

INFLUENCE OF RAINFALL ON THE COMPOSITION OF A TROPICAL AVIAN ASSEMBLAGE IN NORTHEASTERN VENEZUELA

Arnaud Tarroux, Raymond McNeil¹ & Pierre Legendre

Département de Sciences biologiques, Université de Montréal, C.P. 6128, Succ. Centre-ville, Montréal, Québec, Canada H3C 3J7

Abstract. A bird assemblage was sampled every two or three weeks from May 1965 to April 1967 in a semi-arid thorn woodland in northeastern Venezuela, near Cumaná, State of Sucre. Monthly rainfalls varied greatly during the two years; 1965–66 was drier than average, while 1966–67 was rainier than usual. Birds were mist-netted and data on relative abundance, reproduction and moult cycles were compared with rainfall variations through a canonical correspondence analysis. Particular attention was paid to the abundance patterns of the diverse feeding guilds. The migrant or resident status of the species was also taken into account. Birds were expected to respond to higher rainfall levels by greater abundance and species richness. Our results agreed with this hypothesis on the whole, but the influence of rainfall fluctuations differed strongly between species; generally, migrant and/or insectivore species were more influenced than others. The feeding guilds displayed very different abundance patterns. Temporal abundance fluctuations occurred mainly through temporary immigration of transients or boreal and austral migrants. The amplitude of the response of birds to important changes in rainfall was not as high as expected, particularly in the case of the resident species. Hence increased rainfall, through higher food availability, may have profited mostly to migrant species and, to a lesser extent, to residents. *Accepted 28 September 2002.*

Key words: *Rainfall, avian assemblage, bird community, abundance fluctuations, Neotropics, Austral migrants, bird phenology, species diversity.*

INTRODUCTION

Avian assemblages often display temporal variation in structure (Fogden 1972, Poulin *et al.* 1993, Vega & Rappole 1994, Vereá *et al.* 2000) that is induced at various levels by biotic and physical factors. Such factors may be the abundance of resources (Levey 1988, Blake & Loiselle 1991, Poulin *et al.* 1992, Malizia 2001), the occurrence of migrant species (Thiollay 1973, Sinclair 1978, Lefebvre *et al.* 1994, Blake & Rougès 1997), or climate, particularly rainfall fluctuations (Karr 1980, Silkey *et al.* 1999). In seasonal tropical environments, most of the biotic factors appear to be greatly influenced by rainfall fluctuations. This is especially true for the abundance of resources, which directly determines the abundance of birds (Faaborg *et al.* 1984, Blake & Loiselle 1991, Lindsey *et al.* 1997, Bancroft *et al.* 2000). Bird assemblages usually respond to increased rainfall and resource abundance by greater species richness and bird density. Since these climatic variations are seasonal, bird as-

semblages also undergo seasonal fluctuations, leading to lower capture rates during the dry season and higher capture rates during the wet season. In spite of the important number of studies on temporal variations in tropical bird assemblages, it is still difficult to precisely foresee these variations in response to “unusual” environmental conditions. Few researchers have had the opportunity to record the reactions of avian assemblages to exceptional or extreme climatic events like drought (e.g., Faaborg 1982, Smith 1982, Stiles 1992, Jaksic & Lazo 1999). Since these events are frequent in some tropical and subtropical habitats, especially those subjected to highly seasonal climates, it is essential to gather more information on this type of assemblage-environment relationship.

This paper deals with the avian assemblage of a semi-arid region of northeastern Venezuela, monitored from May 1965 to April 1967. Important variations in rainfall were observed during this two-year sampling program (Fig. 1): the first year, 1965–66, was very dry, with an annual rainfall under the normal minimum, while the second, 1966–67, was unusually rainy, with an annual rainfall exceeding the

¹ Correspondence: E-mail: Raymond.McNeil@umontreal.ca

normal maximum. The situation was propitious to a study of the changes in the avifauna between climatically extreme years, since we can consider that the bird assemblage was the same from one year to another. This constituted a lucky opportunity for a field "mensurative experiment" (*sensu* Hurlbert 1984). That the dry and wet years occurred in succession increases their comparability. Accordingly, this study will focus on the changes in number of species and assemblage composition between 1965–66 and 1966–67, and on the relative abundance of the various species, with reference to their feeding guilds and resident or migratory status. Overall, we were expecting greater abundance and diversity during the rainier year. However, as suggested by many authors, the temporal dynamics of the various feeding guilds may vary greatly (Karr 1980, Faaborg *et al.* 1984, Poulin *et al.* 1993) and one of our goals was to evidence this differential variation. We paid particular attention to migratory species and their influence. Abundance variations in relation to rainfall were assessed through multivariate statistical analyses.

MATERIALS AND METHODS

Study area. The study took place near the city of Cumaná, State of Sucre, northeastern Venezuela. This region is characterized by a seasonal semi-arid climate: the rainy season usually occurs from May to October and the dry season from November to April (Sarmiento 1972). The study site (10°25'N, 64°11'W) was located about 5 km south of the Caribbean coast, and elevation was less than 100 m above sea level. The vegetation cover was highly disturbed following the recent development of Cumaná's outlying districts in the 1980s and 90s.

Vegetation. When bird sampling took place, the vegetation was similar to the vegetation of the northern part of the Peninsula of Araya (State of Sucre), described by Guevara de Lampe (1986). Theoretically, it corresponded to a tropical thorn forest (Sarmiento 1972), but actually at the study site it was closer to a tropical thorn woodland (due either to anthropogenic degradation of the thorn forest, or to more drastic climatic conditions associated with the drier limit of the formation). The canopy was more discontinuous than in the thorn forest, with shrubs and columnar cacti up to 5 m high, and there was no layer II (i.e., no trees of 10 to 20 m).

Among the most representative plant families were the Cactaceae, Capparidaceae, Euphorbiaceae, and

Mimosaceae. In this arid environment, plants have developed physiological, morphological, and phenological adaptations to reduce water loss (Tamayo 1967). Vegetative and reproductive activities of the plant community are determined by the annual rainfall pattern (Guevara de Lampe 1986). Three vegetative periods were observed during the sampling, and coincided in general with the vegetation phenology described by Guevara de Lampe (1986) for the Guarapo area, Peninsula of Araya, State of Sucre: (1) from September to January, foliage abundance stabilized and leaf fall began; (2) from February to April (the critical drought period), foliage loss was general among deciduous species; and (3) from May to August, important foliage recovery and growth of vegetative parts occurred. Concerning the reproduction phases, May to August were characterized by peaks in abundance of buds, flowers, and unripe and ripe fleshy fruits. Seeds of herbaceous species were mostly abundant during the second part of the dry season (i.e., from February to April). Flowering rates remained high until January, yet other resources become less abundant as early as late August.

Bird sampling. Data were collected from May 1965 to April 1967. R. McNeil captured birds during sessions of two consecutive days every two or three weeks, using eight to ten mist-nets simultaneously (3x12 m, 4 shelves, 36-mm mesh). A total of 9842 mist-net-hours (MNH, number of nets x number of hours) was carried out in 44 sessions, leading to 3281 captures. Use of mist-nets to evaluate avian relative abundance has been widely discussed, especially in tropical regions, since the method is subject to biases that call for cautious use of the data (MacArthur & MacArthur 1974, Karr 1981a, Pardieck & Waide 1992, Remsen & Good 1996, Silkey *et al.* 1999). The aim of the present study was to compare capture data during two successive years rather than to obtain an exact census of the local populations. The trapping effort averaged 23 hours per session (standard deviation = 2.2 hours), and each hour of the day was sampled at least once during each session. Net shyness was reduced by implementing an 11-day minimum interval between successive sampling sessions, and by a maximum duration of two days for each session (Karr 1981a, Vega & Rappole 1994).

Nets were separated by approximately 60 m. Their initial positions remained the same throughout the two years of sampling. The nets were tied at 0.5 m above ground level, so that they sampled the zone be-

tween 0.5 and 2.5 m high. This should give a good overview of the bird assemblage since the canopy averaged 5 m. Some species, particularly raptors, could not be sampled accurately and were excluded from the data. Poulin (1992) decided not to take the captures of Columbidae into account because they were gregarious or ground-feeding species, thus subject to important variations in capture rates. Of the five species of Columbidae captured during the present study, only the Common Ground Dove (*Columbina passerina*) and the Scaled Dove (*Scardafella squammata*) were kept in the database since they showed normal capture patterns. The other species were too rare and were not used in the statistical analyses. Hummingbirds were also integrated in the database. Although their small mass may influence capture efficiency using 36-mm-mesh nets (Karr 1981a), captures showed enough variation to be taken into account.

Nets were checked every hour on average, in order to reduce physical damage to the birds. Birds were not sampled during the night to prevent the capture of bats. Once captured, birds were identified and banded using a numbered metal ring (USFWS). In addition, moult stage, age, and presence or absence of a brood patch were noted. Age determination was based on the observation of plumage and/or cranial pneumatization, this latter method being described in detail by McNeil (1967) and McNeil & Burton (1972). Birds were classified as juveniles or adults. Moult was not recorded using the indices of Miller (1961), Ashmole (1962), or Spaans (1976) based on the primary moult. In the present study, the body was divided into seven zones, and the wing into eight zones, thus giving a body moult index ranging between 0 and 7 and a wing moult index ranging between 0 and 8. This method, proposed by McNeil (1970) in a study of migrant shorebirds, was easy and fast to use in the field. Six feeding guilds were determined following Hilty & Brown (1986), Poulin *et al.* (1992, 1993, 1994a, 1994b), and Vere *et al.* (2000): granivores (G), granivores-insectivores (GI), frugivores (F), frugivores-insectivores (FI), nectarivores-insectivores (NI), and insectivores (I). The transience rate was calculated for each year and each species when possible. It corresponds to the number of ringed birds that were never recaptured over the total number of birds ringed for that species during the given year. Results are shown in Appendix 1.

Rainfall data. Data concerning rainfall were obtained from the División de Hydrometeorología, Ministerio

de Obras Publicas, Venezuela. They provided monthly cumulative rainfall from May 1965 to April 1967 in Cumaná. Annual rainfall usually ranges from 400 to 700 mm in Cumaná, and rains occur mainly during a short period of about six months, usually representing over 80% of the annual total. From May 1965 to April 1966 rainfall was 255.7 mm, and from May 1966 to April 1967 it was 786.5 mm.

Data analyses. The similarity index of Steinhaus was used to assess abundance variation (1) between successive months (e.g., June–July 1965), and (2) between the same months of the two successive years (e.g., June 1965 and June 1966). This index, which is widely used to compare assemblage composition data, ranges from 0 to 100% depending on the degree of similarity of the two samples considered. It is calculated as follows: $S = 100 [2W/(A+B)]$, where A and B are the total numbers of individuals captured in the first and second samples respectively, and W is the sum of the minimum abundances of the various species, this minimum being defined as the abundance in the sample where the species is the rarest (Legendre & Legendre 1998). The index was computed using The R PACKAGE (Casgrain & Legendre 2001).

Since most of our data did not follow normal distributions, non-parametric tests were used to assess variations of the different variables (Scherrer 1984). For example, a Wilcoxon matched-pairs signed-rank test was used to compare monthly rainfall during the same months on two successive years instead of a matched-pairs parametric t-test. The Wilcoxon test was also used to compare the capture rate or the number of species between corresponding samples of the two successive years. There were only 20 pairs of data between 1965–66 and 1966–67. This is due to the fact that birds were not always sampled regularly, and consequently we had to eliminate the samples that did not have corresponding dates in the previous or following year. The statistical tests were computed using the TRUE EPISTAT statistical package (Gustafson 1994).

Principal component analysis (PCA) was used to compare the abundance patterns between the six feeding guilds. The objects (i.e., the rows) of the data matrix were the sampling dates. Since PCA is not suited for analyzing species abundance raw data, a Hellinger distance transformation was applied to the matrix of guilds abundance, following Legendre & Gallagher (2001). The Hellinger transformation and PCA were conducted using The R PACKAGE. Re-

sults were represented in a correlation biplot in which the correlations between descriptors (i.e., feeding guilds) are proportional to the angles formed by the arrows, ranging from about -1 when they are in perfect opposition, to about $+1$ when they form a zero-degree angle. One may assess the relative positions of the objects along a descriptor by projecting them orthogonally on the arrow representing this descriptor (Legendre & Legendre 1998).

Canonical correspondence analysis (CCA) was also used to analyze the data. This multivariate analysis technique was developed to "assess community composition to known variations in the environment" (ter Braak 1986) and is especially appropriate for species abundance data tables (Legendre & Legendre 1998). It was performed using CANOCO 3.11 (ter Braak 1989). The species composition data were modelled as a function of the monthly rainfall and five other variables: percentages of (1) breeding and (2) moulting individuals, (3) resident juveniles, (4) migratory individuals and (5) species richness. Only resident adults were taken into account to calculate the percentage of breeding individuals. Data on bird abundance correspond to the number of captures per 100 MNH for each species. Rare species (those captured ten times or less in two years) were not used in the CCA, so that we kept only 40 species out of 66. Results are represented in triplot ordination diagrams, where the axes are the first two canonical axes obtained from the analysis. Scaling type 2 was used, so

that distances between species in the diagram approximate to their χ^2 distances.

RESULTS

Monthly rainfall was markedly higher in 1966–67 than in 1965–66 (Wilcoxon matched-pairs signed-rank test, $T = 10$, $n = 12$, $P < 0.05$). Total rainfall during November and December 1966–67 represented 36.9% of the annual total, against 3.6% in 1965–66. The rainy season of 1966–67 received more precipitation and was longer than usual: a major peak occurred in August 1966, but also in November and December, which usually receive little rain and mark the beginning of the dry season (Fig. 1).

The 2341 individuals netted (corresponding to 3281 captures when taking recaptures into account) represented 17 families and 66 species, with three austral and one boreal migrants. A list of the captured species is provided in Appendix 1, with their families, feeding guilds, number of captures and recaptures, and transience rate. Rare species accounted for 39% (26) of the captured species. The Tyrannidae and Emberizidae were the most represented families, with 30.2 and 41.2%, respectively, of the total captures, and 30.3 and 19.7% of the total number of species captured. Since sampling effort (i.e., MNH) was more important during the second year ($MNH_{1965-66} = 4637$, $MNH_{1966-67} = 5205$), bird data were standardized in terms of number of captures per 100 MNH, hence corresponding to capture rates. Capture rates

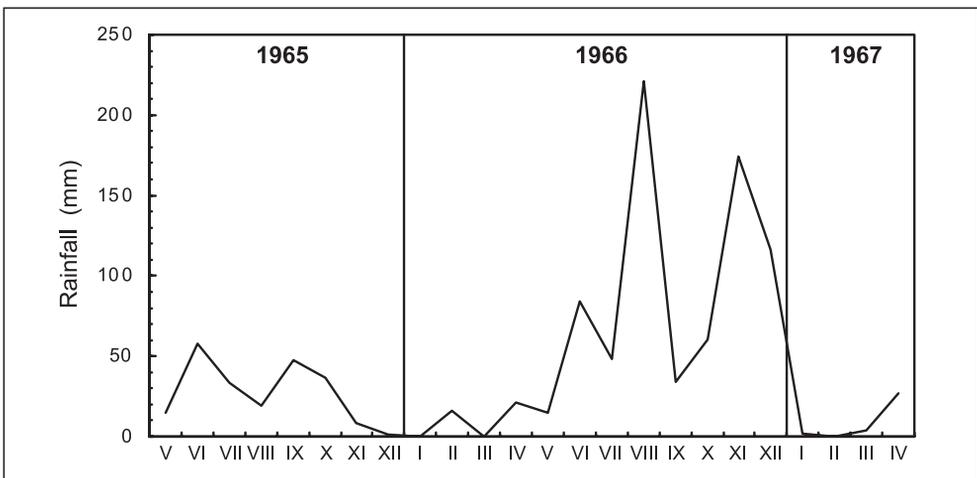


FIG. 1. Monthly rainfalls from May 1965 to April 1967. The X-axis represents time in months.

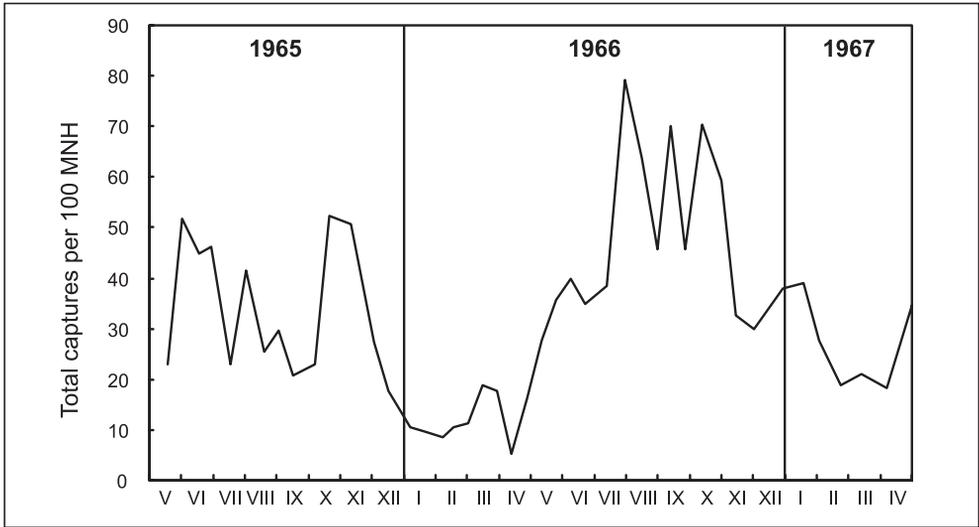


FIG. 2. Number of captures (number of birds per 100 mist-net-hours) from May 1965 to April 1967. The X-axis represents time in months.

(Fig. 2) were significantly higher during 1966–67 than 1965–66 (Wilcoxon matched-pairs signed-rank test, $T = 27$, $n = 20$, $P < 0.005$).

Figure 3 shows the change across time of the cumulative number of species captured. The rate of increase was high at the beginning of the sampling

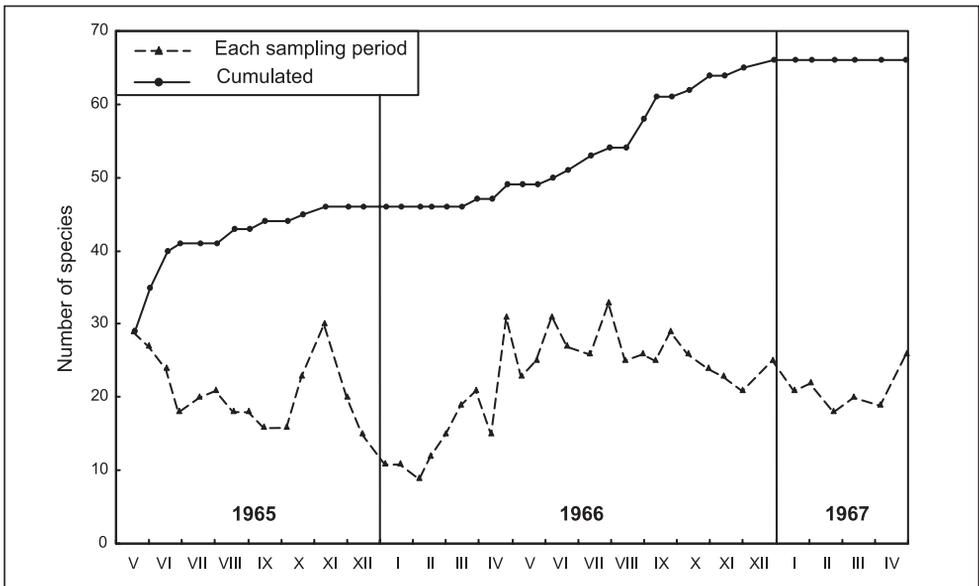


FIG. 3. Number of bird species captured during each mist-netting period, compared to the cumulative number of species captured from May 1965 to April 1967. The X-axis represents time in months.

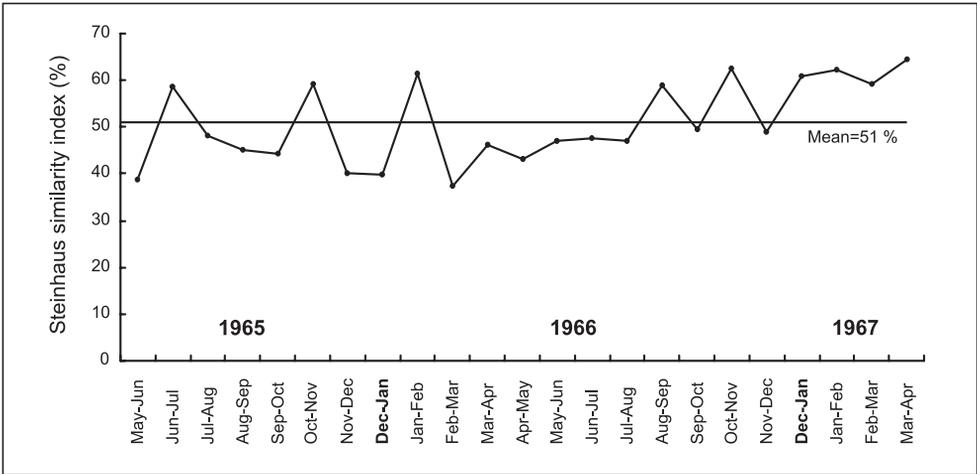


FIG. 4. Steinhaus similarity indices calculated between successive mist-netting periods from May 1965 to April 1967.

program but rapidly stabilized, during the dry season (November to May) of 1965–66, at about 2/3 (46) of the total number of species captured (66). We observed a second increase during the rainy season (August to December) of 1966, that reached the maximum of 66 in December 1966. Hence there was a difference of 20 species between the maximum of 1965–1966 and that of 1966–67. The variation in number of species captured during each netting pe-

riod is also shown on this figure. Although the two years displayed the same cyclic pattern of variation, with lower values during the drought and higher values during the rainy season, the number of species captured per netting period was significantly higher during the second year compared with the first (Wilcoxon matched-pairs signed-rank test, $T = 22$, $n = 20$, $P < 0.001$). The maximum number of species captured on any one date was 33.

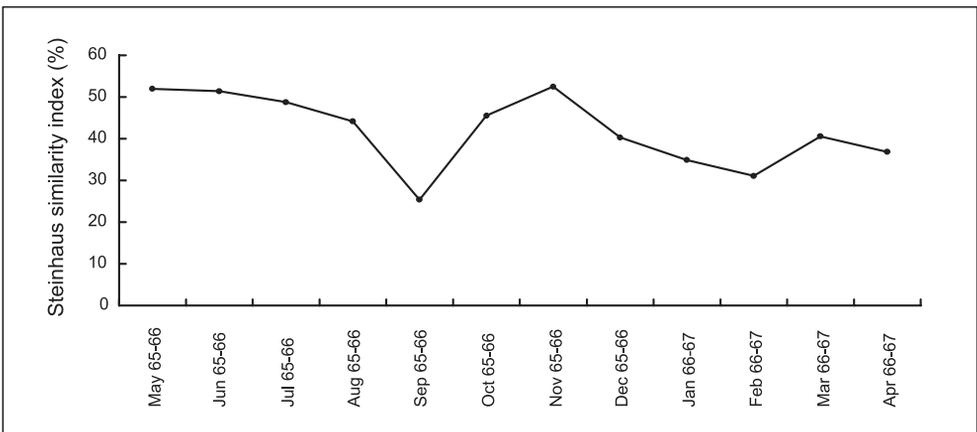


FIG. 5. Steinhaus similarity indices calculated between the corresponding months of the two successive years.

Figure 4 shows the variation of the Steinhaus similarity index calculated between successive months. The values ranged from 37.2 to 64.4%. Although the fluctuations throughout the two years were not of high amplitude, the index had higher values during the second year, indicating that the assemblage structure was more stable (Wilcoxon matched-pairs signed-

rank test, $T = 9, n = 11, P < 0.05$). The same Wilcoxon test was used to show the difference of the transience rate between the two years for the 36 species that were present during both years and were sufficiently abundant (Appendix 1). There was a strong difference, the transience being significantly higher during the first year ($T = 102, n = 36, P < 0.001$).

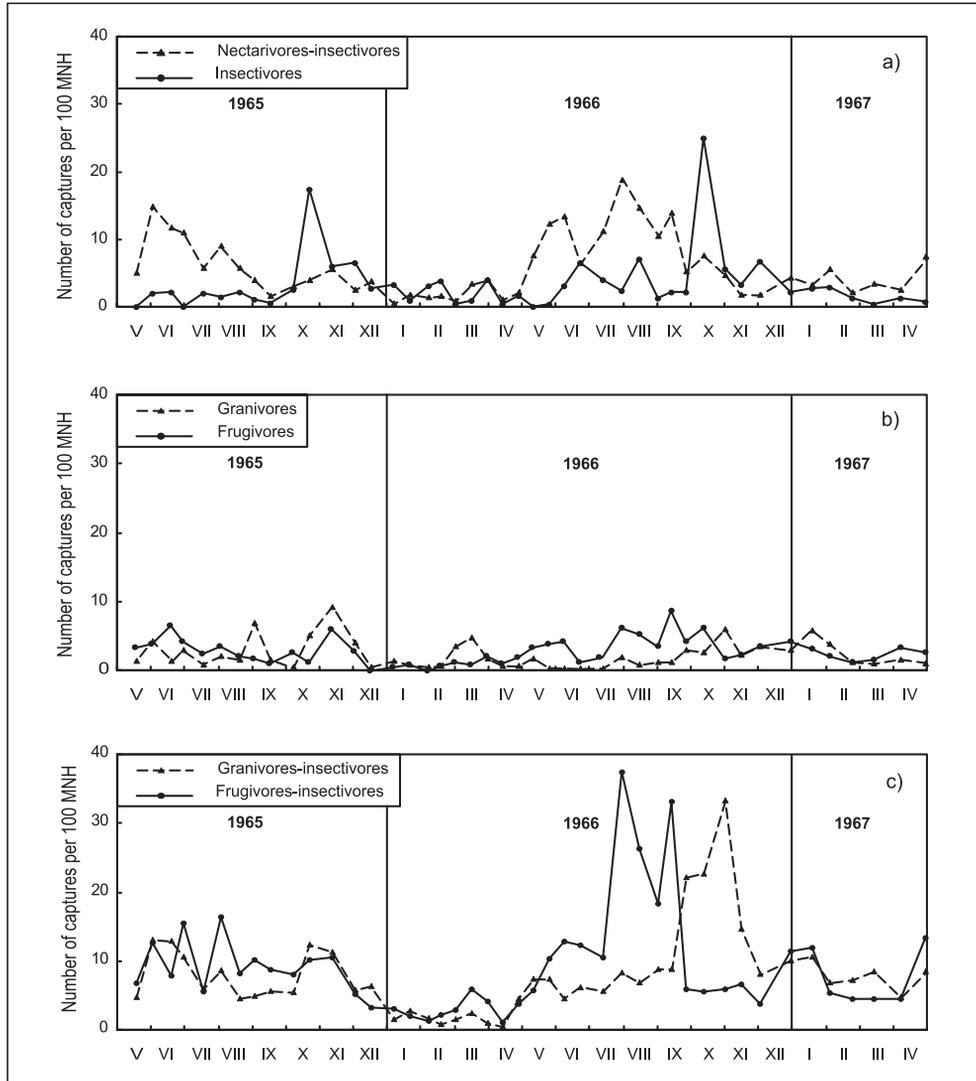


FIG. 6. Number of nectarivores-insectivores, insectivores, frugivores, granivores, frugivores-insectivores, and granivores-insectivores captured from May 1965 to April 1967. The X-axis represents time in months.

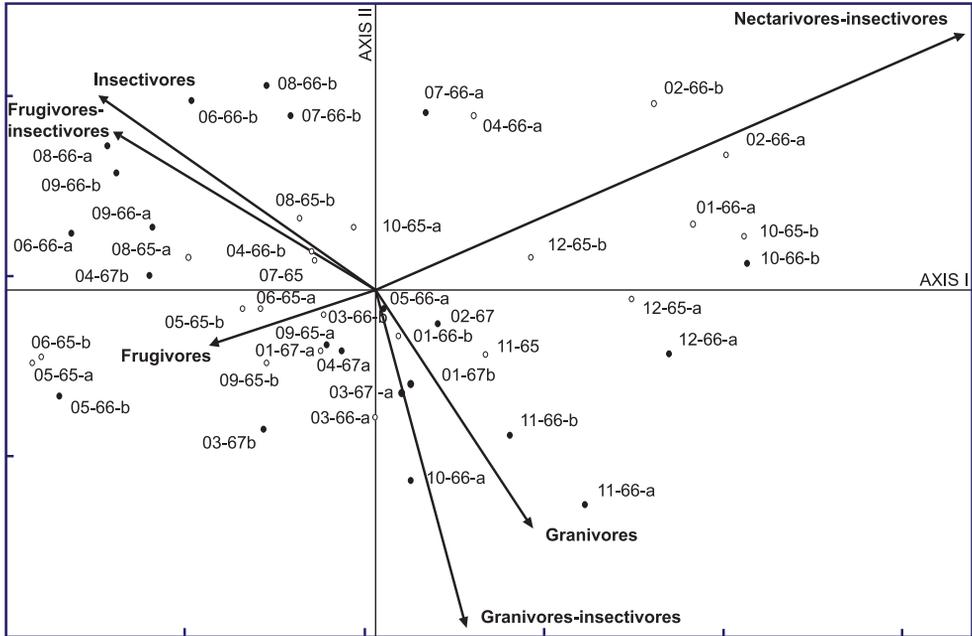


FIG. 7. Correlation biplot obtained by principal component analysis (PCA) displaying the temporal variation of the feeding guilds. The open and filled circles represent the successive mist-netting periods of the first year 1965–66 and 1966–67, respectively. Arrows represent the abundance of the six feeding guilds. Dates are written as follows: 06-66-a or 06-66-b: (06 stands for the month “June”; 66 stands for the year “1966”; “a” stands for the “first half” and “b” for the “second half” of the month concerned, i.e., for the first or the last two weeks).

The values of the Steinhaus similarity index computed between corresponding months of the two successive years are presented in Figure 5. The similarity only averaged 42.6%, showing a relatively poor resemblance between the assemblage compositions of the two years. The lowest value, 25.4%, was reached in September. The index was also low from December to February.

The feeding guilds displayed very different abundances over time (Kendall's coefficient of concordance, $n = 44$, $P = 6$, $W = 0.142$, $P < 0.0001$). Frugivores-insectivores, granivores-insectivores, and insectivores dominated with 29.4, 25.6, and 18.6% of the total captures, respectively. Figure 6 shows the captures throughout the two years for each guild. Frugivorous and granivorous species did not show any marked seasonal increase in the number of birds captured during the second year (Fig. 6b). The four other

guilds (nectarivores-insectivores, frugivores-insectivores, granivores-insectivores, and insectivores) presented cyclic patterns of variation, that were perturbed by a significant rise in the captures during August to November 1966 (Figs. 6a, c). The number of insectivores captured was always low from November to March, but increased at the end of the dry season each year, i.e., in March or April. The lowest capture rates occurred in January and February 1966, but in January and February 1967 they were somewhat higher. The season of abundance lasted five months in 1966–67 compared to three months the previous year. While some guilds, like the frugivores-insectivores and the granivores-insectivores, did not significantly differ in total representation, they differed in that their peaks of abundance were not synchronous: the abundance peak of the granivores-insectivores came after that of the frugivores-insectivores (Fig. 6c). The same was also

observed when comparing the insectivores and the nectarivores-insectivores (Fig. 6a). This latter guild seemed to have a precise cyclic pattern of variation, with significant peaks of abundance in October each year, the highest occurring in 1966–67.

Figure 7 shows the ordination of the sampling dates (objects) and feeding guild abundances (descriptors) in the reduced space formed by the first two PCA axes, which accounted for 43 and 23% of the total variance respectively. These axes were meaningful in that each one accounted for more variance than the corresponding portions of the broken stick null model (Legendre & Legendre 1998). Nectarivores-insectivores appeared to have a very different pattern of temporal variation compared with the other guilds, and particularly frugivores. The granivores and granivores-insectivores were strongly correlated, as were the insectivores and frugivores-insectivores. The latter pair was mainly associated with the rainy period of the second year (June to September 1966). The presence of granivores and granivores-insectivores was associated with the end of the rainy period of 1966–67. The nectarivores-insectivores were mostly present at the end of the rainy season and the beginning of the dry season, especially during the first year. The frugivores did not show any marked trend compared with the other guilds.

Adding the six explanatory variables to the analysis, the first two canonical axes of the CCA explained 25.3 and 7.2%, respectively, of the variance of the data. Both axes were significant (Monte Carlo test under a full model, $P < 0.01$ after 999 permutations). The six explanatory variables explained 53.0% of the variance of the data, and were all significant (Monte Carlo test, 999 permutations, $P < 0.05$).

The CCA triplot was divided into three diagrams (Figs. 8a–c), in order to facilitate reading and interpretation of the results. Six symbols represent the species, divided according to their feeding guilds; only the names of the species playing an important role in the analysis are mentioned. The arrow corresponds to the environmental variable “rainfall”, whereas the lines (without arrowhead) represent the five biotic variables. The positions of the species optima along an explanatory variable can be assessed in Figure 8c by the orthogonal projection of the species points on the explanatory variable-vector, or its extension (Legendre & Legendre 1998).

Figures 8a–b deal respectively with the ordination of the mist-netting periods of the first and second years. In both figures, a line joins the successive dates

of sampling. Since scaling type 2 implies conservation of the chi-square distances between species, it is not well-suited for a detailed comparison of the relationships among the “sites”, i.e., the netting periods. However we can still interpret the positions of the netting periods, which are approximately dispersed in these biplots, as a function of their values along the explanatory variables (ter Braak & Verdonschot 1995). We noted a substantial difference between the cycles of the two years on the biplots. The mist-netting periods of 1965–66 are more tightly grouped in the diagram than those of 1966–67. During the second year, the composition of the bird assemblage differed from the corresponding months of the previous year during June to October (the rainy season). This difference was associated with the increased rainfall of 1966–67, but also with higher species richness. Overall, however, the two years were characterized by similar cyclic patterns of variation.

Figure 8c shows the ordination of the species. Many species are grouped near the origin of the axes. This indicates the absence of important peaks of abundance at particular periods. Most of the species were not strongly associated with rainfall, except the three austral migrants [Swainson’s Flycatcher (*Myiarchus swainsoni*), Slaty Elaenia (*Elaenia strepera*), Small-billed Elaenia (*E. parvirostris*)] whose occurrence was limited to the wetter months of 1966–67. When considering the guilds, the insectivores showed the most important variation, partly due to the presence of boreal [Blackpoll Warbler (*Dendroica striata*)] and austral (Swainson’s Flycatcher and Slaty Elaenia) migratory species that appeared well isolated from the main group. The presence of three other insectivorous species [White-tailed Nightjar (*Caprimulgus cayennensis*), Greenish Elaenia (*Myiopagis viridicata*), Red-eyed Vireo (*Vireo olivaceus*)] was more associated with the breeding period of 1965–66 than with other periods. Frugivores-insectivores also had an eclectic species composition with respect to rainfall with three species [Barred Antshrike (*Thamnophilus doliatus*), White-lined Tanager (*Tachyphonus rufus*), Mouse-colored Tyrannulet (*Phaeomyias murina*)] located far from the drought period (January to March) on the diagram. Granivores, granivores-insectivores and nectarivores-insectivores were associated with the drier months, except for two nectarivores-insectivores, the Copper-rumped (*Amazilia tobaci*) and Ruby-topaz (*Chrysolampis mosquitus*) hummingbirds, which were more abundant at the beginning of the rainy season (May–June). The frugivores, though rather dispersed, were

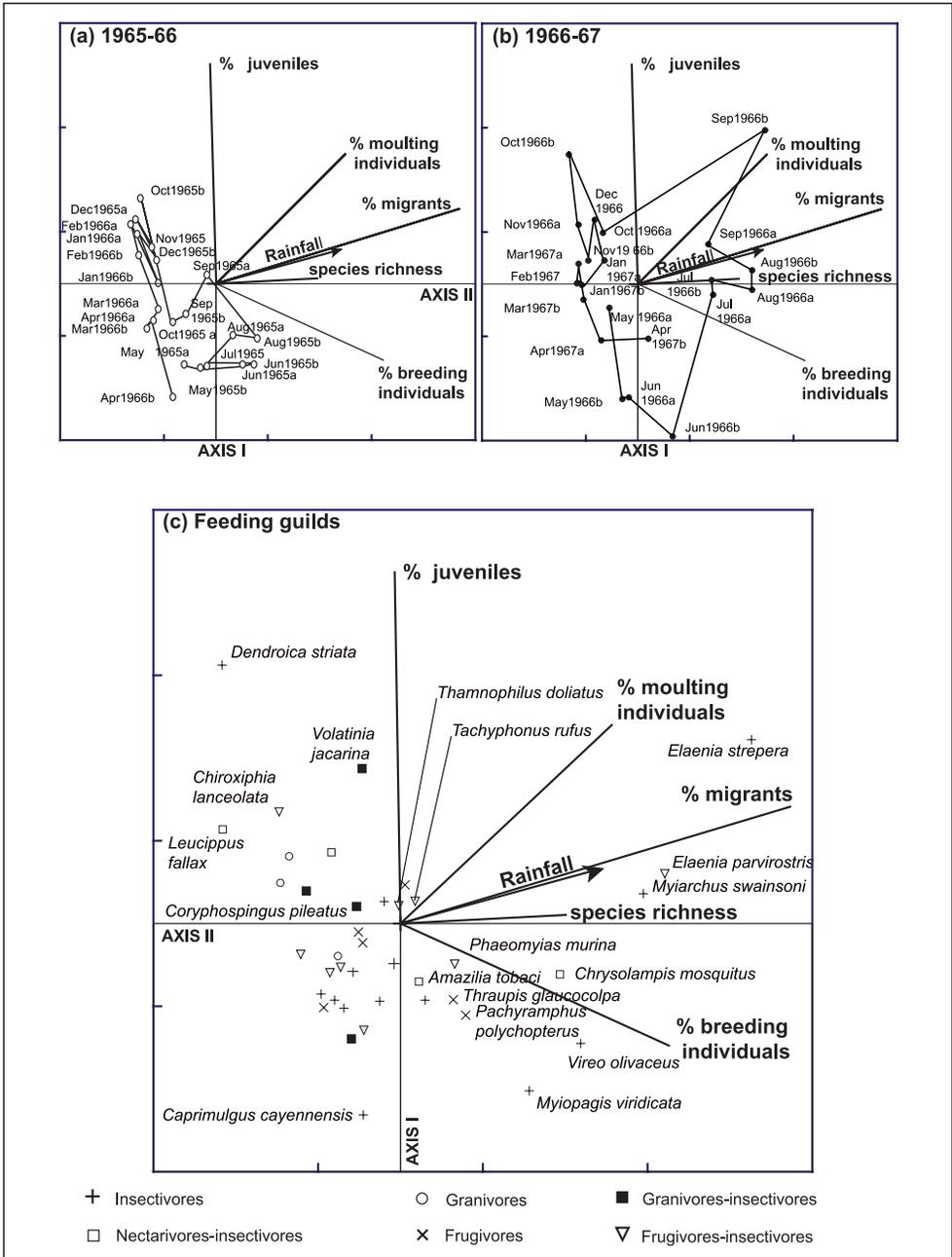


FIG. 8. Biplot diagrams obtained by canonical correspondence analysis (CCA). The results are presented in tree diagrams for clarity. The open and filled circles represent the successive mist-netting periods (a) of 1965–66 and (b) of 1966–67. The feeding guilds of the species are represented by symbols defined under the figure (c). Following months and years, “a” stands for the “first half” and “b” for the “second half” of the month, i.e. for the first or last two weeks.

not clearly influenced by the variables considered here, except for the Glaucous Tanager (*Thraupis glaucocolpa*) and the White-winged Becard (*Pachyrhamphus polychopterus*), which were captured in higher abundance during the breeding season. Overall, the six explanatory variables mainly influenced the abundance patterns of the migratory species, and, if focusing on the guilds, the insectivores.

The biotic variables (i.e., percentages of breeding and moulting individuals, migratory individuals and species richness, but not the percentage of resident juveniles) were well related to rainfall, although this variable did not explain the major part of species variance. Rainfall was clearly a determinant for the attraction of the migratory species and the richness of the assemblage. Its influence on moulting and breeding was less evident, though present. The percentage of juveniles seemed to be relatively independent of all the other explanatory variables and, interestingly, of the percentage of breeding individuals. The proportion of moulting individuals showed a very small positive correlation with the percentage of breeding individuals that indicated the breeding season.

DISCUSSION

Although the mist-netting effort was higher in 1966–67, the difference was not sufficient to explain the increase in new species captured (Fig. 3). The number of new species captured in 1966–67 is clearly associated with the increased rainfall. The total number of species (66) was rather high for this region and vegetation type, especially when taking into account the fact that mist-nets often underestimate the number of species effectively present (Karr 1981b, Vereá & Solorzano 1998). For instance, Poulin *et al.* (1993) found only 39 species during a one-year sampling in an arid thorn scrub of northeastern Venezuela. However, if we adopt the definition of a rare species used by these authors, i.e., a species representing less than 2% of the captures, 78.8% (52) of the species that we captured should be considered rare. Such a proportion is similar to that reported by Vereá & Solorzano (1998) and Vereá *et al.* (2000, 2001) in a tropical deciduous forest of northern Venezuela; it generally characterizes tropical avian assemblages.

The assemblage was clearly dominated, in number of species, by the Emberizidae and Tyrannidae. Seven of the ten most captured species were partial insectivores (FI, GI or NI), but none was strictly insectivorous. Without considering the rare species, the

insectivores represented 35% of the species, but they were less abundant than the frugivores-insectivores and granivores-insectivores. The granivores-insectivores, on the other hand, were very abundant, but they were represented by four species only. Their numerical dominance was due to the very high abundance of one particular species, Pileated Finch (*Coryphospingus pileatus*), which alone accounted for 19% of the total captures. The guilds represented by a few species only tended to be numerically more abundant and *vice versa*. In arid and seasonal environments such as the coastal part of the State of Sucre, natural selection may favour opportunistic and mobile species, which are adapted to follow the temporal variations of the resources (Poulin *et al.* 1993).

Variations in the capture rates agreed with the observations of Poulin *et al.* (1993), who noted a sharp decrease in capture rates at the beginning of the dry season. Species richness (Fig. 3) also followed this pattern, but the greater rainfalls of 1966–67, and particularly the peak in November–December 1966, apparently resulted in a higher number of species in January and February 1967. This increase in species richness was associated with greater capture rates, suggesting that competition was reduced, probably because of a better food supply.

Concerning the overall composition of the assemblage, the Steinhaus similarity index calculated between successive months (Fig. 4) had an average value of 51%, corresponding to a “quite similar” assemblage composition (Vereá *et al.* 2000). Variations of the assemblage composition were especially reduced from December 1966 to April 1967 (values of the index were high and stable throughout this period). These months are usually characterized by the absence of migrant species. The significant rainfalls of November and December 1966 may have enhanced primary productivity and arthropod abundance, thus reducing the need for transience during this period. In our case, these fluctuations were apparently not attributable to occasional captures of birds from the upper vegetation layers, as in Vereá *et al.* (2000), because the low and discontinuous canopy was sampled as well as the lower layers. Actually, this is most probably due to the presence of migrants and to a higher recruitment rate of yearlings.

The fluctuations of the Steinhaus index computed between corresponding months of the successive years (Fig. 5) are indications of yearly changes in assemblage composition. In fact, higher numbers of captures immediately followed the rainy peaks of August 1966

and November–December 1966, thus decreasing the similarity with September and December 1965 to February 1966. Hence rainfall probably modified the composition of the assemblage, but with a time lag. The early dry-season rainfall peaks of November–December 1966 led to more durable modifications of the avian assemblage, since differences with the previous year were observed during at least three consecutive months. The highest values of similarity were reached during the periods May to August and October to November. The first period corresponded to the breeding season: we expected fairly high similarities in assemblage composition between the successive years during these months. However, the similarity overall was low, even when the monthly rainfall was similar between the two years. This suggests (1) that small variations in rainfall had repercussions on the stability of the assemblage structure and (2) that other explanatory variables, or stochastic variations, were involved.

Temporary “invasion” of the area by transient and migratory flocks, due to the patchy distribution of food resources (Martin & Karr 1978, Poulin *et al.* 1993), may play a role in the important short-term fluctuations of abundance observed in these tropical assemblages. This is particularly true for the four migrant species (*Myiarchus swainsoni*, *Elaenia strepera*, *Elaenia parvirostris*, and *Dendroica striata*). The seven *D. striata* individuals captured probably corresponded to a moving migrant flock (Morse 1970) or aggregation, i.e., a group formed of at least two individuals due to a common response to extrinsic factors, such as localized food (Post 1978). Martin & Karr (1978) observed that “birds only spend a short time in a patch if resources are poor”. In fact, *D. striata* was present during one month. As these warblers were absent from the first year of sampling, we are led to believe that our study area corresponded to an occasional stopover on the route to their final wintering destination, probably in southern Venezuela (Bent 1953, Thomas 1993). Latta & Brown (1999) observed *D. striata* in a thorn scrub in the Dominican Republic and suggested that “coastal thorn scrub is important stopover habitat for migrating blackpoll warblers”. Long-term studies are needed to determine if the use of the study site region as a stopover is regular, but our data suggest that its utilization may be restricted to years of high food abundance.

Feeding guilds were differently affected by rainfall fluctuations. Frugivores and granivores were usually captured in low numbers. The PCA ordination

(Fig. 7) clearly isolated the frugivores from the other guilds, although they were not particularly associated with the rainier months. This is probably due to their low abundance, which made the observation of high-amplitude fluctuations difficult.

Tropical insect populations are subject to fluctuations that are not only inherent in their own life cycles (Bigger 1976) but are also influenced by the rainfalls controlling their food resources (Wolda 1978). The insectivorous bird species that we captured were more abundant during the rainy season and during the wetter year. As shown above, abundance peaks of insectivores during the second year were mostly due to the arrival of austral migrants during the rainy season. This period corresponds to the austral winter; this is the first reason why these species appeared to be correlated with rainfall. However, the relevant fact is that captures of *Elaenia parvirostris* and *Myiarchus swainsoni* greatly increased during the wetter year. Populations of strict granivores or frugivores were present throughout the year but were not abundant. Competition against migrants may be difficult and could lessen the benefits of greater food abundance. Concerning the species relying on both arthropods and plants as resources, they may also be efficient competitors against granivores and insectivores because they can switch from one resource to another to face changing conditions in food abundance. This may be especially true during the drought period when resources decline, forcing nectarivores–insectivores, frugivores–insectivores and granivores–insectivores to feed intensively on the remaining arthropods, fruits and seeds. Strict frugivores and granivores do not often switch to other resources when their usual resources become rare.

The lag between the abundance peaks of the frugivores–insectivores and granivores–insectivores, which was not observed during the dry year, was probably not a consequence of a lag between the production of fleshy fruits and seeds but was mainly due to the contributions of *Elaenia parvirostris* and *Coryphospingus pileatus* to the abundance of the frugivores–insectivores and the granivores–insectivores, respectively. *Elaenia parvirostris* usually departs for its southern breeding areas in September or October. The fact that this species was numerically dominant among the frugivores–insectivores explains why this feeding guild declined so rapidly in October 1967 (Fig. 6c). This disappearance did not necessarily indicate a modification of the abundance of their resources.

It is not clear why the abundance peak of the nectarivores-insectivores was so reduced in extent and occurred precisely in October, but McNeil & Rodríguez S. (1985) suggested that the second most abundant species of that guild, Buffy Hummingbird (*Leucippus fallax*), regularly left the thorn scrub habitat to avoid flower rarity and competition from other trochilid species during the rainy season. When it returns in October–November, during a period of greater flower availability (Guevara de Lampe 1986), its abundance may be high but rapidly decreases as food becomes scarce; the species is virtually absent from May to October. Thus the lag between the abundance peaks of nectarivores-insectivores and insectivores may not necessarily be attributed to negative interactions between the two guilds, but rather to intrinsic factors of variation.

Results of the CCA also indicated that guilds differed overall in their reaction to rainfall variations (Fig. 8). Most of the frugivorous and granivorous species are found near the center of the diagram (Fig. 8c), and were seemingly little influenced by the explanatory variables. The results of this analysis are particularly interesting considering the migratory species that were unequivocally more abundant during the rainy season of 1966–67. Rainfall had a positive and almost immediate effect on the species that were more mobile than residents: they could choose the areas where resources were more abundant as winter quarters. The percentage of juveniles was not well explained by rainfall. Actually, clutch size may be strongly influenced by the conditions prevailing during the three months preceding the laying date (Patten & Rotenberry 1999), or even before in some cases (Brown & Li 1996). Our analysis does not take rainfall of the previous months into account, hence the apparent independence we obtained between rain and the percentage of juveniles. Though rainfall undoubtedly influenced flower, fruit, and arthropod abundance at various levels, each species seemed to respond differently. Species with opportunistic feeding behaviour adapted more easily to temporal variations in food level and were dominant during the rainy year of 1966–67. The same appeared to be true for mobile species represented by numerous transient individuals.

This highly unpredictable habitat may have led to the evolution of these behaviours. In our study, despite the fact that monthly rainfall varied greatly between the two years, the response amplitude of the

bird assemblage was not as high as one might have expected. During exceptionally rainy years, bird species do not have enough time (1) to compensate for the “deficit” of individuals and (2) to adjust their population densities to the carrying capacity of the habitat, despite a higher recruitment of yearlings during wet years. Such adjustment is apparently done at the assemblage level by the arrival of migrants that use the area as a stopover or as winter quarters. This characteristic makes this particular environment of great value for avian diversity, since it is regularly used by boreal and austral migrant species, and also by transient species usually living in the adjacent regions.

ACKNOWLEDGMENTS

This study was financed by the Universidad de Oriente (Venezuela), the Université de Montréal, the Natural Sciences and Engineering Research Council of Canada (grant numbers OGP2632 to R. McNeil and OGP7738 to P. Legendre). We are indebted to the Shell Foundation of Venezuela for providing a vehicle during the field work. We thank José Ramón Rodríguez for help with the field work.

REFERENCES

- Ashmole, N.P. 1962. The Black Noddy *Anous tenuirostris* on Ascension Island. Part 1. General Biology. *Ibis* 103b: 235–273.
- Bancroft, G.T., Bowman, R., & R.J. Sawicki. 2000. Rainfall, fruiting phenology, and the nesting season of White-crowned Pigeons in the upper Florida Keys. *Auk* 117: 416–426.
- Bent, A.C. 1953. Life histories of North American wood warblers – Order Passeriformes. Bull. U.S. Natl. Mus. 203, Washington, DC.
- Bigger, M. 1976. Oscillations of tropical insect populations. *Nature* 259: 207–209.
- Blake, J.G., & B.A. Loiselle. 1991. Variation in resource abundance affects capture rates of birds in three lowland habitats in Costa Rica. *Auk* 108: 114–130.
- Blake, J.G., & M. Rougès. 1997. Variation in capture rates of understory birds in El Rey national park, north-western Argentina. *Ornitol. Neotrop.* 8: 185–193.
- Brown, J.L., & S.-H. Li. 1996. Delayed effect of monsoon rains influences laying date of a passerine bird living in an arid environment. *Condor* 98: 879–884.
- Casgrain, P., & P. Legendre. 2001. The R package for multivariate and spatial analysis, Version 4.0 (development release 6. – User’s manual. PDF file accompanying the free-ware. – <<http://www.fas.umontreal.ca/biol/legendre/>>).

- Casgrain, P., & P. Legendre. 2001. The R package for multivariate and spatial analysis. Version 4.0 dl. User's manual. PDF file accompanying the freeware. – <http://www.fas.umontreal.ca/BIOLOGIE/Casgrain/en/labo/R/v4/telecharger.html>.
- Faaborg, J. 1982. Avian population fluctuations during drought conditions in Puerto Rico. *Wilson Bull.* 94: 20–30.
- Faaborg, J., Arendt, W.J., & M.S. Kaiser. 1984. Rainfall correlates of bird population fluctuations in a Puerto Rican dry forest: a nine-year study. *Wilson Bull.* 96: 575–593.
- Fogden, M.P.L. 1972. The seasonality and population dynamics of equatorial forest birds in Sarawak. *Ibis* 114: 307–343.
- Guevara de Lampe, M.C. 1986. Fenología de la vegetación xerofítica de Guarapo-Oturo y Laguna de Cocos (Península de Araya, Estado de Sucre), Venezuela. *Mémoire de maîtrise (M. Sc.)*, Univ. de Montréal, Montréal.
- Gustafson, T.L. 1994. True Epistat reference manual, 5th ed. Epistat services, Richardson, Texas.
- Hilty, S.L., & W.L. Brown. 1986. A guide to the birds of Colombia. Princeton Univ. Press, Princeton, New Jersey.
- Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* 54: 187–211.
- Jaksic, F.M., & I. Lazo. 1999. Response of a bird assemblage in semi-arid Chile to the 1997–1998 El Niño. *Wilson Bull.* 111: 527–535.
- Karr, J.R. 1980. Turnover dynamics in a tropical continental avifauna. *Acta Congr. Int. Ornithol.* 17: 764–769.
- Karr, J.R. 1981a. Surveying birds with mist nets. *Stud. Avian Biol.* 6: 62–67.
- Karr, J.R. 1981b. Surveying birds in the tropics. *Stud. Avian Biol.* 6: 548–553.
- Latta, S.C., & C. Brown. 1999. Autumn stopover ecology of the Blackpoll Warbler (*Dendroica striata*) in thorn scrub forest of the Dominican Republic. *Can. J. Zool.* 77: 1147–1156.
- Lefebvre, G., Poulin, B., & R. McNeil. 1994. Temporal dynamics of mangrove bird communities in Venezuela with special reference to migrant warblers. *Auk* 111: 405–415.
- Legendre, P., & E.D. Gallagher. 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia* 129: 271–280.
- Legendre, P., & L. Legendre. 1998. *Numerical ecology*. 2nd English ed. Elsevier, Amsterdam.
- Levey, D.J. 1988. Spatial and temporal variation in Costa Rican fruit and fruit-eating bird abundance. *Ecol. Monogr.* 58: 251–269.
- Lindsey, G.D., Pratt, T.K., Reynolds, M.H., & J.D. Jacobi. 1997. Response of six Hawaiian forest birds to a 1991–1992 El Niño drought. *Wilson Bull.* 109: 339–343.
- MacArthur, R.H., & A.T. MacArthur. 1974. On the use of mist nets for population studies of birds. *Proc. Natl. Acad. Sci.* 71: 3230–3233.
- Malizia, L.R. 2001. Seasonal fluctuations of birds, fruits, and flowers in a subtropical forest of Argentina. *Condor* 103: 45–61.
- Martin, T.E., & J.R. Karr. 1978. Patch utilisation by migrating birds: resource oriented? *Ornis Scand.* 17: 165–174.
- McNeil, R. 1967. Concerning the cranial development in the Greenish Elaenia, *Myiopagis viridicata* (Vieillot). *Am. Midl. Nat.* 78: 529–530.
- McNeil, R. 1970. Hivernage et estivage d'oiseaux aquatiques nord-américains dans le nord-est du Venezuela (mue, accumulation de graisse, capacité de vol et routes de migration). *Oiseau Rev. Fr. Ornithol.* 40: 185–302.
- McNeil, R., & J. Burton. 1972. Cranial pneumatization patterns and bursa of Fabricius in North American shorebirds. *Wilson Bull.* 84: 329–339.
- McNeil, R., & J.R. Rodríguez S. 1985. Nest, seasonal movements, and breeding of Buffy Hummingbirds in xeric habitats of northeastern Venezuela. *Wilson Bull.* 97: 547–551.
- Miller, A.H. 1961. Molt cycles in equatorial Andean sparrows. *Condor* 63: 143–161.
- Morse, D.H. 1970. Ecological aspects of some mixed species foraging flocks of birds. *Ecol. Monogr.* 40: 119–168.
- Pardieck, K., & R.B. Waide. 1992. Mesh size as a factor in avian community studies using mist nets. *J. Field Ornithol.* 63: 250–255.
- Patten, M.A., & R.T. Rotenberry. 1999. The proximate effect of rainfall on clutch size of the California Gnatcatcher. *Condor* 101: 876–880.
- Post, W. 1978. Social and foraging behavior of warblers wintering in Puerto Rican coastal scrub. *Wilson Bull.* 90: 197–214.
- Poulin, B. 1992. Dynamique temporelle et composition trophique de l'avifaune des milieux xériques du nord-est du Venezuela. Thèse de doctorat (PhD.), Univ. de Montréal, Montréal.
- Poulin, B., Lefebvre, G., & R. McNeil. 1992. Tropical avian phenology in relation to abundance and exploitation of food resources. *Ecology* 73: 2295–2309.
- Poulin, B., Lefebvre, G., & R. McNeil. 1993. Variations in bird abundance in tropical arid and semi-arid habitats. *Ibis* 135: 432–441.
- Poulin, B., Lefebvre, G., & R. McNeil. 1994a. Characteristics of feeding guilds and variations in diets of bird species of three adjacent tropical sites. *Condor* 96: 354–367.
- Poulin, B., Lefebvre, G., & R. McNeil. 1994b. Diets of land birds from north-eastern Venezuela. *Condor* 96: 354–367.
- Remsen, J.V., & D.A. Good. 1996. Misuse of data from mist-net captures to assess relative abundance in bird populations. *Auk* 113: 381–398.
- Sarmiento, G. 1972. Ecological and floristic convergences between seasonal plant formations of tropical and subtropical South America. *J. Ecol.* 60: 367–410.

- Scherrer, B. 1984. Biostatistique. Gaëtan Morin, Chicoutimi, Québec.
- Silkey, M., Nur Nand, N., & G.R. Geupel. 1999. The use of mist-net capture rates to monitor annual variation in abundance: a validation study. *Condor* 101: 288–298.
- Sinclair, A.R.E. 1978. Factors affecting the food supply and breeding season of resident birds and movements of Palaearctic migrants in a tropical African savannah. *Ibis* 120: 480–497.
- Smith, K.G. 1982. Drought-induced changes in avian community structure along a montane sere. *Ecology* 63: 952–961.
- Spaans, A.L. 1976. Moults of flight and tail feathers of the Least Sandpiper in Surinam, South America. *Bird Banding* 47: 59–364.
- Stiles, F.G. 1992. Effects of a severe drought on the population biology of a tropical hummingbird. *Ecology* 73: 1375–1390.
- Tamayo, F. 1967. El espinar costanero. *Bol. Soc. Venez. Cienc. Nat.* 111: 163–168.
- ter Braak, C.J.F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67: 1167–1179.
- ter Braak, C.J.F. 1989. CANOCO – An extension of DECORANA to analyze species-environment relationships. *Hydrobiologia* 184: 169–170.
- ter Braak, C.J.F., & P.F.M. Verdonschot. 1995. Canonical correspondence analysis and related multivariate methods in aquatic ecology. *Aquat. Sci.* 57: 255–289.
- Thiollay, J.M. 1973. Ecologie des migrateurs tropicaux dans une zone pré-forestière de Côte d'Ivoire. *Terre Vie* 27: 268–296.
- Thomas, B.T. 1993. North American migrant passerines at two non-forested sites in Venezuela. *J. Field Ornithol.* 64: 549–556.
- Vega, J.H., & J.H. Rappole. 1994. Composition and phenology of an avian community in the Rio Grande plain of Texas. *Wilson Bull.* 106: 366–380.
- Verea, C., & A. Solorzano. 1998. La avifauna del sotobosque de una selva decidua tropical en Venezuela. *Ornitol. Neotrop.* 9: 161–176.
- Verea, C., Fernando-Badillo, A., & A. Solorzano. 2000. Variación en la composición de las comunidades de aves de sotobosque de dos bosques en el norte de Venezuela. *Ornitol. Neotrop.* 11: 65–79.
- Verea, C., Fernando-Badillo, A., & A. Solorzano. 2001. La comunidad de aves del sotobosque de un bosque deciduo tropical en Venezuela. *Ornitol. Neotrop.* 12: 235–253.
- Wolda, H. 1978. Seasonal fluctuations in rainfall, food and abundance of tropical insects. *J. Anim. Ecol.* 47: 369–381.

30 APPENDIX 1. Total captures and transience rates for each species with reference to families and feeding guilds.

Families (Subfamilies)	Species (English name) ^a	Feeding guilds ^b	Total captures and recaptures	Transience rates (%) ^c 1965–66	1966–67
Columbidae	<i>Claravis mondetourai</i> * (Maroon-chested Ground-Dove)		3	—	100
	<i>Columbina minuta</i> * (Plain-breasted Ground-Dove)		3	—	33
	<i>Columbina passerina</i> (Common Ground-Dove)	GI	104	89	91
	<i>Leptotila verreauxi</i> * (White-tipped Dove)		3	—	100
	<i>Scardafella squamata</i> (Scaled Dove)	GI	24	60	64
	<i>Coccyzus melacoryphus</i> * (Dark-billed Cuckoo)		8	—	75
	<i>Tapera naevia</i> * (Striped Cuckoo)		2	—	100
	<i>Caprimulgus cayennensis</i> (White-tailed Nightjar)	I	18	100	58
	<i>Nyctidromus albigollis</i> * (Common Pauraque)		5	20	—
	<i>Amazilia tobaci</i> (Copper-rumped Hummingbird)	NI	14	83	75
Trochilidae	<i>Chlorostilbon mellisugus</i> * (Blue-tailed Emerald)		8	0	100
	<i>Chrysolampis mosquitos</i> (Ruby-topaz Hummingbird)	NI	46	100	74
	<i>Glaucis hirsuta</i> * (Rufous-breasted Hermit)		1	—	100
	<i>Leucippus fallax</i> (Buffy Hummingbird)	NI	123	97	96
	<i>Galbula ruficauda</i> (Rufous-tailed Jacamar)	I	44	59	71
	<i>Hypnelus ruficollis</i> * (Russet-throated Puffbird)		5	—	100
	<i>Atalapha pilaris</i> * (Pale-eyed Pygmy-Tyrant)		7	100	67
	<i>Cnemotriccus fuscatus</i> * (Fuscous Flycatcher)		28	91	71
	<i>Cyclarhis gujanensis</i> (Rufous-browed Peppershrike)	I	3	—	100
	<i>Elaenia chiriquiensis</i> * (Lesser Elaenia)		2	—	100
Bucconidae	<i>Elaenia flavogaster</i> * (Yellow-bellied Elaenia)	FI	285	100	93
	<i>Elaenia parvirostris</i> (Small-billed Elaenia)	I	61	—	93
	<i>Elaenia strepera</i> (Slaty Elaenia)	I	42	100	67
	<i>Euscarthmus meloryphus</i> (Tawny-crowned Pygmy-Tyrant)		1	100	—
	<i>Fluiccola pica</i> * (Pied Water-Tyrant)	FI	152	52	50
	<i>Hylophilus flavipes</i> (Scrub Greenlet)	FI	72	73	54
	<i>Idioptilon margaritaceiventris</i> (Pearly-vented Tody-Tyrant)		6	60	100
	<i>Inezia subflava</i> * (Pale-tipped Tyrannulet)		1	—	100
	<i>Legatus leucophaius</i> * (Piratic Flycatcher)		3	100	50
	<i>Myiarchus cephalotes</i> * (Pale-edged Flycatcher)		1	100	—
Tyrannidae	<i>Myiarchus ferox</i> * (Short-crested Flycatcher)	I	17	50	93
	<i>Myiarchus swainsoni</i> (Swainson's Flycatcher)	FI	52	72	70

	<i>Myiopagis viridicata</i> (Greenish Elaenia)	I	55	67	49
	<i>Myiophobus fasciatus</i> (Bran-colored Flycatcher)	I	19	75	73
	<i>Pachyramphus polychopterus</i> (White-winged Becard)	FI	24	80	100
	<i>Phacomyias murina</i> (Mouse-colored Tyrannulet)	FI	208	85	64
	<i>Sublegatus arenarum</i> (Scrub Flycatcher)	FI	73	87	50
	<i>Tohnomyias flaviventris</i> (Yellow-breasted Flycatcher)	I	54	68	54
	<i>Chiroxiphia lanceolata</i> (Lance-tailed Manakin)	FI	13	—	100
Pipridae	<i>Synallaxis albenscens</i> * (Pale-breasted Spinetail)		7	67	100
Furnariidae	<i>Campylorhamphus trochilirostris</i> * (Red-billed Scythebill)		1	0	—
Dendrocolaptidae	<i>Xiphorhynchus picus</i> (Straight-billed Woodcreeper)	I	48	52	33
	<i>Formicivora grisea</i> (White-fringed Antwren)	I	95	69	52
Formicariidae	<i>Thamnophilus doliatus</i> (Barréd Antshrike)	FI	44	58	24
	<i>Vireo altiloquus</i> * (Black-whiskered Vireo)	I	1	—	100
Vireonidae	<i>Vireo olivaceus</i> (Red-eyed Vireo)	I	75	68	57
Muscicapidae (Sylviinae)	<i>Poliophtila plumbea</i> (Tropical Gnatcatcher)	I	28	50	44
Muscicapidae (Turdinae)	<i>Turdus leucomelas</i> * (Pale-breasted Thrush)		8	100	71
	<i>Turdus nudigenis</i> * (Bare-eyed Thrush)		1	—	0
Mimidae	<i>Mimus gilvus</i> (Tropical Mockingbird)	FI	13	90	67
Hirundinidae	<i>Steigidopteryx rufficollis</i> * (Rough-winged Swallow)		5	—	0
Emberizidae (Emberizinae)	<i>Arremonops cornirostris</i> (Black-striped Sparrow)	GI	13	100	50
	<i>Coryphospingus pileatus</i> (Pileated Finch)	GI	625	67	55
	<i>Sporophila lineola</i> * (Lined Seedeater)		2	—	100
	<i>Tiaris bicolor</i> (Black-faced Grassquit)	GI	165	80	65
	<i>Volatinia jacarina</i> (Blue-black Grassquit)	GI	14	—	93
Emberizidae (Parulinae)	<i>Dendroica striata</i> (Blackpoll Warbler)	I	10	—	80
	<i>Seturus noveboracensis</i> * (Northern Waterthrush)		1	—	0
Emberizidae (Coerebinae)	<i>Coereba flaveola</i> (Bananaquit)	NI	140	98	71
Emberizidae (Thraupinae)	<i>Tachyphonus rufus</i> (White-lined Tanager)	FI	41	91	73
	<i>Thraupis glaucocolpa</i> (Glaucous Tanager)	FI	48	100	73
Emberizidae (Cardinalinae)	<i>Cyanocampa cyanea</i> (Ultramarine Grosbeak)	GI	100	93	93
	<i>Saltator albicollis</i> (Streaked Saltator)	FI	155	67	68
	<i>Saltator coerulescens</i> (Grayish Saltator)	FI	21	50	54
Emberizidae (Icterinae)	<i>Icterus nigrogularis</i> (Yellow Oriole)	FI	29	100	68

^a Rare species, i.e., those captured less than 10 times, are identified by an asterisk (*).

^b Feeding guilds were determined following Hilty & Brown (1986), Poulin *et al.* (1992, 1993, 1994a, 1994b), & Vereá *et al.* (2000): Granivores (G), granivores-insectivores (GI), frugivores (F), frugivores-insectivores (FI), nectarivores-insectivores (NI) and insectivores (I).

^c Transience rate is the number of ringed birds that were never recaptured over the total number of ringed birds of the species concerned.