Austral
ECOLOGY A Journal of ecology in the Southern Hemisphere

Austral Ecology (2022) **47**, 353–364

Breeding phenology of a terrestrial-breeding frog is associated with soil water potential: Implications for conservation in a changing climate

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Abstract Amphibian breeding is often linked to environmental cues. Given accelerating global climate change and habitat alteration, it is important to understand how environmental changes may affect male calling activity, the necessary precursor to mating. Here, we investigate the calling phenology and activity of *Geocrinia alba*, a critically endangered terrestrial-breeding frog with a highly restricted distribution in southwestern Australia – a region undergoing significant warming and drying. We investigated whether calling periods differed across eight sites during a single breeding season, and the environmental conditions associated with calling activity at the start, peak and end of the calling period. We found consistent and prolonged calling activity over several months of the austral spring, but the length of the calling period varied two-fold across sites, ranging from 3 to 6 months. Initiation of calling by *G. alba* was relatively similar across sites and was associated with warmer temperatures and higher soil water potential. However, the end of the calling period varied from October to January and was significantly associated with decreasing soil water potential. Calling only occurred when soils were close to saturation point, between −8 to −11 kPa, and therefore, breeding opportunities were likely also constrained by the length of time that soils were close to saturation. Changes in the regional climate, such as declining winter rainfall, could result in shorter breeding periods and consequently reduced breeding opportunities. More broadly, our study highlights the sensitivity of amphibians, particularly terrestrial-breeding species, to changes in soil water potential and temperature, and the importance of maintaining suitable hydrological conditions during the breeding period.

Key words: automated recorder, calling activity, *Geocrinia alba*, soil moisture, southwest Australia, temperature.

INTRODUCTION

With climate and environmental change accelerating, it is critical to understand their impacts on breeding activity and phenology (Cohen et al. 2018; Walls et al. 2013; Blaustein et al. 2010). In amphibians, breeding timing and activity, including male calling behaviour, is frequently associated with environmental cues. Rainfall and temperature are primary factors that influence calling activity and breeding of many anurans (e.g. Saenz et al. 2006; Navas 1996; Caldart et al. 2016; Banks and Beebee 1986; Pérez-Granados et al. 2020; Willacy et al. 2015). Other abiotic factors such as humidity (Hauselberger and Alford 2005), wind (Sommers et al. 2018; Oseen and Wassersug 2002) and barometric pressure (Brooke et al. 2000; MacLaren et al. 2018) can also play roles in triggering breeding activity. However, the strength and direction of responses to environmental variables are highly species specific and differ according to reproductive strategy (Oseen and Wassersug 2002; Richter-Boix et al. 2006; Ospina et al. 2013; Plenderleith et al. 2018).

For prolonged breeders, which call continuously for several months, environmental cues for the start and end of the calling period may also differ (Lannoo and Stiles 2017; Oseen and Wassersug 2002). Male anurans with a prolonged breeding strategy call regularly and wait for females, usually while defending a breeding site, and the arrival of receptive females is spread over an extended period (Wells 1977). The duration of calling activity, and hence the breeding period, can be constrained by energy reserves (Wells and Bevier 1997) but can also be linked to environmental cues. For example, in aquatic-breeding anurans, the hydroperiod can be important for determining the length of the breeding period for species that use seasonal or ephemeral water sources (Jakob et al. 2003; Hoffmann 2018).

The timing of breeding activity is crucial for many aspects of animal ecology, such as to coincide with suitable conditions for larval feeding and growth and may be impacted by changes in climate (Visser and

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Accepted for publication October 2021.

doi:10.1111/aec.13122

Both 2005). Warmer conditions are resulting in amphibians breeding earlier (While and Uller 2014) and later (Todd et al. 2011). Drought conditions have also been linked to a decline of calling activity in some species (Jansen et al. 2009) as well as reductions in the length of breeding periods (Lannoo and Stiles 2017). For anurans with terrestrial egg deposition and development, changes in rainfall duration and frequency and consequent changes in soil moisture are predicted to affect calling activity and embryonic survival (Walls et al. 2013; Mitchell 2001, 2002).

Geocrinia alba, the white-bellied frog, is a small (approx 20 mm snout-to-vent length) terrestrial-breeding frog, with a highly restricted and declining distribution (Page et al. 2018). The species is listed as critically endangered (Australian Environment Protection and Biodiversity Conservation Act 1999) and is restricted to specific drainages where breeding occurs in moist soils alongside seasonal streams and headwaters. The species has a prolonged breeding season, typically from September to December, where males advertise for mates by calling from shallow depressions (nests) in the soil, under groundcover such as litter and moss. Egg clutches are laid throughout the calling period (Driscoll 1998; Conroy 2001), and therefore, male calling is a good proxy for the breeding period in *G. alba*.

The restricted area where *G. alba* occurs is experiencing significantly warmer temperatures and reduced rainfall since the 1970s – trends that are projected to continue in the coming decades (Petrone et al. 2010; Charles et al. 2010). Microclimate conditions vary considerably across *G. alba* sites during austral summer and autumn and suggest that hydrological change and the drying climate are the likely drivers of recent population declines (Hoffmann, Williams, et al. 2021; Hoffmann, Cavanough, et al. 2021). However, it is not known whether environmental conditions differ across sites during the breeding season, which occurs during the wetter and cooler months of the austral winter and spring. Furthermore, it is unclear if environmental cues are important for the timing of calling and breeding activity.

Here, we investigate within-species variation in calling phenology and activity across eight *G. alba* populations. We specifically investigated whether calling periods differed across sites, and whether calling activity at the start, peak and end of the calling period was associated with environmental conditions. We hypothesised that the start of the calling season would be cued by increasing temperatures and rainfall events, and that the end of the calling period would be associated with soil drying. Linking calling activity to environmental predictors may reveal potential mechanisms for population declines in this species, and more generally, will be informative for assessing how terrestrial-breeding amphibians may be affected by a drying warming climate.

METHODS

Study species and region

Geocrinia alba is endemic to the Margaret River region of southwestern Australia (Fig. 1), which is characterised by a Mediterranean climate of wet, cool winters and dry, warm summers. The species has an extremely small geographical range with a maximum of 12 km between the furthest extant populations. Frogs occur in isolated sub-populations along seasonal streams and headwaters within tall jarrah (*Eucalyptus marginata*) and marri (*Corymbia calophylla*) forest (Wardell-Johnson and Roberts 1993) and are highly philopatric, with little or no movements between sub-populations (Driscoll 1997). All life stages are terrestrial, with eggs developing endotrophically (without feeding) within concealed shallow depressions in the soil substrate (Anstis 2010). The areas where frogs occur receive runoff and shallow flows in winter months, with the highest rainfalls in June and July. Surface water is generally absent during the warmer summer months.

Acoustic recording

Automated recording units (AudioMoth version 1.1.0) were deployed at eight *G. alba* sites during the 2019 breeding season. Study sites were chosen from sites subject to long-term population monitoring by the Western Australian Department of Biodiversity, Conservation and Attractions. Sites were selected that encompassed the eastern, western and northern extent of the species range, as well as sites that offered a range of microclimate conditions based on Hoffmann et al. (2021). All sites were within protected areas, including Witchcliffe State Forest, Forest Grove National Park and the Boranup section of the Leeuwin Naturaliste National Park (Fig. 1).

Recorders were deployed from the austral winter through to summer (26 June 2019 to 2 February 2020) to capture the entire calling season (based on Driscoll, 1998). Recording units were placed within drainage lines where the Western Australian Department of Biodiversity, Conservation and Attractions monitoring program had previously detected a breeding chorus, and where calling locations during the previous breeding season had been confirmed by EH. Recordings were made concurrently across all sites apart from one logger that was interrupted because it was colonised by ants from 27 October to 19 November 2019.

Acoustic recorders were deployed in a plastic waterproof case with a 5-mm hole covered by water repellent acoustic membrane in front of the microphone. The case was mounted on a metal stake 1 m above ground level, with a small plastic guard sitting above the recorder for added rain protection (Fig. 1). The recording schedule was set to 1 min every hour from 6 pm to 6 am (WAST, GMT+8) as *G. alba* call primarily at night (Driscoll 1998). The recordings were set to a sampling rate of 48 kHz and medium gain (30.6 dB).

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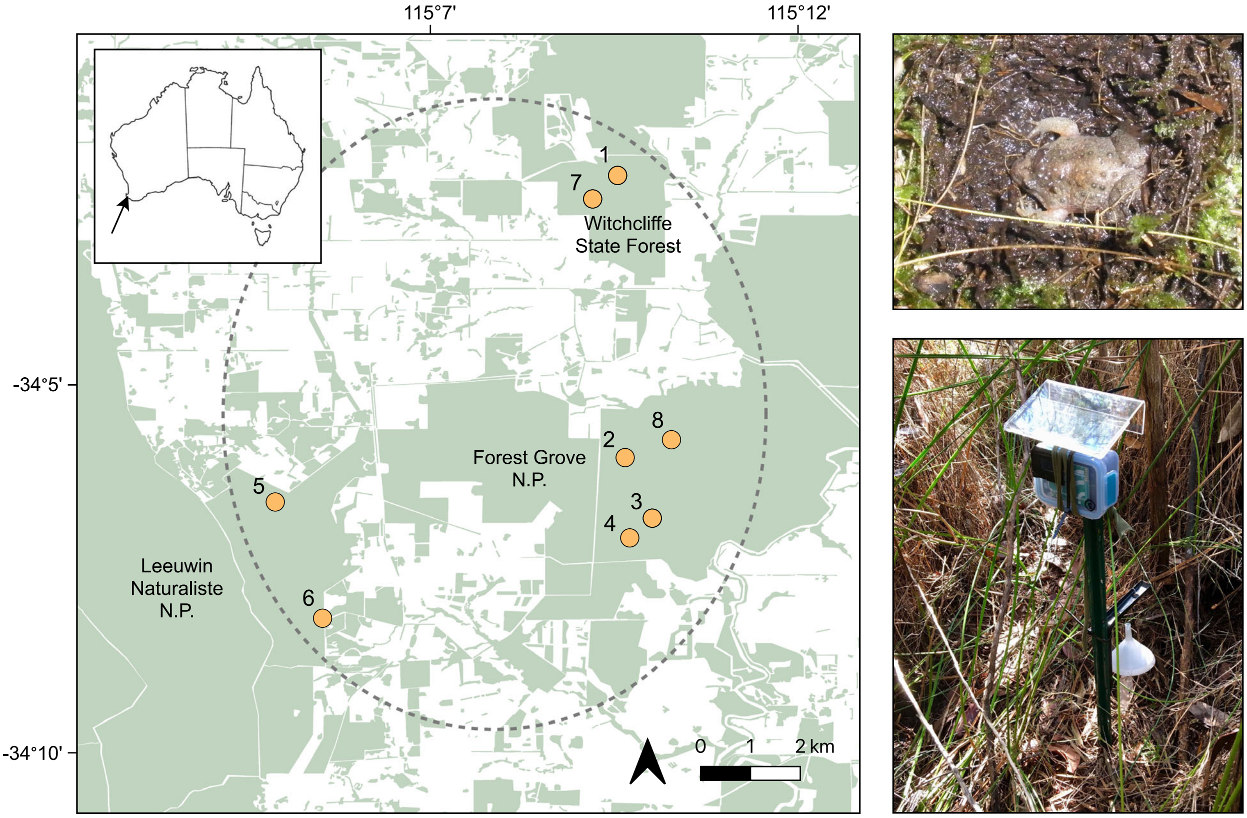

Fig. 1. Location of study sites (orange circles) within the current area of occurrence of *Geocrinia alba* (dashed circle), and images of a male calling from a shallow burrow (top right) and an acoustic recording unit and air temperature logger set up within a breeding site (bottom right). *G. alba* photo credit: Tammy Goad

Environmental variables

To assess the influence of environmental variables on calling behaviour, each recording station was paired with an MPS-6 soil water potential and soil temperature sensor (Decagon Devices, Inc) connected to an EM50 data logger (METER Group, Inc.), and a HOBO pendant temperature logger (UA-001-08). Soil sensors were placed 2 m into the riparian vegetation from the edge of the terrestrial-riparian zone. Soil water potential was recorded, rather than soil moisture content, as it relates directly to water availability for amphibians (Shoemaker et al. 1992), and the measure is independent of soil type and thus was readily comparable across sites. Soil sensors were installed with the ceramic water potential sensor situated approximately 100 mm below the soil surface and the temperature sensor approximately 50 mm below the soil surface. The HOBO temperature logger was suspended 100 mm above the soil surface, underneath a white funnel to shield the logger from UV radiation during daylight (Fig. 1). Sensors were programmed to record hourly.

Rainfall and wind speed were recorded immediately adjacent to one frog site through a HOBO customised sensor unit, and humidity and barometric pressure data were sourced from regional weather stations, located 5–11 km from the study sites (Table 1).

Statistical analysis

Audio recordings were analysed manually by visualising and listening to files in Kaleidoscope (Version 5.4.1, Wildlife Acoustics Inc.). *Geocrinia alba* calls consist of a discrete pulse train of 9–18 pulses (Roberts and Wardell-Johnson 1995), and individual calls could be clearly identified and counted. Call counts were then used as a measure of calling activity (calls per minute; Nelson and Graves, 2004; Hauselberger and Alford, 2005; Williams et al., 2013). Although manually scanning files was time intensive, it provided more accurate and detailed counts of calling activity than could be achieved with automated software (Kaleidoscope Pro).

To increase efficiency, audio files were subset to three audio files per day, based on when calling activity was highest. Preliminary analysis found that calling activity peaked after sunset and dropped off throughout the night (Appendix S1: Fig. S1). Therefore, we analysed daily recordings from the first, third and fifth recording after sunset to account for changing sunset time and to capture the periods of highest calling activity. We identified the number of calls in each recording (number of calls/minute) and summed them across the three time periods for each night as an index of calling activity for each night. To visualise calling activity over the 2019–2020 breeding season

Table 1. Environmental variables recorded during the *Geocrinia alba* breeding season 2019–2020

Variable	Description	Location	Device
Soil water potential	Soil water potential (kPa) at 100 mm depth	All sites	MPS-6
Soil temperature	Soil temperature (°C) at 50 mm depth	All sites	MPS-6
Air temperature	Air temperature (°C) at 100 mm height above soil	All sites	HOBO pendant
Rainfall	Daily total rainfall (mm)	Site GA37C	Davis® 0.2mm rain gauge S-RGF-M003
Wind speed	Wind speed (m s^{-1})	Site GA37C	Davis® anemometer S-WCF-M003
Relative humidity	Relative humidity (%)	Witchcliffe	BOM Stn. 009746
Barometric pressure	Atmospheric pressure reduced to mean sea level (hPa)	Witchcliffe	BOM Stn. 009746

BOM – Bureau of Meteorology.

[Correction added on 6 November 2021 after the first publication: Rows “Soil temperature” and “Air temperature” have been corrected for text formatting and placement.]

across the eight sites, we calculated the relative calling activity for each site. This was calculated as the calling activity for each night, divided by the maximum calling activity recorded for that site. Relative calling activity varies from 0 to 1 and was used for comparing the calling activity periods across sites.

To confirm the first and last calling dates at each site, all hourly audio files for each night (from 6 pm to 6 am) were scanned to determine when the earliest and latest call was detected. The ten nights prior and following these dates were also examined to confirm they were the first and last call recordings for each site. The calling period for each site was calculated as the number of days from the first to the last call detected for each site (Saenz et al. 2006).

Generalised linear mixed models were used to investigate associations between calling activity and environmental variables using the ‘glmmTMB’ package in R (Brooks et al. 2017; R Core Team 2019) (Table 1). We used a correlation matrix to inspect for evidence of collinearity, and pairs of environmental variables were identified as highly correlated if $r > 0.7$ (Dormann et al. 2013) (Appendix S1: Table S1). Soil temperature was correlated with air temperature ($r = 0.81$). We retained soil temperature in our analysis, as male *G. alba* call from the soil surface and therefore their body temperatures were predicted to be more closely associated with soil temperature than air temperature (Brown and Brown 1977).

To detect and differentiate cues at the start, peak and end of the seasonal calling period, we analysed data separately for each time period. The start of the calling period was defined as the 4 weeks before and after calling commenced at each site (i.e. 8 weeks). Similarly, the end of calling period included the 4 weeks before and after calling ceased at each site. In contrast, the peak calling period was the core calling period, excluding the first and last four weeks of calling. The time before and after calling was included to compare conditions before or after calling occurred (e.g. Oseen and Wassersug, 2002).

Calling activity data were analysed with a Poisson distribution for the start and end calling periods (as data were negatively skewed) and a Gaussian distribution for the peak calling period. Environmental predictors were scaled and centred to have a mean of 0 and standard deviation of 1 (Harrison et al. 2018), allowing for comparison of effect sizes (Grueber et al. 2011). All models included site as a random variable to account for spatial autocorrelation, and an autoregressive structure of order 1 for date to account for temporal autocorrelation.

We used a multimodel information-theoretic approach, where inference is based on a candidate model set, which can be more robust than single model methods (Burnham and Anderson 2002). We compared and ranked candidate models with all variable subsets of the global model by Akaike’s Information Criterion (AIC) and calculated averaged parameter values for models with highest support ($\Delta AIC_C \leq 2$ with the top-ranked model) using the ‘modavg’ function in the ‘MuMIn’ package (Bartoń 2019).

All global models were checked for overdispersion, deviation of simulated residuals, zero-inflation and autocorrelation using the ’DHARMa’ package (Hartig 2020). The amount of variance explained by the fixed effects in each global model (with all environmental predictors) for the start, peak and end of calling periods was approximated by calculating the marginal coefficient of determination (marginal-R^2; Nakagawa & Schielzeth, 2013).

An ANOVA was used to explore differences in environmental conditions across sites, with an autoregressive model of order 1 for date to account for temporal autocorrelation. Post-hoc comparisons were made using Tukey’s honest significant difference tests.

RESULTS

Environmental conditions

Temperature increased throughout the sampling period of 26 June 2019 to 2 February 2020 (Appendix S1: Fig. S2). Mean nightly air temperatures (during sampling hours) ranged from 4.6 to 25.7°C (mean 12.2°C) and soil temperatures ranged from 10.6 to 19.2°C (mean 14.3°C) (Appendix S1: Table S2), and varied significantly across sites (air temperature: ANOVA, $F_{(7,1784)} = 21.44$, $P < 0.0001$; soil temperature: ANOVA, $F_{(7,1784)} = 7.86$, $P < 0.0001$). Mean soil water potentials ranged from −176.1 to −8.6 kPa and also varied significantly across sites (ANOVA, $F_{(7,1784)} = 28.68$, $P < 0.0001$). Mean daily precipitation ranged from 0 mm to 30.2 mm and decreased over the study period (Appendix S1: Fig. S2). The total rainfall over the study period was 404 mm.

Calling phenology

Initiation of *G. alba* calling varied by 22 days across sites (21 July to 12 August) and showed similar timing in the increase of calling activity at all sites, with the exception of GA37E (Fig. 2, Appendix S1: Table S3). Notably, GA37E was significantly cooler than all other sites at the start of the calling season (ANOVA, $F_{(7,600)} = 59.84$, $P < 0.0001$; Tukey's honest significant difference, $P < 0.05$). Calling was prolonged, with calling activity occurring on most days during the calling period at each site (mean = 95% of days), but there was considerable nightly variation in calling activity across all sites (Fig. 2).

The date that *G. alba* calling ended varied substantially across sites, ranging from 31 October 2019 to 11 January 2020 (a difference of 72 days) (Fig. 2; Appendix S1: Table S3). The total calling period (from first to last day of calling) differed by 90 days across sites (range 84–174 days). The duration of the calling period was positively associated with the maximum number of calls detected for each site ($R^2 = 0.66$, $F_{(1,\ 6)} = 11.74$, $P = 0.014$; $r = 0.81$) (Appendix S1: Table S3).

Calling activity related to environmental parameters

Calling activity at the start of the breeding period was associated with warmer temperatures and higher soil water potential at sites (Fig. 3a; Appendix S1: Fig. S3). Temperature and water potential had similar importance, with both occurring in all top models and had similar effect sizes (Table 2, Fig. 3a). Calling activity during the peak calling season was positively associated with soil temperature, which had the largest effect size (Fig. 3b). Calling during the peak period was also positively associated with soil water potential and wind speed, although wind speed had a small effect size, indicating it was less important.

Environmental variables explained the most variation (40.9%) in calling activity at end of the calling period (Table 2). Calling activity at the end of breeding period was positively associated with soil water potential, and this variable had the largest effect size (Fig. 3c). That is, calling decreased significantly with decreasing soil water potential at the end of the breeding season (Appendix S1: Fig. S3). Calling at the end of the season was also associated with lower barometric pressure; however, the effect size was negligible. Rainfall and relative humidity were not significant predictors of calling activity at any time.

Across the entire breeding season, calling only occurred when soil temperatures were between 10.0 and 18.7°C and when soil water potentials ranged between −8 and −11 kPa when soils were close to their saturation point (Fig. 4).

DISCUSSION

Identifying environmental associations with anuran calling activity is important for understanding breeding biology as well as assessing the vulnerability of species to hydrological and climatic changes. Here, we found that the calling phenology of *G. alba* varied considerably across a small geographic range and was associated with environmental cues – primarily soil water potential and temperature. Further, our findings suggest that the climatic and hydrological changes affecting *G. alba* habitats are likely to reduce breeding activity. Given these environmental factors also affect survival and translocation success (Hoffmann, Williams, et al. 2021), the overall situation is concerning for this critically endangered species.

Differences in phenology

The duration of calling periods differed two-fold (~3 to 6 months) across eight sites throughout the species' small distribution. As the length of the calling season was correlated with the number of calls detected at a site, it likely reflects the number of males at each site (Nelson and Graves 2004). However, individual *G. alba* males can call for up to 126 nights (Driscoll 1996), which is a longer calling period than we observed at two sites, where calling periods were 84 and 114 days. Furthermore, as there is little turnover in calling males during the breeding season (Driscoll 1998), male calling duration may have been limited by suitable conditions at the site. Calling is energetically costly (Prestwich 1994; Wells 2001), and the calling period can be limited by food resources (McCauley et al. 2000) or males' energy reserves (Wells and Bevier 1997). Male *G. alba* lose body condition over the calling period, up to a third

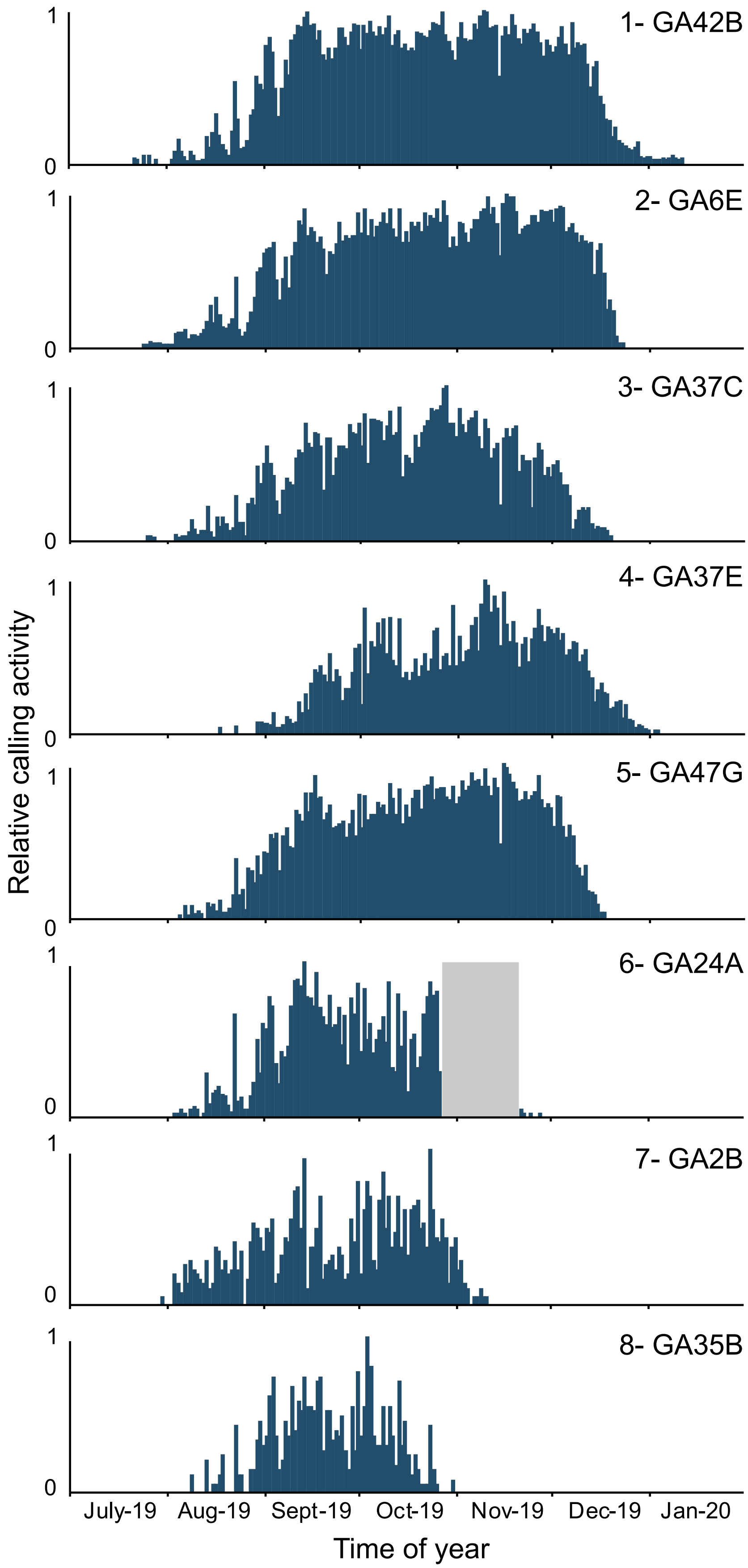

Fig. 2. *Geocrinia alba* relative calling activity over the 2019 breeding season across eight sites (July 2019 to January 2020). Grey area indicates missing data at GA24A

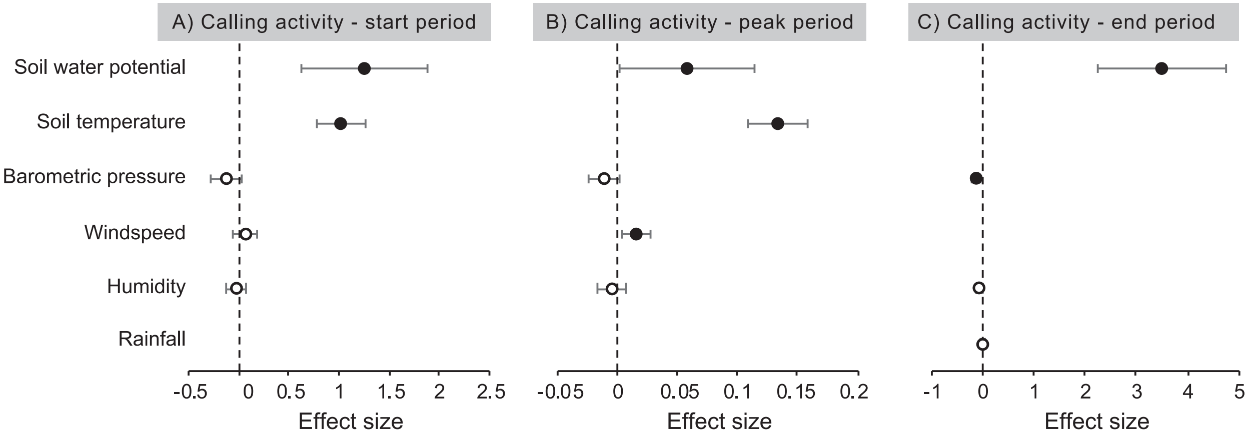

Fig. 3. Factors affecting the calling activity during the start (a), peak (b) and end (c) of the *Geocrinia alba* breeding period. Values are average model coefficients (effect sizes) calculated for variables included in the top model sets ($\Delta AIC \leq 2$). Error bars indicate 95% confidence intervals. Filled circles indicate model-averaged regression slopes that are considered statistically significant (their confidence intervals do not span zero). All variables were standardised (mean = 0, SD = 1) before analysis to allow comparison. Missing effect sizes are those that did not appear in the highest-ranked ($\Delta AIC \leq 2$) models

Table 2. Best approximating general linear mixed-effect models ($\Delta AIC \leq 2$) predicting *Geocrinia alba* calling activity during the start, peak and end of the breeding period, as a function of environmental variables

Candidate model	df	logLik	AIC	Δi	Wi	MarginalR^2
Start of calling period						16.7
Baro + SoilTemp + Soil WP	7	-669.05	1352.4	0	0.35	
SoilTemp + Soil WP + Windspeed	7	-669.65	1353.6	1.21	0.19	
SoilTemp + Soil WP	6	-670.76	1353.7	1.36	0.18	
Baro + RH + SoilTemp + Soil WP	8	-668.93	1354.2	1.83	0.14	
Baro + SoilTemp + Soil WP + Windspeed	8	-668.98	1354.3	1.93	0.13	
Peak calling period						29.7
Baro + SoilTemp + SoilWP + Windspeed	9	377.12	-735.93	0	0.49	
SoilTemp + SoilWP + Windspeed	8	375.51	-734.77	1.16	0.28	
Baro + RH + SoilTemp + SoilWP + Windspeed	10	377.41	-734.44	1.49	0.23	
End of calling period						41.0
Baro + SoilWP	6	-780.00	1572.2	0	0.47	
Baro + RH + SoilWP	7	-779.26	1572.8	0.58	0.35	
Baro + Rainfall + SoilWP	7	-779.96	1574.2	1.98	0.18	

Models are ranked according to Akaike's information criterion (AIC). The number of degrees of freedom, log-likelihood, AIC, AIC differences (Δi) and Akaike weights (Wi) are shown for each model, as well as the marginal (fixed effects) R^2 for each of the global models containing all predictor variables.

Baro, barometric pressure; SoilTemp, soil temperature; SoilWP, soil water potential; RH, relative humidity.

of their body weight (Conroy 2001), and therefore, longer calling may also reflect that males have better body condition at those sites. Environmental variables also explained substantial variation in calling activity at the end of the calling period, which was largely attributed to differences in soil water potential, indicating that site wetness likely limits the length of *G. alba's* calling period.

Importance of environmental conditions

High soil water potential was a consistent predictor of calling activity at frog sites for the entire calling period, as calling only occurred when soils were close to saturation (between −8 and −11 kPa). Rainfall in the region is highest in June and July, the two months preceding calling; however, the significant positive relationship with soil water potential and calling activity at the start of the calling period indicated that soils were still wetting toward full saturation. Soil water potential is an important driver of the hydration state of terrestrial frogs and is a key factor in the choice of suitable terrestrial nest sites. For example, in the terrestrial-breeding frog *Pseudophryne bibronii*, a manipulative experiment showed that males called and mated more when they occupied wetter nest sites, and so their hydration state

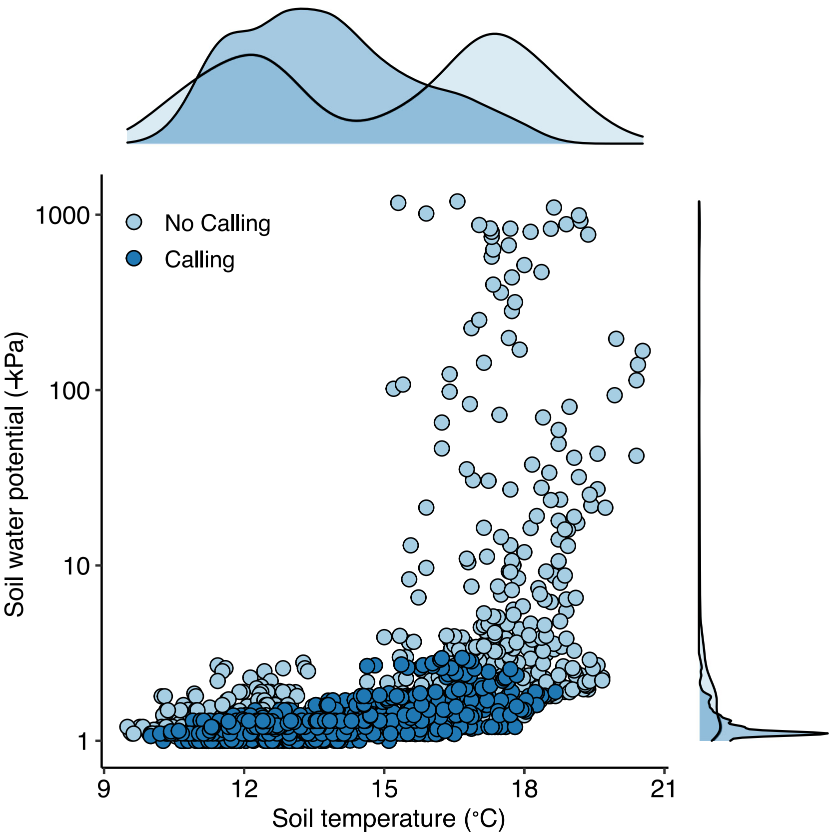

Fig. 4. Relationship between soil temperature (°C) and soil water potential (-kPa) during calling (dark blue) and non-calling (light blue) periods during the *Geocrinia alba* breeding season. Peripheral density plots (top and right panels) show the frequency distribution of values for each variable (for both calling and non-calling periods) and highlight that calling occurred nearly exclusively when soils were saturated. Soil water potential is scaled to the difference from the maximum water potential (between 8 and 9 -kPa) +1 at each site to account for differences in saturation points across sites and for clearer visualisation on a logarithmic scale

was linked to reproductive success (Mitchell 2001). Similarly, females may prefer and lay more eggs in wetter nests, as demonstrated in the related terrestrial-breeding *Pseudophryne coriacea* (O'Brien et al. 2021), and therefore, males directly benefit by calling from wetter nest sites. In *G. alba*, embryos develop to metamorphosis entirely within the nest site and male fitness would be optimised by calling from depressions in wetter (but not flooded) soils, and at times that eggs could continue to develop without risk of desiccation. The relationship between calling activity and soil water potential was strongest at the end of the calling period when calling dropped abruptly as soils decreased in water potential (i.e. began drying). Despite that all sites likely received similar rainfall given their close proximity, the timing of soil drying varied considerably across sites. The variation in drying dates could reflect differences in soil type and consequent water retention capability, catchment area and vegetation cover, distance from headwater, aspect and/or groundwater depth and inflows.

Soil temperatures were also significantly associated with calling activity during the start and peak calling period, with more calling activity detected on warmer nights. Temperature is well known as an important driver of anuran breeding and activity, and many species have preferred environmental temperature ranges for calling (Navas 1996; Pérez-Granados et al. 2020; Saenz et al. 2006; Llusia et al. 2013). We found *G. alba* called well across a broad range of temperatures, but less often at cool and warm extremes (Fig. 4). As ectotherms, environmental temperatures significantly influence anuran body temperatures and consequently the physiological processes involved in call production, and anuran call rates generally increase with temperature (Prestwich 1994; Navas and Bevier 2001). Thus, high calling activity (calls per minute) was likely in part due to warmer soil temperatures increasing call rates (Zweifel 1959; Gayou 1984). However, this relationship was not significant at the end of the calling period (Fig. 3c), when declining soil moisture drove the cessation of calling.

Impact of a regional drying trend

The association between soil water potential, soil temperature and calling activity indicates that *G. alba* breeding behaviour is sensitive to changing climatic conditions. As with many Mediterranean biomes, the southwest region of Australia is drying and warming (Petrone et al. 2010; Charles et al. 2010). Comparison of the total rainfall and mean temperature in 2019 to the long-term average (1961–1990) showed this study occurred in a significantly drier and warmer year than average (Hoffmann, Cavanough, et al. 2021). Warmer winter temperatures may result in an earlier onset of calling (Blaustein et al., 2010), although soil water potential was similarly important as a cue at the start and end of the calling period. Increasingly dry conditions may result in both a later 'wetting' and earlier 'drying' of soils at frog breeding sites (Smettem et al. 2013), and consequently, a later start and earlier end to the calling period. This could result in a shorter available breeding period, as female breeding cues can be driven by male calling (O'Brien et al. 2021).

During the *G. alba* breeding season, clutches are laid throughout the male calling period, over many months, and peak clutch production can be relatively late in the calling season (Driscoll 1998; Conroy 2001). The extended breeding season may be important for spreading reproductive effort and staggering the development of clutches through time to reduce the impact of stochastic events on nest survival. If the breeding period is shorter, all eggs likely experience similar conditions and the likelihood of all nests being lost at a site by an extreme event such as a flood, fire or heatwave increases. *Geocrinia alba* populations are particularly sensitive to stochastic events, as they have low fecundity and low adult survival (Conroy 2001; Driscoll 1999). Therefore, higher risk of nest mortality to stochastic events could have substantial impacts on populations.

Unexplained calling variation

This study found some strong relationships between soil temperature and water potential with calling activity; however, a considerable amount of variation in calling activity was unexplained. There may be other environmental variables important for calling activity that we did not include, such as photoperiod (Both et al. 2008; Canavero and Arim 2009) and moon phase (Grant et al. 2013). In addition, variation in calling can be related to endogenous cues, such as the concentration of reproductive hormones (Yamaguchi and Kelley 2002), or social cues, which can be stronger drivers of calling than environmental factors in some species (Brooke et al. 2000; Höbel 2017).

Conservation and management implications

In addition to gaining a better understanding of species breeding ecology, knowledge of environmental cues and the conditions experienced during the breeding season could assist with captive breeding. To date, captive breeding of *G. alba* has had variable success and been unpredictable, despite development of successful techniques for a closely related species (Mantellato et al. 2013). Mimicking natural environmental conditions, such as the range and fluctuations in soil moisture and temperatures observed in the wild, may help stimulate the calling of males in captivity. This in turn could increase female breeding behaviour which is often associated primarily with social cues (Höbel 2017) and male calls have a stimulatory effect on the reproductive physiology of females, such as increasing estrogen or maintaining reproductive condition (Lea et al. 2001; Lynch and Wilczynski 2006).

Our study provides new information that could improve the timing of frog monitoring surveys currently used for determining presence and population estimates (Department of Parks and Wildlife 2015). Conducting acoustic surveys shortly after sunset, and on warmer nights, should increase the chance of detecting *G. alba*. We also found that frogs called on most nights during the breeding period, even when few frogs were present at a site. Although the seasonal timing of calling activity was site specific, males called reliably throughout September and October across all sites, and where soils stayed saturated, males continued consistently into December. More broadly, our study highlights the sensitivity of amphibians, particularly terrestrial-breeding species, to changes in soil water potential and temperature. The significant association between calling phenology and soil water potential emphasises the need for protecting the winter flows of headwater and seasonal streams in *G. alba* habitats. Regional changes to stream flow because of lower rainfall may be difficult to mitigate, but approaches such as environmental watering may be useful for preventing premature drying of key sites (Shoo et al. 2011; Hoffmann 2018). Any proposals for local impacts such as installation of new dams or land use changes upstream of populations should be critically examined for their likely impacts on *G. alba* breeding sites.

ACKNOWLEDGEMENTS

We thank the Western Australian Department of Biodiversity, Conservation and Attractions, particularly Kim Williams and Christine Taylor, for site access and assistance with field logistics. We are grateful to Dale Roberts for discussions regarding frog acoustics, loaning audio equipment and comments on a draft manuscript. This research was completed under a DBCA Regulation 4 Permit and University of Western Australia Animal Ethics Permit RA/3/100/1554 and was supported by the Australian Government's National Environmental Science Program through the Threatened Species Recovery Hub, the Forrest Research Foundation, the Mohamed bin Zayed

Species Conservation Fund, the Holsworth Wildlife Research Endowment and The Ecological Society of Australia.

CONFLICTS OF INTEREST

The authors declare that they have no conflict of interest.

AUTHOR CONTRIBUTION

Emily P. Hoffmann: Conceptualization (lead); Formal analysis (lead); Funding acquisition (supporting); Methodology (lead); Visualization (lead); Writing-original draft (lead); Writing-review & editing (equal). **Nicola Mitchell:** Funding acquisition (lead); Supervision (lead); Writing-review & editing (equal).

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SUPPORTING INFORMATION

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

Fig. S1 Average number of *Geocrinia alba* calls and time of night (sites $n = 8$) on the 15th of each month from August to December 2019.

Fig. S2 Environmental conditions during sampling hours over the study period (26 June 2019 to 2 February 2020) including, (a) daily precipitation and mean soil water potential, (b) maximum soil (orange) and air temperature (red), (c) relative humidity (grey) and barometric pressure (black) and (d) wind speed

Fig. S3 Relative calling activity (grey) of *Geocrinia alba* across the breeding season, contrasted with soil water potential (top panel) and temperature (bottom panel).

Table S1 Half matrix of Spearman's rank correlations between environmental variables.

Table S2 Summary of environmental conditions at *G. alba* sites during the study period (26 June 2019 to 2 February 2020).

Table S3 Summary table of the calling period for eight *Geocrinia alba* sites.

doi:10.1111/aec.13122