

## NEOTROPICAL AUSTRAL MIGRANT LANDBIRDS: POPULATION TRENDS AND HABITAT USE IN THE CENTRAL MONTE DESERT, ARGENTINA

VÍCTOR R. CUETO<sup>1,4</sup>, JAVIER LOPEZ DE CASENAVE<sup>1</sup>, AND LUIS MARONE<sup>2,3</sup>

<sup>1</sup>*Desert Community Ecology Research Team (Ecodes), Departamento de Ecología, Genética y Evolución, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Piso 4, Pabellón 2, Ciudad Universitaria, C1428EHA Buenos Aires, Argentina*

<sup>2</sup>*Desert Community Ecology Research Team (Ecodes), IADIZA Institute, CONICET, Casilla de Correo 507, 5500 Mendoza, Argentina*

<sup>3</sup>*Centro de Estudios Avanzados en Ecología y Biodiversidad (CASEB), Pontificia Universidad Católica de Chile, Alameda 340, Santiago, Chile*

**Abstract.** We studied density changes of two groups of Neotropical austral migrant landbirds—the South American temperate-tropical (SATT) and cold-temperate (SACT) migratory systems—in the main habitat types of the central Monte desert of Argentina (open *Prosopis flexuosa* woodland and *Larrea cuneifolia* shrubland) over 10 years. Five species, all tyrant flycatchers (Tyrannidae) made up SATT, whereas only two of the seven species of SACT were tyrannids. Densities of both SATT and SACT were higher in open woodland than in shrubland. SATT density did not differ among years, but SACT density did, having lower values in 1994 in both habitats. In subsequent years, SACT densities increased but did not reach values similar to those previous to 1994. The decline in 1994 coincided with a two-year drought period that began in 1993, but lower density in the following years did not appear to be related to climatic conditions in the study area, suggesting a low capacity of SACT species to recover population abundance after periods of stress. In contrast, SATT density was not associated with local climatic conditions, possibly because several SATT species used the study area only as a stopover site. During the breeding season, birds of both migratory systems disproportionately use the open woodland, which offers more sites to nest and feed than does the shrubland. Although most SATT and SACT species are abundant and not currently of conservation concern, human activities in the central Monte desert promote the structural simplification of the habitat, which could threaten future populations of Neotropical austral migrant landbirds in this ecosystem.

**Key words:** Argentina, density fluctuations, desert, drought effects, habitat use, Neotropical austral migrants.

### Migrantes Australes del Neotrópico: Tendencias Poblacionales y Uso del Hábitat en el Desierto del Monte Central, Argentina

**Resumen.** Durante 10 años estudiamos las variaciones en la abundancia de las aves migrantes australes del Neotrópico en los principales tipos de hábitat del Monte central (Argentina): los bosques abiertos de *Prosopis flexuosa* y los arbustales de *Larrea cuneifolia*. Las especies pertenecen a dos sistemas migratorios de América del Sur: el sistema templado-tropical (SATT) y el frío-templado (SAFT). El SATT estuvo compuesto por cinco especies de la familia Tyrannidae, mientras que en el SAFT sólo dos especies de las siete que lo forman pertenecen a esa familia. La densidad del SATT y SAFT fue mayor en el bosque abierto que en el arbustal. La densidad del SATT no mostró variaciones estadísticamente significativas entre años, mientras que la densidad del SAFT difirió estadísticamente entre los años estudiados. Registramos bajas densidades de las especies del SAFT durante 1994 en los dos tipos de hábitats. En los años siguientes la densidad de SAFT incrementó, pero no alcanzó valores similares a los registrados antes de 1994. La disminución de SAFT en 1994 estuvo relacionada con un periodo de sequía de dos años que comenzó en 1993, pero la menor densidad en los años siguientes no estuvo relacionada con las condiciones climáticas en el área de estudio. Esto sugiere una baja capacidad de recuperación de las poblaciones de las especies del SAFT después de sufrir un periodo de restricciones ambientales. En cambio, la densidad de SATT no estuvo asociada con las condiciones climáticas locales, en parte debido a que varias especies de este grupo utilizarían el área como sitio de descanso. El análisis del uso de hábitat claramente sugiere que las aves de los dos grupos migratorios usan los bosques abiertos de *P. flexuosa* durante la estación reproductiva. La mayor complejidad estructural del bosque abierto ofrece más sitios para nidificar y alimentarse que el arbustal. Aunque la mayoría de las especies de estos dos grupos son abundantes y no presentan problemas de conservación, las actividades humanas en el desierto del Monte generan una simplificación estructural del hábitat, que podrían llevar a que las aves migrantes australes del Neotrópico enfrenten un escenario crítico para su conservación en este ecosistema.

Manuscript received 22 February 2007; accepted 12 November 2007.

<sup>4</sup>E-mail: vcuetto@ege.fcen.uba.ar

## INTRODUCTION

The South American bird migratory systems are, as a whole, the third largest in species number worldwide and the largest in the Southern Hemisphere (Chesser 1994). The particular geography of South America critically influences these migratory systems because the Andes mountain range, the main geographic barrier for bird dispersal, runs parallel to the displacement of migratory birds between breeding and wintering areas (reviewed by Chesser 1994). Knowledge about these migratory systems is still fragmented (Jahn et al. 2004, Stiles 2004), despite advances in understanding aspects of the evolution and geographic distribution of this group of birds. Examples of such advances include a general theory on South American migrant bird evolution proposed by Chesser and Levey (1998) and a model for the evolution of Swainson's Flycatcher (*Myiarchus swainsoni*) migration postulated by Joseph et al. (2003). Furthermore, general surveys concerning geographic distribution (Chesser 1994, 1997, Hayes et al. 1994, Joseph and Stockwell 2000) and seasonality (Cueto and Lopez de Casenave 2000a, Malizia 2001, Jahn et al. 2002, Codesido and Bilenca 2004) of migrant landbirds in South America as well as detailed descriptions of the geographic distribution of several bird species (Marantz and Remsen 1991, Chesser and Marín 1994, Cardozo da Silva 1995, Capllonch and Lobo 2005) have been published in the last 15 years. However, no parallel advances in the knowledge of population dynamics and habitat use of Neotropical austral migrant species have been reported (Stotz et al. 1996).

In order to understand the causes of variation in the abundance of bird populations, it is essential to consider the intrinsic, demographic characteristics of populations (e.g., birth and death rates, migration), along with external factors such as food supply, interspecific competition, or predators, given that the latter factors would constitute the ultimate causes of year-to-year or between-site variation in bird populations (Newton 1998). Several authors have reported important changes in population abundance of North American migratory birds (Sauer and Droege 1992, James et al. 1992) in undisturbed (Holmes and Sherry 2001) as well as disturbed habitats (Robbins et al. 1989, James et al. 1996). These studies have shown how several environmental factors may act to make bird population sizes fluctuate. For example, breeding success of Black-throated Blue Warblers (*Dendroica caerulescens*) is associated with increases in the abundance of food resources resulting from the positive phase of the El Niño-Southern Oscillation (ENSO) event (Sillet et al. 2000). Precipitation anomalies also associated with ENSO promote cascading effects on marine and mainland ecosystems of western South America (Jaksic 2001). For example, population sizes of Darwin's finches increased by an order of magnitude (Gibbs and Grant 1987, Grant and Grant 1987), and individuals bred more successfully after wet years associated with El Niño on the

Galápagos Islands (Grant et al. 2000). Landbird assemblages in semiarid Chile also reached maximum richness and density after El Niño events (Jaksic and Lazo 1999). Effects of ENSO on the biota of areas located to the east of the Andes are, by contrast, less known.

Birds may be viewed as possessing an internal image or template of what constitutes a suitable habitat, based on several "habitat cues" (e.g., vegetation structure, floristic composition) that provide information on food abundance and availability of feeding or nesting sites (Wiens 1989). The identification of habitat cues permits a better understanding of bird-habitat relationships for the development of conservation and management strategies for bird populations (Verner et al. 1986). Many Nearctic-Neotropical migrant landbirds use forests in their breeding range although they are habitat generalists in their wintering range (Hagan and Johnston 1992). In contrast, Neotropical austral migrant landbirds generally breed in open or scrubby habitats (Chesser 1994) and appear to show little habitat specificity on their winter ranges (Stotz et al. 1996). In east-central Argentina, Neotropical austral migrants select woodlands with more complex vegetation structure (Cueto and Lopez de Casenave 2000b), in part because these habitats offer more foraging microhabitats (Cueto and Lopez de Casenave 2002). Migrant landbirds might show a similar pattern of habitat use in the central Monte desert (Cueto et al. 2006).

Here we assess population fluctuations of several Neotropical austral migrant bird species in the main habitats of the central Monte desert—open woodlands of *Prosopis flexuosa* and *Larrea cuneifolia* shrublands—in order to determine patterns of habitat use and the effect on population dynamics of wet and dry periods across 10 years. Furthermore, we discuss the role of ENSO phases on bird population changes in the central Monte desert.

## METHODS

### BIRD SPECIES AND STUDY SITE

In the Neotropical region, there are at least four migratory bird systems (Joseph 1997). We follow the classification proposed by Joseph (1997), focusing on South American Temperate-Tropical (hereafter SATT) and South American Cool-Temperate (hereafter SACT) Migration Systems. In Argentina, SATT is composed of species that breed in temperate zones of the country and spend the austral winter in the warm, humid tropical latitudes of South America. Bird species within SACT, in turn, breed in cool-temperate zones of south and central Argentina and spend the austral winter in northern Argentina, southern Bolivia, southern Brazil, and Paraguay. Migrant status of birds at our study site was determined using records on species occurrences taken seasonally over more than a decade (Marone 1992, Lopez de Casenave

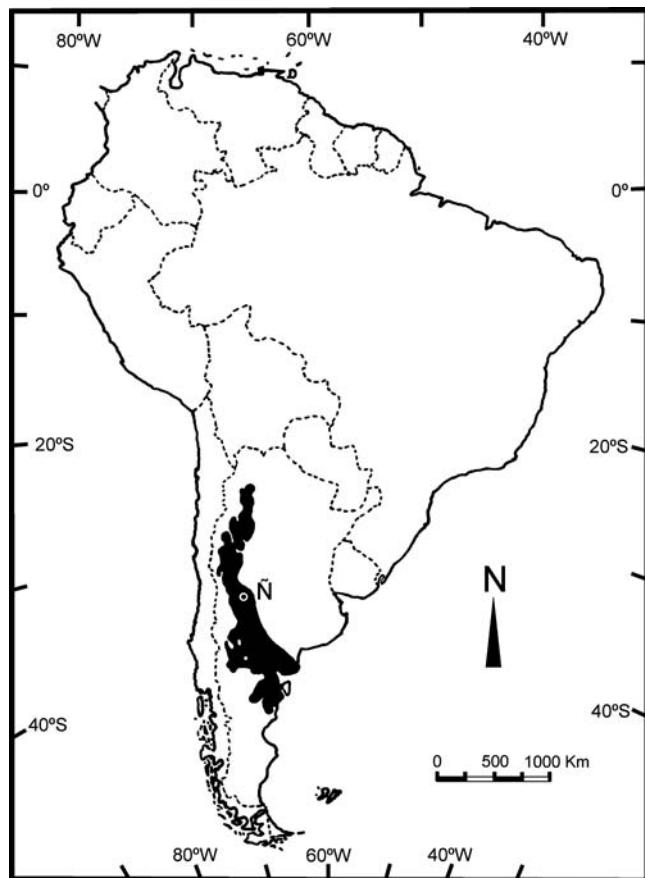


FIGURE 1. Geographical extent of the Monte desert (shaded area) in South America in which migrant landbirds were studied (1985–1988; 1993–1998). The white circle (labeled Ñ) indicates the location of the Ñacuñán Reserve.

2001). Migrant species were assigned to SATT or SACT following Joseph (1996, 2003).

We use in this study the name *Serpophaga griseiceps* (Gray-crowned Tyrannulet). This corresponds to an undescribed species of *Serpophaga* tyrannulet that Straneck (1993) considered to *S. griseiceps* (Herzog and Mazar Barnett 2004). Although Straneck's revalidation of the taxon appears to be unsubstantiated, and the assignment of the taxon name could be invalid, both his description of plumage and spectrograms of vocalizations coincide with those of individuals observed in our study site. Thus, we are presenting here population trends and habitat use for a taxon that awaits formal description (Herzog and Mazar Barnett 2004).

We conducted our study at the Biosphere Reserve of Ñacuñán (34°03'S, 67°54'W), located in the central Monte desert, Argentina (Fig. 1). The landscape of the reserve is mainly an open woodland intersected by variably sized tracts of shrubland. The open woodland is a matrix of nonthorny tall shrubs (mainly *Larrea divaricata*), with thorny trees (*Prosopis*

*flexuosa* and *Geoffroea decorticans*) and thorny tall shrubs (*Capparis atamisquea* and *Condalia microphylla*; Marone 1991, Milesi et al. 2002). Nonthorny tall shrubs (*Larrea cuneifolia*) dominate the shrubland, with a low cover of thorny trees and thorny tall shrubs (Marone 1991, Milesi et al. 2002). Grass cover (e.g., *Pappophorum* spp., *Trichloris crinita*, *Setaria leucopila*, *Sporobolus cryptandrus*, *Digitaria californica*, *Aristida* spp.) is similar in both habitat types. The open woodland has higher vertical complexity (three vegetation strata) than the shrubland (two strata; Marone 1991). Climate is dry and temperate, with hot summers and cold winters. On average, >75% of annual rainfall (349 mm,  $n = 31$  years) occurs during the growing season (October–March). For a complete description of the study area, see Lopez de Casenave (2001).

#### BIRD SAMPLING

We sampled bird populations in austral spring (October–November) during two periods: 1985–1988 and 1993–1998, and estimated bird abundance using the variable-width strip transect method (Emlen 1977). For each species, we defined a trailside strip narrow enough to permit detection of cues (e.g., songs, calls, and sightings) produced by birds. Strip width was set for each species as the distance from the trail at which detection of all cues begins to decline (list of widths will be furnished upon request). Birds were counted in 200 m-long transects established in both the open woodland (three transects in 1993 and four in other years) and the shrubland (four transects in 1985–1988 and three in 1993–1998). Sampling was not conducted under inclement weather (Verner 1985). We recorded the presence of individuals (using visual or aural cues) on both sides of the survey trail during the first four hours after sunrise (Verner 1985). Only birds using the sampling area were recorded (i.e., birds that flew across the strip transect were not included). In each year of sampling, each transect was surveyed several times (4–10 surveys), alternating the order of sampling of transects on successive days. Transects in both habitat types were surveyed on the same days. Abundances obtained in all surveys of each transect were averaged to obtain the bird density per transect for each year (Emlen 1977). Therefore, we used as a replicate the average density of each transect, avoiding temporal pseudoreplication for statistical purposes. Bird counts for 1985–1988 were recalculated from Marone (1990).

#### RAINFALL PATTERNS

Precipitation data were available from the weather station maintained in the Reserve of Ñacuñán since 1972. We considered wet or dry years to be those with annual rainfall one standard deviation respectively above or below the average annual rainfall of the 31-year period of climatic data for Ñacuñán Reserve (Ropelewski and Folland 2000).

TABLE 1. Species composition and mean annual breeding density (1985–1988; 1993–1998; average  $\pm$  SD) of South American Temperate-Tropical (SATT) and South American Cool-Temperate (SACT) Neotropical austral migratory systems. Birds were counted in the main habitat types of the Ñacuñán Reserve, central Monte desert, Argentina (open woodland of *Prosopis flexuosa*, and *Larrea cuneifolia* shrubland). Dashes indicate the absence of a species.

Species	Family	Migratory system	Open woodland (individuals ha <sup>-1</sup> )	Shrubland (individuals ha <sup>-1</sup> )
White-crested Elaenia <i>Elaenia albiceps</i>	Tyrannidae	SATT	0.1 $\pm$ 0.1	0.07 $\pm$ 0.10
Southern Scrub-Flycatcher <i>Sublegatus modestus</i>	Tyrannidae	SATT	0.02 $\pm$ 0.04	—
Crowned Slaty-Flycatcher <i>Griseotyrannus aurantioatrocristatus</i>	Tyrannidae	SATT	0.09 $\pm$ 0.10	0.02 $\pm$ 0.03
Fork-tailed Flycatcher <i>Tyrannus savana</i>	Tyrannidae	SATT	0.002 $\pm$ 0.005	—
Swainson's Flycatcher <i>Myiarchus swainsoni</i>	Tyrannidae	SATT	—	0.004 $\pm$ 0.010
Pale-breasted Spinetail <i>Synallaxis albescens</i>	Furnariidae	SACT	0.2 $\pm$ 0.2	0.04 $\pm$ 0.05
Gray-crowned Tyrannulet <i>Serpophaga griseiceps</i>	Tyrannidae	SACT	1.6 $\pm$ 0.5	0.3 $\pm$ 0.2
Black-crowned Monjita <i>Xolmis coronatus</i>	Tyrannidae	SACT	0.01 $\pm$ 0.01	0.02 $\pm$ 0.04
White-tipped Plantcutter <i>Phytotoma rutila</i>	Cotingidae	SACT	0.2 $\pm$ 0.1	0.01 $\pm$ 0.03
House Wren <i>Troglodytes musculus</i>	Troglodytidae	SACT	0.2 $\pm$ 0.2	0.03 $\pm$ 0.05
White-banded Mockingbird <i>Mimus triurus</i>	Mimidae	SACT	0.3 $\pm$ 0.2	0.05 $\pm$ 0.06
Cinnamon Warbling-Finch <i>Poospiza ornata</i>	Emberizidae	SACT	0.9 $\pm$ 0.8	0.6 $\pm$ 0.5

#### STATISTICAL ANALYSES

We used two-way analysis of variance to assess differences in both SATT and SACT abundance among habitat types, years, and the interaction of habitat and year. Given that we had an unequal number of replicates per cell, we used the Type III method to compute the sum of squares (Shaw and Mitchell-Olds 1993). Comparisons of treatments after ANOVA were performed using the Kramer modification of Tukey's test (Day and Quinn 1989). Raw data were square root transformed (Zar 1996). In order to maintain the experimentwise error rate, we did not analyze year-to-year abundance variations between habitats at the species level. Had we analyzed such information by adjusting alpha levels (Rice 1989), we would have reduced statistical power of the test due to small sample size, making it impossible to reject any null hypothesis for the single-species analyses. Thus, abundance fluctuations at the species level were assessed only through exploratory data analyses.

We evaluated the relationship between total density of each migrant group (i.e., the sum of open woodland and shrubland densities) and total precipitation from 1 October of the year preceding transect counts through 30 September of the year of bird sampling. By doing this, we included the rainfall of the previous growing season (October–March) in the total precipitation value prior to bird counts. We used simple regression analysis to test the relationships among these variables. Residuals of regression were screened for normality and highly influential outliers (defined as cases with a Cook's distance in excess of  $\pm 2.0$ ; Cook and Weisberg 1982). When such a case was detected, the analysis was repeated omitting the outlier, and results reported. Descriptive statistics represent averages  $\pm$  SD. All statistical analyses were conducted using Statistica Version 6.0 (StatSoft 2001), with significance accepted at  $P \leq 0.05$ .

#### RESULTS

Five species of the Tyrannidae composed SATT (Table 1), although two dominated numerically: the Crowned Slaty-Flycatcher (*Griseotyrannus aurantioatrocristatus*) and White-crested Elaenia (*Elaenia albiceps*; 34% and 58% of the overall annual average breeding density, respectively). Other species were less abundant or of more sporadic occurrence at the reserve (Southern Scrub-Flycatcher, *Sublegatus modestus*, 6%; Swainson's Flycatcher, *Myiarchus swainsoni*, 1%; and the Fork-tailed Flycatcher, *Tyrannus savana*, <1%). SATT density in the open woodland was higher than in the shrubland ( $F_{1,53} = 8$ ,  $P < 0.01$ ; Fig. 2A), and there was no statistical difference among years ( $F_{9,53} = 1.4$ ,  $P = 0.22$ ), although we observed an increase in the density of this group between 1993 and 1995 (Fig. 2A). The habitat  $\times$  year interaction was not statistically significant ( $F_{9,53} = 1$ ,  $P = 0.46$ ). The most common SATT species, the Crowned Slaty-Flycatcher and White-crested Elaenia, had similar patterns of habitat use. They were more abundant in the open woodland, although the latter had a higher density in the shrubland during 1995 (Fig. 3).

Seven species from six different families composed SACT (Table 1). The most abundant species of this group were the Gray-crowned Tyrannulet (*S. griseiceps*) and Cinnamon Warbling-Finch (*Poospiza ornata*; 43% and 33% of the overall annual average breeding density, respectively). Other species in the group were less abundant (White-banded Mockingbird, *Mimus triurus*, 7%; Pale-breasted Spinetail, *Synallaxis albescens*, 6%; White-tipped Plantcutter, *Phytotoma rutila*, 6%; and House Wren, *Troglodytes musculus*, 5%) or rare (Black-crowned Monjita, *Xolmis coronata*, <1%). SACT density differed between habitats, being higher in open woodland than in shrubland ( $F_{1,53} = 151$ ,  $P < 0.01$ ; Fig. 2B). This group also showed statistically significant density fluctuations

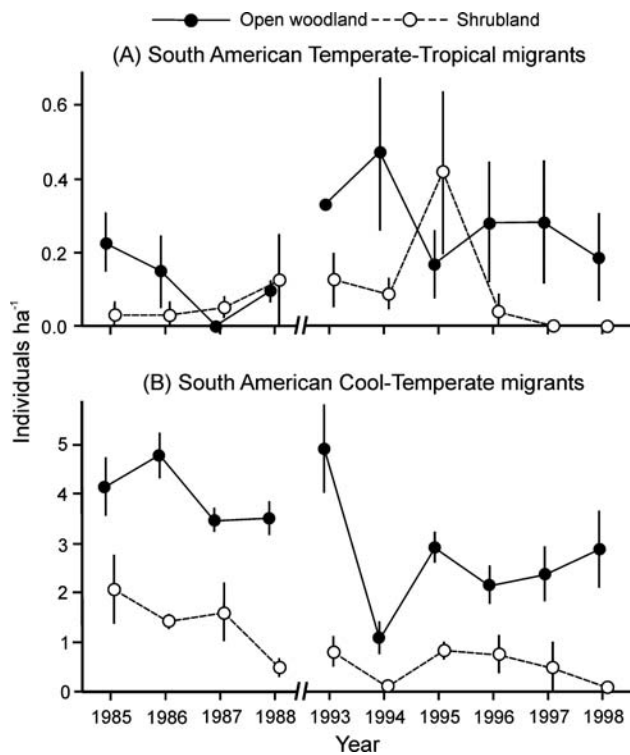


FIGURE 2. Annual breeding density values (average  $\pm$  SD) of (A) South American Temperate-Tropical and (B) South American Cool-Temperate Neotropical austral migrant landbirds in open woodland and shrubland at *Ñacuñán* Reserve, central Monte desert, Argentina (1985–1988; 1993–1998). Note that vertical axes differ in scale between graphs.

among years ( $F_{9,53} = 8.7$ ,  $P < 0.01$ ; Fig. 2B). The interaction between habitat and year was not statistically significant ( $F_{9,53} = 1.6$ ,  $P = 0.13$ ). Densities in 1994 were lower in both habitats relative to that in the other years (Kramer modification of Tukey's test,  $P < 0.05$ ; Fig. 2B). In subsequent years, the density increased but did not reach the relatively high values of the years before 1994. At the species level, all SACT species had higher densities in open woodland than in shrubland (Fig. 4) and experienced a density decline in 1994, with the exception of the White-tipped Plantcutter, which showed a moderate density decline, and the Pale-breasted Spinetail, which increased in abundance during that year. The Cinnamon Warbling-Finch, White-banded Mockingbird, and House Wren were absent on transects during 1994, while the Gray-crowned Tyrannulet showed the lowest breeding density records in that year out of the 10 years of the study. After 1994, the Gray-crowned Tyrannulet and Pale-breasted Spinetail increased in density to levels similar to those of the years before 1994 (although the latter species only during 1996 and 1997), while the other species were less abundant or were not recorded (e.g., House Wren; Fig. 4D).

During this study, there were two wet years (1985 and 1997) and four dry years (1986, 1988, 1993, and 1994) at

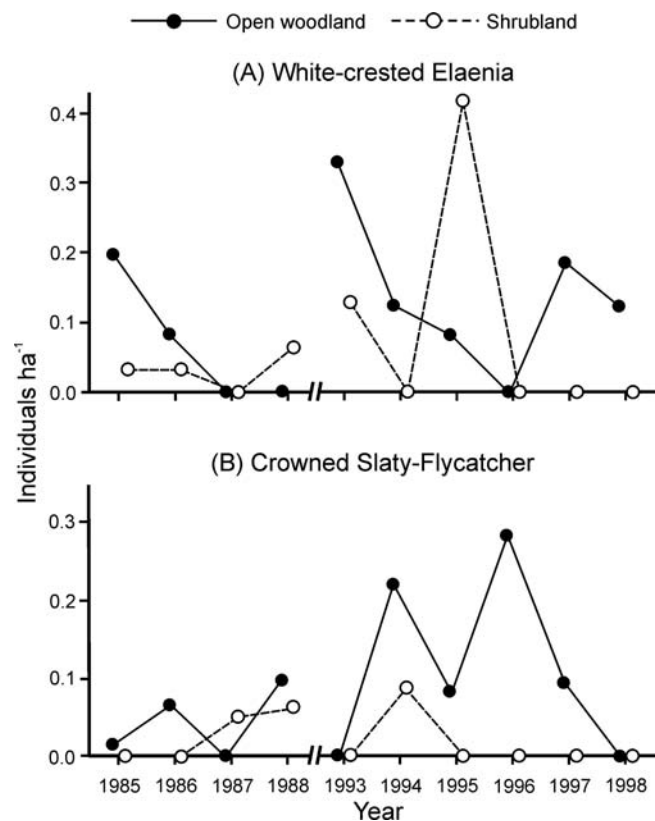


FIGURE 3. Annual breeding density values of the (A) White-crested Elaenia and (B) Crowned Slaty-Flycatcher, the most common South American Temperate-Tropical Neotropical austral migrant landbird species in open woodland and shrubland at *Ñacuñán* Reserve, central Monte desert, Argentina (1985–1988; 1993–1998). Note that vertical axes differ in scale between graphs.

*Ñacuñán* (Fig. 5). According to simple regression analyses, SATT and SACT total breeding densities were not associated with previous annual rainfall ( $r^2 = 0.2$ ,  $F_{1,8} = 2.3$ ,  $P = 0.17$  and  $r^2 = 0.1$ ,  $F_{1,8} = 0.9$ ,  $P = 0.37$ , respectively; Fig. 6). However, residual analysis for SACT indicated that 1998 was an outlier for previous annual rainfall (1998 Cook's distance = 2.6). This year could be an outlier because bird populations suffering a 1994 decline may have had a time lag in their response to a high rainfall increase during 1997 (e.g., see House Wren, White-banded Mockingbird, and Cinnamon Warbling-Finch in Fig. 4D–F). When the 1998 datum was omitted from the simple regression analysis, SACT total breeding density was significantly positively related to previous annual rainfall ( $r^2 = 0.5$ ,  $F_{1,7} = 7.8$ ,  $P = 0.03$ ).

## DISCUSSION

The two South American landbird migration systems studied demonstrate remarkable differences in several regards. Tyrannidae species compose SATT, whereas in SACT, only

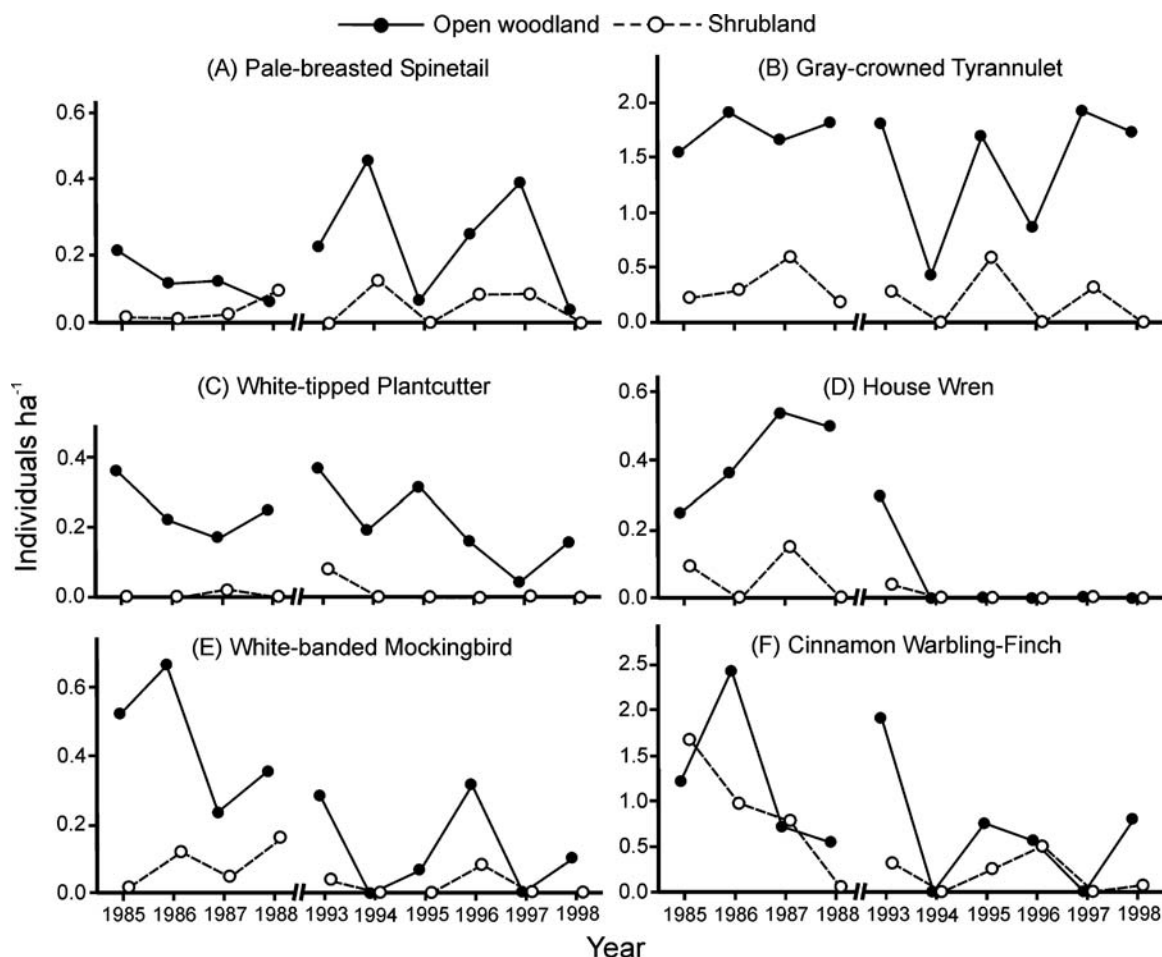


FIGURE 4. Annual breeding density values of the (A) Pale-breasted Spinetail, (B) Gray-crowned Tyrannulet, (C) White-tipped Plantcutter, (D) House Wren, (E) White-banded Mockingbird, and (F) Cinnamon Warbling-Finch—the most common South American Cool-Temperate Neotropical austral migrant landbird species in open woodland and shrubland at Ñacuñán Reserve, central Monte desert, Argentina (1985–1988; 1993–1998). Note that vertical axes differ in scale among graphs.

two of seven species come from this family. This taxonomic difference could have effects on species population abundance in both groups. All SATT species depend mainly on insects for food; in contrast, several SACT species depend on different food types. Among the most common bird species in SACT are a seedeater (the Cinnamon Warbling-Finch), an herbivore-frugivore (the White-tipped Plantcutter), and an omnivore (the White banded Mockingbird; Canevari et al. 1991). Thus, future research on the food resources used by SATT and SACT species may prove to be a fruitful line of research toward explaining the notable differences in abundance and the contrasting population trends between both migrant groups.

Two of five species that form SATT in Ñacuñán (the White-crested Elaenia and Crowned Slaty-Flycatcher) were abundant in most years, whereas the remaining three species reached low densities or were only occasionally recorded. With the exception of the Black-crowned Monjita, SACT species were common in spring–summer, and all species bred in

Ñacuñán (Mezquida and Marone 2001). Among SATT species, the White-crested Elaenia and Swainson's Flycatcher did not breed at Ñacuñán (Mezquida 2002) and may have used the reserve as a stopover site. The main breeding area of the White-crested Elaenia is located in Patagonian forests (Canevari et al. 1991), and at Ñacuñán, individuals of this species are commonly observed during spring. They appear abruptly for a few weeks and soon diminish noticeably in number and disappear after spring (LdeC, pers. obs.). The Crowned Slaty-Flycatcher was the only abundant SATT species recorded during the study period that exhibited high breeding success at Ñacuñán (Mezquida and Marone 2001).

Both groups of Neotropical austral migratory birds also differed in population trends. Birds within SACT showed breeding density fluctuations that related positively with previous annual rainfall, but SATT birds did not. Lower abundance of SACT species was observed especially during the second year of a two-year drought (1993 and 1994), suggesting that

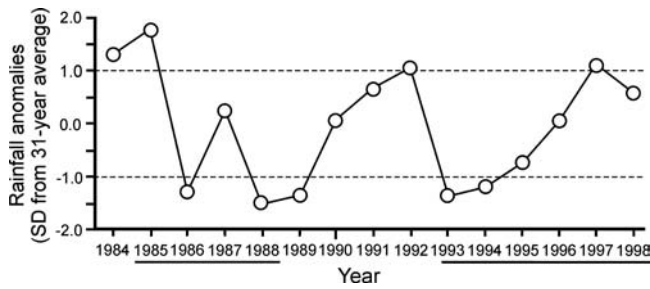


FIGURE 5. Annual rainfall anomalies at Ñacuñán Reserve, central Monte desert, Argentina (1984–1998). Values are expressed in standard deviations from the average of the 31-year period of climatic data at Ñacuñán Reserve. Wet or dry years were those with annual rainfall respectively above or below one standard deviation (dashed lines) of the mean. The black line below years indicates when Neotropical austral migrant landbirds were sampled at Ñacuñán.

dry conditions persisting for more than one year could have a greater negative impact on populations of SACT species. That the density of SACT in 1986 did not diminish (as in 1993) despite annual rainfall in that year being similarly low to that of 1993 or 1994 supports this idea. Furthermore, the effect of the 1993–1994 drought period on SACT species appears to have lasted until the end of our study in 1998. Population abundance of SACT species other than the Gray-crowned Tyrannulet did not return to values similar to those previous to 1994, suggesting a low capacity of most SACT species to recuperate abundances after a potentially severe climatic perturbation. This delay could be related to reproductive constraints. For example, after two years of moderate or no breeding (1995–1996 and 1996–1997), the Cinnamon Warbling-Finch returned to breed in substantial numbers at Ñacuñán in the wet 1997–1998 breeding season (Mezquida and Marone 2003). However, nest success of this and another SACT species, the White banded Mockingbird, were very low due mainly to nest predation (8.4% and 9.6%, respectively; Mezquida and Marone 2001), supporting the hypothesis that density recovery of SACT species is constrained at the reproductive stage. In contrast to SACT, SATT species abundance was not associated with rainfall patterns. In sum, population cycles of SACT species appear to be more tightly associated with local conditions than those of SATT species, possibly because the abundances of the latter are more affected by processes occurring in other parts of their annual range, such as the wintering grounds.

Large-scale climate patterns have important effects on terrestrial ecosystems (Stenseth et al. 2002). For example, the ENSO event appears to govern a portion of rainfall anomalies in western South America, where wetter conditions occur during El Niño phases and drier conditions during La Niña phases (Holmgren et al. 2001). Such fluctuations often markedly affect island and mainland bird assemblages in this part of South America (Grant and Grant 1987, Jaksic and Lazo 1999). Nev-

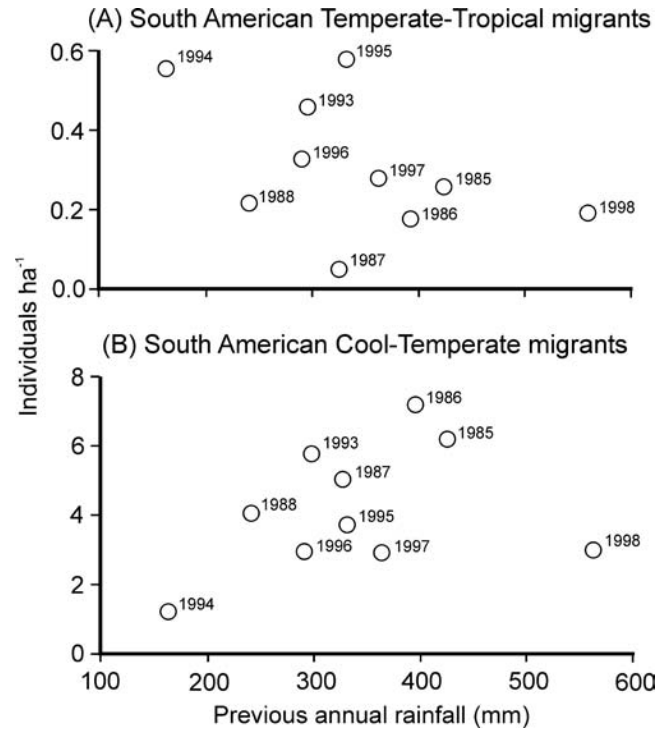


FIGURE 6. Relationship between total breeding density (i.e., the sum of open woodland and shrubland breeding densities) of (A) South American Temperate-Tropical and (B) South American Cool-Temperate Neotropical austral migrant landbirds and previous annual rainfall (from 1 October of the year preceding transect counts through 30 September of the year of sampling) at Ñacuñán Reserve, central Monte desert, Argentina. Note that vertical axes differ in scale between graphs. Numbers next to each data point indicate the years when Neotropical austral migrant landbirds were sampled at Ñacuñán.

ertheless, we did not find any relationship between annual rainfall at Ñacuñán and El Niño or La Niña phases. Although two El Niño (1986–1987 and 1997–1998) and one La Niña (1988–1989) events occurred while we studied bird population dynamics at Ñacuñán, annual rainfall was not in close agreement with the anomalies expected by the ENSO model. Our results are consistent with the conclusions of Compagnucci et al. (2002), who showed that, at regional scales, wet and dry periods are not strongly associated with El Niño or La Niña events in west-central Argentina. Although the ENSO signal may be less clear on the east than on the west side of the Andes, the hypothesis of large-scale climatic phenomena—other than ENSO—influencing SACT bird species abundance in the central Monte desert cannot easily be rejected. The major moisture sources east of the Andes in austral South America are the equatorial-tropical South Atlantic Ocean as well as the Brazilian humid forests (Wang and Paegle 1996). A South American tropical-subtropical climatic connection seems to be the result of a meridional low-level jet east of the Andes, which enhances the influx of moisture to subtropical Argentina (Nogués-Paegle and Mo 1997, Saulo et al. 2000, Doyle and Barros 2002).

Whether these oceanic-atmospheric connections are responsible for rainfall anomalies at Ñacuñán and ultimately for SACT density variations requires further study.

Migrant SATT and SACT species showed similar patterns of habitat use: both were more abundant in open woodland than in shrubland. The open woodland offers more nesting sites than the shrubland because birds rarely use *Larrea* spp. shrubs (Mezquida 2004) for nesting, in spite of its high availability in both habitat types (Marone 1991). Instead, they intensively use the tree *Geoffroea decorticans* (Mezquida 2002, 2004), which is more common in the open woodland (Marone 1991). The Crowned Slaty-Flycatcher used that tree exclusively for nesting (Mezquida 2002), and 95% and 57% of the nests constructed by the Gray-crowned Tyrannulet and Cinnamon Warbling-Finch, respectively, were also on *Geoffroea decorticans* (Mezquida and Marone 2000, Mezquida 2004). Therefore, the nesting requirements of some Neotropical austral migrants may be a central cause of the habitat use patterns reported here. However, availability of food and foraging sites could also contribute to the pronounced habitat partitioning by migrant landbird species in Ñacuñán. For example, the Crowned Slaty-Flycatcher is an aerial insectivore that uses tall trees as a perch for passive searching for prey (Lopez de Casenave et al. 1998, Lopez de Casenave et al. 2008). Birds foraging on vegetation (e.g., the Gray-crowned Tyrannulet, White-crested Elaenia, Pale-breasted Spinetail, House Wren; Lopez de Casenave et al. 2008) may also find more foraging sites in open woodland because there are more vegetation strata than in shrubland. The White-tipped Plantcutter is an arboreal herbivorous species which feeds heavily on leaves and buds of *Prosopis flexuosa* and *Geoffroea decorticans* (Lopez de Casenave et al. 2008). Thus, differences in food abundance between habitats could also explain the pattern of habitat use of these species.

Knowledge of the habitat requirements of Neotropical austral migrants could provide important information for the development of effective conservation plans for arid and semiarid landscapes of Argentina. Current degradation of Argentinean dry forests is so pronounced that their demise is considered one of the most serious ecological catastrophes in South America (Redford et al. 1990). More than 70% of the 700 000 km<sup>2</sup> of woody vegetation in arid and semiarid Argentina has been lost due to conversion to agriculture, livestock production, logging, and fire (Mateucci et al. 1999). Livestock production and logging continue to affect vegetation structure in the fields around Ñacuñán (Asner et al. 2003), leading to structural simplification of the landscape (Roig 1982). A similar pattern of woodland use has been recorded in other Monte desert areas (Villagra et al. 2004). Taking into account human land use in this ecosystem, Neotropical austral migrants could be facing a grim future in the Monte desert. Thus, it will be important to pay close attention to bird population trends in this arid landscape as well as on their winter ranges.

Future research on bird migration in South America needs to focus on the mechanisms underlying the population trends of Neotropical austral migrants (Jahn et al. 2006). In the central Monte desert, we still need information on the demography and site fidelity of SATT and SACT species as well as on the population connectivity between breeding and wintering areas. Knowledge of where these populations spend the winter could be very important, because El Niño promotes dramatic increases in rainfall in northeastern Argentina, southeastern Brazil and Paraguay but drought conditions in the wet tropics of South America (Holmgren et al. 2001). Thus, ENSO phases could have notable and different consequences for SATT or SACT populations in their wintering areas. Furthermore, long-term monitoring of these migrant populations in the central Monte desert could help us to understand how biological systems respond to current and future challenges—such as climate change—facing our planet.

#### ACKNOWLEDGMENTS

This study was originally presented at a symposium-workshop of the Seventh Neotropical Ornithological Congress held at Puyehue (Chile), 3–11 October 2003. We are grateful to Alex Jahn, Doug Levey and Kim Smith for inviting us to participate. We thank Alex Jahn and Celeste Saulo for constructive discussion and reviews of the manuscript, and Rosa Compagnucci and Celeste Saulo for their kindness explaining the dynamics of austral South American climate. David Dobkin and one anonymous referee provided numerous constructive comments for improving our paper. Fieldwork in Ñacuñán was supported by MaB-UNESCO, the Association of Field Ornithologists, the Manomet Bird Observatory, PROCINAMACN, CONICET (through PIP 6141), Universidad de Buenos Aires (through UBACyT X/144) and Agencia Nacional de Promoción Científica y Tecnológica (most recently through PICT 01-12199). This is contribution No. 57 of the Desert Community Ecology Research Team (Ecodes) of IADIZA Institute (CONICET) and FCEyN (Universidad de Buenos Aires).

#### LITERATURE CITED

- ASNER, G. O., C. E. BORGHI, AND R. A. OJEDA. 2003. Desertification in central Argentina: changes in ecosystem carbon and nitrogen from imaging spectroscopy. *Ecological Applications* 13:629–648.
- CANEVARI, M., P. CANEVARI, G. R. CARRIZO, G. HARRIS, J. RODRIGUEZ MATA, AND R. J. STRANECK. 1991. Nueva guía de las aves argentinas. Fundación Acindar, Buenos Aires, Argentina.
- CAPLLONCH, P., AND R. LOBO. 2005. Contribution to the knowledge of migration of three *Elaenia* species (Tyrannidae) from Argentina. *Ornitología Neotropical* 16:145–161.
- CARDOZO DA SILVA, J. M. 1995. Seasonal distribution of the Lined Seedeater. *Bulletin of the British Ornithologists' Club* 115:14–21.
- CHESSER, R. T. 1994. Migration in South America: an overview of the austral system. *Bird Conservation International* 4:91–107.
- CHESSER, R. T. 1997. Patterns of seasonal and geographical distribution of austral migrant flycatchers (Tyrannidae) in Bolivia. *Ornithological Monographs* 48:171–204.
- CHESSER, R. T., AND D. J. LEVEY. 1998. Austral migrants and the evolution of migration in New World birds: diet, habitat, and migration revisited. *American Naturalist* 152:311–319.



- CHESSER, R. T., AND M. A. MARÍN. 1994. Seasonal distribution and natural history of the Patagonian Tyrant (*Colorhamphus parvirostris*). *Wilson Bulletin* 106:649–667.
- CODESIDO, M., AND D. N. BILENCA. 2004. Variación estacional de un ensamble de aves en un bosque subtropical semiárido del Chaco argentino. *Biotropica* 36:544–554.
- COMPAGNUCCI, R. H., E. A. AGOSTA, AND W. M. VARGAS. 2002. Climatic change and quasi-oscillations in central-west Argentina summer precipitation: main features and coherent behaviour with southern African region. *Climate Dynamics* 18:421–435.
- COOK, R. D., AND S. WEISBERG. 1982. *Residuals and influence in regression*. Chapman and Hall, New York.
- CUETO, V. R., AND J. LOPEZ DE CASENAVE. 2000a. Seasonal changes in bird assemblages of coastal woodlands in east-central Argentina. *Studies on Neotropical Fauna and Environment* 35:173–177.
- CUETO, V. R., AND J. LOPEZ DE CASENAVE. 2000b. Bird assemblages of protected and exploited coastal woodlands in east-central Argentina. *Wilson Bulletin* 112:395–402.
- CUETO, V. R., AND J. LOPEZ DE CASENAVE. 2002. Foraging behavior and microhabitat use of birds inhabiting coastal woodlands in east central Argentina. *Wilson Bulletin* 114:342–348.
- CUETO, V. R., J. LOPEZ DE CASENAVE, M. C. SAGARIO AND J. DAMONTE. 2006. Relación aves-vegetación: importancia de los algarrobales para la avifauna del desierto del Monte, p. 244–236. *In* A. Brown, U. Martínez Ortiz, M. Acerbi and J. Corcuera [EDS.], *La situación ambiental argentina 2005*. Fundación Vida Silvestre Argentina, Buenos Aires, Argentina.
- DAY, R. W., AND G. P. QUINN. 1989. Comparisons of treatments after an analysis of variance in ecology. *Ecological Monographs* 59:433–463.
- DOYLE, M. E., AND V. R. BARROS. 2002. Midsummer low-level circulation and precipitation in subtropical South America and related sea surface temperature anomalies in the South Atlantic. *Journal of Climate* 15:3394–3410.
- EMLEN, J. T. 1977. Estimating breeding season bird densities from transect counts. *Auk* 94:455–468.
- GIBBS, H. L., AND P. R. GRANT. 1987. Ecological consequences of an exceptionally strong El Niño event on Darwin's finches. *Ecology* 68:1735–1746.
- GRANT, P. R., AND B. R. GRANT. 1987. The extraordinary El Niño event of 1982–83: effects on Darwin's Finches on Isla Genovesa, Galápagos. *Oikos* 49:55–66.
- GRANT, P. R., B. R. GRANT, L. F. KELLER, AND K. PETREN. 2000. Effects of El Niño events on Darwin's finch productivity. *Ecology* 81:2442–2457.
- HAGAN, J. M., III, AND D. W. JOHNSTON [EDS.]. 1992. *Ecology and conservation of Neotropical migrant landbirds*. Smithsonian Institution Press, Washington, DC.
- HAYES, F. E., P. A. SCHARF, AND R. S. RIDGELY. 1994. Austral bird migrants in Paraguay. *Condor* 96:83–97.
- HERZOG, S. K., AND J. MAZAR BARNETT. 2004. On the validity and confused identity of *Serpophaga griseiceps* Berlioz 1959 (Tyrannidae). *Auk* 121:415–421.
- HOLMES, R. T., AND T. W. SHERRY. 2001. Thirty-year bird population trends in an unfragmented temperate deciduous forest: importance of habitat change. *Auk* 118:589–609.
- HOLMGREN, M., M. SCHEFFER, E. EZCURRA, J. R. GUTIÉRREZ, AND G. M. J. MOHREN. 2001. El Niño effects on the dynamics of terrestrial ecosystems. *Trends in Ecology & Evolution* 16:89–94.
- JAHN, A. E., S. E. DAVIS, AND A. M. SAAVEDRA ZANKYS. 2002. Patterns of austral bird migration in the Bolivian Chaco. *Journal of Field Ornithology* 73:258–267.
- JAHN, A. E., D. J. LEVEY, J. E. JOHNSON, A. M. MAMANI, AND S. E. DAVIS. 2006. Towards a mechanistic interpretation of bird migration in South America. *Hornero* 21:99–108.
- JAHN, A. E., D. J. LEVEY, AND K. G. SMITH. 2004. Reflections across hemispheres: a system-wide approach to New World bird migration. *Auk* 121:1005–1013.
- JAKSIC, F. M. 2001. Ecological effects of El Niño in terrestrial ecosystems of western South America. *Ecography* 24:241–250.
- JAKSIC, F. M., AND I. LAZO. 1999. Response of a bird assemblage in semiarid Chile to the 1997–1998 El Niño. *Wilson Bulletin* 111:527–535.
- JAMES, F. C., C. E. MCCULLOCH, AND D. A. WIENDENFELD. 1996. New approaches to the analysis of population trends in land birds. *Ecology* 77:13–27.
- JAMES, F. C., D. A. WIENDENFELD, AND C. E. MCCULLOCH. 1992. Trends in breeding populations of warblers: declines in the southern highlands and increases in the lowlands, p. 43–56. *In* J. M. Hagan III and D. W. Johnston [EDS.], *Ecology and conservation of Neotropical migrant landbirds*. Smithsonian Institution Press, Washington, DC.
- JOSEPH, L. 1996. Preliminary climatic overview of migration patterns in South American austral migrant passerines. *Ecotropica* 2:185–193.
- JOSEPH, L. 1997. Towards a broader view of neotropical migrants: consequences of a re-examination of austral migration. *Ornitología Neotropical* 8:31–36.
- JOSEPH, L. 2003. Predicting distribution of South American migrant birds in fragmented environments: a possible approach based on climate, p. 263–283. *In* G. A. Bradshaw and P. A. Marquet [EDS.], *How landscapes change*. Springer-Verlag, Berlin, Germany.
- JOSEPH, L., AND D. STOCKWELL. 2000. Temperature-based models of the migration of Swainson's Flycatcher (*Myiarchus swainsoni*) across South America: a new use for museum specimens of migratory birds. *Proceedings of the Academy of Natural Sciences of Philadelphia* 150:293–300.
- JOSEPH, L., T. WILKE, AND D. ALPERS. 2003. Independent evolution of migration on the South American landscape in a long-distance temperate-tropical migratory bird, Swainson's Flycatcher *Myiarchus swainsoni*. *Journal of Biogeography* 30:1–13.
- LOPEZ DE CASENAVE, J. 2001. *Estructura gremial y organización de un ensamble de aves del desierto del Monte*. Ph.D. dissertation, Universidad de Buenos Aires, Buenos Aires, Argentina.
- LOPEZ DE CASENAVE, J., V. R. CUETO, AND L. MARONE. 2008. Seasonal dynamics of guild structure in a bird assemblage of the central Monte desert. *Basic and Applied Ecology* 9:78–90.
- LOPEZ DE CASENAVE, J., J. P. PELOTTO, S. M. CAZIANI, M. MERMOZ, AND J. PROTOMASTRO. 1998. Responses of avian assemblages to a natural edge in a Chaco semiarid forest in Argentina. *Auk* 115:425–435.
- MALIZIA, L. R. 2001. Seasonal fluctuations of birds, fruits, and flowers in a subtropical forest of Argentina. *Condor* 103:45–61.
- MARANTZ, C. A., AND J. V. REMSEN. 1991. Seasonal distribution of the Slaty Elaenia, a little-known austral migrant of South America. *Journal of Field Ornithology* 62:162–172.
- MARONE, L. 1990. *Ensamblajes de aves en la Reserva de la Biosfera de Ñacuñán: patrones y procesos de organización espacio-temporal*. Ph.D. dissertation, Universidad Nacional de San Luis, San Luis, Argentina.
- MARONE, L. 1991. Habitat features affecting bird spatial distribution in the Monte desert, Argentina. *Ecología Austral* 1:77–86.
- MARONE, L. 1992. Estatus de residencia y categorización trófica de las especies de aves en la Reserva de la Biosfera de Ñacuñán, Mendoza. *Hornero* 13:207–210.

- MATEUCCI, S. D., O. T. SOLBRIG, J. MORELLO, AND G. HALFFTER. 1999. Biodiversidad y uso de la tierra: conceptos y ejemplos de Latinoamérica. Editorial de la Universidad de Buenos Aires, Buenos Aires, Argentina.
- MEZQUIDA, E. T. 2002. Nidificación de ocho especies de Tyrannidae en la Reserva de Nacuñán, Mendoza, Argentina. *Hornero* 17:31–40.
- MEZQUIDA, E. T. 2004. Nest site selection and nesting success of five species of passerines in a South American open *Prosopis* woodland. *Journal of Ornithology* 145:16–22.
- MEZQUIDA, E. T., AND L. MARONE. 2000. Breeding biology of Gray-Crowned Tyrannulet in the Monte desert, Argentina. *Condor* 102:205–210.
- MEZQUIDA, E. T., AND L. MARONE. 2001. Factors affecting nesting success of a bird assembly in the central Monte Desert, Argentina. *Journal of Avian Biology* 32:287–296.
- MEZQUIDA, E. T., AND L. MARONE. 2003. Comparison of the reproductive biology of two *Poospiza* warbling-finches of Argentina in wet and dry years. *Ardea* 91:251–262.
- MILESI, F. A., L. MARONE, J. LOPEZ DE CASENAVE, V. R. CUETO, AND E. T. MEZQUIDA. 2002. Gremios de manejo como indicadores de las condiciones del ambiente: un estudio de caso con aves y perturbaciones del hábitat en el Monte central, Argentina. *Ecología Austral* 12:149–161.
- NEWTON, I. 1998. Population limitation in birds. Academic Press, London.
- NOGUÉS-PAEGLE, J., AND K. C. MO. 1997. Alternating wet and dry conditions over South America during summer. *Monsoon Weather Review* 125:279–291.
- REDFORD, K. H., A. TABER, AND J. A. SIMONETTI. 1990. There is more to biodiversity than the tropical rain forest. *Conservation Biology* 4:328–330.
- RICE, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43:223–225.
- ROBBINS, C. S., J. R. SAUER, R. S. GREENBERG, AND S. DROEGE. 1989. Population declines in North American birds that migrate to the Neotropics. *Proceedings of the National Academy of Sciences USA* 86:7658–7662.
- ROIG, F. A. 1982. Cuyo, p. 61–100. *In* Fundación Miguel Lillo and Sociedad Argentina de Botánica [EDS.], *Conservación de la vegetación natural en la República Argentina*. Fundación Miguel Lillo, Tucumán, Argentina.
- ROPELEWSKI, C. F., AND C. K. FOLLAND. 2000. Prospects for the prediction of meteorological drought, p. 21–41. *In* D. A. Wilhite [ED.], *Drought: a global assessment*. Routledge Press, New York.
- SAUER, J. R., AND S. DROEGE. 1992. Geographic patterns of population trends of Neotropical migrants in North America, p. 26–42. *In* J. M. Hagan III and D. W. Johnston [EDS.], *Ecology and conservation of Neotropical migrant landbirds*. Smithsonian Institution Press, Washington, DC.
- SAULO, A. C., M. NICOLINI, AND S. C. CHOU. 2000. Model characterization of the South American low-level flow during the 1997–1998 spring–summer season. *Climate Dynamics* 16:867–881.
- SHAW, R. G., AND T. MITCHELL-OLDS. 1993. ANOVA for unbalanced data: an overview. *Ecology* 74:1638–1645.
- SILLETT, T. S., R. T. HOLMES, AND T. W. SHERRY. 2000. Impacts of a global climate cycle on population dynamics of a migratory songbird. *Science* 288:2040–2042.
- STATSOFT, INC. 2001. STATISTICA for Windows. Version 6.0. StatSoft, Inc., Tulsa, OK.
- STENSETH, N. C., A. MYSTERUD, G. OTTERSEN, J. W. HURRELL, K. S. CHAN, AND M. LIMA. 2002. Ecological effects of climate fluctuations. *Science* 297:1292–1296.
- STILES, F. G. 2004. Austral migration in Colombia: the state of knowledge, and suggestions for action. *Ornitología Neotropical* 15 (Suppl.): 349–355.
- STOTZ, D. F., J. W. FITZPATRICK, T. A. PARKER, AND D. K. MOSKOVITS. 1996. *Neotropical birds: ecology and conservation*. University of Chicago Press, Chicago.
- STRANECK, R. J. 1993. Aportes para la unificación de *Serpophaga sub-cristata* y *Serpophaga munda*, y la revalidación de *Serpophaga griseiceps* (Aves: Tyrannidae). *Revista del Museo Argentino de Ciencias Naturales “Bernardino Rivadavia,” Serie Zoología* 16:51–63.
- VERNER, J. 1985. Assessment of counting techniques. *Current Ornithology* 2:247–302.
- VERNER, J., M. L. MORRISON, AND C. J. RALPH. 1986. *Wildlife 2000: modeling habitat relationships of terrestrial vertebrates*. University of Wisconsin Press, Madison, WI.
- VILLAGRA, P. E., M. A. CONY, N. G. MANTOVÁN, B. E. ROSSI, M. M. GONZÁLEZ LOYARTE, R. VILLALBA, AND L. MARONE. 2004. Ecología y manejo de los algarrobales de la Provincia Fito-geográfica del Monte, p. 1–32. *In* M. F. Arturi, J. L. Frangi, and J. F. Goya [EDS.], *Ecología y manejo de bosques nativos de Argentina*. Editorial Universidad Nacional de La Plata, La Plata, Argentina.
- WANG, M., AND J. PAEGLE. 1996. Impact of analysis uncertainty upon regional atmospheric moisture flux. *Journal of Geophysical Research* 101:7291–7303.
- WIENS, J. A. 1989. *The ecology of bird communities*. Cambridge University Press, Cambridge, UK.
- ZAR, J. H. 1996. *Biostatistical Analysis*. 3rd ed. Prentice Hall, Upper Saddle River, NJ.