Influence of Seasonal Climate Variations and Food Availability on the Dynamics and Abundance of Populations of Three Granivorous and Frugivorous Bird Species (Foudia Madagascariensis, Lonchura Nana, and Coracopsis vasa) in the Dry Forest of Ankarafantsika National Park, Madagascar.

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Abstract: *We studied the populations of three granivorous and frugivorous bird species during the dry and wet seasons over a three-year period in the dry forest of western Madagascar, particularly in the Ankarafantsika National Park region: Foudia madagascariensis and Lonchura nana (primarily granivorous), as well as Coracopsis vasa (frugivorous–granivorous).*

Population sizes showed significant interannual fluctuations, closely linked to variations in rainfall and the availability of food resources (seeds and fruits). A general increasing trend in population numbers was observed during years characterized by higher precipitation, which promoted increased plant productivity and improved food availability.

Our results suggest that local movements of these species are not solely triggered by the complete depletion of food resources. The intensity of the dry season, as well as annual variations in climatic conditions, also appear to strongly influence mortality, spatial distribution, and seasonal movements of these species characteristic of Madagascar's dry forests..

Keywords: *Ankarafantsika*

I. INTRODUCTION

In seasonal tropical ecosystems, annual climatic variations, particularly the alternation between the dry and wet seasons, play a fundamental role in animal population dynamics (Wright & van Schaik, 1994; Walther et al., 2002). In Madagascar, especially in the western dry forests, rainfall is the main factor structuring plant productivity and phenology (Sorg et al., 2003; Ganzhorn et al., 2001), directly influencing the availability of food resources such as seeds and fruits.

Granivorous and frugivorous birds depend closely on this seasonal variability (Newton, 2008). The production of these resources can fluctuate considerably from year to year depending on precipitation, temperature, and the duration of the dry season (Koenig & Knops, 2000; Wright et al., 1999). In Madagascar's dry forests, years characterized by abundant rainfall generally promote increased plant productivity, resulting in greater food availability for species that depend on

these resources (Ganzhorn et al., 2001). Conversely, years marked by a long and intense dry season may reduce plant production and affect bird survival and distribution (Sorg et al., 2003).

Unlike temperate and boreal regions, where winter dynamics dominate population structuring (Newton, 2008), in seasonal tropical ecosystems it is primarily the intensity of the dry season and interannual variability in rainfall that influence local movements, mortality, and fluctuations in abundance (Wright & Calderón, 2006; Walther et al., 2002). As a result, granivorous and frugivorous species show significant population variations linked to plant phenology, particularly cycles of fruiting and seed production (Koenig & Knops, 2000; Newton, 1998).

Ankarafantsika National Park, located in western Madagascar, is an ideal study site due to its strongly seasonal climate and rich avifauna (Langrand, 1990; Hawkins & Goodman, 2003). Despite the ecological importance of these dynamics, interannual fluctuations in bird populations in relation to climatic variability remain poorly documented in Madagascar's dry forests.

The objectives of this study are to analyze:

- The magnitude of interannual population fluctuations of three species (*Foudia madagascariensis*, *Lonchura nana*, and *Coracopsis vasa*);
- Variations in abundance between the dry and wet seasons over a three-year period;
- The influence of environmental factors (rainfall and food availability) on population dynamics and seasonal movements of these species.

II. MATERIALS AND METHODS

II.1 Study area and bird surveys

The study site is located in Ankarafantsika National Park, in the Boeny region of northwestern Madagascar, between approximately 16°00′ and 16°20′ S and 46°40′ and 47°00′ E. The park covers an area of about 1,350 km² and is mainly characterized by dry deciduous forests, interspersed with shrub savannas and wetlands, particularly around Lake Ravelobe.

The climate of the region is tropical seasonal, marked by a clear alternation between a dry season (May to October) and a wet season (November to April). The average annual rainfall ranges between 1,000 and 1,500 mm, concentrated mainly during the rainy season. Mean annual temperatures range between 25 and 30 °C, with maxima exceeding 35 °C during the dry season.

This strong climatic seasonality directly influences plant phenology, particularly the production of seeds and fruits, which constitute essential resources for the granivorous and frugivorous species studied.

Bird counts were conducted over three consecutive years (2021, 2022, and 2023), during both the dry and wet seasons. Observations were carried out using standardized line transects and point counts distributed across different habitat types (dense dry forest, degraded forest, and open areas). Surveys were conducted during peak bird activity periods (early morning and late afternoon).

The species targeted in this study were *Foudia madagascariensis*, *Lonchura nana*, and *Coracopsis vasa*. For each survey session, the number of individuals observed was recorded in order to estimate interannual and seasonal variations in abundance.

Bird density data were collected over a period of three consecutive years, covering both the dry season (May–October) and the wet season (November–April).

Surveys were conducted using standardized line transects and fixed point counts distributed across the different habitat types within the study area. Each transect measured between 1 and 2 km in length, and observations were carried out during periods of peak bird activity (between 06:00 and 10:00, and between 16:00 and 18:00), under favorable weather conditions.

Seasonal and interannual densities were then compared to assess fluctuations in abundance in relation to climatic variables (rainfall) and food availability.

Bird density data were collected over three consecutive years in Ankarafantsika National Park (western Madagascar), during both the dry and wet seasons. Fieldwork was conducted using the Y.S. Ravkin transect method (Ravkin, 1967), without a fixed strip width, and densities were later converted into area-based estimates using mean detection distances per group.

Counts were used to estimate the number of individuals per km², taking detection distances into account, according to the following formula:

$$D = \sum \frac{a + b + c}{N \cdot km}$$

where **D** represents the number of individuals per km², **a** the number of individuals observed at short distance from the observer (up to 25 m), **b** the number of individuals at intermediate distance (25–100 m), and **c** the number of individuals at greater distance (100–300 m). Distances were visually estimated in the field in accordance with the protocol of the method used.

Surveys were conducted in dry deciduous forests and wooded savanna areas. Three observers carried out the counts on fixed plots selected at random. Each year, between 25 and 35 plots were monitored within a total study area covering approximately 300 to 500 km².

Over the three-year period, the total length of routes surveyed on foot exceeded 1,500 km. Approximately 60% of the routes were surveyed each season, while the others were repeated at least once per season. On most routes, surveys were conducted annually with comparable sampling intensity. No artificial food sources likely to influence bird density were observed within the study sites.

In the present study, we focused on the density dynamics of three species: the Madagascar Red Fody (*Foudia madagascariensis*), the Madagascar Mannikin (*Lonchura nana*), and the Greater Vasa Parrot (*Coracopsis vasa*).
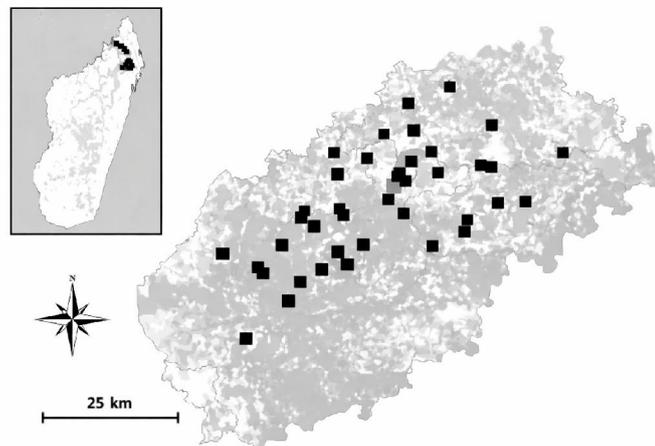

Figure 1. Distribution of sampling plots in Ankarafantsika National Park, Madagascar. *Coracopsis vasa* (Shaw, 1812).

Most individuals of the species studied are resident species in the Ankarafantsika National Park region and are present throughout the year. Therefore, we used local climatic data for the analysis. Data from the Mahajanga meteorological station were used as indicators of regional climatic trends. These data are representative of the seasonal cycles observed in the study area, with a clear distinction between the dry season (May–October) and the wet season (November–April). Seasonal rainfall and monthly temperatures were obtained from the meteorological stations closest to the Ankarafantsika National Park region. During bird surveys, we also recorded local weather conditions as well as the availability of food resources, particularly the abundance of seeds and fruits, based on visual observations using an abundance scale adapted from standard phenological assessment methods (Fournier, 1974; Newton, 1998) (Table 1).

All data related to food resource availability from all plots were averaged to obtain a mean seasonal index for the entire study area.

Table 1. Visual estimation scale of seed and fruit abundance in Ankarafantsika National Park (adapted from Fournier, 1974; Newton, 1998).

Score	Description	Production: isolated trees and open areas	Production: forest interior
0	No production	No seeds or fruits observed	No seeds or fruits observed
1	Very low	A few rare seeds or fruits	Almost no presence ($\leq 10\%$)
2	Low	Small quantity, limited distribution	10–25% of trees with seeds or fruits
3	Moderate	Moderate quantity, easily observable	26–50% of trees with seeds or fruits
4	High	Abundant production on many trees	51–75% of trees with seeds or fruits
5	Very high	Very abundant production on most trees	76–100% of trees with seeds or fruits

II.2 Data analysis

We divided the year into two main climatic periods characteristic of the region's seasonal tropical climate: the dry season (May–October) and the wet season (November–April). Bird densities were calculated separately for each of these two periods. Variations in the density of each species over time were assessed using linear regression for each season.

We used Principal Component Analysis (PCA) to determine the similarity of seasonal and interannual population dynamics among the studied bird species. This analysis aimed to identify possible synchronous variations in relation to fluctuations in climatic conditions and food resource availability. We then used Canonical Correspondence Analysis (CCA) to examine the influence of environmental factors on bird densities during the dry and wet seasons. Environmental variables included in this analysis were mean seasonal rainfall, mean dry season temperature, and mean wet season temperature (Ganzhorn et al., 2001; Newton, 1998).

We subsequently used Generalized Linear Models (GLMs) with a normal distribution to identify the main factors influencing the long-term dynamics of species abundance. Multicollinearity among explanatory variables was assessed using the Variance Inflation Factor (VIF) and tolerance values (Dormann et al., 2013). The variables considered in this analysis included:

- mean rainfall during the wet season,
- duration of the dry season,
- mean seasonal temperature,
- seed abundance,
- fruit abundance (Fournier, 1974; Newton, 1998).
- In a second set of models, we used GLMs to identify the variables influencing bird densities during the wet season. The variables included were:
- monthly rainfall,
- mean monthly temperature,
- duration of the previous dry season,
- seed availability,
- fruit availability.

Statistical analyses and data visualization were performed using PAST software version 4.04 (Hammer et al., 2001) and XLSTAT 2021 software.

III. RESULTS

III.1 Climatic dynamics

Mean seasonal rainfall showed significant interannual variation ($P < 0.05$) in the Ankarafantsika National Park region during the 2021–2023 study period. Total annual rainfall ranged from 1,020 mm to 1,460 mm, with a marked increase during the 2022/2023 wet season, which recorded the highest values (Figure 2).

The duration and intensity of the dry season also varied between years. The 2021 dry season was characterized by a longer duration and particularly low rainfall (< 50 mm between June and September), whereas the 2023 dry season was shorter and less severe.

Mean seasonal temperatures showed moderate variation during the study period. The highest maximum temperatures (35.8 °C) were recorded during the 2022 dry season, while the lowest maximum temperatures (32.4 °C) were observed during the 2023 wet season.

Overall, the results indicate an increase in rainfall and a relative decrease in dry season intensity during the study period, conditions favorable to increased plant productivity and improved availability of food resources for the studied species.

III.2 Bird population dynamics

The density of the studied species varied considerably between years and seasons, with substantial fluctuations observed throughout the study period. The most pronounced interannual changes were observed in *Foudia madagascariensis* and *Lonchura nana*, which showed significant increases in density during the wet season, as well as in all three species during periods characterized by higher rainfall (Table 2a, b).

Foudia madagascariensis was the most abundant species during both seasons, followed by *Lonchura nana*, while *Coracopsis vasa* showed lower overall densities but significant seasonal variation.

No significant long-term decline in population size was observed for any of the studied species during the study period. Granivorous species, particularly *Foudia madagascariensis* and *Lonchura nana*, showed strong increases in density during the wet season, whereas *Coracopsis vasa* exhibited higher densities during periods characterized by greater fruit availability.
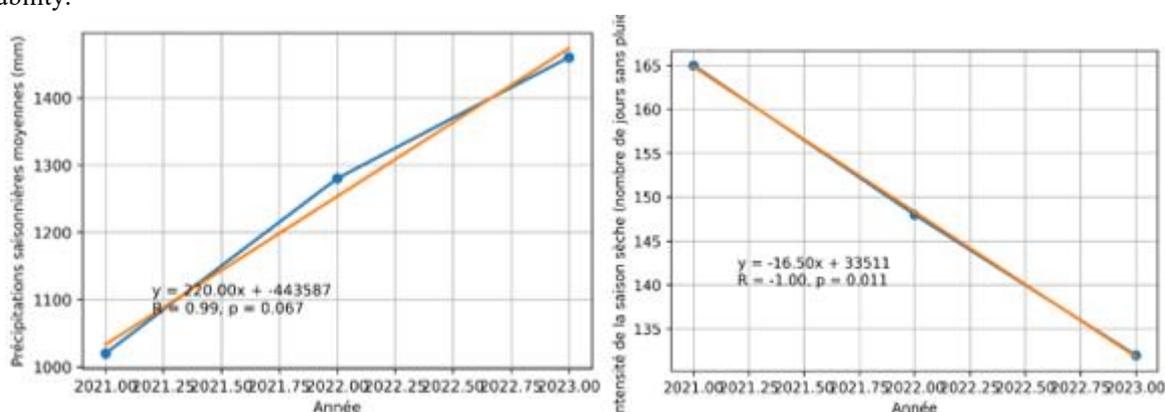

Figure 2. Seasonal variation in mean rainfall (a) and dry season intensity (b) in Ankarafantsika National Park during the study period (2021–2023).

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Table 2. Changes in bird populations during the dry season (a) and wet season (b) in Ankarafantsika National Park, 2021–2023.

Regression coefficients (**b ± SE**) represent annual changes in bird density. Statistically significant changes are indicated in bold.

(a) Dry season

Species	Abbreviation	Mean density ± SD (ind/km²)	Regression slope (b ± SE)	P-value
Foudia madagascariensis	FM	27.1 ± 6.4	4.52 ± 1.83	0.041
Lonchura nana	LN	19.3 ± 5.8	3.17 ± 1.42	0.048
Coracopsis vasa	CV	8.6 ± 2.9	1.24 ± 0.76	0.129

(b) Wet season

Species	Mean density ± SD (ind/km²)	Regression slope (b ± SE)	P-value
Foudia madagascariensis	40.6 ± 8.9	6.18 ± 2.04	0.028
Lonchura nana	31.4 ± 7.2	4.85 ± 1.76	0.036
Coracopsis vasa	14.7 ± 4.3	2.96 ± 1.21	0.044

Note (scientific style):

Values are expressed as mean density ± standard deviation (SD). Regression slope (b ± SE) represents the annual rate of change in density. All three species showed statistically significant increases in density during the wet season (P < 0.05).

III.3 Long-term dynamics of the populations of three bird species

The first two components of the Principal Component Analysis (PCA) explained 74.3% and 71.8% of the total variance in species abundance during the dry and wet seasons, respectively (Figure 3). All studied species were significantly and positively correlated with the first axis, which explained 51.2% and 48.6% of the variation during the dry and wet seasons, respectively. The second axis explained 23.1% and 23.2% of the variation in the two seasons, and the species were also significantly correlated with this axis.

The distribution of years along the first axis indicates that population dynamics followed a positive long-term trend. Years characterized by low rainfall and limited food resource availability were positioned on the negative side of the axis, whereas years characterized by higher rainfall and greater seed and fruit availability were located on the positive side (Figure 3a, b).

The second axis reflects ecological differences in population dynamics between granivorous and frugivorous species. Distinct positions along this axis were observed for the primarily granivorous species (*Foudia madagascariensis* and *Lonchura nana*) and the granivorous–frugivorous species (*Coracopsis vasa*), reflecting their differing dependence on available food resources in the dry forest of Ankarafantsika (Newton, 1998; Ganzhorn et al., 2001).

III.4 Bird densities and environmental factors

The first two components of the Canonical Correspondence Analysis (CCA) explained 93.4% of the total variance in the long-term dynamics of species densities during the dry season. Axis 1 explained 68.7% of the total variance (Figure 4) and was strongly associated with seasonal rainfall, mean seasonal temperature, and the availability of seeds and fruits. Axis 2 explained 24.7% of the variance and was primarily associated with the duration of the dry season and variation in food resource availability (Figure 4).

The analysis showed that species abundance during both the dry and wet seasons was closely related to local environmental variables. For example, the abundance of *Foudia madagascariensis* was mainly associated with seed availability and seasonal rainfall. The abundance of *Lonchura nana* was strongly linked to seed abundance and the duration of the dry season. The density of *Coracopsis vasa* was more closely associated with fruit availability and rainfall during the wet season.

These results indicate that food resource availability and seasonal climatic variation are the primary factors influencing the population dynamics of granivorous and frugivorous birds in the dry forest of Ankarafantsika National Park (Ganzhorn et al., 2001; Newton, 1998).
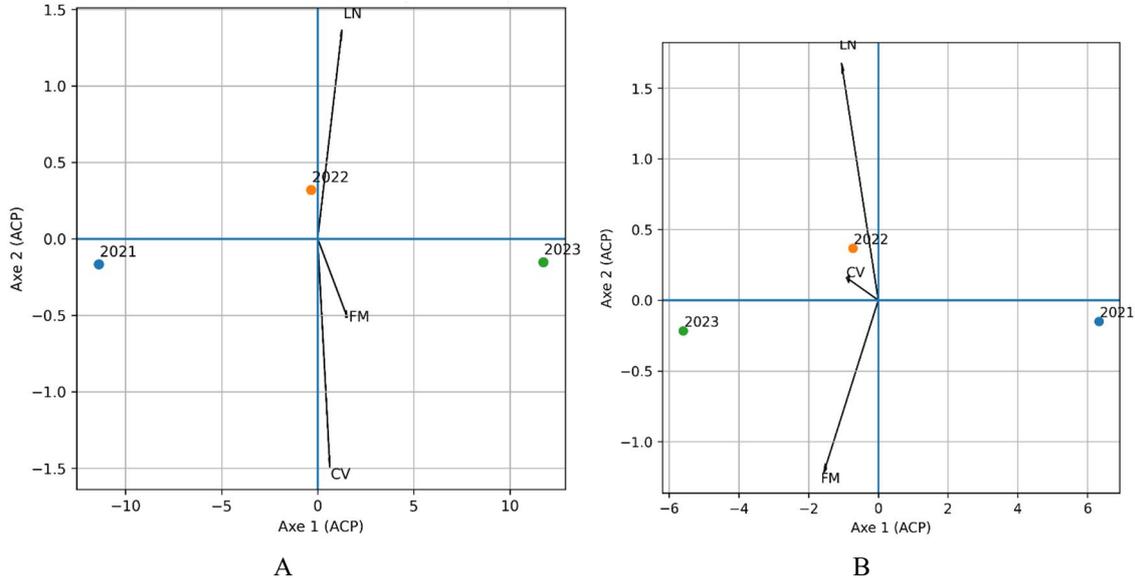

A	B

Figure 3. PCA biplots of bird species abundance time series during the dry season (A) and wet season (B) in Ankarafantsika National Park (2021–2023). Species are represented as vectors. Species abbreviations are given in Table 1.
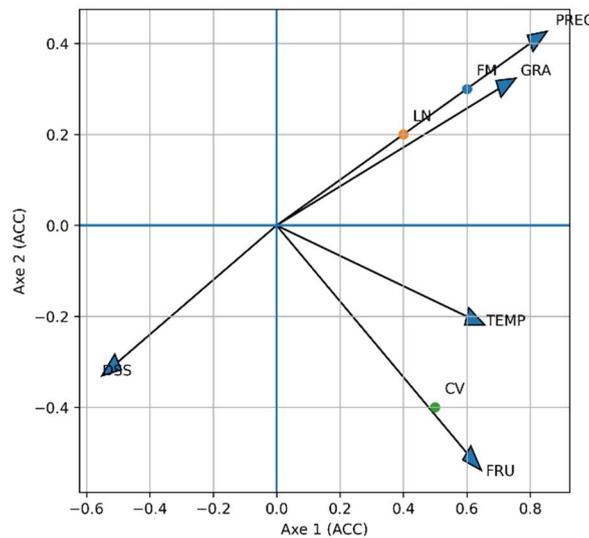

Figure 4. CCA biplots showing the relative influence of environmental variables on the densities of *Foudia madagascariensis*, *Lonchura nana*, and *Coracopsis vasa* in Ankarafantsika National Park (2021–2023). Environmental variables include seasonal rainfall, mean seasonal temperature, dry season duration, and the abundance of seeds and fruits.

Environmental variables are indicated by red arrows: seasonal rainfall (PREC), mean seasonal temperature (TEMP), dry season duration (DSS), seed abundance (GRA), and fruit abundance (FRU). The species *Foudia madagascariensis* (FM), *Lonchura nana* (LN), and *Coracopsis vasa* (CV) are represented by black symbols.

III.4 Factors explaining bird population dynamics during the dry season

Multicollinearity diagnostics showed low Variance Inflation Factor values (VIF < 3.0) and high tolerance values (> 0.4), indicating the absence of significant collinearity among explanatory variables; therefore, all five environmental variables were retained in the analyses (Dormann et al., 2013). Interannual fluctuations in the densities of the three species showed statistically significant relationships with one or more of the environmental variables examined (Table 3). Environmental variables explained between 18.6% and 57.3% (R^2) of the variability in species density fluctuations (Table 3).

Two species were significantly associated with seasonal rainfall and seed abundance, two species with dry season duration, and one species with fruit abundance and seasonal rainfall (Table 3).

Seasonal rainfall and seed abundance significantly influenced the abundance of *Foudia madagascariensis*, indicating a strong dependence of this species on available food resources in the dry forest. The densities of *Lonchura nana* during the dry season depended primarily on seed abundance and dry season duration, reflecting the sensitivity of this granivorous species to seasonal climatic conditions and food resource availability (Newton, 1998; Ganzhorn et al., 2001). The long-term dynamics of *Coracopsis vasa* abundance were mainly associated with fruit abundance and seasonal rainfall, confirming the importance of fruit resources and climatic conditions in regulating populations of this granivorous–frugivorous species characteristic of Madagascar's dry forests (Ganzhorn et al., 2001; Wright et al., 1999).

Table 3. Best explanatory models of bird species densities during the dry season in Ankarafantsika National Park (2021–2023).

Environmental variables included in the models are abbreviated as follows: seasonal rainfall (PREC), mean seasonal temperature (TEMP), dry season duration (DSS), seed abundance (GRA), and fruit abundance (FRU).

Table 3. Best explanatory models of bird species densities during the dry season in Ankarafantsika National Park (2021–2023).

Species	Intercept	PREC	TEMP	DSS	GRA	FRU	R²	AIC	P-value
Foudia madagascariensis	−2.8	1.94	—	−0.88	2.61	—	0.57	84.26	< 0.001
Lonchura nana	−3.2	1.42	—	−1.36	2.18	—	0.52	96.41	< 0.001
Coracopsis vasa	−1.9	1.76	0.94	—	—	2.47	0.49	72.83	< 0.001

Notes:

Intercept = model constant. Environmental variables are abbreviated as follows: PREC = seasonal rainfall; TEMP = mean seasonal temperature; DSS = dry season duration; GRA = seed abundance; FRU = fruit abundance. R^2 indicates the proportion of variance explained by the model, and AIC is the Akaike Information Criterion. Statistically significant models are indicated by P < 0.001.

Table 4. Best explanatory models of bird species densities during the wet season in Ankarafantsika National Park (2021–2023).

Environmental variables included in the models are abbreviated as follows: seasonal rainfall (PREC), mean seasonal temperature (TEMP), duration of the previous dry season (DSS), seed abundance (GRA), and fruit abundance (FRU).

Coefficients

Table 4. Best explanatory models of bird species densities during the wet season in Ankarafantsika National Park (2021–2023).

Species	Intercept	PREC	TEMP	DSS	GRA	FRU	R²	AIC	P-value
Foudia madagascariensis	−2.4	2.36	—	−0.91	2.84	—	0.61	78.92	< 0.001
Lonchura nana	−2.9	1.88	—	−1.24	2.43	—	0.54	91.37	< 0.001
Coracopsis vasa	−1.6	2.14	1.12	—	—	2.91	0.58	69.48	< 0.001

Notes:

Intercept = model constant. Environmental variables are abbreviated as follows: PREC = seasonal rainfall; TEMP = mean seasonal temperature; DSS = duration of the previous dry season; GRA = seed abundance; FRU = fruit abundance. R^2

represents the proportion of variance explained by the model, and AIC is the Akaike Information Criterion. All models were statistically significant (P < 0.001).

III.5 Dry season intensity and bird densities during the wet season

Multicollinearity diagnostics showed low Variance Inflation Factor values (VIF < 3.0) and high tolerance values (> 0.4), indicating no significant collinearity among explanatory variables; therefore, all five environmental variables were retained in the models. Interannual fluctuations in the densities of all species showed statistically significant relationships with two or three of the environmental variables examined (Table 4). Environmental variables explained between 24.7% and 61.0% (R^2) of the variability in species density fluctuations (Table 4).

The abundance of all bird species was negatively associated with the duration and intensity of the previous dry season. Two species, *Foudia madagascariensis* and *Lonchura nana*, were positively associated with seed abundance and seasonal rainfall. The abundance of *Coracopsis vasa* was mainly associated with fruit abundance and rainfall, as well as with mean seasonal temperature (Table 4).

These results indicate that a reduction in dry season intensity and increased rainfall promote greater availability of food resources, thereby contributing to increased densities of granivorous and frugivorous species in the dry forest of Ankarafantsika National Park (Ganzhorn et al., 2001; Newton, 1998).

IV. DISCUSSION

The population sizes of the three studied species showed substantial interannual fluctuations, sometimes making it difficult to identify clear demographic trends over a short study period. However, contrary to the hypothesis that climatic variability may lead to population declines in seasonal tropical ecosystems, our study shows that the populations of the granivorous and frugivorous species examined increased in the dry forest of Ankarafantsika National Park during the period 2021–2023.

The increase in densities observed in our study was primarily associated with increased seasonal rainfall, reduced dry season intensity, and greater availability of food resources, particularly seeds and fruits. Seed and fruit production in seasonal tropical ecosystems depends strongly on climatic conditions, especially rainfall and temperature (Ganzhorn et al., 2001; Wright et al., 1999). Years characterized by higher rainfall promote increased plant productivity, resulting in greater food availability for granivorous and frugivorous species.

In our study area, species densities varied significantly between the dry and wet seasons, confirming the importance of climatic seasonality in regulating tropical bird populations (Newton, 1998). Granivorous species, particularly *Foudia madagascariensis* and *Lonchura nana*, showed the greatest increases in density during the wet season, reflecting their direct dependence on seed availability. Similarly, *Coracopsis vasa* showed higher densities during periods characterized by greater fruit availability, confirming the key role of fruit resources in the population dynamics of this granivorous–frugivorous species (Ganzhorn et al., 2001).

The results of the Principal Component Analysis (PCA) revealed both similarities and differences in the population dynamics of the studied species. Granivorous species showed similar responses to variations in seed availability, whereas *Coracopsis vasa* showed a response more closely associated with fruit availability and rainfall. These differences reflect species-specific ecological adaptations and their dependence on different types of food resources (Newton, 1998).

The Canonical Correspondence Analysis (CCA) identified the main environmental factors influencing species densities. Seasonal rainfall and food resource availability were the primary factors affecting bird density variation. The duration and intensity of the dry season had a negative effect on species abundance, likely due to reduced food availability during this period (Ganzhorn et al., 2001; Wright et al., 1999).

Contrary to the assumption that movements of granivorous and frugivorous birds are driven solely by local resource depletion, our results suggest that seasonal climatic conditions also play a major role in population regulation. A longer and more intense dry season may reduce food availability and increase mortality, whereas a more favorable wet season may enhance survival and reproduction (Newton, 1998).

Our findings are consistent with other studies conducted in tropical ecosystems, which have shown that rainfall is a key factor influencing animal population dynamics (Wright & van Schaik, 1994; Walther et al., 2002). Interannual variation in rainfall can lead to significant fluctuations in food resource availability, thereby influencing species distribution and abundance (Ganzhorn et al., 2001).

It is important to note that bird population dynamics in seasonal tropical ecosystems are influenced by a complex combination of environmental factors. Food resource availability, seasonal climatic conditions, and species-specific ecological adaptations interact to determine the observed variations in abundance. Therefore, a comprehensive understanding of population dynamics requires long-term studies spanning multiple climatic cycles.

Overall, our study highlights a strong relationship between seasonal climatic variability, food resource availability, and the population dynamics of granivorous and frugivorous birds in the dry forest of Ankarafantsika National Park. The results suggest that climate change, particularly variation in rainfall and dry season duration, may have significant effects on the structure and dynamics of bird communities in seasonal tropical ecosystems.

These findings emphasize the importance of long-term monitoring of bird populations in Madagascar's dry forests to better understand the effects of climatic variability on biodiversity and to contribute to species conservation in the context of global climate change (Ganzhorn et al., 2001; Newton, 1998).

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