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Research Article

# Acoustic monitoring of invasive species: Continental patterns in calling activity of the invasive cane toads

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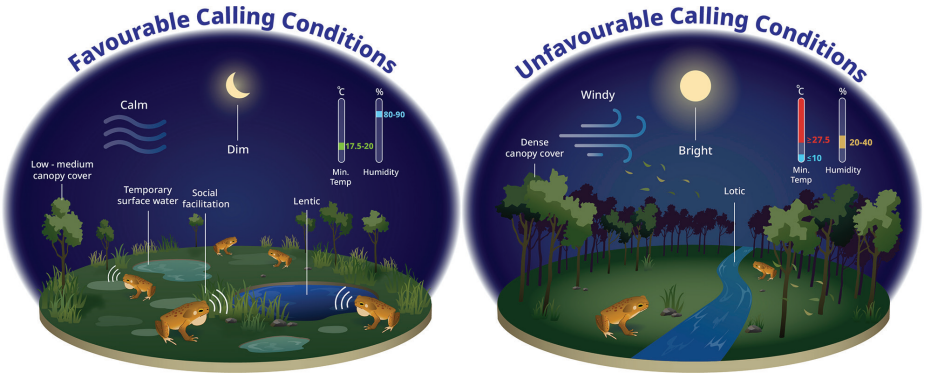
## Abstract

Invasive populations are managed most effectively when surveillance aligns with periods and places of maximal activity. Understanding the conditions influencing breeding of invasive species may help provide information for studies of population dynamics and range expansion. Despite their continued successful advances, the patterns and drivers of invasive cane toad (*Rhinella marina*) calling activity, as a signal of potential breeding activities, remain poorly resolved at broad scales in Australia. Using continent-wide passive acoustic recording data paired with a machine-learning acoustic classifier, we describe patterns in cane toad choruses across most of their current range in Australia, spanning three States and climate zones (~ 15° latitude and 27° longitude). A total of 163,701 minutes of cane toad calls from 33,799 nights of recordings showed that they chorused nearly year-round, with seasonal peaks. Cane-toad calling probability and intensity increased on dark, calm, humid nights and near lentic systems or temporary water, with low- to medium- canopy cover and decreased with increasing wind and moonlight. Social cues appeared important: prior-week calling activity strongly elevated both probability and intensity of calling. Interestingly, temperature effects were context-dependent, without a prior chorus, calling probability and intensity peaked at moderate temperatures; following chorusing, both metrics remained high across a broader thermal range. However, variable importance differed amongst climate zones: atmospheric and lunar factors were more influential for initiating choruses in subtropical and semi-arid sites, whereas habitat and hydrology contributed more to sustaining choruses in the Tropics. Together, these results reveal a detailed picture of cane toad calling ecology in Australia, identifying when, where and under what conditions chorusing is favoured. More broadly, this study demonstrates the value of ecoacoustics for investigating vocal invasive species at large spatial scales and provides a useful basis for future monitoring and modelling.

## Graphical abstract

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**Key words:** ANURAN, Australian Acoustic Observatory, ecoacoustics, machine learning, passive acoustic monitoring

## Introduction

Biological invasions cause substantial ecological problems worldwide (Pimentel et al. 2001; Peller and Altermatt 2024), impacting ecosystem services, altering food webs and posing threats to native biodiversity (Charles and Dukes 2007; Strayer 2010; Mollot et al. 2017), with outcomes that depend on species' biology, phenology and the components of the recipient community (Wolkovich and Cleland 2011; Ricciardi et al. 2013; Gallardo et al. 2016). Rates of invasive-species introduction are projected to rise (Seebens et al. 2021), and climate change is expected to alter the range, abundance and impacts of invaders (Dukes and Mooney 1999; Hellmann et al. 2008; Bellard et al. 2013). Understanding the timing and drivers of key behaviour, such as aggregation and reproduction, reveals how invaders respond to seasonality, weather and local habitat structure, which, in turn, can provide information for understanding of their adaptation and likelihood of spreading, improving monitoring and management. In anurans, chorusing provides an observable signal of aggregation and reproduction. Thus, a broad-scale study of chorusing in an invasive amphibian would provide insights useful for surveillance of vocal, invasive species.

Cane toads (*Rhinella marina*), listed amongst the world's top 100 worst invasive species (Lowe et al. 2000), have successfully invaded more than 20 countries (Lever 2001), becoming a global invader with one of the highest combined environmental and socioeconomic impacts (Measey et al. 2016). In Australia, they are widespread across the north and east and continue to expand, particularly into northern Western Australia (Doody et al. 2018) and they pose a serious conservation concern. Although cane toads have been the focus of extensive research, with decades of work documenting substantial ecological impacts (reviewed by Shine (2010)) and describing aspects of reproduction and calling behaviour (e.g. Semeniuk et al. (2007); Yasumiba et al. (2016); Brodie et al. (2021)), broad-scale patterns and drivers of calling remain insufficiently resolved. Existing studies suggest cane-toad breeding is quite plastic and that environmental effects are relatively weak or inconsistent compared to other frogs (Brodie et al. 2021, 2025); however, these studies are typically small in spatial and temporal extent, limiting inference about the underlying processes. A shift from site-specific patterns to general mechanisms at broader spatial and temporal scales can clarify which drivers are consistent, which are context-dependent and how they interact. Studying the drivers of cane toad chorusing would sharpen our understanding of their phenology and reveal conditions under which calling activities start and persist across Australia's diverse habitats, knowledge that may also inform management in other countries they have invaded.

As male anurans, including cane toads, advertise acoustically and aggregate at waterbodies, their activity is well suited to detection with passive acoustic monitoring (PAM) (Lassandro et al. 2025). PAM is an emerging remote sensing approach now widely used in anuran research, because it operates continuously with minimal disturbance, scales to large deployments and provides call detections from remote sites, supporting inferences about occupancy (e.g. Wood et al. (2023)), phenology (e.g. Oliver et al. (2018)), and calling patterns (e.g. Kaczmarski et al. (2025)). It enables direct tests of environmental influences on chorusing (e.g. Desjonquères

et al. (2022)) and it is increasingly used in invasive-species studies (e.g. Hofstadter et al. (2022); Ribeiro Jr et al. (2022); Amorim et al. (2023); Kimura et al. (2025); Leung et al. (2025)). The Australian Acoustic Observatory (A2O), a continent-wide acoustic sensor network (Roe et al. 2021), offers extensive acoustic coverage for such analyses. The A2O consists of 62 active monitoring sites, across seven major ecoregions in Australia, including habitats ranging from rainforests to arid landscapes, capturing diverse, real-world acoustic environments (Roe et al. 2021). Previous work identified cane toad occurrence at more than 20 sites within this network, spanning the Northern Territory, Queensland and Western Australia (Leung et al. 2025). This broad coverage provides an opportunity to evaluate cane toad calling across large spatial and temporal gradients in Australia and to identify the conditions that promote reproductive activity.

In most anurans, breeding cycles are strongly influenced by seasonal variation in temperature and rainfall (Helm et al. 2013) and chorusing often occurs on warm, humid nights as an adaptive response to the environment (Oseen and Wassersug 2002). Moonlight, wind, hydrology and vegetation structure also affect calling behaviour (Johnson and Batie 2001; Lichtenberg et al. 2006; Brown 2013; Suárez et al. 2016). Cane toads broadly follow this template, but calling is only weakly and inconsistently tied to nightly conditions compared with many frogs (Brodie et al. 2021). Cane-toad chorusing can persist, or recur, in cool, dry periods (Brodie et al. 2021) and experimental field studies show strong phonotaxis, i.e. males orient and move towards conspecific calls, using chorusing to locate aggregations (Yasumiba et al. 2015; Clarke et al. 2019). Indeed, in some frog species, social cues can outweigh abiotic drivers triggering and sustaining chorusing (Brooke et al. 2000; Llusia et al. 2013; Höbel 2017). Together, these lines of evidence suggest that both abiotic conditions and social dynamics may shape chorus initiation and persistence in cane toads.

In this study, we leverage the acoustic recordings from the A2O and a machine-learning detection tool, to characterise the spatio-temporal dynamics of cane toad calling across most of their Australian range (Cutajar et al. 2025). Our goals were: (i) to describe broad spatio-temporal patterns in cane-toad calling across Australia and (ii) to quantify environmental, habitat and possibly social drivers of chorusing, at two complementary scales. Accordingly, we fitted two models: a calling-probability model (whether calling occurred on a given night) and a calling-intensity model (minutes of calling on nights when calling occurred), identifying key factors that initiate and sustain cane-toad chorus. We then assessed whether predictor importance was consistent across climate zones. Given Australia's continental breadth and pronounced climatic gradients, these cross-zone analyses provide a comprehensive picture of cane-toad calling ecology and are likely informative for other invaded countries with comparable environments, supporting local inference using acoustic monitoring.

Building on these ideas and beyond examining the effects of general environmental conditions, we test whether cane toad chorusing exhibits temporal persistence, consistent with social facilitation across multiple timescales. Previous work has shown that nightly cane toad chorusing is autocorrelated across successive nights and is not fully explained by weather, suggesting additional drivers of calling activity (Brodie et al. 2021). Moreover, chorusing episodes may promote the arrival of additional males and females at breeding sites (Schwarzkopf and Alford 2007; Yasumiba et al. 2015; Clarke et al. 2019). Thus, we predict that

both calling on the previous night and cumulative calling over preceding days, would increase the likelihood and duration of subsequent calling, consistent with possible social-facilitation effects on toad chorusing. In addition, rainfall can stimulate toad movement to breeding sites (Schwarzkopf and Alford 2002), but sites with permanent water may provide breeding opportunities even in the absence of recent rain. Conversely, at sites lacking permanent water, rainfall may create temporary breeding opportunities, such as ephemeral pools, which are widely used by frogs for breeding following re-watering events (e.g. Anstis (2013); Hoffmann (2018)). We therefore explore whether calling activity responded more strongly to cumulative rainfall across sites without permanent water, as rainfall pulses may alter breeding opportunities across habitat contexts. Together, these lines of evidence could reveal if both abiotic conditions and social dynamics may shape the initiation and persistence of cane-toad choruses.

## Materials and methods

### Study area and audio data collection

All cane toad detections used in this study were derived from previous research, in which Leung et al. (2025) developed a custom acoustic classifier using the BirdNET algorithm and manually labelled data from the A2O (see Leung et al. (2025) for full details on recogniser development, testing and performance). We analysed audio recordings from 41 A2O sites across Australia, where cane toads may occur, according to observational records (Atlas of Living Australia 2024). Acoustic data spanned February 2019 to September 2023, although the exact period of data availability varied amongst acoustic recording units (ARUs) and some gaps occurred because of technical issues (Suppl. material 1: fig. S1). Recordings between 18:00 h and 06:00 h were processed using a trained classifier. Because cane toads typically chorus for at least some minutes and detected single calls are unlikely to be correct, using contextual data (calls occurring around a detected call) can be useful to decide whether a detection is correct. Thus, we refined our detection patterns using a thresholding framework that incorporated contextual information from aggregated time-series features (see Singer et al. (2024); Leung et al. (2025) for full details on aggregating time series thresholding). To ensure adequate data for inference, sites with sparse or inconsistent signals (≤ 500 total detections and ≤ 5 detection nights) were excluded, yielding 21 sites (out of 26 toad-positive sites) across the Northern Territory, Queensland and Western Australia. A conditional inference tree optimisation on this revised dataset identified the final thresholding rule (± 12 h average confidence > 0.5163 and maximum confidence > 0.997), producing 3,274,015 three-second detections from ~ 405,588 h of audio with 95.6% precision and 80.8% recall.

### Drivers of cane toad calling activity

To characterise environmental influences on calling, we first assembled a set of weather predictors using each ARU location and a range of gridded environmental data sources. Daily scale weather predictors, including rainfall (mm), minimum air temperature (°C), vapour pressure (hPa) and relative humidity at minimum temperature (%) were obtained from the SILO climate database at a spatial

resolution of 0.05° × 0.05° (Queensland Government 2024). Hourly cloud cover and wind components were extracted from the ECMWF Reanalysis v.5 dataset at spatial resolution of 0.25° × 0.25° (Copernicus Climate Change Service [C3S] 2023; Hersbach et al. 2023). For both datasets, values were assigned to each ARU using the nearest grid cell. As cumulative rainfall lagged over several days affects vocalisation patterns (Caldart et al. 2016; Schalk and Saenz 2016; Brodie et al. 2021), we also computed cumulative rainfall totals at 3-, 5-, 7-, 10- and 14-day lags. To calculate wind speed (m $s^{-1}$), we used the east-west directional component (10 m u-component, ws, m $s^{-1}$) and the north-south component (10 m v-component, m $s^{-1}$) according to the formula: $ws = \sqrt{(u^2+v^2)}$. All hourly data were aggregated to nightly averages, calculated from 18:00–06:00 h, to match the temporal resolution of our aggregated acoustic detections.

Recognising that moon illumination and seasonality can influence toad calling (Brodie et al. 2021; Thompson et al. 2022), we first derived mean moonlight intensity using the moonlit R package (Śmielak 2023). Moon phase alone is not a good proxy for ground-level illumination (Śmielak 2023), so we used moonlit to estimate clear-sky astronomical night-time illumination for each ARU from its latitude, longitude, elevation and time zone and modelled its interaction with cloud cover to better reflect variation in realised ground-level illumination. To represent seasonality, we used day-of-year (DOY) encoded with circular terms, $\sin(2\pi \cdot DOY/365)$ and $\cos(2\pi \cdot DOY/365)$, derived from each ARU's local timestamp to capture annual periodicity without an artificial year-end break.

Brown (2013) and Brodie et al. (2021) demonstrated that calling activity on one night increases both the probability and intensity of calling on the following night, suggesting a social facilitation effect. To detect if this effect might be important in our data, we included in our models: (i) a previous-night calling indicator (0/1) in both models and (ii) model-specific prior-week activity terms: in the probability model, the number of calling nights in the preceding seven days and in the intensity model, the log of total calling minutes over the preceding seven days. These predictors allowed us to test whether an initial calling event increases the chance of calling on subsequent nights and whether recent activity lengthens later calling bouts.

In addition to these behavioural predictors, we incorporated habitat and hydrological predictors that often influence frog calling activity, but are rarely examined in acoustic studies of cane toads. These included habitat openness (Vignoli et al. 2014), percentage vegetation cover (Lichtenberg et al. 2006) and the proximity and characteristics of nearby waterbodies (Suárez et al. 2016; Annich 2017). Because no single hydrology dataset covered all waterbodies in the areas where our ARUs were placed, we merged the four national hydrology datasets: the Australian Hydrological Geospatial Fabric (Bureau of Meteorology 2025a), Digital Earth Australia Waterbodies v.3.0 (Dunn et al. 2024), National Catchment Boundaries v.1.1.4 (Stein et al. 2011) and the Geofabric V3x Surface Hydrology Network (Bureau of Meteorology 2025b). In QGIS v. 3.36.2, we first created a 264-m (radius) buffer around each ARU, chosen based on the average nightly movement distance of cane toads (Kelly et al. 2023). From this merged hydrological layer, we measured the distance to the nearest waterbody using QGIS's Distance to nearest hub function. We then classified the nearest waterbody's flow regime according to its feature type from the attributes of the merged hydrology layer, for example, reservoirs, ponds and lakes were classified as lentic, while rivers, creeks and channels were classified as lotic. Finally, within the buffer zone, we assessed each waterbody's

permanence, which was categorised as absent, temporary or perennial, directly from the layer's attribute data. We used the Digital Earth Australia Land Cover Level 3 dataset (Tissott et al. (2025); via the Esri web service) to extract percentage vegetation cover at each ARU. From the layer's herbaceous/woody classes (4–15%, 15–40%, 40–65%, > 65%), we collapsed the original six habitat/cover categories into a three-level canopy cover factor to improve interpretability, reduce sparse strata and avoid conflating vegetation with hydrology (several of the original six classes partially tracked the levels of the water permanence variable). Specifically, we defined low canopy level as "4–15% herbaceous" and "15–40% herbaceous," medium canopy level as "40–65% herbaceous" and "15–40% woody" and high canopy level as "40–65% woody" and "> 65% woody".

## Statistical analysis

We began by filtering our ARUs to include only those with at least ten nights of calling data and we removed nights from each ARU's record without corresponding data for the lagged-calling predictor (i.e. nights with missing recordings in the preceding seven nights), resulting in 21,823 nights of data analysed (sites = 17, ARU = 46). All continuous predictors were standardised to zero mean and unit variance to aid model convergence and to make effect sizes directly comparable. Finally, we included ARU nested within each site as a random effect to account for repeated measures at each location.

To tease apart the drivers of: (i) the probability that cane toads would call, versus (ii) the intensity of cane-toad calling once it occurred, we fitted two parallel generalised linear mixed models using glmmTMB (Brooks et al. 2017). The probability model used a binomial (logit) link with a binary response (1 = at least one call, 0 = no calls) and represented call or chorus initiation, i.e. whether calling occurred on a given night. The intensity model used a gamma distribution with a log link and a continuous response (minutes of calling, excluding zeros), that is, it examined variation in calling duration on nights when calling occurred. Together, this two-part framework is conceptually similar to a hurdle approach, separating the transition from no calling to calling from the amount of calling once that threshold is crossed. Both models shared the same suite of abiotic and biotic predictors: daily weather (temperature, vapour pressure, humidity, wind speed), rainfall (daily and multi-day lags), date-of-year (DOY), moonlight, waterbody characteristics (distance, flow regime, permanence), habitat structure (canopy cover) and lagged-calling predictors.

We translated the temporal hypothesis (probability of calling) and exploratory rainfall analysis (persistence of calling) into explicit model terms as follows. To describe temporal persistence, we included two complementary lagged-calling measures representing different timescales of recent activity. First, we included an interaction between binary lagged calling and nightly temperature, to test whether the effect of temperature on calling probability and intensity differed depending on whether a chorus had occurred on the previous night. Second, we included a prior-week calling term in both models to assess whether recent calling activity accumulated across multiple nights, using the count of call-positive nights in the preceding seven nights for the probability model and total calling minutes in the preceding seven nights for the intensity model. To explore whether rainfall-associated calling responses varied with habitat context, we included an interaction be-

tween accumulated multi-day rainfall and waterbody type at the ARU (factor with levels of absent, temporary, perennial) in the probability model. Both temperature and the prior week's calling variable were modelled with second-degree polynomials to capture potential non-linear responses.

We began fitting both the probability and intensity models with the full set of predictors, plus the random intercept, then iteratively screened for multicollinearity by computing model-based variance-inflation factors (VIFs) with the performance package (Lüdecke et al. 2021), dropping the highest-VIF predictor until all VIFs were ≤ 5 (James et al. 2013). Next, to choose the optimal rainfall window, we compared alternative rainfall specifications — same-day rainfall, single accumulated windows (3, 5, 7, 10, 14 days) and combinations of daily and accumulated, fitting otherwise identical models and ranking them by Akaike's Information Criterion (AIC; Bozdogan (1987); Suppl. material 1: table S1). This component of the analysis was exploratory, as cumulative rainfall metrics are commonly used in frog calling studies and calling can persist for several days after rainfall events; we therefore could not assume that calling reflected only an immediate response to precipitation and considered cumulative rainfall windows to capture possible lagged or build-up effects (e.g. Caldart et al. (2016); Schalk and Saenz (2016); Brodie et al. (2021)). We retained the rainfall term(s) with the lowest AIC for each response. For both models, we generated simulated residuals with the DHARMa package (Hartig and Hartig 2017) and inspected them visually. We applied tests for uniformity, dispersion and outliers for both models and zero-inflation for the probability model. We also tested temporal autocorrelation by aggregating residuals by ARU-night and running DHARMa's temporal autocorrelation test. We summarised fit with marginal and conditional $R^2$ (Nakagawa and Schielzeth 2013) and assessed out-of-sample predictive performance via temporally blocked five-fold cross-validation. Observations were ordered by time and partitioned into five consecutive temporal blocks; models were trained on four blocks and evaluated on the remaining block in turn. For the probability model, the area under the receiver operating characteristic curve (ROC AUC) was computed with pROC (Robin et al. 2011) and the intensity model's agreement between observed and predicted values was quantified by Lin's concordance correlation coefficient (CCC; Lin (1989)) using DescTools (Signorell et al. 2025). We performed all the analyses with R version 4.2.3 (R Core Team 2023).

The equation and the definitions of each predictor from the final selected models were as follows:

(1) Probability model

$$\begin{aligned} logit\left(p_{\{ij(s)\}}\right) = {} & \beta_0 + \beta_1 FR_{j(s)} + \beta_2 WP_{j(s)} + \beta_3 MMI_{ij} + \beta_4 DCC_{ij} + \\ & \beta_5 RH_{\{ij\}} + \beta_6 WS_{\{ij\}} + \beta_7 CC_{j(s)} + \beta_8 SL7_{ij} + \beta_9 SL7_{ij}^2 + \\ & \beta_{10(BLC_{ij} \times T_{min}, ij)} + \beta_{11(BLC_{ij} \times T_{min}, ij^2)} + \gamma^T s\left(DOY_{ij}\right) + \\ & \beta_{14(CR7_{ij} \times WP_{j(s)})} + \beta_{15} DR_{ij} + b_{0s} + b_{j(s)} \end{aligned}$$

(2) Intensity model

$$\begin{aligned} \log\left(E\left[Y_{ij(s)}\right]\right) = {} & \beta_0 + \beta_1 FR_{j(s)} + \beta_2 WP_{j(s)} + \beta_3 MMI_{ij} + \beta_4 DCC_{ij} + \\ & \beta_5 RH_{ij} + \beta_6 WS_{ij} + \beta_7 CC_{j(s)} + \beta_8 SL7_{ij} + \beta_9 SL7_{ij}^2 + \\ & \beta_{10(BLC_{\{ij\}} \times T_{min}, ij)} + \beta_{11(BLC_{ij} \times T_{min}, ij^2)} + \gamma^T s\left(DOY_{ij}\right) + \\ & \beta_{14} CR3_{ij} + b_{0s} + b_{j(s)} \end{aligned}$$

where:

$p_{ij(s)}$ (probability) or $Y_{ij(s)}$ (intensity) is the model-predicted response for night $i$ at ARU $j$ nested within site $s$;
$\beta_0$ is is the intercept term;
$\beta_1$– $\beta_{11}$ are the coefficients for the main effects of flow regime, water permanence, mean moonlight intensity, cloud cover, daily rainfall, relative humidity at minimum temperature, wind speed, canopy cover, prior-week calling and the interaction between lagged calling and the linear and quadratic terms of minimum temperature; $\gamma^T s(DOY_{ij})$ represented circular day-of-year terms, capturing annual seasonality, computed from each ARU's local date.

In the probability model, $\beta_{14}$ represented the interaction between 7-day cumulative rainfall and water permanence and $\beta_{15}$ represented the effect of daily rainfall, whereas, in the intensity model, $\beta_{14}$ represented the effect of 3-day cumulative rainfall. Random effects include a site intercept $b_{0S}$ and an ARU intercept nested within site, $b_{j(s)}$.

The response of broadly distributed frogs to weather and habitat can vary amongst climate zones (Forti et al. 2022; Thompson et al. 2022). To assess whether the same drivers held across climates and against spatial heterogeneity, we stratified our data, based on the Köppen Climate Classification (Peel et al. 2007; Bureau of Meteorology 2025c). Each ARU was assigned to one of six major classes: equatorial, tropical, subtropical, desert, grassland (which we termed 'semi-arid' to separate it from our vegetation classifications) and temperate. Our modelling set contained no desert or temperate sites and only a single equatorial site, so we conducted zone-specific analyses for tropical, subtropical and semi-arid (grassland) zones (Suppl. material 1: fig. S2). Within each zone, we fitted two GLMMs: a probability model (binomial) and a calling-intensity model (gamma). To keep models interpretable, we restricted candidates to main effects (omitting the interaction hypothesis terms used in the global models) and iteratively screened predictors to VIF ≤ 5. After finalizing the zone-specific formulas (six models total), we quantified variable importance with drop-one ΔAIC: for each predictor (or block), we refitted the model without each predictor and recorded the AIC increase relative to the full model (larger ΔAIC indicates greater contribution; Anderson and Burnham (2002); Burnham and Anderson (2004); Burnham et al. (2011)). We also report evidence ratios (ER = exp[ΔAIC/2]) for each variable and treat ER ≥ 10 as strong support (Anderson and Burnham 2002). During the preparation of this work, ChatGPT was used only to check grammar and improve readability. After using this tool, all authors reviewed and edited the content.

## Results

### Calling patterns overview

The analysed recordings spanned approximately 33,799 nights from February 2019 to September 2023, with calling present on 12.5% of nights (mean ± SD = 59.6 ± 69.8 calling nights per ARU; Suppl. material 1: fig. S1, table S2). The westernmost detection occurred at Uunguu Indigenous Protected Area (ARU replicate: Dry A; 14.8183°S, 125.7080°E), the northernmost at Steve Irwin Wildlife Reserve (ARU replicate: Dry B; 12.3691°S, 142.2046°E) and the southernmost at Mourachan (ARU replicate: Wet A; 27.7837°S, 149.0089°E) (Fig. 1, Suppl. material 1: table S2). Amongst the sites where calls were detected, Rinyirru National Park had the highest proportion of calling nights, approximately 43.8% of data-available nights, whereas

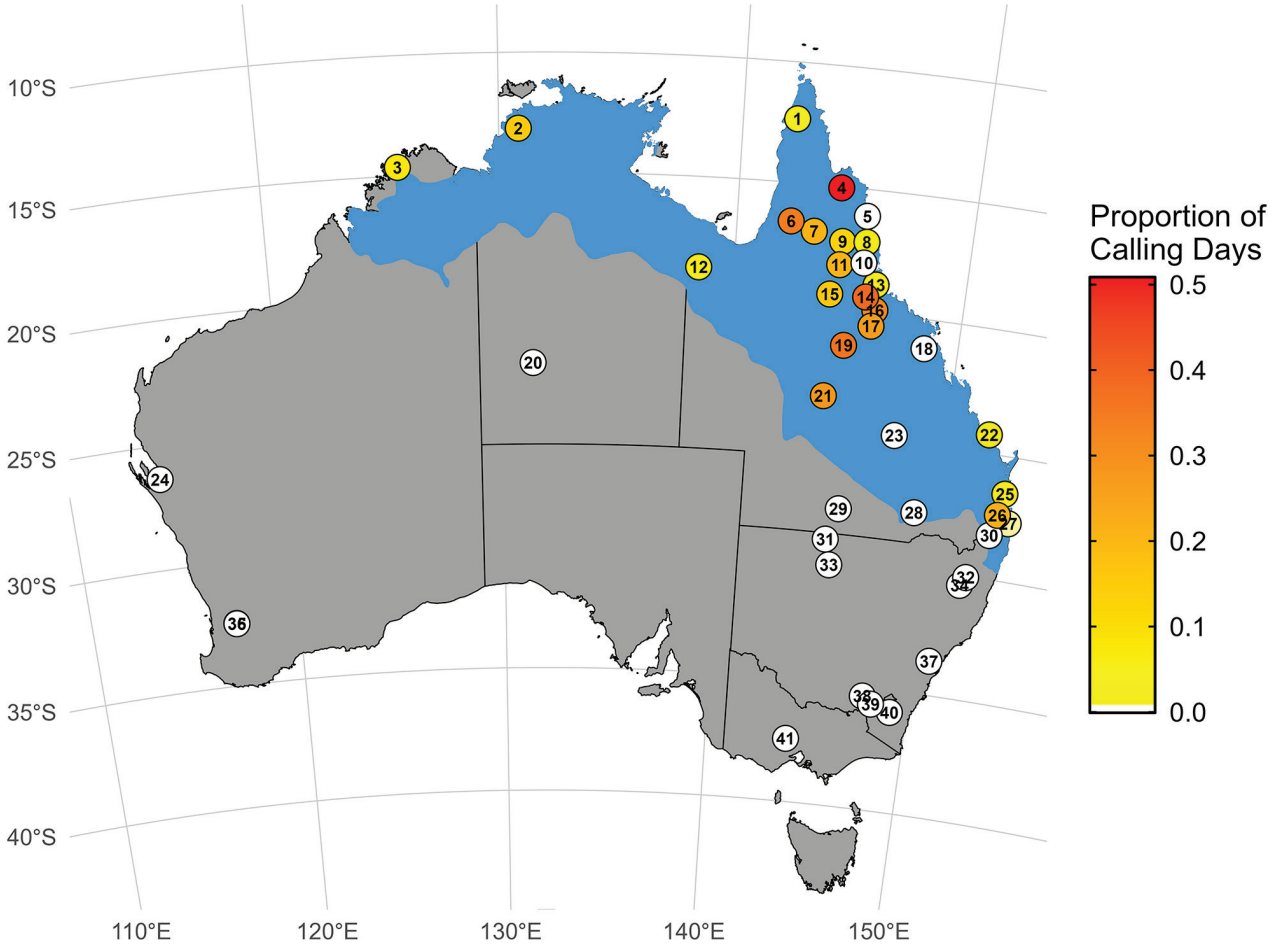


**Figure 1.** Map of Australia showing the proportion of nights with detected cane-toad calling at each A2O site, calculated as the average across ARUs within a site, using the full dataset (all sites, including those later filtered in analyses). Each circle marks a site (ARU-averaged) and is coloured by the proportion of calling nights (white = 0%, then yellow–orange, to red ≥ 50%). Numbers identify sites and correspond to the numbering used in Figs 2, 3. The blue shaded area indicates the current distribution of cane toads in Australia (Cutajar et al. 2025).

Mourachan accounted for the lowest (0.26%; Fig. 1). In terms of cumulative calling effort, of the 163,700.8 total minutes detected, Spyglass registered the greatest average calling intensity (17,385 min), while Carnarvon recorded the least (1.1 min).

Across the continental time series, cane toad calling was detected year-round, but both its timing and intensity varied markedly amongst sites (Fig. 2). When pooled across all ARUs, calling began to increase in late October, coinciding with the onset of the wet season and peaked sharply between March and April and then declined through late June and July (red curve, Fig. 2). Most individual sites reached their highest calling activity either in the early wet season (October–December) or the late wet season (March–April), with only occasional or sporadic calling during the dry season. Notably, Rinyirru and Wambiana maintained relatively continuous, more evenly distributed calling throughout the year (Fig. 2). Despite spanning over 15° of latitude (~ 12.37°S–27.78°S), there was no consistent latitudinal gradient in monthly calling patterns.

At the diel scale, calling occurred over the entire night (18:00–06:00 h) at all sites (Fig. 3). Calling typically began shortly after sunset, at around 18:00 h in the dry season and around 18:30–19:00 h in the wet season. Both rose quickly to a plateau in about an hour, then fell off and reached another plateau again at around 22:00 h, but gradually tapered off afterwards (red curve, Fig. 3). Individual

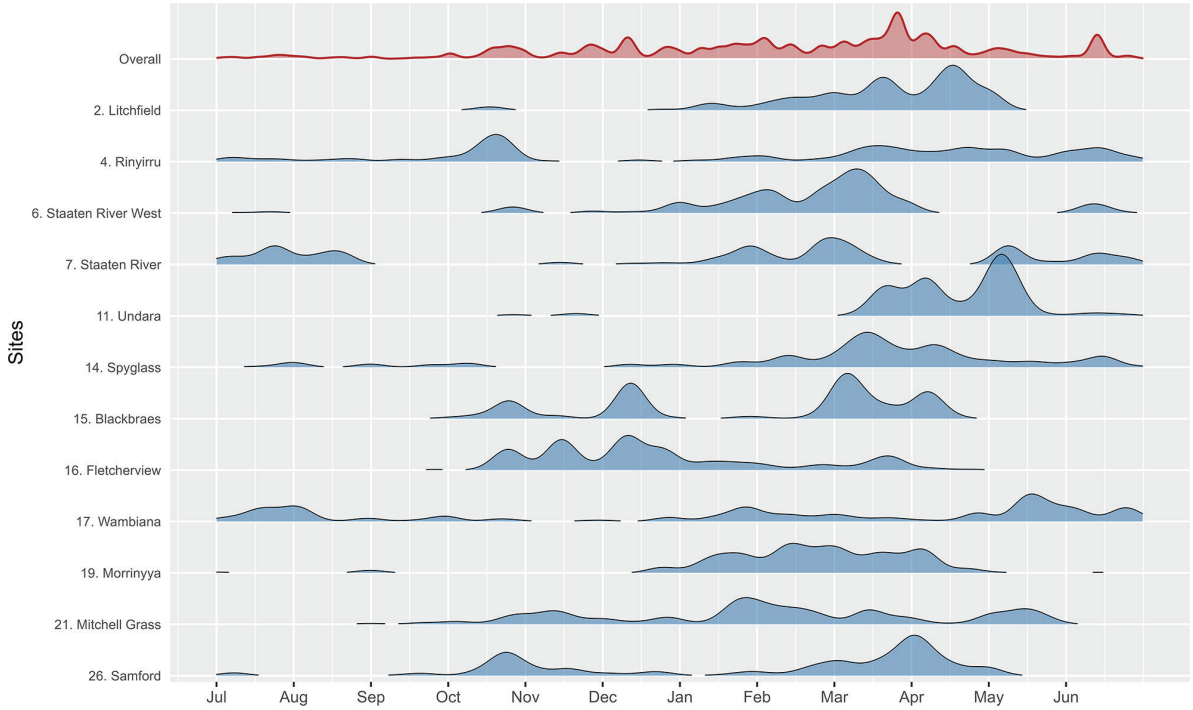


**Figure 2.** Monthly cane-toad calling at selected A2O recording sites (blue) and across all sites combined (red). We only showed individual sites with at least 60 unique nights of detection, ordered from north to south by latitude. Site numbers correspond to those shown in Fig. 1. Each blue ridge shows the kernel density of nightly calling detections for one site and the red ridge at the top shows the weighted overall density (all sites considered equally), computed on the full dataset (all sites, including those filtered in analyses).

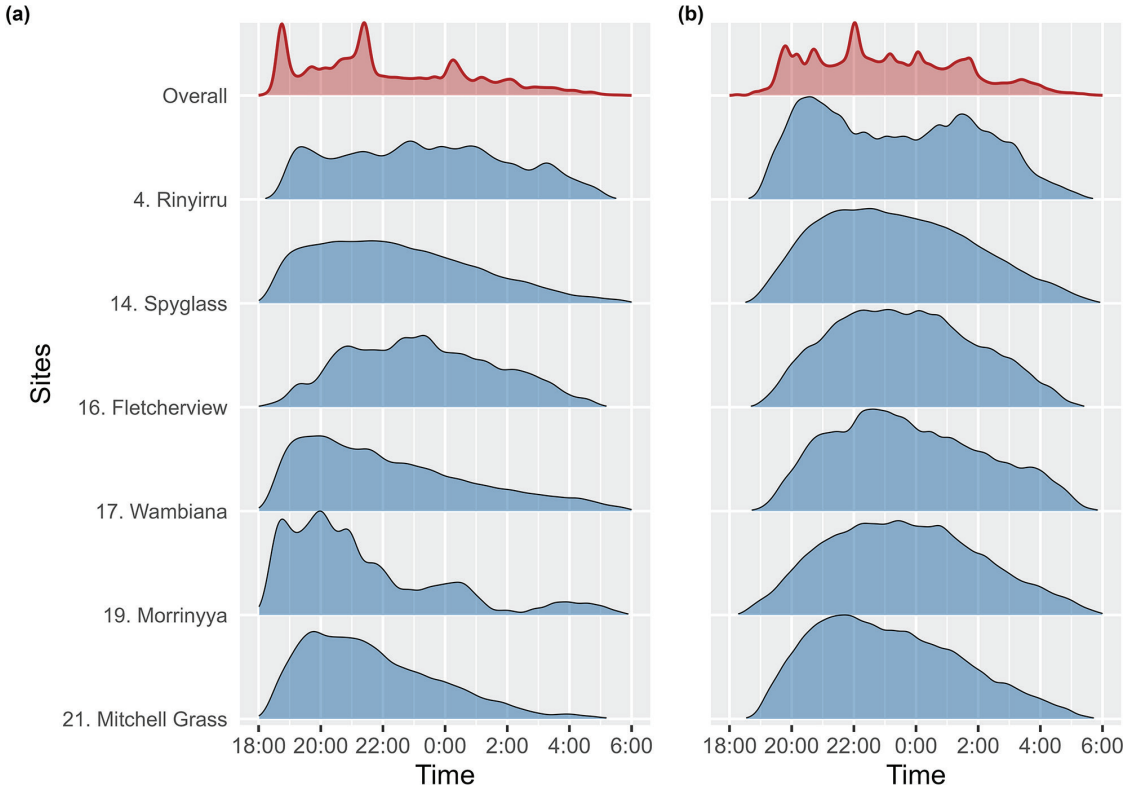


**Figure 3.** Nightly cane-toad calling activity by: dry season (**a**) (May–October) and wet season (**b**) (November–April). Site numbers correspond to those shown in Fig. 1. For each panel, blue ridges show kernel-density estimates of cane toad detections for individual recording sites (only individual sites with data in all 12 hourly bins), ordered from north to south by latitude. The red ridge at the top is the weighted overall density (all sites considered equally), computed on the full dataset (all sites, including those filtered in analyses).

sites showed smooth, hump-shaped trends and the onset of calling occurred earlier in the dry season than in the wet season (blue curve in Fig. 3); calling ramped up immediately after dusk, remained high through late evening and then waned. Relative to the dry season, the wet season had a later onset of calling activity and sustained elevated activity later into the night (often past midnight) and showed higher overall levels (blue curve, Fig. 3). Most sites followed this pattern; the main exception was Morrinya in the dry season, which exhibited a sharp post-dusk surge and earlier decline. Across the seven focal sites (≈ 15–23.5°S), diel timing was broadly consistent, with no clear latitudinal trend.

## Calling probability model

Residual diagnostics indicated minor departure from uniformity, but no major issues (see Suppl. material 1: figs S3–S5 for details). The final model showed that nearly all environmental and behavioural predictors influenced nightly cane toad calling probability, except for DOY and daily total cloud cover (Fig. 4; Suppl. material 1: table S3). Calling probability was notably higher near lentic waterbodies compared to lotic ones ($\beta$ = –0.39, $p$ < 0.001). Relative to sites without a waterbody, calling probability was higher at sites with temporary bodies ($\beta$ = 0.29, $p$ = 0.031), while the effect of perennial waterbodies was positive, but less clear ($\beta$ = 0.34, $p$ = 0.083). Daily rainfall was negatively associated with calling probability, although statistically supported, the estimated effect size was small ($\beta$ = –0.10, $p$ < 0.001). Relative humidity at minimum temperature had a strong positive effect ($\beta$ = 0.38, $p$ < 0.001), while calling probability declined with increasing daily mean moonlight intensity ($\beta$ = –1.6, $p$ < 0.001) and wind speed ($\beta$ = –0.21, $p$ < 0.001), suggesting that toads were less likely to call on bright or windy nights. Calling probability was highest in sites with low canopy cover and was significantly greater than at sites with medium- or high-canopy cover, whereas medium- and high-canopy-cover sites did not differ from each other (Fig. 4).

Regarding behavioural influences, recent calling activity influenced calling probability markedly. Calling probability increased steeply with the cumulative number of calling nights in the preceding week (linear term $\beta$ = 0.54, $p$ < 0.001), although the effect diminished at higher levels (quadratic term $\beta$ = –0.02, $p$ < 0.001; Fig. 4; Suppl. material 1: table S3). This pattern is consistent with temporal persistence in calling activity and possible positive feedback from social facilitation. Secondly, the interaction between 7-day cumulative rainfall and water permanence was significant, with rainfall positively affecting calling only at sites lacking permanent waterbodies ($\beta$ = 0.09, $p$ < 0.001) and with temporary water ($\beta$ = 0.04, $p$ = 0.004), while perennial waterbodies showed no clear rainfall-related increase (Fig. 4). Lastly, the interaction between lagged calling and minimum temperature was significant for both the linear (Lag calling 0 $\beta$ = 0.44, $p$ < 0.001; Lag calling 1 $\beta$ = 0.45, $p$ < 0.001) and quadratic terms (Lag calling 0 $\beta$ = –0.61, $p$ < 0.001; Lag calling 1 $\beta$ = 0.34, $p$ < 0.001), reflecting differing temperature response, depending on whether calling occurred the previous night (Suppl. material 1: table S3). When there was no prior calling, the relationship was hump-shaped, with calling most likely at an intermediate minimum temperature (Fig. 4). In contrast, when calling had occurred the previous night, calling activity was less a function of temperature, more likely to occur at cooler and very warm temperatures than when there was no calling the previous night (Fig. 4).

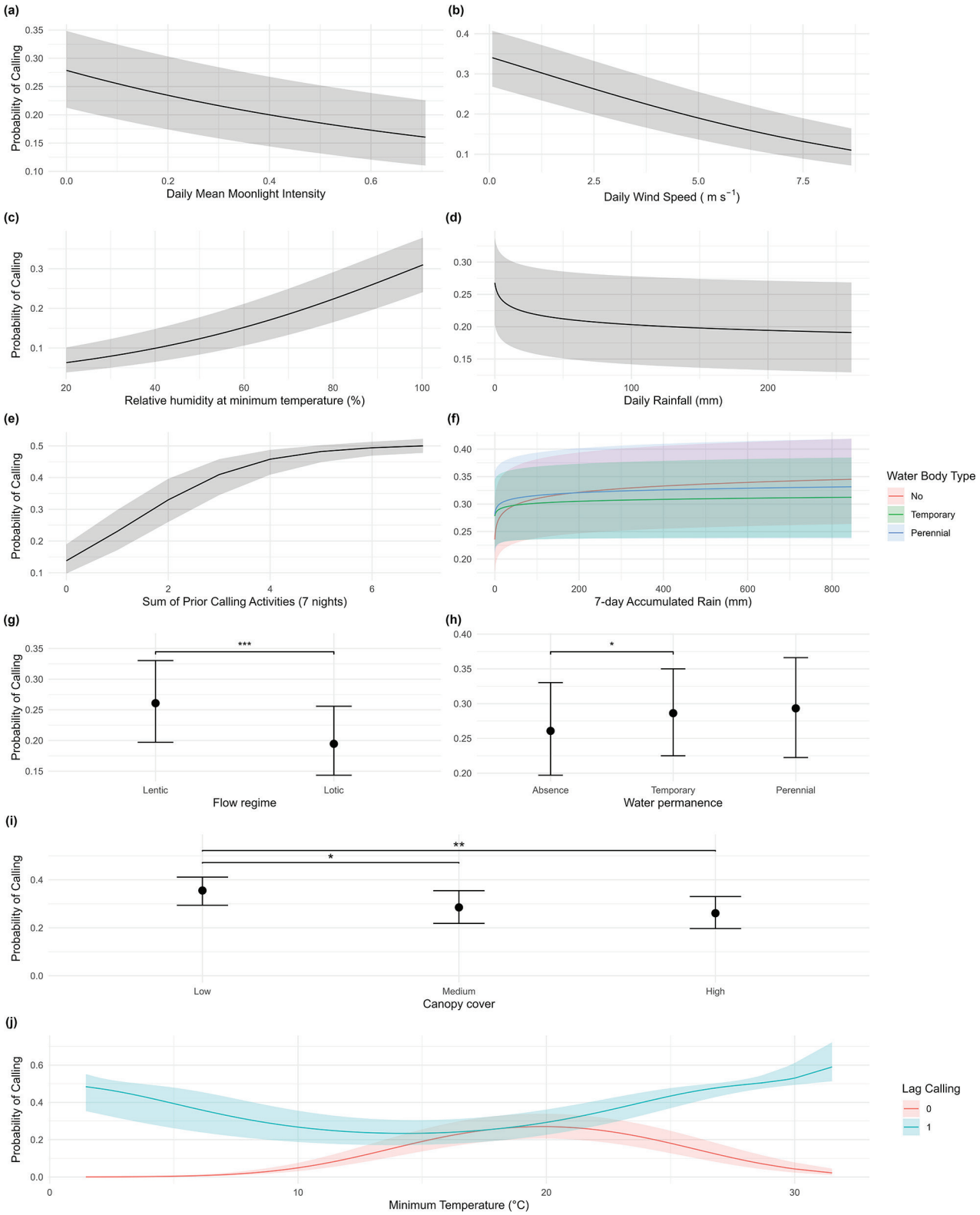


**Figure 4.** Predicted partial effects of significant abiotic, biotic and behavioural drivers on the nightly probability of cane-toad calling from the binomial GLMM. **a.** Daily mean moonlight intensity; **b.** Daily wind speed; **c.** Relative humidity at minimum temperature; **d.** Daily rainfall; **e.** Sum of prior calling activity over the previous 7 nights; **f.** Interaction between 7-day accumulated rainfall and waterbody type; **g.** Flow regime; **h.** Water permanence; **i.** Canopy cover; **j.** Interaction between minimum temperature and lagged calling. Estimated marginal means were computed to conduct pairwise comparisons between flow regime, water permanence and canopy cover groups using the emmeans package in R (Lenth 2024), horizontal bars with asterisks indicate significant pairwise differences (Tukey-adjusted): $p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***).

Overall, the model explained a substantial portion of variance (conditional $R^2$ = 0.500), with fixed effects alone accounting for 46.7% (marginal $R^2$; Suppl. material 1: table S3). Under temporally structured holdout within the observed dataset, the model achieved an AUC of 0.853, indicating good discrimination between calling and non-calling nights (Suppl. material 1: fig. S6). Random intercepts captured appreciable amongst-site heterogeneity ($\sigma^2$ = 0.168; $\sigma$ = 0.410) and a smaller, but non-zero ARU effect within sites ($\sigma^2$ = 0.043; $\sigma$ = 0.207), indicating mild residual differences in baseline calling probability both amongst sites and amongst recorders at the same site, beyond the fixed predictors (Suppl. material 1: figs S7, S8).

## Calling intensity model

Residual diagnostics indicated mild departure from uniformity, but no major issues (see Suppl. material 1: figs S9, S10 for details). Several environmental and behavioural predictors were associated with calling duration on call-positive nights, except for daily total cloud cover and DOY_sin (Fig. 5; Suppl. material 1: table S4). Consistent with the probability model, calling intensity was significantly lower near lotic waterbodies compared to lentic ones ($\beta$ = –0.74, $p$ < 0.001). Sites with temporary waterbodies exhibited greater calling intensity than those without water ($\beta$ = 0.48, $p$ = 0.008), while the effect at perennial waterbodies was positive, but lacked statistical support ($\beta$ = 0.42, $p$ = 0.2). Relative humidity at minimum temperature ($\beta$ = 0.17, $p$ < 0.001) and 3-day accumulated rainfall ($\beta$ = 0.05, p < 0.001) influenced calling intensity positively. Conversely, daily wind speed and mean moonlight intensity had negative effects on calling intensity ($\beta$ = –0.15, $p$ < 0.001; $\beta$ = –0.54, $p$ = 0.002, respectively), indicating that toads called for less time in windy conditions or on brighter nights. DOY_cos showed a negative effect ($\beta$ = –0.20, $p$ < 0.001) and exhibited a mild increase in calling intensity during early- to mid-July, when combining with DOY_sin (Fig. 5). Amongst canopy cover categories, both low- and mid- showed significantly higher calling intensity than sites with dense canopy cover ($\beta$ = 0.72, $p$ < 0.001; $\beta$ = –0.87, $p$ < 0.001, respectively; Fig. 5; Suppl. material 1: table S4).

Behavioural predictors showed patterns like those in the probability model. The linear effect of cumulative calling minutes over the previous seven nights had positive estimated effects, but were not statistically supported ($\beta$ = 0.11, $p$ = 0.08; Suppl. material 1: table S4). The quadratic term showed a positive effect ($\beta$ = 0.03, $p$ < 0.001), indicating a non-linear increase in calling intensity with recent calling effort. When no prior calling occurred, calling intensity exhibited a hump-shaped response to minimum temperature, peaking at moderate temperatures (linear term $\beta$ = 0.21, $p$ = 0.002; quadratic term $\beta$ = –0.47, $p$ < 0.001; Fig. 5). This relationship flattened with prior calling, as reflected in a poorly-supported quadratic term ($\beta$ = –0.01, $p$ = 0.9). The interaction between lagged calling and minimum temperature showed a notably positive estimated effect in the linear term ($\beta$ = 0.23, $p$ < 0.001), indicating that previous calling activity was associated with greater subsequent calling intensity, a pattern consistent with temporal persistence and possible social facilitation.

Overall, the model explained a significant portion of variance (conditional $R^2$ = 0.597), with fixed effects alone accounting for 48.8% (marginal $R^2$; Suppl. material 1: table S4). Under temporally blocked cross-validation, the concordance correlation coefficient (CCC) between observed and predicted calling duration was 0.546 (Suppl. material 1: fig. S11), indicating useful, but imperfect

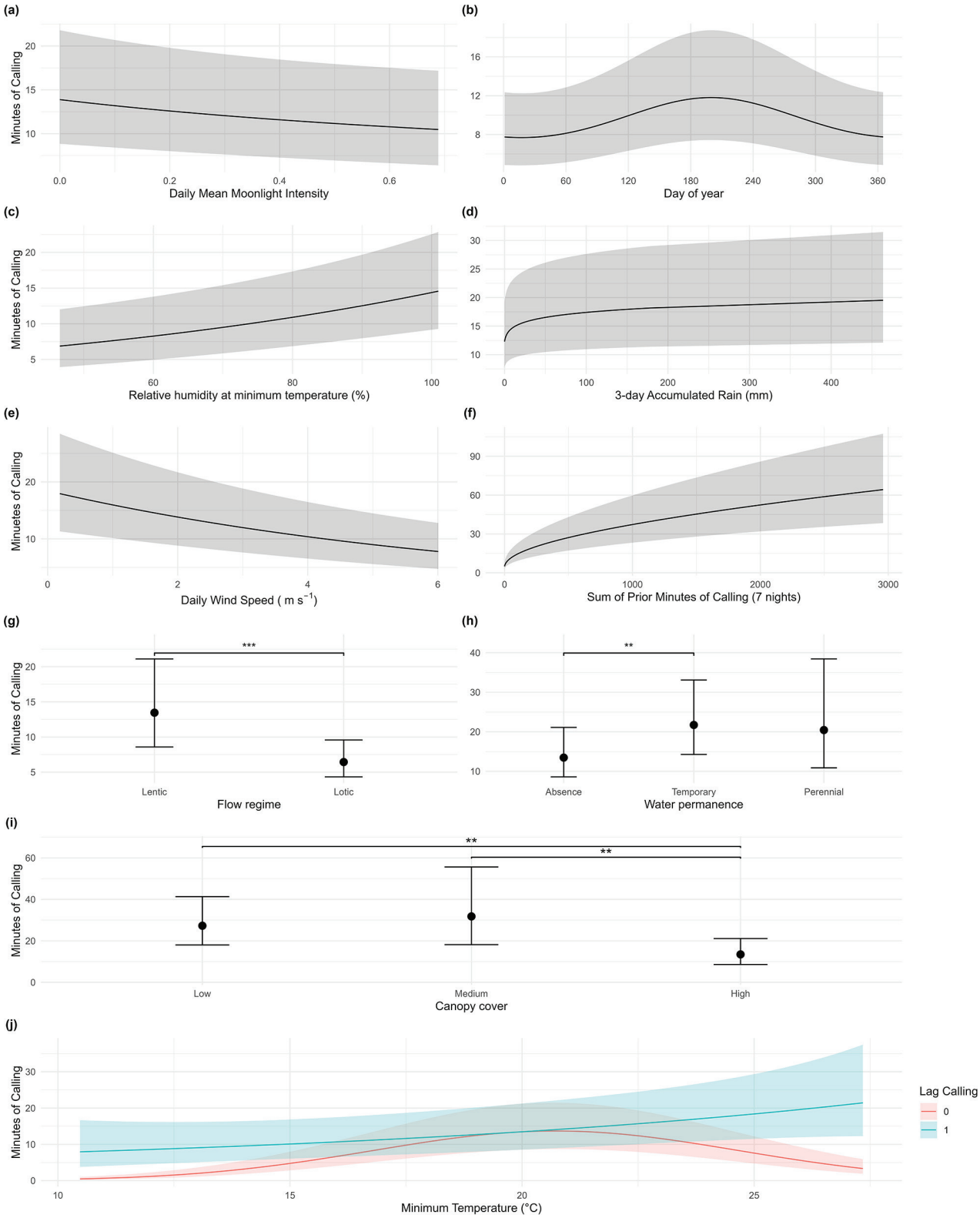


**Figure 5.** Predicted partial effects of significant abiotic, biotic and behavioural drivers on the nightly intensity of cane-toad calling from the gamma GLMM. **a.** Daily mean moonlight intensity; **b.** Day of year; **c.** Relative humidity at minimum temperature; **d.** 3-day accumulated rainfall; **e.** Daily wind speed; **f.** Sum of prior calling minutes over the previous 7 nights; **g.** Flow regime; **h.** Water permanence; **i.** Canopy cover; **j.** Interaction between minimum temperature and lagged calling. Estimated marginal means were computed to conduct pairwise comparisons between flow regime, water permanence and canopy cover groups using the emmeans package in R (Lenth 2024), horizontal bars with asterisks indicate significant pairwise differences (Tukey-adjusted): $p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***).

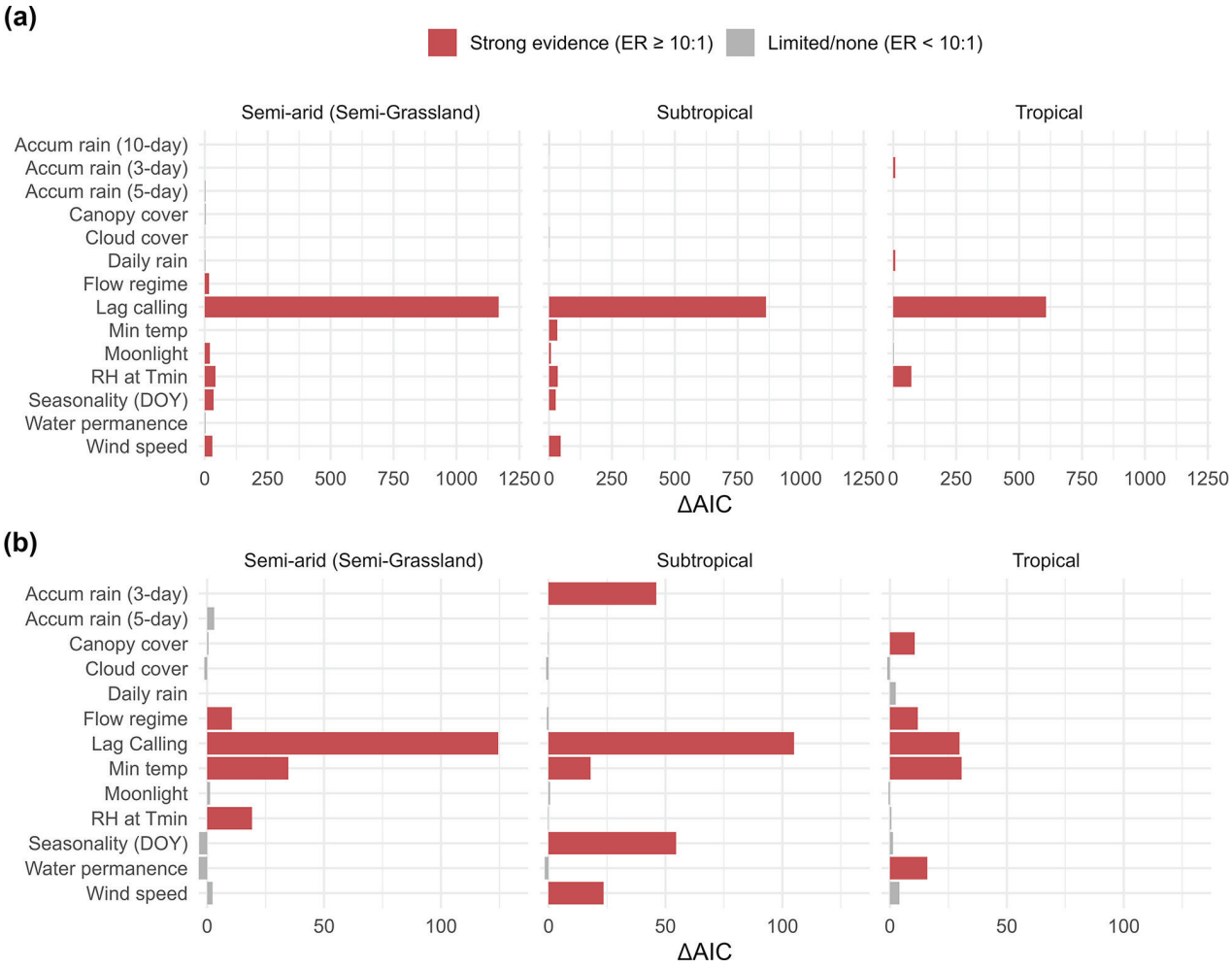


**Figure 6.** AIC-based variable importance by climate zone for calling probability (**a**) (binomial GLMM) and calling intensity (**b**) (gamma GLMM), calculated separately for semi-arid (semi-grassland), subtropical and tropical zones. Bars show the increase in the Akaike Information Criterion (AIC) when the named predictor block is removed from the full model (ΔAIC = AICreduced – AICfull); larger ΔAIC indicates a greater contribution of that block to model fit. Red bars denote strong evidence (evidence ratio ER ≥ 10:1, where ER = exp[ΔAIC/2]; Burnham and Anderson (2004)); grey bars indicate limited or no evidence (ER < 10:1).

predictive performance within the observed dataset. Random effects indicated much larger variability amongst ARUs within a site than amongst sites: ARU-within-site ($\sigma^2$ = 0.246; $\sigma$ = 0.496) versus amongst site ($\sigma^2$ = 0.024; $\sigma$ = 0.154; Suppl. material 1: figs. S12, S13), indicating substantial fine-spatial-scale differences in calling intensity amongst ARUs at a site.

## Climate-stratified models

We stratified the analyses by Köppen climate classifications (Fig. 6a) and fitted separate models for calling probability and intensity for tropical (n = 15 ARUs), subtropical (n = 17) and semi-arid (grassland) zones (n = 13). For calling probability, previous night calling overwhelmingly dominated model fit in every zone (ER ≫ 10; Fig. 6b) consistent with a strong social-facilitation effect on starting choruses. Relative humidity was also important across zones and moonlight, seasonality (DOY) and wind speed were additionally influential in the semi-arid (grassland)

and subtropical zones (ER > 10). Nevertheless, once lagged calling was included, the support for other predictors was comparatively much weaker within each zone. For calling intensity, the drivers varied by climate (Fig. 6c). Although lagged calling ranked highest in the semi-arid (grassland) and subtropical models, flow regime, minimum temperature and humidity also contributed meaningfully in the semi-arid (grassland) zone, while high cumulative rainfall, seasonality (DOY), low wind speed and high minimum temperature supported longer bouts in the subtropics. In the Tropics, high minimum temperature had the greatest weight, followed by lagged calling; other influential terms (ER > 10) were primarily habitat characteristics (canopy cover, flow regime and water permanence).

## Discussion

Here, leveraging a continent-wide acoustic dataset and a custom-trained machine-learning classifier, we present a broad picture of cane toad calling behaviour. By modelling both nightly calling probability and calling intensity, we show that toad chorusing is governed by a nuanced interplay of abiotic drivers (e.g. wind, temperature, moonlight), habitat context (waterbody availability and flow regime, vegetation structure) and strong behavioural effects (i.e. prior calling). Zone-stratified variable-importance patterns supported this view: recent calling consistently carried the strongest signal predicting both intensity and probability of calling, moisture-related conditions and temperature were broadly influential and the balance of weather versus habitat effects shifted amongst climate zones. These results clarify when and where in Australia cane toads are most likely to call and for how long. By showing that broad passive acoustic networks, coupled with a machine-learning classifier, can resolve chorusing phenology and its drivers at scale, this study highlights ecoacoustics as a useful approach for invasive-species acoustic monitoring and research. While our focus is cane toads, the framework and key cues identified here may offer a useful point of reference for understanding and monitoring of other vocal invasive species around the world.

### Spatio-temporal calling patterns

*A priori*, one might expect calling to occur on fewer nights in cooler and drier or range peripheral regions, but we did not observe this. Our site-level map of proportions of nights upon which calling occurred (Fig. 1) spans both the core and peripheral regions of cane toad occurrence in Australia (Atlas of Living Australia 2024; Cutajar et al. 2025). No simple latitudinal gradient emerges, although we acknowledge there are coverage gaps along southern Queensland's east coast and in parts of the Northern Territory and Western Australia. Calling-night proportions peak in the tropical and subtropical zones of northern Queensland, which also constitute the heart of the species' current range (Fig. 1; Cutajar et al. 2025).

Across our 21 sites, cane toads display near-year-round calling activity, with pronounced peaks in the mid-to-late wet season (Fig. 2). This pattern aligns with regional studies in tropical Australia (Brodie et al. 2021), where calling occurred, albeit at lower rates, through the dry months (Fig. 2). We detected no consistent latitudinal gradient in monthly activity: there were also occasional winter choruses at southern sites, indicating that climate or geography alone does not fully explain calling behaviour. From a management perspective, these findings suggest that

surveillance may need to extend beyond the wet season even in some marginal areas, because low-level calling associated with possible breeding activity can still occur outside the main calling period.

Within nights, calling occurred from shortly after sunset until dawn across all sites (18:00–06:00 h; Fig. 3), with a rapid increase after dusk and one or two evening peaks. Onset occurred later in the wet than in the dry season, consistent with longer photoperiods and delayed darkness and dry-season calling was generally of lower intensity and shorter duration, likely reflecting cooler nocturnal temperatures. This seasonal contrast was weakest at the only tropical site (Rinyirru), where more stable temperatures allowed elevated calling to persist longer than at subtropical sites. The overall trend is the mean of site-level curves, so its shape can be influenced by differences in photoperiod across latitude (~ 15.5°) and variation in the availability of recording data. Even across the smaller latitudinal spread amongst the listed sites (~ 8.5°; tropical to subtropical), we saw no clear latitudinal shift in chorus timing. Rather, we observed seasonal shifts in the beginning and end of calling, the peak period and activity levels. Notably, the intensity of elevated calling in the dry season shortened from ~ 6.5 h at Rinyirru to ~ 5–6 h at Spyglass/Fletcherview to ~ 2–3 h at Wambiana, Moorrinya and Mitchell Grass. Although daytime audio was not analysed, the strong dusk-to-dawn signal matches the species' nocturnal ecology (Doody et al. 2019). Such prolonged nocturnal occupancy of the acoustic space, combined with the year-round activity we observed, could raise the possibility of acoustic interference with co-occurring native frog species and merits further investigation (e.g. Bleach et al. (2015); Allen-Ankins and Schwarzkopf (2022); Hopkins et al. (2023)).

## Environmental, habitat, and behavioural drivers of calling

Humidity and rainfall are well-established drivers of anuran breeding activity across tropical and temperate systems (Donnelly and Guyer 1994; Brooke et al. 2000; Hatano et al. 2002; Steelman and Dorcas 2010; Llusia et al. 2013; Brodie et al. 2021, 2025), reflecting amphibians' strong dependence on water and sensitivity to moisture regimes (Feder and Burggren 1992; Wells and Schwartz 2007). In our study, high relative humidity at the nightly minimum temperature had a clear positive effect on both calling probability and intensity, although this effect was substantially stronger for the probability of calling (Figs 4, 5; Suppl. material 1: tables S2, S3). This pattern could be explained by a water-balance mechanism: high humidity reduces evaporative water loss and the energetic cost of calling, acting primarily as a trigger for chorus initiation rather than a dominant contributor to chorus continuation, a pattern that was also observed in a native Australian frog (*Cophixalus ornatus*; Hauselberger and Alford (2005)). By contrast, rainfall effects are scale- and context-dependent, some species respond to short lags or multi-day accumulations, others show weak or even negative responses (e.g. Ospina et al. (2013); Steen et al. (2013); Brodie et al. (2025)). Here, same-day rainfall slightly reduced calling probability and did not affect intensity (Figs 4, 5; Suppl. material 1: tables S2, S3), plausibly due to storm noise and immediate disturbance, choruses often start after, not during, rainfall events. In turn, accumulated rainfall boosted calling intensity with 3-day totals and increased calling probability where permanent water was absent (evidenced by the 7-day rainfall × no-water site interaction) (Figs 4, 5; Suppl. material 1: tables S1, S3,

S4). Rainfall-window selection was exploratory, however and the best-supported windows should not be interpreted as uniquely identified timescales: in the calling-probability model, the 7-day window had the lowest AIC, but the 3-day and 5-day windows also had ΔAIC values ≤ 2, while in the calling-intensity model, the 3-day window was best supported, but the 5-day and 7-day windows were also competitive (Suppl. material 1: table S1). This suggests that cane toad calling is associated with short-term accumulated rainfall over multiple plausible lag windows of several days. Accumulated rainfall likely forms ephemeral ponds at otherwise dry sites, reflecting the requirement for movement to the calling site and social dynamics: toads must leave refuges and converge on breeding sites and calling can intensify as additional individuals join choruses on post-rain nights (Saenz et al. 2006; Fouquet et al. 2020). These outcomes align with previous work on cane toads showing stronger effects on calling of multi-day rainfall than of same-day rain (Brodie et al. 2021, 2025). Notably, we detected a negative same-day rainfall effect on calling probability; although modest in magnitude relative to other predictors, it underscores the importance of distinguishing immediate weather from accumulated moisture and water availability. However, rainfall may also affect acoustic detectability, by increasing background noise and masking calls. Taken together, these results suggest that humidity may be more closely linked to chorus initiation, whereas cumulative rainfall may better reflect the short-term hydrological conditions that create or expand potential breeding opportunities, especially in landscapes lacking permanent waterbodies.

As chorusing is nocturnal, nightly minimum temperature is a better proxy for the thermal conditions experienced during calling than daytime maxima. In our models, minimum temperature was a strong predictor of both calling probability and intensity, with hump-shaped relationships on nights without prior calling that are consistent with the thermal performance breadth reported for anuran calling (Llusia et al. 2013; Figs 4, 5; Suppl. material 1: tables S2, S3). Although its apparent effect size was not the greatest amongst predictors, minimum temperature was the only single covariate that pushed predicted calling activity towards zero across the observed range (Figs 4, 5; Suppl. material 1: tables S2, S3). From our results, calling was least likely to initiate or persist below roughly 6–7 °C (Figs 4, 5), matching reports of no chorusing when overnight minima fell below 7 °C in northern Australia (Brodie et al. 2021) and the broader activity range documented for adult cane toads (≈ 6 °C to > 40 °C; Zug and Zug (1979)).

Interestingly, after a chorus the previous night, the impact of minimum temperature was different. When there was previous activity, calling was more likely to happen on cool or warm nights and nightly calling tended to last longer as minimum temperature increased (Figs 4, 5; Suppl. material 1: tables S2, S3). Ecologically, we suggest this indicates that social context is reshaping the cost-benefit trade-off, once a chorus was underway. Once a chorus was active the previous night, the decision environment changes, social cues signal that mates and competitors are present, many males are already at or near water. Warm nights often coincide with higher humidity that retains heat and reduces desiccation risk. Greater water availability and the reproductive payoff (e.g. greater female attendance, reduced male–male competition, reduced predation risk and a better overall environment for tadpole growth; Crump (1974); Toft (1985); Duellman (1989); Donnelly and Guyer (1994)) of an active chorus may outweigh physiological costs, sustaining or even increasing calling activity. The elevated calling probability under

cool conditions may indicate carry-over social facilitation: because calling rarely begins on cold nights, once a chorus is underway, social cues may maintain calling despite temperatures that would otherwise suppress initiation. In short, prior-night calling, together with minimum temperature, was pivotal for chorus perpetuation. If toads had called the night before, they would be more likely to call again the next night, across a wider range of night-time temperatures.

The amount of prior-week calling was one of the strongest predictors for both calling probability and intensity (Figs 4, 5; Suppl. material 1: tables S2, S3). Each additional night of recent calling sharply increased the chance that toads would call again, but the positive effect plateaued after several consecutive nights. This pattern fits carry-over occupancy: once males had moved to water and a chorus had formed, it is possible many remained at or near the site, so calling again costs little, but eventually activity plateaus as energetic reserves are depleted, receptive females become scarce or the site reaches an acoustic or reproductive carrying capacity. Calling intensity showed a different response to calling on previous nights: it changed little with a small amount of recent activity, then tended to increase once chorusing had been sustained for several nights. This escalation is consistent with social facilitation, because prior calling signals that mates and competitors are present and increases the payoff of continued effort. Simply put, prior-week calling reflects genuine behavioural persistence. Once calling gets underway, social and logistical carry-over and not just nightly conditions keeps calling elevated across successive nights.

Among environmental predictors, moonlight was especially influential: toads called less often and for shorter periods on brighter nights (Figs 4, 5; Suppl. material 1: tables S2, S3). Importantly, our moonlight estimates represent clear-sky astronomical illumination rather than realised ground-level brightness, which may be modified locally by cloud cover, vegetation screening, and topographic context (Vignoli et al. 2014). In spite of these potential additional sources of variation influencing the variable we used, the reduced calling we observed aligns with reports of reduced anuran and specifically cane toad calling activity on bright nights (Johnson and Batie 2001; Pena et al. 2008; Brodie et al. 2025), as well as field evidence that cane toad trapping rates drop under strong moonlight (Muller and Schwarzkopf 2018), suggesting a potential suppressive effect on cane toad activity. We did evaluate a moonlight × cloud cover interaction during model development, as a closer proxy for realised ground-level illumination, but this term was not retained during model selection and remained uninformative even when fitted without collinear terms. Reduced calling on brighter nights is consistent with predator-avoidance behaviour, as greater nocturnal illumination may increase conspicuousness to predators (reviewed in Grant et al. (2013)). In general, moonlight had an obvious suppressive impact on calling in our study, although the mechanism for this is not known. Further studies should observe toad behaviour in relation to direct measures of ground-level illumination to clarify this mechanism.

Day-of-year showed a modest, but significant association with nightly calling intensity, reflecting a subtle seasonal signal (Fig. 5; Suppl. material 1: table S4). Having held the spatial differences (random effect) and nightly conditions (other covariates) constant, cane-toad choruses were slightly longer (more minutes per night) in the dry season (May–September), whereas DOY did not affect the probability of calling initiation (Suppl. material 1: table S3). We interpret this as a small

residual seasonal pattern not captured by our covariates. Whereas many studies report non-linear DOY-calling relationships or strong seasonal effects with summer or wet-season peaks (e.g. Schalk and Saenz (2016); Thompson et al. (2022); Brodie et al. (2025)), our result suggests that, when calling occurs in the dry season, it tends to last a little longer, an effect that is modest relative to the main environmental and social predictors (Fig. 5), but for which the cause is unclear.

Calling declined on windier nights (Figs 4, 5; Suppl. material 1: tables S2, S3). Wind can increase evaporative water loss and convective cooling, elevate locomotor costs and degrade acoustic transmission (attenuation, scattering, rustle noise), all of which are consistent with negative effects on anuran calling (Oseen and Wassersug 2002; Steelman and Dorcas 2010; Brodie et al. 2025). For cane toads specifically, having limited resistance to desiccation and often calling on open ground, near open water, both pathways are plausible: windier conditions likely impose higher water-balance costs, while also lowering signal-to-noise ratios by wind-driven turbulence and vegetation noise. We cannot fully eliminate effects of detectability bias on our data (Gjelland and Hedger 2013), but the negative effects are concordant with a trapping study also reporting reduced activity under windy conditions (Muller and Schwarzkopf 2018).

Across sites, temporary waterbodies supported higher calling probability and longer bouts than locations without surface water, whereas perennial waterbodies were not consistently different from either category (Figs 4, 5; Suppl. material 1: tables S2, S3). A similar pattern has also been reported for frog communities in South Australia (Hoffmann 2018), supporting the idea that ephemeral ponds offer short, predator-poor breeding opportunities, whereas permanent waterbodies are more likely to harbour fish and large aquatic insect larvae that prey on eggs and tadpoles, depressing reproductive activity (Eterovick and Sazima 2000; Prado et al. 2005; Spencer and Wassens 2009; Lowe et al. 2015). Beyond predator avoidance, multiple lines of evidence indicate that ephemeral pools compress amphibian reproductive cycles: following re-watering events, diverse species initiate breeding as a single rapid pulse (e.g. *Litoria raniformis*, *L. dumerilii*; Anstis (2013); Hoffmann (2018)). Although continuous breeders use permanent water in dry periods (e.g. Prado et al. (2005)), cane toads are opportunistic and not strictly continuous everywhere (Fig. 2); where temporary habitats are available, they likely prefer them, to capitalise on favourable conditions for larval development. Hydrology also mattered via flow regime: cane toads are more likely to call and call more, at lentic water than at lotic channels (Figs 4, 5; Suppl. material 1: tables S2, S3), matching their tendency to spawn in still pools and avoid flowing water (Hagman and Shine 2006, 2007) and their preference for quiet water in their native range (Evans et al. 1996). Together, these mechanisms explain why temporary waterbodies stood out relative to no-water sites, while perennial systems showed no uniform effect on propensity to call, and they align with our broader result that multi-day rainfall pulses facilitate calling where standing water is otherwise scarce. In practice, ephemeral, still waters emerge as key foci for calling activity and monitoring.

Toads called most often in open habitats with little canopy cover and calling bouts tend to last longer at sites with low- to moderate canopy (Figs 4, 5; Suppl. material 1: tables S2, S3). Sites with low- to moderate canopy are usually dominated by short vegetation (grasses) and with only modest coverage of woody plants (roughly up to ~ 40%). Cane toads typically breed on relatively open ground with sparse vegetation (Hagman and Shine 2006, 2007; Semeniuk et al. 2007; Mayer et

al. 2015), prefer waterbodies with little emergent cover in their native range (Evans et al. 1996) and avoid overhanging vegetation (Zug and Zug 1979). Dense cover likely hampers acoustic communication by attenuating calls and shortening effective transmission distance (MacLaren et al. 2018) and may cool waterbodies and decrease the rate of tadpole development. In short, cane toads most often initiate choruses in open, low-canopy habitats, whereas sustained calling is less common in dense woodlands or forests.

## Variable importance across climate zones

Stratifying sites by Köppen climate zones (tropical, subtropical, semi-arid [grassland]) largely reinforced the overall picture (Fig. 6, Suppl. material 1: fig. S1). Prior-night calling (putative social facilitation) was the most consistent predictor of chorus re-initiation across all zones, with relative humidity also important for determining whether calling occurred and minimum temperature important for determining chorus length (Fig. 6). Other drivers varied by climate: the probability of calling was more influenced by wind, moonlight and seasonality (DOY) in subtropical and semi-arid sites, whereas habitat features (canopy cover, flow regime, water permanence) were more important in the Tropics (Fig. 6). In all regions analysed, relative humidity, wind speed and moonlight had larger effects on whether calling occurred than on how long choruses lasted, suggesting they mainly influence chorus initiation rather than persistence, consistent with the partial-effect estimates from the global models (Figs 4, 5). DOY contributed more to calling probability in subtropical than in tropical or semi-arid regions, paralleling a prior Australian acoustic study (Thompson et al. 2022) that observed a similar regional contrast, supporting this interpretation. This pattern likely reflects stronger seasonality in subtropical regions, especially at our two southernmost subtropical sites near the temperate boundary, where warm–wet windows are short (Suppl. material 1: fig. S2). In the semi-arid [grassland] zone, the strong role of humidity in determining calling occurrence mirrors previous findings (Thompson et al. 2022) and accords with amphibians' heightened hydric sensitivity in moisture-limited systems (Cruz-Piedrahita et al. 2018). In the Tropics, the prominence of habitat variables in calling activity likely reflects that ambient conditions are closer to the species' optimal climatic niche, so weather becomes less of a limitation, making local habitat structure the primary constraint on sustaining choruses. Overall, variable importance differed slightly by climate zone: atmospheric and lunar cues mattered most for initiating choruses in subtropical and semi-arid zones, while habitat features contributed to sustaining them in the Tropics. Prior-night calling is important everywhere and minimum temperature is a key driver of calling intensity across all zones. These zone-specific patterns help clarify how calling correlates vary across broad environmental settings and may support more targeted interpretation of acoustic activity by climate zone. Because our analysis spans a broad spatial extent (~ 15° of latitude and 27° of longitude; Suppl. material 1: table S2) and a wide climatic gradient (tropical, subtropical, semi-arid), these results provide a practical reference for investigators in other invaded regions with comparable environments, providing information for survey timing, prioritisation of environmental conditions and study design.

The strong site effects we observed may also be ecologically informative. In the calling-probability model, site-level variance exceeded within-site variance,

suggesting that broader, site-scale differences contributed more strongly to whether calling occurred at all than did fine-scale differences amongst recorder locations. This pattern is consistent with variation amongst sites in broader ecological contexts not fully captured by the predictors included in the model, such as longer-term climatic setting, hydrological dynamics, habitat configuration or other unmeasured aspects of site suitability. By contrast, the effect of within-site variance was larger in the calling-intensity model (Suppl. material 1: figs S12, S13), indicating that calling duration varied more strongly at finer spatial scales within sites. This is more likely associated with local differences where breeding aggregations formed relative to individual recorders, including variation in chorus size or concentration of calling males, although other factors, such as vegetation screening, background noise and distance to calling individuals and breeding grounds, may also contribute to local variation.

Several limitations should be considered when interpreting these results. First, because calling activity was inferred from passive acoustic detections, some environmental predictors may influence both behaviour and detectability. Stronger wind and heavy rainfall may reduce acoustic detectability by increasing background noise and lowering signal transmission, but they are also biologically plausible constraints on activity (e.g. Muller and Schwarzkopf (2018)) and severe rainfall or flooding can negatively affect frogs by disrupting calling conditions and breeding habitat (Walls et al. 2013; Bieri and Rowley 2026). Second, the environmental predictors used here were derived from gridded datasets and nightly summaries and, therefore, may not fully capture the fine-scale microclimatic and within-night conditions experienced by calling individuals, although it is important to note that these types of errors tend to increase variation and make our ability to discern patterns less likely, rather than making it likely we will detect spurious relationships. Third, although behavioural predictors captured important temporal structure in the data, some temporal dependence may still remain, particularly for calling intensity. However, our temporally blocked cross-validation and residual checks should reduce concern that the main results are purely artefacts of leakage or unmodelled autocorrelation. Lastly, although the dataset spans up to approximately four years, we did not model year as an explicit effect, because our focus was on observation-level environmental and behavioural correlates rather than interannual trend estimation. Environmental covariates were matched to each observation, so much of the relevant temporal variation was incorporated directly into the models. Nevertheless, broader year-to-year differences were not explicitly partitioned and unmeasured annual variation, such as shifts in habitat condition, hydrology or population dynamics, may still contribute to residual variation. Future work could address these limitations by pairing passive acoustic monitoring with on-site microclimate measurements and higher-resolution environmental data to better align local vegetation, hydrology and microclimatic conditions with calling behaviour and by embedding routine site visits within monitoring programmes to ground-truth ecological patterns. For example, brief microhabitat surveys, abundance indices (e.g. using chorus counts, acoustic arrays or mark–recapture) and checks for independent breeding evidence (eggs or tadpoles or both) could help determine whether acoustic detections reflect cane toad occurrence alone or breeding-related activity. Such integration would strengthen ecological interpretation of acoustic monitoring and improve its value for future research and management. More broadly, acoustic detections could support future modelling of cane toad

calling activity under changing environmental conditions, including possible links to emerging breeding opportunities under climate change (e.g. Desjonquères et al. (2022)) and extending passive acoustic monitoring towards range edges may improve coverage of calling activity in invasion-prone areas. Preliminary experience also suggests that the cane-toad classifier used in this study (Leung et al. 2025) may have broader utility beyond Australia: it generally performed well in a Japanese acoustic dataset, despite the presence of a native frog species with a potentially confusing vocalisation (*Nidirana okinavana*) that was not included in the training data (K. Kimura, personal communication, 4 June 2025), suggesting potential for future evaluation in other invaded regions.

## Conclusions

In Australia, cane toads are amongst the most widespread and ecologically damaging invasive vertebrates (Shine 2015). More broadly, they are also recognised as a globally important invader, ranking amongst the alien amphibians with the greatest combined environmental and socioeconomic impacts (Measey et al. 2016). Several studies discovered climate potential for further range expansions in Australia (Kearney et al. 2008; Andersen et al. 2021), highlighting the value of stronger ecological understanding of cane toad activity patterns for future invasion research. Passive acoustic monitoring enables continuous observation of behaviour across complex habitats and extensive space–time scales, especially in remote, under-surveyed regions. Using a continent-scale acoustic network, paired with environmental and habitat data, we characterised broad spatial, seasonal and nocturnal patterns of cane toad calling across Australia. The most consistent correlates of chorusing were low moonlight, low wind, higher relative humidity, the presence of lentic or temporary water and recent calling activity. Minimum temperature influenced chorus initiation, especially when no chorus had been active the previous night. The strong effect of prior-night calling was consistent with temporal persistence and possible social facilitation. However, the relative contributions of these variables were different across semi-arid (grassland), subtropical and tropical zones. Beyond the Australian case, our approach provides a practical example of how ecoacoustics can help identify environmental and behavioural correlates of activity in vocal invasive species across large spatial scales. For cane toads and other invasive toads in comparable climatic and habitat settings, these findings provide a useful reference for future monitoring and ecological investigation. Further progress will depend on linking acoustic monitoring with on-site microclimate measurements, higher-resolution environmental data and independent field evidence of breeding and abundance, particularly at range edges and invasion fronts.

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## Additional information

### Conflict of interest

The authors have declared that no competing interests exist.

### Ethical statement

No ethical statement was reported.

### Artificial Intelligence (AI) use

Regarding the use of AI in the preparation of this manuscript, the authors declare the following:
During the preparation of this work, ChatGPT was used to check grammar and improve readability. After using this tool, all authors reviewed and edited the content as needed.

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### Author contributions

Franco Ka Wah Leung: Conceptualisation, Methodology, Software, Validation, Formal Analysis, Investigation, Writing – Original Draft, Visualisation. Slade Allen-Ankins: Conceptualisation, Methodology, Validation, Writing – Original Draft, Writing – Review and Editing, Supervision, Project administration. Lin Schwarzkopf: Conceptualisation, Methodology, Validation, Writing – Original Draft, Writing – Review and Editing, Supervision, Project administration, Funding acquisition.

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### Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

## Supplementary material 1

### Model diagnostics and performance

Authors: Franco Ka Wah Leung, Slade Allen-Ankins, Lin Schwarzkopf

Data type: docx

Explanation note: Supplementary tables and figures.



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