Passive acoustic monitoring and deep learning reveal spatiotemporal patterns in gibbon calling behaviour associated with habitat and climate variables

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Abstract

1. Understanding the basic ecology of endangered species is essential for effective conservation, yet this remains challenging for elusive species inhabiting tropical forests. For the endangered Bornean white-bearded gibbon (*Hylobates albibarbis*), basic ecological information remains limited. Most research on the species is restricted to peat swamp forests, while little is known from other forest types that make up a large part of its range. Passive acoustic monitoring provides an opportunity to study vocal behaviour to obtain such ecological insights, while enabling research across larger spatial and temporal scales than previously possible.
2. We deployed eight autonomous recording units across three forest types in Central Kalimantan, Indonesia, collecting 23,244 hours of acoustic data over 18 months. A pretrained deep learning automated detector was applied to identify great calls, performed by female gibbons as part of morning duets and a key indicator for comparing population density. We identified 83,956 great calls and examined how daily call rates varied across habitats and in response to seasonal rainfall (as an indicator of resource fluctuations).
3. Daily call rates did not differ significantly among forest types but showed significant temporal variation over the survey period. Higher call rates occurred during months with greater rainfall, consistent with seasonal resource availability driving vocal activity. To clarify this effect, we investigated the short-term effects of weather and found that rainfall on the day before observation reduced both call rates and the probability of calling, while rainfall two days prior increased calling activity, suggesting compensatory vocal behaviour.
4. Our findings highlight the need to account for variable vocalisation rates in acoustic monitoring, particularly when evaluating the additive effects of habitat loss and climate change on species behaviour and ecology. We emphasise the importance of considering phenological factors when interpreting calling activity and the value of incorporating spatial data to strengthen ecological inferences from acoustic datasets. Furthermore, this study demonstrates the power of deep learning for large-scale, long-term monitoring of species’ vocal behaviour, providing valuable ecological insights across increasingly broad spatiotemporal scales.

Introduction

Effective conservation action requires an understanding of the basic ecology of threatened species, including distribution, habitat use, and the limiting factors on their population density (Rushton et al., 2004). However, obtaining such information is particularly challenging for animals inhabiting tropical rainforests, which are among the most biodiverse and threatened biomes on Earth. This is due to limitations on direct observation caused by dense foliage, human-avoidance behaviour, and the inaccessibility of habitats to researchers (Zwerts et al., 2021). The gibbons (family Hylobatidae) of Southeast Asia are a taxonomic group that exemplify these challenges. Despite 19 of the 20 species being classified as Endangered or Critically Endangered by the IUCN Red List of Threatened Species, key ecological knowledge remains limited (IUCN, 2025). For example, while the boundaries of species' ranges may be well known, occupancy and population density distributions within those ranges, and how these may be affected by habitat variation, remain largely unknown (Cheyne et al., 2016; Geissmann, 2007). Furthermore, where detailed knowledge from direct observation does exist, it is typically restricted to small geographic areas and a limited number of habituated individuals; meanwhile, there is a severe lack of data on gibbons outside of protected areas (Cheyne et al., 2023).

The Bornean white-bearded gibbon (*Hylobates albibarbis*) is endemic to southern Borneo, occurring within Indonesia's Central Kalimantan and West Kalimantan provinces, south of the Kapuas River and west of the Barito River (Marshall et al., 2020). Variation in soil types and elevation has given rise to a range of forest types in this area, with distinctly different tree species compositions (Anirudh et al., 2025). This botanical variation among forest types can be expected to influence the distribution of gibbons across their range, as has been observed in relation to canopy height (Hamard et al., 2010). Gibbons are primarily frugivorous and folivorous, and, because they live in small family groups in fixed territories, localised fruit availability and temporal variation therein are likely key limiting factors on gibbon population density (Marshall, 2009; Marshall & Leighton, 2006). Such temporal variation can differ greatly among forest types, with some showing masting, whereby mass fruiting events in some years are interspersed by a varying number of lean years, whereas other types show either no or limited masting but may show varying degrees of intra-annual variation in response to seasonal variation in rainfall (Curran & Leighton, 2000; Morrogh-Bernard, 2009; van Schaik & Pfannes, 2005). Currently, most research on *H. albibarbis* ecology and behaviour has been conducted in a few non-masting peat swamp forest locations, while little is known from other forest types that make up a large part of the species' range (Cheyne et al., 2016).

Most gibbon species perform elaborate long-range vocalisations in the form of sex-specific songs that are coordinated as morning duets by territorial mated pairs (Geissmann, 2002). These duets typically consist of introductory, interlude and great call sequences, with the latter being the most stereotyped and easily identifiable component (Geissmann, 2002). The great call sequence, comprising the female great call, often followed by a male coda, serves as a key indicator for comparing population density, as its presence indicates a mated pair (Gilhooly et al., 2015). These duets serve multiple functions, including mediating intergroup spacing, maintaining the pair bond, mate defence, and advertising attributes of the individual or pair (Cowlishaw, 1992; Geissmann & Orgeldinger, 2000; Mitani, 1985). Studies of gibbon songs have been used to identify species (Cheyne et al., 2024), determine phylogenetic relationships (Thinh et al., 2011), estimate population density (Cheyne et al., 2016), assess spatial distribution (Okuda et al., 2022), and identify individuals (Clink et al., 2017). Recent advances in passive acoustic monitoring (PAM) and machine learning have further expanded the scope of such research by improving the efficiency of collecting and analysing acoustic data while enabling research across larger spatial and temporal scales than previously possible (Stowell, 2022; Wich & Piel, 2021).

The deployment of PAM arrays in diverse forest types across a landscape provides the opportunity to infer differences in gibbon population densities among habitats from the frequency of songs detected in recordings over prolonged periods. It should, however, be noted that the relationship between song frequency and population density may not be linear, as gibbon singing has been shown to be density dependent, wherein animals sing less frequently in areas with fewer neighbouring groups (Brockelman & Srikosamatara, 1993; Yin et al., 2016). While this relationship may complicate direct interpretation, differences in population densities among habitats can therefore be expected to manifest as amplified differences in relative song frequencies. Further, singing is energetically costly, and gibbons have been observed to produce shorter songs and call less frequently during periods of low fruit abundance (Cowlishaw, 1996). Therefore, temporal variation in song frequency could reflect changes in the timing of peaks and troughs in resource abundance in different habitat types.

A potentially complicating factor in deriving temporal variation in resource abundance from gibbon song frequency is their short-term response to overnight or morning rainfall, which is more likely in the rainy season. This seasonal increase in rainfall is typically associated with peaks in animal-dispersed fruit abundance (Morrogh-Bernard, 2009; van Schaik & Pfannes, 2005). However, rainfall generally reduces both the duration and probability of pairs engaging in song duets, possibly because rainy or windy conditions impair sound transmission, reducing the effectiveness of long-range vocal communication, and/or because the increased energetic cost of overnight thermoregulation may cause gibbons to prioritise foraging over singing the following morning (Brockelman & Srikosamatara, 1993; Cheyne, 2008; Clink et al., 2020; Mitani, 1985). Together, these factors contribute to gibbons singing on fewer days during months with higher rainfall (Mitani, 1985). Higher song frequency during the rainy season is therefore likely to be consistent with the hypothesis that song frequency is associated with resource availability, while higher song frequency in the dry season would indicate that the short-term effects of weather are the more important driver. Moreover, the cumulative impact of consecutive missed song duets due to adverse weather remains unclear. Gibbons may compensate for missed duets by increasing vocal effort on fair-weather days, or the suppressive effect of rainfall on duetting may diminish over consecutive rainy days as the social costs of missing duets are compounded.

Here, we use an 18-month acoustic data set collected using a PAM array deployed in a mosaic lowland forest landscape in southern Borneo. We utilise a deep learning detector developed by Owens et al. (2024) to automatically identify *H. albibarbis* great calls. We investigate how patterns of *H. albibarbis* great calls vary across habitats and in response to changing seasonal conditions. Specifically, we test the following hypotheses: (1) the number of great calls detected per day differs among habitat types, which may reflect differences in population density; (2) the number of great calls detected per day varies seasonally, with temporal trends differing among habitats, which may reflect changes in resource availability and the timing of peaks and troughs in resource abundance in different habitat types; (3) the number of great calls detected per day is positively associated with seasonal rainfall, despite the negative short-term effects of rainfall on calling activity, which would suggest that song frequency is associated with resource availability.

Methods

Study site

The long-term acoustic dataset used in this study derives from the Mungku Baru Education and Research Forest (MBERF), a ~50 km^2 area of tropical rainforest in Central Kalimantan Province, Indonesia (1°39'S 113°44'E). The MBERF lies in the centre of the wider Rungan forest landscape, which spans approximately 1,500 km^2 between the Kahayan and Rungan rivers, north of the provincial capital of Palangka Raya (*Figure 1)*. This landscape represents the largest area of continuous unprotected lowland rainforest remaining on the island of Borneo (Afitah & Purnama, 2021) and is home to an estimated ~4,000 *H. albibarbis* individuals, making the region critically important for the conservation of the species (Buckley et al., 2018). Despite this, the forests here are under threat from the conversion of primary forest to oil palm and acacia plantations, expansion of coal mining concessions, gold mining in surrounding rivers, wildlife hunting, and forest fires. Ongoing wildlife monitoring has been recommended to strengthen the case for increased protection and fully realise the conservation potential of the Rungan forest landscape (Anirudh et al., 2025; Buckley et al., 2018).

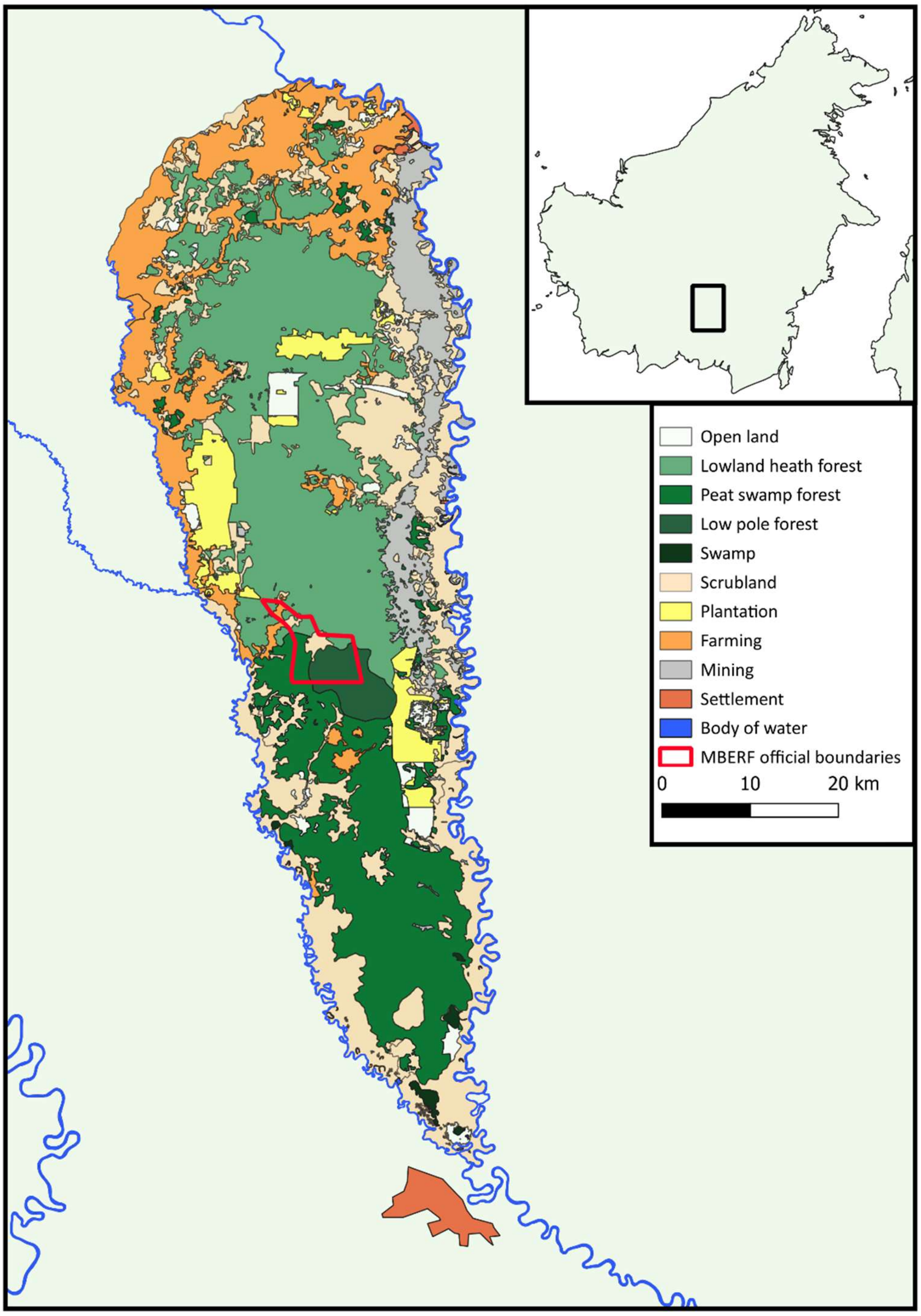

Figure 1. Map of the Rungan forest landscape within Borneo, showing the official land designations and the location of the Mungku Baru Education and Research Forest (MBERF; General Directorate of Forestry Planning and Environmental Management, Indonesian Ministry of Forestry, 2020).

The MBERF comprises a mosaic of different habitats, including three predominant forest types: ‘lowland heath’ (known locally as kerangas), ‘low-pole peat swamp’ (low pole), and ‘mixed swamp’, with the latter representing a transitional habitat between the former two

(Anirudh et al., 2025). Compared to low pole, lowland heath has taller trees (average height ~18 m) and greater tree diversity (12.05-15.74 species/100 stems). Low pole, on the other hand, has an average tree height of 14.90 m, lower tree diversity (6.43 species/100 stems), and is characterised by a low, open canopy. Mixed swamp has the highest tree diversity (19.67 species/100 stems). As a transitional habitat, mixed swamp exhibits a gradient from tall continuous to low discontinuous canopy cover (Anirudh et al., 2025). The northern part of the MBERF also features an area that was impacted by a tornado event in 2006 and is characterised by windblown trees and dense regrowth, forming a low, discontinuous canopy.

Data collection

Eight autonomous recording units (ARUs; Song Meter SM4, Wildlife Acoustics, Maynard, Massachusetts) were deployed in the MBERF by W.M.E. and E.E. from July 2018 to December 2019. The ARUs were placed on trees, 5 m above the ground, in a dispersed grid with approximately 1,200 m between devices. This placement ensured full coverage of the study area while aiming to minimise overlapping detections of ape calls between neighbouring ARUs. Playback experiments indicate that gibbon great calls can be detected in recordings from distances of 500 m or more (Erb, unpublished data). The ARU grid was designed to sample each of the habitats within the MBERF, wherein three were deployed in lowland heath, three in low pole, and two in mixed swamp habitats (*Figure 2*).

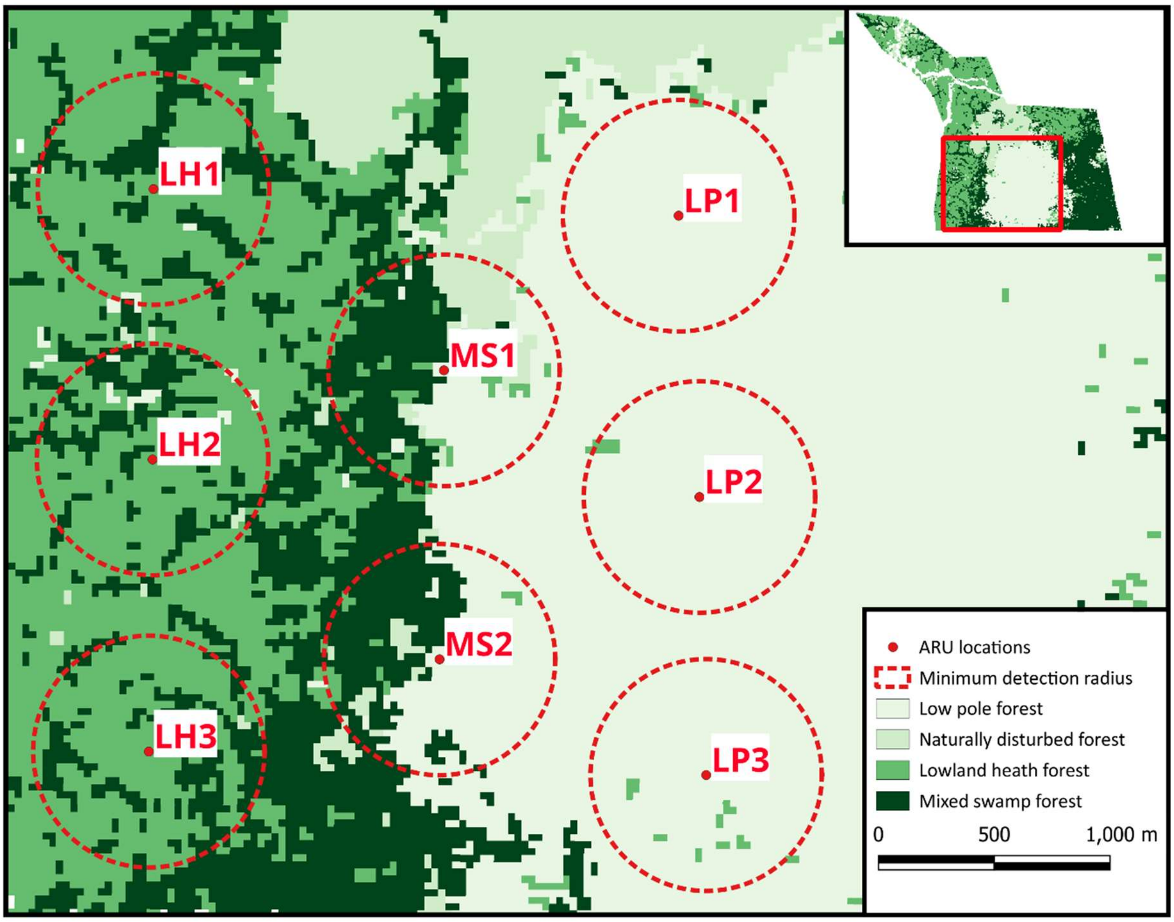

Figure 2. Map of the Mungku Baru Education and Research Forest) showing the distribution of different habitat types over the survey area and the location of the autonomous recording units (ARUs; Buckley et al., 2018). The dashed red circles represent a predicted minimum 500m detection radius around each ARU, based on playback experiments (Erb, unpublished data). The ARU labels correspond to the forest type where each device was deployed (LH – lowland heath, MS - mixed swamp, LP - low pole).

The ARUs were programmed to record daily from 4 am to 6 pm (local time, UTC +7) to capture the predawn and diurnal period of ape calling. These used default settings [sensitivity of -35 6 4 dB (0 dB ¼ 1 V/pa at 1 kHz), dynamic range of 14-100 dB sound pressure level (SPL) at 0 dB gain, microphone gain of 16 dB, and inbuilt preamplifier gain of 26 dB] and recorded on two channels with a sampling rate of 24 kHz. Audio was captured in 16-bit waveform audio file format (WAV) and saved as 1-hour files. Memory cards and batteries were changed every two weeks. Due to logistical and technical difficulties, devices did not always record continuously throughout the full survey period. To ensure full coverage of gibbon duets, we selected files recorded between 04:00 and 10:00 and only included days with no missing data. The average number of survey days per recorder was 484 (range = 429–498 of a possible 535 days; *Table S1, supplementary material*). The resultant dataset contained 23,244 hours of audio.

To detect *H. albibarbis* great calls, we applied the automated detector described in Owens et al. (2024). The detector splits audio files into 28s segments with a 27s overlap and assigns each segment a confidence score (ranging from 0 to 1), with higher scores indicating greater confidence in the presence of a great call. We used a confidence score threshold of 0.78 to balance precision (the proportion of true positive predictions among all positive predictions) and recall (the proportion of true positive predictions among all actual positive instances), enabling reliable detection while minimising false positives (Owens et al., 2024). Neighbouring segments with scores above the threshold were grouped into detections and exported as selection tables using Raven Pro 1.6 (K. Lisa Yang Center for Conservation Bioacoustics, 2024). Selection tables were processed in R (R Core Team, 2023; see Owens et al., 2024) to estimate the number of great calls per day at each ARU, henceforth *daily call rate*, which served as the basis for subsequent analysis. Since the identity of calling individuals was unknown, *daily call rate* is a measure of daily calling activity within the vicinity of each ARU, but not an accurate estimate of the number of calling individuals or groups.

To estimate rainfall variables for our study site, we used the PERSIANN-CDR dataset, a high-quality climate data record of precipitation with a spatial resolution of 0.25 degrees (~25 km) (Ashouri et al., 2015). This dataset is generated by applying the PERSIANN algorithm (Hsu et al., 1997) to the GridSat-B1 infrared data archive from geostationary earth-orbiting satellites (Knapp et al., 2011). We chose the PERSIANN-CDR dataset as it represents the nearest and most comprehensive rainfall data available for the study site. We accessed monthly and daily rainfall accumulations from July 2018 to December 2019 for the coordinates 1°45' S, 113°48' E, approximately 11 km from the centre of the ARU grid, downloaded from the CHRS data portal (Center for Hydrometeorology and Remote Sensing, University of California, Irvine).

Response variable	Description
Daily call rate	Number of great calls detected per day at each ARU
Daily call presence	Binary variable indicating presence (1) or absence (0) of a great call at each ARU on a given day
Predictor variable	
Habitat	Habitat type in which the ARU was located
Month	Month-year of data collection
Daily rainfall	Total daily rainfall (mm)
Monthly rainfall	Total monthly rainfall (mm)
Hour	Recording hour
Call quality	Description of the clarity of great call annotations: ‘*clear*’, ‘*faint*’, or ‘*very faint*’ (see Owens et al. 2024)
Random effect	
ARU	Unique ID of each recording unit

Table 1. Summary of response variables, predictor variables and random effects included in models for validation and data analysis.

Detector validation

To evaluate the precision of the automated detector across conditions, we visually assessed a subset of detections using Raven Pro 1.6 (K. Lisa Yang Center for Conservation Bioacoustics, 2024). Specifically, we reviewed all detections from one randomly selected date per month between July 2018 and December 2019, restricted to dates when recordings were available from all ARUs (n = 864 sound files). This yielded 2,923 detections in 326 sound files. Detections were annotated as true positives (TPs) if they overlapped with a great call or false positives (FPs) if they did not. We fitted a generalised linear model (GLM) with a quasibinomial distribution, using the log-odds of TPs relative to FPs as the response variable. *Month*, *ARU* and *hour* (*Table 1*) were added as categorical predictor variables to assess whether these factors accounted for variation in precision. As the survey period did not include every month in each year, *month* was treated as a categorical variable representing unique month-year combinations. Nested models were compared using analysis of variance (ANOVA).

To evaluate recall, we assessed detector performance relative to a manually annotated test dataset comprising 522 great calls in 90 sound files described in Owens et al. (2024). Great calls were annotated as TPs if they overlapped a model detection, and false negatives (FNs) if they did not. A GLM with a quasibinomial distribution was fitted with the log-odds of TPs relative to FNs as the response variable. *Call quality* (*Table 1*), *month*, *ARU* and *hour* were included as categorical predictor variables to assess their effect on recall. Additionally, to test if the effect of *call quality* varied by *ARU*, *hour* and *month*, we tested models including interaction terms between *call quality* and each of these variables. Model selection was performed using ANOVA.

For the best-fitting models for both precision and recall, we computed estimated marginal means using the R package "emmeans" (Lenth, 2025) to assess detector performance across predictor variables. Pairwise post hoc comparisons were conducted with Tukey adjustments for multiple testing. Confidence intervals for observed precision and recall were calculated using Wilson's method to provide robust interval estimates. Finally, to assess whether variation in precision could be explained by the number of great calls for each condition, we tested for correlations between precision and the number of TPs for significant predictor variables using Spearman's rank correlation.

Data analysis

To test whether *daily call rate* varies among habitat types (*hypothesis 1*), and seasonally, with temporal trends differing among habitats (*hypothesis 2*), we fitted a generalised linear mixed model (GLMM) with a zero-inflated negative binomial (ZINB) distribution using the R package "glmmTMB" (Brooks et al., 2017). This incorporates excess days with zero detected calls and accounts for overdispersion in the count data (Stoklosa et al., 2022). *ARU* was included as a random effect to account for variation in *daily call rate* among recording units within the same habitat, and to avoid pseudo-replication. *Daily call rate* was treated as the response variable, and we investigated the effects of *habitat*, *month*, and their interaction.

To test *hypothesis 3*, that *daily call rate* is positively associated with seasonal rainfall, we fitted a GLMM with a ZINB distribution with *daily call rate* as the response variable, *ARU* as a random effect, and *monthly rainfall* as the predictor variable. To clarify the short-term effects of rainfall on calling activity, we also tested for a lag effect of *daily rainfall* on both *daily call rate* and *daily call presence* (*Table 1*). For *daily call rate*, we fitted a GLMM with a ZINB distribution and *ARU* as a random effect. For *daily call presence,* we fitted a GLMM using the R package "lme4" (Bates et al., 2015), specifying a binomial distribution, *daily call presence* as the response variable, and *ARU* as a random effect. For both analyses, we first assessed the effect of *daily rainfall* one day prior to observation, then successively added lagged *daily rainfall* variables up to five days prior. Rainfall on the day of observation was excluded, as it could encompass rainfall occurring after the morning song bout.

Nested model comparisons were conducted using ANOVA and model fit was evaluated using Akaike's Information Criterion (AIC) and Bayesian Information Criterion (BIC).

Results

Detector validation

To assess potential factors influencing the precision of the automated detector, we fitted a GLM with a quasibinomial distribution, using the log-odds of TPs relative to FPs as the response variable and *month, ARU* and *hour* as categorical predictor variables. Initial model fitting suggested that *month* improved overall model fit (F = 2.127, p < 0.01). However, examination of individual *month* coefficients revealed no significant effects for any specific month, with some months showing extremely large standard errors indicative of sparse data. Therefore, *month* was excluded from the final model, which included *ARU* and *hour* as predictors (*Figure S1, supplementary material*). Precision varied across ARUs, with LH3 showing the highest precision (0.962, 95% CI: 0.942–0.975) and LP3 the lowest (0.716, 95% CI: 0.648–0.775). Post hoc pairwise comparisons indicated that precision was significantly higher at LH1 (p < 0.05) and LH3 (p < 0.001) compared to LP3. No other pairwise differences among ARUs were statistically significant after adjustment. Precision also varied significantly by *hour*. The highest precision occurred at 6 am (0.982, 95% CI: 0.973–0.988) and the lowest at 4 am (0.238, 95% CI: 0.165–0.329). Pairwise comparisons showed that precision was significantly lower at 4 am than all other hours of the morning, except for 9 am (p = 0.328). Additionally, precision at 6 am was significantly higher than at 8 am (p < 0.001) and 9 am (p < 0.001). Precision was positively associated with the number of TPs for both *ARU* (ρ = 0.929, p < 0.01) and *hour* (ρ = 0.943, p < 0.05; *Figure S2, supplementary material*). This suggests that, in some conditions, a lower occurrence of great calls may account for the observed reduction in precision, as would be expected given a constant FP rate.

For recall, we also fitted a GLM with a quasibinomial distribution, this time using the log-odds of TPs relative to FNs as the response variable and *call quality*, *month*, *ARU* and *hour* as categorical predictor variables. The best-fitting model included *call quality* as the sole predictor (*Figure S3, supplementary material*). We then tested interaction terms between *call quality* and the other predictor variables, with only the *call quality x month* interaction being significant (F = 2.15, p < 0.05). However, examination of individual interaction coefficients again revealed extremely large standard errors indicative of sparse data, so interactions were excluded. Recall varied by *call quality*, with the greatest recall observed for “clear” calls (0.951, 95% CI: 0.920–0.971) and the lowest for “very faint” calls (0.406, 95% CI: 0.332–0.485). All pairwise comparisons were significant, showing that recall decreased with *call quality*.

Detector output

Over the survey period, 83,956 *H. albibarbis* great calls were identified by the automated detector across all habitats and ARU devices, with a mean of 10,545 (range: 6,463 at LP3 – 14,915 at LH3, SD = 2,756) great calls per ARU. The mean *daily call rate* per ARU, including days without calls, ranged from 13.0 (LP3) to 31.4 (LH3), with an overall mean of 21.7 (SD = 5.6) calls per day. Great calls were detected across the entire 04:00-10:00 period, with half of all detected great calls occurring between 05:57 and 06:57, and a mean time of 06:32 (*Figure 3)*.

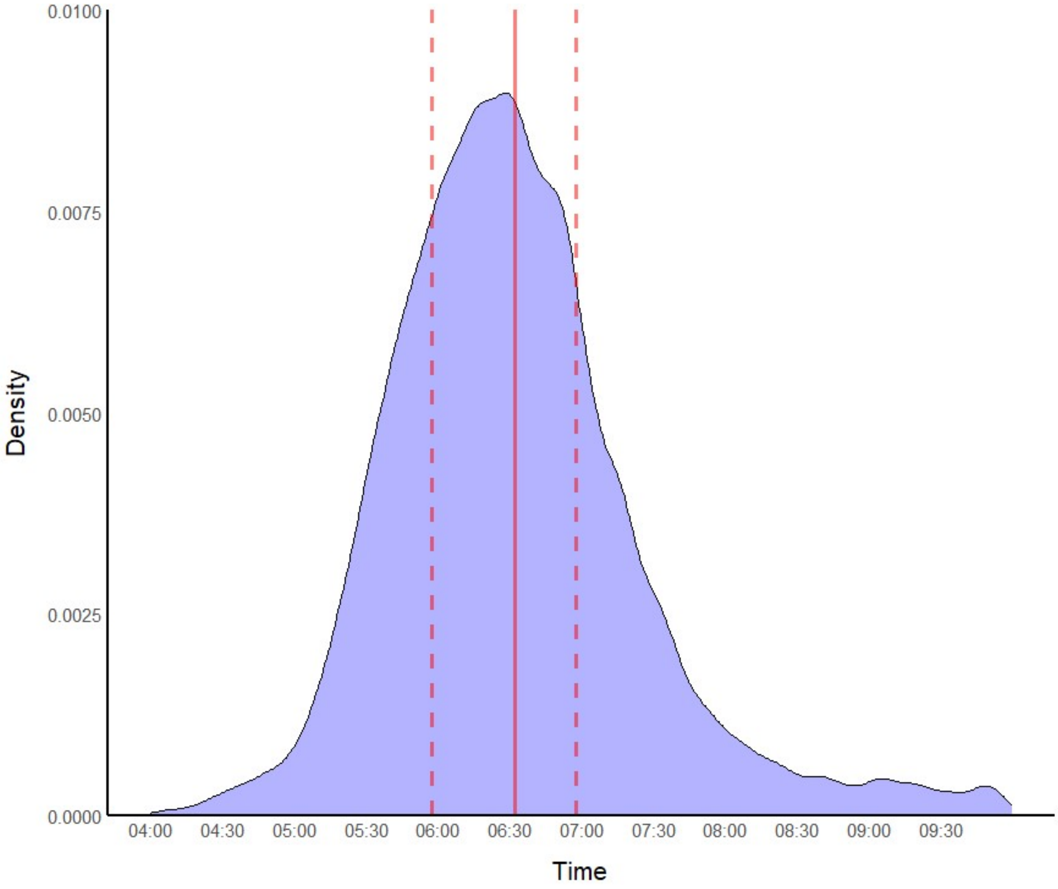

Figure 3. Density plot showing the temporal distribution of 83,956 great call detections between 04:00 and 10:00. The solid red line indicates the mean detection time, and the dashed red lines indicate the interquartile range.

Hypotheses 1

To test whether daily call rates differ among habitat types, we added *habitat* to the *month*-only model, which resulted in a non-significant improvement in model fit ($\chi^2 = 4.957$, $p = 0.084$). Although the *month + habitat* model had the lowest AIC, the difference was not substantial enough to justify the inclusion of *habitat* (ΔAIC = 0.96), consistent with the ANOVA and BIC results (*Table S2, supplementary material*). While visual inspection of the data suggested habitat differences (*Figure* 4), there was insufficient evidence to support a meaningful effect of *habitat* on *daily call rate*.

Hypothesis 2

To test whether daily call rates vary seasonally, with temporal trends differing among habitats, we examined the effect of *month* and its interaction with *habitat*. Including *month* as a predictor significantly improved model fit compared to a model with *habitat* alone ($\chi^2 = 170.044$, $p < 0.001$). The *month*-only model also had the lowest BIC and the second-lowest

AIC (*Table S2, supplementary material*), indicating significant temporal variation in the rate of detected great calls over the survey period. Compared to July 2018, the most notable peak occurred in February 2019 (z = 4.470, $p < 0.001$), while June 2019 showed a significant decrease in *daily call rate* (z = -2.689, $p < 0.01$; *Table S3, supplementary material*). Further, including an interaction between *habitat* and *month* did not significantly improve model fit compared to a model with only the main effects ($\chi^2 = 30.029$, p = 0.663), suggesting that temporal variation in *daily call rate* did not differ significantly across habitat types.

Hypothesis 3

To test *hypothesis 3*, we examined the relationship between *daily call rate* and *monthly rainfall*. *Monthly rainfall* was positively associated with *daily call rate* (z = 5.41, $p < 0.001$), supporting the hypothesis that *daily call rate* is positively associated with seasonal rainfall. However, this relationship was not consistent across all months. For example, the rate of detected great calls was lower in November 2018 and December 2019 than in the preceding month despite high rainfall accumulation (*Figure 4*).

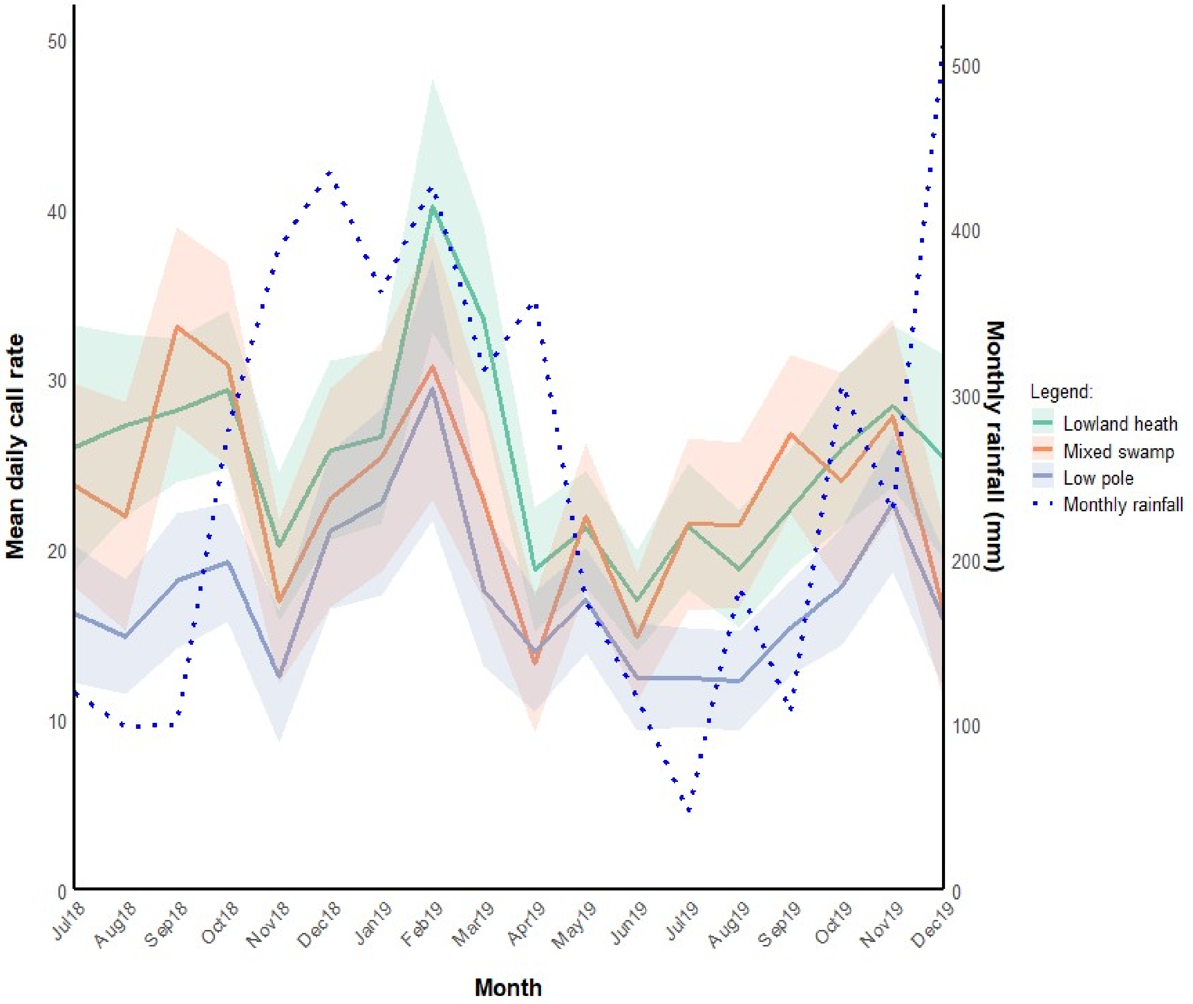

Figure 4. Line graph showing the mean daily call rate (number of great calls detected per day) per month across habitats and monthly rainfall. Shaded areas indicate 95% confidence intervals around the means.

To clarify the short-term effects of rainfall on calling activity, we examined how *daily call rate* and *daily call presence* were influenced by rainfall on the previous day up to five days prior. For *daily call rate*, model comparison indicated that the best-fitting model included rainfall up to the previous four days, which significantly improved model fit compared to a model that included only three days of prior rainfall ($\chi^2 = 10.787$, $p < 0.01$) and had the lowest AIC (*Table S4, supplementary material*). The best-fitting model showed that rainfall one day prior to observation had a negative effect on daily calling rates ($z = -9.320$, $p < 0.001$; *Figure 5a*). Rainfall two and four days prior had a positive effect on daily calling rates ($z = 6.940$, $p < 0.001$, $z = 3.250$, $p < 0.01$, respectively), while rainfall three days prior had a negative effect ($z = -2.910$, $p < 0.01$).

For *great call presence*, model comparison indicated that the best-fitting model included rainfall up to the previous three days, which significantly improved model fit compared to the model that included only two days of prior rainfall ($\chi^2 = 7.906$, $p < 0.01$) and had the lowest AIC (*Table S5, supplementary material*). The best-fitting model showed that rainfall one day prior to observation had a negative effect on the probability of calling ($z = -14.573$, $p < 0.001$; *Figure 5b*). Rainfall two days prior had a positive effect on the probability of calling ($z = 4.549$, $p < 0.001$), while rainfall three days prior had a negative effect ($z = -2.851$, $p < 0.01$).

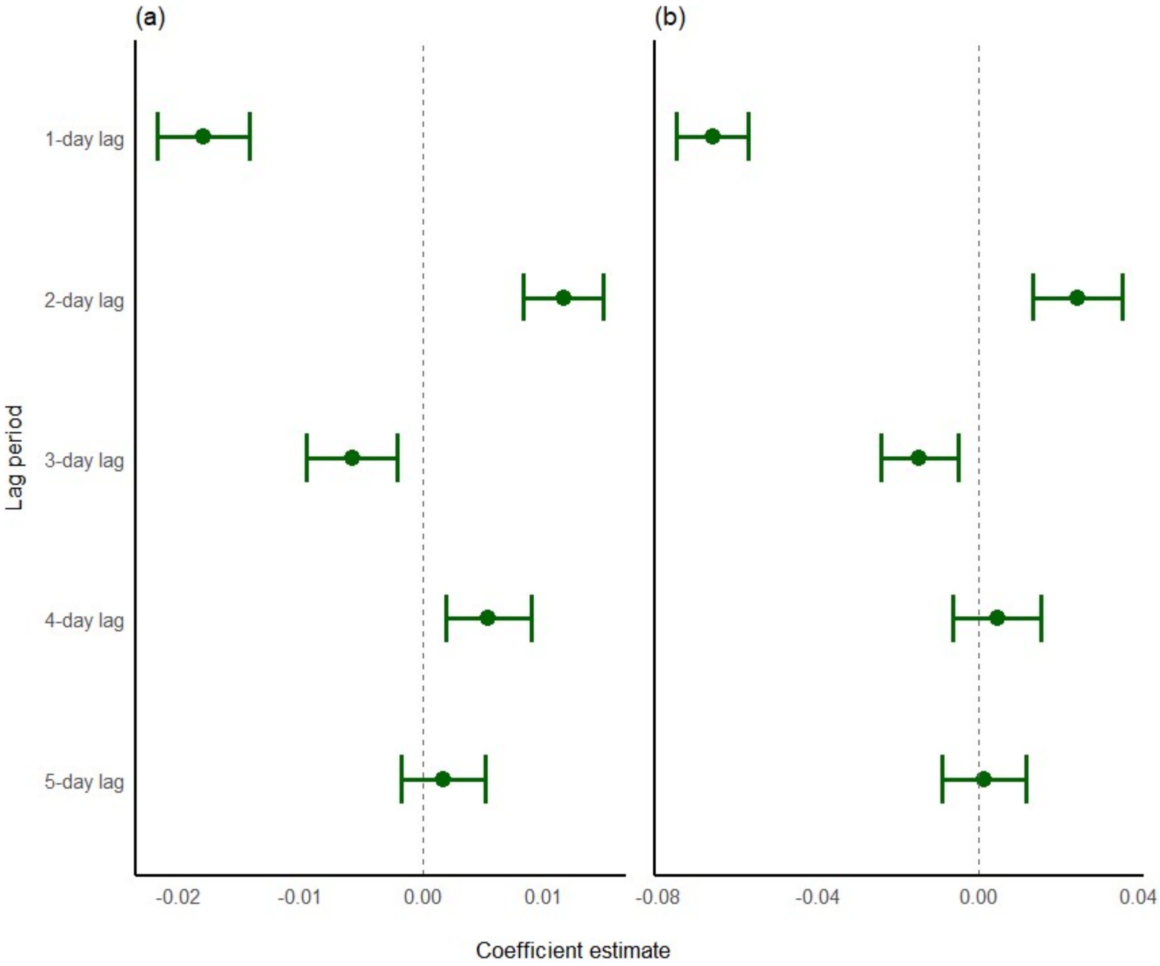

Figure 5. Coefficient estimates (with 95% confidence intervals) for daily rainfall lagged by 1-5 days prior to observation, predicting (a.) log daily call rate (the number of great calls detected per day) and (b.) the log-odds of daily call presence, defined as the presence (1) or absence (0) of great call detections at each ARU on a given day.

Discussion

Studying the ecology of elusive species inhabiting tropical forests remains challenging, such as for *H. albibarbis*, where large parts of the species' range remain understudied. To address this, we deployed eight ARUs across a mosaic lowland forest landscape over 18 months to examine differences in calling patterns among forest types and assess the effects of environmental factors on vocal behaviour. Our results highlight spatiotemporal variability in *H. albibarbis* vocalisation rates, shaped by rainfall patterns, suggesting an influence of seasonal fluctuations in resource availability.

We found insufficient evidence to conclude that the daily rate of detected great calls differed significantly among habitats. This contrasts with our expectations, as low pole has a lower discontinuous canopy cover, which has been associated with lower gibbon densities (Hamard et al., 2010), and lower densities are in turn associated with lower song rates

(Brockelman & Srikosamatara, 1993; Yin et al., 2016). In Sebangau National Park, previous studies have presumed a low to near-zero population density in low pole, observing infrequent duetting and a single gibbon sighting in this habitat (Buckley et al., 2006; Cheyne et al., 2008). Our results show consistent detection of great calls from ARUs placed in low pole, suggesting that breeding groups are present within, or at least bordering, this habitat, and that low pole may be more suitable for gibbons than previously assumed.

However, direct habitat comparisons are complicated by the small number of sampling locations, with only 2-3 replicates per habitat, which limits statistical power and increases the influence of site-specific factors or individual variation in calling behaviour. For example, the effective detection area of each ARU was not entirely homogeneous, and ARUs deployed in low pole may acoustically sample small pockets of more suitable gibbon habitat. Additionally, the distance that great calls propagate may vary across habitats (Erb, unpublished data), meaning detection ranges may vary between ARUs. Consequently, calls may have been detected from adjacent habitats with higher group densities, potentially inflating observed great call rates. Furthermore, ARUs located centrally within a group's home range may detect fewer calls than those positioned at the boundary between multiple groups, where calls from a greater number of individuals may be recorded. Finally, consistent differences in the rate of detected calls across ARUs may reflect variation in individual or group-level calling behaviour that does not necessarily correspond to group density (Clink et al., 2020); for instance, the number of great calls can be influenced by pair-bond strength (Ma et al., 2022). Additional spatial context, particularly empirical estimates of effective detection ranges for both ARUs and the automated detector, would enable clearer interpretation of habitat-related patterns in future studies. Furthermore, applying acoustic localisation methods, such as the time difference of arrival technique (Lellouch et al., 2025), would allow calls to be clustered spatially to identify distinct groups, providing more precise estimates of group density.

We observed significant seasonal variation in the rate of detected great calls, with distinct peaks and troughs in calling activity across months. Call rates increased during wetter periods, despite the negative short-term effects of rainfall on calling activity, suggesting that song frequency reflects resource availability. Given that the rainy season is associated with peaks in animal-dispersed fruit abundance (Morrogh-Bernard, 2009; van Schaik & Pfannes, 2005), this is consistent with Cowlishaw (1996), who found that duet frequency and duration are greater during periods of high fruit availability. Notably, monthly variation in daily call rates in our study was broadly consistent across habitats. While the underlying mechanisms behind this pattern remain unclear, this could suggest that fruiting responses to rainfall across the three predominant forest types are similar, or that the key food species driving temporal variation in calling activity are present in all three habitats. These findings highlight the value of incorporating phenological data in future studies. Examining fluctuations in the availability of key food species alongside gibbon vocal activity could help clarify the causal links between resource abundance and calling behaviour and potentially allow gibbon vocal patterns to serve as an indicator of habitat productivity over time.

Alongside this seasonal pattern, our analyses indicate that short-term rainfall significantly influences calling behaviour at daily scales. Rainfall on the day prior to a song duet had a significant negative effect on both daily call rate and the probability of calling, possibly due to increased energetic costs of overnight thermoregulation associated with adverse weather (Cheyne, 2008; Clink et al., 2020). This may explain the lower rate of detected great calls during the onset of the rainy season in November 2018 and December 2019, when resource availability would also be low due to a lagged fruiting response to rainfall. Interestingly, rainfall two days prior was associated with an increase in calling activity, suggesting that gibbons may compensate for missed song duets by increasing vocal effort the following day, potentially to mitigate the cumulative social costs of reduced calling. We also observed significant positive and negative effects of rainfall three- and four-days prior, though further investigation using higher-resolution rainfall data may be required to clarify these interactions. Understanding how short-term rainfall influences gibbon singing behaviour is particularly important, since vocally derived population estimates rely on call probability correction factors to account for days when singing does not occur (Brockelman & Ali, 1987; Cheyne et al., 2016).

The occurrence of the El Niño weather event in 2019 may have further influenced observed patterns of calling activity. This event triggered drought and resulted in forest fires across Borneo, which blanketed large areas in a smoke haze and increasing levels of harmful pollutants such as $PM_{2.5}$ and carbon monoxide, particularly from September to November 2019 (Yokelson et al., 2022). Wildfire smoke has been shown to negatively affect *H. albibarbis* singing behaviour, reducing both the number of singing days per month and the length of song bouts, potentially due to respiratory stress (Cheyne, 2008). Similarly, Erb *et al.* (2023) found that Bornean orangutans (*Pongo pygmaeus wurmbii*) perform fewer long calls per day when exposed to increased air pollution from wildfire smoke. Although it remains unclear whether wildfire smoke directly influenced our results, our study highlights the importance of accounting for underlying variation in vocal patterns when examining the additive effects of wildfire smoke or other anthropogenically exacerbated factors. Future studies should compare smoke and non-smoke conditions during the same season to control for seasonal differences and better isolate the effects of wildfire smoke on vocal behaviour.

The performance of the automated detector varied significantly across ARUs, times of day, and the quality of the target calls. However, it is unlikely that this substantially affected our findings, and observed temporal variation in daily call rates is more likely attributable to ecological processes rather than fluctuations in detector precision or recall. While the lower precision for LP3 may have contributed to an inflated daily call rate in low pole due to a higher number of false positive detections, this ARU also recorded the fewest calls. Similarly, although precision was lowest for files recorded at 4 am, this accounted for a relatively small proportion of total detections. The markedly low precision in files during this hour is likely due to the presence of male solo calls preceding the duet (Clink et al., 2020), some of which were misclassified as great calls. Furthermore, precision for both *ARU* and *hour* was correlated with the number of true positives present, suggesting a relatively stable false positive rate, which would result in lower precision where great calls are scarce. Therefore, caution is warranted when interpreting daily call rates during off-peak calling hours and in low-density populations. As expected, recall varied with *call quality*, since "clear" calls are more likely to originate closer to the ARU than "very faint" calls. Further investigation into the relationship between detection probability and distance to the call source would help to contextualise this relationship. Overall, our validation process highlights the importance of comprehensive performance assessment when interpreting the output of automated detectors in ecological applications. Special attention should be given to generating test datasets to ensure robust detector performance, especially when applying automated detection across different locations, habitats, and time periods.

This study highlights the advantages of applying automated detection to acoustic data when studying species' vocal behaviour. Although frequent maintenance of ARUs was required, conducting manual acoustic surveys at eight locations over an equivalent time period would be unfeasible. Furthermore, the 23,244-hour dataset was analysed by our automated detector in only ~123 hours. Unlike manual acoustic surveys, our approach allows for continuous monitoring without the presence of human observers, which can influence vocal behaviour. The scalability of this method from single-site to landscape-level monitoring provides opportunities to study species' distributions and responses to environmental or anthropogenic factors across habitats and over extended time periods. For example, our findings suggest that lowland heath forests support healthy gibbon populations, as evidenced by the relatively high call rates recorded in this habitat. Although widespread, lowland heath forests have often been overlooked in conservation planning due to misconceptions about their biodiversity and ecological productivity (Anirudh et al., 2025). Our results challenge this perception by highlighting the importance of lowland heath for endangered *H. albibarbis*, thereby strengthening the case for protecting this habitat type in future conservation strategies.

Supplementary material

Supplementary tables and figures are provided below.

Acknowledgements

We acknowledge Universitas Muhammadiyah Palangkaraya and Borneo Nature Foundation for access to and support in the MBERF, as well as the Indonesian government for permission to perform this research [RISTEK-DIKTI Permit Nos. 189/SIP/FRP/E5/Dit.KI/VI/2018 and 43/E5/E5.4/SIP.EXT/2019 (W.M.E.)]. We thank Rido for his invaluable support in deploying and maintaining the ARUs and data in the field. In addition, we acknowledge the contributions of the Indigenous Dayak Ngaju community of Mungku Baru, including Pak Edo, Pak Yuli, Pak Viktor, and Rico, who supported the data collection. The authors would like to acknowledge the use of the University of Exeter's Advanced Research Computing facilities in carrying out this work. Please note the following sponsors of this research, awarded to W.M.E.: Primate Conservation, Incorporated; British Academy; Conservation International; American Association of Physical Anthropologists; International Primatological Society; and American Institute for Indonesian Studies. A.F.O., F.J.F.V., K.J.H., M.A.I., T.T.C., and W.M.E. developed the project and concept; E.E. and W.M.E. deployed and curated the acoustic dataset; M. and S.M. provided permissions and guidance for field study design and execution; A.F.O. and M.S. carried out batch processing of the acoustic dataset; A.F.O. drafted the manuscript to which all other authors then contributed to produce the final version.

Conflict of Interest

The authors have no conflicts to disclose.

Ethics Approval

Ethical approval was provided by the University of Exeter (Application ID 1845574), BRIN (Application No. 22 022 023 000 026), and Institutional Animal Care and Use Committee of Rutgers, the State University of New Jersey Protocol No. PROTO201800073.

Data availability

All data and scripts necessary to replicate the results will be made available prior to submission.

ARU	Jul-18	Aug-18	Sep-18	Oct-18	Nov-18	Dec-18	Jan-19	Feb-19	Mar-19	Apr-19	May-19	Jun-19	Jul-19	Aug-19	Sep-19	Oct-19	Nov-19	Dec-19	Total
LH1	15	20	30	31	23	29	25	28	31	30	31	30	31	25	30	31	30	29	498
LH2	1	9	30	22	30	27	24	28	31	29	31	30	31	26	28	18	28	8	429
LH3	12	30	30	31	30	26	23	27	31	30	31	28	30	26	25	26	22	23	475
MS1	16	20	30	31	30	27	24	28	31	30	31	30	24	26	30	28	30	24	490
MS2	14	24	30	31	30	24	23	28	31	30	31	30	30	26	30	23	30	28	493
LP1	17	30	21	31	30	27	24	27	31	30	30	30	30	25	29	26	30	25	493
LP2	14	31	30	31	30	27	24	27	31	30	31	30	31	26	30	23	30	22	498
LP3	17	31	30	31	30	25	24	26	31	30	31	30	29	23	30	26	28	27	498

Table S1. The number of survey days for each ARU per month.

Model	df	AIC	BIC	ΔAIC
habitat + month	23	30897.15	31041.18	0.00
month	21	30898.11	31029.61	0.96
habitat x month	57	30935.12	31292.06	37.97
habitat	6	31033.20	31070.77	136.05

Table S2. Model fit comparisons for hypotheses 1 and 2. Generalised linear mixed models with a zero-inflated negative binomial distribution and random effect of recording unit were fitted to test the effects of habitat, month, and their interaction on daily call rate.

Month	Estimate	SE	z-value	p-value
August 2018	0.039	0.116	0.335	0.738
September 2018	0.223	0.111	2.013	0.044*
October 2018	0.247	0.111	2.228	0.026*
November 2018	-0.074	0.116	-0.636	0.525
December 2018	0.162	0.114	1.423	0.155
January 2019	0.273	0.117	2.345	0.019*
February 2019	0.501	0.112	4.470	<0.001***
March 2019	0.210	0.111	1.899	0.058
April 2019	-0.216	0.112	-1.924	0.054
May 2019	-0.036	0.110	-0.325	0.745
June 2019	-0.300	0.112	-2.689	0.007**
July 2019	-0.162	0.111	-1.463	0.144
August 2019	-0.174	0.114	-1.518	0.129
September 2019	-0.033	0.110	-0.304	0.761
October 2019	0.060	0.113	0.529	0.597
November 2019	0.245	0.111	2.208	0.027*
December 2019	0.038	0.119	0.317	0.751

*Table S3. Effects of month on daily call rate relative to July 2018. Results are from a generalised linear mixed model with a zero-inflated negative binomial distribution, random effect of recording unit, and month as a fixed effect. Significance codes: $p < 0.05$ *, $p < 0.01$**, $p < 0.001$***.*

No. of lagged days	df	AIC	BIC	ΔAIC
1	5	30972.93	31004.24	65.85
2	6	30918.82	30956.40	11.74
3	7	30915.87	30959.70	8.79
4	**8**	**30907.08**	**30957.18**	**0.00**
5	9	30908.16	30964.52	1.08

Table S4. Model fit comparisons for daily call rate and lagged daily rainfall. Generalised linear mixed models with a zero-inflated negative binomial distribution and random effect of recording unit were fitted. Models include daily rainfall accumulations from one day prior up to the specified number of lagged days.

No. of lagged days	df	AIC	BIC	ΔAIC
1	3	2842.954	2861.740	21.840
2	4	2827.020	2852.068	5.906
3	**5**	**2821.114**	**2852.424**	**0.000**
4	6	2822.339	2859.911	1.225
5	7	2824.282	2868.116	3.168

Table S5. Model fit comparisons for daily call presence and lagged daily rainfall. Generalised linear mixed models with a binomial distribution and random effect of recording unit were fitted. Models include daily rainfall accumulations from one day prior up to the specified number of lagged days.

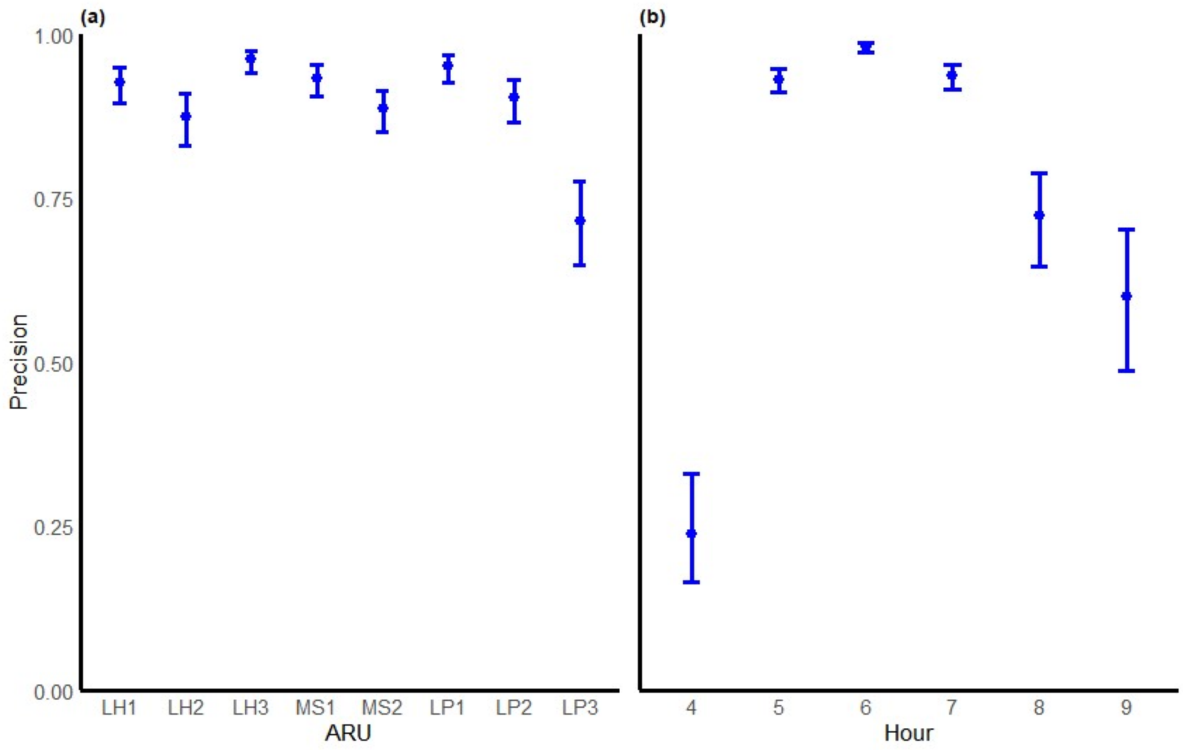

Figure S1. Precision of the automated detector by ARU (a.) and hour (b.) with 95% Wilson confidence intervals.

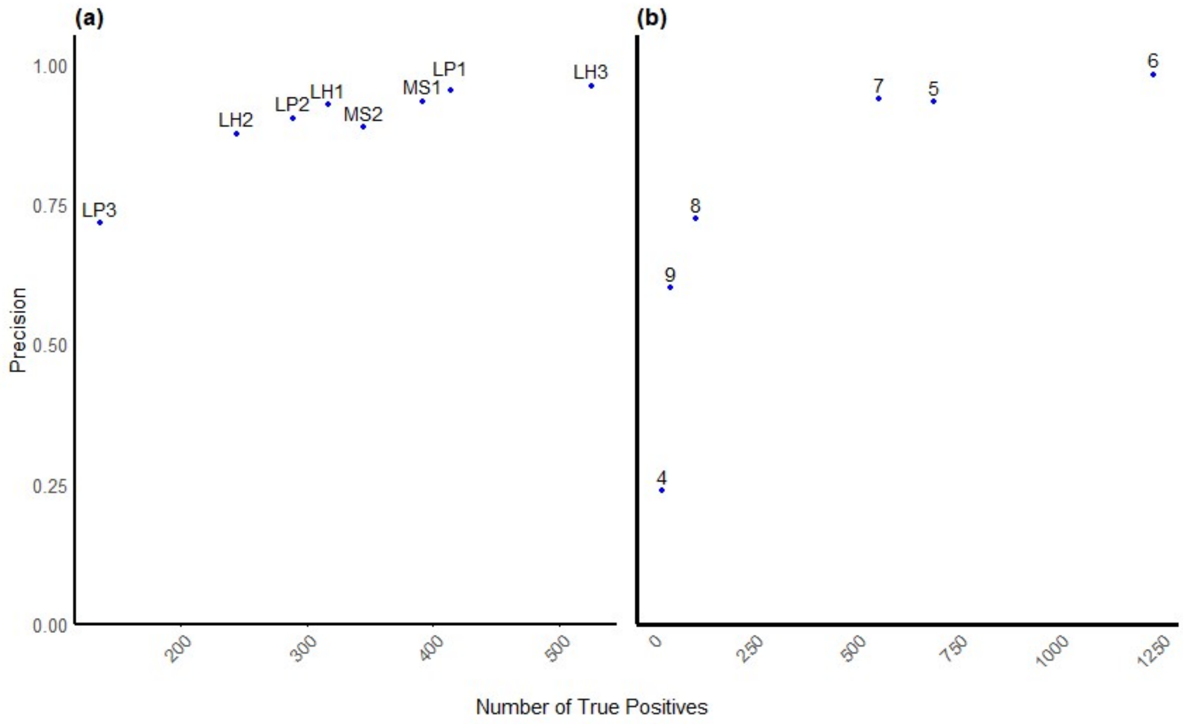

Figure S2. Precision of the automated detector by ARU (a.) and hour (b.) relative to the total number of true positives.

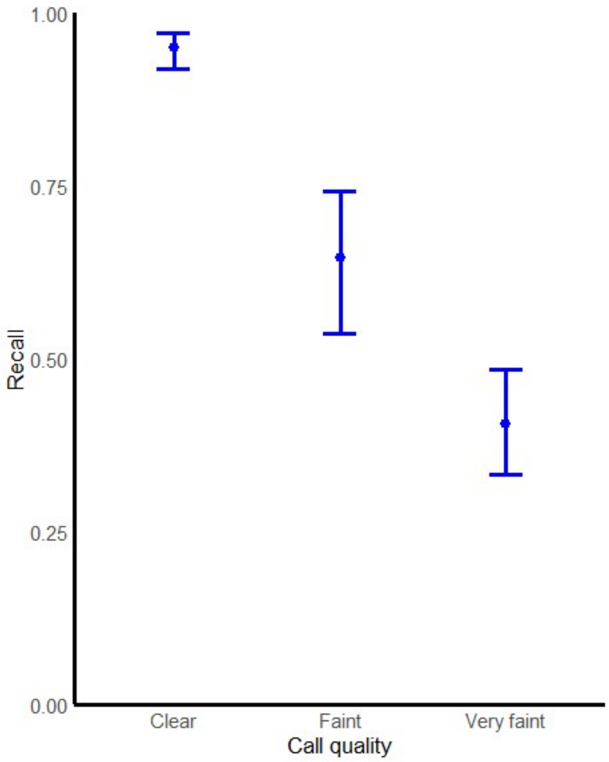

Figure S3. Recall of the automated detector by call quality with 95% Wilson confidence intervals.

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