brumm, 2004; Fuller et al., 2007; Miller, 2006; Mockford & Marshall, 2009; Nemeth & Brumm, 2009).

Amphibians are affected by anthropogenically modified landscapes, including cities (Callaghan et al., 2021), with relatively high proportions of threatened species among vertebrate taxa (Hoffmann et al., 2010; Rodrigues et al., 2014), but their adaptations to these environments remain largely unknown. Some frog species change their call frequencies, amplitude or call rate with anthropogenic noise (e.g. traffic or engine noise; Cunnington & Fahrig, 2010; Hoskin & Goosem, 2010; Parris et al., 2009; Sun & Narins, 2005), but these responses are species specific, with inconsistencies among species (Roca et al., 2016; Sun & Narins, 2005). Our understanding of amphibian behavioural responses to anthropogenic habitat

modification largely comes from small-scale studies of calling (e.g. a single pond, or a single city; but see Mitchell et al., 2020) or one anthropogenic variable (e.g. noise or light pollution; Shannon et al., 2016). There is a need to understand the generality of responses to habitat modification across a range of species and their habitats using geographically broad data.

We used acoustic data from a continental-scale citizen science project (FrogID; Rowley et al., 2019) to investigate how anthropogenic habitat modification affected frog breeding and calling behaviour, across a range of species. First, we examined how breeding phenology changed along an anthropogenic modification gradient. This gradient was represented by a continuous index that quantified the intensity of land modification, from unmodified to highly modified, based on the presence of human stressors, including human settlement and agriculture (Kennedy et al., 2019). We used species' calling seasons as a proxy for their breeding seasons, given that calling is a precursor to frog breeding and vocalizations closely track breeding phenology (Hoffmann & Mitchell, 2021; Klaus & Lougheed, 2013; Larsen et al., 2021; Willacy et al., 2015). Then, we analysed calls from a subset of species to determine whether call characteristics changed along an anthropogenic modification gradient.

2 | MATERIALS AND METHODS

2.1 | FrogID dataset

We obtained acoustic data from FrogID, an Australia-wide citizen science project based on audio recordings of frog advertisement calls (Rowley et al., 2019). Citizen scientists submitted 20–60 s recordings, containing one or more species of calling frogs, via a smartphone application which recorded the location, date and time of recording. Experts validated each recording, identifying all calling frog species. We collated data from 10 October 2017 to 19 May 2021, excluding recordings with uncertain locations (i.e. accuracy >3 km; more stringent filtering, excluding recordings with accuracy >1 km, did not affect the results; Table S1). Most recordings (96.8%) were accurate to ≤1 km, and 89.5% were accurate to ≤100 m (Figure S11).

2.2 | Breeding phenology

We divided Australia into square grid cells per 0.1 degrees (∼11.1 km) of latitude and longitude and assigned each FrogID observation to a grid cell according to its location. Observations on the border of two grid cells (0.3% of records; 759/226,820) were assigned to both grid cells, but we also tested the effect of omitting these records and results were unchanged (Table S1). We used Google Earth Engine (Gorelick et al., 2017) to calculate the average global human modification (GHM) index (Kennedy et al., 2019) within each grid cell, as a proxy for the intensity of anthropogenic habitat modification

(Figure 1). The GHM index measures global human land modification and is a continuous index ranging from 0 (no human impact) to 1 (high impact). It is based on 13 anthropogenic stressors within five major categories (human settlement; agriculture; transport, mining and energy production; and electrical infrastructure); it is strongly correlated with other common measures of anthropogenic impact including human population density and night-time lights (see Figure S7).

We removed duplicate FrogID records (observations of the same species from the same location [latitude and longitude] and date) and included only grid cells with at least 20 unique observations of a species, from across three or more days of the year (data aggregated across all years; Li et al., 2021). Most grid cells were considerably better sampled than this (average of 3.3±2.4 species in each grid cell; each combination of species and grid cell had 79.2±158.0 observations from across 38.5±36.8 days; all values are mean±standard deviation [SD]). We omitted species represented in less than 10 grid cells from analyses. This threshold maximized our species sample size (42/204 [20.6%] species remained) while ensuring sufficient grid cells per species for statistical analyses (see below for details).

For each species in each grid cell (i.e. for all species-grid cell combinations), we estimated the start ('onset': 5th percentile of calling), middle ('median': 50th percentile) and end ('offset': 95th percentile) of the breeding season (nth day of year) using the R package 'phenesse' (Belitz, Campbell, & Li, 2020). The phenesse estimator is a Weibull-parameterized estimator, generating robust phenological estimates for any percentile of a distribution from sparsely sampled presence-only data (Belitz, Larsen, et al., 2020). Our minimum sample size of 20 observations was conservative given reliable and accurate estimates can be obtained using as few as 10 observations (see Figures S1–S4; Belitz, Larsen, et al., 2020). Onset and offset were defined as the 5th and 95th percentiles of calling, respectively, as these can be estimated with greater accuracy than the absolute start or end of the breeding season (Belitz, Larsen, et al., 2020). We also estimated the duration of the breeding season within each grid cell, calculated as the number of days between these defined onset and offset days.

Since many species bred throughout December and January (summer), we could not use actual nth day of year as measures for the onset, median and offset of the breeding season because
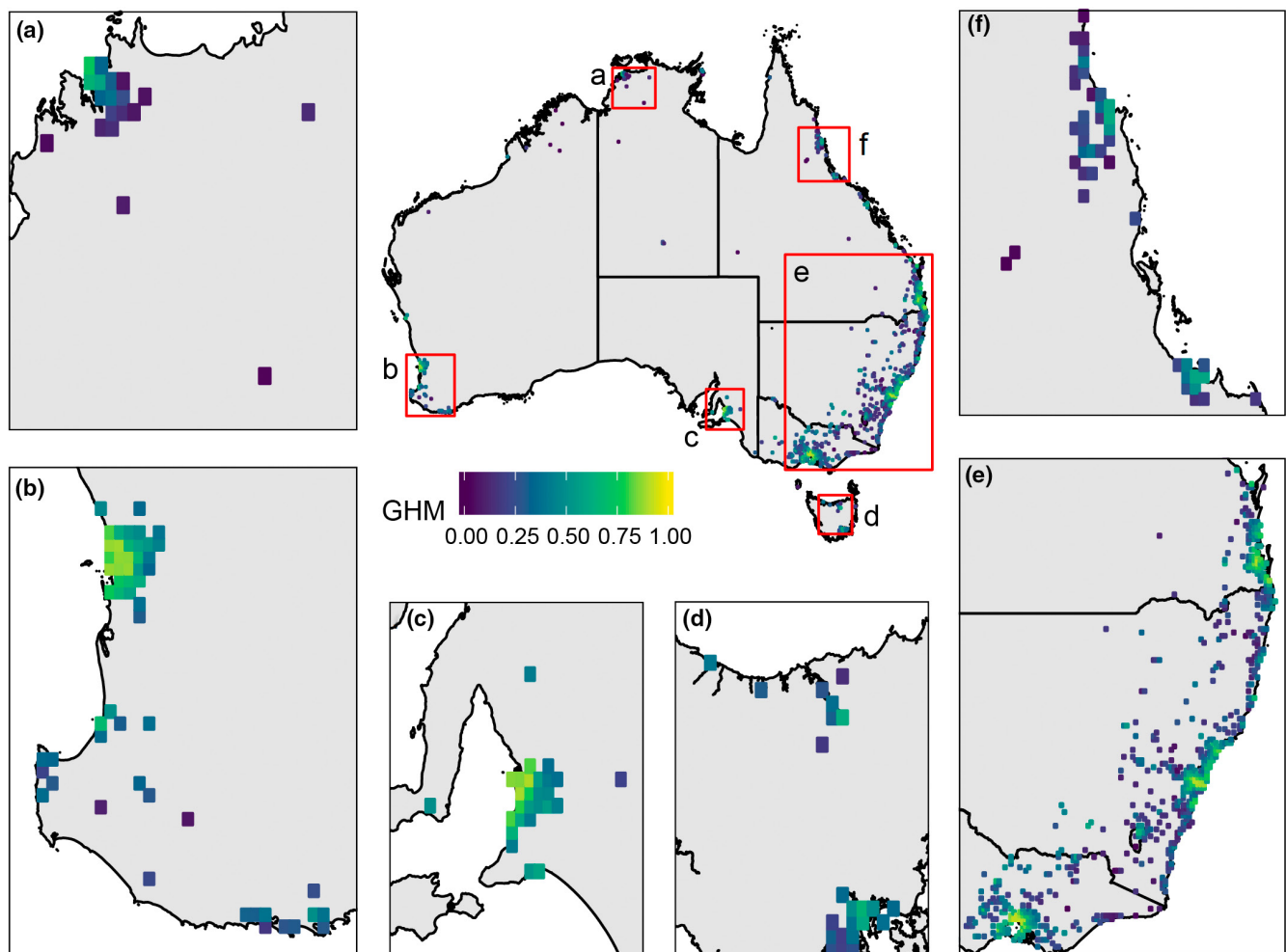

FIGURE 1 Locations of analysed grid cells across Australia where there were breeding season estimates (onset, offset, median and duration) for least one frog species, and their corresponding global human modification index (GHM; 0 [no modification]—1 [high modification]), with inset maps (a–f) of enlarged grid cells (each 0.1×0.1 decimal degrees in size; approximately 11.1×11.1 km).

it resulted in discontinuities between *n*th day 366 (31 December) and *n*th day 1 (1 January) in statistical models. For example, for the tusked frog (*Adelotus brevis*), the middle (median) of the breeding season occurred between *n*th day 285 (October) and day 52 (February), depending on the grid cell. Since we needed to recognize days 1–52 (January–February) as a continuation from days 285 to 366 (October–December) for linear modelling, we set day 1 to be a day in the middle of each species' non-breeding period and calculated the nth day of year of the onset, median and offset of the breeding season relative to this. For example, for *A. brevis*, which typically bred from June to April, day 1 was set to early May (day 122; 1 January was originally considered day 1). After this adjustment, the median day of year of breeding occurred between days 163 and 296 (cf days 285–52), eliminating discontinuities.

For some species-grid cell combinations, the breeding duration was estimated to be more than 366 days (110/2863, 3.8%). We set these values to 366 to represent year-round breeding, obviously excluding onset, median and offset estimates. Furthermore, some offset estimates could not be accurately determined (i.e. offset was estimated to occur on nth day of year >366, outside of the expected range: days 1–366) and were therefore removed (few species with extended breeding seasons, e.g. *Crinia signifera*, *Litoria ewingii* and *Litoria verreauxii*). To test the sensitivity of our results across grid sizes, we repeated all analyses using grid cells per 0.25 and 0.05 degrees of latitude and longitude (approximately 27.8 and 5.6 km, respectively). As the results were similar across all grid sizes (see Tables S2 and S3), we only present results from 0.1-degree grid cells.

2.3 | Call characteristics

To explore whether call characteristics changed along an anthropogenic modification gradient, we selected three frog species for acoustic analyses—the Striped Marsh Frog (*Limnodynastes peronii*), Peron's Tree Frog (*Litoria peronii*) and Green Tree Frog (*Litoria caerulea*)—according to the following criteria: (1) large number of recordings available for analyses, (2) recordings were distributed across a large geographical area to allow spatially broad analyses and (3) recordings were available from both anthropogenically modified and relatively unmodified habitats to allow exploration of relationships between calling and habitat modification. We randomly selected 300 FrogID recordings for each species, excluding recordings submitted from the same location on the same or successive nights to reduce non-independent data. We used Google Earth Engine (Gorelick et al., 2017) and the latitude and longitude of each recording to calculate the intensity of habitat modification at each recording location. We used the same GHM index used in the breeding phenology analyses, but rather than calculating average values within grid cells, we calculated the average GHM index within a 1 km buffer of each recording location, given susceptibility of frogs to nearby anthropogenic disturbances (e.g. roads; Villaseñor

et al., 2017). To ensure the buffer encompassed the survey site, we removed recordings with location accuracy >1 km.

For acoustic analyses, recordings were converted from AAC to WAV format (sampling rate of 44.1 kHz with 16 bits per sample) using a VLC Media Player (http://www.videolan.org/). We removed recordings from analyses if calls of individual frogs could not be identified due to background noise or multiple overlapping calls of different individuals. We then determined the call duration, call repetition rate, intercall interval, calling effort and call dominant frequency (see Table 1 for definitions of call variables; Köhler et al., 2017) from each recording, using Raven Pro 1.5.0 with a time resolution of 5.8 ms and a frequency resolution of 86.1 Hz (Hann window; FFT length = 512). For *Lit. peronii*, which has a more complex call consisting of a series of notes (rather than a single note, as in *Lim. peronii* and *L. caerulea*; Figure 2), we also counted number of notes per call and quantified note repetition rate.

In each recording, we measured all the calls of a single individual (3–34 calls [mean ± SD in parentheses; 14 ± 7] per recording of *Lim. peronii*; 1–24 calls [5 ± 4] per recording of *Lit. peronii* and 5–107 calls [38 ± 20] per recording of *L. caerulea*) and used the average values for each individual for subsequent statistical analyses (i.e. individuals as the unit of replication; Köhler et al., 2017). Some call variables could not be measured in all recordings. For example, we retained recordings containing a single high-quality (e.g. high amplitude) *Lit. peronii* call (*n* = 13) to calculate call duration, call dominant frequency, notes per call and note repetition rate, but not call repetition rate, intercall interval or calling effort because calculating these variables required a minimum of two calls per recording.

Frog calls can be influenced by environmental temperature (Köhler et al., 2017) and so we estimated the temperature at the time of recording (to the nearest hour). We obtained the daily minimum and maximum temperatures from the nearest weather station, extracting the data using the 'bomrang' package (Sparks et al., 2020) in R. We used the 'chillR' package (Luedeling, 2019) to interpolate any missing daily temperature records (using the minimum and maximum temperatures in the 15 days before and after the date of recording) and to generate an hourly temperature record (from daily minimum and maximum temperatures) (Mitchell et al., 2020).

2.4 | Statistical analyses

We used timing of breeding seasons and call characteristics of the different frog species as response variables in our models. To examine whether frog breeding phenology was related to anthropogenic habitat modification, we used linear mixed-effects models with the phenological estimate (duration of the calling season in days, or the *n*th day of year of the onset, median or offset of the calling period) as the response variable and modification intensity (GHM index) as the predictor variable. We included the grid cell (grid ID) and species as random intercept terms, with a random slope for the effect of modification on each species. All analyses were performed in R version 3.6.2 (R Core Team, 2019).

Call characteristic	Definition and response variable used in analysis
Call duration	The duration (s) of a single call; measured from the start to the end of the call (a distinct vocalization, separated from other calls by silent intervals that are usually much longer than the call)
Call repetition rate	The ratio of the number of calls to the duration in which the calls were made; given as the number of calls per minute
Intercall interval	The interval (s) between two consecutive calls; measured from the end of the call to the start of the next call
Calling effort	The proportion of calling within a signalling period. The ratio of the call duration to the call period (call duration plus intercall duration)
Call dominant frequency	The frequency (Hz) of the call that contains the greatest sound energy
Notes per call	The number of notes (the main subunit of a call) in one call. Calls can consist of one note (e.g. *Limnodynastes peronii* and *Litoria caerulea*) or multiple notes (in which 100% amplitude modulation occurs between notes, but this interval is short relative to the call duration; e.g. *Lit. peronii*)
Note repetition rate	The number of notes per second within a call, calculated as the ratio of the number of notes to the duration in which the notes were made

TABLE 1 Definitions of frog call variables (Köhler et al., 2017), quantified from Australia-wide audio recordings submitted to the FrogID project, which were independently used in analyses to test their relationships to anthropogenic habitat modification

Models were fitted using the 'lme4' package (Bates et al., 2015) and *p*-values were calculated using the 'lmerTest' package (Kuznetsova et al., 2017). Normal quantile and residual plots of the models did not reveal noticeable deviations from model assumptions. To test for effects of sampling biases (e.g. more records in more modified areas), we randomly subsampled the data so that grid cells had the same number of observations and reran the models. Results were essentially unchanged (Table S1), indicating that sampling bias did not explain the results.

To examine the relationships between call characteristics and the anthropogenic modification gradient, we fitted a generalized additive model for each call variable (Table 1) for each species. The call variable was the response variable and the GHM index was the predictor variable. Day of year, geographical location (latitude and longitude) and temperature were added into the model as smoother covariates given their influence on frog calling (Mitchell et al., 2020). Correlations between model predictors were minimal (Figure S13). Data were normally distributed or otherwise log-transformed (see Table 4).

Recognizing that the GHM index represents cumulative human stressors, we separately analysed two components of modification, urbanization and agriculture, to better understand their relative impacts on breeding phenology and call variables (see Materials S1). We repeated the statistical analyses with VIIRS night-time light (Elvidge et al., 2017; Mills et al., 2013) and cropland extent data (Global Food-Support Analysis Data Cropland Extent; Teluguntla et al., 2015), respectively, as the predictor variables. Analyses performed using the urbanization index and the GHM index revealed very similar results, indicating that trends observed along the modification gradient can at least be attributed to urban impacts (Tables S4 and S6; Figure S9).

3 | RESULTS

3.1 | Breeding phenology

We analysed 42 species (17% of Australia's frog species), meeting the minimum criteria (see methods), representing 226,820 observations from 872 unique grid cells. Each species had at least 419 total observations; each species-grid cell combination had 79 ± 158 (mean ± SD) observations. Results were consistent, regardless of grid cell size (see Tables S2 and S3). The duration of the calling season was significantly positively related to increasing habitat modification (Table 2). Calling seasons were 22.9 ± 8.25 days (SE) longer in the most highly modified areas (170.7 days; GHM = 1), compared to unmodified areas (147.8 days; GHM = 0; Figure 3a). All 42 species increased the duration of their calling season with increasing anthropogenic modification (Figure 4a). The Western Banjo Frog (*Limnodynastes dorsalis*) increased its calling season duration the most, with a 33.7-day difference between the most highly modified and unmodified regions. Conversely, the Eastern Banjo Frog (*Limnodynastes dumerilii*) had the shortest increase in calling season duration, with an 11.6-day difference between the most highly modified and unmodified regions.

Frogs started calling significantly earlier (earlier onset of calling season) with increasing anthropogenic habitat modification (Table 2; Figure 3b), resulting in these longer calling seasons. Of the 42 species examined, 40 species (95%) started calling earlier (Figure 4b, blue points, negative values), but two species started calling slightly later (Figure 4b, blue points, positive values) with increasing habitat modification. *Litoria rothii* had the largest trend towards earlier calling seasons (62.3 days earlier) while *Heleioporus eyrei* had the largest
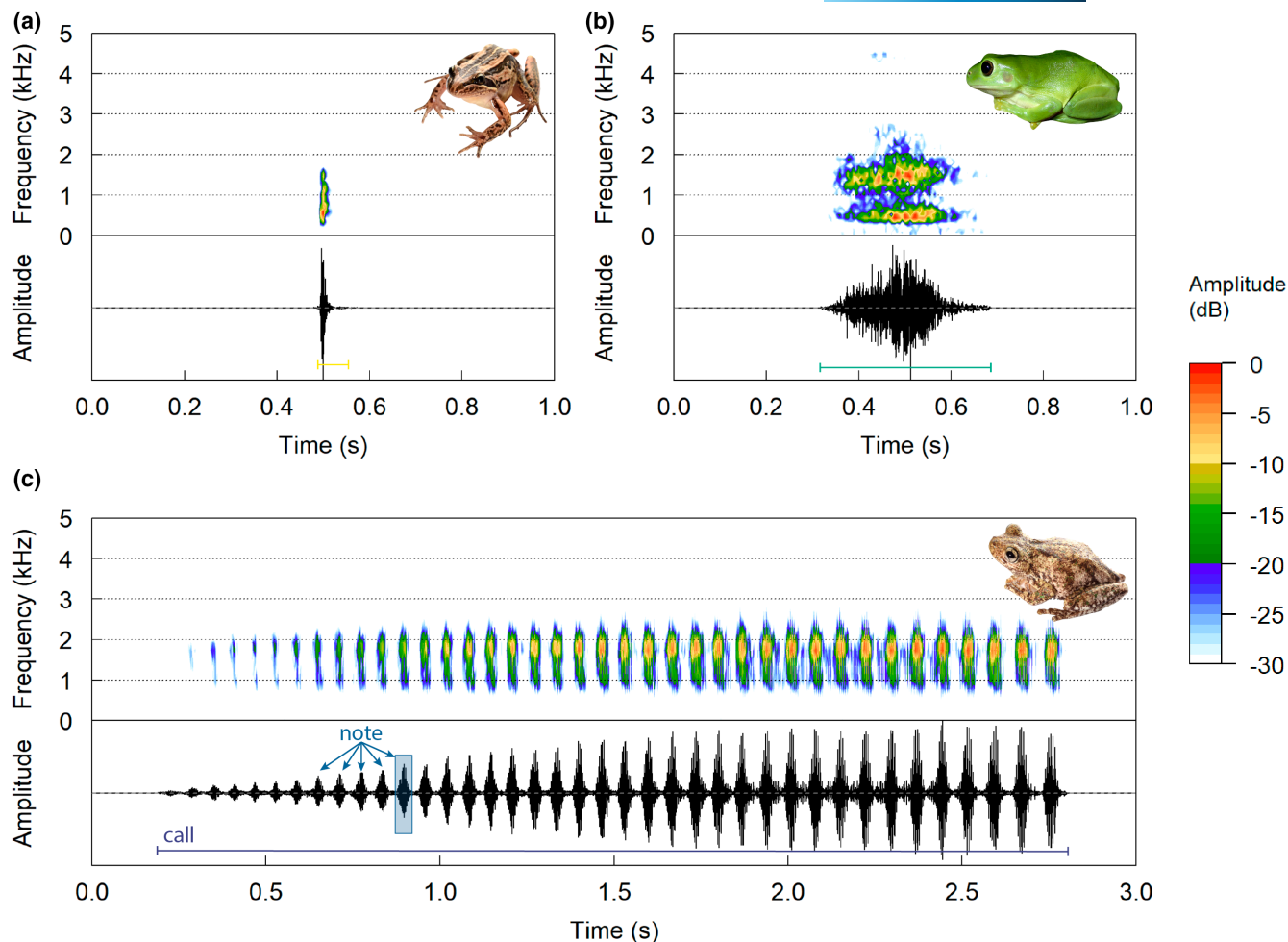
FIGURE 2 Examples of spectrograms (top; showing the frequency [Hz] and amplitude [dB] of sound over time) and oscillograms (bottom; showing relative changes in amplitude over time) of single calls of (a) *Limnodynastes peronii*; (b) *Litoria caerulea* and (c) *Litoria peronii*, with coloured lines below oscillograms indicating call duration. Calls of *Limnodynastes peronii* and *L. caerulea* consist of a single note. Calls of *L. peronii* consists of a series of notes; a single note is highlighted in the blue rectangle.

TABLE 2 Results of linear mixed-effects models examining the relationships between anthropogenic habitat modification (global human modification index, GHM) and breeding phenology (duration of the calling season in days; start of the calling season [onset; 5th percentile; day of year, DOY]; median DOY of calling [50th percentile]; and end of the calling season [offset; 95th percentile; DOY]), with sample size (N), and significance at $p < .05$ in bold

Response variable	Term	Estimate	SE	p	N
Duration	Intercept	147.773	8.653	**<0.001**	2863
	GHM	22.904	8.251	**0.008**	
Onset	Intercept	128.547	4.299	**<0.001**	2753
	GHM	−31.711	6.402	**<0.001**	
Median	Intercept	204.75	3.705	**<0.001**	2753
	GHM	−18.918	4.925	**<0.001**	
Offset	Intercept	267.003	5.196	**<0.001**	2514
	GHM	3.142	5.611	0.578	

trend towards later calling seasons (3.8 days later) with increasing habitat modification. The middle of the calling season (median day of calling) was also significantly associated with the intensity of habitat modification (Table 2), occurring earlier with increasing modification for most species (41/42, 98%). On average, the middle of the calling season occurred 18.9 days earlier in the most highly modified, compared to unmodified, areas (Table 2; Figure 3c). Unlike the start and middle of the breeding season, the end (offset) of the calling season was unrelated to the intensity of anthropogenic habitat modification, varying among species (Table 2). As modification levels increased,
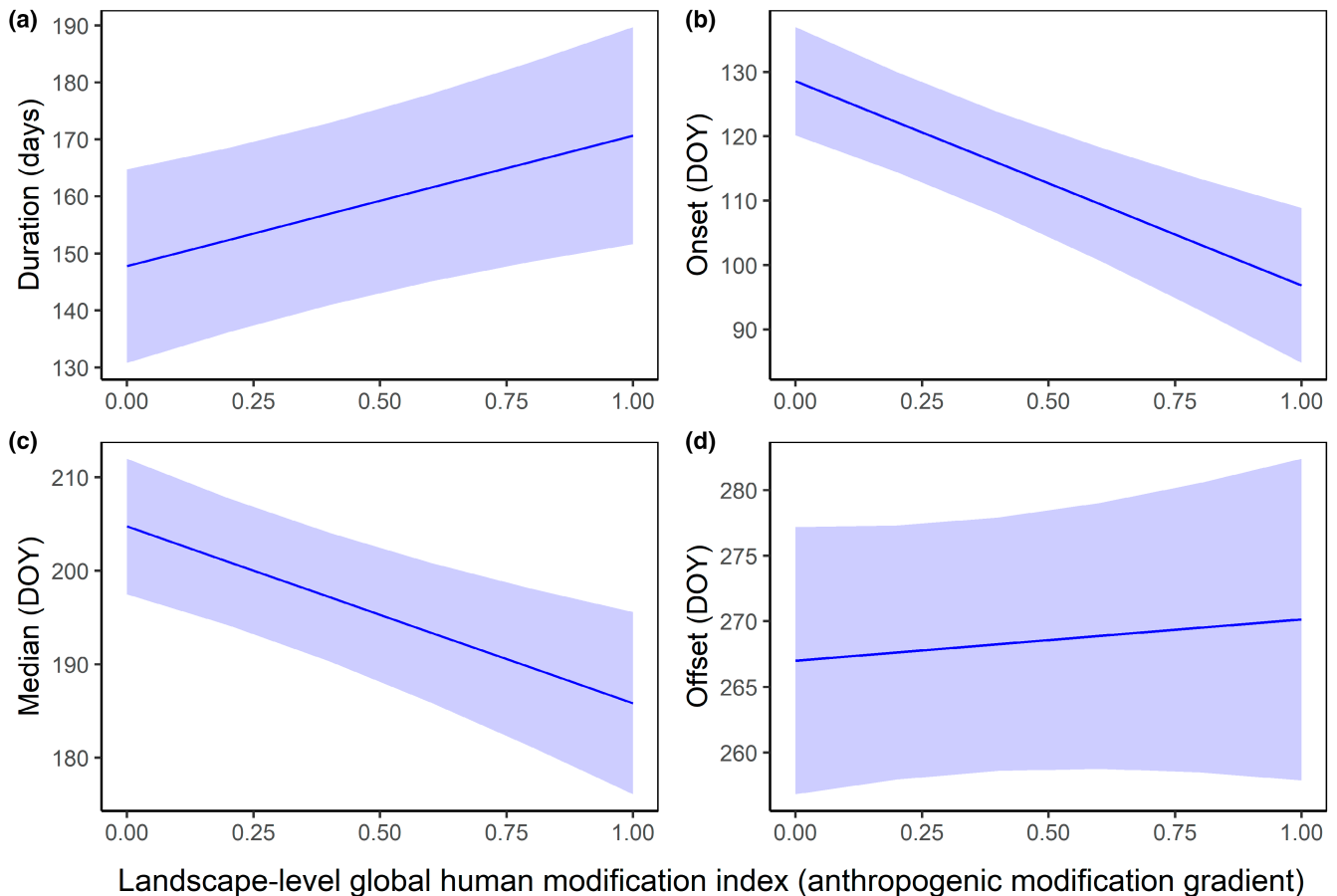
FIGURE 3 Predictions from linear modelling (with 95% confidence intervals) relating frog breeding phenology (a) duration of the calling season; (b) start of calling season (5th percentile; day of year, DOY); (c) median DOY of calling (50th percentile); (d) end of calling season (95th percentile; DOY) to the global human modification index (0 (no modification)—1 (high modification); 0.1-degree grid cells, approximately 11.1 km × 11.1 km).

calling seasons ended earlier for 17 species (40%; Figure 4b, red points, negative values) but later for 25 species (Figures 3d and 4b, red points, positive values).

3.2 | Call characteristics

We quantified call variables from 441 recordings (131 *Lim. peronii*, 171 *L. caerulea* and 139 *Lit. peronii*). They were all highly variable within each species (Table 3; Figure S14). However, none of the measured call variables were related to the intensity of anthropogenic habitat modification (Table 4 and Table S8). Some call variables were associated with air temperature, geographical location (latitude and longitude) or day of year, but this varied among species, with no consistency. For *Lim. peronii*, the call duration and calling effort varied significantly with temperature, while call duration also varied significantly with location (Table 4). For *L. caerulea*, call repetition rate, intercall interval and call dominant frequency were significantly related to geographical location, whereas call duration, repetition rate and intercall interval varied significantly with temperature (Table 4). The duration of *Lit. peronii* calls, the mean number

of notes per call and note repetition rate varied significantly with day of year; dominant frequency and note repetition rate varied with location; and note repetition rate was additionally significantly associated with temperature (Table 4).

4 | DISCUSSION

Our multispecies continental-scale study showed large-scale changes in frog breeding phenology, surprisingly consistent across all 42 species examined, along an anthropogenic modification gradient. Where humans have highly modified habitats with buildings, roads, lights and other stressors (Kennedy et al., 2019), frogs had extended breeding seasons compared to less modified areas, primarily because they bred earlier (Table 2 and Figure 4). The phenological trends—significantly earlier start and middle, but no significant change to the end, of the breeding season with increasing habitat modification (Figure 3)—highlight complex environmental cueing of breeding phenology. Frog call characteristics were unrelated to habitat modification (Table 4), but the large variation in calls (Table 3) could potentially represent behavioural
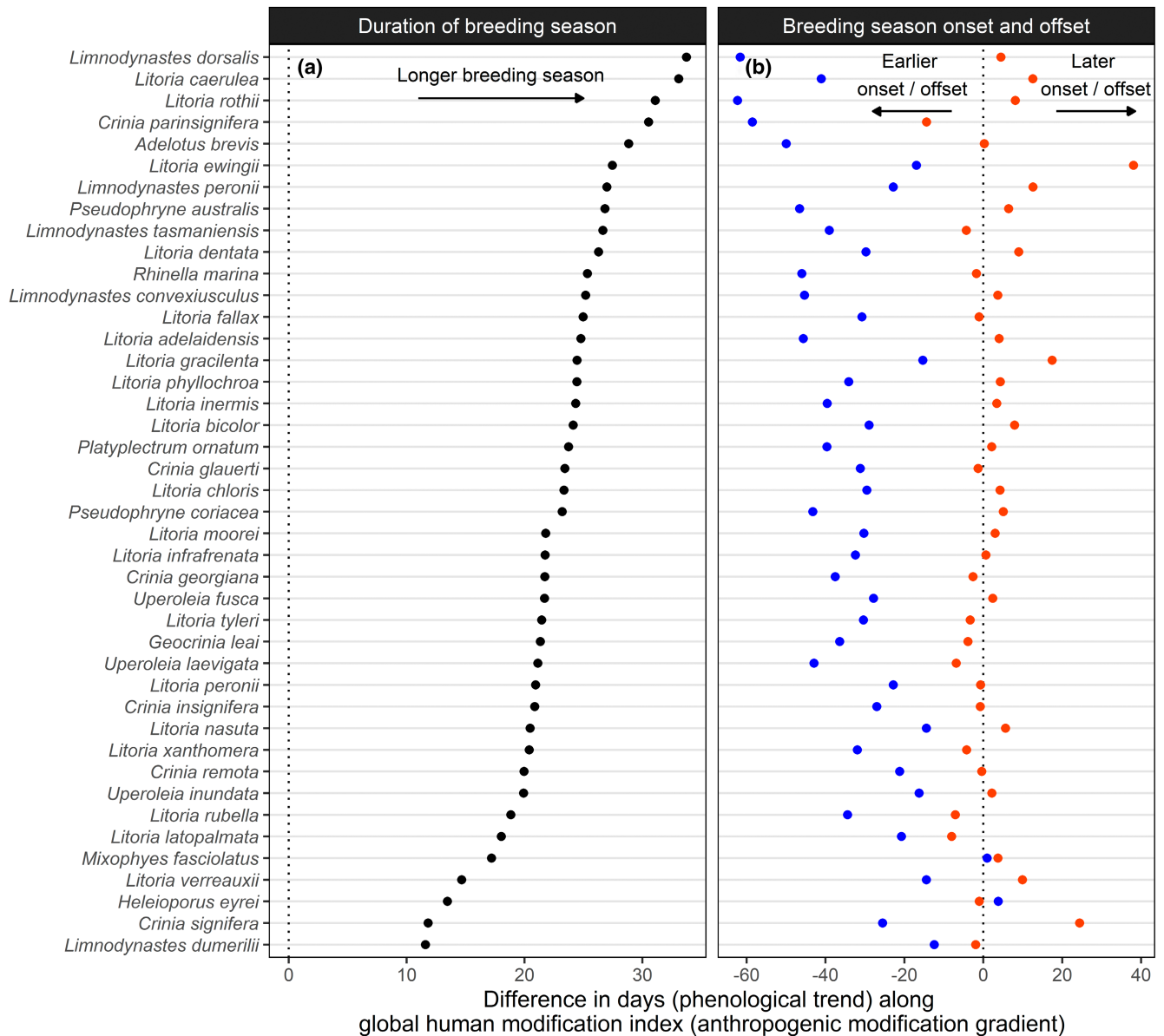
FIGURE 4 Differences in days from the value expected under null hypothesis (0, i.e. no relationship between breeding phenology and intensity of anthropogenic habitat modification) in (a) duration (black) and (b) onset (blue) and offset (red) of the breeding season for each species, along an (increasing) global human modification index (anthropogenic modification gradient; 0 [no modification]—1 [high modification]).

flexibility that is important for keeping up with anthropogenic changes. These behavioural responses could have important ecological implications.

4.1 | Breeding phenology

Amphibian breeding seasons are highly labile compared to other animal and plant taxa (Parmesan, 2007). Amphibians can breed a month or more earlier every decade with climate change and even average rates of change can be more than double that of other taxa (Parmesan, 2007; Todd et al., 2011; While & Uller, 2014). Similarly, our study showed that frog breeding season durations

differed by as many as 33.7 days (average 22.9 days; Table 2) along an anthropogenic modification gradient. The consistency of response was unexpected, given the diversity of phenological responses among amphibians, even when relatively few species are examined (Parmesan, 2007; Todd et al., 2011). They highlight the potential far-reaching impacts of the Anthropocene on communities of organisms. They also align with increasing understanding of the effects of urbanization on breeding phenology, where there is earlier breeding or mating of plants (Neil & Wu, 2006), birds (Møller et al., 2015), ants (Chick et al., 2019; Hart et al., 2018) and mosquitoes (Townroe & Callaghan, 2014), compared to non-urban habitats (but see Fisogni et al., 2020). This can be coupled with extended breeding seasons (e.g. Møller et al., 2015 and this

TABLE 3 Summary statistics (mean, standard deviation, minimum values, maximum values and sample size) for each of the seven call variables in relation to the three frog species analysed

Call variable	Species	Mean ± SD	Minimum	Maximum	N
Call duration (s)	*Lim. peronii*	0.065 ± 0.037	0.016	0.205	131
	L. caerulea	0.255 ± 0.059	0.123	0.449	170
	Lit. peronii	1.752 ± 0.620	0.342	5.542	139
Call repetition rate (calls/min)	*Lim. peronii*	17.980 ± 8.062	0.486	48.211	131
	L. caerulea	106.296 ± 25.669	16.044	183.214	171
	Lit. peronii	7.803 ± 5.602	1.598	32.304	127
Intercall interval (s)	*Lim. peronii*	3.945 ± 2.536	1.122	22.294	131
	L. caerulea	0.361 ± 0.288	0.095	3.460	170
	Lit. peronii	9.846 ± 7.171	0.501	35.542	126
Calling effort (call duration/call period)	*Lim. peronii*	0.022 ± 0.017	0.003	0.107	131
	L. caerulea	0.463 ± 0.096	0.259	0.774	170
	Lit. peronii	0.226 ± 0.140	0.041	0.740	125
Dominant frequency (Hz)	*Lim. peronii*	1007.456 ± 326.733	339.119	1948.775	131
	L. caerulea	900.858 ± 378.016	362.969	1741.811	170
	Lit. peronii	1862.490 ± 214.467	1248.950	3014.650	139
Notes per call	*Lit. peronii*	28.469 ± 9.959	3.333	83.000	120
Note repetition rate (notes/s)	*Lit. peronii*	16.473 ± 3.854	6.851	27.154	120

Call variable	Species	GHM index	Day of year	Location (latitude, longitude)	Hourly temp	N
Call duration	*Lim. peronii*	0.569	0.081	**0.049**	**0.002**	102
	L. caerulea	0.721	0.224	0.203	**<0.001**	157
	Lit. peronii	0.290	**0.015**	0.440	0.465	110
Call repetition rate	*Lim. peronii*	0.718	0.247	0.470	0.061	102
	L. caerulea	0.130	0.496	**0.003**	**<0.001**	158
	*Lit. peronii**	0.149	0.265	0.078	0.341	98
Intercall interval	*Lim. peronii**	0.659	0.124	0.163	0.067	102
	*L. caerulea**	0.229	0.812	**0.015**	**0.002**	157
	*Lit. peronii**	0.147	0.549	0.699	0.276	97
Calling effort	*Lim. peronii**	0.184	0.154	0.176	**0.006**	102
	*L. caerulea**	0.144	0.512	0.164	0.415	157
	*Lit. peronii**	0.205	0.771	0.872	0.439	96
Dominant frequency	*Lim. peronii*	0.414	0.397	0.462	0.406	102
	L. caerulea	0.415	0.440	**<0.001**	0.656	157
	Lit. peronii	0.336	0.126	**<0.001**	0.492	110
Notes per call	*Lit. peronii*	0.313	**0.002**	0.176	0.133	96
Note repetition rate	*Lit. peronii*	0.578	**0.010**	**0.002**	**<0.001**	96

TABLE 4 Statistical output (*p*-values, significance at *p* < .05 in bold) of generalized additive models examining relationships between call variables (*indicates log-transformed variables) and anthropogenic habitat modification (global human modification index, GHM), day of year, location, and temperature for the three frog species analysed

Note: N represents sample size. See Table S8 for detailed model outputs.

study), but in some plants, extended breeding has been linked to a later end (rather than an earlier start) to the breeding season (Li et al., 2021). Environmental cues are variously affecting reproduction of different species in urban environments.

We speculate that many different confounding and interacting factors could be contributing to these phenological changes, including temperature, rainfall and hydrology (Diamond et al., 2014; Li et al., 2019). Though the modification (GHM) index reflects

multiple human stressors, urban factors were likely important drivers of frog responses (Table S4 and Figure S9). Increasing temperatures are occurring with climate change and urban heat island (UHI) effects, contributing to earlier reproductive phenology in various taxa (plants, Neil & Wu, 2006; vertebrates and invertebrates, Parmesan, 2007). The combination of UHI effects and climate change may also be driving earlier breeding phenology for some frog species, as temperature can be an important cue for the initiation of breeding—emergence from overwintering sites, and commencement of breeding migrations and oviposition (Arietta et al., 2020; Gibbs & Breisch, 2001; Reading, 1998). A temporal analysis of frog reproduction in low modified and highly modified areas might show a shift with climate change. However, increasing temperature does not explain why autumn- and winter-breeding species (where increasing temperature presumably does not cue breeding, e.g. *Crinia georgiana*, *Crinia insignifera*, *Geocrinia leai*) exhibited earlier and longer (rather than shorter or unchanged) breeding seasons in modified areas (Figure 4).

Altered hydrology in modified environments, including increased runoff and flooding caused by large areas of impervious surfaces, and more extreme rainfall events (Pathirana et al., 2014), may also influence frog breeding phenology via effects on hydroperiods and stream flow (Hamer & McDonnell, 2008; Todd et al., 2011). Stormwater management and direct alteration of waterbodies (e.g. filling and draining) can change hydroperiods (Hamer & McDonnell, 2008), with urban areas generally supporting permanent waterbodies with relatively few temporary ponds (Oertli & Parris, 2019); this could affect timing of breeding for aquatic-breeding frogs. Indeed, most of the examined species typically breed in permanent water bodies (8/42; 19%) or a combination of permanent and ephemeral waterbodies (26/42; 62%; Liu et al., 2021; Murray et al., 2011). Year-round presence of suitable breeding habitat may stimulate these species to extend their breeding period. Similarly, changes to vegetation and soil type in anthropogenically modified environments may affect soil water potential and consequently alter breeding periods of terrestrial frogs (Hoffmann & Mitchell, 2021).

However, climate is probably not the only factor, given that urbanization drives bird (Møller, 2009) and plant (Li et al., 2021) breeding phenology after accounting for climate. Artificial lights can disrupt the photoperiod or lunar-related cues for frog breeding (Arietta et al., 2020; Grant et al., 2009). Environmental pollutants (including artificial lights) can also affect endogenous variables, such as reproductive hormones and stress levels (Forsburg et al., 2021), disrupting breeding behaviours (Gorissen et al., 2005; Hayes et al., 2010; Yamaguchi & Kelley, 2003). However, this explanation seems incongruous with our observed phenological trends (i.e. earlier and extended breeding). Increased resources in urban (compared to rural) landscapes are another possible driver of earlier and longer breeding seasons in anthropogenically modified areas, enabling species to maintain energy reserves and body condition for breeding for longer (Hoffmann & Mitchell, 2021; McCauley et al., 2000; Møller et al., 2015).

More research into the relative importance of environmental variables is needed but, given the end of breeding seasons was

unrelated to habitat modification (Table 2 and Figure 3), it is plausible that frogs are sensitive to different cues throughout the season (Grant et al., 2009). Environmental cues may strongly determine the start and peak of breeding, but the end of breeding may be less labile. Additionally, different species' breeding seasons may be variably constrained by these cues. Though all examined species had extended breeding seasons and most started breeding earlier in modified areas (Figure 4), the drivers behind specific phenological patterns, such as the relative magnitude of species' trends, are unclear. Exploring relationships between species' phenological trends and their ecological, physiological and behavioural traits may help to identify important drivers.

A key question is whether these changes can help species cope in modified landscapes. Earlier and extended breeding seasons can benefit frogs. Earlier breeding typically results in earlier metamorphosis, larger body size at autumn and, ultimately, improved overwintering survival and larger clutches (Altwegg & Reyer, 2003; Loman, 2009), while extended breeding seasons can create additional breeding opportunities (Juncá & Rodrigues, 2006). Frogs may be breeding earlier in modified habitats to capitalize on higher quality or more abundant food (Loman, 2009); they may be tracking shifts in insect phenology observed in urban areas (Hart et al., 2018), given their dependence on insects (Le et al., 2020). Phenological flexibility may be an important determinant of persistence in anthropogenically modified environments (Belitz et al., 2021). Breeding when resources and environmental conditions are not conducive to reproduction can cause failed reproduction, high larval mortality, increased competition and predation among sympatric species and, in more extreme cases, population declines and local extinctions (Klaus & Lougheed, 2013; Mayor et al., 2017; Todd et al., 2011). Phenological mismatches have occurred between migratory birds and their food resources (Mayor et al., 2017; Wanless et al., 2009), and plants and their insect pollinators (Hegland et al., 2009; Kudo & Ida, 2013). However, knowledge of whether similar mismatches are occurring among frogs, whether phenological changes can compensate for these and the consequences of altered frog phenology, remains limited.

Phenological changes are not necessarily adaptive. First, they did not seem to be related to the relative tolerance of individual species to anthropogenically modified habitats (Liu et al., 2021). For example, the responses of tolerant species such as *Litoria infrafrenata* and *Litoria moorei* were similar to less tolerant species such as *Geocrinia leai* and *Uperoleia laevigata* (Figure 4; Liu et al., 2021). Second, earlier breeding can decrease juvenile survival in cold climates as earlier laid eggs can be more susceptible to freezing and can take longer to develop (Loman, 2009), increasing the risk of predation (Chivers et al., 2001). Furthermore, if anthropogenically modified habitats function as ecological traps (i.e. species show a preference for habitats that reduce fitness), negatively impacting offspring survival and growth (Sievers et al., 2018), then changing breeding phenology may have no fitness benefits. Given the energetic costs of calling and increased risk of predation (Lemckert & Shine, 1993; Sullivan & Kwiatkowski, 2007), longer calling seasons in modified environments could even be maladaptive, representing wasted efforts.

4.2 | Call characteristics

Contrasting the strong phenological trends, there was no consistent pattern in the temporal or spectral properties of frog calls along an anthropogenic modification gradient (Table 4 and Figure S14). Our findings contradicted local and regional studies showing different bird call spectral properties between urban and rural populations (Mockford & Marshall, 2009) and changes to frog call characteristics with traffic noise (Cunnington & Fahrig, 2010; Hoskin & Goosem, 2010; Parris et al., 2009). However, they were consistent with a continental-scale acoustic assessment of red tree frogs (*Litoria rubella*), where calls were similarly variable and unrelated to an urbanization gradient (Mitchell et al., 2020). While we used a common dataset (audio recordings from the FrogID project), our findings were derived independently following standard acoustic analysis protocols. Together, they suggest that acoustic changes are not detectable at large scales when multiple anthropogenic stressors are examined simultaneously, possibly because calls exhibit plasticity in response to local noisy conditions (Cunnington & Fahrig, 2010) which are not consistent across broad scales (along large modification gradients). The type of modification may also be important. If anthropogenic noise is an important driver of acoustic changes, then calling patterns may emerge along an urbanization gradient, but not along a gradient of increasing agricultural modification. However, we examined whether call variables changed along urban and agricultural gradients (Tables S6 and S7) and found no consistent responses along either gradient, suggesting that broad-scale changes to habitat modification are unlikely in the examined species.

Alternatively, population-level shifts in call characteristics may be occurring but developing slowly (Parris et al., 2009); frogs may be changing call characteristics not measured here (e.g. amplitude; Halfwerk et al., 2015; but see Love & Bee, 2010); or broad-scale acoustic changes may be occurring among some, but not all species (Cunnington & Fahrig, 2010; Roca et al., 2016). Like *Litoria rubella*, our three analysed species are relatively tolerant of anthropogenically modified habitats (Liu et al., 2021) and may not be representative of all species. High variability within these species' calls (Table 3 and Figure S14; Weaver et al., 2020) may reflect their behavioural flexibility, which potentially contributes to their success in variably modified landscapes (Mitchell et al., 2020). However, some of this variability may be driven by environmental variables such as temperature (Mitchell et al., 2020; Parris et al., 2009). The role of call variability in breeding success in modified environments remains largely untested, providing opportunities to explore in both urban and non-urban adapted frogs.

5 | CONCLUSIONS

Humans are rapidly changing the planet in the Anthropocene, with significant ecological and evolutionary consequences. Understanding how these changes affect different species, across different life-history stages, remains important in predicting ecological and conservation ramifications. Our continental-scale citizen science data allowed us to examine these changes across a large suite of frog species, revealing consistent associations between phenology and anthropogenic habitat modification. The causes and long-term consequences remain unknown but are likely to be important. There is an opportunity to extend our understanding of the role of environmental variables in breeding phenology, and to assess the fitness consequences of phenological change by examining fecundity, breeding success and survival of frogs in modified habitats. Nonetheless, our research provides an important first look into frog breeding phenology along an anthropogenic modification gradient.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The complete raw dataset is not fully available due to sensitivities in relation to locations of rare or threatened species and citizen scientist information (Rowley & Callaghan, 2020). However, the data, with sensitive species' localities removed or buffered, are made available annually (Rowley & Callaghan, 2020; data available at GBIF: https://doi.org/10.15468/wazqft and FrogID: https://www.frogid.net.au/explore). The processed breeding phenology estimates (duration, onset, median and offset of the breeding season) and call characteristic data, and the code to reproduce our results are available on GitHub (https://github.com/liugracie/human_impacts_on_frog_phenology_and_calls) and are archived at Zenodo (https://doi.org/10.5281/zenodo.6939509).

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