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RESEARCH ARTICLE

How to count bird calls? Vocal activity indices may provide different insights into bird abundance and behaviour depending on species traits

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Abstract

1. Passive acoustic monitoring (PAM) has become an important tool for surveying birds, and there is a growing demand for approaches to obtain abundance and behavioural information from PAM recordings. Changes in bird populations have been assessed by counting recorded calls and calculating the vocal activity rate (VAR, i.e. the number of calls per recording time). However, bird calls could be counted in various ways and depending on species traits, these call counts could give us different insights on bird abundance, vocal behaviour and/or habitat use.

2. Our study had two goals: (1) to present and evaluate two new indices based on call counts, the detection rate (DR, i.e. the number of 1-min recordings in which the presence of a target vocalization is detected) and the maximum count per minute (MAX, i.e. the maximum number of calls found in a 1-min recording); and (2) to present a conceptual framework showing how the interpretations of VAR, DR and MAX could depend on the index and on species traits.

3. For three Neotropical bird species with distinct traits, we calculated VAR, DR and MAX based on PAM data from 25 sites in the Yucatan Peninsula (Mexico) that varied in their degree of anthropogenic habitat disturbance. We found moderate to high correlations between the indices and higher temporal variability in VAR compared to DR and MAX. We also found different effect sizes of habitat disturbance on the three species and indices.

4. We suggest that DR might be a more reliable index of relative abundance than VAR for species whose calling behaviour exhibits a high cue rate and that MAX may be suitable for estimating family or flock size in gregarious birds. Our findings show the potential usefulness of developing new indices based on call counts to generate ecological hypotheses and assess changes in bird abundance and behaviour.

1 | INTRODUCTION

Habitat loss and modification are major threats to animal biodiversity in tropical forest regions around the world (Barlow et al., 2018). To evaluate the effects of such threats, birds are often used as a focal taxon (Şekercioğlu, 2012; Whelan et al., 2015). In this context, passive acoustic monitoring (PAM) has become increasingly popular as an effective method for conducting bird surveys (Sugai et al., 2019). PAM uses autonomous recording units (ARUs) that capture acoustic information, which can be stored and used for a variety of purposes. This method is especially suitable for sampling highly vocal species and can be very useful in habitats where dense vegetation hampers visual detection, such as tropical forests (Darras et al., 2019).

Anthropogenic disturbances of tropical forests affect bird species in different ways (Newbold et al., 2013). On the one hand, forest-specialists are highly vulnerable to disturbances (e.g. toucans, Martínez-Ruiz et al., 2021), while some habitat-generalists can increase in abundance with progressing disturbance (e.g. brown jays, Jones, 2020). On the other hand, disturbances may not only affect a species' abundance but can cause changes in behaviour, including its vocal behaviour (Gil et al., 2015; Kirschel et al., 2009) and/or patterns of habitat use (Graham, 2001). Although PAM has primarily been used to detect species presence, data from recordings can also be used to assess changes in abundance (Pérez-Granados & Traba, 2021) and behaviour (Pérez-Granados & Schuchmann, 2020a).

Methods for estimating absolute abundance (e.g. distance sampling, sonogram analysis, cue counting; see Pérez-Granados & Traba, 2021 for a detailed review) are not easily applicable because they require additional information and equipment (Marques et al., 2013). Thus, indices of relative abundance (i.e. any measurable correlate of absolute abundance; Hopkins & Kennedy, 2004) have been proposed as a more convenient alternative, as they only assume a positive correlation between a species' absolute abundance and the number of vocalizations on a single recording (Pérez-Granados, Bota, et al., 2019). For example, ecoacoustic indices, which employ mathematical formulas to characterize the soundscape (Alcocer et al., 2022), have been utilized as proxies of avian abundance and diversity (Bradfer-Lawrence et al., 2020; Orben et al., 2019). In contrast, vocal activity indices, which are also derived from soundscape recordings, rely on the identification and quantification of target vocalizations from focal species. The vocal activity rate (VAR), which is the number of calls per recording time, is such an index (Pérez-Granados, Bota, et al., 2019; Pérez-Granados & Traba, 2021).

Vocal activity rate assumes that as more birds occur in an area, more calls of the species are emitted and recorded. However, although variation in VAR across sites may reflect differences in species abundance, it could also indicate differences in vocal behaviour (Pérez-Granados & Schuchmann, 2020a; Upham-Mills et al., 2020) or

other aspects of behaviour such as habitat use, that is the time a bird spends in a particular part of its habitat (which in turn affects how much time it spends near a recording device). Distinguishing between potential causes of variation in VAR is difficult because it is often unknown whether multiple calls were made by one or more individuals (but see Ntalampiras & Potamitis, 2021) and because this index does not take into consideration the temporal patterns of bird vocalizations. Here, we argue that recorded calls can be counted in different ways, and that some types of counts may correlate more strongly than others with behaviour or abundance, depending on the species' traits.

We introduce two new indices obtained by counting calls in ways in which the temporal patterns of bird vocalization are taken into consideration: (1) the detection rate (DR), which we defined as the number of 1-min recordings in which the presence of a target vocalization is detected, per recording time; and (2) the maximum count per minute (MAX), which we defined as the highest number of calls found in a 1-min recording within the total recording time (Figure S1). The first goal of our study was to evaluate the performance of DR and MAX in comparison to VAR. We compared values of VAR, DR and MAX for three bird species with different traits. We used recordings derived from a long-term PAM project in the Yucatan Peninsula (Mexico) where sites with varying levels of habitat disturbance were monitored. We obtained values of the indices during the non-breeding season for three resident bird species:

(i) The collared forest-falcon (*Micrastur semitorquatus*, hereafter 'the falcon'), a territorial, forest-dependent, solitary raptor (forming pairs only during the breeding season) with a habitat preference for old-growth forest (Martínez-Ruiz, 2021). Territories are defended more strongly, that is through longer vocalization sequences, in higher-quality habitat (i.e. areas with high forest cover; Martínez-Ruiz et al., 2016). Hence, its vocal behaviour depends on the level of habitat disturbance. Territories can overlap (Martínez-Ruiz et al., 2016), thus some variation in abundance across sites is expected (0–2 individuals).

(ii) The grey-headed tanager (*Eucometis penicillate*, hereafter 'the tanager') lives in pairs or small family groups consisting of parents and their juvenile offspring (Baker & Burns, 2020). Although group size may vary among sites due to differential reproduction, it remains stable before the breeding season (which starts in March; Baker & Burns, 2020) with groups only consisting of pairs during that time. This species shows a low to moderate degree of territoriality, such that home ranges of different groups can overlap (Baker & Burns, 2020). Thus, much of the variation in bird abundance across sites is expected to be due to variation in the number of groups (Figure 1). The tanager is threatened by deforestation (Ridgely & Tudor, 2009), which

reduces the availability of its main food resource, insects escaping from army ants (Roberts et al., 2000). Therefore, habitat disturbance can negatively influence species abundance (Kumar & O'Donnell, 2007).

(iii) The black-headed saltator (*Saltator atriceps*, hereafter 'the saltator') lives in groups of 3–10 individuals. Therefore, variation in group size is expected among sites. No information on territoriality is available (Deshwal et al., 2020). This generalist species benefits from habitat disturbance (Patten et al., 2010), being less common in pristine forest (Deshwal et al., 2020). Habitat disturbance may thus positively influence the abundance of this species.

The second goal of our study was to propose a conceptual framework that includes several bird traits that we believe can strongly affect the number of calls recorded in PAM and can thus influence how the results obtained using different indices (DR, MAX and VAR) ought to be interpreted (Figure 1, Figure S1). The traits we focus on are the vocal activity period, the cue rate, the degree of territoriality, the social organization and the pattern of habitat use of a species.

Vocal activity period and cue rate are two aspects of vocal behaviour that are directly related to the temporal pattern of a bird's vocalization. Vocal activity periods are those times in a day when birds show heightened vocal activity (Aide et al., 2013). In full-day PAM recordings, more vocalizations will be captured when the vocal activity period of a species at a site is longer. When PAM schedules are set to interval recording, recording hours should align with vocal activity periods to ensure bird detection. It is also important to consider that vocal activity periods may vary due to environmental conditions such as background noise (Dorado-Correa et al., 2016; Gil et al., 2015; Gentry & Luther, 2017). The cue rate (Sebastián-González et al., 2018), also called repetition rate (Wheatcroft, 2015) or song rate (Upham-Mills et al., 2020), refers to the number of vocalizations emitted by an individual in a short time period (Price, 2013; Suthers, 2004). Thus, a high cue rate causes vocalizations to be temporally clumped on a recording. High cue rates are common in songs (Pérez-Granados et al., 2018; Price, 2013), alarm calls (Suzuki, 2016), contact calls (Meaux et al., 2023), and territorial calls (Enriquez-Rocha & Rangel-Salazar, 2001). Cue rates can vary with breeding status (Upham-Mills et al., 2020), resource availability, and the presence of competitors and predators (Clay et al., 2012; Morales et al., 2014; Wheatcroft, 2015), and have been used to estimate absolute bird abundance in some methodological approaches (e.g. cue counting: Sebastián-González et al., 2018; Pérez-Granados et al., 2021; sonogram analysis: Drake et al., 2016).

Other traits that can affect the interpretation of call counts on a recording are the species' degree of territoriality and social organization. For example, in highly territorial solitary species, neighbouring territories have little overlap (Robinson & Terborgh, 1995) and most recorded vocalizations stem from the same few individuals. Thus, differences in call counts between two sites would mainly reflect differences in vocal behaviour rather than differences in abundance. Calls can also be temporally clumped when multiple individuals vocalize during the same time, which occurs in species with a gregarious social organization (i.e. birds living in families or flocks). In this case, call counts contain information on both vocal behaviour and abundance. Finally, bird species differ in how they use their habitat. Consequently, the more time a bird spends near an ARU, the more of its calls will be recorded.

In our framework, we propose that indices obtained from different types of call counts can correlate more strongly with abundance or vocal behaviour, depending on what traits a species possesses (Figure 1). We suggest that all three indices (DR, MAX, VAR) may correlate with some aspect of abundance (number of individuals, number of groups and/or group size), but that they differ in how bird traits may influence them. We propose that VAR may be influenced by up to three traits: length of the vocal activity period, cue rate and/or habitat use. DR, which only reflects how often a target vocalization is detected in 1-min recordings, is expected to be less affected by the cue rate, but more by the length of the activity period and/or habitat use. MAX, which is obtained from a single short time sequence (i.e. from one 1-min recording), should mostly be affected by cue rates. MAX may therefore also serve as an indicator of activity bursts, that is of behaviour or events related to increased cue rates (e.g. mate attraction: Upham-Mills et al., 2020; predator presence: Wheatcroft, 2015; food abundance: Clay et al., 2012; territorial competition: Morales et al., 2014). We also argue that for solitary species, particularly territorial ones, DR and VAR are likely to be more strongly correlated with abundance than MAX, because MAX mainly reflects cue rates in those species (unless cue rates vary very little, in which case the three indices would be highly correlated with one another). In contrast, for gregarious species, we propose that VAR may indicate group size and/or number of groups, while DR would most strongly correlate with the number of groups, and MAX with group size (Figure 1).

To explore the applicability of our framework, we performed three analyses to (i) assess the strength of correlations between the three indices, (ii) quantify the indices' temporal variability within monitoring sites and (iii) determine how the indices' relationships with anthropogenic habitat disturbance vary among species. We reasoned that the strength of correlations among the indices might indicate to what extent they are shaped by the same factors. We expected the correlations between VAR and MAX and between VAR and DR to be stronger than the correlations between DR and MAX, because the former pairs have common sources of variation, while the latter pair does not (Figure 1; Prediction 1).

Within sites, the abundance of resident bird species is expected to remain relatively constant during a 4-month period in the non-breeding season, whereas vocal behaviour of birds can show short-term temporal changes (Pérez-Granados & Schuchmann, 2020a). Therefore, the within-site variability of our indices in the four-month period serves as an indicator of their sensitivity to changes in vocal behaviour. According to our framework, VAR is affected by two aspects of vocal behaviour (cue rate and length of the vocal activity period). Thus, we expected VAR to show higher temporal variability compared to DR, which we assume to be mainly affected by the
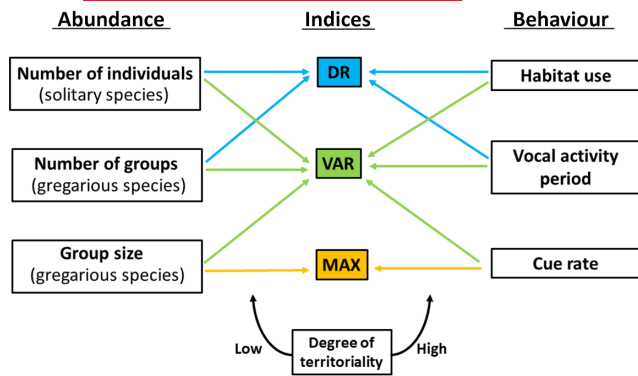
FIGURE 1 Conceptual framework showing the proposed strongest correlations (straight coloured arrows) between vocal activity indices (DR, VAR, MAX; coloured boxes) and aspects of species abundance (boxes to the left) for solitary bird species (Number of individuals) and for gregarious species (number of groups and Group size) as well as behaviour (boxes to the right). VAR is the number of detected calls per recording time; DR is the number of 1-min recordings in which at least one call is present, per recording time; MAX is the maximum number of calls found in a 1-min recording within the total recording time. Aspects of behaviour, such as habitat use and vocal behaviour (length of vocal activity period and cue rate) can affect the number of calls recorded through PAM and thus influence the values of the indices. The emission of multiple redundant calls in a short time determines the cue rate and causes temporal clumping of calls, whereas the length of vocal activity periods refers to the total time during a day when individuals are vocally active. Here, by habitat use we refer to the time birds spend near an ARU within their habitat. We propose that indices that are affected by fewer behavioural aspects might have stronger correlations with abundance and vice versa. For solitary species, DR and VAR are expected to be more strongly correlated with species abundance than MAX because the latter index is sensitive to temporal clumping of calls, and would thus mostly reflect cue rates. For gregarious species, VAR is expected to be similarly correlated with group size and with the number of groups, while DR should be more strongly correlated with the number of groups, and MAX with group size. We also expect that VAR is equally affected by the cue rate and the length of the vocal activity period, while DR is more strongly affected by the length of the vocal activity period, and MAX is not affected by it. VAR and DR are likely to be affected by habitat use, but MAX less so. Finally, a species' degree of territoriality is expected to affect the strength of the correlations (curved black arrows): low territoriality should yield stronger correlations between the indices and bird abundance, while high territoriality should yield stronger correlations between indices and behavioural aspects, since the higher the degree of territoriality, the less variability in the number of individuals is expected to occur at a site. ARU, autonomous recording unit; DR, detection rate; MAX, maximum count per minute; PAM, passive acoustic monitoring; VAR, vocal activity rate.

length of the vocal activity period, and compared to MAX, which we assume to be mainly affected by the cue rate (Prediction 2). Finally, we expected that the effect sizes of anthropogenic habitat disturbance would vary among species and indices, depending on how the species behaviour and abundance are affected by disturbance (Prediction 3).

2 | MATERIALS AND METHODS

2.1 | Study area

We collected data at 25 sites in the Lake Bacalar region (18.6783° N, 88.3924° W) of the Yucatan Peninsula (Mexico). The region comprises a mosaic of large patches of semideciduous tropical forest in various stages of succession, smaller patches of agricultural fields and areas covered by urban infrastructure (Huchin Ochoa et al., 2022). The climate is characterized by mean annual temperatures of 24°–28°C and rainfall of 1100–1500 mm (Huchin Ochoa et al., 2022). Rainfall is seasonal, with a rainy period between June and October (>100 mm/ month) and a dry period between November and May (<100 mm/ month); occasional cold fronts can occur between October and April (Tobó Velázquez et al., 2019). Monitoring sites were established in late successional and mature forest patches on the western side of Lake Bacalar, where the urban expansion is concentrated (Figure S2). We obtained permission from local landowners and land managers, and systematically selected sites in areas with varying degrees of anthropogenic disturbance, maintaining a minimum distance of 1 km between sites. Research complied with protocols approved by the Secretaría del Medio Ambiente y Recursos Naturales [SEMARNAT: 479 SGPA/DGVS/03005/19].

2.2 | Anthropogenic habitat disturbance

First, we developed a land-cover map using the JavaScript API Code Editor in Google Earth Engine with open-access satellite imagery from the Sentinel-2 Multispectral Instrument (MSI, 10 m/ pixel resolution; Abdi, 2020; Rapinel et al., 2019; see Appendix S2 in Supplementary Information for details). Second, habitat disturbance was assessed as the amount of urban area (i.e. urban infrastructure in terms of roads and buildings) around monitoring sites (see Section 2.5).

2.3 | PAM surveys and the semi-automated detection process

We installed one ARU per site; we used 18 Audiomoth (v.1.1.0 and 1.2.0, openacousticdevices.info) and seven SM4 (Wildlife Acoustics). ARUs were attached to tree trunks or branches at breast height and were active for 4 months (November 2021 to February 2022) outside the breeding season of the three focal bird species. Each ARU was set to record for 1 min every 6 min between 5:00 AM and 07:00 PM (UTC-5), for a maximum of 140 min per day (48.000 Hz sampling rate, medium gain for Audiomoth and default gain of 48 dB for SM4 ARUs). However, due to technical failures and corrupted data, recording efforts differed among sites and months (Figure S3).

As target vocalizations, we chose the territorial-defence call (a high-amplitude vocalization) for the falcon, the contact call (a vocalization used for group communication) for the tanager and the

common song for the saltator (Figure S4).We used the open-access ARBIMON Pattern Matching tool (Rainforest Connection, https://arbimon.rfcx.org) for scanning recordings to detect vocalizations of the three bird species. We first performed a random manual scan of our recordings to select examples with optimal signal-to-noise ratios of the target vocalizations (one per species). These examples were used as templates for the Pattern Matching analysis to systematically detect target vocalizations in the 1-min recordings (threshold settings depended on the detectability of target vocalizations found during pilot trials: 0.3 for the falcon and the saltator; 0.2 for the tanager, see Appendix S1 in Supplementary Information for details). The resulting recording list (including information on site ID, date and time of recording) was validated by two of us (MBJ and AT) to exclude false-positive hits and manually count the number of detected target vocalizations within 1-min recordings. We evaluated the performance of the ARBIMON Pattern Matching tool for each species and found a recall rate of 0.86 for the falcon, 0.77 for the tanager and 0.59 for the saltator (see Appendix S1 for details). Precision was 0.02 for the falcon, 0.01 for the tanager and 0.09 for the saltator.

2.4 | Vocal activity indices

We calculated DR, MAX and VAR for each of the 4 months in our study period (November and December 2021, January and February 2022) for each monitoring site and for each species. Calculating vocal activity indices based on an adequate monitoring period is essential to account for daily variation in vocal activity when aiming to determine relative abundance (Hopping & Klinck, 2021; Pérez-Granados, Gómez-Catasús, et al., 2019). For this purpose, we chose 1 month as a conservative time period, based on recommendations from previous studies (Pérez-Granados & Schuchmann, 2020a: 3–15 days; Pérez-Granados, Gómez-Catasús, et al., 2019: minimum 9 days; Abrahams, 2019: 1 month). DR was the number of 1-min recordings in which the target vocalization was detected at least once per total recording time within a survey month (rounded to the nearest integer), and VAR was the total number of target vocalizations counted per total recording time within a survey month (rounded to the nearest integer). Total recording time varied among sites and months and averaged 2,966 min (Figure S3). We converted the total recording time to days (= $\frac{minutes}{60*24}$) to ensure that the resulting values of DR and VAR were not excessively small. MAX was the maximum number of target vocalizations found in a 1-min recording in each month. We consider a time interval of 1 min as suitable for calculating MAX as it is sufficiently short not to be affected by the length of the vocal activity period, while sufficiently long to capture the collective calling of group members.

2.5 | Data analysis

First, to determine the strength of the association between the indices, we ran Spearman rank correlations between each pair of indices for each species. For this calculation, we determined the three indices for each site and month while excluding months in which a target vocalization was not detected (i.e. we excluded zeroes; $N = 51$ for the falcon, $N = 44$ for the tanager, $N = 28$ for the saltator per index). Second, to compare the temporal variability of the three indices, we used the coefficient of variation (CV) as a scale-independent measure of data dispersal (Abdi, 2010). CVs were calculated for each site, based on the index values obtained in each of the months for each of the three species. CVs were calculated only for sites in which a species was detected in at least three of the 4 months (11 sites for the falcon, 7 sites for the tanager, 4 sites for the saltator) and only for months with species detection, because our objective was to examine to what extent indices varied when a species was present. The CVs showed a normal error distribution ($N = 66$, Shapiro–Wilk test: $W = 0.9765$, $p = 0.243$); therefore, we ran a linear mixed model using the *lme4* package (Bates et al., 2015) in R (v.4.1.2, R Core Team, 2021) to test for differences among the CVs of the three indices (fixed factor). Species and monitoring sites were included as random factors, with species nested within sites. We checked if the corresponding null model was equally plausible (i.e. had a ΔAICc <2) than our model, which would indicate a lack of support for the influence of the fixed factor (Burnham & Anderson, 2002).

Finally, to evaluate the effect of anthropogenic habitat disturbance on the indices, we first determined the scale of effect for each bird species (Miguet et al., 2016) by evaluating 5 spatial scales (buffers of 100–500 m radius around monitoring sites; see Appendix S3 in Supplementary Information for details). Subsequently, we used the *glmmTMB* package (Brooks et al., 2017) in R to run generalized linear mixed models (GLMM) using data from all 25 sites. For each species, we generated three sets of GLMM using DR, VAR and MAX as response variables. In each set, the full model contained the *z*-standardized amount of urban area around monitoring sites (at its scale of effect) as a fixed predictor factor, ARU model (SM4 or Audiomoth) and survey month as fixed control factors and site ID as random factor. We tested the full models for overdispersion based on simulation-based unconditional nonparametric dispersion tests using the *DHARMa* package (Hartig, 2018) before creating all possible additive model combinations using the *MuMIn* package in R (Barton, 2018). We then calculated model-averaged parameter estimates and summed Akaike weights to assess the relative importance of anthropogenic habitat disturbance as a predictor of each index. We checked if the corresponding null models were among the highest-ranking models (ΔAIC <2). To visualize results, we used the *sjplot* package (Lüdecke, 2021) to back-transform model-averaged covariate estimates and their standard errors from the logit scale to the original scale.

3 | RESULTS

In a total of 294,548 1-min recordings, we detected target vocalizations in 219 recordings at 18 sites for the falcon, 98 recordings

at 21 sites for the tanager and 72 recordings at 12 sites for the saltator. The falcon was detected primarily in the morning (05:00–09:00 AM) and afternoon hours (5:00–7:00 PM; Figure S5) with vocal activity bursts between 06:00 and 07:00 AM and between 06:00 and 07:00 PM (Figure S6a). The tanager and the saltator were detected throughout the entire day (Figure S5), with vocal activity bursts between 06:00 and 10:00 AM for the saltator, whereas no clear bursts were evident for the tanager (Figure S6b,c). DR values were lower than VAR and MAX for all species (Figure 4; Table S1) at all sites (Figure S7). Median VAR values were higher than MAX at most sites for the falcon, whereas no clear ranking of median VAR and MAX was evident for the tanager and saltator (Figure S7).

3.1 | Correlations between indices

For each species, we found positive correlations between the three indices. The correlations were stronger between VAR and DR, and between VAR and MAX, compared to those between DR and MAX (Figure 2).

3.2 | Temporal variability of indices

On average, the coefficient of variation was higher for VAR compared to DR and MAX (Figure 3; Table S2), indicating higher temporal variability in the former index.
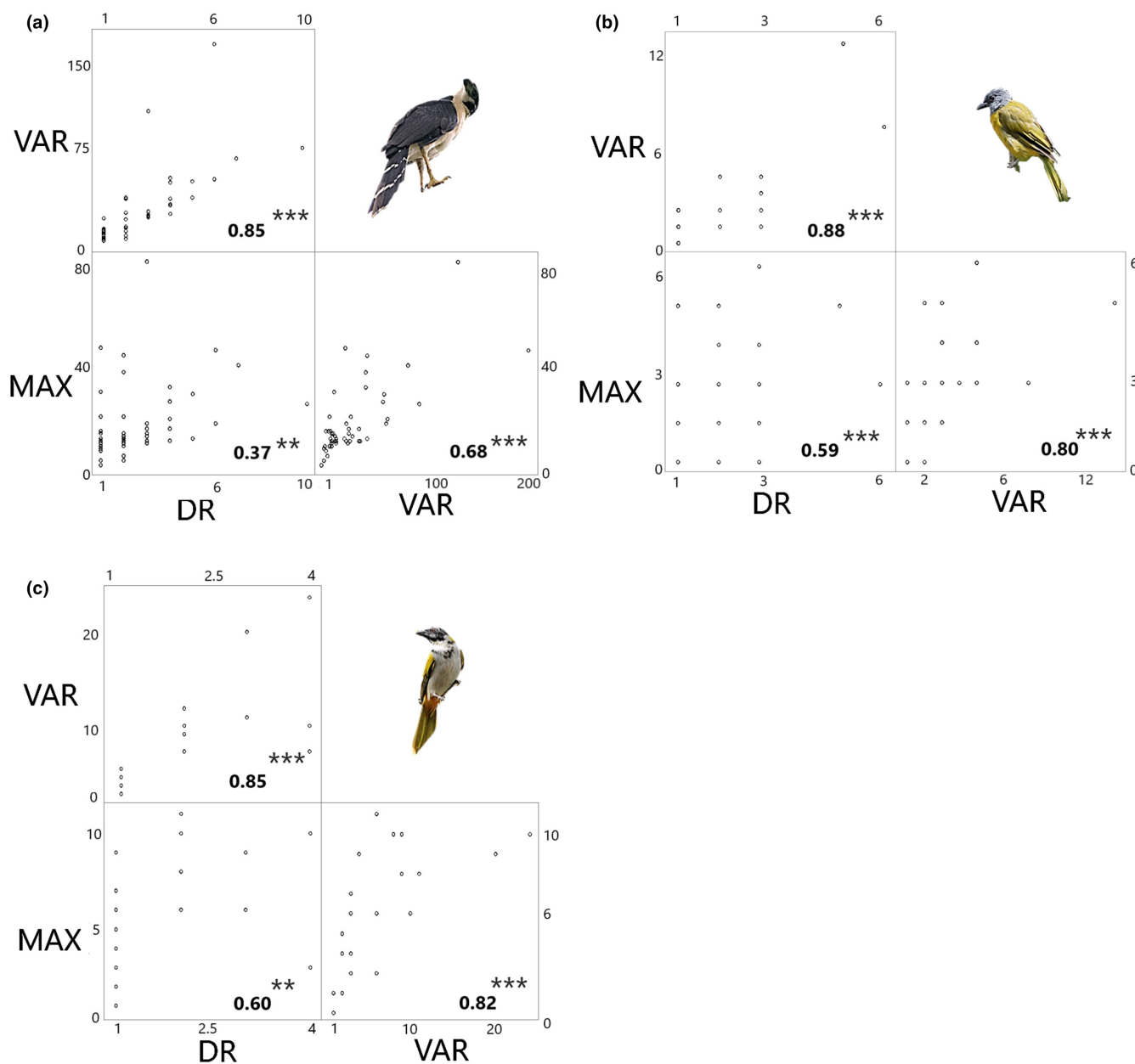

FIGURE 2 Correlations between the indices, VAR, DR and MAX, for the falcon (a), the tanager (b) and the saltator (c). Numbers within panels are the values of the Spearman correlation coefficient (***$p < 0.001$; **$p < 0.01$). DR, detection rate; MAX, maximum count per minute; VAR, vocal activity rate.

3.3 | Effects of habitat disturbance on the indices

The largest effect of anthropogenic habitat disturbance was found in the 500-m buffer for the falcon and the tanager, and in the 200-m buffer for the saltator (Table S3). The amount of urban area ranged from 0 to 11.2% (median = 1.4%) in the 500-m buffers and from 0 to 7.6% (median = 0.2%) in the 200-m buffers. The full GLMM sets showed good fit when using a negative-binomial distribution for the falcon (p_{DR} = 0.704; p_{VAR} = 0.240, p_{MAX} = 0.168), the tanager (p_{DR} = 0.760; p_{VAR} = 0.864, p_{MAX} = 0.752) and the saltator

FIGURE 3 Boxplots showing the coefficients of variation (CV) as indicative of the temporal variability in the values of the three indices (DR, VAR and MAX). The lower and upper whiskers are minimum and maximum values, the lower and upper box limits are the first and third quartiles, the horizontal black lines are the medians and the dots are outliers. Different letters above bars identify statistical differences (see Table S2 for detailed statistical output). DR, detection rate; MAX, maximum count per minute; VAR, vocal activity rate.
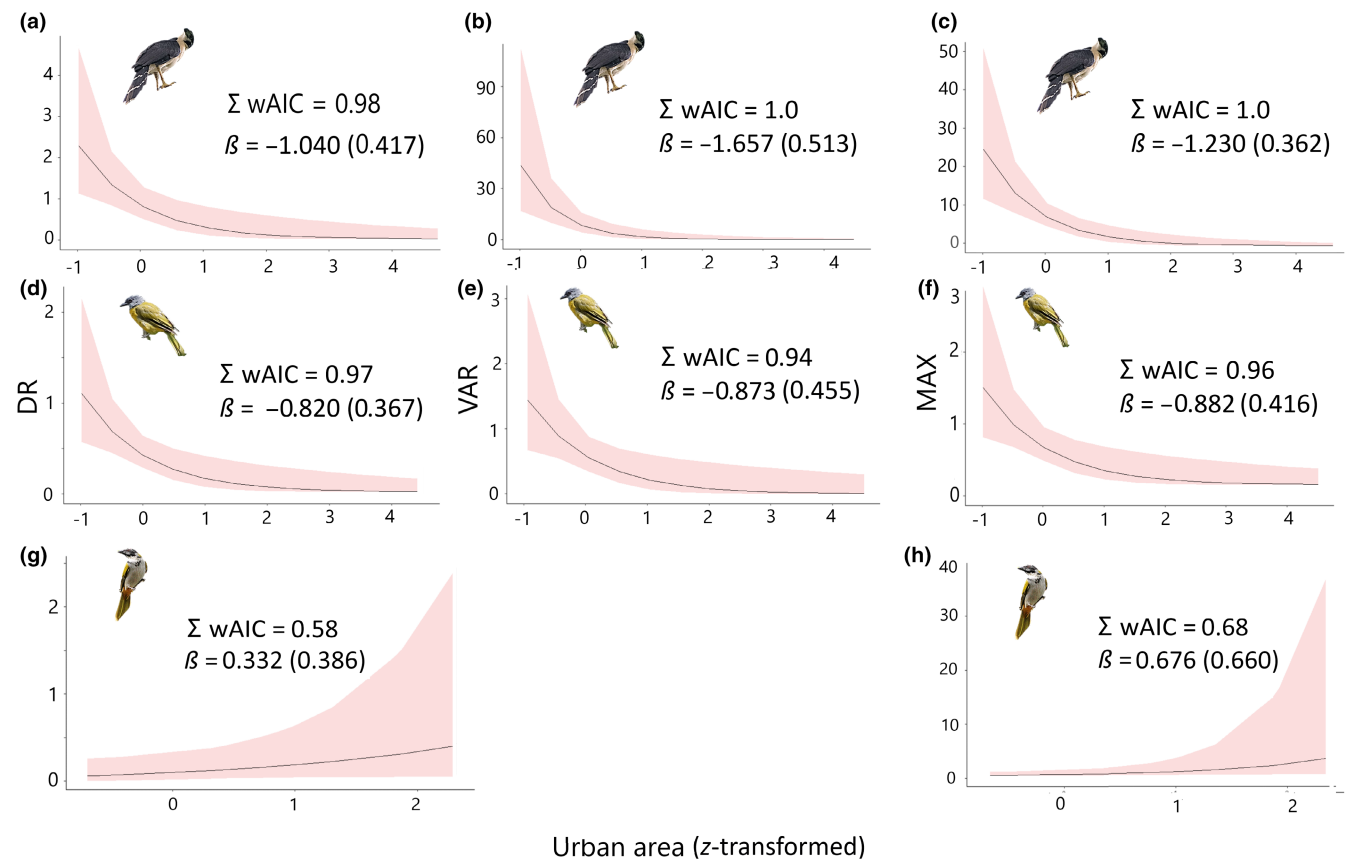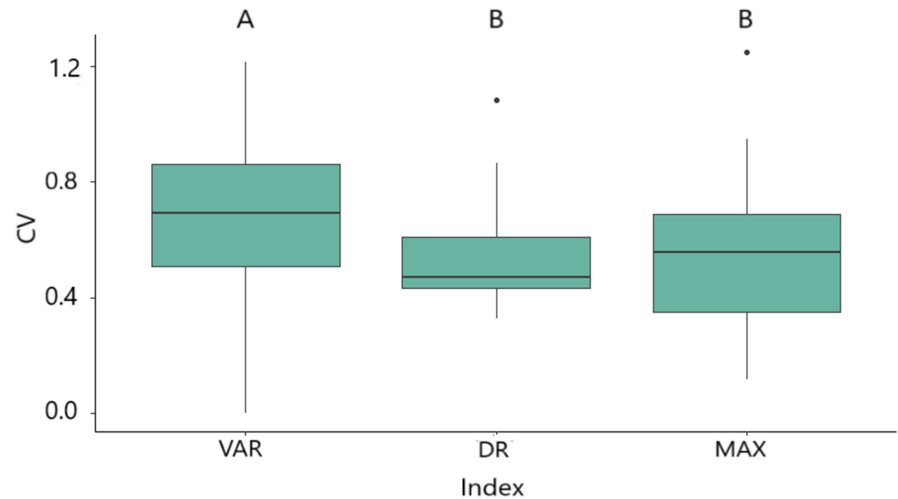

FIGURE 4 Effects of anthropogenic habitat disturbance (amount of urban area) on DR (a, d, g), VAR (b, e) and MAX (c, f, h) for the falcon (a–c), the tanager (d–f) and the saltator (g, h). Each panel includes the values of the summed Akaike weights (Σ wAIC) and the model-averaged covariate estimates (ß and its standard error within parentheses) over all candidate models. VAR results for the saltator are not presented because the null model was among the highest-ranking models. Shaded areas represent 95% confidence intervals. Note that y-axis scales were adjusted in each graph for optimal visual representation. DR, detection rate; MAX, maximum count per minute; VAR, vocal activity rate.

($p_{DR} = 0.584$; $p_{VAR} = 0.616$, $p_{MAX} = 0.464$). Only in the case of VAR for the saltator, was the null model among the highest-ranking models ($\Delta AIC = 1.92$), indicating lack of evidence for the effect of anthropogenic habitat disturbance. We found strong evidence of negative effects of habitat disturbance in the falcon and the tanager using all indices (all Σ wAIC >0.9; Figure 4). In the case of the saltator, there was weaker evidence for a positive effect of anthropogenic habitat disturbance when using MAX (Σ wAIC = 0.68) and DR (Σ wAIC = 0.58; Figure 4). VAR showed the largest effect size (i.e. the highest coefficient estimate) for the falcon, whereas MAX had the largest effect size for the tanager and the saltator. Survey month and ARU model had weak effects on all indices (Table S4).

4 | DISCUSSION

For three bird species, we compared three indices obtained from call counts from PAM recordings. DR and MAX, the novel indices we proposed, correlated more strongly with VAR than with each other in all three species, in accordance with Prediction 1. This suggests that DR and MAX are influenced by different species traits, and that they share more sources of variation with VAR than with one another. In accordance with Prediction 2, VAR showed higher temporal variability than DR and MAX, indicating that the latter two are probably less affected by short-term changes in vocal behaviour, which in turn suggests that in some cases they may be more adequate proxies of bird abundance. All three indices responded to anthropogenic habitat disturbance, but effect sizes differed depending on the species/index combination, in accordance with Prediction 3. Our results indicate that the biological information that can be obtained from different indices may depend on the index and on species traits. With our framework, we propose that for some bird species, depending on their degree of territoriality and social organization, indices can be more useful for assessing changes in abundance, whereas for other species, indices may be more strongly associated with some behavioural aspect (vocal behaviour or habitat use). Thus, it is crucial that future PAM studies consider which index is more appropriate to obtain the desired information for a particular bird species. Our study also suggests that, when little ecological and behavioural information about a bird species is available, the simultaneous use of multiple indices can be helpful in inferring some of the missing information.

4.1 | Temporal variability of the indices

Our study revealed that VAR had higher temporal variability compared to DR and MAX. These results support our argument that DR and MAX may be less affected by changes in vocal behaviour than VAR. As we propose in our framework, VAR is likely to be affected by both the cue rate and the length of the vocal activity period, whereas DR and MAX are each affected by only one of these factors (Figure 1). We believe that this makes DR a potentially more accurate proxy of the number of individuals in the case of solitary species, and MAX a more accurate proxy of group size in the case of gregarious species, compared to VAR. To test these claims, however, future studies will need to assess the relationships of DR and MAX with abundance estimates obtained through other methods (e.g. point counts), as has already been done for some species in the case of VAR (see Table 2 in Pérez-Granados & Traba, 2021).

Because our study focused on resident bird species and was conducted during the non-breeding season, we can exclude the possibility that the indices were affected by temporal changes in abundance due to migration or reproduction. However, we cannot exclude the possibility of small temporal changes in group sizes of both gregarious species (e.g. due to changes in food availability within the 4-month study period; Silk et al., 2014). Nevertheless, such changes should have affected both VAR and MAX similarly. Yet, we found higher temporal variability in VAR, indicating that aspects of vocal behaviour that do not affect MAX, such as the length of vocal activity periods, probably contributed to the variability in VAR. Although several studies have reported seasonal differences in VAR (Pérez-Granados et al., 2020; Pérez-Granados & Schuchmann, 2020a, 2020b), it remains unknown whether these seasonal patterns are due to changes in the length of vocal activity periods or changes in cue rates.

In theory, all three vocal activity indices could be used to estimate absolute abundances, using regressions of call counts on bird abundance obtained through validation datasets (as done for VAR: Pérez-Granados & Traba, 2021). However, given the temporal variability we observed in the indices, particularly in VAR, caution is needed when using such regressions. Large validation datasets are likely necessary to obtain accurate and precise regression coefficients, capable of offsetting large variability in vocal behaviour.

4.2 | Responses of the indices to anthropogenic habitat disturbance

In the falcon, a solitary species, the three indices had strong negative associations with anthropogenic habitat disturbance. Because this species is highly territorial, indices, in particular MAX, are assumed to reflect mainly cue rates (Figure 1). Thus, the pattern observed for MAX is in accordance with results of a previous study showing that this species decreases its territorial-defence cue rate in areas with higher levels of habitat disturbance (Martínez-Ruiz et al., 2016). The same authors observed that individuals defended larger territories as the amount of degraded habitat within their territory increased, possibly to compensate for reduced food availability. Thus, population density of this species most likely decreases in areas of greater habitat disturbance, which aligns with the results we obtained for VAR. Reflected in the largest coefficient estimate, VAR exhibited the strongest response to habitat disturbance. This result suggests that VAR may be a more sensitive indicator of habitat disturbance. Yet, this index does not discriminate whether abundance, habitat use, or vocal behaviour are being affected more strongly by habitat disturbance. In such cases, by including information of DR and MAX, in

addition to VAR, we may reach clearer conclusions. For example, in the case of the falcon, since the coefficient estimates were higher for MAX and VAR than for DR, one could infer that cue rate (reflected in MAX and VAR but not DR) is more strongly impacted by habitat disturbance than abundance, the length of the vocal activity period, or habitat use (i.e. factors that influence DR but not MAX in solitary species).

In the tanager, an insectivorous species that lives in pairs during the non-breeding season, again all three indices showed negative associations with habitat disturbance. We expected to find these associations with DR and VAR, since it is likely that fewer groups occur in disturbed habitat where food availability is scarce (Kumar & O'Donnell, 2007; Ridgely & Tudor, 2009). However, we did not expect an effect on MAX. According to our framework, MAX should mainly reflect group size in gregarious species (Figure 1). Thus, since group size was believed to remain stable (2 individuals) before the breeding season (Baker & Burns, 2020), we expected no response of MAX to habitat disturbance. Yet, not only was MAX negatively affected by habitat disturbance, but it also showed the largest effect size. Baker and Burns (2020) reported that family groups of the tanager stay together up to 7 months after the offspring hatch and then separate, but that occasionally family members rejoin until the next breeding season. If this occurred at our study site, our result could indicate that larger groups caused by the rejoining of family members are less likely in disturbed habitat, possibly due to increased resource competition (Rylander, 2021).

Maximum count per minute can also be indicative of cue rates. Contact calls, which is the vocalization type we used for the tanager, are used for cohesion and movement coordination within groups (Kondo & Watanabe, 2009), and are associated with social contexts (Radford & Ridley, 2008), rather than with environmental conditions (Meaux et al., 2023). Consequently, we reasoned that a direct effect of habitat disturbance on cue rates would be unlikely in this species. However, an indirect effect, mediated through group size, could be possible. It has been shown that individuals increase their cue rates in contact calls with increasing group size (Meaux et al., 2023; Striedter et al., 2003). Thus, in the tanager, the lower values of MAX observed at sites with greater anthropogenic habitat disturbance might represent a combination of smaller group sizes due to family members not rejoining and decreased cue rates due to smaller group sizes.

The difficulty of accurately interpretating vocal activity indices increases when there is less information on the natural history of a target species available. In such cases, the use of multiple indices can be helpful to gain insights and/or generate hypotheses on the effects of habitat disturbance. This is the case of the saltator, a gregarious habitat generalist for which we have even less information than for the other two species. We found that, in this species, habitat disturbance had a moderate positive effect on MAX and a weak positive effect on DR. These results are consistent with previous findings on the saltator, which describe it as a generalist species that is positively impacted by habitat disturbance (Patten et al., 2010). However, we found no positive effect of habitat disturbance on VAR. By comparing the responses

of the three indices, we may infer that group size and/or cue rates (as measured by MAX) are probably the aspects more likely affected (positively) by habitat disturbance, while the variability in VAR introduced by other aspects (the number of groups, habitat use, and the length of the vocal activity period) was too high to detect a significant effect of habitat disturbance. The case of the saltator, along with the examples from the other two species, illustrate how our proposed framework can facilitate the generation of hypotheses to stimulate additional research on bird behaviour.

4.3 | DR and MAX as novel vocal activity indices

While our results show that DR and MAX are closely related to VAR and reveal the effects of habitat disturbance on bird populations, further research is needed to test the assumptions that underlie our conceptual framework (Figure 1), such as DR hardly being influenced by cue rate or group size, and MAX being sensitive to both. Studies carrying out PAM and observer-based surveys simultaneously could aid in testing our proposed interpretations of DR and MAX, as has been previously done for VAR (e.g. Pérez-Granados, Bota, et al., 2019) and for ecoacoustic indices (Allen-Ankins et al., 2023). We believe that DR (and possibly MAX in the case of gregarious species) have the potential to be less variable proxies of relative bird abundance than VAR. In addition, they are easier to calculate. In our case, whereas calculating VAR required counting all target vocalizations recorded, determining MAX required counting calls only for the fraction of recordings with high call numbers. Similarly, determining DR solely required a count of the recordings in which the target vocalization was present, without the need of counting individual calls. Counting effort depends on the software used, the recording schedule, and how indices are adjusted (see below). Given that fully automated detection of target vocalizations is yet unfeasible in most cases (Tuia et al., 2022), differences in manual processing effort is an important consideration when designing PAM studies.

Whether DR and MAX correlate strongly with species abundance, vocal behaviour, and/or other behaviours such as habitat use, is likely influenced by the time intervals used to calculate the indices. In our study, we recorded 1 min every 6 min, resulting in DR having a maximum value of 1 for every 6-min interval and MAX being limited to the number of vocalizations emitted within 1 min. However, the index parameters can be adjusted to any recording period, depending on the vocal behaviour shown by the species of interest. For example, while DR as calculated in our study was adequate for the falcon, since the average length of its territorial-defence-call sequence is 5.9 min (Martínez-Ruiz et al., 2016), it would be less appropriate for a species such as the ferruginous pygmy-owl (*Claudidium brasilianum*), which is known to vocalize in sequences of up to 5 h (Proudfoot et al., 2020). Therefore, careful consideration must be given to the appropriate time interval used to count calls (similarly to when calculating ecoacoustic indices: Metcalf et al., 2021), to ensure that the calculated indices provide the expected information. We recommend gathering as much information as possible on the

vocal behaviour of the species of interest from the literature, existing recordings, or field observations, before defining index parameters, and interpreting index values obtained through call counts from PAM recordings.

In addition to the aspects considered here (length of activity period, cue rate, habitat use, territoriality, social organization), other species traits and survey characteristics can influence how strongly vocal activity indices correlate with animal abundance and/or behaviour, including home-range size, the chosen target vocalization, and the spatial setup of monitoring sites. For example, certain types of vocalizations are density-dependent, such that individuals vocalize at higher rates when more birds are present in an area (Veech et al., 2016). This is the case for the falcon, a species that emits territory-defence calls more frequently when more conspecifics there are in the vicinity (Martínez-Ruiz et al., 2016). In such cases, indices incorporating such aspects of vocal behaviour (such as VAR) can be useful for assessing abundance changes. This might be an additional reason why we found VAR to have the largest effect size in the falcon. The choice of target vocalization can also influence the interpretation of the calculated index. For example, when using a song as the target vocalization for a gregarious species (as we did for the saltator), MAX might be more likely to capture individuals from multiple groups, compared to when using a contact call (as we did for the tanager). This is because songs are often more concentrated around sunrise and sunset (see Figure S6c), increasing the chances of multiple groups singing simultaneously, whereas contact calls have broader vocal activity periods (Pérez-Granados et al., 2018; see Figure S6b). Furthermore, the target vocalization may be emitted only by certain individuals, resulting in indices that might represent only a subset of the population. For instance, if only adult males of a species emit the target vocalization, indices may reflect only their abundance, and an estimation for the rest of the population needs to be based on the species typical ratio of adult males to females and juveniles. Unfortunately, information on basic behavioural aspects, such as vocal repertoire, is limited for many Neotropical birds (Ruelas Inzunza et al., 2023), making it challenging to select target vocalizations based on their functions and sound characteristics.

5 | CONCLUSIONS

Based on our findings and the conceptual framework presented, we offer some recommendations on the use of vocal activity indices derived from counting calls in PAM recordings. First, it is necessary to consider whether the research question requires an index of relative abundance, an index of vocal behaviour or some other behavioural aspect, or an index that is correlated with both abundance and behaviour. Second, it is advisable to gather comprehensive information on the species' traits and consider how these traits may influence call counts obtained in different ways. Third, decisions can then be made regarding the choice of target vocalization and index, and the design of the recording schedule (if applicable).

The selection of indices based on call counts derived from PAM recordings should be tailored to each study, according to the species traits, target vocalizations, the recording schedule, and the specific research objectives. We believe that the framework we present offers valuable guidance for choosing indices. Looking ahead, there is potential to expand this framework to address scenarios where more complex relationships between species abundance, behaviour, and traits may be at play. This might include species occurring in mixed flocks (Kajiki et al., 2018) or non-gregarious species forming occasional flocks in response to factors such as food availability (Fraga, 2020). With this study, we intend to encourage the exploration of alternative approaches to obtain vocal activity indices from PAM recordings, other than the VAR index. We also aim to open a fruitful discussion on the need to consider species traits to adequately interpret the information contained in different indices based on call counts.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Example of how bird species traits (e.g. degree of territoriality and social organization) can impact patterns of vocalization recordings.

Figure S2. Map of the study area in Mexico, with locations of the 25 monitoring sites labelled with their ID.

Figure S3. PAM monitoring effort per site during the 4-month study period.

Figure S4. Example spectrograms of vocalizations used in our study to detect *Micrastur semitorquatus* (territorial-defense call), *Eucometis penicillata* (contact call), and *Saltator atriceps* (common song) (from left to right).

Figure S5. Temporal distribution of detection events for the three bird species surveyed in our study.

Figure S6. Temporal distribution of recordings used to determine MAX for (a) *Micrastur semitorquatus*, (b) *Eucometis penicillata* and (c) *Saltator atriceps*.

Figure S7. Median index values per site across survey months for (a) *Micrastur semitorquatus*, (b) *Eucometis penicillata* and (c) *Saltator atriceps*.

Table S1. Numbers of days with at least one detection and the three vocal activity indices per species, site, and survey month.

Table S2. Model-averaged covariate estimates for the effect of vocal activity index on the coefficient of variation (CV) across months as indicator of temporal variability.

Table S3. R^2 values of generalized linear models predicting detection frequency from the proportion of urban area in spatial buffers of different sizes for the three bird species.

Table S4. Model-averaged covariate estimates and summed Akaike weights (Σ wAIC) over all candidate models of the effects of ARU model and survey month on vocal activity indices.

Appendix S1. ARBIMON Pattern Matching configuration and performance.

Appendix S2. Description of the land cover map development.

Appendix S3. Determination of scales of effect.