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SEASONAL AND YEAR-TO-YEAR FLUCTUATIONS OF BIRD POPULATIONS AND GUILDS IN THE MONTE DESERT, ARGENTINA

LUIS MARONE
Área de Investigaciones de las Zonas Áridas
CRICYT-Mendoza Casilla de Correo 507
5500 Mendoza
República Argentina

Abstract.—The density variations (at local and regional scales) of the eight most common bird species and of the five bird guilds present in the Biosphere Reserve of Ñacuñán during the winter, spring and summer of 1985–1988 were studied. Both bird populations and guilds underwent important seasonal and year-to-year fluctuations. Local fluctuations of populations and guilds that were stable at a regional scale may be the result of the movement of individuals between sites within an unsaturated environment. Several bird species and guilds showed this pattern in Ñacuñán. Granivorous species reached their maximum density in summer, the season of minimum seed availability in Ñacuñán, and were more scarce in spring. As seeds are the most important limiting resource for granivores in arid zones, this evidence supports the existence of seed surplus in the reserve. On the other hand, granivores were significantly less abundant in 1988, coinciding with a dry period that had begun in Sep. 1987. Thus, granivores in Ñacuñán did not seem to track their resources seasonally, but they might occasionally be limited by unusual periods of seed shortage. The abundance of insectivorous guilds seems not to have been affected by the period of drought. These guilds underwent important seasonal fluctuations, however, as they were more abundant in summer, and reached lowest densities in winter. As winters would be periods of arthropod shortage, migration of arthropod consumers may be an effective way to avoid these periods.

FLUCTUACIONES ESTACIONALES E INTERANUALES DE POBLACIONES Y GREMIOS DE AVES EN EL DESIERTO DEL MONTE, ARGENTINA

Sinopsis.—De 1985 a 1988 se estudiaron las variaciones en densidad local y regional de las ocho especies de aves más comunes y de los cinco gremios de aves presentes en la Reserva de la Biósfera de Ñacuñán, durante el invierno, la primavera y el verano. Tanto las poblaciones como los gremios sufrieron importantes fluctuaciones estacionales e interanuales. Las fluctuaciones locales de poblaciones o gremios regionalmente estables pueden interpretarse como el resultado del movimiento de individuos entre sitios en un ambiente insaturado. Varias especies y gremios de aves mostraron este tipo de patrón en Ñacuñán. Las especies granívoras fueron más abundantes en el verano, la temporada en donde hay menor disponibilidad de semillas en Ñacuñán, y más escasas en la primavera. Como las semillas son el recurso limitante más importante para los granívoros en zonas áridas, nuestra evidencia ofrece apoyo a la hipótesis de la existencia de excedentes de semillas en la reserva. Por otra parte, la abundancia de especies granívoras fue significativamente menor durante 1988, coincidiendo con un período de sequía que comenzó en septiembre de 1987. En resumen, las aves granívoras no parecen rastrear el nivel estacional de sus recursos, pero podrían ser limitadas ocasionalmente por inusitados períodos de déficit de semillas. El período de sequía parece no haber afectado la densidad de los gremios insectívoros, pero estos gremios sufrieron importantes fluctuaciones estacionales: alcanzaron máxima abundancia en verano, y mínima en invierno. Debido a que los inviernos podrían constituir períodos de déficit en la disponibilidad de artrópodos, la migración de las aves que los consumen puede ser un efectivo mecanismo para evitar estos períodos de escasez.

The role of interspecific competition in the organization of bird assemblages has not been entirely established, partly because the detection of competition in nature is difficult. For this reason, the extent to which field evidence upholds or contradicts the assumptions of competition theory has been proposed as an alternative to the classical search for patterns of competition in natural communities (Grant 1986). The most restrictive assumption of the theory is that potentially competitive populations coexist in or close to equilibrium, determined by resource limitation (Wiens 1983). The existence of populations limited by their resources has been tested in a number of environments with different results (Cody 1981, Dunning and Brown 1982, Grant 1986, Wiens 1974). Though classical competition theory assumes that resource levels remain stable, and that they constantly limit the size of their consumer populations (Chesson and Case 1986), competition may also manifest itself when resources fluctuate and bird consumers track their fluctuations by maintaining a dynamic balance (Cody 1981), or during "ecological crunches" in variable environments (Wiens 1977).

Though North and South American deserts have seasonal climates, in which bird resources fluctuate in a cyclic and predictable way, year-to-year climatic variations may be drastic and unpredictable (Raitt and Pimm 1976, Wiens 1974). Plants and animals are adapted to seasonal climatic variations. Seed production, for instance, closely depends on rainfall (Brown et al. 1979), and seed availability in the bank shows a seasonal pattern, usually reaching maximum levels during the dry season (Capurro and Bucher 1986). Nevertheless, total seed biomass is affected by the precipitation of the previous growing season (Dunning and Brown 1982), which is quite variable in arid zones. In addition, in North American deserts arthropod biomass increases during warm and wet seasons (Maurer 1985, Raitt and Pimm 1976), and the number and biomass of locusts, ants, scorpions, spiders and other arthropods increases in the wettest areas and throughout the environment after rainfall in the Monte Desert (Mares et al. 1977).

In this paper I analyze the seasonal and year-to-year fluctuations of bird populations and guilds, and their possible relationship with resource levels, to detect evidence of ecological saturation and equilibrium in bird assemblages of the Monte Desert.

MATERIALS AND METHODS

I conducted this study in the Biosphere Reserve of Ñacuñán (34°02′S, 67°58′W), located in the Monte Desert, Argentina (Morello 1958). The reserve is an open forest of mesquite (*Prosopis flexuosa*) with abundant shrub (especially *Larrea* spp.) and grass covers. In the winter, spring and summer of 1985–1988 I made bird censuses in four 4-ha sites (AA, JA, AJ, JJ) selected at random within the reserve, by using the strip transect method (Burnham et al. 1980). Every transect was run several times on each sampling occasion (mean = 8), after sunrise for no more than 4 h, and during the last 3 h of daylight. Densities of the eight most common species, which accounted for more than 75% of records, were estimated, as well as densities of the five trophic guilds present in Ñacuñán (Capurro and Bucher 1982, 1986; Marone 1990; see Appendix); (1) terrestrial granivores; (2) tree herbivores; (3) insectivores that feed on surfaces (ground, bark or leaves) by gleaning, digging or pecking; (4) insect-hunters that use short flights among the foliage; (5) insect-hunters that use long flights (their prey remaining in the air or on the ground). Birds of prey were not considered because estimates of their density cannot be derived from the field method used.

Abundances of bird guilds and populations were assessed at both local (in each one of the four sites) and regional scales (grouping all four sites, which were thus considered as spatial replications).

The climate in Ñacuñán is remarkably seasonal, with cold and dry winters, and warm and relatively rainy summers. Mean fall-winter temperature (April–August) is usually less than 10 C, and the average of precipitation (±SD) was 53.9 ± 32.0 mm n = 17 yr. The mean temperature during the breeding season (September–March) exceeds 20 C, and precipitation averages 279.0 ± 77.1 mm. The winters of 1986, 1987 and 1988 were relatively dry, and so were the 1987–1988 and 1988–1989 breeding seasons (Fig. 1). Climatic data were obtained from the station located within the reserve, which belongs to the Centro Regional de Investigaciones Científicas y Tecnológicas, Mendoza.

Winter seed availability in the reserve was inferred based on the total grass aerial production of the previous growing season (September–March) calculated after Seligman et al. (1992), and on the precipitation for the identical period. To determine spring-summer seed availability, the same estimates were used, but this time applied to the previous year (September–August). The model by Seligman et al. (1992) assesses the forage production of C_4 grasses (100% of Ñacuñán grass species), which show an opportunistic growth when summer precipitation occurs, but cannot grow when temperature remains below a certain threshold (approximately 10 C). In unusually rainy winters, forb cover may increase remarkably in Ñacuñán (Guevara et al. 1973), and forbs contribute their seeds to the bank of the next growing season. As production of forb species is not evaluated by the model, precipitation was also used as an estimate of seed biomass.

The statistical significance of variation in bird density between years and seasons was tested with one-way analyses of variance (ANOVA). When ANOVA assumptions were violated, data were analyzed by using the nonparametric Kruskal-Wallis test (Sokal and Rohlf 1981). The association between density of consumer birds and estimates of the level of their resources was analyzed with Pearson's product-moment correlation based on data corresponding to the 4 yr of study. To eliminate the effect of differences between sites, density data on every site were normalized (divided by the site mean density, calculated over the 4 yr).

RESULTS

Density fluctuations and ecological saturation.—Figures 2 and 3 show the local and regional density of both the five guilds and the eight most

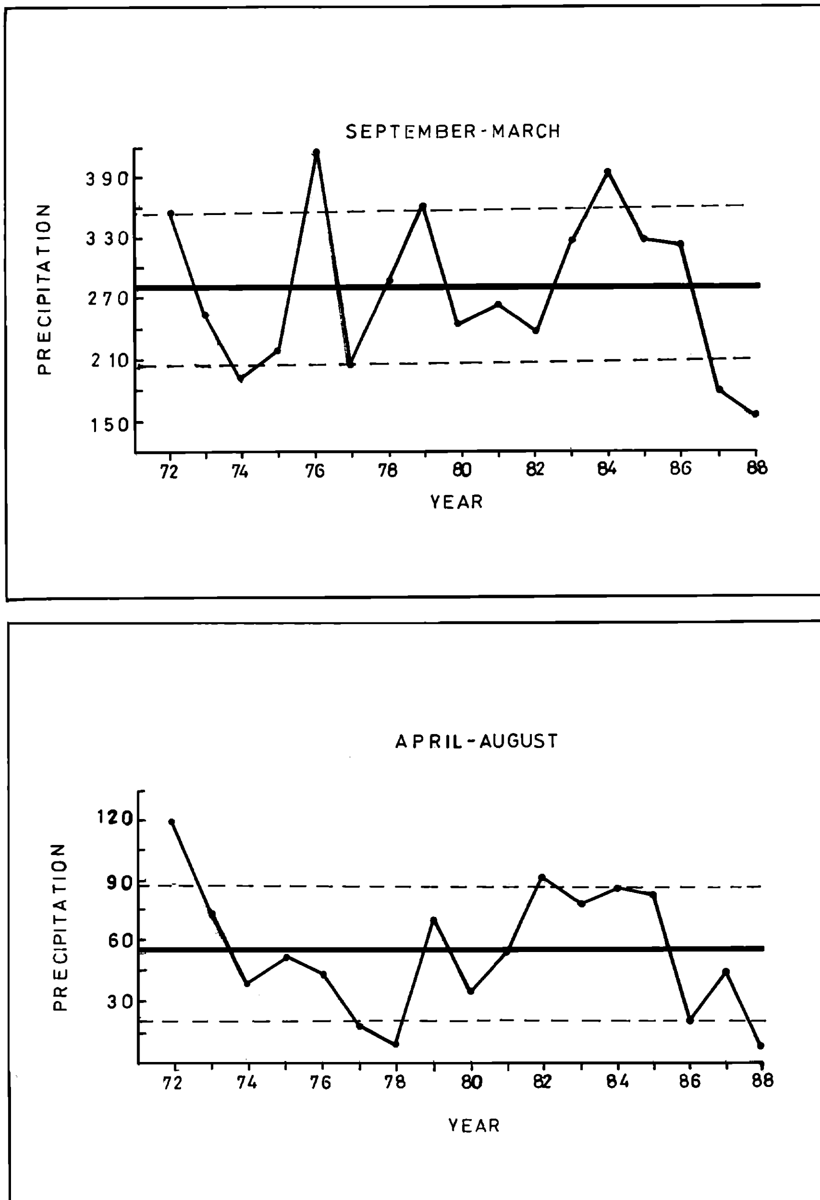


FIGURE 1. Upper part: Precipitation in mm (●) during the breeding season (September of the year indicated to March of the following year). Lower part: Precipitation during the fall–winter season (April–August). Records correspond to the 1972–1989 period in the Biosphere Reserve of Ñacuñán. Solid lines stand for the mean precipitation of each season, and dashed lines for the standard deviation.

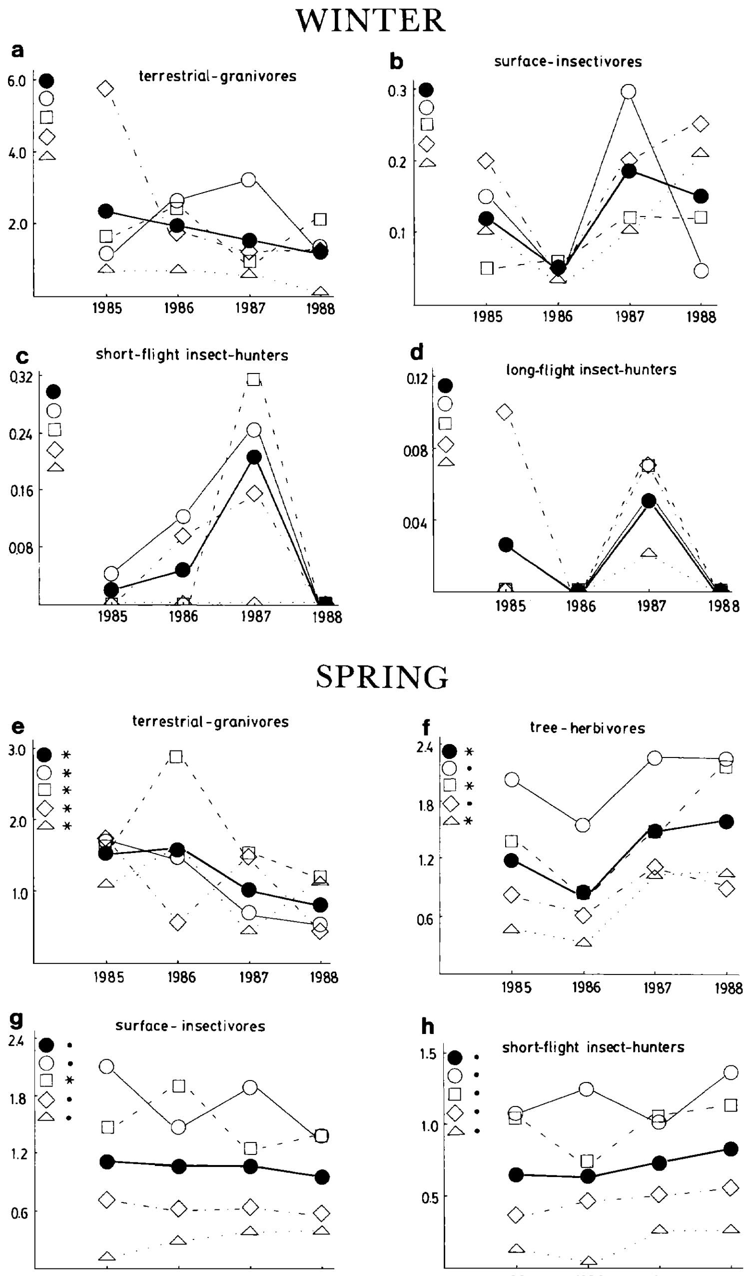
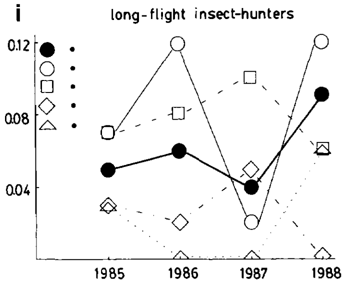


FIGURE 2. Mean density (individuals/ha) of bird guilds during the winter (a–d), spring (e–i) and summer (j–n) of 1985–1988, in the Reserve of Ñacuñán, at regional (●) and local scales (AA: ○, JA: □, AJ: ◇, JJ: △). The statistical significance of the density



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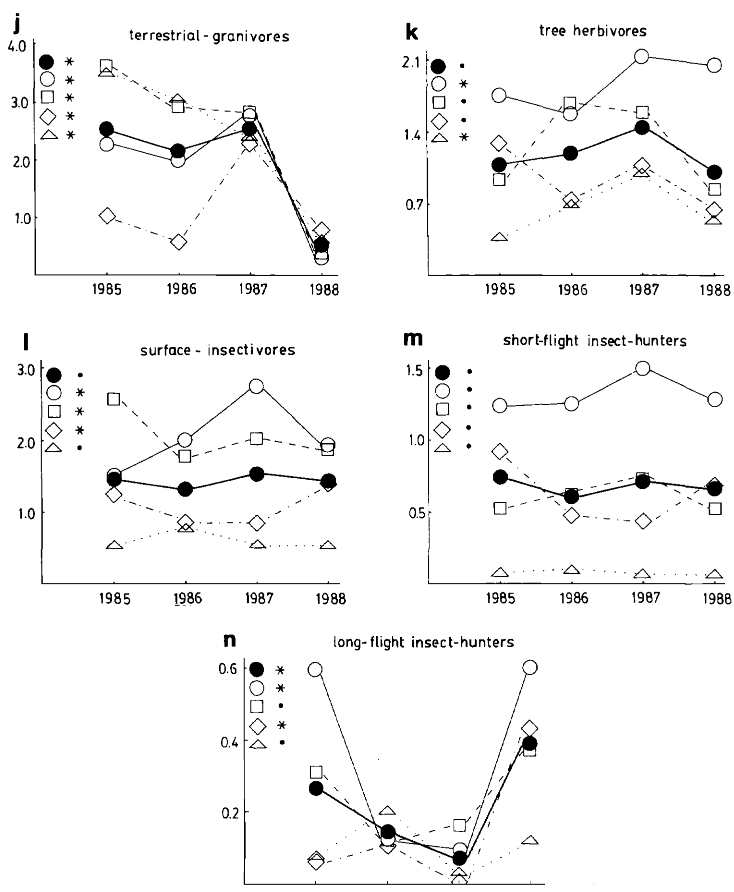

changes between years was analyzed through ANOVA, or the non-parametric Kruskal-Wallis test when ANOVA assumptions were violated (this analysis was carried out only for spring and summer samples) (*: $P < 0.05$, ●: $P > 0.05$).

SPRING

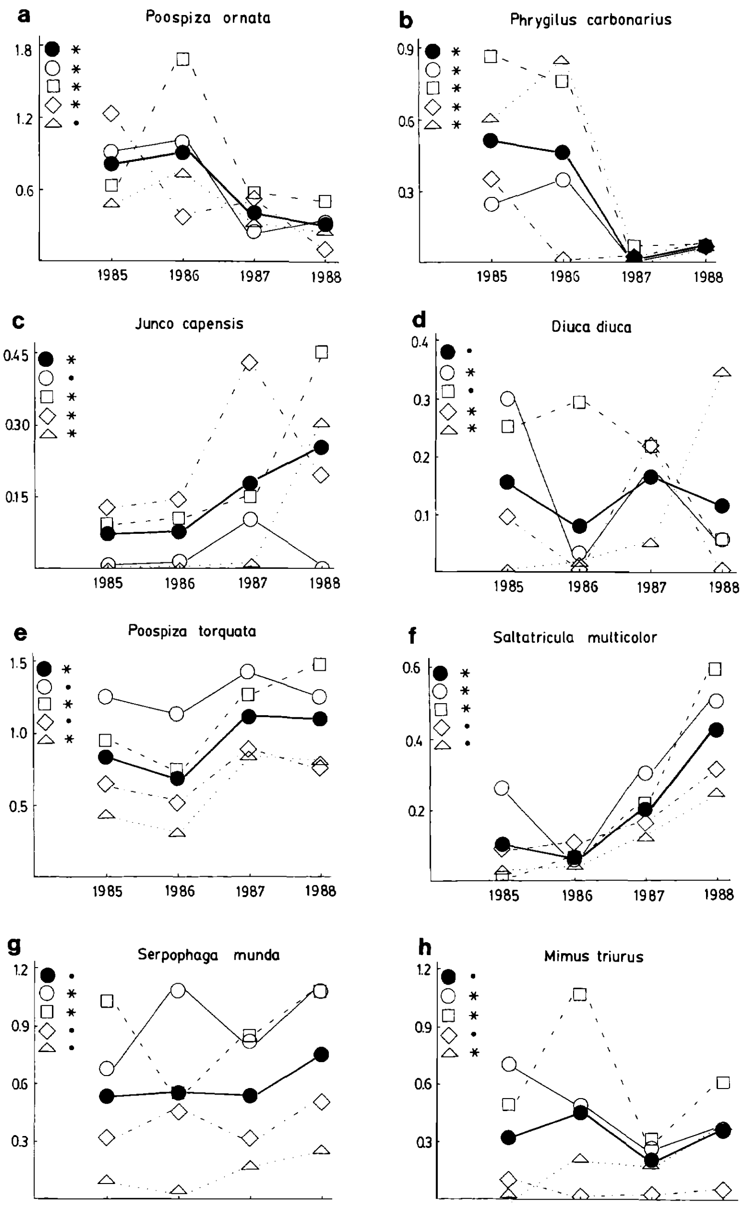

FIGURE 3. Mean density (individuals/ha) of the eight most common bird species during the spring (a–h) and summer (i–p) of 1985–1988, in the Reserve of Ñacuñán, at regional (●) and local scales (AA: ○, JA: □, AJ: ◇, JJ: △). The statistical significance of the

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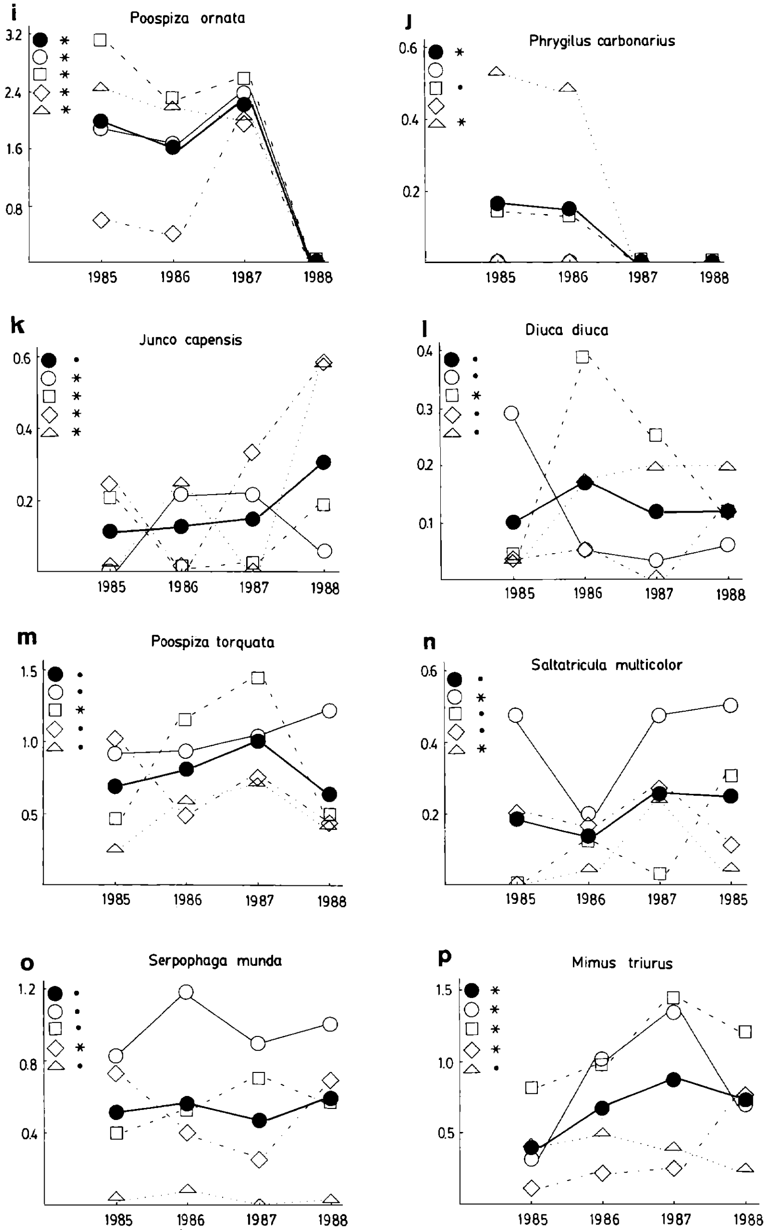

density changes between years was analyzed through ANOVA, or the non-parametric Kruskal-Wallis test when ANOVA assumptions were violated (*: $P < 0.05$, ●: $P > 0.05$).

common species present during the spring and summer of the 4 yr studied. In spring 60% and in summer 80% of guilds underwent significant year-to-year fluctuations at regional or local scales, whereas all eight species experienced changes in spring and summer. Obviously, this scenario does not show a stable equilibrium, but, ecological saturation might still exist if bird populations fluctuated as a result of a close tracking between consumer species and their resources. It is hard to test this prediction without detailed measurement of the resources involved (Wiens 1986). Nevertheless, a way still exists to falsify the ecological saturation hypothesis.

Year-to-year changes in regional bird density would provide a more faithful image of the variations in their resources than would changes in local density, because the latter may be prone to sampling errors in unsaturated habitats (Wiens 1981, 1986). Year-to-year local-density fluctuations of species that were regionally stable during the same period must be the result of intra-habitat migrations within an unsaturated environment. In spring, surface insectivores showed local changes in density, in spite of being regionally stable. In summer, tree herbivores and surface insectivores showed similar changes (Fig. 2). Out of the eight most common species, three in spring (*Diuca diuca, Serpophaga munda* and *Mimus triurus*) and five in summer (*Junco capensis, Diuca diuca, Saltatricula multicolor, Poospiza torquata* and *Serpophaga munda*) underwent local but not regional changes (Fig. 3). This pattern could be interpreted as indirect evidence of lack of ecological saturation of the environment.

Evidence of limitations imposed by food shortage.—Table 1 shows the seasonal fluctuations of every trophic guild based on 4-yr sampling. The species consuming plant material from among the foliage during the breeding season feed on seeds on the ground, or next to it, during the winter. These species (*Poospiza torquata* and *Saltatricula multicolor*) form mixed flocks with terrestrial granivores (*Junco capensis* and *Diuca diuca*) in winter, bringing about high variance in winter samples. This variance makes comparisons between seasons quite difficult. Density of terrestrial granivores reached its maximum in summer, and its minimum in spring. Density of tree herbivores remained invariable throughout the breeding season. Insectivores were significantly more abundant in the breeding season, particularly in summer (except for short-flight insect-hunters that remained unchanged in spring and summer) (Table 1).

The correlation between precipitation in the previous growing season and density of terrestrial granivores was not significant in winter ($r = 0.45$, df = 14, $P > 0.05$). The abundance of this guild in winter was not correlated with the total grass aerial production either ($r = 0.40$, df = 14, $P > 0.10$). In the breeding season, instead, granivore density was positively and significantly correlated with the two estimates of seed biomass. In spring, the correlation coefficient between granivore density and precipitation was $r = 0.70$ (df = 14, $P < 0.01$), and in summer $r = 0.52$ (df = 14, $P < 0.05$). In spring, the correlation between granivores and

TABLE 1. Mean seasonal densities (individuals/ha) and standard deviation of bird trophic guilds in the Biosphere Reserve of Ñacuñán based on 4 yr sampling of four 4-ha sites. The statistical significance of density variations was assessed through ANOVA (F) and the non-parametric Kruskal-Wallis test (H). Degrees of freedom are indicated in parentheses.

Guilds	Winter (n = 120)	Spring (n = 164)	Summer (n = 118)	
Terrestrial granivores	1.73 ± 3.23	1.35 ± 0.98	2.13 ± 1.28	H(2) = 39.5*
Tree herbivores	—	1.19 ± 0.79	1.21 ± 0.77	F(1,280) = 0.1
Surface insectivores	0.13 ± 0.19	1.06 ± 0.79	1.44 ± 0.91	H(2) = 182.8*
Short-flight insect-hunters	0.09 ± 0.21	0.67 ± 0.56	0.65 ± 0.59	H(2) = 114.1*
Long-flight insect-hunters	0.02 ± 0.07	0.05 ± 0.12	0.19 ± 0.26	H(2) = 48.4*

* $P < 0.001$.

grass aerial production was $r = 0.52$ (df = 14, $P < 0.05$), and in summer $r = 0.59$ (df = 14, $P < 0.05$).

In spring precipitation in the previous year was negatively correlated with the density of both tree herbivores ($r = -0.71$, df = 14, $P < 0.01$) and short-flight insect-hunters ($r = -0.61$, df = 14, $P < 0.05$). On the other hand, this precipitation was neither significantly correlated with the abundance of surface insectivores ($r = -0.13$, df = 14, $P > 0.50$) nor with that of long-flight insect-hunters ($r = -0.10$, df = 14, $P > 0.50$). During the summer, precipitation was not significantly correlated with the abundance of tree herbivores ($r = 0.02$, df = 14, $P > 0.50$), surface insectivores ($r = -0.05$, df = 14, $P > 0.50$), short-flight insect-hunters ($r = 0.22$, df = 14, $P > 0.40$), or long-flight insect-hunters ($r = -0.14$, df = 14, $P > 0.50$).

DISCUSSION

The avifauna of Ñacuñán is far from stable from year-to-year. During this study, both species and guilds underwent important fluctuations in their abundances (Figs. 2 and 3). Part of these fluctuations may result from processes that affect bird species in areas outside the reserve (Wiens 1974). In Ñacuñán there are several important migrant species (Marone 1991). Out of the eight most common species, three are summer residents (*Serpophaga munda, Poospiza ornata* and *Mimus triurus*), and three other species, though having a permanent population dwelling in Ñacuñán, receive migratory contributions throughout the year (*Poospiza torquata, Junco capensis* and *Diuca diuca*). Therefore, disregarding the factors to which bird species are subject outside the reserve is risky.

The year-to-year species dynamics are not consistent with the existence of a stable equilibrium (Chesson and Case 1986). Moreover, the analysis of population and guild fluctuations at regional and local scales rendered indirect evidence in agreement with the predictions of the hypothesis of an unsaturated habitat. Bird species might not saturate the environment because of a series of factors that prevent them from taking advantage of the periods of abundance in a quick and efficient manner (e.g., limitation of nesting sites and density-independent winter mortality) (Wiens 1974).

As restrictions on population sizes will be manifest only during periods of resource shortage, seasonal fluctuations of guilds will then reflect the variations in their resources only if they become seasonally scarce, and year-to-year fluctuations of guilds will reflect resource variations only in years of actual resource shortage.

Seasonal dynamics.—Terrestrial granivores were more scarce in spring, and more abundant in summer (Table 1). The spring decline is related to the period of minimum annual level of seeds in the bank, due to the sustained predation to which seeds were subject during the winter, and to the germination brought about by the first rains. Capurro and Bucher (1982) recorded maximum seed availability during the dry season (April–September) in the arid Chaco of Argentina, an environment climatically and floristically similar to the Monte Desert. If this could be extrapolated to Ñacuñán, the period of maximum granivore abundance (summer) would not coincide with that of greater seed availability on the ground. There are two alternative explanations: either terrestrial granivores incorporate other elements in their diet in summer, or seed surplus is usual in Ñacuñán.

Insectivores were more abundant in the breeding season, during which their numbers increased gradually towards the summer (except for short-flight insect-hunters). The seasonal dynamics of these birds would corresponds quite closely with the abundance of their resources. About 63% of insectivores that hunt in flight, and 21% of surface insectivores, are summer residents in Ñacuñán (Marone 1990). Winters are probably periods of food shortage for these birds (Mares et al. 1977, Raitt and Pimm 1976), and migration would be their strategy to avoid them (Wiens 1974).

Year-to-year dynamics.—This study included a period of potential seed shortage: precipitation during the 1987–1988 and 1988–1989 breeding seasons was well below the average (Fig. 1, note that both years were the driest of the entire record). The 1988–1989 breeding season was not only preceded by a dry year, but was a dry season in itself, thus representing an event of unlikely occurrence in Ñacuñán.

On the basis of the above, a hypothesis can be proposed that terrestrial granivores underwent seed shortage in the spring and summer of 1988–1989. The correlation between granivore density and seed production estimates was significant and positive during the breeding seasons when the records of the 4 yr were included, but it lost significance when the 1988–1989 season was left out of the analysis (precipitation vs. granivores in spring $r = 0.55$, df $= 10$, $P > 0.05$, and in summer $r = -0.24$, df $=$ 10, $P > 0.40$; grass production vs. granivores in spring $r = 0.15$, df $=$

10, $P > 0.50$, and in summer $r = -0.46$, df = 10, $P > 0.10$). This evidence supports the hypothesis that terrestrial granivores would not usually saturate the environment, though they would suffer occasional ecological "bottle-necks" in exceptionally dry years. Thus, competition for food between the species of this guild might occur in an intermittent fashion.

On assessing the maximum summer abundance of granivores, I considered the alternative of their incorporating a proportion of arthropods in their diet so as to reach maximum abundance when seed accumulation is not at its highest point. If this is true, this guild would not have decreased abruptly in the summer of 1988, whereas both surface insectivores and short-flight insect-hunters remained stable (Fig. 2). *Poospiza ornata,* a summer-dwelling granivorous species that reached high densities in previous summers (80% of the guild records), arrived at the reserve in Sept. 1988, and deserted it in December showing its facultative migration capability, probably in response to resource shortage (Fig. 3).

The year-to-year correlation analysis between granivore density and seed production estimates in winter yielded no significant results. Winters are most unlikely to be subject to seed shortage because they are precisely the season of greatest seed availability.

Tree herbivores and short-flight insect-hunters were negatively and significantly correlated with precipitation level in spring, whereas such correlation was not significant in summer. Both guilds also coincided in their seasonal dynamics: almost non-existent during the winter, they reached maximum abundance in spring and remained constant throughout the breeding season (Table 1). The pattern shared by these guilds is suggestive because their species depend on mesquite for food, feeding on buds and phitophagous insects from among the foliage, respectively. It has been shown that *Prosopis* leaves have a high nutritive value during spring in North American deserts (Barth 1975, Maurer 1985), and that such value increases after rainy winters (Cates and Rhoades 1977). In Ñacuñán, on the other hand, the hydric status of mesquite would be independent of rains (B. Cavagnaro, pers. comm.). Without knowledge of the factors that affect the phenology of mesquite in the Monte Desert, it is not possible to make an in-depth analysis of the negative correlation pattern found between precipitation and abundance of these guilds in spring.

The abundances of surface insectivores and long-flight insect-hunters were not correlated with precipitations, thus they do not seem to have been affected by the period of drought that started in September 1987 (Fig. 2). The food resources of these birds may have been not so drastically affected by drought as was the seed production of grasses and forbs.

I conclude that terrestrial granivores did not track the seasonal fluctuations of their resources probably because these birds are not usually limited by seed levels. In the year-to-year analysis, instead, this guild underwent an abrupt density decrease. It is suggestive that this density fall coincided with an unusual period of drought, which surely affected the main source of food of the guild (seeds of plants showing an opportunistic growth when rainfall occurs). On the other hand, the period of drought seems not to have affected the abundance of insectivorous guilds. These guilds, however, would track quite closely the seasonal variations in their resources: winters would be periods of arthropod shortage and a great number of arthropod consumers would abandon the reserve in such season. For these guilds, migration arises as an effective way to avoid the periods of food shortage.

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APPENDIX. Specific composition of each bird guild. Species cited have been observed at least on one occasion in one of the sampling sites. Scientific names after Olrog (1978).

Bird guilds	Species in each guild
Terrestrial-granivores	*Eudromia elegans*
	Columba livia
	Columba maculosa
	Zenaida auriculata
	Sicalis luteola
	Diuca diuca
	Phrygilus carbonarius
	Junco capensis
	Poospiza ornata
	Carduelis magellanica
Tree-herbivores	*Cyanoliseus patagonus*
	Myiopsitta monacha
	Phytotoma rutila
	Saltator aurantiirostris
	Poospiza torquata
	Saltatricula multicolor
Surface-insectivores	*Rhinocrypta lanceolata*
	Mimus triurus
	Sturnella supercilliaris
	Pseudoseisura lophotes
	Coccyzus cinereus
	Colaptes melanolaimus
	Drymornis bridgesii
	Lepidocolaptes angustirostris
	Upucerthia certhioides
	Leptasthenura aegithaloides
	Synallaxis albescens
	Certhiaxis pyrrohophia
	Tripophaga spp.
	Troglodytes aedon
Short-flight insect-hunters	*Anairetes flavirostris*
	Stigmatura budytoides
	Serpophaga munda
	Elaenia albiceps
Long-flight insect-hunters	*Empidonomus aurantioatrocristatus*
	Pyrocephalus rubinus
	Myiarchus tyrannulus
	Tyrannus melanocholicus
	Tyrannus savana
	Xolmis coronata