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INFLUENCE OF RAIN ON THE BREEDING AND MOLTING PHENOLOGY OF BIRDS IN A THORN WOODLAND OF NORTHEASTERN VENEZUELA

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Resumen. – Influencia de la lluvia sobre la fenología de la reproducción y muda de las aves en un bosque espinoso del noreste de Venezuela. – En ese estudio, monitoreamos durante dos años consecutivos la comunidad de aves de un bosque espinoso situado cerca de Cumaná, Estado de Sucre, al Noreste de Venezuela. Las aves fueron capturadas con redes de neblina cada dos o tres semanas. Todos los individuos fueron anillados y liberados, y datos sobre edad, muda, y presencia o ausencia de parche de incubación fueron obtenidos para cada ave capturada. Los dos años del estudio se caracterizaron por importantes variaciones en cuanto a la abundancia de lluvias. Durante el primer año, la estación lluviosa fue relativamente corta con precipitaciones anuales (255,7 mm) inferiores al mínimo promedio normal. Por el contrario, el segundo año se caracterizó por una estación lluviosa mas larga con precipitaciones anuales tres veces (786,5 mm) mas abundantes que durante el primer año. La sucesión de un año inusualmente seco por uno excepcionalmente húmedo presentó una oportunidad para comparar la influencia de variaciones climáticas de alta amplitud sobre los ciclos de reproducción y muda de las aves. Describimos las variaciones de los ciclos de reproducción y muda principalmente al nivel de comunidad. El incremento de las precipitaciones durante el segundo año influenció particularmente la abundancia de juveniles, pero no afectó realmente los ciclos de reproducción y muda. Los periodos de reproducción y muda fueron controlados por momento en que se iniciaron las lluvias, no por su abundancia.

Abstract. – In this study we sampled during two successive years (1965–1967) the bird community of a thorn woodland near Cumaná, State of Sucre, northeastern Venezuela. Birds were mist-netted every two or three weeks. All individuals were banded and released, and data on age, molt stage and presence or absence of a brood patch were obtained for each captured bird. These two years of sampling were characterized by important rainfall fluctuations. The first year had a relatively short wet season, with an annual rainfall (255.7 mm) under the normal average minimum. On the contrary, the second year had a longer wet season and received three times more rain (786.5 mm) than the first year. The succession of unusually dry and wet years constituted an opportunity to compare the influence of high-amplitude climatic variations on the breeding and molting cycles of birds. The variations of the breeding and molt 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 really breeding and molting cycles. The breeding and molt periods were controlled by the timing of rains, not by their abundance. *Accepted 20 December 2002.*

Key words: Bird community, rainfall, breeding, molt, phenology, tropics, Venezuela.

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 the sea-

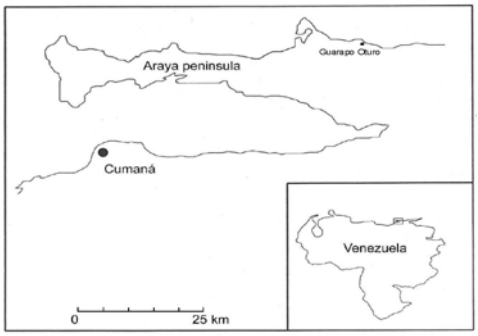

FIG. 1 . Map of the northeastern coast of Venezuela showing the relative positions of Cumaná and Guarapo Oturo (Araya Peninsula), where similar studies were undertaken.

sonal cycle of reproduction in tropical arid or semi-arid seasonal environments (Gilliard 1959, Snow & Snow 1964, Boag & Grant 1984). Usually in wetter zones, where the dry season is shorter and of low amplitude, birds avoid breeding 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 & Smith 1955, Beals 1970). When seasonal variations of environmental factors are less marked, as in tropical wet forests, other factors such as the presence of migrants during certain periods of the year may induce circannual cycles in breeding (e.g., Miller 1963). Existence of a well-defined breeding period may have consequences on the prebasic (i.e., postnuptial) molt. Although these two resource-demanding activities of the life cycle are usually considered to be mutually exclusive in an individual (Pitelka 1958; Miller 1961, 1963; Fogden 1972), it is not rare to observe an overlap between breeding and molting in certain species (Foster 1975, 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, the amount of 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 (Tarroux *et al.* 2003.). Birds have thus to deal with two principal elements, rain distribution and competitive pressures, 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 (1965–1966), rainfall was below the normal average minimum, with an annual total of 255.7 mm. By contrast, the second year (1966–1967) was unusually rainy, with a long wet season and an annual total of 786.5 mm, three times that of 1965–1966. Given this tremendous variability, we were expecting a strong influence of rainfall fluctuations on the birds' biological cycles. Breeding and molting cycles were first described at the community level. A few target species were then studied more precisely to determine the influence of the heavy rainfalls of 1966–67.

Study area and methods

Study area. 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 km south of the Caribbean coast. It has now disappeared because of the development of the city of Cumaná's outlying districts.

The vegetation of the study areas and neighboring areas is similar to the vegetation of Guarapo Oturo, in the northern part of the Peninsula of Araya, described by Guevara de Lampe (1986). Theoretically, it should correspond to a tropical thorn forest as described by Sarmiento (1972) but, actually, at the study site in 1965–1967, 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 vegetation formation). The canopy in thorn woodland is more discontinuous than in the thorn forest, with shrubs and columnar cacti up to 5 m high, and there is no layer II (i.e., no trees from 10 to 20 m).

Among the most representative plant families are the Cactaceae, Capparidaceae, Euphorbiaceae, and Mimosaceae (Sarmiento 1972, Guevara de Lampe 1986). In this arid environment, plants have developed physiological, morphological, and phenological adaptations to reduce water loss (Tamayo 1967). Vegetative and reproductive activities of the plant community are determined by the annual rainfall pattern (Guevara de Lampe 1986). Three vegetative periods were observed during the sampling period. They coincide with the vegetation phenology described by Guevara de Lampe (1986) for the Guarapo area: (1) from September to January, foliage abundance stabilizes and leaf fall begins; (2) from February to April (the critical drought period), the foliage loss is generalized among deciduous species; and (3) from May to August, important foliage recovery and growth of the vegetative parts occur. Concerning the reproduction phases, May to August are featured by peaks in abundance of buds, flowers, and unripe and ripe fleshy fruits; up to 50% of the total plant species in the thorn woodland are concerned. Seeds of herbaceous species are abundant mostly during the second part of the dry season (i.e., from February to April). Flowering rates remain high until January, yet other resources become less abundant as soon as late August (Tamayo 1967, Guevara de Lampe 1986).

Methods. Data were collected from May 1965 to April 1967. Birds were captured during sessions of 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 2-day sessions, leading to the capture of 3281 birds. Use of mist-nets to evaluate avian relative abundances has been widely discussed, especially in tropical regions, since the method is subjected to biases which call for cautious use of the data (MacArthur & MacArthur 1974, Karr 1981, Pardieck & Waide 1992, Remsen & Good 1996, Silkey *et al.* 1999). The aim of the present study was to compare capture data during two successive years rather than to obtain an exact census of the local populations. The 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 & Rappole 1994).

The mist-nets were set approximately 60 m apart from one another. Their initial positions remained the same during 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 above the ground. This should give a good overview of the bird community since the canopy height

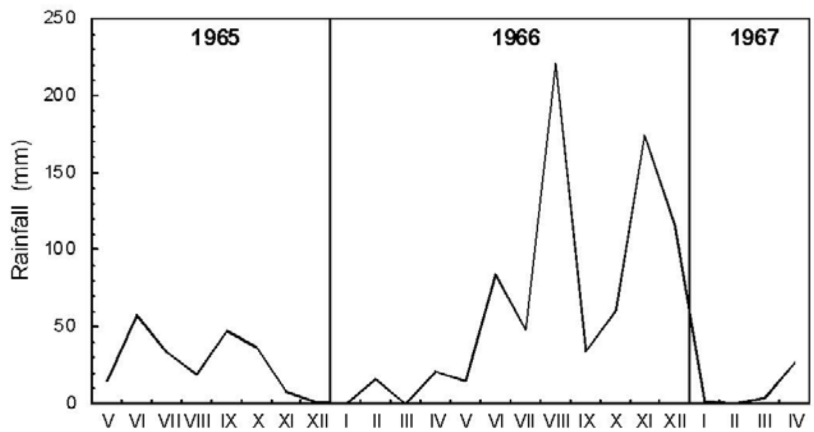

FIG. 2 . Variations of monthly rainfall from May 1965 to April 1967 in the region of Cumaná, State of Sucre, Venezuela.

averaged 5 m. Some species, particularly raptors, could not be sampled adequately and were excluded from the data.

Nets were checked every hour on average, in order to reduce physical damages to birds. Sampling was not carried out during the night, due particularly to the presence of numerous bats which were frequently caught in the nets. After identification, captured birds were banded using a numbered metal ring (U.S.F.W.S.). Molt stage, age, and presence or absence of a brood patch were noted for each bird. Age determination was based on the observation of plumage and/or cranial pneumatization through the skin, this latter method being described in detail by McNeil (1967) and McNeil & Burton (1972). Molt was not recorded with the indices of Miller (1961), Ashmole (1962) or Spaans (1976) which are based on primary molt. Instead, we divided the body in seven zones, and the wing in eight zones, thus giving a body molt index ranging between 0 and 7 and a wing molt index ranging between 0 and 8. The seven body zones correspond to the seven major pterylae, 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 of migrant shorebirds (McNeil 1970), and is easy and fast to use in the field. Reproductive condition was assessed by the presence or absence of a brood patch. Hence our data do not give information on the beginning of the reproduction period *sensu stricto* but rather on the period that follow it. A species was considered to be breeding when at least one individual was found to have an active brood patch. Results were associated with the proportion of juveniles present in the resident population. In other words, we did not take into account the austral and boreal migratory species, which did not breed in the study area. Four species were studied in greater detail, as they were sufficiently numerous and were present in at least 75% of the mist-netting sessions: Pileated Finch (*Coryphospingus pileatus*), Bananaquit (*Coereba flaveola*), Mouse-colored Tyrannulet (*Phaeomyias murina*) and Black-faced Grassquit (*Tiaris bicolor*).

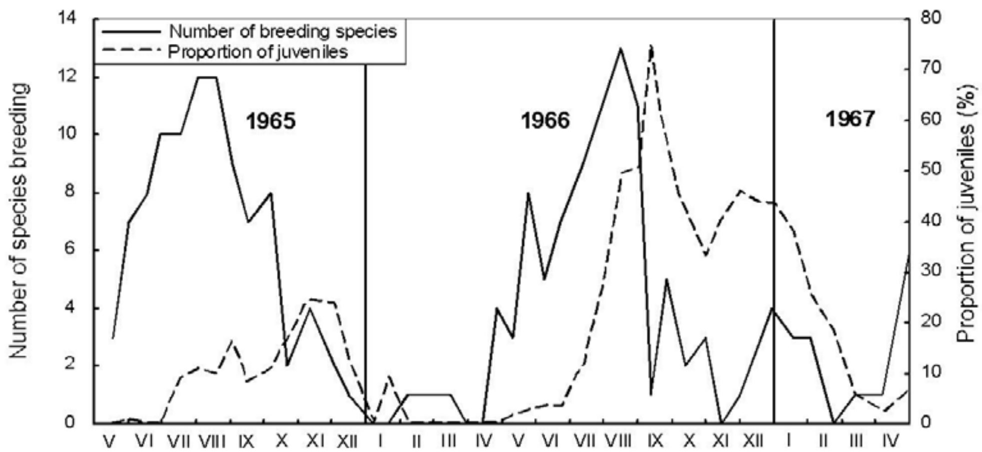

FIG. 3. Variation in the number of breeding species and the proportion of juveniles from May 1965 to April 1967.

Data concerning rainfall were obtained from the División de Hydrometerología, Ministerio de Obras Públicas, Venezuela. These data included monthly cumulative rainfall in Cumaná from May 1965 to April 1967. Annual rainfall usually ranges from 400 to 700 mm, and rains occur mainly during a period of about 6 months, usually representing over 80% of the annual total. 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). As mentioned earlier, 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 molting. A Wilcoxon matched-pairs signed rank test was used to assess the differences between 1965–66 and 1966–67 concerning the breeding and molting 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 molting). 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).

RESULTS

A total of 66 species in 17 families were mist-netted during 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.

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

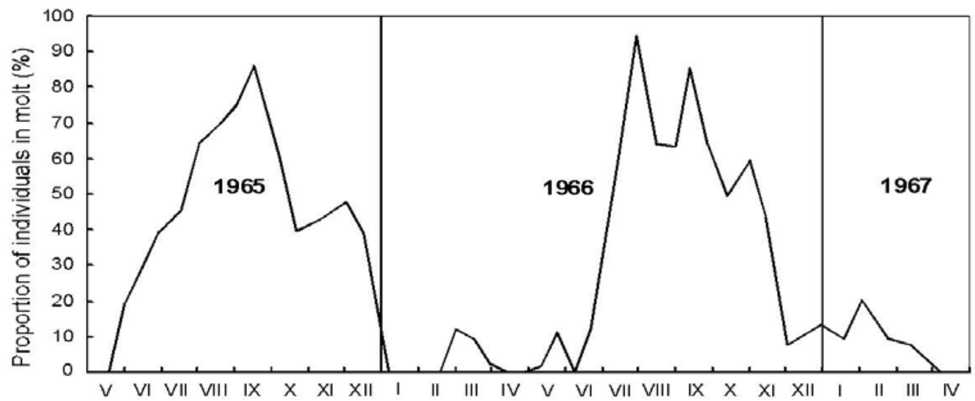

FIG. 4. Variation in the number of molting individuals of all species from May 1965 to April 1967.

(Fig. 3) in the permanent resident population (thereafter called "residents", as opposed to austral or boreal migrants). 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 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 molting 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 1966–67 (Wilcoxon matched-pairs signed rank test, $T = 0$, $P < 0.00001$), reaching a high of 75% in September 1966, against a high of only 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 there was virtually no rainfall. There was no exceptional breeding activity in November and December 1966, compared to the same months of 1965 (see Figs 2 and 3). The difference between the two years rests mainly on the months of January and February 1967, when Rufous-browed Peppershrikes (*Cyclarhis gujanensis*), Tawny-crowned Pygmy Tyrants (*Euscarthmus meloryphus*), White-fringed Antwrens (*Formicivora grisea*), Scrub Greenlets (*Hylophilus flavipes*), and Black-faced Grassquits 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 molt, 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 molting at the individual level. Most of the time molt was initiated at the end of breeding, just after hatching. No important variation in the molt cycle was found between the two years, except that the molt period was shorter by one month during the second year. There were still some species (ranging from two to seven) in molt from January to February 1967, but this phenomenon was not

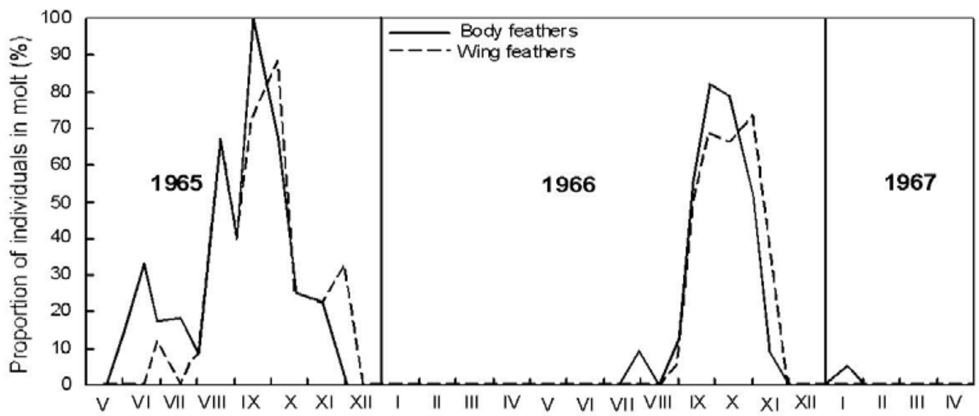

FIG. 5. Variation in the proportion of molting Pileated Finches (*Coryphospingus pileatus*) from May 1965 to April 1967.

observed during the previous year. The species molting from January to February 1967 were not those that started to breed during this same period.

In Pileated Finches, Bananaquits, Mouse-colored Tyrannulets, and Black-faced Grassquits, wing molt was almost always accompanied by body feathers molt, but usually took place over a shorter period than body molt, i.e., began later and/or ended sooner. The molt patterns differed from one species to another, without showing any marked trend. The important short-term fluctuations that molt cycle displayed in three of the four above-mentioned species (Bananaquit, Mouse-colored Tyrannulet, and Black-faced Grassquit) made interpretation difficult. The small number of observations made us decide not to include these results in this paper. Nevertheless, molt was strongly associated with the rainy season. The molt cycle of the Pileated Finch was well defined (Fig. 5), and appeared to be shorter during the second year. Although Pileated Finches were particularly numerous during the second year, they were rarely captured with brood patches. There is no doubt, however, that this species breeds in the region of our study site (Meyer de Schauensee & Phelps 1978, Poulin *et al.* 1992), and that it probably bred nearby in 1965–1967.

DISCUSSION

Even though rainfall patterns were almost identical at the beginning of both wet seasons, differences were rather marked later in the breeding season, once hatching had begun. Although the rainy season lasted longer during the second year of our study, there was no important increase in reproductive activity during the breeding period of the wetter year. The most probable explanation of this pattern 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, a finding that agrees with the results of Poulin *et al.* (1992) in the same region. This time lag corresponds to the time needed for incubating and raising nestlings 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 juvenile abundance was synchronized with the rainfall maximum of August 1966. It has been demonstrated that in seasonal arid habitats in Neotropical areas, the first rains may be used as a cue for the initiation of nest construction and breeding (Wunderle 1982, Boag & Grant 1984, Poulin *et al.* 1992) and that most species breed preferentially during the first part of the wet season (Cruz & Andrews 1989). This allows the rearing of juveniles during the most propitious period for their development, i.e., when food is most abundant. Poulin *et al.* (1992) showed that arthropod abundance played a major role for all species during breeding, even for frugivores or granivores, as these birds often feed insects to their fledglings (Wunderle 1982, Malizia 2001). In the tropics, arthropod population fluctuations usually follow rainfall fluctuations (Sinclair 1978, Janzen 1973). Therefore, the influence of a climatic event depends not only on its amplitude, but also on the moment during which 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 favorable to breeding success depending on its timing. The species in our study area had but one successful brood per breeding season. It appeared more profitable for birds to breed just once but more efficiently, obtaining a higher reproductive success from a single brood. It has been shown that, for some species, renesting can take place either when the first breeding attempt aborted or when conditions for breeding, e.g., resulting from a longer rain season, lasted for longer periods (Serventy & Marshall 1957, Boag & Grant 1984). However we found no evidence of such behavior in our study area even after the rainfall peaks of November and December 1966, except for the few species that bred in January and February 1967. Most of the juveniles captured from January 1967 to April 1967 had already been mist-netted in September or October 1966. Hence they were not the result of a second wave of reproduction that could have occurred in November or September 1966.

During the first rainfall peak of August 1966, as mentioned above, most of the species were still breeding, and started molting just afterwards. Molt was thus associated with the energetically demanding period of feeding nestlings, and the presence of brood patches and molt overlapped for a longer period than in passerines of south-central Brazil (Marini $ Durães 2001). However, we found some individuals breeding and molting synchronously, but this phenomenon was not common, and molt, associated with the rearing of nestlings, 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 strongly suggests that food levels were sufficiently high, compared to the previous year, to enable birds to attempt this. 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 emigration of young out of the study area. This emigration generally indicates a rarefaction of the resources that might have occurred after the onset of the second breeding period.

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

In conclusion, we confirm the fact, observed in our area and elsewhere, that rainfall greatly influences avian reproduction, particularly in seasonal semi-arid or arid regions of the tropics. However this influence may express itself in various degrees and at various stages during the breeding cycle. In our study, rainfall increased mostly during the second part of the rainy season. Hence its influence was very significant on the fledging period. Although we are not sure whether the increase in the proportion of juveniles in 1966, compared to the previous year, was due to a better survival rate or to a diminution of the emigration rate, we believe that it was probably a combination of these two elements.

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