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Influence des variations saisonnières et annuelles de la pluviosité  
sur la composition, la reproduction et la mue d'une communauté  
aviaire au Nord-est du Venezuela

par  
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Ce mémoire intitulé :

Influence des variations saisonnières et annuelles de la pluviosité sur la  
composition, la reproduction et la mue d'une communauté aviaire  
au Nord-est du Venezuela

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a été évalué par un jury composé des personnes suivantes :

Georg Baron	président rapporteur
Raymond McNeil	directeur de recherche
Jean-Pierre Simon	membre du Jury

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## Sommaire

Ce mémoire porte sur l'analyse de données qui furent récoltées de mai 1965 à avril 1967 au Nord-est du Venezuela. Il s'agit de données sur les cycles d'abondance, de reproduction et de mue d'un peuplement d'oiseaux vivant dans un bois tropical épineux semi-aride. Les patrons de pluviosité des deux années d'échantillonnage furent très différents, la première année étant anormalement sèche et la seconde anormalement humide. Le but était de mettre en évidence les conséquences de ces fluctuations climatiques sur les divers cycles biologiques de ce peuplement aviaire.

Le présent ouvrage a été organisé en deux parties sous forme d'articles scientifiques. Le premier article étudie, à l'aide d'analyses quantitatives multidimensionnelles, les variations d'abondance et de composition du peuplement en fonction du facteur pluie. Il y est plus particulièrement question des variations spécifiques à chaque guildes alimentaire, ainsi que de l'influence des espèces migratrices sur les fluctuations d'abondance que l'on observe à l'échelle du peuplement. Le second article traite des cycles de reproduction et de mue selon une approche descriptive.

Bien que les variations de pluviosité aient eu une influence nette, elles ne se sont pas manifestées exactement de la façon dont nous l'avions envisagé au départ. Ainsi, l'année la plus pluvieuse fut plus profitable aux migrateurs qu'aux résidents. Au niveau des cycles de mue et de reproduction, les pluies ont influencé principalement les taux de survie ou de recrutement des juvéniles.

**Mots-clés** : Oiseaux · Tropiques · Bois épineux · Saisons · Guildes alimentaires

## Abstract

This work is based on data that were collected from May 1965 to April 1967 in northeastern Venezuela. The data concern the cycles of abundance, reproduction and molt of the avian community of a semi-arid tropical thorn woodland. Rainfall patterns differed greatly between the two sampling years, the first one being unusually dry while the second one was very wet. The aim of the study was to feature out the consequences of these climatic fluctuations on the biological cycles of the bird community.

The thesis is divided in two parts corresponding to two articles. The first article studies, through multidimensional quantitative analyses, the variations of abundance and composition of the avian community. A special attention is paid to the specific variations of each feeding guild, and to the influence of migrating species on the abundance fluctuations at the community level. The second article analyses reproduction and molt cycles with a descriptive approach. Although rainfall variations significantly influenced the bird community, the influence was not in the predicted direction. The rainy year seemed actually more profitable to the migrants than to the residents. Concerning the reproduction cycles, the influence of rainfall was observed mainly on the survival and recruitment rates of juveniles.

**Key words :** Birds · Feeding guilds · Seasons · Thorn woodland · Tropics

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## Liste des sigles et des abréviations

PCA	Principal component analysis
CCA	Canonical correspondence analysis
MNH	Mist-net hours
G	Granivores
F	Frugivores
I	Insectivores
GI	Granivores-insectivores
FI	Frugivores-insectivores
NI	Nectarivores-insectivores

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## **Introduction générale**

La présente recherche se situe dans le domaine de l'écologie des peuplements aviaires. Le but était de mettre en évidence, à l'aide d'outils statistiques appropriés, l'influence des variations saisonnières et annuelles de pluviosité sur divers aspects de l'écologie d'un peuplement aviaire tropical. Bien que ce thème ait déjà été abordé dans d'autres études, les données sur lesquelles ce travail s'est basé semblaient suffisamment originales pour justifier que l'on s'y attarde une fois de plus. Les données expérimentales furent récoltées de mai 1965 à avril 1967 au Nord-est du Venezuela par R.McNeil. J'ai moi-même effectué la revue des articles scientifiques, l'ensemble des analyses statistiques ainsi que la rédaction des deux manuscrits en vue d'une soumission dans deux revues scientifiques spécialisées. L'apport des coauteurs des deux articles consistait en la revue et la correction du texte et des analyses statistiques.

Les variations temporelles d'abondance sont caractéristiques de la plupart des espèces d'oiseaux tropicaux (Loiselle, 1988; Poulin et al. 1993). Ces variations sont en général reliées à la quantité et à la qualité des ressources, lesquelles dépendent principalement, dans les habitats saisonniers, de la répartition et de l'importance des pluies (Leck, 1972; Karr, 1976; Wolda, 1978; Blake and Loiselle, 1991; Poulin et al., 1992 et 1993). De nombreuses études se sont portées sur l'influence que la variation saisonnière de certains facteurs environnementaux comme la pluie peut avoir sur différents aspects de l'écologie des oiseaux (Keast, 1968; Leck, 1972; Loiselle, 1988; Blake and Loiselle, 1991; Jaksic and Lazo, 1999; Bancroft et al. 2000). Il en ressort qu'en plus d'influencer l'abondance globale et la composition des peuplements, la pluviosité a aussi des répercussions majeures sur les cycles de reproduction et de mue. Cependant l'impact des variations annuelles de la pluviosité a été plus rarement abordé. On peut donc se demander comment les peuplements aviaires s'adaptent, à court terme, aux variations des patrons de pluviosité (i.e., la quantité de pluie mais

aussi la répartition des pluies au cours du cycle annuel) entre plusieurs années successives. Ceci semble particulièrement important dans les milieux où ces variations sont de forte amplitude.

La corrélation positive entre l'abondance des oiseaux et la pluviosité est communément admise en ce qui concerne les régions tropicales où sévit une saison sèche plus ou moins longue, que ce soit à l'intérieur d'un cycle annuel (Levey, 1988; Poulin et al. 1993) ou bien d'une année à l'autre (Faaborg et al. 1984). Ces fluctuations d'abondance sont habituellement accompagnées de variations similaires au niveau de la richesse spécifique, c'est-à-dire du nombre d'espèces observées. L'influence de la pluie est indirecte et se manifeste surtout par des changements saisonniers du niveau des ressources alimentaires (Faaborg et al. 1984; Martin and Karr, 1986; Blake and Loiselle, 1991; Lindsey et al. 1997), à savoir la biomasse végétale (les fleurs, les fruits charnus ou secs et les feuilles; voir par exemple Guevara de Lampe, 1986) et les arthropodes (Sinclair, 1978; Poulin et al. 1993; Lefebvre et al. 1994). Ainsi, durant certaines périodes de l'année, les oiseaux sont soumis à des réductions drastiques de la quantité de ressources disponibles. Pour faire face à ce phénomène plusieurs stratégies ont été développées, parfois simultanément, comme l'adoption de régimes alimentaires peu spécialisés ou opportunistes (Poulin, 1992), ou bien l'existence de déplacements saisonniers chez certaines espèces, dites transitoires, vers des zones voisines plus riches en ressources (Sinclair, 1978; Poulin et al. 1993).

Les cycles de mue et de reproduction sont, aussi, largement saisonniers chez les oiseaux tropicaux (Friedmann and Smith, 1950; Snow and Snow, 1964; Hau et al. 1999; Marini and Durães, 2001). Cependant, contrairement aux régions tempérées, les facteurs environnementaux qui régissent la périodicité de ces cycles dans les régions tropicales sont moins évidents. Dans les zones subéquatoriales (latitude inférieure à  $15^\circ$ ), les variations annuelles dans la photopériode journalière sont d'amplitude relativement faible (Hau et al. 1999), et il est depuis longtemps supposé que les

oiseaux de ces régions ne peuvent véritablement les utiliser pour ajuster leur cycle reproducteur (Skutch 1950; Moreau, 1950; Miller, 1959; Fogden, 1972). Plusieurs études ont démontré, depuis les années 1940, qu'un grand nombre d'espèces d'oiseaux tropicaux sont sensibles et répondent aux changements de la longueur du jour qui se produisent aux latitudes tempérées (e.g., Rollo and Domm, 1943, *in* Hau et al. 1999). Pourtant, une grande partie des études subséquentes portant sur des espèces tropicales dans leur propre milieu se sont concentrées sur la pluviosité ou la nourriture comme facteurs principaux (e.g. : Wolf, 1970; Poulin et al. 1992 et 1993; Brown and Li, 1996; Bancroft et al. 2000). Et il apparaît en effet que ces facteurs sont prépondérants en tant qu'initiateurs ou régulateurs des cycles de reproduction (Feinsinger and Swarm, 1982; Wunderle Jr. 1982; Boag and Grant, 1984). En fait, comme le mentionnent Hau et al. (1999), lorsqu'il s'agit d'espèces qui vivent en milieux ouverts ou perturbés, l'influence de ces facteurs surpasse souvent celles de facteurs plus discrets, tel que le photopériodisme. Ceci contraste avec les milieux fermés de sous-bois, qui subissent théoriquement un effet tampon relativement aux facteurs climatiques. L'influence du photopériodisme serait donc relativement restreinte dans les milieux subéquatoriaux ouverts, particulièrement lorsque les conditions climatiques sont extrêmes et soumises à des variations saisonnières marquées.

La partie expérimentale de la présente étude fut réalisée en périphérie de Cumaná, sur la côte Nord du Venezuela, c'est-à-dire à une latitude d'environ 10°N. Cette région est caractérisée par un climat saisonnier semi-aride. Les données, récoltées sur deux années consécutives (mai 1965 à avril 1966 et mai 1966 à avril 1967) par R. McNeil, concernent plusieurs aspects de l'écologie du peuplement d'oiseaux de cette région, en particulier les patrons d'abondance, de reproduction et de mue. Le recueil des données était effectué par la capture d'oiseaux à l'aide de filets japonais de 3 x 12 m. Les oiseaux étaient bagués et relâchés après la prise en note des diverses variables étudiées.

Les détails des techniques utilisées seront abordés plus loin dans les sections consacrées à la méthodologie.

Le milieu dans lequel l'étude fut conduite correspondait théoriquement, à ce moment-là, à un bois tropical épineux, selon la définition de Sarmiento (1972). Ce dernier définissait dans son étude quatre strates végétales : (I) avec des arbres supérieurs à 20 m, (II) avec des arbres entre 10 et 20 m, (III) avec des espèces ligneuses entre 2 et 10 m et (IV) avec des arbustes et des espèces succulentes entre 50 cm et 2 m de haut. Notre site d'étude n'était composé que des strates III et IV, et la strate III, très ouverte, ne dépassait pas 5 m de hauteur. La strate herbacée était discontinue et très réduite durant les mois les plus secs (janvier à mars). En réalité le milieu se situait à un stade intermédiaire entre le bois épineux ("thorn woodland") et la formation arbustive épineuse ("thorn scrub"), à cause notamment d'une quantité importante de cactacées présentes à la fois dans les strates III et IV. Les périodes végétatives seront abordées plus loin mais de façon assez générale, car aucune donnée précise à ce sujet ne fut récoltée durant la phase expérimentale de l'étude. C'est pourquoi il sera fait référence principalement aux travaux de Guevara de Lampe (1986) et Poulin (1992) qui furent conduits dans des milieux similaires, dans la même région du Venezuela.

Le climat est caractérisé par une saison sèche très marquée, qui a lieu habituellement de novembre à avril. Il arrive fréquemment qu'aucune goutte de pluie ne tombe pendant deux ou trois mois consécutifs durant cette période. La pluviosité annuelle varie normalement entre 400 et 700 mm de pluie, dont 80% en moyenne tombent durant la saison des pluies, soit de mai à octobre. Cependant cette pluviosité peut varier de façon substantielle d'une année à l'autre et se trouver en dehors de ces limites. Durant la période l'échantillonnage, 255.7 mm de pluie sont tombés la première année et 786.5 mm la seconde année. À l'augmentation significative de pluviosité durant la seconde année était aussi associée une prolongation de la période des pluies, avec l'occurrence de deux pics importants en novembre et décembre 1966. Les données sur le peuplement aviaire ont



donc été recueillies durant deux années consécutives dont les patrons de pluviosité respectifs différaient grandement. Cette situation, exceptionnelle, nous a permis d'évaluer d'une part les variations temporelles de la composition d'un peuplement d'oiseaux tropicaux de milieu semi-aride en fonction de la pluviosité, et d'autre part sa phénologie (*sensu* Poulin et al. 1992), c'est-à-dire les relations entre les cycles de reproduction et de mue et les variations saisonnières des pluies. Deux approches différentes ont été adoptées pour étudier (1) les variations temporelles d'abondance et de composition et (2) les cycles biologiques cités plus haut (reproduction et mue).

La première partie cherche à expliquer, par l'intermédiaire d'analyses quantitatives multidimensionnelles, à quel point la composition du peuplement aviaire a pu, dans son ensemble, être affectée par les variations brutales de pluviosité qui furent enregistrées. Une attention particulière a été portée aux patrons d'abondance relatifs aux diverses guildes alimentaires représentées au sein de ce peuplement, ainsi qu'au rôle des espèces migratrices (australes et boréales) qui utilisent plus ou moins régulièrement cette zone comme site d'hivernage. Comme mentionné plus haut, les conditions climatiques durant les deux années d'échantillonnage furent exceptionnelles, et par le fait même justifient une étude, même simplement descriptive, des données recueillies. Le fait que l'échantillonnage ait été réparti sur deux années successives (au lieu de deux années isolées) dégageait l'étude de certains biais et constituait donc un avantage. Par exemple le site était inchangé d'une année à l'autre et la végétation n'avait pas subi de modifications majeures, d'origine anthropiques ou non, qui auraient pu avoir des conséquences sur la composition du peuplement aviaire et éventuellement sur les cycles biologiques des oiseaux. De plus les données étaient récoltées régulièrement, toutes les deux ou trois semaines, pendant deux ans. En ce sens cette étude constituait ce que Hurlbert (1984) nomme "*mensurative experiment*" : bien que seules deux années soient comparées, chacune d'elle était constituée de plus d'une vingtaine d'échantillons et il s'agissait donc d'analyser deux groupes de mesures et non pas seulement deux mesures. Les

deux méthodes d'analyse quantitative multidimensionnelle utilisées pour ce travail sont l'analyse en composantes principales et l'analyse canonique des correspondances. Elles seront décrites ultérieurement en détail mais l'on peut déjà signaler que pratiquement elles ne comparent pas deux années l'une à l'autre, mais bel et bien les 44 échantillons (i.e., les 44 résultats issus des séances de captures) entre eux. Cela signifie que, d'un point de vue statistique, elles sont valides et solides car le nombre d'observations est suffisant. C'est l'interprétation qui en est faite qui permet de regrouper les dates d'échantillonnage en deux groupes correspondant aux deux années consécutives (cf. Fig. 8a et b p. 46). Ces analyses consistent en fait à mettre en évidence l'existence d'une corrélation entre l'abondance des espèces d'oiseaux et la pluviosité ainsi qu'à montrer quelle fraction de la variance observée au niveau de l'abondance peut-être expliquée par les divers facteurs environnementaux. Il est vrai que l'interprétation de ces variations ne peut mener à une généralisation ou une modélisation des effets de la pluie sur la composition et les cycles biologiques du peuplement aviaire en question. Il faudrait pour cela effectuer un échantillonnage sur un nombre d'années beaucoup plus grand. Néanmoins cela permet, d'une part, de décrire efficacement les phénomènes qui ont pu être mis en cause temporairement sur le site d'étude et, d'autre part, d'avoir une idée assez précise des phénomènes plus généraux à moyen et long terme qui ont une influence sur le peuplement aviaire. Cela revient finalement à définir cette étude comme étant plutôt de nature exploratoire que confirmatoire.

La seconde partie de l'étude repose sur une approche plus descriptive, et s'attache principalement à observer et analyser les variations qui ont pu avoir lieu, entre 1965-66 et 1966-67, dans le déroulement des cycles de reproduction et de mue, à l'échelle du peuplement ou de l'espèce dans certains cas. L'ensemble de ce travail permettra de dégager en partie les fondements adaptatifs de ce peuplement face aux importantes variations climatiques de son environnement.

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**Article 1**

**Influence of rainfall on the composition of a tropical  
avian community in northeastern Venezuela**

Arnaud Tarroux · Raymond McNeil · Pierre Legendre

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**Abstract**

A bird community was sampled every two or three weeks from May 1965 to April 1967 in a semi-arid thorn woodland in northeastern Venezuela. 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 to 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 globally agreed with this hypothesis but the influence of rainfall fluctuations differed strongly among species; generally, migrants 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 considering the resident species. Hence increased rainfall, through higher food availability, may have profited mostly to migrant species and, to a lesser extent, to the residents.

**Key words** avian community · rainfall · abundance · feeding guild · tropics



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## Introduction

Avian communities often display temporal variation in structure (Fogden, 1972; Poulin et al. 1993; Vega and Rappole, 1994; Vereá et al. 2000), which is induced at various levels by biotic and physical factors. Such factors may be the abundance of resources (Levey, 1988, Blake and Loiselle, 1991; Poulin et al. 1992; Malizia, 2001), the occurrence of migrant species (Thiollay, 1973; Sinclair, 1978; Lefebvre et al. 1994; Blake and Rougès, 1997), or climate, and particularly rainfall fluctuations (Karr, 1980; Silkey, 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, i.e., individuals and species (Faaborg et al. 1984; Blake and Loiselle, 1991; Lindsey et al. 1997; Bancroft et al. 2000). In spite of the important number of studies on temporal variations in tropical birds communities, it is still difficult to foresee precisely these variations in response to "unusual" environmental conditions. Few researchers had the opportunity to report the reactions of avian assemblages to exceptional or extreme climatic events like drought (e.g., Faaborg, 1982; Smith, 1982; Stiles, 1992; Jaksic and 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 community-environment relationship.

This paper deals with the avian community of a semi-arid region of northeastern Venezuela, monitored from May 1965 to April 1967. Important variations in rainfall were observed during this two-years sampling programme (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 normal maximum. The situation was ideal for a study of the changes in the avifauna between climatically extreme years. 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 community 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. Globally, 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 have been assessed through multivariate statistical analyses.

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## Methods

### Study area

The study took place near the city of Cumaná, State of Sucre, northeastern Venezuela. This region is characterised 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. Its vegetation cover was highly disturbed following the development of Cumaná's outlying districts in the 80's.

### 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 anthropic 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 column cacti up to 5 m high, and there was no layer II (i.e., no trees from 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 loss of water (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 globally coincided with the vegetation phenology described by Guevara de Lampe (1986) for the Guarapoto area, Peninsula of Araya, State of Sucre: (1) from September to January, foliage abundance stabilised and leaf fall began; (2) from February to April (the critical drought period), the foliage loss was generalised among deciduous species; and (3) from May to August, important foliage recovery and growth of the vegetative parts occurred. Concerning the reproduction phases, May to August were featured 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 soon as late August.

#### Bird sampling

Data were collected from May 1965 to April 1967. R. McNeil captured birds during two consecutive days every two or three weeks, using eight to ten mist-nets simultaneously (3 x 12 m, 4 shelves, 36-mm mesh). A total of 9842 mist-net-hours (MNH, number of nets x number of hours) were carried out in 44 sessions, leading to 3281 captures. Use of mist-nets to evaluate avian relative abundance has been widely discussed, since the method is subject to biases which call for a

cautious use of the data (MacArthur and MacArthur, 1974; Karr, 1981a; Pardieck and Waide, 1992; Remsen and Good, 1996; Silkey et al. 1999). The aim of the present study was to compare capture data between two successive years and the comparison should be valid since biases were the same in both years. The trapping effort averaged 23 hours per session (standard deviation = 2.2 hours), and each period of the day was sampled at least once during each session. Net shyness was reduced by implementing an 11-day minimum interval between successive samplings, and by a maximum duration of two days for each session (Karr, 1981a; Vega and 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 between 0.5 and 2.5 m high. This should give a good overview of the bird community since the canopy averaged 5 m. Some species, particularly raptors, could not be sampled correctly 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.

In order to reduce physical damage to the birds, nets were checked every hour on average. 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 (U.S.F.W.S.). In addition moult stage, age, and presence or absence of a brood patch were noted. We did not use the indices of Miller (1961), Ashmole (1962), or Spaans (1976), which are based on the moult of the primary feathers, to record

the moult index. 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 gave interesting results in a study on shorebirds (McNeil, 1970), and was of easy and fast use in the field. Six feeding guilds were determined following Hilty and Brown (1986), Poulin et al. (1992, 1993, 1994a and b), and Vereá et al. (2000): granivores (G), granivores-insectivores (GI), frugivores (F), frugivores-insectivores (FI), nectarivores-insectivores (NI), and insectivores (I). No distinction was made between the different types of insectivores (e.g., flycatchers or gleaners). Indeed we think the feeding behaviour had little or even no incidence on the capture rates, since the canopy was low and all species were supposed to fly within the vertical range of the mist-nets. 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 concerning rainfall were obtained from the *División de Hydrometeorología, Ministerio de Obras Públicas, 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 community

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 respectively in the first and second samples, and W is the sum of the minimum abundance of the various species, this minimum being defined as the abundance in the sample where the species is the rarest (Legendre and Legendre, 1998). The index was computed using the R Package (Casgrain and 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 components 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 analysing species abundance raw data, a Hellinger distance transformation was applied to the matrix of guilds abundance, following Legendre and Gallagher (2001). The Hellinger transformation and PCA were conducted using the R Package.

Canonical correspondence analysis (CCA) was also used to analyse 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 and Legendre, 1998). It was performed using Canoco 3.11 (ter Braak, 1989). The species composition data were modelled as a function of the monthly rainfalls and five other variables: percentages of (1) breeding and (2) moulting individuals, (3) resident juveniles, (4) migratory individuals and (5) the 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 over 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 among species in the diagram approximate their  $\chi^2$  distances.

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## 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, with reference to their families, feeding guilds, number of captures-recaptures, and transience rate. Rare species accounted for 39% (26) of the captured

species. The Tyrannidae and Emberezidae were the most represented families, with respectively 30.2 and 41.2% of the total captures, and 30.3 and 19.7% of the total number of species captured. Since sampling effort (in MNH) was more important during the second year ( $MNH_{1965-66} = 4637$ ,  $MNH_{1966-67} = 5205$ ), bird data were standardised in terms of number of captures per 100 MNH, hence corresponding to capture rates. Capture rates (Fig. 2) were significantly more important during 1966-67 than in 1965-66 (Wilcoxon matched-pairs signed-rank test,  $T = 27$ ,  $n = 20$ ,  $P < 0.005$ ).

Figure 3 shows the evolution across time of the cumulated number of species captured. The rate of increase was high at the beginning of the sampling programme but rapidly stabilised, 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, which 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 period 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, there were differences between 1965-66 and 1966-67. The number of species captured during netting periods was significantly lower during the first year, compared to the second (Wilcoxon matched-pairs signed-rank test,  $T = 22$ ,  $n = 20$ ,  $P < 0.001$ ). The maximum number of species captured at any one date was 33.

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 community structure was more stable (Wilcoxon matched-pairs signed-rank test,  $T = 9$ ,  $n = 11$ ,  $P < 0.05$ ). The same Wilcoxon test was used to feature 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). There was a strong difference, the transience being very significantly higher during the first year ( $T = 102$ ,  $n = 36$ ,  $P < 0.001$ ).

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 community 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 abundance 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 respectively 29.4, 25.6, and 18.6% of the total captures. 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, which were perturbed by an important rise of the captures during August to November 1966 (Figs. 6a and 6c). 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 in 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 important 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 abundance (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 and Legendre, 1998). Results were represented in a correlation biplot in which the correlation between two descriptors (i.e., feeding guilds) is 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 and Legendre 1998). Nectarivores-insectivores appeared to have a very different pattern of temporal variation compared to the other guilds, and particularly frugivores. The granivores and granivores-insectivores were strongly correlated, and so 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 to the other guilds.

Adding the six explanatory variables to the analysis, the first two canonical axes of the CCA explained respectively 25.3 and 7.2% 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 (a, b, and c in Fig. 8), 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 Fig. 8c, by the orthogonal projection of the species points on the explanatory variable-vector, or its extension (Legendre and Legendre, 1998).

Figures 8a and 8b 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 among 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 and 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 community 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. Globally, however, the two years were characterised by similar cyclic patterns of variations.

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 (*M. swainsoni* and *E. strepera*) 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 to the breeding period of 1965-66 than to 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 dryer 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 not clearly influenced by the variables considered here, except for the Glaucous Tanager, *Thraupis glaucocolpa* and the White-winged Becard, *Pachyramphus polychopterus*, which were captured in higher abundance during the breeding season. Globally, 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 the species variance. Rainfall was clearly determining for the attraction of the migratory species and the richness of the community. 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, noteworthy, of the percentage of breeding individuals. The proportion of moulting individuals presented a very small positive correlation with the percentage of breeding individuals that indicates the breeding season.

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## Discussion

Although the mist-netting effort was higher in 1966-67, the difference was not sufficient to explain the increase of 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 and Solarzano, 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 and Solarzano (1998) and Vereá et al. (2000, 2001) in a tropical deciduous forest of northern Venezuela; it generally characterises tropical avian communities.

The community was clearly dominated, in number of species, by the Emberezidae 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 contrary, 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, *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 of the capture rates agreed with the observations of Poulin et al. (1993) who noticed 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 community, the Steinhaus similarity index calculated between successive months (Fig. 4) had an average value of 51%, corresponding to a "quite similar" community composition (Verea et al. 2000). Variations of the community 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 characterised by the absence of migrant species. The important rainfalls of November and December 1966 may have enhanced primary productivity and arthropod abundance, thus reducing the need of 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 Verea 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 community 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 community, but with a time lag. The early dry-season rainfall peaks of November-December 1966 led to more durable modifications of the avian

community, 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 community composition between the successive years during these months. However, the similarity was globally 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 community 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 and Karr, 1978; Poulin et al. 1993), may play a role in the important short-term fluctuations of abundance observed in these tropical communities. 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 by at least two individuals due to a common response to extrinsic factors, such as localised food (Post, 1978). Martin and 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 and Brown (1999) observed *D. striata* in a thorn scrub of 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 region of the study site as a stopover is regular, but our data suggest that its utilisation may be restricted to years of high food abundance.

Feeding guilds were differently affected by rainfall fluctuations. Frugivores and granivores were usually little captured. 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 insects 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. Actually, this period corresponds to the austral winter; this is the first reason why these species appeared to be correlated to rainfall. However, the relevant fact is that the captures of *Elaenia parvirostris*, and *Myiarchus swainsoni*, were greatly improved 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 a 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 use to switch to other resources when their usual resources rarefy.

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. *E parvirostris* usually departs to 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 abundance of their resources.

It is not clear why the abundance peak of the nectarivores-insectivores was so reduced in extent and precisely occurred in October, but McNeil and Rodríguez (1985) suggested that the second most abundant species of that guild, *Leucippus fallax*, was regularly leaving the thorn scrub habitat to avoid flower rarity and competition from other trochilid species during the rainy season. When it comes back in October-November, during a period of greater flower availability (Guevara de Lampe, 1986), its abundance may be high but rapidly decreases as food rarefies; the species becomes 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 globally differed in their reaction to rainfall variations (Fig. 8). Most of the frugivorous and granivorous species are found near the centre 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 for winter quarters the areas where resources were more abundant. 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 and Rotenberry, 1999) or even before in some cases (Brown and 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 flowers, fruits, and arthropod abundance at various levels, each species seemed to respond differently. Species with opportunistic feeding behaviour adapted more easily to temporal variations of 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 community was not as high as one might have expected. During exceptionally rainy years, bird species do not have enough time (1) to compensate the "deficit" of individuals and (2) to adjust their population densities to the carrying capacity of the habitat, despite a more important recruitment of yearlings during wet years. Such adjustment is apparently done at the community 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.

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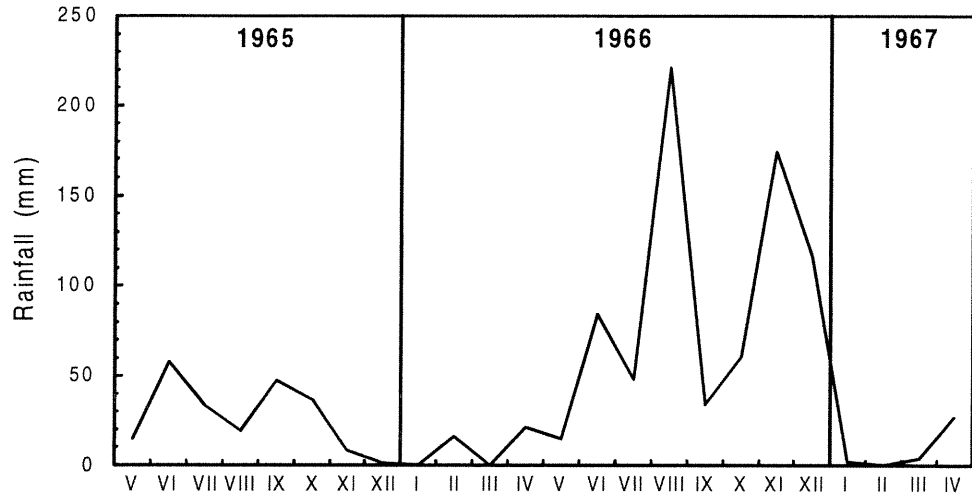
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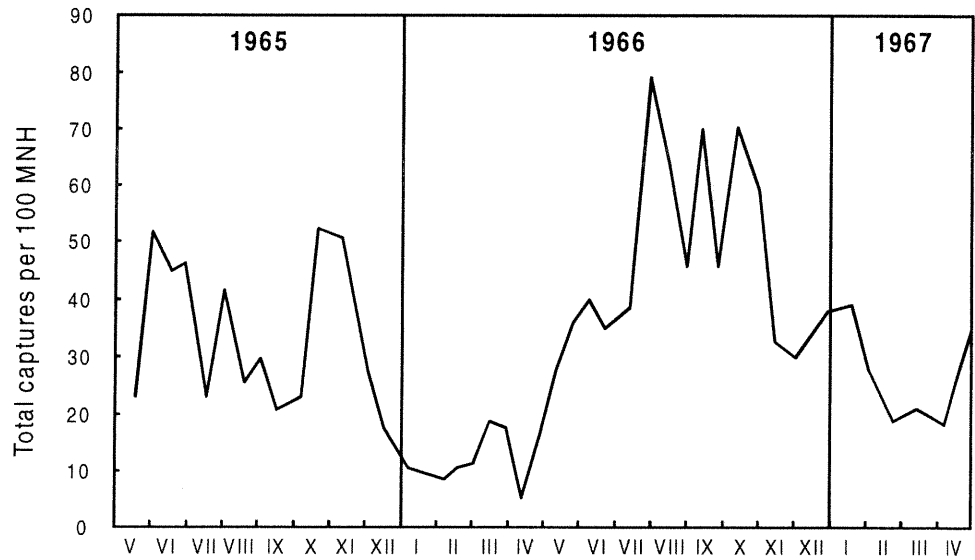
## Figures

- Figure 1 Monthly rainfalls from May 1965 to April 1967.
- Figure 2 Number of captures (number of birds per 100 mist-net-hours) from May 1965 to April 1967.
- Figure 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.
- Figure 4 Steinhaus similarity indices calculated between successive mist-netting periods from May 1965 to April 1967.
- Figure 5 Steinhaus similarity indices calculated between the corresponding months of the two successive years.
- Figure 6 Number of nectarivores-insectivores, insectivores, frugivores, granivores, frugivores-insectivores, and granivores-insectivores captured from May 1965 to April 1967.
- Figure 7 Correlation biplot obtained by principal component analysis (PCA) displaying the temporal variation of the feeding guilds. The empty and full 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.

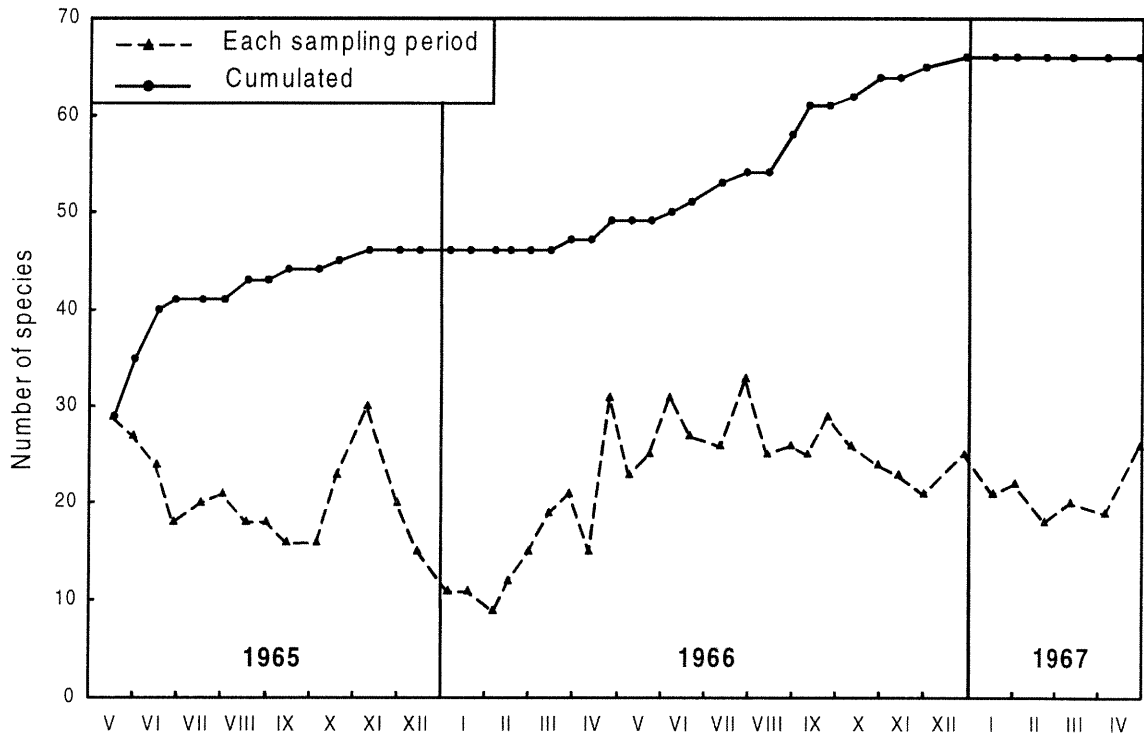
Figure 8      Biplot diagrams obtained by canonical correspondence analysis (CCA). The results are presented in three diagrams for clarity. The empty and full circles represent the successive mist-netting periods (a) of 1965-66 and (b) of 1966-67. (c) The feeding guilds of the species are represented by symbols defined under the figure.



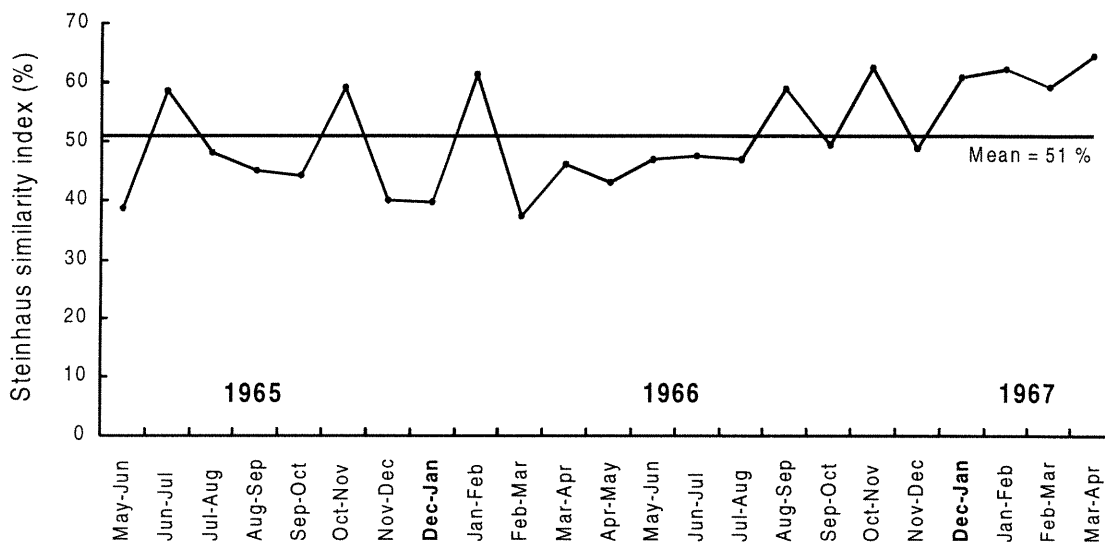
Tarroux et al., Fig. 1



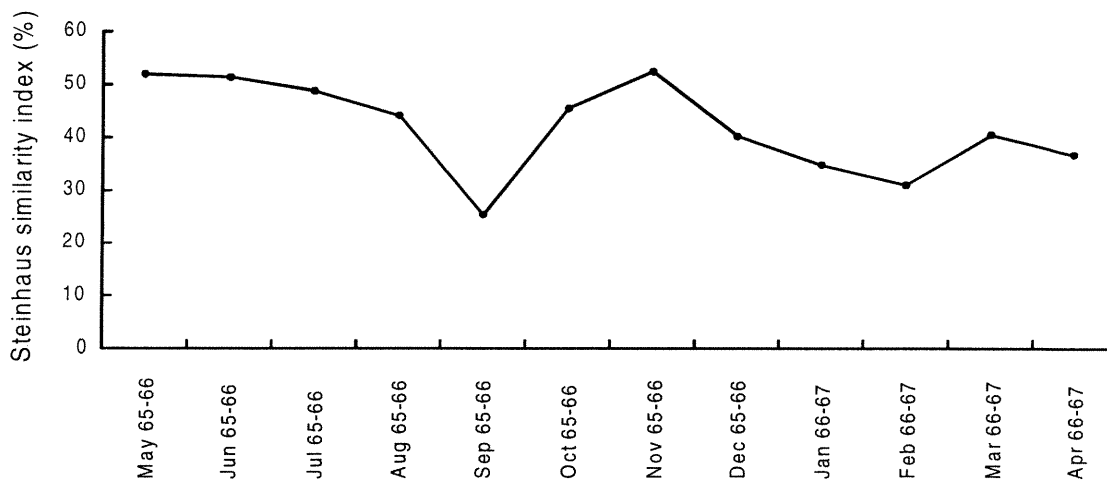
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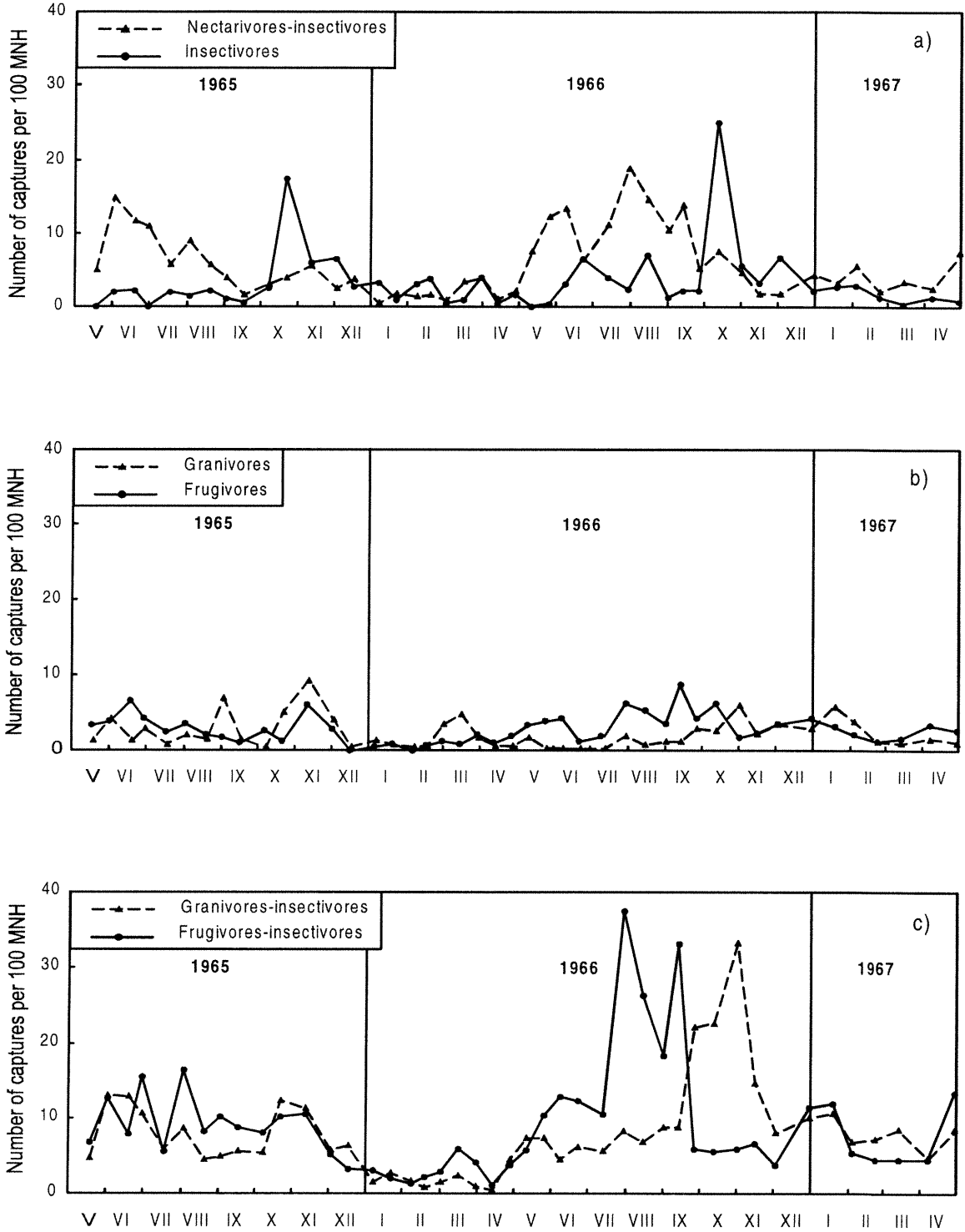
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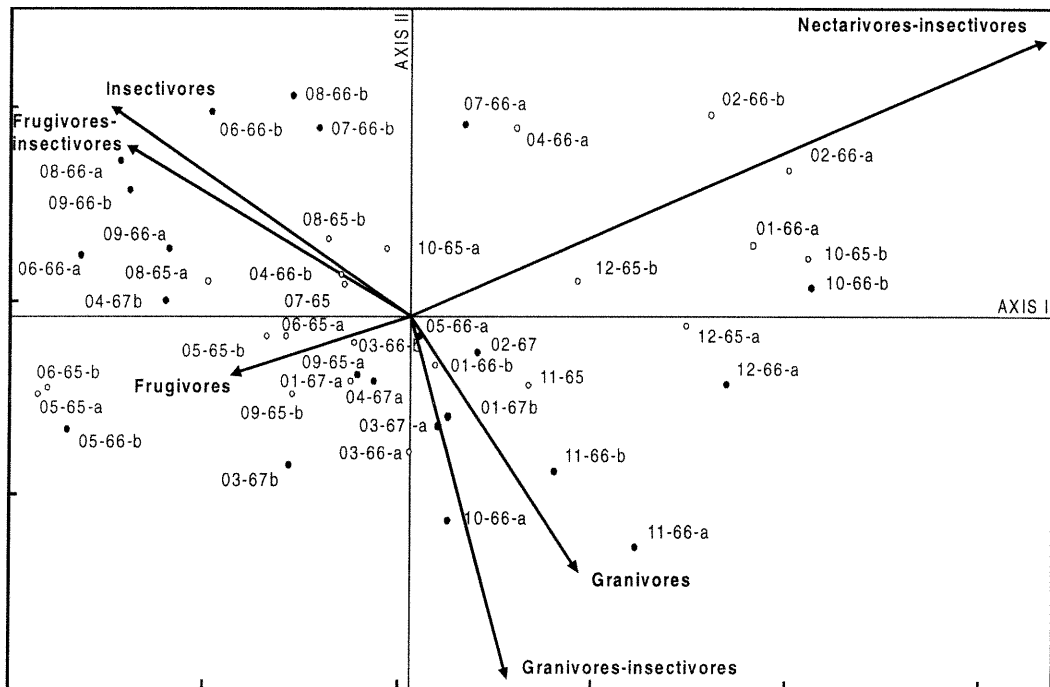
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Tarroux et al., Fig. 5

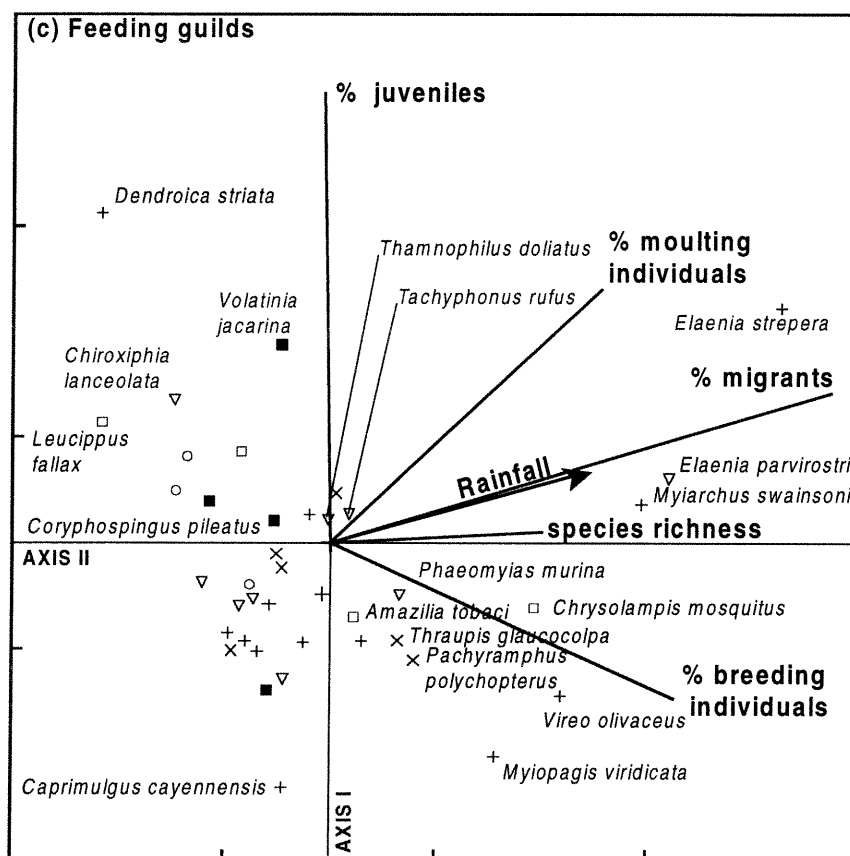
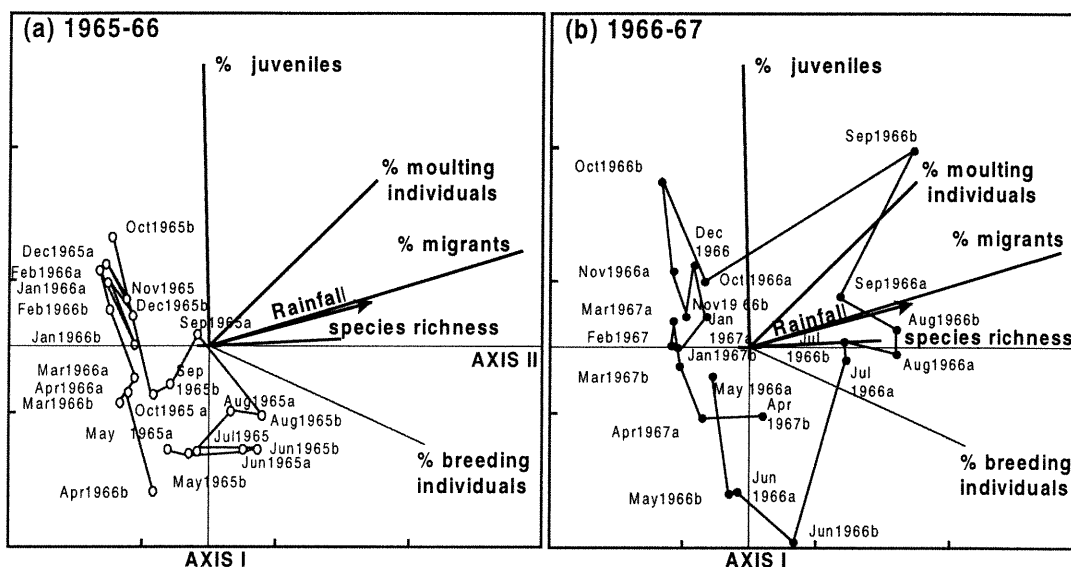


Tarroux et al., Fig. 6



Tarroux et al., Fig. 7





- + Insectivores
- Granivores
- Granivores-insectivores
- Nectarivores-insectivores
- × Frugivores
- ▽ Frugivores-insectivores

Tarroux et al., Fig. 8

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

Families (Subfamilies)	Species (English name) <sup>a</sup>	Feeding guilds <sup>b</sup>	Total captures and recaptures	Transience rates (%) <sup>c</sup>
			1965–66	1966–67
Bucconidae	<i>Hypnelus ruficollis</i> (Russet-throated Puffbird)		1	100
Caprimulgidae	<i>Caprimulgus cayennensis</i> (White-tailed Nightjar)	I	18	58
Columbidae	<i>Nyctidromus albicollis</i> (Pauraque)		5	–
	<i>Claravis mondetoura</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	91
	<i>Leptotila verreauxi</i> (White-tipped Dove)		3	100
	<i>Scardafella squammata</i> (Scaled Dove)	GI	24	64
Cuculidae	<i>Coccyzus melacoryphus</i> (Dark-billed Cuckoo)		8	75
	<i>Tapera naevia</i> (Striped Cuckoo)		2	100
Dendrocolaptidae	<i>Campilorhamphus trochilirostris</i> (Red-billed Scythebill)		1	–
	<i>Xiphorhynchus picus</i> (Straight-billed Woodcreeper)	I	48	33
Emberizidae (Cardinalinae)	<i>Cyanocompsa cyanea</i> (Ultramarine Grosbeak)	GI	100	93
	<i>Saltator albicollis</i> (Streaked Saltator)	FI	155	68
Emberizidae (Coerebinae)	<i>Saltator coerulescens</i> (Grayish Saltator)	FI	21	54
	<i>Coereba flaveola</i> (Bananaquit)	NI	140	71
Emberizidae (Emberizinae)	<i>Arremonops cornirostris</i> (Black-striped Sparrow)	GI	13	50
	<i>Coryphospingus pileatus</i> (Pileated Finch)	GI	625	55

Appendix 1. Continued.

Families (Subfamilies)	Species (English name) <sup>a</sup>	Feeding guilds <sup>b</sup>	Total captures and recaptures	Transience rates (%) <sup>c</sup>	
				1965–66	1966–67
Emberizidae (Emberizinae)	<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 (Icterinae)	<i>Icterus nigrogularis</i> (Yellow Oriole)	FI	29	100	68
Emberizidae (Parulinae)	<i>Dendroica striata</i> (Blackpoll Warbler)	I	10	–	80
	<i>Seiurus noveboracensis</i> (Northern Waterthrush)		1	–	0
Emberizidae (Thraupinae)	<i>Tachyphonus rufus</i> (White-lined Tanager)	FI	41	91	73
	<i>Thraupis glaucocolpa</i> (Glaucous Tanager)	FI	48	100	73
Formicariidae	<i>Formicivora grisea</i> (White-fringed Antwren)	I	95	69	52
	<i>Thamnophilus doliatus</i> (Barred Antshrike)	FI	44	58	24
Furnariidae	<i>Synallaxis albescens</i> (Pale-breasted Spinetail)		7	67	100
Galbulidae	<i>Galbula ruficauda</i> (Rufous-tailed Jacamar)	I	44	59	71
Hirundinidae	<i>Steigodopteryx rufficollis</i> (Rough-winged Swallow)		5	–	0
Mimidae	<i>Mimus gilvus</i> (Tropical Mockingbird)	FI	13	90	67
Muscicapidae (Sylviinae)	<i>Polioptila 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
Pipridae	<i>Chiroxiphia lanceolata</i> (Lane-tailed Manakin)	FI	13	–	100

**Appendix 1. Continued.**

Families (Subfamilies)	Species (English name) <sup>a</sup>	Feeding guilds <sup>b</sup>	Total captures and recaptures	Transience rates (%) <sup>c</sup>
				1965–66    1966–67
Trochilidae	<i>Amazilia tobaci</i> (Copper-rumped Hummingbird)	NI	14	83    75
	<i>Chlorostilbon mellisugus</i> (Blue-tailed Emerald)		8	0    100
	<i>Chrysolampis mosquitus</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
Tyrannidae	<i>Atalotriccus pilaris</i> (Pale-eyed Pygmy-Tyrant)		5	100    33
	<i>Cnemotriccus fuscatus</i> (Fuscous Flycatcher)		7	100    67
	<i>Cyclarhis gujanensis</i> (Rufous-browed Peppershrike)	I	28	91    71
	<i>Elaenia chiriquensis</i> (Lesser Elaenia)		3	–    100
	<i>Elaenia flavogaster</i> (Yellow-bellied Elaenia)		2	–    100
	<i>Elaenia parvirostris</i> (Small-billed Elaenia)	FI	285	100    93
	<i>Elaenia strepera</i> (Slaty Elaenia)	I	61	–    93
	<i>Euscarthmus meloryphus</i> (Tawny-crowned Pygmy-Tyrant)	I	42	100    67
	<i>Fluvicola pica</i> (Pied Water-Tyrant)		1	100    –
	<i>Hylophilus flavipes</i> (Scrub Greenlet)	FI	152	52    50
<i>Idioptilon margaritaceiventris</i> (Pearly-vented Tody-Tyrant)	FI	72	73    54	
<i>Inezia subflava</i> (Pale-tipped Tyrannulet)		6	60    100	
<i>Legatus leucophaeus</i> (Piratic Flycatcher)		1	–    100	

**Appendix 1. Continued.**

Families (Subfamilies)	Species (English name) <sup>a</sup>	Feeding guilds <sup>b</sup>	Total captures and recaptures	Transience rates (%) <sup>c</sup>	
				1965–66	1966–67
Tyrannidae	<i>Myiarchus cephalotes</i> (Pale-edged Flycatcher)		3	100	50
	<i>Myiarchus ferox</i> (Short-crested Flycatcher)		1	100	–
	<i>Myiarchus swainsoni</i> (Swainson's Flycatcher)	I	17	50	93
	<i>Myiarchus tyrannulus</i> (Brown-crested 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>Pachyrhamphus polychopterus</i> (White-winged Becard)	FI	24	50	100
	<i>Phaeomyias murina</i> (Mouse-colored Tyrannulet)	FI	208	85	64
	<i>Sublegatus arenarum</i> (Scrub Flycatcher)	FI	73	87	50
	<i>Tolmomyias flaviventris</i> (Yellow-breasted Flycatcher)	I	54	68	54
Vireonidae	<i>Vireo altiloquus</i> (Black-whiskered Vireo)		1	–	100
	<i>Vireo olivaceus</i> (Red-eyed Vireo)	I	75	68	57

<sup>a</sup> Rare species, i.e. those captured less than 10 times, are in grey.

<sup>b</sup> Feeding guilds were determined following Hilty and Brown (1986), Poulin et al. (1992, 1993, 1994a, 1994b), and Vereza et al. (2000): granivores (G), granivores-insectivores (GI), frugivores (F), frugivores-insectivores (FI), nectarivores-insectivores (NI) and insectivores (I).

<sup>c</sup> Transience rate is the number of ringed birds that were never recaptured over the total number of ringed birds for the species concerned.

**Article 2**

**Breeding and moulting phenology of birds in a seasonal environment  
of northeastern Venezuela**

Arnaud Tarroux · Raymond McNeil

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**Abstract**

In this study we sampled a bird community during two successive years in a thorn woodland of northeastern Venezuela. Birds were mist-netted every two or three weeks and age, moult stage and presence or absence of a brood patch were noted. These two years of sampling were characterised by important rainfall fluctuations. The first year had a relatively short wet season, with an annual rainfall under the minimum average. On the contrary, the second year had a longer wet season and received more rain than the maximum annual average. The succession of unusually dry and wet years constituted an opportunity to compare the influence of high-amplitude climatic variations on the breeding and moulting cycles of birds. We expected a strong influence of rainfall on the breeding activity, and to a lesser extent on moult. The variations of the biological cycles were described mainly at the community level. It appeared that the increase of rainfall during the second year influenced particularly the fledglings abundance, but not appreciably breeding and moulting cycles. Timing of rainfall also played an important role.

**Key words** Bird community · rainfall · breeding · moult · tropics

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## Introduction

Tropical bird communities may present very different patterns of reproduction depending on the region they inhabit, and more specifically on the climate of this region (Beals, 1970). Rainfall has long been considered as the main external factor controlling reproduction in tropical arid or semi-arid seasonal environments (Gilliard, 1959; Snow and Snow, 1964; Boag and Grant, 1984). Usually in wetter zones, where the dry season is short and of low amplitude, birds avoid to breed during heavy rains (Moreau, 1950). But this cycle is reversed in tropical arid or semi-arid regions where the breeding period occurs during the rainy season, whether rains are heavy or not (Friedmann and Smith, 1955; Beals, 1970). When seasonal variations of environmental factors are less marked, like in tropical wet forests, other factors such as the presence of migrants during certain periods of the year may induce circannual cycles in breeding (Miller, 1963). Existence of a well-defined breeding period may have consequences on the prebasic (i.e., postnuptial) moult. Although these two phenomena are usually considered as mutually exclusive (Pitelka, 1958; Miller, 1961 and 1963), it is not rare to observe breeding and moulting overlap in certain species (Hahn et al., 1992), especially in regions where the period of resources abundance is short (Holmes, 1966).

The study we present here was carried out from May 1965 to April 1967 in a tropical thorn woodland of northeastern Venezuela, corresponding to a tropical semi-arid climate with a highly seasonal repartition of rainfall (Sarmiento, 1972; Poulin, 1992). In addition, rainfall is subjected to high-amplitude yearly fluctuations, and the beginning and end of the rainy season may vary greatly from one year to another. Annual rainfall usually ranges from 400 to 700 mm, and rains occur mainly during a period of about 6 months (May to October), usually representing over 80% of annual total. The avian community of this region is also greatly influenced by migrants and transient species that more or less regularly invade the area, owing to the fluctuating resources abundance (Tarrowx et al.



*In prep.*). Birds have thus to deal with these two principal elements to adjust their breeding cycles, considering that reproduction success should increase following higher resource levels and/or lower competition. During the first year of sampling, rainfall was below the normal average, with an annual total of 255.7 mm. On the contrary, the second year was unusually rainy, with a longer wet season and an annual total of 786.5 mm. This exceptional succession of two extreme years was an unlooked-for opportunity to study the short-term adaptation mechanisms of this avian community to such climatic events. We were in fact expecting a strong influence of the rainfall fluctuations on the birds' biological cycles, without knowing exactly at which stage of the reproduction cycle this influence would be the most important. Breeding and moulting cycles were firstly described for the community level in order to reveal the general patterns involved. A few species were then observed more precisely to determine the specific influence of the heavy rainfall variations.

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## Study site

The study was conducted near the city of Cumaná, State of Sucre, northeastern Venezuela (Fig. 1). This region is characterised 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 situated about 5 kilometres south of the Caribbean coast. Its vegetation cover was highly disturbed following the development of Cumaná's outlying districts in the 80's.

When bird sampling took place, the vegetation was similar to the vegetation of Guarapo Oturo, in the northern part of the Peninsula of Araya, 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 anthropic 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 column cacti up to 5 m high, and there was no layer II (i.e., no trees from 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 loss of water (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 globally coincide with the vegetation phenology described by Guevara de Lampe (1986) for the Guarapo area: (1) from September to January, foliage abundance stabilised and leaf fall began; (2) from February to April (the critical drought period), the foliage loss was generalised among deciduous species; and (3) from May to August, important foliage recovery and growth of the vegetative parts occurred. Concerning the reproduction phases, May to August were featured 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 soon as late August.

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## Methods

Data were collected from May 1965 to April 1967. Birds were captured by R. McNeil during two consecutive days every two or three weeks, using eight to ten mist-nets simultaneously (3 x 12 m, 4 shelves, 36-mm mesh). A total of 9842 mist-net-hours (MNH, number of nets x number of hours) were carried out in 44 sessions, leading to 3281 captures. Use of mist-nets to evaluate avian relative abundances has been widely discussed, since the method is subjected to a bias which calls for a cautious use of the data (MacArthur and MacArthur, 1974; Karr, 1981; Pardieck and Waide, 1992;

Remsen and Good, 1996; Silkey et al, 1999). The aim of the present study was to compare capture data between two successive years and the comparison should be valid since biases were the same in both years. The trapping effort averaged 23 hours per session, and each period of the day was sampled at least one time each session. Net shyness was reduced by implementing an 11-day minimum interval between successive samplings, and by a maximum duration of two days for each session (Karr, 1981; Vega and Rappole, 1994).

The mist-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 between 0.5 and 2.5 m high. This should give a good overview of the bird community since the canopy averaged 5 m. Some species, particularly raptors, could not be sampled correctly and were excluded from the data.

In order to reduce physical damages to birds, nets were checked every hour in average. Sampling was not carried out during the night to prevent the capture of bats. Captured birds were identified and banded using a numbered metal ring (U.S.F.W.S.). Moulting stage, age, and presence or absence of a brood patch were noted for each capture. We did not use the indices of Miller (1961), Ashmole (1962), or Spaans (1976), which are based on the moult of the primary feathers, to record the moult index. In our case, the body was divided in seven zones, and the wing in eight zones, thus giving a body moult index ranging between 0 and 7 and a wing moult index ranging between 0 and 8. The seven body zones correspond to the seven major pterygiae, i.e. the capital, spinal, caudal, humeral, femoral, crural and ventral tracts. The wing was divided as follows: primaries, secondaries, greater primary coverts, greater secondary coverts, median primary coverts, lesser coverts, marginal coverts and underwing coverts. This method has given interesting results in a study on shorebirds (McNeil, 1970), and was of easy and fast use in the field. The reproductive condition was assessed

by the presence of a brood patch. A species was considered breeding when at least one individual was found with an active brood patch. Results were associated with the proportion of juveniles present in the resident population, i.e., not taking into account the austral and boreal migratory species, which did not breed in the study area. Four species were studied more specifically, as they were sufficiently numerous and were present at least in 75% of the mist-netting sessions: the Pileated Finch (*Coryphospingus pileatus*), the Bananaquit (*Coereba flaveola*), the Mouse-colored Tyrannulet (*Phaeomyias murina*) and the Black-faced Grassquit (*Tiaris bicolor*).

Data concerning rainfall were obtained from the *División de Hydrometeorología, Ministerio de Obras Publicas, Venezuela*. They gave monthly cumulative rainfall from May 1965 to April 1967, in Cumaná. Annual rainfall usually ranges from 400 to 700 mm, and rains occur mainly during a short period of about 6 months, usually representing over 80% of 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.

Spearman rank correlations were calculated to evaluate the relationships between rainfall and breeding and moulting. A Wilcoxon matched-pairs signed rank test was used to feature the differences between 1965-66 and 1966-67 concerning the breeding and moulting activity of birds. There were only 20 pairs of data between 1965-66 and 1966-67 for each variable (i.e., number of resident adults having a brood patch, proportion of juveniles in the resident population and proportion of residents moulting). 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. Nonparametric tests were chosen because most of the variables were not normally distributed. All tests were performed using the True Epistat statistical package (Gustafson, 1994).

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## Results

A total of 66 species (17 families) were mist-netted throughout the two years of sampling, including three austral (Swainson's Flycatcher, *Myiarchus swainsoni*, Slaty Elaenia, *Elaenia strepera*, and Small-billed Elaenia, *E. parvirostris*) and one boreal (Blackpoll Warbler, *Dendroica striata*) migratory species. From May 1965 to April 1966, rainfall was 255.7 mm and from May 1966 to April 1967, it was 786.5 mm. The timing of rainfalls throughout the year is as important as the annual total. In our study area, two major peaks of 220.8 and 173.9 mm were observed in August and November 1966, respectively. In one month (August 1966) the study area received almost as much rain as the total of the previous year (May 1965 to April 1966; see Fig. 2).

Breeding activity at the community level was determined firstly by the number of permanent resident species with a brood patch, and secondly by the proportion of juveniles (Fig. 3) in the permanent resident population (thereafter called "residents", in opposition to the austral or boreal migratory species). The main breeding period was largely limited to the wet season of both years, i.e., from April-May to October-November (Fig. 3). Rainfall was significantly and positively correlated with the breeding activity (Spearman rank correlation,  $r = 0.42$ ,  $P < 0.005$ ), the proportion of juveniles ( $r = 0.32$ ,  $P < 0.05$ ) and the proportion of moulting individuals ( $r = 0.45$ ,  $P < 0.005$ ). The first captures of juveniles occurred about one month after the appearance of brood patches on adults.

There was no significant difference between the number of resident species breeding in 1965-66 and 1966-67 (Wilcoxon matched-pairs signed rank test,  $T = 74$ ,  $P > 0.9$ ). Nevertheless, the proportion of juveniles in the resident population was significantly higher during the rainy year of 1966-67 (Wilcoxon matched-pairs signed rank test,  $T = 0$ ,  $P < 0.00001$ ), reaching as much as 75% in September 1966, against 24% in November of the previous year (see Fig 3).

From May 1966 to April 1967, each sample contained at least a few juveniles, even from January to March 1967 when rainfall was virtually absent. There was no exceptional breeding activity in November and December 1966, compared to the same months of 1965 (see Fig. 2 and 3). The difference between the two years relied mainly on the months of January and February 1967, since the Rufous-browed Peppershrikes (*Cyclarhis gujanensis*), the Tawny-crowned Pygmy-tyrants (*Euscarthmus meloryphus*), the White-fringed Antwrens (*Formicivora grisea*), the Scrub Greenlets (*Hylophilus flavipes*), and the Black-faced Grassquits (*Tiaris bicolor*) captured during this period were breeding. The Scrub Greenlet was the only species found breeding during the same period of the previous year.

The onset of moult, at the community level, was similar from one year to another: it occurred in May-June, and corresponded to the beginning of the breeding period (Fig. 4). However, there were only few observations of simultaneous breeding and moulting at the individual level. Most of the time moult was initiated at the end of breeding, just after hatching. There was still some species (one to seven) in moult from January to March 1967, but this phenomena was unnoticed the previous year. No correspondence was found between the species moulting from January to March 1967 and those who started to breed in January or February of the same year. Globally, there was no important variation in the moult cycle between the two years, excepting that moult period was shorter by one month the second year.

In Pileated Finches, Bananaquits, Mouse-colored Tyrannulets, and Black-faced Grassquits, the wing moult was almost always accompanied by body feathers moult, but usually took place over a shorter period than body moult, i.e., began later and/or ended sooner. The moult patterns differed from one species to another, without showing any marked trend. The important short-term

fluctuations that moult cycle displayed in three of the above-mentioned species (Bananaquit, Mouse-colored Tyrannulet, and Black-faced Grassquit) made interpretation difficult, or simply hazardous: it was due to a small number of observations, and we decided not to include these results in this paper. Nevertheless, the moult was strongly associated with the rainy season. The moult cycle of the Pileated Finch was well defined (Fig. 5), and appeared to be shorter during the second year. Pileated Finches, though particularly numerous during the second year, were rarely captured with brood patches. There is no doubt, however, that this species bred in the region of our study site (Meyer de Schauensee and Phelps, 1978; Poulin et al. 1992).

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## Discussion

Rainfall patterns were almost identical at the beginning of both wet seasons. Difference was rather marked further in the breeding season, once hatching had begun. Although the rain season lasted longer during the second year, there was no important increase in the reproductive activity during the breeding period of the wetter year. The most probable explanation is that the breeding season started long before the first rainfall peak and, when this peak occurred, in August 1966, most of the species were already breeding or rearing nestlings. The first juveniles were captured one month after the beginning of the breeding season. It is in accordance with the results of Poulin et al. (1992) in the same region. This lag corresponds to the time needed for incubation and nestling raising since, when juveniles were mist-netted they were already almost fully independent from their parents. The influence of rainfall was apparently stronger on the juveniles themselves as the peak of juveniles abundance was synchronised with the rainfall maximum of August 1966. It has been demonstrated that in seasonal arid habitats, the first rains may be used as a cue for the initiation of nest construction and breeding (Wunderle, 1982; Boag and Grant, 1984; Poulin et al. 1992) and that

most of the species breed preferentially during the first part of the wet season (Cruz and Andrews, 1989). This allows the rearing of juveniles during the period the most propitious to their development, i.e., when food abundance is at a maximum. Poulin et al. (1992) showed that arthropods abundance played a major role for all species during breeding, even for frugivores or granivores which often feed their fledglings on insects (Wunderle, 1982; Malizia, 2001); in the tropics, arthropods populations usually follow rainfall fluctuations (Sinclair, 1978; Janzen, 1973). Therefore, the influence of a climatic event depends on its amplitude, but also on the moment it takes place. In the same way that the timing of drought periods may lessen reproductive success (Smith, 1982), exceptional rainfall should be more or less favourable to breeding success depending on its timing. In our study area, it appeared more profitable for birds to breed just one time but more efficiently, obtaining a better reproductive success from a single brood. Some species may renest either when the first breeding attempt aborted or when conditions for breeding, e.g., resulting from a longer rain season, last for longer periods (Serventy and Marshall, 1957; Boag and Grant, 1984). However there was no evidence of such behaviour, even after the rainfall peaks of November and December 1966, except for the few species that bred in January and February 1967. The juveniles captured from January 1967 to April 1967 had, most of the time, already been mist-netted in September or October 1966. Hence they were not issued from a second wave of reproduction that could have occurred in November or September 1966.

During the first peak of August 1966, as mentioned above, most of the species were still breeding, and started moulting just after. Moulting was thus associated with the energetically demanding period of nestling feeding. Though we found some individuals breeding and moulting synchronously, this phenomena was not generalised, and moulting, associated with the rearing of the nestling, could have reduced the feasibility of a second breeding in autumn 1966. The fact that a few species decided to breed just during the drought period of 1966-67 indicates that food levels were sufficiently



high, compared to the previous year. This was probably a consequence of the rainfall peaks of November and December 1966. However, the proportion of juveniles continued to decrease sharply during this period, most probably because of young emigration. This emigration generally indicates a rarefaction of the resources that might have occurred after the onset of the second breeding period.

Moult seemed much more independent from rainfall fluctuations than reproduction. Though it was well correlated with rainfall, it seemed more difficult for birds to delay or modify their moult cycle, particularly once they have bred. Hence moult might be more directly related to the end of the reproduction than to rainfall. The shorter moult period during the wet year may be explained by a greater resources abundance, which allowed birds to complete their moult more rapidly. However we also lack data on individuals to confirm this hypothesis.

In conclusion, we suggest that rainfall may greatly influence avian reproduction, particularly in seasonal semi-arid or arid regions. However this influence may express itself at various degrees and stages during the breeding cycle. In this study, rainfall increased mostly during the second part of the rainy season. Hence its influence was very significant on the fledging. It is not sure if the increase in the proportion of juveniles in 1966, comparatively to the previous year, was due to a better survival rate or to a diminution of the emigration rate. Actually, it is probably a combination of these two elements.

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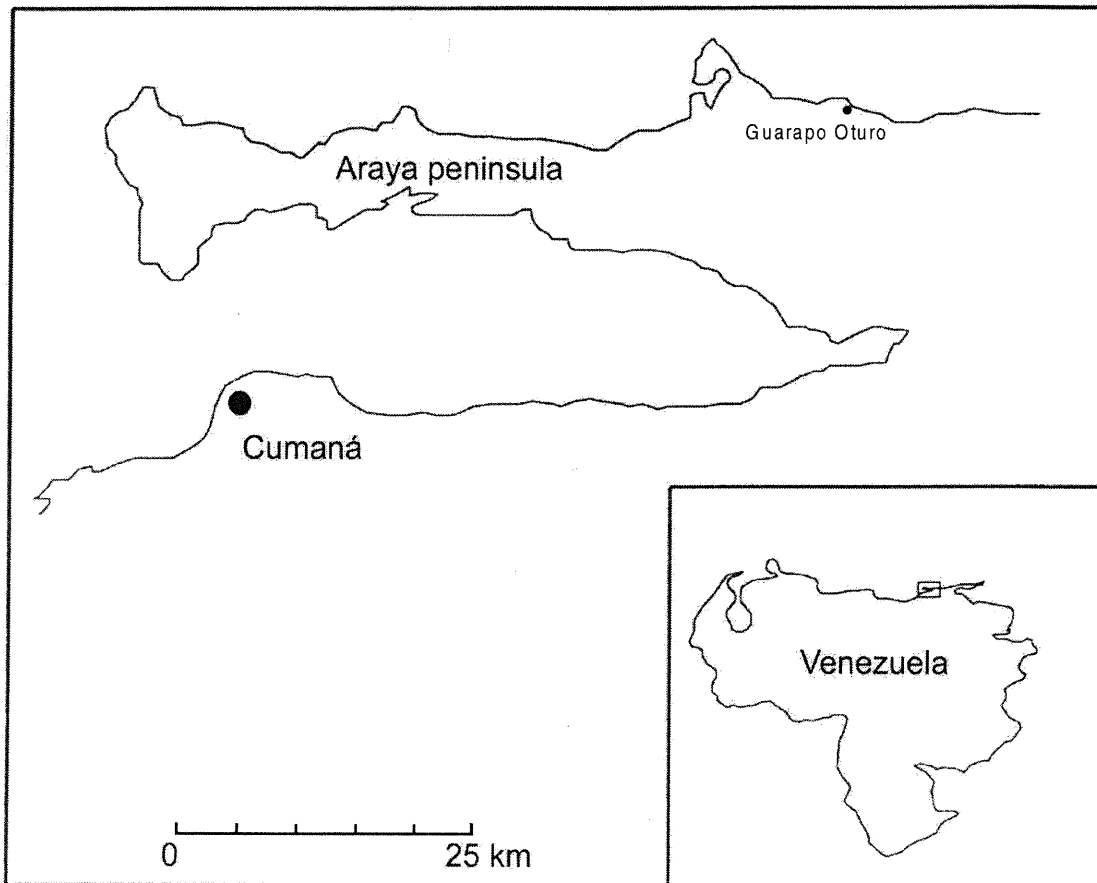
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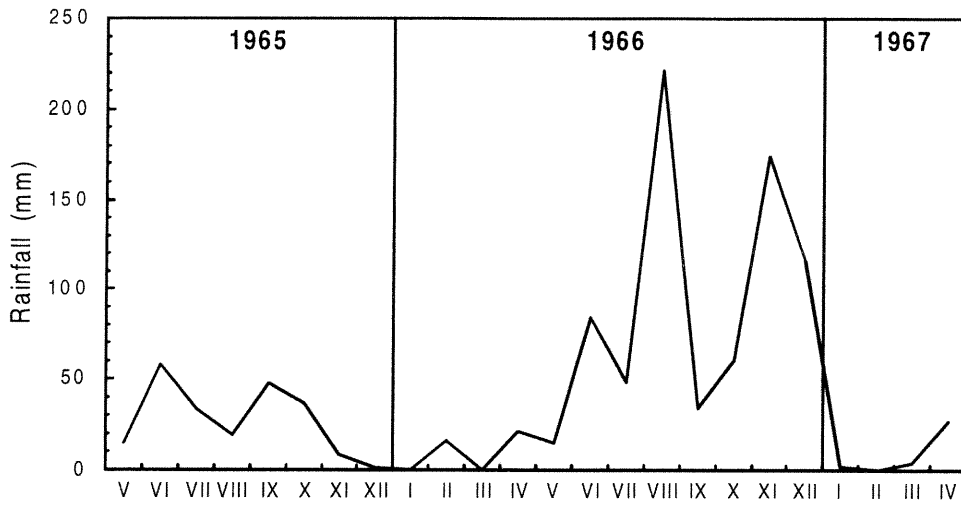
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## Figures

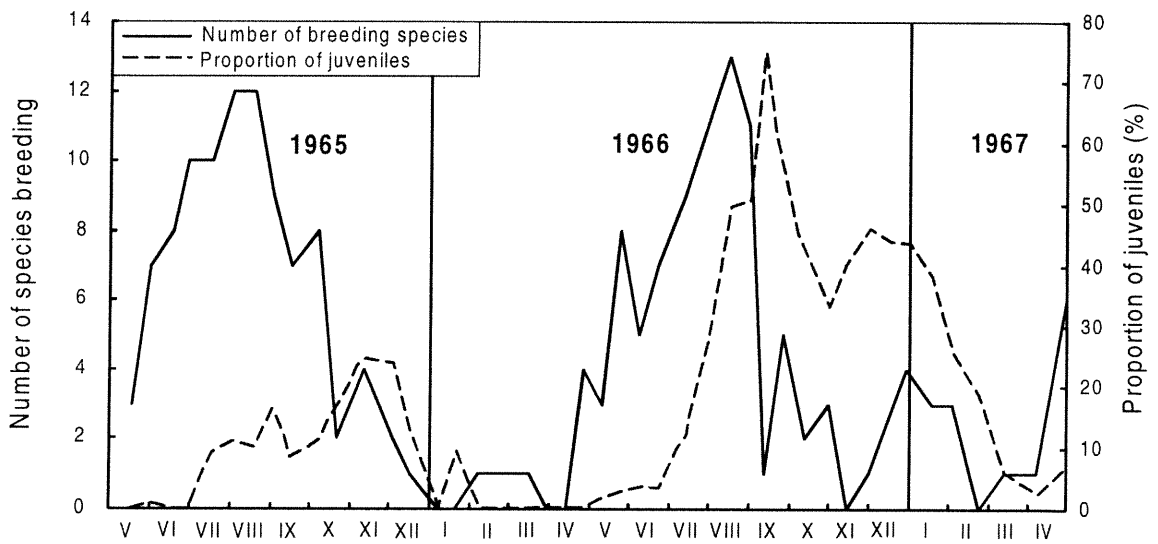
- Figure 1 Map of the northeastern coast of Venezuela showing the relative positions of Cumaná and Guarapo Oturo (Araya Peninsula), where similar studies were undertaken.
- Figure 2 Variations of monthly rainfall from May 1965 to April 1967 in the region of Cumaná, State of Sucre, Venezuela.
- Figure 3 Variation in the number of breeding species and the proportion of juveniles from May 1965 to April 1967.
- Figure 4 Variation in the number of moulting individuals of all species from May 1965 to April 1967.
- Figure 5 Variation in the proportion of moulting Pileated Finches (*Coryphospingus pileatus*) from May 1965 to April 1967.



Tarroux and McNeil, Fig. 1

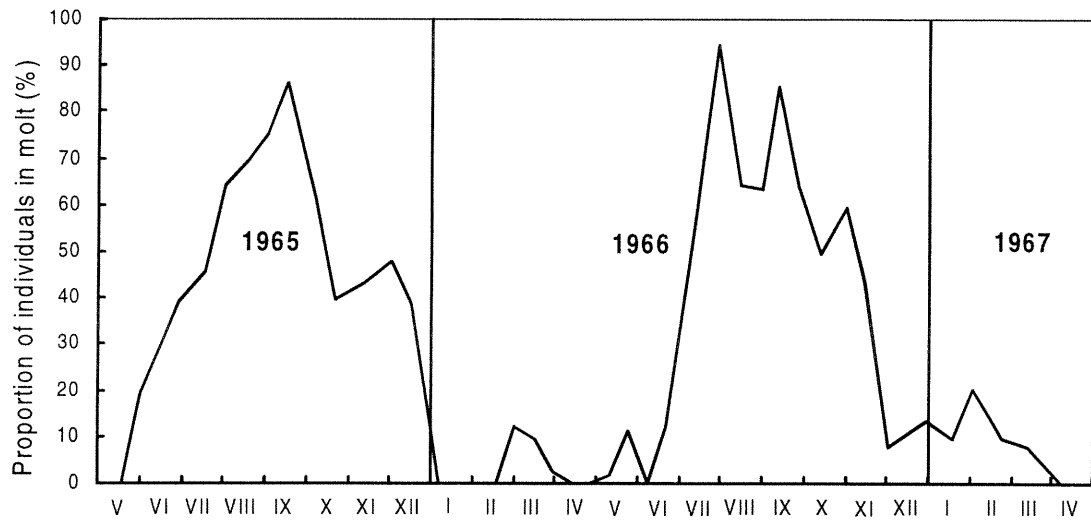


Tarroux and McNeil, Fig. 2

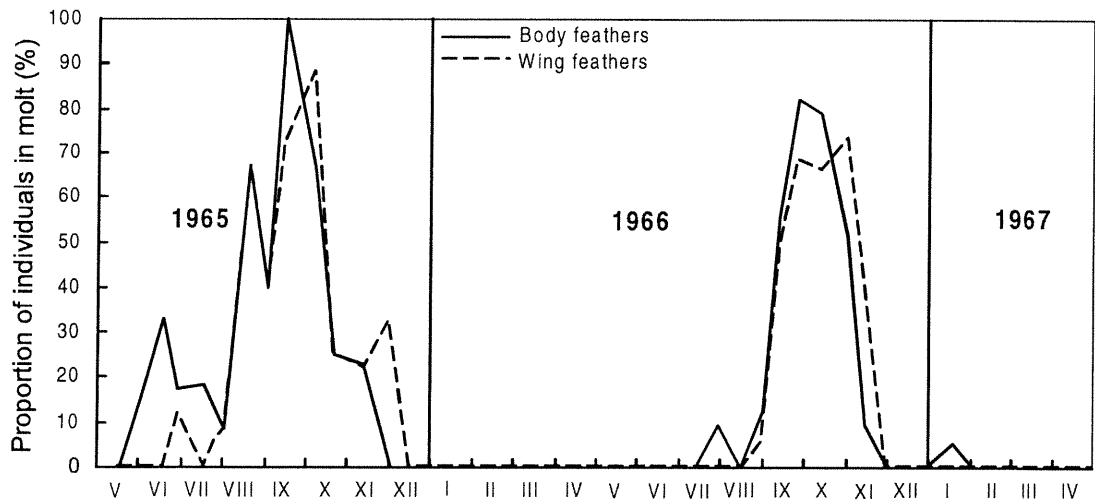


Tarroux and McNeil, Fig. 3





Tarroux and McNeil, Fig. 4



Tarroux and McNeil, Fig. 5

## **Conclusion générale**

Le bois tropical épineux dans lequel cette étude fut conduite est un milieu semi-aride sujet à d'importantes variations annuelles de pluviosité. Ces variations concernent aussi bien la quantité que la répartition de la pluie au long du cycle annuel. Face à cette variabilité les oiseaux de cette région du Nord-est Vénézuélien ont développé des comportements ou des habitudes particulières. Ainsi la majorité des espèces sont caractérisées par un régime alimentaire mixte, généralement partiellement insectivore. Ceci leur permet de s'ajuster plus facilement aux fluctuations des ressources engendrées par la variabilité du climat. En ce qui concerne les cycles de mue et reproduction, nous avons montré qu'ils sont largement associés aux mois où la pluviosité et, par conséquent, l'abondance des ressources, sont les plus élevées.

À l'issue de cette étude, il est apparu que lors d'années exceptionnellement pluvieuses l'ensemble des espèces résidentes n'était pas à même de profiter pleinement de l'augmentation des ressources, contrairement aux espèces migratrices. L'adaptation aux fluctuations du niveau des ressources a semblé se produire de deux façons : (1) par des déplacements sur de courtes distances (espèces ou individus transitoires) et (2) par un recrutement plus important des juvéniles de l'année en cours. En revanche, nos résultats n'ont montré aucune augmentation, d'une part, de l'intensité de la reproduction et, d'autre part, de la durée de la période reproductive. La proportion de juvéniles capturés au filet caractérise généralement le succès reproducteur et, dans le cas présent, il était nettement plus élevé la seconde année. Cela traduisait aussi le fait que même après l'acquisition de leur indépendance, les juvéniles n'ont pas quitté la région immédiatement, grâce à une plus grande disponibilité de nourriture qui réduisait d'autant la compétition avec les adultes.

Les augmentations ou diminutions rapides d'abondance étaient dues en majeure partie aux espèces transitoires ou migratrices, qui se déplaçaient généralement en groupes. À l'inverse, les phénomènes comme le recrutement des juvéniles se traduisaient par des fluctuations plus graduelles d'abondance, et leur impact à l'échelle du peuplement se définit probablement à plus long terme que

les "invasions" irrégulières d'espèces migratrices. Cela signifie que, selon notre échelle temporelle d'observation, les influences à court terme étaient plus susceptibles d'être identifiées, mais il aurait été intéressant de pouvoir continuer l'échantillonnage l'année suivante afin de mesurer les conséquences durables des variations climatiques. L'imprévisibilité de la quantité et de la répartition des pluies ne permet probablement pas aux espèces résidentes de s'adapter à court terme aux variations. Ceci est donc compensé en grande partie par l'arrivée des espèces migratrices.

Il peut paraître surprenant que l'activité reproductrice en tant que telle n'ait pas augmenté durant la seconde année, c'est-à-dire que le nombre d'individus qui se sont reproduits n'ait pas suivi l'accroissement de la pluviosité. Ceci est probablement dû, en partie, au fait que les pluies les plus importantes ont eu lieu vers la fin de la période de reproduction, voire après pour les pics de novembre et décembre 1966. Cependant il est envisageable que l'année précédente, qui fut anormalement sèche, ait aussi influencé le comportement reproducteur des oiseaux l'année suivante. Le grand nombre de juvéniles observés par la suite peut s'expliquer principalement par un taux de survie plus élevé. Ceci aurait constitué un moyen plus efficace de profiter des soudaines augmentations du niveau de ressources, alors qu'une augmentation de l'effort reproductif tôt dans la saison des pluies, qui n'avait pas encore connu une pluviosité exceptionnelle, ne garantissait pas un niveau de ressources suffisant dans les mois suivants. Le cycle de mue, quand à lui, a montré relativement peu de différence entre l'année pluvieuse et l'année sèche.

Il apparaît finalement que les cycles de reproduction et de mue, bien que très fortement associés à la saison des pluies, sont relativement indépendants des fluctuations imprévisibles de pluviosité. Que l'année soit pluvieuse ou non, il est presque certain que la plus grande partie des pluies se concentreront dans une période bien définie, soit de mai à octobre, voire exceptionnellement décembre. Cela signifierait que même dans un environnement dont les principaux facteurs sont sujets à une grande variabilité, les cycles biologiques de certains

peuplements animaux sont tout de même basés sur les caractéristiques les plus cycliques et régulières de ces facteurs. Les ajustements ont alors lieu à un autre niveau, comme la survie des juvéniles ou l'immigration, temporaire ou non, d'individus provenant de régions voisines.