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VOCAL REPERTOIRE OF PLUSH-CRESTED JAY (*Cyanocorax chrysops*): VOCALIZATIONS AND MIMICRY

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ABSTRACT: Vocal communication plays a fundamental role in birds, particularly in gregarious species such as jays. However, the diversity and function of their vocalizations remain poorly known in many Neotropical jay species. In this study, we describe and characterize part of the vocal repertoire of the Plush-crested Jay (*Cyanocorax chrysops*), a social species distributed in the tropical and subtropical forests of South America. To do so, we combined focal recordings of four groups in the Yungas ecoregion with acoustic records from repositories and continuous recordings made with a passive recorder. From the focal recordings, we identified seven vocalization types, distinguishable by their spectro-temporal structure and their auditory similarity. Multivariate acoustic analysis showed that the vocalizations occupy differentiated acoustic regions, although some are similar to each other. Some vocalizations could be associated with specific behavioral contexts, particularly alarms and group movements. In addition, the analysis of recordings from repositories revealed two vocalizations that suggest possible imitations of raptors of the genera *Micrastur* and *Astur*. The analysis of 117 hours of passive recordings allowed us to explore a possible variation in the relative frequency of use of the different vocalizations, in which certain vocalizations would apparently dominate the repertoire and vary in their emission throughout the day. Overall, these results show that *C. chrysops* has a structured and diverse vocal repertoire, consistent with what has been observed in other social corvids, and they provide new information on the use of acoustic signals in species of this group.

KEYWORDS: *acoustic activity patterns, behavioral ecology, bioacoustics, Corvidae, Tucumán*

The vocal repertoire of bird species and its function within a behavioral context have intrigued numerous researchers over time (Hardy 1979, Alonso 2001, Elie et al. 2011, Leighton & Birmingham 2021). Vocalizations can be directed at interspecific or intraspecific individuals, and in gregarious species intraspecific vocalizations are linked to group activities, such as moving together, maintaining cohesion, and alerting others to predators (Hardy 1979). Among gregarious birds, corvids are particularly interesting because they have a vocal repertoire that covers many of these functions and, in some cases, shows a high degree of flexibility and complexity (Hardy 1979).

Corvids (family Corvidae) stand out among passerine birds for frequently performing complex behaviors and for having a high degree of encephalization (the ratio between brain size and body size; Taylor 2014). Globally, the family has been widely studied because it accounts for the largest number of behavioral innovations in foraging and tool use compared with other bird groups, as well as for behaviors such as social learning, intraspecific cooperation, and flexibility in communication systems, particularly in complex social contexts (Emery et al. 2007a, Taylor 2014, Lambert et al. 2019). However, despite their broad behavioral and cognitive diversity, knowledge of vocal communication is uneven, and vocal repertoires have not been described for most species in the family (Kovářová et al. 2025). In this context, exploring the vocal repertoire of different corvid groups is

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key to understanding how communication systems diversify within the family.

The 'New World jays' are a group of American corvids belonging to several genera (e.g., *Aphelocoma*, *Cyanocitta*, *Cyanocorax*, *Cyanolyca*, and *Gymnorhinus*; Espinosa de los Monteros & Cracraft 1997) and have different types of vocalizations that can be associated with specific behavioral contexts, such as group movement and alerting to dangerous situations (Rosa et al. 2016). The genus *Cyanocorax* comprises 19 species (AviList 2025) and is one of the most morphologically diverse lineages among the corvids of the Americas, with a distribution extending from southern North America to northern and central South America. Species in this genus show considerable variation in body size and plumage coloration (Bonaccorso et al. 2010) and are characterized by forming relatively stable social groups and maintaining frequent social interactions (Emery et al. 2007b). However, the vocal repertoire has been studied in only a few species of the genus *Cyanocorax*, such as the Azure Jay (*Cyanocorax caeruleus*; Dos Anjos & Vielliard 1993). The Plush-crested Jay (*Cyanocorax chrysops*) is a conspicuous and gregarious species, common in open and ecotonal environments, where it forms stable groups (Kazue Uejima et al. 2012). This conspicuousness is not only visual but also acoustic, since individuals vocalize frequently and strikingly during their social interactions. Nevertheless, despite the prominence of these vocalizations in the species' daily behavior, the available knowledge on the structure, diversity, and function of its vocal repertoire remains limited, and the most recent studies come from Brazil, where they focused on a single vocalization type, the 'social call', with subtle acoustic differences between groups (Brunetta 2009). Thus, we do not know the complete vocal repertoire of the species, how the different vocalization types differ acoustically, in which situations the vocalizations are emitted, or how the vocal activity of the species varies throughout the day. This lack of information limits our understanding of the role that acoustic communication would play in the social organization and group interactions of the species.

The aim of this study is to describe and characterize part of the vocal repertoire of the Plush-crested Jay and, in particular, that of the subspecies *C. chrysops tucumanus*, based on recordings of groups in the Yungas ecoregion of northwestern Argentina. To do so, we combined field observations, acoustic analyses, and automatic detection tools. Specifically, we aimed to: (1) Identify and qualitatively classify the different vocalization types present in the repertoire of *C. chrysops* based on their acoustic structure and auditory similarity. (2) Explore the association between vocalization types and behaviors, particularly in situations of movement, feeding, and alarm. (3) Quantitatively assess whether the qualitatively defined vocalization types differ in their spectro-temporal characteristics by means of multivariate acoustic analyses. (4) Quantify the relative frequency of emission of the different vocalizations using automatic detection tools (based on a machine learning model). (5) Examine the temporal variation in the emission of vocalizations throughout the day and evaluate possible patterns in the vocal activity of the species. Together, these analyses provide an integrated characterization of part of the vocal repertoire of the Plush-crested Jay.

METHODS

Study area

We conducted the study in Tucumán province, in northwestern Argentina, located in the Yungas ecoregion. This ecoregion is one of the main subtropical montane forest systems of South America and is characterized by a marked altitudinal gradient that determines changes in vegetation structure and environmental conditions (Brown et al. 2002). We carried out the work in three large areas located in the transition zone between the piedmont forest and the montane forest. Both strata have a seasonal climate regime, with a period of heavy rains between November and March, followed by a prolonged dry season (Hunzinger 1997). Within the three areas, we established four sites where independent groups of Plush-crested Jays had been found during previous walks (Fig. 1). Two sites, which we named IER and IER–Antayacu, were located in Parque Sierra San Javier (26°46'S, 65°20'W), near the Instituto de Ecología Regional (IER), in Yerba Buena department. At each of the Parque Sierra San Javier sites, we found a group of jays occupying the forest, which is in a good state of recovery after its productive use (Grau et al. 1997). The third site corresponds to an adjacent semi-urban area (26°48'S, 65°19'W), where a resident group of Plush-crested Jays uses a mosaic of remnant native vegetation, gardens, and green spaces. The fourth site corresponds to Proyecto Seamos Bosques (26°30'S, 64°53'W), located near the town of El Cajón, in Burruyacú department. Proyecto Seamos Bosques is a large area (5650 ha) where a restoration project of canopy trees is being carried out, together with areas in a good state of conservation. As such, the area hosts several independent groups of jays, but in this study

we focused on only one group (26°30'S, 64°53'W). The dominant vegetation at all study sites includes tree species such as *Tipuana tipu* and *Enterolobium contortisiliquum*, while in some sectors vegetation associated with the montane forest can be found, with species such as *Ocotea puberula* (Lauraceae), *Juglans australis*, and *Blepharocalyx salicifolius* (Brown et al. 2002). Together, these environments form a heterogeneous landscape where areas of native forest, modified sectors, and semi-urban environments coexist, conditions under which the Plush-crested Jay forms stable and vocally active social groups.

Qualitative identification of vocalizations and association with behavioral contexts

Between September and November 2025, we recorded Plush-crested Jays during two morning field trips to the Parque Sierra San Javier area, one visit to the Proyecto Seamos Bosques area, and opportunistically in the semi-urban area. Once a group was located, we made focal recordings of different individuals; in all cases, we sought to record each individual only once each time we found a group. This yielded 24 recordings from four different groups (Fig. 1), although, given the social nature of the species, in the subsequent analyses we could not clearly assign each vocalization to an individual, since many vocalizations occur synchronously from several individuals. The 24 recordings obtained during the field trips were inspected aurally and visually in Raven Pro 1.6.5 (K. Lisa Yang Center for Conservation Bioacoustics at the Cornell Lab of Ornithology 2026) using standardized spectrograms (Hann window, FFT size 512, 50% overlap), in order to identify and preliminarily classify the different vocalization types. This initial stage consisted of a qualitative classification, based on the auditory similarity of the sounds and the structure observed in the spectrograms. Each vocalization type identified was grouped and named with an onomatopoeia representative of its characteristic sound (e.g., *kekeke*, *kiu*, *maullido* ['meow'], among others; Fig. 2).

For each recording, we made voice notes with information on the behavior observed in the focal individuals. The behaviors observed were summarized in three main categories: (1) movement, when the individual was moving as its predominant activity or moved after emitting the vocalization; (2) feeding, when the individual was foraging, which could include short movements associated with this activity; (3) alarm, when the presence of a potential predator (a raptor that feeds on other birds) was recorded within 20 m of the recorded individuals. These behaviors were associated with the vocalization type only when they were clearly identifiable. We made all recordings with a Zoom H1essential recorder equipped with a unidirectional parabola and a stereo microphone (CrakeSound), protected with a windscreen. A small number of recordings (n = 8) was additionally obtained

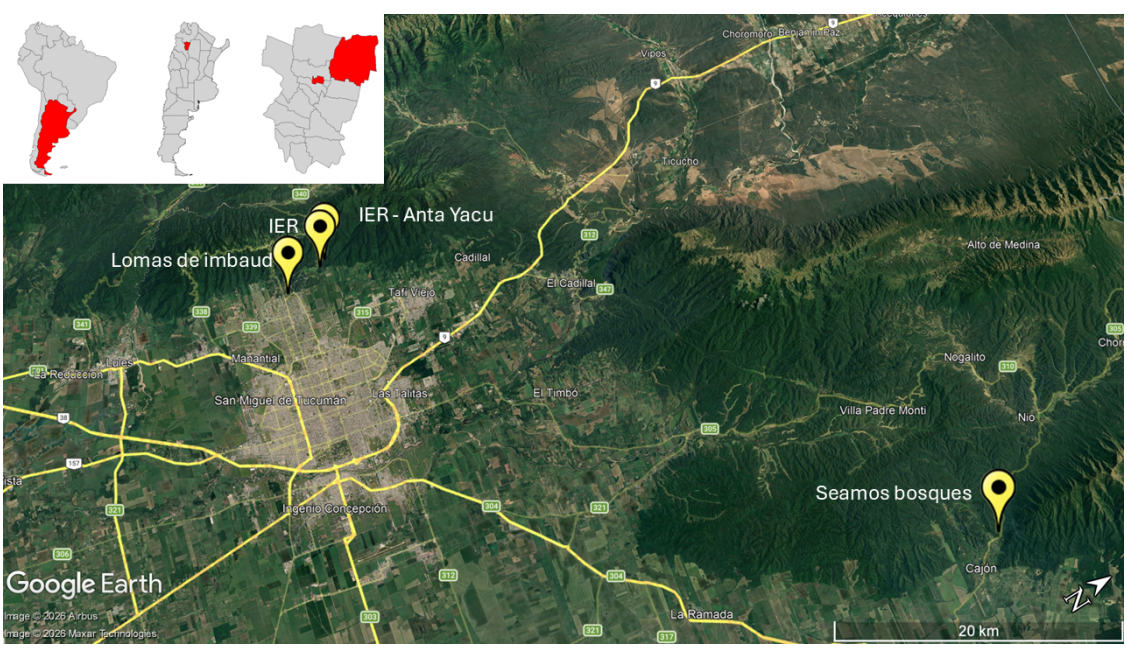


Figure 1. Map showing the sampling sites where 24 recordings of the Plush-crested Jay (*Cyanocorax chrysops*) were obtained in Burruyacú and Yerba Buena departments, Tucumán province, Argentina.

with a mobile phone using the Merlin app (Cornell Lab of Ornithology 2026), and all recordings were made in *.wav* format, 32 bits.

Measurement of acoustic variables and quantitative validation of vocalization types

We analyzed a total of 44 recordings of Plush-crested Jays from three sources: 24 of our own recordings made in Tucumán province from September to November 2025 (see section '*Qualitative identification of vocalizations and association with behavioral contexts*'), 18 recordings obtained from the Xeno-canto platform (www.xeno-canto.org, up to February 2026), selected because they represented northwestern Argentina (eight from Jujuy province, ten from Salta) and contained vocalizations identifiable as belonging to this species, and finally two vocalizations outside this selection: an opportunistic recording from the Proyecto Seamos Bosques group made in 2023, and a Xeno-canto recording from Misiones province that we decided to include in our analyses of the vocal repertoire because of the unique characteristics of these vocalizations. We used the 24 field recordings to inspect those obtained from repositories and to classify the vocalizations according to the qualitatively identified vocalization types. Vocalizations that did not resemble the qualitatively identified types (Fig. 2) were discarded. From each recording, we selected only one event of each different vocalization type, keeping the events with the best signal-to-noise ratio to extract acoustic variables (e.g., recording 1 contained different vocalization types, *kiu* and *kia*, with several repetitions; in that case, in that case, we selected only one repetition per vocalization type and measured its acoustic variables and its acoustic variables measured). Some recordings contained sounds that were classified as imitations (see '*Results*' section).

To acoustically characterize each vocalization, we extracted seven variables in Raven Pro 1.6.5 (K. Lisa Yang Center for Conservation Bioacoustics at the Cornell Lab of Ornithology 2026) from standardized spectrograms (Hann window, FFT size 512, 50% overlap): peak frequency (Peak Freq), 90% duration (Dur 90%), 95th-percentile frequency (Freq 95%), 5th-percentile frequency (Freq 5%), 90% bandwidth (bandwidth 90%), and the means of the 5% and 95% frequency contours; in addition, two variables were calculated, the standard deviation of the upper and lower frequency contours (C95 SD and C05 SD, respectively), giving a total of nine acoustic variables measured. The standard deviation of the upper and lower frequency contours is related to the temporal modulation of each contour throughout the vocalization and is not directly available in Raven. Therefore, we calculated the standard deviation in R from the frequency values of all spectrogram windows spanning each vocalization (window size = 512 samples, overlap = 50%), obtaining one value per contour for each vocalization. Because the sampling rate of the recordings was heterogeneous, each contour was

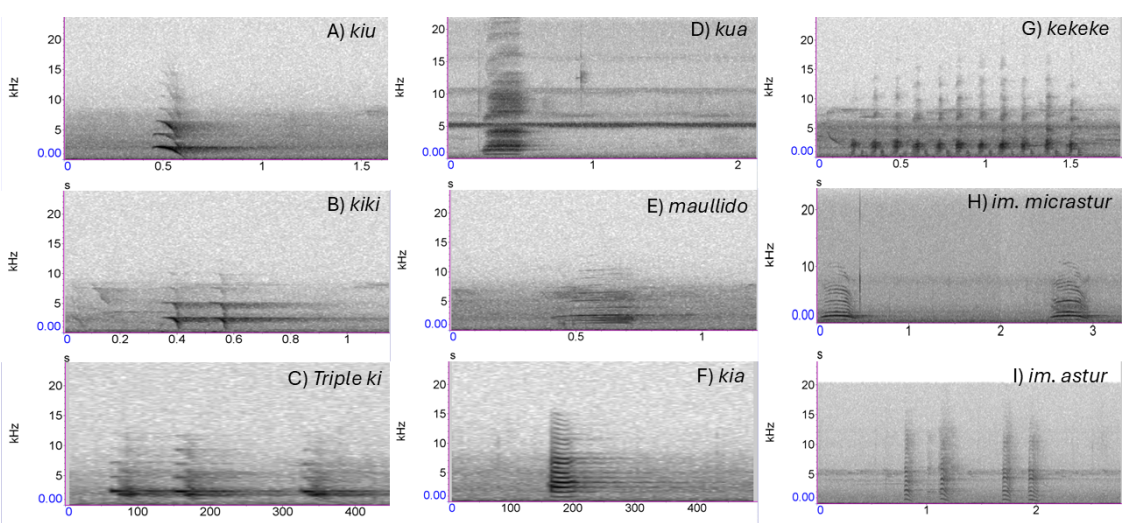


Figure 2. Standardized spectrograms (Hann window, FFT size 512, 50% overlap). One example of each of the seven vocalization types identified in the Plush-crested Jay (*Cyanocorax chrysops*) is shown: *kiu* (A), *kiki* (B), *triple ki* (C), *kua* (D), *maullido* (E), *kia* (F), *kekeke* (G). The two vocalizations categorized as imitations are also shown: imitation of the Collared Forest-Falcon (*Micrastur semitorquatus*; H), recorded at Proyecto Seamos Bosques, September 2023, and imitation of the Bicolored Hawk (*Astur bicolor*; I), obtained from xeno-canto (XC337874). Spectrograms were generated with Raven Pro 1.6.5.

interpolated to 100 equidistant points before calculating the standard deviation, ensuring comparability among vocalizations.

To evaluate the acoustic separation between vocalization types, we performed an exploratory linear discriminant analysis (LDA) on the standardized variables, including all events of the vocalization types from the different recordings from northwestern Argentina (n = 67). Variable selection aimed to minimize redundancy among predictors by discarding those strongly correlated with each other (Pearson correlation, $|r| \geq 0.85$); bandwidth 90% was excluded because of its high correlation with Freq 95% (r = 0.96), and the contour means were excluded because of their correlation with Freq 95% (r = 0.87) and Freq 5% (r = 0.85), respectively. The statistical significance of the differences between groups was evaluated by PERMANOVA (adonis2, *vegan* package; using 999 permutations, Oksanen et al. 2025), restricting permutations within each source recording (strata = recording ID) in those cases in which recordings contained more than one vocalization type, to control for the non-independence of vocalizations from the same audio file. The PERMANOVA was performed only with the classes with $n \geq 4$ (*kiu*, *maullido*, *kiki*, *triple ki*, and *kekeke*; n = 63 vocalizations from 38 recordings), excluding *kia* (n = 1) and *kua* (n = 3), because their sample sizes were too small to perform the permutation; the *Micrastur semitorquatus* imitation (n = 2), from a single 2023 recording; and the *Astur bicolor* imitation, because it was a recording from northeastern Argentina. The assumption of homogeneity of multivariate dispersion was checked with betadisper with 999 permutations. Post hoc pairwise comparisons between classes were performed with individual PERMANOVAs, correcting p-values with the FDR method (false discovery rate, Benjamini–Hochberg). All analyses were performed in R v4.3.1 (R Core Team 2023).

Training and evaluation of the automatic model and analysis of temporal patterns of vocal activity

To explore the daily vocal activity pattern of the Plush-crested Jay, we used passive recordings obtained in the semi-urban area with a SongMeter Mini recorder for nine days (3 to 11 October 2025), placed 50 cm above the ground. The recorder was set to record 1 h continuously every hour from ~ 05:00 h to ~ 19:00 h (thus providing recordings from 05:00 to 06:00 h, from 06:00 to 07:00 h, etc.). This allowed us to obtain 117.3 h of continuous recording. During this period, we did not make direct recordings of the same group to avoid pseudoreplication. Thus, to quantify the relative frequency of the different vocalization types in long-duration recordings, we implemented an automatic detection approach using BirdNET Analyzer v2.4.0 (Kahl et al. 2021), a tool based on convolutional neural networks trained for sound recognition. Based on the vocalization types defined in the previous qualitative classification, we trained a specific model to recognize the different vocalization types of the Plush-crested Jay. We used the default hyperparameters: 50 epochs, batch size of 32, learning rate of 0.0001. We did not apply data augmentation (mixup or upsampling) or the autotune function. We worked with the 24 recordings made in Tucumán province, where each recording was manually inspected and segmented into fragments of up to 3 s, corresponding to different vocal events of each vocalization type per recording (the 3 s range is the one used by the model). The final training set included only the vocalization types with enough representation to allow the model to learn (minimum per vocalization type: 6; maximum: 27, of *kekeke*, *kia*, *kiu*, *kiki*, *triple ki*, and *maullido*). In addition to the vocalization types, an additional class called *noise* was included, comprising environmental sounds such as background noise, heterospecific vocalizations, and anthropogenic sounds (e.g., vehicles). The inclusion of this class would allow the classifier to distinguish between the target vocalizations and other acoustic events present in the recordings. The recordings used for training varied both in duration (always within the 3 s limit) and in signal quality, since they came from individuals recorded at different distances and in different contexts (both in semi-urban and non-urban areas). This variability would provide the model with more representative examples of the acoustic conditions present in the recordings obtained from the automatic recording devices.

During training, BirdNET Analyzer processes recordings in 3 s time windows, automatically extracting spectro-temporal features used by the neural network for classification. To evaluate the generalization ability of the model and maximize the use of the available recordings, we implemented a four-fold cross-validation procedure. For each vocalization type, recordings were randomly divided into four approximately equal subsets (folds). Model training and validation were repeated four times, using three subsets for training and the remaining one for validation. In this way, each recording was used once for validation and three times for training. Thus, the performance of the training procedure was estimated by four-fold cross-validation; the final model applied

to the passive recordings was trained with all clips. This procedure reduced the bias associated with the relatively small size of the dataset and provided multiple independent estimates of model performance. For each repetition of the cross-validation process, BirdNET Analyzer generates a confusion matrix. From these results, the following evaluation metrics were calculated: precision (true positives/(true positives + false positives)), recall (true positives/(true positives + false negatives)), F1-score, the area under the ROC curve (AUROC), and the area under the precision–recall curve (AUPRC). Model performance indicated a moderate discrimination ability in all repetitions. Mean AUROC was 0.86 (range: 0.82–0.91), indicating a limited ability of the model to distinguish between positive and negative cases. Similarly, mean AUPRC was 0.65 (range: 0.53–0.74), suggesting performance that can be improved in terms of precision and recall, considering the probable class imbalance in the dataset. The F1-score at the optimized threshold was relatively low ($\bar{x}$ = 0.07; Table 1), reflecting the difficulty of simultaneously maximizing precision and recall in a context of imbalanced classes (some vocalization types were represented by 6 clips and others by 27), although this allows us to explore possible variation in the vocal use of the species throughout the day. Because the classifier produces confidence values of membership for each class, we used this value as a criterion to evaluate the reliability of the predictions. Detections were considered high-confidence only when the estimated confidence values were ≥ 0.85. Occurrences that exceeded this confidence threshold, without manual validation, were subsequently used to estimate the relative frequency of the different vocalization types emitted by the Plush-crested Jay in the recordings analyzed.

Once the model was trained and evaluated, it was applied to the set of recordings obtained with the automated recorders installed in the semi-urban study area. This procedure allowed us to analyze a large volume of continuous recordings automatically. We compiled all detections with an estimated confidence value ≥ 0.85. Because BirdNET Analyzer evaluates recordings in 3 s time windows, each detection corresponds to the presence of a vocalization within that window. In this way, we quantified the number of 3 s windows in which each vocalization type was detected at least once in the recordings analyzed. Finally, detections were aggregated temporally as an hourly average over the nine days, to estimate the frequency of emission of vocalizations per minute of recording. This aggregation also allowed us to explore a possible variation in the emission rate of the different vocalization types throughout the day, considering the time of each recording window.

RESULTS

Qualitative identification of vocalizations and association with behavioral contexts

We made a total of 24 independent focal recordings of Plush-crested Jays from four different groups, distributed as follows: Group 1 (IER): seven recordings; Group 2 (IER–Antayacu): six recordings; Group 3 (semi-urban area): eight recordings; and Group 4 (Proyecto Seamos Bosques): three recordings. We identified seven vocalization types that could be clearly distinguished by their spectro-temporal structure and their auditory similarity (Figs. 2 & 3). These vocalizations were classified with onomatopoeias representative of their characteristic sound: *kekeke*, *kiki*, *kia*, *kiu*, *kua*, *maullido*, and *triple ki* (Figs. 2 & 3). Although we did not obtain enough data to statistically evaluate which behaviors would be associated with each vocalization, our field observations suggest an association between sound and behavior in six different recordings (each with different vocalization types). We recorded two vocalization types (*kiu* and *maullido*; Figs. 2A & 2E) emitted in contexts associated with the presence of raptors and potential predators. The *kiu* vocalization was recorded in the presence of a Barred Forest-Falcon (*Micrastur ruficollis*) at the

Table 1. Summary of the results of the four-fold cross-validation of the recognition model for the vocalization types of the Plush-crested Jay (*Cyanocorax chrysops*). Values correspond to the macro-average of the seven classes (six vocalization types and noise) in each fold. F1 (threshold opt): F1-score at the optimized threshold; AUPRC: area under the precision–recall curve; AUROC: area under the ROC curve. The low F1 values indicate a reduced detection ability with the current volume of training data, so the detections obtained with this model are considered exploratory.

Metric	Fold 1	Fold 2	Fold 3	Fold 4	Mean
F1 (threshold opt)	0.02	0.07	0.11	0.08	0.07
AUPRC	0.63	0.53	0.74	0.68	0.65
AUROC	0.82	0.86	0.91	0.83	0.86

Proyecto Seamos Bosques site, with mobbing behavior toward the individual, as well as of a Collared Forest-Falcon (*Micrastur semitorquatus*) at the IER–Antayacu site, which was vocalizing near where the group of jays was. We also recorded this vocalization when a Roadside Hawk (*Rupornis magnirostris*) at IER flew close to the canopy (approximately 20 m above the ground). In the encounter between the jays and the Roadside Hawk, the *maullido* vocalization was emitted interspersed within the same vocal sequence in which *kiu* was recorded. Regarding movement behavior, the *kekeke* vocalization (which is performed while stationary, but with the body moving up and down emphatically, as if shaking the branch on which the individual is perched; Fig. 2G) appeared in two movement situations, interspersed with the *kiki* vocalization. As for feeding behavior, no clear association was detected between a particular vocalization type and this behavior (although the vocalizations called *kiki* and *kia* were recorded during feeding events; Figs. 2B & 2F). Finally, the analysis of opportunistic recordings and of those from acoustic repositories revealed two vocalizations that suggest possible imitations of raptors. One of them corresponds to an opportunistic recording made in 2023 at Proyecto Seamos Bosques (Tucumán, Argentina; GM), whose vocal structure suggests a possible imitation of the Collared Forest-Falcon (Figs. 2H & 4A). The second corresponds to a recording available on xeno-canto (XC337874) from Misiones province, whose acoustic structure shows similarities with the vocalizations of the Bicolored Hawk (*Astur bicolor*; Figs. 2I & 4B). The Plush-crested Jay's imitation of the Collared Forest-Falcon's song approximates the latter species in its central dimensions, where the measured peak frequency is similar (1266 Hz in the imitation vs. 1125 Hz in the Collared Forest-Falcon's vocalization), and the 90% duration is longer in the imitation (0.31 s vs. 0.26 s, approximately 19% longer). The most marked difference appears in the upper contour (95%), where in the jay's imitation it rises to much higher frequencies (around 4500 Hz), covering a wider and higher-pitched range than the Collared Forest-Falcon's vocalization. As for the imitation of the Bicolored Hawk, the imitation would correspond to only part of a more complete vocalization of the raptor, but when the elements of both

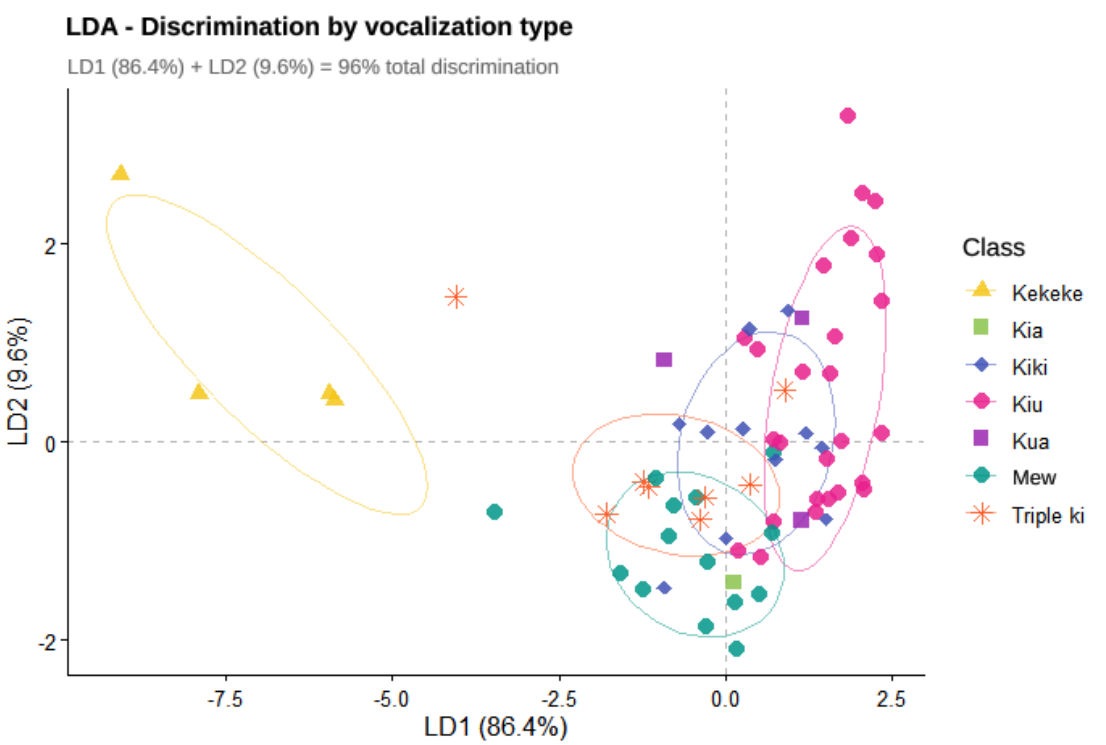


Figure 3. Linear discriminant analysis (LDA) of the vocalization types of the Plush-crested Jay (*Cyanocorax chrysops*), with 24 recordings from Tucumán province from September to November 2025 and 18 recordings from the xeno-canto platform (eight from Jujuy, ten from Salta). The first two discriminant axes (LD1 and LD2) are shown, which together explain 96% of the variance between classes (LD1 = 86.4%; LD2 = 9.6%). Each point represents a vocalization, and colors and symbols indicate the vocalization type (see legend in the plot). Ellipses correspond to 95% confidence intervals assuming a bivariate normal distribution. LD1 was determined mainly by vocalization duration (90% duration); LD2, by the variability of the lower frequency contour (SD contour 5%). Abbreviations: LD = linear discriminant function; SD = standard deviation. The standardized discriminant coefficients of each variable are given in Table 2.

vocalizations are considered separately, both share the same frequency contour pattern (5% and 95%), so that the Plush-crested Jay's imitation reproduces the spectro-temporal shape of the Bicolored Hawk's natural call. The main difference is in frequency level, where the imitation keeps the shape of the contour but at higher frequencies, with a peak approximately 63% higher (3750 Hz vs. 2295 Hz), in addition to a slightly longer 90% duration (0.06 s in the imitation vs. 0.05 s in the raptor's call). This suggests that the Plush-crested Jay emits a sound similar in the shape of the vocalization but has greater difficulty matching and precisely sustaining the frequency of the Bicolored Hawk.

Acoustic variables and quantitative validation of vocalization types

The analysis of our own 24 recordings made for this study and the 18 from xeno-canto from Salta and Jujuy provinces allowed us to classify the following vocalization types, which we associated with the previously identified categories: *kiu* (n = 26), *maullido* (n = 14), *kiki* (n = 11), *triple ki* (n = 8), *kekeke* (n = 4), *kua* (n = 3), *kia* (n = 1; Figs. 2 & 3). The LDA (linear discriminant analysis) discriminated the vocal classes along two main axes that together explained 96% of the discriminant variation (LD1: 86.4%; LD2: 9.6%). In the discriminant space, *kekeke* separated clearly from the rest of the classes along LD1, while the rest of the vocalizations were distributed at positive LD1 values, with a partially overlapping internal structure in which *maullido* occupied the lower region (negative LD2 values), *kiu* extended toward high LD1 and LD2 values, and *kiki* and *triple ki* were in a central position, overlapping with both. The classes with the fewest records (*kia* and *kua*) fell within the dispersion of the majority classes (Fig. 3). The ordination of vocalization types was determined mainly by vocalization duration (90% duration), which was the variable with the greatest weight on LD1 (Table 2), followed by peak frequency and the variability of the lower frequency contour (SD Contour 5%). The second axis (LD2) was associated with the variability of the frequency contours, both lower and upper (Table 2). The global PERMANOVA showed significant differences between the vocalization types analyzed within the multivariate acoustic space ($F_{4,58}$ = 4.14; R^2 = 0.22; p < 0.05; permutations were restricted by the ID of each recording). The test of homogeneity of dispersions (betadisper) was not significant ($F_{4,58}$ = 1.20; p = 0.34), indicating that the results would reflect the separation of the acoustic centroids of each class and not unequal dispersion. Post hoc pairwise comparisons between classes (pairwise PERMANOVA corrected for multiple comparisons using the Benjamini–Hochberg false discovery rate adjustment) revealed that all vocalization types differed significantly from at least one of the other types. The *kekeke* vocalization showed the greatest acoustic differentiation, differing significantly from the other four vocalization types

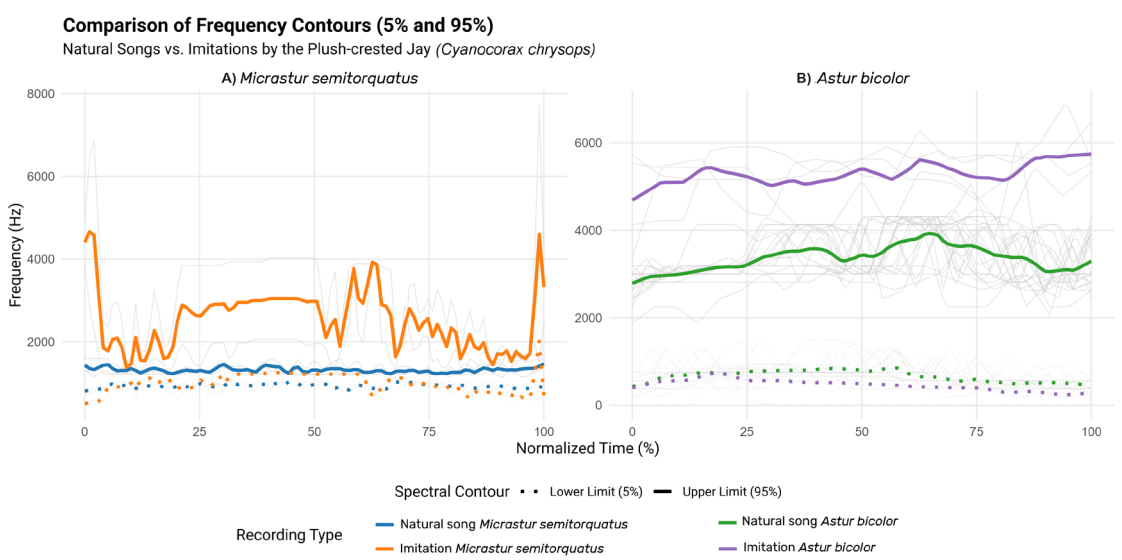


Figure 4. Frequency contours at the 5% (dotted line) and 95% (solid line) levels for vocalizations categorized as imitations of raptors, standardized to 100 time windows. Thin gray lines show the individual contours of each vocalization analyzed; colored lines represent the mean contour of each recording. (A) Light blue shows the natural song of the Collared Forest-Falcon (*Micrastur semitorquatus*), recorded in Concepción department, Tucumán, in February 2024, and orange shows its imitation by the Plush-crested Jay (*Cyanocorax chrysops*). (B) Green shows the natural song of the Bicolored Hawk (*Astur bicolor*), recorded at Proyecto Seamos Bosques in September 2023, and purple shows the imitation by the Plush-crested Jay.

compared (*kiki*, *kiu*, *maullido*, and *triple ki*; all $p < 0.05$; Fig. 3). It was followed by *kiu*, which differed from three vocalization types (*maullido*, *triple ki*, and *kekeke*; $p < 0.05$), then *triple ki* and *maullido*, which differed from two vocalization types (*kekeke* and *kiu*; $p \leq 0.05$). Finally, the *kiki* vocalization type differed significantly only from *kekeke* ($p < 0.05$).

Automatic detection and analysis of temporal patterns of vocal activity

The analysis of 117.3 hours of passive recordings showed that *kekeke* was the most frequently detected vocalization of the Plush-crested Jay, accounting for 63% of the species' detections (det), followed by *kia* and *kiu* (71.8 det/h; $n = 8419$; Fig. 5). The least frequent vocalizations were *kiki* (13.5 det/h; $n = 1583$), *triple ki* (7.7 det/h; $n = 898$), and *maullido* (3.0 det/h; $n = 347$). Together, these last three vocalizations accounted for less than 4% of all detections recorded, while *kekeke* and *kia* accounted for 75% of the total, which would suggest that these two vocalizations make up the core of the vocal repertoire of the group studied during the nine days of recording.

Regarding vocal activity throughout the day, the analysis of automatic detections revealed different patterns depending on the vocalization class (Fig. 6). In general terms, the mean detection rate (black line) remained relatively low and stable throughout the day, with a marked peak during the first sampling hour (~ 05:00 h, ~ 20%), followed by a pronounced decrease toward 06:00–07:00 h (~ 6–7%) and a slight upward trend during the afternoon hours. This general pattern, however, is not reflected in each vocalization class. Specifically, the *kekeke* vocalization (Fig. 2G), potentially associated with movement behavior, was the dominant class throughout the sampling period; it showed its highest detection rate at dawn (05:00 h, ~ 63%), followed by an abrupt drop during the early morning hours (06:00–08:00 h, ~ 13%) and a second sustained increase toward midday and the afternoon (13:00–19:00 h, ~ 25–33%). This bimodal pattern would suggest greater movement activity both at dawn and during the second half of the day. The *kia* vocalization (Fig. 2F) also showed relatively high detection levels at dawn (~ 49% at 05:00 h), with a gradual decrease toward 07:00–08:00 h (~ 13%) and more constant values during the rest of the day (~ 14–16%). Unlike *kekeke*, *kia* did not show a clear second evening peak, but rather moderate and relatively constant activity during the central hours of the day.

The vocalizations that appeared to be associated with alarm contexts, *kiu* and *maullido* (Figs. 2A & 2E; see above in the Results section: Qualitative identification of vocalizations and association with behavioral contexts), had considerably lower detection rates throughout the day. However, *kiu* showed a particular pattern, with two relatively discrete detection peaks around 07:00 h and 18:00–19:00 h, coinciding precisely with the times when other vocalizations, particularly *kekeke* and *kia*, would reach their minimum values or showed a marked decrease in their detection rate. The *maullido* showed even lower values and no clear temporal pattern, which could indicate that its emission responds to specific stimuli rather than to a defined temporal pattern. Finally, *kiki* and *triple ki* (Figs. 2B & 2C) had the lowest detection rates of the set (~ 1–4%), with no evident temporal patterns.

DISCUSSION

In this study, we described and characterized part of the vocal repertoire of the Plush-crested Jay, combining field observations, vocalizations available in repositories, multivariate acoustic analyses, and automatic detection tools applied to passive recordings. With this approach, we identified seven main vocalization types that could be distinguished both by their spectro-temporal structure and by their auditory similarity, and we report potential vocal imitations of raptors. The acoustic analyses showed that these vocalizations occupy differentiated acoustic regions, which supports part of the qualitative classification into discrete categories. We also report possible associations between vocalizations and their role as alarm signals emitted in response to potential predators and group movement behaviors. Finally, the analysis of automatic detections in continuous recordings suggested potential differences in the relative frequency of use and in the activity patterns throughout the day among the different vocalization types, although the performance of the detection model still needs to

Table 2. Standardized coefficients of the linear discriminant analysis of the qualitatively identified vocalization types of the Plush-crested Jay (*Cyanocorax chrysops*) ($n = 67$). The two axes together capture 96% of the discriminant variation between vocalization types.

Variable	LD1	LD2
Peak frequency (Hz)	-0.34	-0.19
Duration (90%)	-2.13	0.54
Frequency (95%)	0.24	-0.03
Frequency (5%)	0.09	0.37
SD Frequency contour 95%	-0.11	0.35
SD Frequency contour 5%	0.33	1.07

be improved to confirm these patterns. Thus, these results suggest that the vocal repertoire of the Plush-crested Jay is composed of acoustically differentiated signals that could play different roles in the social and behavioral dynamics of the species.

Diversity and structure of vocalizations

Vocalizations in corvids can vary depending on the behavioral context or the environment in which they are produced (Kovářová et al. 2025), and they can even vary according to the message to be transmitted, for example, the degree of threat in the case of an alarm vocalization (Hardy 1979, Ellis 2008). In our study, we found at least nine distinguishable vocalization types in the Plush-crested Jay (seven in focal group recordings and two potential imitations from repositories and opportunistic recordings from previous years) and, although we recognize that this is only a small portion of the probable repertoire, our findings are consistent with what has been reported for the family Corvidae. In particular, we found vocalizations linked to group movement, such as those that occurred in the morning and afternoon to initiate movement. In addition, there were vocalizations that we could not associate with a clear behavioral pattern but that could be associated, for example, with group territorial defense, as has been described in the Steller's Jay (*Cyanocitta stelleri*; Harvey et al. 2024). Finally, there were those linked to the presence of predators, to alert other individuals. It has been described for the White-throated Magpie-Jay (*Cyanocorax formosus*) that the duration of the vocalization and the rate at which it is produced vary according to the level of threat. The relationship described indicates that the greater the degree of threat, the shorter the calls and the higher their rate (Ellis 2008). Although we did not evaluate the intensity of the response in our study, since it belongs to the same genus, we believe it is plausible that this behavior may also be found in the Plush-crested Jay. At the same time, at our study sites and during our limited study period, we did not find courtship or nesting situations that would have allowed us to evaluate vocalizations linked to the individual defense of the nest or territory. However, in the genus *Cyanocorax*, vocalizations that elicit responses from males when females are fertile have been described (Ellis 2009), so it would be important to look for reproductive events and study the vocalizations of the Plush-crested Jay at these times. Finally, in the genus *Cyanocorax*, vocal variation has been documented at the individual, group, and even geographic levels (Hardy 1979, Rosa & Dos Anjos 2022). In this regard, our findings do not allow us to

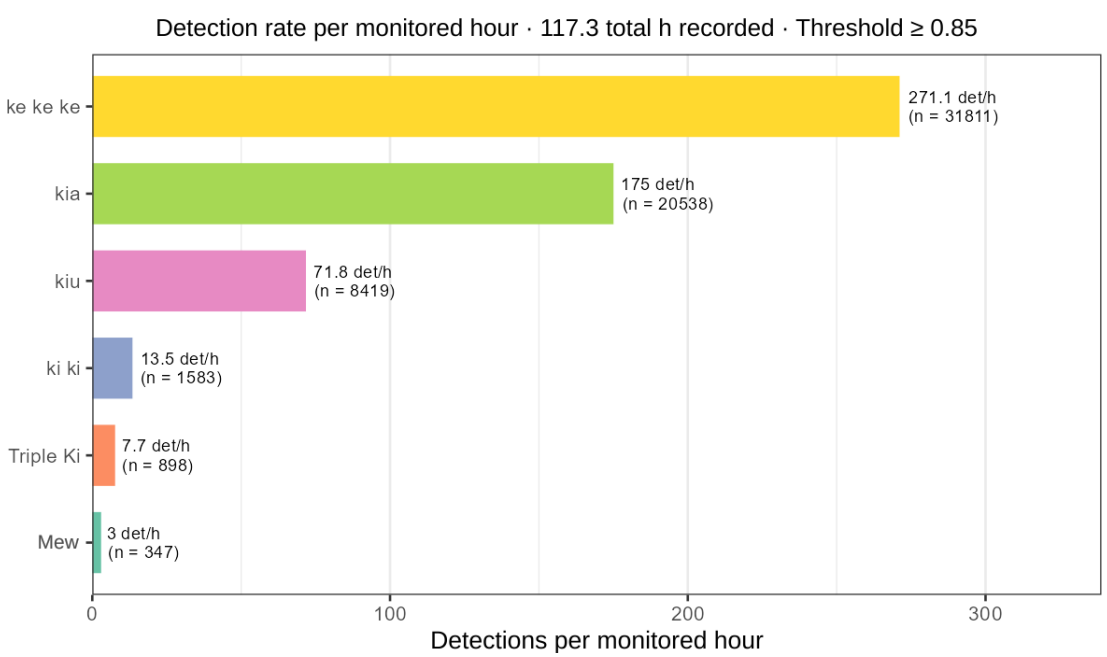


Figure 5. Detection rate per monitoring hour of each vocalization type of the Plush-crested Jay (*Cyanocorax chrysops*), obtained by automatic detection from passive recordings at the semi-urban site, Tucumán, during 3–11 October 2025 with a SongMeter Mini passive recorder. Detections were generated with BirdNET Analyzer, keeping only those with a confidence value ≥ 0.85. Bars indicate the number of detections per monitored hour (det/h) and, in parentheses, the total number of detections (*n*) accumulated over a total of 117.3 h of recording. Detections may include false positives; therefore, relative frequencies should be interpreted as exploratory.

evaluate differences between groups and individuals, but in the future, the analysis of daily vocal patterns in different groups could provide additional evidence to better understand the origin and magnitude of this variability.

Automatic detections and vocal activity pattern

The study of the vocal activity of birds is key to understanding their biology, as well as to contributing to their conservation and to the development of management strategies (Baldo & Mennill 2011, Lavariega et al. 2019, Pérez-Granados & Schuchmann 2021). In this exploratory and descriptive study, we identified different potential patterns of vocal activity throughout the day depending on the vocalization class recorded, which would suggest that vocalizations reflect different behavioral contexts. In particular, the *kekeke* vocalization, which we were able to associate with movement, showed a marked peak during the early morning hours, followed by a decrease toward midday, which could reflect rhythms of movement and rest of the species throughout the day. On the other hand, the *kiu* vocalization, linked to alarm contexts in response to predators, showed a bimodal pattern, with greater emission at both dawn and dusk. This pattern could coincide with times of greater activity of potential predators, such as crepuscular raptors (e.g., Collared Forest-Falcon; Bierregaard et al. 2020) or some owl species (Enríquez 2015). Although bird species have activity peaks at dawn and dusk, our results show that this pattern does not appear equally across all vocalization types, reinforcing the idea of a specific relationship between vocalization type and the temporal pattern of vocalization. In social species, complexity in vocal emission patterns is especially relevant, since the function of vocalizations goes beyond the classic roles associated with territoriality and reproduction (Kroodsma & Byers 1991). Thus, in gregarious species, vocalizations can serve functions linked to group cohesion, coordination of movements, and recognition between individuals, including the identification of group members and of strangers. For this reason, interpreting patterns of vocal activity involves considering both the competitive interactions and the cooperative dynamics that structure social life in gregarious species. Moreover, the study of vocal activity is a valuable tool for exploring the behavioral ecology of social species such as the Plush-crested Jay.

Although we consider that the general patterns of relative use and temporal variation of vocalizations captured at the aggregate level are informative and are based on a large volume of data and on the application of high-confidence thresholds, our results should be interpreted in the context of certain limitations, and the detections made with the model we trained using BirdNET should be considered exploratory. On the one hand, the limitations are associated with the low

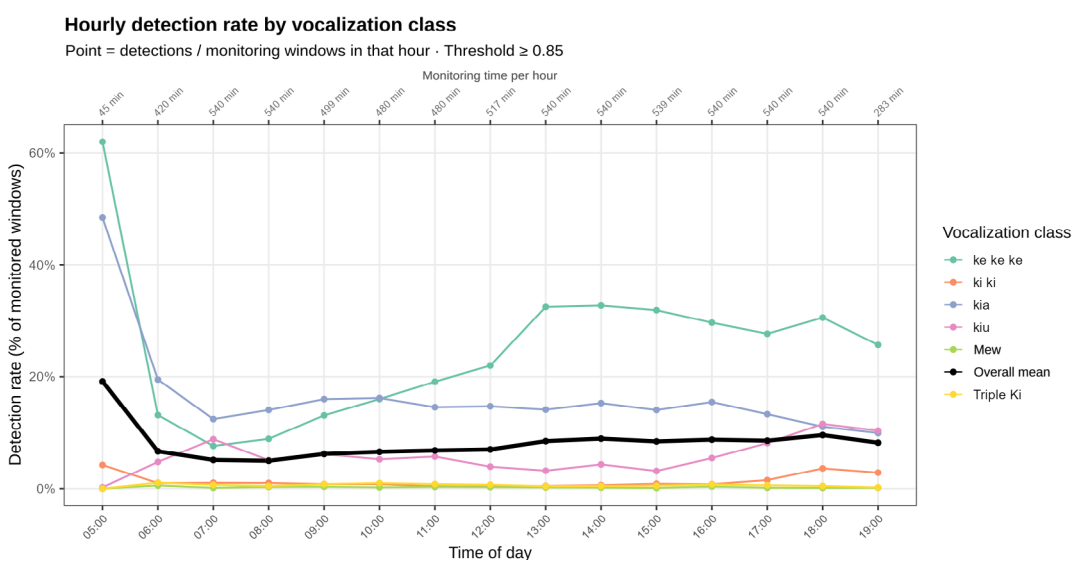


Figure 6. Vocal activity of the Plush-crested Jay (*Cyanocorax chrysops*) throughout the day according to the type of vocalization identified from passive recordings obtained in the semi-urban area, Tucumán, during 3 to 11 October 2025. *Y*-axis values were calculated from the total number of possible detection windows (3 s) and represent the percentage of time windows in which each vocalization class was detected relative to the windows in which the species was detected. Detections should be considered exploratory until confirmed with a better-performing model. The black line represents the overall mean acoustic activity of the species during the recording period.

number of replicates at the spatial and group scale and with the possible presence of false positives, since we did not validate all detections manually. On the other hand, the study focused on a single group (semi-urban area), during a limited period (nine days), and mainly during the breeding season in northwestern Argentina (Auer et al. 2007), and we did not include climatic factors in our analyses. In addition, variation in vocalizations has been documented at both the intraspecific and regional levels in birds (Medina & Francis 2012, García et al. 2014), and even within the genus *Cyanocorax* (Rosa & Dos Anjos 2022), so the patterns observed can be expected to vary compared with other groups of jays. Nevertheless, these results constitute a first quantitative description of the vocal activity of the Plush-crested Jay and a replicable methodological basis for future studies with greater temporal and spatial coverage. Consequently, future studies that incorporate a larger number of groups, broader seasonal coverage, and a more complete characterization of the vocal repertoire with larger training volumes will allow a deeper understanding of these patterns. Finally, this work adds to a growing body of studies (e.g., Pérez-Granados & Schuchmann 2021) that highlight the potential of passive recording tools and automated analysis to generate continuous data and provide new perspectives on the study of the acoustic ecology of birds.

Possible cases of mimicry

In the family Corvidae, at least 39 species have been described that imitate vocalizations of at least 13 different bird genera, including raptors (Wascher et al. 2025). This value, equivalent to 30% of the species in the family, contrasts with the prevalence of this trait in the suborder Passeri as a whole (8.9%), suggesting a particularly marked presence of vocal mimicry in corvids (Goller & Shizuka 2018, Wascher et al. 2025). Our study reveals at least two potential imitations by the Plush-crested Jay, which we compared with natural vocalizations: the imitation of the Collared Forest-Falcon and that of the Bicolored Hawk, the imitation of the Collared Forest-Falcon having already been described in Brazil by Martos-Martins & Donatelli (2018).

Although the imitation of potential (and potentially known) predators is not currently considered to have a single specific function, there are different hypotheses about its role in different contexts. On the one hand, Harvey et al. (2024) suggest that mimicry could be more related to social activities than to the presence of a predator, becoming more frequent during the breeding season, and that it could be associated with nest defense or warning the partner. In this sense, predator mimicry could also be linked to mate searching, under the assumption that an individual able to perform them accurately has the ability to recreate heterospecific sounds and a high cognitive level, and is therefore considered a better potential mate (Taylor 2014). On the other hand, in other species of the genus *Cyanocorax*, it has been suggested that the imitation of raptors is used as a deception mechanism to deter other species and steal food. This has been mentioned for the White-naped Jay (*C. cyanopogon*), which emits imitations of the Roadside Hawk toward primates (Barbosa da Silva 2020), and for the Green Jay (*Cyanocorax yncas*) imitating an accipitrid to deter Plain Chachalaca (*Ortalis vetula*; Giese & Hall 2024). In our study, the alarm signal that appeared in the three encounters with different predators was the vocalization we called *kiu*; we did not observe a link between the species imitated and the raptor present (e.g., when we recorded a Collared Forest-Falcon near the IER–Antayacu group). This would suggest that raptor imitations could also be emitted as a deception mechanism and, taken together, that the vocalizations of potential predators are not learned by mistake but have an adaptive evolutionary function (Wascher et al. 2025).

CONCLUSION

Our study provides new details on vocal communication in the Plush-crested Jay, showing that the species has a structure of acoustically distinguishable vocalizations associated with behavioral situations, and that the use of certain vocalizations would be distributed differentially throughout the day. The detection of possible imitations of raptors adds to the recognized vocal plasticity of the family Corvidae; although the function of these imitations is still debated, their presence in the Plush-crested Jay raises questions about their possible role in social interactions, territory defense, or deception strategies that remain to be evaluated. In this context, our results highlight the Plush-crested Jay as a model gregarious species for exploring the link between communication and cognition. Finally, we highlight the need for future studies that evaluate a larger number of vocalization types, integrate experimental approaches, and continue recording the species in order to train a more complete model with more vocalization types and in different seasons of the year.

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USE OF ARTIFICIAL INTELLIGENCE

Grammarly was used for spelling, grammar, and style review of the text. In addition, Gemini was used for assistance with and debugging of the R script used to produce the contour plots comparing natural vocalizations and imitations. All suggestions generated by these tools were reviewed, evaluated, and validated by the authors.

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