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Dawn chorus succession in a lowland rainforest of Papua New Guinea

Master's thesis

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Annotations

This thesis examines the patterns and ecological significance of bird vocalizations during the dawn chorus in the rainforests of Papua New Guinea. Specifically, it aims to identify the species involved, analyze their songs, and understand the influence of environmental factors. To accomplish this, the study employs a combination of field recordings, phylogenetic analysis, and statistical methods to elucidate the complex interactions between avian species and their habitats. The findings of this study contribute to the broader understanding of biodiversity and ecosystem dynamics in tropical rainforests.

Declaration

I declare that I am the author of this qualification thesis and that in writing it, I have used the sources and literature displayed in the list of used sources only.

České Budějovice,

Date: 07.12.2023

Sofía Medellín B.

Sofía Medellín-Becerra

Table of Contents

<i>1. Introduction</i>	1
<i>2. Methods</i>	5
<i>2.1 Study area</i>	5
<i>2.2 Audio Analysis</i>	5
<i>2.3 Dawn Chorus at civil twilight</i>	7
<i>2.4 Phylogenetic analysis</i>	7
<i>2.5.1 Chi-Squared</i>	7
<i>2.5.2 Mixed Linear Model</i>	8
<i>3. Results</i>	9
<i>3.2 Vocal activity patterns</i>	11
<i>3.3 Vocal activity distribution by order</i>	12
<i>3.4 Vocal activity distribution by habitat</i>	14
<i>3.5 Vocal activity distribution by feeding guild</i>	16
<i>4. Discussion</i>	18
<i>4.1 Vocal Activity Patterns</i>	18
<i>4.2 Taxonomical Order</i>	19
<i>4.3 Habitat</i>	20
<i>4.4 Feeding Guild</i>	20
<i>4.5 Weight</i>	20
<i>5. Conclusions</i>	21
<i>6. References</i>	22
<i>Appendix</i>	27
<i>Phylogenetic tree of birds</i>	28
<i>Figure 7 Phylogenetic tree of the species singing during the dawn chorus.</i>	29

List of figures

- Figure 1.** Map of Papua New Guinea and the four study sites in Madang Province6
- Figure 2** Horizontal bar plots showing the frequency of different study sites, avian orders, habitats, and feeding guilds in the dataset, using the 'magma' palette. Each plot is sorted in descending order of frequency..... 10
- Figure 3** Ridge plot representing the most common activity time for each species in relation to the civil twilight adjusted for each day in minutes. The width of each ridge indicates the variability or spread of the activity times. Narrow ridges suggest that the activity time for that species is very consistent, while wider ridges indicate more variability. The order of the succession is given in descending order for each species 12
- Figure 4** Violin plot indicating the distribution of the counts or observations by order, Cuculiformes with a mean of 22.0 minutes; Passeriformes with a mean of 15.0 minutes; Psittaciformes with a mean of -60.0 minutes; Coraciiformes with a mean of 15.2 minutes; Columbiformes with a mean of 47.8 minutes..... 13
- Figure 5** Violin plot indicating the distribution of the counts or observations by habitat. It displays the bird's habitat as canopy, with a mean of 21.8 minutes; understory with a mean of 12.0 minutes; and Both (often observed in canopy and understory) with a mean of 12.0 minutes..... 15
- Figure 6** Violin plot indicating the distribution of the counts or observations by Feeding guild. It displays the bird's feeding guild as frugivore with a mean of 74.9 minutes; frugivore/insectivore, with a mean of -0.05 minutes; herbivore, with a mean of 63.0 minutes; insectivore, with a mean of 16 minutes and insectivore/nectivore, with a mean of 74.9 minutes..... 17
- Figure 7** Phylogenetic tree of the species singing during the dawn chorus.29
- Figure 8** Photographs of the listed birds A. *Cacatua galerita*, B. *Microdynamis parva*, C. *Chrysococcyx minutillus*, D. *Cacomantis variolosus*, E. *Ceyx Lepidus*, F. *Melidora macrorrhina*, G. *Tanyptera galatea*, H. *Ptilinopus magnificus*, I. *Ducula pinon*, J. *Ducula*

zoeae, K. *Toxorhamphus novaeguineae*, L. *Mino dumontii*, M. *Poecilodryas hypoleuca*, N. *Xanthothis flaviventer*, O. *Philemon meyeri*, P. *Philemon novaeguineae*, Q. *Pachycephala simplex*, R. *Monarcha chrysomela*, S. *Pitohui kirhocephalus*, T. *Rhipidura rufiventris*, U. *Ptilorrhoa caerulescens*, V. *Ptilorrhoa leucosticta*. All pictures were taken by Katerina Sam and downloaded from the website <https://pngbirds.myspecies.info>.30

List of tables

Table 1 Estimated marginal means (Emmeans) for the orders Columbiformes, Coraciiformes, Cuculiformes, and Passeriformes, along with their standard errors (SE), degrees of freedom (df), and 95% confidence intervals (lower.CL, upper CL)	14
Table 2 Estimated marginal means (Emmeans) for the habitats Canopy, Understory and Both, along with their standard errors (SE), degrees of freedom (df), and 95% confidence intervals (lower.CL, upper CL).....	16
Table 3 Estimated marginal means (Emmeans) for the feeding guilds Frugivore, Insectivore and Frugivore/Insectivore, along with their standard errors (SE), degrees of freedom (df), and 95% confidence intervals (lower.CL, upper CL).....	18
Table 4 Values of the Mixed Linear Model using species as the intercept and random effect. The standardized weight, feeding guild, habitat and order were used as fixed effects.....	27
Table 5 Chi-Squared tests for the categorical variables taxonomical order, habitat, feeding guild and species.	28

1. Introduction

The dawn chorus is an intricate acoustic phenomenon in birds, most notably among passerines, although not exclusive to this order (Kroodsma, 1976; McNeil et al., 2005). This synchronized song performance plays diverse roles in avian behavior and ecology, serving functions from territorial defense to mate attraction (Moran et al., 2019; Kunc et al., 2005). Among the various hypotheses that have been proposed to explain the dawn chorus, I focus on three that are particularly relevant to the scope of this thesis because of their empirical support and explanatory power across multiple bird species and habitats.

First, the acoustic transmission hypothesis relies on the well-documented atmospheric conditions of early morning, which are known to enhance sound propagation, making them a biologically plausible explanation for the timing of the chorus (Henwood & Fabrick, 1979; Brenowitz, 1982). Secondly, the stochastic energy storage hypothesis proposes that the participation of birds in the dawn chorus is determined by the variability of their energy reserves at dawn (Hutchinson, 2002). This hypothesis emphasizes the connection between physiological state and behavioral expression in birds. It states that birds with sufficient energy reserves are capable of engaging in the energetically demanding singing task, which fulfills important functions in territorial defense and mate attraction. On the other hand, birds with limited energy reserves may refrain from participating in the chorus to prioritize foraging. This illustrates the adaptive strategies that birds use to manage their energy resources depending on their ecological and social context. (Staicer et al., 1996). Lastly, the foraging efficiency hypothesis proposes that the onset of the dawn chorus is influenced by the ambient light levels at dawn, which are typically insufficient for effective foraging. In the early morning light, birds encounter difficulties in visually locating and capturing their food, resulting in less efficient foraging. Consequently, birds may engage in alternative beneficial activities, such as singing, during this time (Kacelnick, 1979). The low light conditions at dawn also play a role in predation risk. Predators are less active at this time, which reduces the risk to birds when they engage in conspicuous behaviours such as singing. The dawn would be a safer time for birds to sing loudly and extensively. According to the hypothesis, as light levels increase and foraging becomes more efficient and less risky, birds shift their focus from singing to foraging (Berg et al., 2006). Taken together, these hypotheses provide a multifaceted view, integrating physical, physiological, and ecological perspectives that are

most relevant to understanding the complex phenomenon of the dawn chorus within the context of this thesis.

Intersexual interactions, such as self-advertisement and mate stimulation, are some of the functions of these vocalizations as they promote the mating process (Otter and Ratcliffe, 1993; Welling et al., 1995). These song-mediated interactions facilitate imperative ecological behaviors such as social communication, territory acquisition, and defense against conspecifics (Foote et al., 2008). The dawn chorus also functions as an indicator of habitat quality and species diversity in avian ecology (Marler et al. 1992) and serves as an early anti-predator warning system when birds alter their chorus in response to potential threats (Blumstein et al., 2011). Moreover, a recent study highlighted that the occurrence of dawn and dusk choruses can be influenced by the dynamics of male-female interactions, particularly in relation to the absence of the mate, adding a new dimension to our understanding of this complex vocal behavior (Schlicht et al., 2023).

Several determinants interact and modulate the intensity, timing, and composition of the dawn chorus. Abiotic factors, particularly the timing of sunrise, influence the dawn chorus, with birds initiating their vocalizations earlier as the time of sunrise shifts to an earlier hour (Brown 1962). The presence of both sunlight and moonlight serves as a trigger to initiate the dawn chorus (Leopold and Eynon 1961). For instance, cooler temperatures and increased humidity can suppress bird activity by impeding foraging and movement (Avery and Krebs 1984). Under these conditions, the activity of both nocturnal and diurnal predators is also reduced (Henwood and Fabrick 1979, Cuthill and Macdonald, 1990). This decrease in predator activity lowers the risk associated with vocal displays during the dawn chorus, which could otherwise reveal a bird's location (Cuthill and Macdonald, 1990). Additionally, the acoustic attributes of the early morning environment, generally characterized by lower wind speed and less background noise, are favorable for sound propagation, allowing vocalizations to maintain their intensity over greater distances (Dabelsteen and Mathevon, 2002; Brown and Handford, 2003). Environmental factors, such as cloud cover, time of year, seasonality and precipitation can delay or affect the onset of the dawn chorus (Allen 1913; Davis 1958; Slagsvold 1977; Thomas 1999; Thomas et al. 2002; Miller 2006; Hasan, 2010).

The timing of the dawn chorus is also influenced by a number of social and individual factors. The social benefits of singing in the early morning apply to a wide range of species

(Staicer et al., 1996). One of these benefits is that dawn songs are used to attract mates and strengthen bonds (Cachpole & Slater, 2008). Another example is social cohesion for species living in groups, where the dawn chorus indicates the location and status of group members (Berg et al 2006). Intrinsic factors, that are both structural (eye size) and time dependent (reproductive stage), also affect the timing of the dawn chorus within and between species (Mace 1987; Berg et al. 2006).

These favorable acoustic conditions must be weighed against the limited visibility at dawn, which hinders typical diurnal activities, such as foraging and visual communication (Kacelnik, 1979; Amrhein and Erne, 2006). However, this dim light environment is exploited by birds with anatomical adaptations, i.e., larger eyes, enabling them to engage earlier in the dawn chorus while maintaining some degree of visual awareness of their surroundings (Thomas et al., 2002; McNeil et al., 2005). Although larger eyes provide advantages under low-light conditions, they also come at a cost. These include increased aerodynamic and energetic costs during flight, as carrying a larger payload requires more energy (Laughlin, 1995). Additionally, maintaining numerous nerve cells in a larger eye requires substantial energy (Laughlin et al., 1998). Furthermore, larger eyes are more susceptible to damage that could affect the long-term survival of a bird (Harper, 1988). Consequently, the size of a bird's eye reflects a balance between the benefits and costs associated with visual adaptations, shaped by its ecological niche and foraging strategy (Motani et al. 1999; Land & Nilsson 2002). Although several studies have explored the relationships between eye size, brain size, body size, and feeding strategies in birds (Brooke et al., 1999; Garamszegi et al., 2002; Rojas et al. 1999), there is still a need for comprehensive analyses across bird species. Such analyses using modern phylogenetic comparative methods (Berg et al, 2006; Chen et al., 2015) can provide deeper insights into how visual adaptations have evolved in response to specific ecological demands.

The dawn chorus has been extensively studied in different geographical contexts. In temperate regions, research has primarily focused on the oscine radiation of passerine birds, with studies highlighting factors such as atmospheric conditions favorable to sound transmission at dawn and the role of vocal communication in territory defense (Henwood & Fabrick, 1979; Thomas et al., 2002). In the Neotropics, the dawn chorus is characterized by a greater diversity of participating species, including a substantial number of suboscine and non-passerine taxa. The study by Berg et al. (2006) in the Neotropical forests of Ecuador, for

instance, provides insights into the phylogenetic and ecological determinants of the dawn chorus, emphasizing the role of foraging strata and light levels in determining the timing and participation of various bird species. This research highlights that while some mechanisms driving the dawn chorus are universally applicable across regions, such as the inefficient foraging hypothesis, the ecological and evolutionary nuances of different biomes play a critical role in shaping these complex vocal behaviors.

The habitat in which birds reside has a significant influence on the manifestation and structure of the dawn chorus. Forested environments with their stratified layers and varying foliage density lead to a complex gradient of light conditions (Berg et al., 2006). This layered structure results in varying light penetration that affect birds' behavioral responses in the early morning hours. For instance, birds that perched higher in the canopy, or opted for elevated singing perches, tended to have higher light availability than their conspecifics in the lower layers (Hunter, 1980; Barker and Mennill, 2009). The preference by many birds for higher perches, especially those foraging in lower layers or even on the forest floor, may be attributed to the better advantage point and lower risk of predation. The foraging height and diet may also play a role in determining the timing of the dawn chorus. Observations in East Asian mountain forests have shown that bird species that forage in lower layers of the forest tend to begin singing earlier than those inhabiting the upper layers (Chen et al., 2015). This suggests that the foraging height and diet of avian species can have a significant impact on the timing of the dawn chorus.

Research on the neotropics have included eye size, body mass, foraging height, and phylogenetic independent contrasts to understand their role in the timing of the dawn chorus. It was found that, while both eye size and foraging height play a primary role in determining the time of the dawn chorus, other ecological factors such as phylogenetic lineage and morphological traits play a secondary role and should be taken into account to understand this behavior more thoroughly (Berg et al., 2006).

Previous research conducted in Papua New Guinea investigated the feeding guild of birds and their body weight in relation to an elevational gradient, discovering a significant decrease in the mean body weight of insectivorous bird species at higher elevations (Sam et al., 2017). These results highlight the complex relationship between environmental factors such as altitude and key biological characteristics such as body size in birds. Although studies

examining the connection between body size and feeding guild have been conducted in this region, specific aspects of the dawn chorus have not been extensively studied in relation to these variables. This presents an opportunity for further research to explore how factors such as body size and feeding guild may influence avian vocal behavior during the dawn chorus.

This thesis aims to understand the intricate patterns of dawn chorus succession within an avian community in Papua New Guinea. It seeks to address the factors that could influence the timing of songs among various species based on ecological, morphological, and phylogenetic variables.

2. Methods

2.1 Study area

The research site at Baitabag, nestled in the lowlands of Madang Province in Papua New Guinea, is a mid-sized fragment of primary forest stretching over 600 ha. Situated at coordinates (5° 8' 36.6" S – 145° 34' 23.52" E), with an elevation of 100 m asl amidst a landscape that has been increasingly shaped by human activities since the 1980s. The mosaic of primary and secondary forests that once surrounded local villages has been transformed into a landscape intensively managed for slash-and-burn agriculture, with young secondary forests rising from abandoned gardens alongside deforested village settlements and plantations. These areas are still predominantly covered by continuous forests, although they are facing increasing logging pressures. The climate of Baitabag is characterized by humidity and a notable, albeit mild, dry season from July to September. The average annual rainfall is approximately 3600 mm. The forest features closed canopies with an average height of approximately 35 meters and an open understory, lacking distinct stratification, which is a typical feature of the region's forested landscapes (Sam, 2014).

2.2 Audio Analysis

One AudioMoth recorder was placed in the primary lowland forest in Baitabag, Papua New Guinea (5° 8' 36.6" S – 145° 34' 23.52" E) (**Figure 1**). The recorder was placed inside a plastic bag 1.50 m above the ground, configured with a sample rate of 44 kHz, and recorded in WAV format. The AudioMoth device was set to record three minutes (180 s) every 10 minutes (600 s) all day for a month in April and May 2022 (end of the rainy season), recording a total of 32 days at four different study sites separated by 1.0 km. The recorder

was reallocated to a new site every 7 days. The data from the 3rd study site, as well as two days from the 4th study site, was not used because it continuously rained during the recording period. The recordings were visually analyzed using Raven Pro. 1.5.0. software (Bioacoustics Research Program, Cornell Lab of Ornithology, 2017) and the package “seewave” (Sueur et al. 2008) to visually compare different vocalizations in R 4.0.2. (R. Core Team, 2021). All recordings were analyzed with a Hamming window and a Fast Fourier Transformation (FFT) length of 1024 and 95% overlap. Xeno-canto <www.xeno-canto.org> was used to download and identify the songs of the expected species based on point counts from previous studies and only songs were considered, discarding calls. Each song was isolated and identified manually; they were compared with the songs already reported in xeno-canto for that site, and their ID was again confirmed by experts. Annotations of each individual song were made in Raven for each species and each study site manually for the entire day and sampling period.

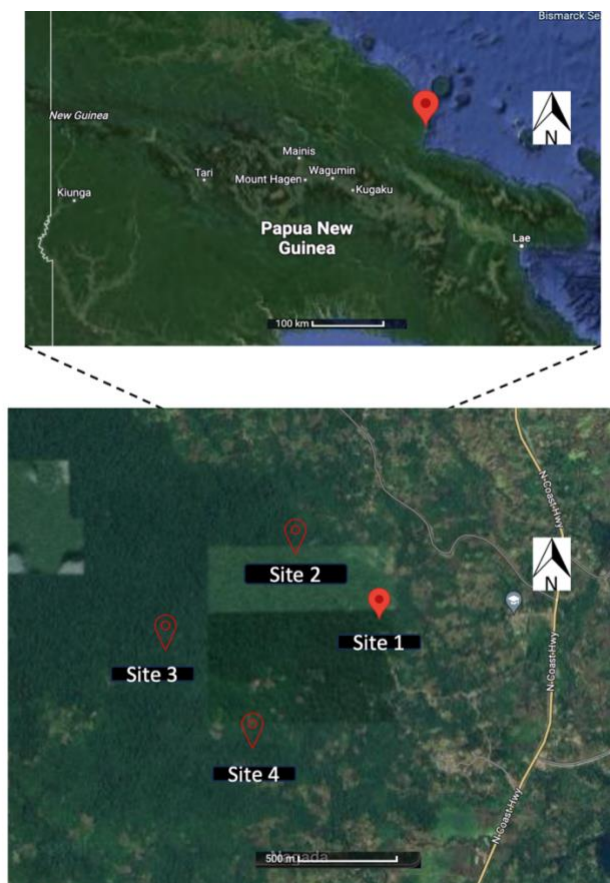


Figure 1. Map of Papua New Guinea and the four study sites in Baitabag.

2.3 Dawn Chorus at civil twilight

The civil twilight is a period of time that occurs after sunset or before sunrise, during which the sky is partially illuminated, allowing for outdoor activities to take place without the need for additional lighting. The onset of civil twilight is signaled by the sun being approximately 6 degrees below the horizon, as measured from its geometric center. This period comes to an end as the sun rises in the morning or sets in the evening. To study dawn chorus succession, only the morning hours were filtered from the recordings. The exact hours of the civil twilight were obtained from <https://www.timeanddate.com>, the time of the civil twilight in the first day was at 5:57 and the time for the last day was 5:54. Each observation was corrected as [Observation time – Civil Twilight] to obtain the number of minutes before, during, and after the civil twilight, a song was recorded.

2.4 Phylogenetic analysis

After downloading the ND2 DNA sequences of all focal species from NCBI (as FASTA files), a multispecies alignment was obtained using MAFFT (Katoh & Standley, 2013) (with 1000 replicates of the Maxiterate algorithm. The alignment was then checked in Geneious Prime (Kearse et al., 2012) for potential errors and exported as a PHYLIP file. Finally, we used IQTREE2 (Minh et al., 2020) for phylogenetic inference with 1000 ultra-fast bootstrap iterations and the bnni option for optimization of the UltraFast Bootstrap (Hoang et al., 2017), alrt correction, and MFP option for extended model selection.

2.5 Statistical analysis

2.5.1 Chi-Squared

In this study, the chi-square (χ^2) test was employed as a statistical tool to examine the association between categorical variables, specifically feeding guild, phylogenetic order, species, and habitat. The Chi-Squared test is a non-parametric method used to determine whether there is a statistically significant difference in the frequency distribution of categories across different groups. This test computes the sum of the squared differences between the observed (O) and expected (E) frequencies, divided by the expected frequencies, across all categories of each variable. The formula for the test statistic is $\chi^2 = \sum [(O - E)^2/E]$,

where Σ denotes the summation over all categories. A higher χ^2 value indicated a greater disparity between the observed and expected frequencies, suggesting a potential association between the variables. The significance of the χ^2 statistic was assessed against a chi-squared distribution, with degrees of freedom calculated as $(\text{number of rows} - 1) \times (\text{number of columns} - 1)$. A p-value is then derived, which indicates the probability of observing a χ^2 value as extreme as or more extreme than the one calculated if the null hypothesis of independence is true. This test allows for effective analysis of the distribution patterns and associations among species and ecological factors.

2.5.2 Mixed Linear Model

Linear Mixed-Effects Models (LMMs), or hierarchical linear models, incorporate both fixed and random effects (Pinheiro and Bates 2000). In this study, a LMM was employed to analyze the relationship between the time of singing during the dawn chorus (dependent variable) and various ecological variables. The package, ‘lme4’ (Bates et al., 2015) was used to create and analyze the model and ‘ggplot2’ (Wickman, 2016) to visualize the data. Each observation was defined as an individual song per species displayed before or after the civil twilight (150) in minutes and annotated alongside their respective time and date. The fixed effects in this model included several key ecological factors: Weight (centered and measured in grams, using an average per species), Habitat (categorized as Canopy, Understory, and Both), Feeding Guild (categorized as Frugivore, Insectivore, and Both), and Taxonomical Order (Passeriformes, Columbiformes, Coraciiformes, and Cuculiformes).

These fixed effects estimate common relationships shared across the entire dataset, capturing the average influence of these ecological variables on the timing of species activity. In contrast, the random effects in this model were captured through the intercept, which was modeled for Species. This approach allowed us to account for the intrinsic differences among species that might influence their singing behavior relative to civil twilight. By treating Species as a random intercept, we acknowledged that each species might have a unique baseline level of the dependent variable. These models are particularly useful for analyzing data that exhibit correlations and nonconstant variability (Galecki and Burzykowski, 2013), and are prevalent in many ecological studies where the assumptions of independence among observations are not met. By adopting LMMs in this study, it was possible to gain more accurate and interpretable insights into the effects of different ecological factors on the timing

of species activity relative to civil twilight, thereby enriching our understanding of ecological processes and relationships.

The Estimated Marginal Means (EMMs) method was used for this study using the package in R 'emmeans' (Lenth, 2023). This method is commonly utilized in the context of linear models, to conduct post-hoc pairwise comparisons. This approach was particularly critical for assessing the mean response levels across different factors, such as habitat types, avian orders, and feeding guilds, while controlling for other variables in the model. To discern specific differences between group levels, a Tukey honest significant difference test was integrated with the EMMs. This combination allowed for a robust analysis of the interaction effects and pairwise comparisons, ensuring that the observed differences in means were not only statistically significant but also accounted for multiple testing to control the type I error rate. The use of EMMs, therefore, provided a nuanced understanding of how habitat, order, and feeding guild contribute to the observed patterns in the data, highlighting the ecological and behavioral nuances among the bird species studied.

3. Results

3.1 Exploratory data analysis of the avian community

Distinct patterns were observed in the distribution of the study sites, avian orders, habitats, and feeding guilds (**Figure 2**). In the Study Site category, 'site_1' emerges as the most frequently sampled location, accounting for 917 observations. In contrast, 'site_4' is the least represented, with only 249 observations, likely due to filtering the data after it rained for two days. For the same reason the third study site could not be included at all. Regarding avian orders, Passeriformes stood out as the most prevalent, with 1054 records. This prominence may reflect ecological dominance or broader geographical distribution. On the other hand, Psittaciformes is the least common order, represented by only 15 observations and only one species singing, *Cacatua galerita*. Regarding the habitat, the understory represents the majority of observations, comprising 853 entries. The category 'Both,' indicating understory and canopy habitat type is least observed, with 217 entries.

Lastly, in the feeding guild category, insectivores were the most common with 992 instances. The least represented guild was herbivore, with only 16 instances, reflecting a more

specialized diet for *Cacatua galerita*, highlighting it as an outlier species in different variables. These findings show the diverse distribution, habitat preference, and feeding behavior of avian species in the study sites, providing insights into ecological dynamics and resource utilization across different bird groups. These patterns suggest that ecological adaptation to diet and habitat plays a significant role in determining the distribution and abundance of avian species in a given area.

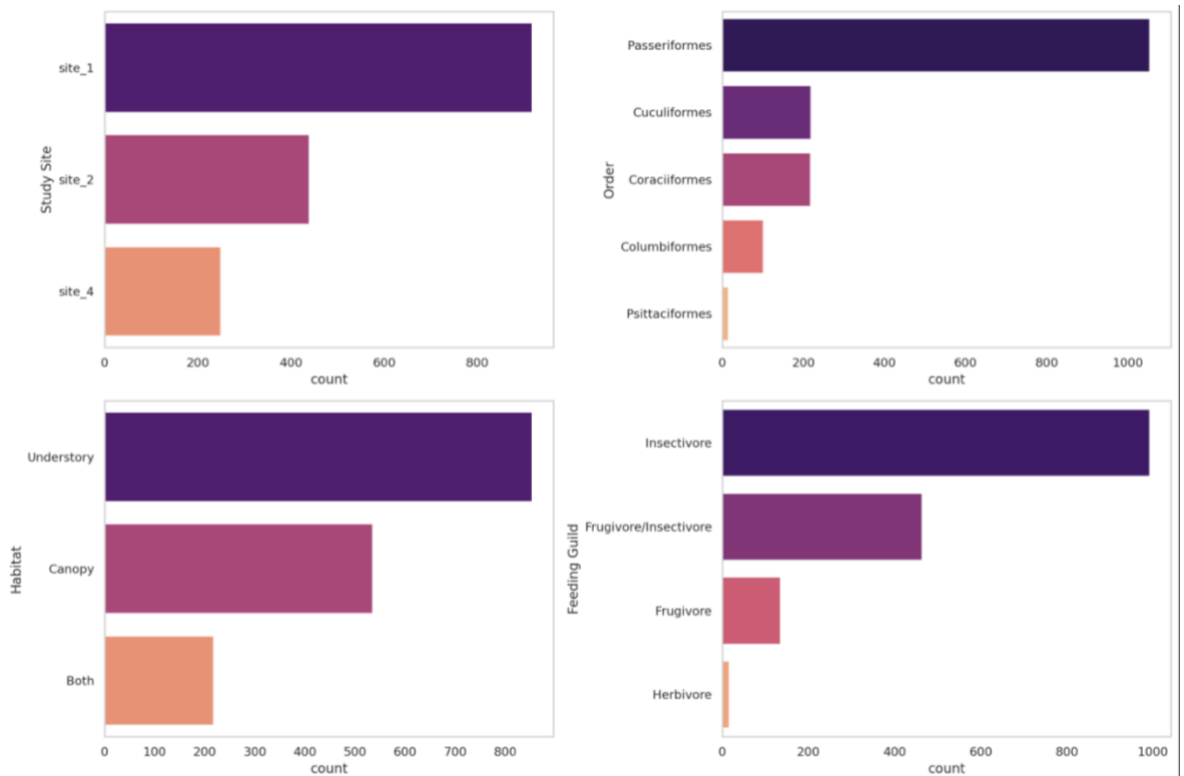


Figure 2 Horizontal bar plots showing the frequency of different study sites, avian orders, habitats, and feeding guilds in the dataset, using the 'magma' palette. Each plot is sorted in descending order of frequency.

The species identified during the dawn chorus were as listed from

<https://pngbirds.myspecies.info>:

Sulphur-crested cockatoo	<i>Cacatua galerita</i>
Chestnut-breasted Cuckoo	<i>Cacomantis castaneiventris</i>
Brush Cuckoo	<i>Cacomantis variolosus</i>
Golden monarch	<i>Carterornis chrysomela</i>
Variable dwarf kingfisher	<i>Ceyx lepidus</i>
Long-billed cuckoo	<i>Chrysococcyx megarhynchus</i>
Little bronze cuckoo	<i>Chrysococcyx minutillus</i>

Pinon's imperial pigeon	<i>Ducula pinon</i>
Zoe's imperial pigeon	<i>Ducula zoeae</i>
Hook-billed Kingfisher	<i>Melidora macrorrhina</i>
Dwarf koel	<i>Microdynamis parva</i>
Yellow-faced myna	<i>Mino dumontii</i>
Grey whistler	<i>Pachycephala simplex</i>
New Guinea friarbird	<i>Philemon novaeguineae</i>
Meyer's friarbird	<i>Philemon meyeri</i>
Northern Variable Pitohui	<i>Pitohui kirhocephalus</i>
Black-sided Robin	<i>Poecilodryas hypoleuca</i>
Wompoo Fruit Dove	<i>Ptilinopus magnificus</i>
Blue Jewel-babbler	<i>Ptilorrhoa caerulescens</i>
Spotted Jewel-babbler	<i>Ptilorrhoa leucosticta</i>
Northern Fantail	<i>Rhipidura rufiventris</i>
Common Paradise Kingfisher	<i>Tanysiptera galatea</i>
Yellow-bellied Longbill	<i>Toxorhamphus novaeguineae</i>
Tawny-breasted Honeyeater	<i>Xanthotis flaviventer</i>

3.2 Vocal activity patterns

A total of 24 species were observed, some species, such as *Melidora macrorrhina*, *Cacatua galerita*, *Tanysiptera galatea*, *Poecilodryas hypoleuca*, and *Microdynamis parva*, show a peak in activity that occurs just before civil twilight, as the ridge peaks in the negative time range. Other species, such as *Chrysococcyx minutillus*, *Ceyx lepidus*, *Caterornis chrysomela*, *Ptilinopus magnificus*, and *Pachycephala simplex*, have their activity peak well after civil twilight, as evidenced by the ridge peaking around 100 min after civil twilight. Species such as *Philemon buceroides novaeguineae*, *Ducula pinon*, and *Toxorhamphus novaeguinae* appeared to have a relatively flat distribution, indicating less variation in the timing of their activity in relation to civil twilight (**Figure 3**).

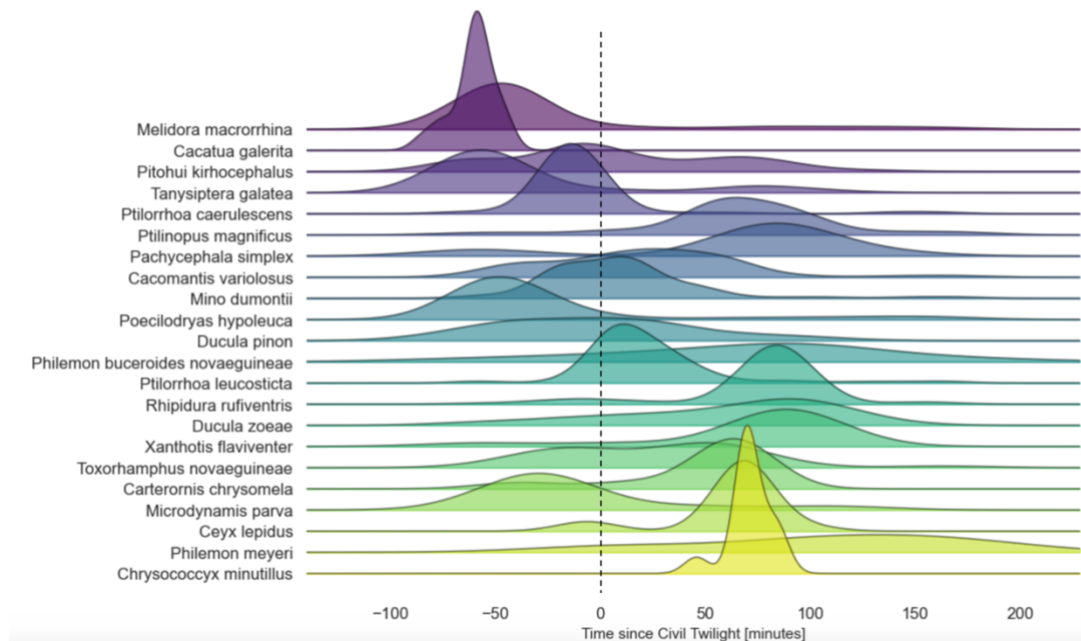


Figure 3 Ridge plot representing the most common activity time for each species in relation to the civil twilight adjusted for each day in minutes. The width of each ridge indicates the variability or spread of the activity times. Narrow ridges suggest that the activity time for that species is very consistent, while wider ridges indicate more variability. The order of the succession is given in descending order for each species.

3.3 Vocal activity distribution by order

The analysis of the temporal activity of birds in relation to the civil twilight revealed a different distribution according to taxonomic orders (**Figure.4**). Columbiformes, with 122 observations, performed their singing activity with a mean of 60.20 and a standard deviation of ± 47.8 minutes after the civil twilight (median = 57, range = (-71) – 176)). In contrast, birds from the Coraciiformes order had 231 observations and performed their singing activity -23.37 ± 55.66 minutes after the civil twilight (median = 47, range = (-87) - 163).

Cuculiformes had 225 observations, 22.18 ± 45.64 minutes after the civil twilight (median = 18 range = ((-71) – 176), reflecting a more balanced temporal distribution around twilight.

The largest group, Passeriformes, with 1119 observations, showed a mean of 15 ± 53.23 minutes, indicating a slight inclination towards post-twilight activity, although with considerable spread (median = 5, range = (-74) – 176). Finally, Psittaciformes, although the smallest group with only 16 observations, demonstrated a markedly different pattern, with a mean of -60.1 ± 9.96 minutes after the civil twilight, primarily occurring well before civil twilight (median = 59, range = (-84) – (-47)).

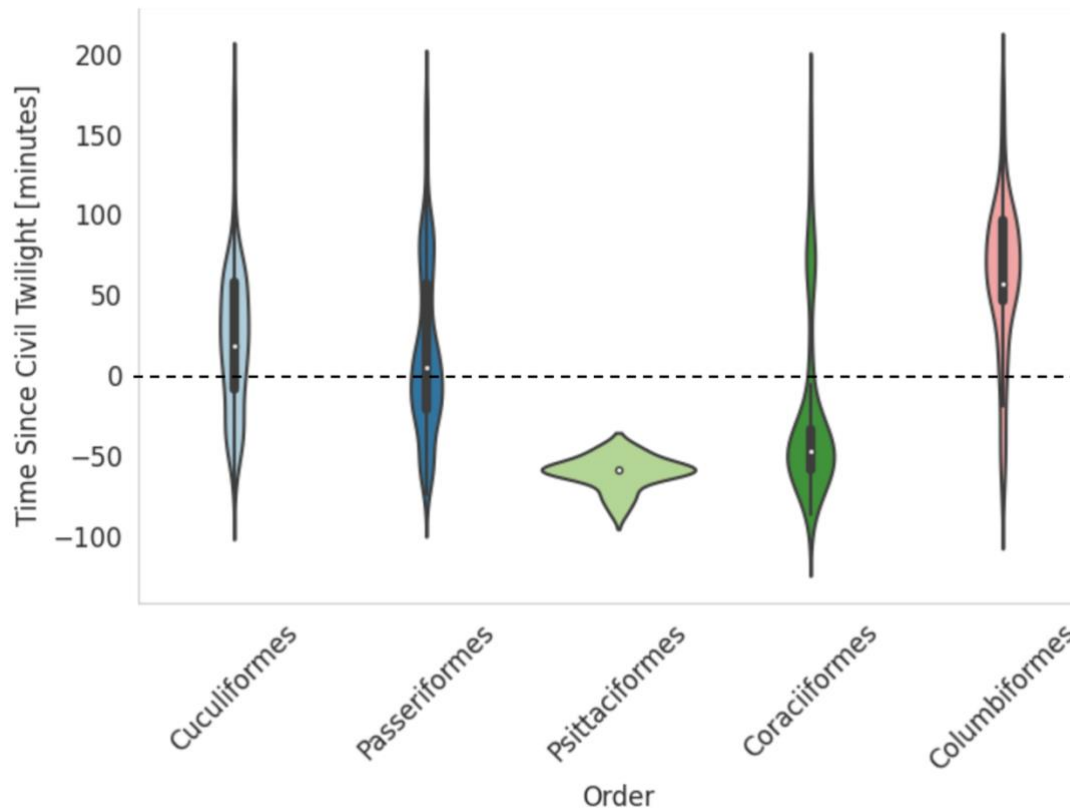


Figure 4 Violin plot indicating the distribution of the counts or observations by order, Cuculiformes with a mean of 22.0 minutes; Passeriformes with a mean of 15.0 minutes; Psittaciformes with a mean of -60.0 minutes; Coraciiformes with a mean of 15.1 minutes; Columbiformes with a mean of 47.8 minutes.

The estimated marginal means (EMMeans) exhibited considerable variability across different orders of birds. Columbiformes displayed the highest mean, while Coraciiformes had the lowest mean. Notably, the confidence intervals associated with each order were extensive, indicating a significant degree of uncertainty in the estimates. The estimated mean for Cuculiformes and Passeriformes and Columbiformes was not significantly different from zero at the 5% level. When examining the contrasts, the differences in means involving Columbiformes when compared with other orders exhibited lower p-values, yet none reached statistical significance under the common threshold of 0.05. Even though there are numerical distinctions, these are not statistically significant. Similarly, the contrasts not involving Columbiformes, such as Coraciiformes vs. Cuculiformes, Coraciiformes vs. Passeriformes and Cuculiformes vs. Passeriformes show exceedingly high p-values, indicating no significant differences between the means of these orders.

Table 1 Estimated marginal means (EM means) for the orders Columbiformes, Coraciiformes, Cuculiformes, and Passeriformes, along with their standard errors (SE), degrees of freedom (df), and 95% confidence intervals (lower CI, upper CI)

Order	EM mean	SE	df	Lower CI	Upper CI
Columbiformes	140.81	45.5	11.6	41.31	240.3
Coraciiformes	2.64	27.1	11.7	-56.58	61.9
Cuculiformes	7.26	28.1	12.6	-53.65	68.2
Passeriformes	26.00	15.9	11.6	-8.88	60.9
Contrast	Estimate	SE	df	T ratio	P value
Columbiformes - Coraciiformes	138.17	53.4	11.5	2.588	0.0975
Columbiformes - Cuculiformes	133.55	58.3	11.9	2.290	0.1554
Columbiformes - Passeriformes	114.81	51.7	11.4	2.220	0.1755
Coraciiformes - Cuculiformes	-4.62	37.4	12.0	-0.123	0.9993
Coraciiformes - Passeriformes	-23.36	26.9	11.6	-0.867	0.8215
Cuculiformes - Passeriformes	-18.74	28.8	12.2	-0.650	0.9137

3.4 Vocal activity distribution by habitat

In examining the variance in minutes since civil twilight across various habitats (**Figure 5**), it was possible to observe different patterns based on the bird's preferred habitat. The category 'Both,' encompassing 233 observations, shows a mean of 3.5 ± 65.3 minutes (median = -34, range = (-87) – 163), indicating a broad spread in activity times with respect to civil twilight. Activity range in this category reflects a highly variable pattern. Contrastingly, birds singing in the canopy have a total of 558 observations, exhibit a mean of 21.8 ± 46.8 minutes (median = 17, range = (-71) – 176), suggesting activities tend to occur more frequently after civil twilight. The range in this habitat spans from a considerable time before to after twilight, with a narrower distribution compared to birds singing in both, canopy and understory, habitats.

The 'Understory' habitat, represented by 960 observations with a mean of 12 ± 57 minutes (median = (-1), range = (-74) – 176). These data indicate a slight leaning towards post-twilight activity, but with a substantial range, extending both before and after civil twilight. These insights revealed the intricate relationship between avian temporal activity and habitat. The observed variations across the 'Both,' 'Canopy,' and 'Understory' habitats are indicative of different ecological behaviors or adaptational strategies. Particularly, the contrast between the relatively more consistent post-twilight activities in 'Canopy' and 'Understory' habitats

and the highly variable patterns in the 'Both' category, underscores the complexity of avian activities in relation to their environmental niches.

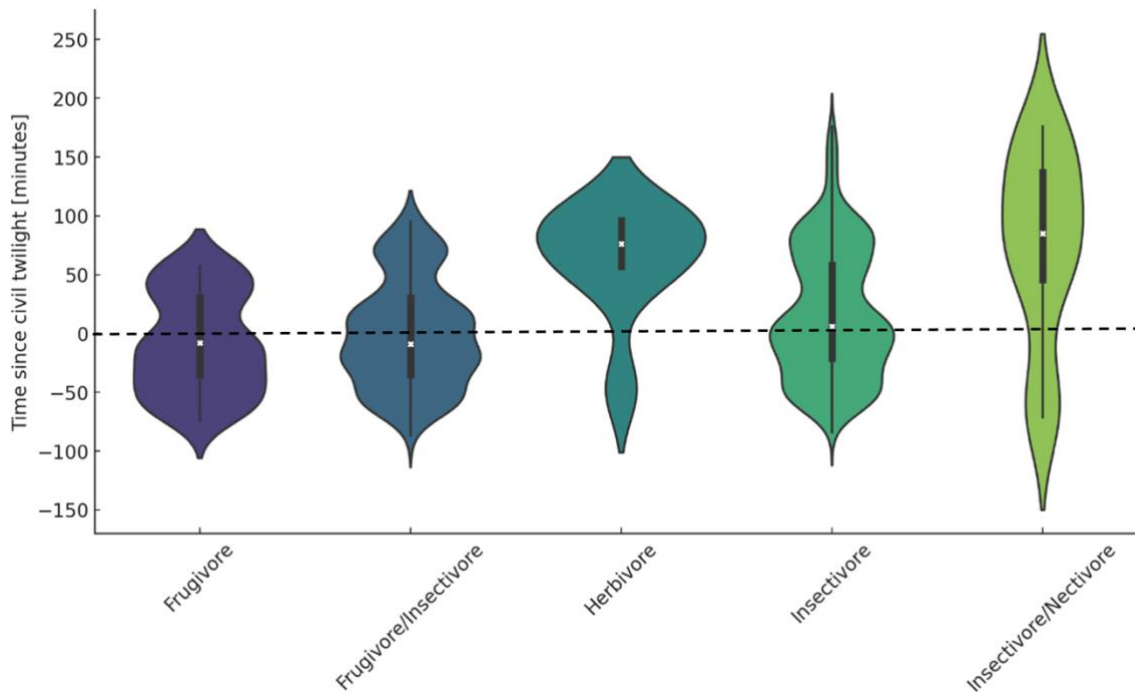


Figure 5 Violin plot indicating the distribution of the counts or observations by habitat. It displays the bird's habitat as canopy, with a mean of 21.8 minutes; understory with a mean of 12 minutes; and Both (often observed in canopy and understory) with a mean of 12 minutes.

For each type of habitat analyzed, the EM Means exhibited a considerable degree of variation (**Table 2**). Birds from the canopy showed the highest adjusted mean, suggesting a substantial mean estimate that excludes zero. Followed by the 'Both' habitat, with a wide confidence, and the Understory had the lowest mean; both intervals span zero, indicating that these means are not significantly different from zero at the 5% significance level. Contrast analyses further illuminate these relationships; however, the p-values for the differences between habitats are all above the 0.05 threshold. This suggests that despite the numerical disparities in EM Means, they do not translate into statistically significant differences at the 5% level. The largest observed mean difference between 'Canopy' and 'Understory' habitats is 44.6, yet the associated p-value of 0.2259 indicates that this difference, while substantial, does not achieve statistical significance, possibly due to the high variability within the data or small true effect sizes relative to the sample sizes used.

Table 2 Estimated marginal means (EM means) for the habitats Canopy, Understory and Both, along with their standard errors (SE), degrees of freedom (df), and 95% confidence intervals (lower CL, upper CL).

Habitat	EM mean	SE	df	Lower CI	Upper CI
Both	46.9	24.8	11.9	-7.22	101.0
Canopy	65.1	20.2	12.5	21.22	109.0
Understory	20.5	18.2	11.8	-19.25	60.3
Contrast	Estimate	SE	df	T ratio	P value
Both - Canopy	-18.2	28.5	12.2	-0.640	0.8012
Both - Understory	26.3	25.3	11.6	1.041	0.5672
Canopy - Understory	44.6	25.4	12.1	1.754	0.2259

3.5 Vocal activity distribution by feeding guild

Frugivore birds (**Figure 6**), exhibited a total of 387 observations and display a mean of -8.94 ± 47.6 minutes (median = (-8), range = (-71) – 176), indicating activities occurring around twilight. 'Frugivore/Insectivore', showed a total of 210 observations with a mean of 0.05 ± 56.4 minutes, (median = (-9), range = (-74) – 176). Herbivores, represented by fewer observations, present a markedly different pattern, since it only has one representative species. This feeding guild had 16 observations, a mean of 63.5 ± 46 minutes (median = 76.5, range = (-47) – 96), predominantly reflecting post-twilight activities.

Insectivores formed a large group with 992 observations and a mean of 16.9 ± 55 minutes (median = 6, range = (-87) – 176. Lastly, the 'Insectivore/Nectivore' guild, though smaller in size, exhibits 35 observations, a distinct pattern with a mean of 74.9 ± 80 minutes (median = 85, range = (-71) – 176), primarily indicative of activities well after civil twilight. This analysis highlights the varied temporal behaviors among different feeding guilds in relation to civil twilight, reflecting their unique ecological adaptations and foraging strategies. The range and average singing time since civil twilight values for each guild underscore the diversity of avian activities, particularly showing the contrast between guilds like frugivores and herbivores in their temporal preferences.

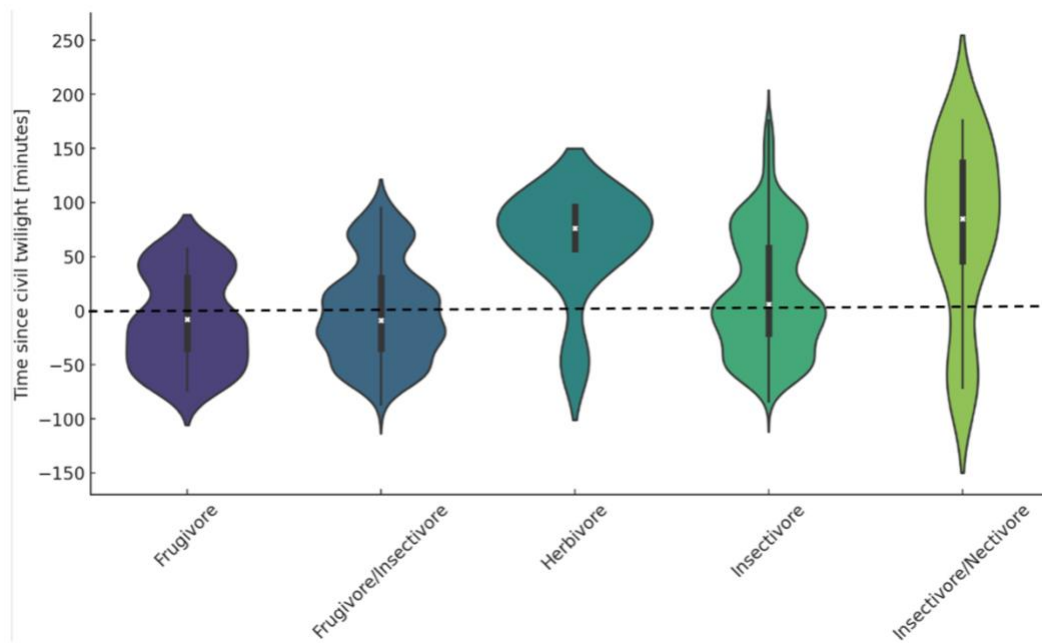


Figure 6 Violin plot indicating the distribution of the counts or observations by Feeding guild. It displays the bird's feeding guild as frugivore with a mean of 74.9 minutes; frugivore/ insectivore, with a mean of -0.05 minutes; herbivore, with a mean of 63 minutes; insectivore, with a mean of 16 minutes and insectivore/nectivore, with a mean of 74.9 minutes.

When evaluating the EM Means for various feeding guilds, it becomes evident that there exists a noticeable variation among the groups. The frugivore guild showed a considerable degree of uncertainty around its estimate. In contrast, the frugivore/insectivore guild displayed a higher estimate, which does not include zero. The insectivore guild's mean had a narrower confidence interval, also above zero, indicating a significant difference from zero. Regarding pairwise contrasts between the feeding guilds, no statistically significant differences were observed at a significance level of 0.05. The p-values suggest that although the observed differences in means are numerically discernible, they do not reach the threshold of statistical significance. This may indicate that there are no meaningful differences in the feeding behaviors captured by these guild categories or that the sample sizes might be insufficient to detect such differences.

Table 3 Estimated marginal means (Emmeans) for the feeding guilds Frugivore, Insectivore and Frugivore/Insectivore, along with their standard errors (SE), degrees of freedom (df), and 95% confidence intervals (lower.CL, upper CL).

Feeding Guild	EM mean	SE	df	Lower CI	Upper CI
Frugivore	14.1	26.9	12.0	-44.57	72.8
Frugivore/Insectivore	69.5	28.9	12.4	6.75	132.2
Insectivore	48.9	16.0	11.7	14.01	83.9
Contrast	Estimate	SE	df	T ratio	P value
Frugivore - (Frugivore/Insectivore)	-55.3	38.7	12.2	-1.431	0.3566
Frugivore - Insectivore	-34.8	34.6	11.9	-1.006	0.5871
(Frugivore/Insectivore) - Insectivore	20.5	27.9	12.4	0.734	0.7484

For the statistical analysis, the species that had only one observation during the entire sampling period were filtered out, as well as nocturnal species, such as *Podargus papuensis*, even though they sang during dawn, their songs starts even before astronomical twilight, around midnight, and they did not belong to the dawn chorus succession. Since the variables weight and body size are correlated, we chose only weight for the statistical analysis to avoid redundancy. The feeding guilds of the filtered species included herbivores and nectivores, which is the reason why they appear in the initial analysis, but as outliers, they add unwanted noise to the model.

4. Discussion

4.1 Vocal Activity Patterns

The order Passeriformes dominated the study with 1054 records, reflecting its dominance and wide geographic distribution and singing activity, consistent with established understanding of avian biodiversity and bioacoustic patterns in the neotropics (Berg et al., 2006). However, the lower occurrence of Psittaciformes, particularly *Cacatua galerita*, may indicate a specialized ecological niche or limited distribution within the study area. The majority of observations (853 records) indicate that avian species prefer understory habitats, possibly due to the abundant food resources and protection from aerial predators (Loiselle & Blake, 1990). However, the lower observation count for species singing in both canopy and the understory (217 records) may indicate a more selective habitat preference or species-specific behaviors that need to be analyzed in detail in future studies (Collins et al., 1990).

The analysis of vocal activity patterns in relation to civil twilight in bird species in Papua New Guinea revealed different temporal niches. Early singing species such as *Melidora macrorrhina* and *Cacatua galerita*, which peak just before civil twilight, may use dawn conditions to maximize song transmission, supporting the acoustic transmission hypothesis, but direct measurements of temperature and humidity are needed to further explore this result (Henwood & Fabrick, 1979). This time of day is characterized by lower environmental noise and usually stable atmospheric conditions that may facilitate signal transmission over greater distances (Brenowitz, 1982). Late vocalizers, such as *Chrysococcyx minutillus* and *Ptilonopus magnificus*, whose peak activity occurs after civil twilight, may be responding to other selective pressures, such as the availability of food resources or social interactions within the bird community (Thomas et al., 2002). This delayed activity could also be a strategy to avoid predation, as predators may be less active after dawn (Krams, 2001). The consistent activity, displayed by species such as *Philemon buceroides novaeguineae* and *Ducula pinon*, suggests a more general behavior that is less tied to the specifics of twilight. These species may be less dependent on the visual cues that influence the behavior of other species, or they may be less vulnerable to predation, allowing them more flexible song timing (Catchpole & Slater, 2008).

4.2 Taxonomical Order

The temporal niches of the various avian orders show different trends. Columbiformes are often active after twilight, which could be due to their diet, since they belong to the frugivore/insectivore feeding guild, or to predator avoidance tactics, where visibility is crucial (Henwood and Fabrick, 1979). Coraciiformes and Psittaciformes, on the other hand, generally start their activities before civil twilight, possibly to avoid daytime predators, to reduce competition for sound space, or to forage crepuscular insects (Kacelnik, 1979). The contrasting temporal behaviors between orders, such as pre-twilight activities of Coraciiformes and Psittaciformes compared to the post-twilight tendencies of Columbiformes, Cuculiformes, and Passeriformes, may indicate evolutionary adaptations aimed at minimizing interspecific competition for resources or acoustic interference (Staicer et al., 1996).

4.3 Habitat

The wide distribution of singing activity in birds inhabiting both the canopy and the understory suggests a high degree of behavioral flexibility. These birds may be generalists able to utilize resources in both the canopy and understory, which could be an advantage in environments with fluctuating conditions (Sam et al., 2017). The tendency for singing activity to occur more frequently in the canopy after civil twilight and a similar weak tendency in the understory may reflect a strategy to avoid predators or optimize foraging when light conditions are more favorable. This behavior could also be influenced by the physical structure of habitats, which affects sound transmission and influences communication strategies (Bradbury & Vehrencamp, 2011). The contrast between the relatively consistent post-twilight activity in the canopy and understory, and the variable patterns in species singing in both strata, highlights the complexity of avian behaviors. Birds adapted to specific strata, such as the canopy, may have evolved traits that enable their survival in these environments, such as specialized foraging techniques or predator avoidance behaviors (Farina, 2015).

4.4 Feeding Guild

The altitude of the study area was 100 m above sea level, and at low altitudes, frugivores are relatively the most common feeding guild (Sam et al., 2017). With 134 observations, these results indicate a low number of strict frugivores. However, it is important to note, that the earlier study relied both on visual and acoustic identifications conducted throughout the day, while my own data use only acoustic identification from morning hours. In contrast to frugivores, both frugivores and insectivores and strict insectivores were recorded a total of 463 and 992 times, respectively. Strict insectivores, insectivores/nectivores, and insectivores/frugivores all have early vocal activity, starting at least 100 min before civil twilight. Insectivores/nectivores were mainly active after the twilight, which could be related to the highest availability of insects and nectar, but are among the feeding guilds with fewer observations, totaling 35 counts. This is consistent with studies that have found low counts of nectivorous species at lower altitudes (Sam et al., 2017).

4.5 Weight

Previous research has suggested that body size plays a secondary role in the timing of the dawn chorus compared to other morphological characteristics; and some studies have even

found insignificant trends (Berg et al., 2006). In this study, both body size and weight were positively correlated, but to avoid redundancy, only the variable weight was chosen as a fixed effect. The results of the mixed linear model revealed that weight was negatively associated with the timing of the dawn chorus, as indicated by a coefficient of -19.61. However, this association was not statistically significant, suggesting that while there was a trend indicating that heavier birds might sing earlier or later than lighter birds, this trend was not strong enough to be considered reliable within the context of this study. The lack of statistical significance implies that weight may not be a critical factor in determining the timing of the dawn chorus for the species studied.

5. Conclusions

The conclusions of this study highlight recognizable patterns in the distribution of birds, habitats, and feeding behavior. The high number of observations at site 1 is due to the fact that more days were available for the analyses, and that it rained at the other study sites. The dominance of Passeriformes is consistent with their known ecological prevalence, in contrast to the few observations of Psittaciformes, suggesting niche specialization.

Temporal activity patterns around civil twilight were diverse. Early vocalizers, perhaps exploiting optimal dawn conditions, contrasted with active species after twilight, possibly adapted to predation risks or resource availability. The variation in singing activity suggests that the ecological adaptations and feeding strategies of birds are closely linked to their temporal niches, with habitat preference playing a pivotal role in their daily routines.

Overall, these findings underscore the complexity of avian life, emphasizing the importance of ecological adaptations in the spatial distribution and temporal activity of birds, which has implications for their conservation and for understanding the bird community dynamics. However, literature indicates that eye size is the primary estimator for predicting the succession of the dawn chorus. For future studies, it is recommended to measure eye size and other morphological traits directly in the field.

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Appendix

Table 4. shows the results of the mixed linear model taking as fixed effects weight, order, habitat and feeding guild, and as intercept and random effect species. The intercept suggests that when all the other variables are zero, the response variable starts at 113.46. Weight had a negative relationship with the response (-19.61), but this was not statistically significant ($p = 0.0828$). Habitat type did not significantly affect the response, as indicated by the p-values for both canopy and understory. Foraging guilds, compared to the reference category, show higher estimates for frugivores/insectivores and insectivores alone, but again, these are not statistically significant. Orders Coraciiformes, Cuculiformes, and Passeriformes show significant negative effects on the response variable, with p-values indicating statistical significance at 0.05, suggesting that these orders may have a substantial and statistically significant influence on the response variable being measured.

Table 4 Values of the Mixed Linear Model using species as the intercept and random effect. The standardized weight, feeding guild, habitat and order were used as fixed effects.

	Estimate	Std. Error	df	t-value	Pr(> t)
(Intercept)	113.46	48.88	11.51	2.321	0.0395*
Weight	-19.61	10.40	12.48	-1.886	0.0828.
HabitatCanopy	18.24	28.49	12.24	0.640	0.5338
HabitatUnderstory	-26.35	25.31	11.63	-1.041	0.3191
F_guild_Frugivore/Insectivore	55.33	38.67	12.24	1.431	0.1775
F_guild_Insectivore	34.82	34.59	11.99	1.007	0.3340
OrderCoraciiformes	-138.17	53.39	11.58	-2.588	0.0243*
OrderCuculiformes	-133.55	58.33	12.00	-2.290	0.0410*
OrderPasseriformes	-114.81	51.71	11.49	-2.220	0.0474*

Table 5, which present the results of the chi-square tests examining the associations between various avian characteristics, indicate that there are statistically significant interdependencies among species, habitats, feeding behaviors, and taxonomic orders. The association between avian species and their respective habitats was found to be highly significant (chi-square =

3394, $df = 40$, $p < 2.2e-16$), suggesting that there is a strong correlation between specific species and their preferred habitats. This implies that habitat selection is closely connected to species-specific ecological adaptations and requirements. Similarly, a pronounced relationship was observed between species and their feeding habits (chi-square = 3394, $df = 40$, $p < 2.2e-16$). This suggests that dietary preferences are intrinsically linked to species characteristics.

The analysis also revealed a significant association between species and their taxonomic order (Chi-square = 5091, $df = 60$, $p < 2.2e-16$), highlighting classification of species within orders that likely share common evolutionary traits and ecological niches. When examining the relationship between habitat types and feeding behaviors, the analysis showed a substantial association (Chi-square = 588.36, $df = 4$, $p < 2.2e-16$), indicating that different habitats provide distinct resources and conditions that influence the feeding strategies of resident species. Additionally, the tests comparing habitat types with taxonomic orders (Chi-square = 939.69, $df = 6$, $p < 2.2e-16$) and feeding behaviors with orders (Chi-square = 670.82, $df = 6$, $p < 2.2e-16$) revealed significant associations. These results emphasize the interplay between broader taxonomic classification, habitat preferences, and feeding habits, reflecting the evolutionary and ecological diversity within avian taxa.

Table 5 Chi-Squared tests for the categorical variables taxonomical order, habitat, feeding guild and species.

Categories	Chi-Squared	P-Value
Order and Species	5091.00	<0.001
Order and Habitat	939.69	<0.001
Order and Feeding Guild	670.81	<0.001
Species and Habitat	3394.00	<0.001
Species and Feeding Guild	3390.00	<0.001
Habitat and Feeding Guild	588.35	<0.001

Phylogenetic tree of birds

The cladogram **Figure 7** represents the phylogenetic relationships between several bird species classified by order. At the top, *Cacatua galerita*, a cockatoo species, was selected as the outgroup because it was the only species representative of its order and outliers in the other statistical analyses. Cuculiformes, Coraciiformes, and Columbiformes, each represented by a few species, suggest less diversity within these orders or less sampling in this study.

Passeriformes, highlighted in blue, show rich diversity, with multiple branches indicating a high degree of evolutionary divergence among these species. This diversity within Passeriformes is typical given its status as the largest bird order, encompassing more than half of all bird species. The tree structure, with branching points, reflects the evolutionary history and relationships, with closely related species branching off more recently than less related species.

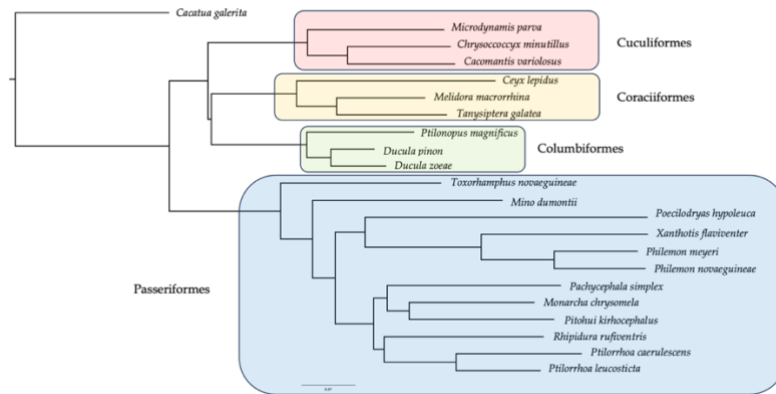


Figure 7 Phylogenetic tree of the species singing during the dawn chorus.

Photos of birds



Figure 8 Photographs of the listed birds A. *Cacatua galerita*, B. *Microdynamis parva*, C. *Chrysococcyx minutillus*, D. *Cacomantis variolosus*, E. *Ceyx lepidus*, F. *Melidora macrorrhina*, G. *Tanysiptera galatea*, H. *Ptilinopus magnificus*, I. *Ducula pinon*, J. *Ducula zoeae*, K. *Toxorhamphus novaeguineae*, L. *Mino dumontii*, M. *Poecilodryas hypoleuca*, N. *Xanthothis flaviventer*, O. *Philemon meyeri*, P. *Philemon novaeguineae*, Q. *Pachycephala simplex*, R. *Monarcha chrysomela*, S. *Pitohui kirhocephalus*, T. *Rhipidura rufiventris*, U. *Ptilorrhoa caerulea*, V. *Ptilorrhoa leucosticta*. All pictures were taken by Katerina Sam and downloaded from the website <https://pngbirds.myspecies.info>.