

SEASONAL AND MULTIANNUAL PATTERNS IN AVIAN ASSEMBLAGE STRUCTURE AND COMPOSITION IN NORTHERN CHILEAN THORN-SCRUB

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Abstract. The species composition of the Chilean avifauna is well-defined taxonomically but is not well known ecologically. We sampled avian communities at a biosphere reserve in coastal north-central Chile in three seasons over six years (18 surveys total) and characterized them in terms of community structure and composition. The avifauna ($S = 56$ species) was dominated by insectivores ($S = 20$), carnivores ($S = 14$), and granivores ($S = 13$), with lesser contributions by omnivores ($S = 5$), nectarivores ($S = 2$), folivores ($S = 1$), and one vagrant piscivore. The fauna varied greatly between summer and winter, and in most years the breeding season also was distinct. Eighteen species constituted a core group of residents observed in nearly all surveys, but at least 15 species were nomadic or migratory. Our site supported more insectivorous species in winter but more granivores and omnivores in the breeding season, although this observation may be confounded by species' detectability. The structure of the set of species was nested temporally, but this was not clearly caused by seasonal influx supplementing a core fauna of residents. Ordination clearly segregated all three seasons, except for one survey that was explained by very dry conditions in that year. Further research will quantify productivity and demographic responses to long-term climatic variation to compare avian and mammalian patterns with respect to extrinsically generated pulses in resources (e.g., El Niño/Southern Oscillation).

Key words: avian community structure, avian diversity, biosphere reserve, Chile, migration, seasonality, semiarid thorn scrub.

Patrones Estacionales y Multianuales en la Estructura y Composición de Ensamblajes de Aves en el Matorral Espinoso del Norte de Chile

Resumen. La composición de especies de la avifauna de Chile está bien definida taxonómicamente pero no es bien conocida en términos ecológicos. Muestreamos las comunidades de aves en una reserva de biosfera en la costa nor-central de Chile en tres estaciones a lo largo de seis años (18 muestreos en total) y las caracterizamos en términos de estructura y composición de la comunidad. La avifauna ($S = 56$ especies) estuvo dominada por insectívoros ($S = 20$), carnívoros ($S = 14$) y granívoros ($S = 13$), con una menor contribución de omnívoros ($S = 5$), nectarívoros ($S = 2$), folívoros ($S = 1$) y una especie piscívora vagabunda. La fauna varió enormemente entre el verano y el invierno, y en la mayoría de los años la estación reproductiva también fue distintiva. Dieciocho especies representaron un grupo central de residentes observados en casi todos los muestreos, pero al menos 15 especies fueron nómades o migratorias. Nuestro sitio albergó más especies insectívoras en invierno pero más granívoras y omnívoras en la estación reproductiva, aunque esta observación puede estar distorsionada por la detectabilidad de las especies. La estructura del grupo de especies estuvo temporalmente anidada, pero esto no estuvo claramente causado por un influjo estacional suplementando una fauna núcleo de residentes. La ordenación segregó claramente las tres estaciones, excepto por un muestreo que estuvo explicado por condiciones muy secas en ese año. Estudios suplementarios cuantificarán la productividad y las respuestas demográficas a la variación climática de largo plazo para comparar los patrones de aves y mamíferos con respecto a pulsos de recursos generados externamente (e.g., El Niño/Oscilación del Sur).

INTRODUCTION

The avifaunas of temperate arid and semiarid regions of southern South America are well-characterized taxonomically but with few exceptions are rather poorly studied ecologically. In

Argentina, extensive work has documented spatial and temporal patterns at the Ñacuñan Biosphere Reserve (Marone et al. 2000, 2008, Lopez de Casenave et al. 2008). For example, at Ñacuñan as well as at Parque Nacional Bosque de Fray Jorge in northern Chile, research has documented the trenchant role of

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birds as seed predators in temperate South America (Lopez de Casenave et al. 1998, Marone et al. 2000, 2008, Kelt et al. 2004a, b). Basic patterns in assemblage composition, however, remain only moderately understood, and at relatively few localities. Here again, Ñacuñan stands out for the extent of such monitoring (Cueto et al. 2008). The only other site that has received more than relatively short-term effort is near Aucó, located in the northern Mediterranean region of Chile ca. 110 km SSE of Fray Jorge. There, Jaksic and Lazo (1999) reported on variation in the structure and composition of the avian assemblage through a strong El Niño. Although their data were limited to a single fixed-width transect in each of two habitats (north- and south-facing slopes on opposing sides of a ravine) they documented substantial variation in abundance and diversity over 5 years. A second general area on which surprisingly little information has been published is the extent of seasonal and multi-year variation in avifaunal structure and composition in temperate South America. Generally, temperate-zone avifaunas are strongly influenced by seasonal immigration and emigration of migrants (Chesser 1994, Joseph 1997, Berthold et al. 2003, Faaborg et al. 2010). Although this is well-known for arid and semiarid regions (Keast 1959, Brown 1986, Wiens 1991, Dean 2004), few studies have addressed the ecological role or influence of seasonal migrants in temperate South America. This ignorance is more troubling given recent evidence for changes in avian migratory behavior in the face of climate change (e.g., Cotton 2003, Møller 2011, Saino et al. 2011). The general lack of ecological insight into the avifaunas of this region is additionally problematic given that Chile's Mediterranean region is one of the most imperiled parts of the country and a recognized biodiversity hotspot (Myers et al. 2000).

We have been monitoring the avian assemblage at Fray Jorge since 2004, in part for comparison with long-term research at this site on plants, small mammals, and predators (Meserve et al. 2003, 2009, 2011, Gutiérrez et al. 2010). Although we envision assessing small birds' demographic responses to variation in abiotic factors caused by the El Niño Southern Oscillation (ENSO), no such events occurred during the period reported on here. Here we characterize the avifauna at Fray Jorge in three seasons (summer, winter, breeding) across six years (2004–2010), and we apply a series of analyses to test related hypotheses pertaining to how assemblage composition and structure vary seasonally and annually.

We begin by comparing community metrics (diversity, evenness, species richness) and trophic structure across seasons and years, evaluating the hypothesis that assemblage structure and trophic composition vary seasonally (reflecting seasonal presence of migrant species) but not annually (since these data all pertain to a period lacking strong climatic variation). We then evaluate temporal patterns in assemblage nestedness. A series of communities or surveys is considered to be perfectly nested when each species is present in all communities or on all surveys with more species than the most depauperate community

or survey in which that species occurs (Patterson and Atmar 1986). The factors underlying nested structure are numerous and range from sampling artifacts to selective colonization or extinction and the influence of environmental heterogeneity (reviewed in Ulrich et al. 2009). However, if avifaunas are compositionally constrained in sequential surveys, then we would expect a suite of species to constitute a faunal core, with nomadic and migratory species ("satellite" species sensu Hanski 1982) entering and leaving according to resource availability. Consequently, we predict that faunal structure should be nested over time (Elmendorf and Harrison 2009). Finally, we quantify seasonal and annual patterns in avifaunal composition in multidimensional space. As above, we predict that assemblage composition should differ seasonally but not annually, reflecting predictable but divergent sets of species in each season, and we assessed this by using multivariate ordination and associated metrics. We compare the avifauna at our site with that at Aucó and with the limited data available on similar habitats elsewhere. These analyses demonstrate that the avifauna of this region has relatively predictable patterns of structure and composition, and they provide a foundation against which we anticipate comparing data from more productive years associated with El Niño Southern Oscillation (e.g., Bolger et al. 2005, Styrsky and Brawn 2011; but see Stutchbury et al. 2009).

METHODS

STUDY SITE

Our study site is in Fray Jorge (71° 40' W, 30° 38' S), located on the coast of Chile near the northern extreme of the Mediterranean region. Fray Jorge is a biosphere reserve and has been protected from grazing and disturbance since 1941 (Squeo et al. 2004). As such, it is a biological oasis surrounded by highly disturbed and increasingly agricultural terrain (Bahre 1979). We studied birds in thorn scrub in the Quebrada de las Vacas, located immediately inland from a coastal range (the Altos de Talinay) rising to 450 m elevation. Coastal fog deposits considerable moisture in these hills, allowing for the persistence of relict temperate rainforests (del-Val et al. 2006, Squeo et al. 2006) and for high percolation to groundwater. The climate is semiarid Mediterranean with 90% of the ~131 mm of annual precipitation (measured since 1989 at a meteorological station on site) falling in winter (May–September). Summers are warm and dry, although fog and coastal clouds are common. Vegetation generally is spiny and drought-deciduous or evergreen, with heavy shrub cover (ca. 50–60%; Meserve et al. 2009) and understory herbs on a primarily sandy substrate (Gutiérrez et al. 2010); it is characterized as coastal matorral steppe (Gajardo 1994).

In February 2004 we established eight point-count transects at ~1-km intervals along a north–south gradient through the Quebrada de las Vacas. Each transect comprised four stations at 250-m intervals, oriented east–west. We used

variable-distance point counts at each station to sample avian diversity and abundance (Bibby et al. 2000). Using detection curves, we determined that 8 min was sufficient to characterize the avifaunal richness at a given point, and since March 2004 we have surveyed these points every summer (February–March) and winter (usually August), and in all but one year (2005) we also surveyed in the spring breeding season (October–November); here we report data through March 2010. Surveys were conducted within an hour after sunrise (finished by 10:00) on days with suitable conditions (low wind, no rain). The 32 points were repeated once to provide two estimates of numbers; the full survey generally lasted four consecutive days (two observers per survey period). Field workers also recorded additional bird species that were observed during surveys but not on point counts (e.g., while traversing to the next station).

STATISTICAL ANALYSES

We estimated population density with the program Distance 6.0 (Thomas et al. 2009). In general, we followed the procedures and recommendations of Buckland et al. (2001) and Thomas et al. (2010). For species detected an average of ≥ 30 times per session, we visually inspected the data for outliers and set a truncation distance that excluded the most distant 5–10% of observations to avoid excess adjustment terms for the detection function (Buckland et al. 2001). Because distance estimates were frequently rounded, we defined intervals that did not coincide with customary rounding points. This helped prevent rounded distance estimates from falling into incorrect distance intervals (Thomas et al. 2010). We fit uniform, half-normal, and hazard-rate functions with cosine, Hermite, and simple polynomial adjustments. When no single model clearly outperformed the others (on the basis of Akaike's information criterion, AIC), we selected all models with $\Delta AIC < 2$ and applied model averaging (Burnham and Anderson 2002). We estimated precision by bootstrapping with 1000 replicates. We refer to species so analyzed as category 1 species.

To estimate the density of less frequently observed species (< 30 detections per session; category 2 species), we first pooled observations of the species by season. Next, we generated an estimate of the effective detection radius during each season by following the same procedure used to generate detection functions for frequently observed (category 1) species. Finally, we calculated the density of the species during each session by dividing the number of birds observed by the effective survey area as per Spiegel et al. (2006). This analysis assumed that a species' detectability during a particular season remained the same across years.

We calculated Shannon–Wiener species diversity (H') and assemblage evenness (H'/H'_{\max}) for each survey period and compared these across seasons with repeated-measures analysis of variance (rmANOVA) in which years were treated as repeated measures. We allocated species to one of

seven trophic groups (Table 1) on the basis of the literature (references in Table 1) and compared both species richness (S) and population densities across seasons. Because our data are limited to 21 surveys over 3 seasons, however, a multivariate ANOVA was not feasible. We ordinated richness and densities for 5 trophic groups (excluding herbivores and piscivores, which included only one species each) with principal components analysis (PCA) using a correlation matrix, then evaluated significant axes ($\lambda > 1$) with ANOVA (SAS Proc Mixed) with a first-order autoregressive covariance structure. When ANOVA on PCA axes justified further analysis, we applied ANOVA (Proc Mixed) to assess seasonal variation in S and density by trophic group. Because analyses on multiple trophic groups are not independent we applied the sequential Bonferroni adjustment to critical values to assess emerging patterns conservatively (Holm 1979, Rice 1989); Bonferroni adjustments have been controversial (Garcia 2003, Moran 2003), so we present both raw and adjusted P -values for verification of our interpretations.

Nestedness may be quantified in various ways, most typically by tallying unexpected presences or absences (Ulrich et al. 2009). We assessed the nestedness of the Fray Jorge avifauna over time with the algorithm BINMATNEST (Rodríguez-Girones and Santamaria 2006), which improves upon some concerns with the nestedness-temperature calculator (NTC; Atmar and Patterson 1993) and, like the latter metric, calculates a “characteristic temperature” that reflects deviation from perfect nestedness and in theory ranges from zero to 100. We applied BINMATNEST to test the hypothesis of no nested structure in our 18 surveys. As input parameters we used 200 random matrices, a starting population size of 50, 20 individuals selected in each generation, and 5000 generations.

Finally, we ordinated our data by nonmetric multidimensional scaling (NMS) in PC-ORD version 5.32 (McCune and Mefford 2006). NMS is fundamentally different from other ordination techniques in that only the rank order of inter-object distances is used (James and McCulloch 1990). Because variables themselves are not employed in the analyses, NMS is useful for representing relationships among variables but is not as useful (as PCA, for example) for formulating hypotheses about causal relationships among variables (James and McCulloch 1990). It is worth noting that the proportion of variance explained on NMS axes is not necessarily a monotonically declining function of axis rank. We used Sorensen's distance measure as this is robust to outliers and has been demonstrated to be very effective with community data (Beals 1984, McCune et al. 2002), and we applied varimax rotation to our data. NMS operates by iteratively seeking the best positions of n entities (e.g., sites, time periods, etc.) in k dimensions (e.g., ordination axes) such that the stress of this k -dimensional relationship is minimized (Prentice 1977, McCune et al. 2002).

Within ordination space we applied multi-response permutation procedures (MRPP) in PC-ORD to test the

TABLE 1. Species documented during surveys at Bosque Fray Jorge National Park, Chile. Scientific and English names from Remsen et al. (2011); dietary categories taken from Jaksic and Lazo (1999) except where noted in footnotes. Residency status based on our observations.

Species	Abbreviation	Category	Diet ^a	Status
Tinamiformes, Tinamidae				
Chilean Tinamou <i>Nothoprocta perdicaria</i>	CHTI	1	Gran	Resident
Galliformes, Odontophoridae				
California Quail <i>Callipepla californica</i>	CAQU	1	Gran	Resident
Suliformes, Sulidae				
Peruvian Booby <i>Sula variegata</i>	PEBO	2	Pisc	Occasional
Pelecaniiformes, Threskiornithidae				
Black-faced Ibis <i>Theristicus melanopis</i>	BFIB	2	Carn	Occasional
Accipitriformes, Accipitridae				
Variable Hawk <i>Geranoaetus polyosoma</i>	VAHA	1	Carn	Resident
Cinereous Harrier <i>Circus cinereus</i>	CIHA	2	Carn	Occasional
White-tailed Kite <i>Elanus leucurus</i>	WTKI	1	Carn	Summer migrant
Black-chested Buzzard-Eagle <i>Geranoaetus melanoleucus</i>	BCBE	1	Carn	Resident
Harris's Hawk <i>Parabuteo unicinctus</i>	HAHA	1	Carn	Resident
Falconiformes, Falconidae				
Aplomado Falcon <i>Falco femoralis</i>	APFA	1	Carn	Resident, uncommon
Peregrine Falcon <i>Falco peregrinus</i>	PEFA	2	Carn	Resident, uncommon
American Kestrel <i>Falco sparverius</i>	AMKE	2	Carn ^a	Resident
Chimango Caracara <i>Milvago chimango</i>	CHCA	1	Carn ^b	Resident
Gruiformes, Rallidae				
Plumbeous Rail <i>Pardirallus sanguinolentus</i>	PLRA	2	Insect ^c	Occasional
Charadriiformes, Charadriidae				
Southern Lapwing <i>Vanellus chilensis</i>	SOLA	2	Insect ^d	Uncommon resident ^e
Columbiformes, Columbidae				
Picui Ground Dove <i>Columbina picui</i>	PGDO	2	Gran	Resident but uncommon in park ^f
Chilean Pigeon <i>Patagioenas araucana</i>	CHPI	1	Gran	Resident
Eared Dove <i>Zenaida auriculata</i>	EADO	1	Gran	Resident
West Peruvian Dove <i>Zenaida meloda</i>	PADO	2	Gran	Occasional ^g
Caprimulgiformes, Caprimulgidae				
Band-winged Nightjar <i>Caprimulgus longirostris</i>	BWNI	2	Insect	Resident
Strigiformes, Strigidae				
Short-eared Owl <i>Asio flammeus</i>	SEOW	2	Carn	Resident
Burrowing Owl <i>Athene cunicularia</i>	BUOW	1	Carn	Resident
Austral Pygmy-Owl <i>Glaucidium nana</i>	APOW	1	Carn	Resident
Apodiformes, Trochilidae				
Giant Hummingbird <i>Patagona gigas</i>	GIHU	1	Nect	Resident
Green-backed Firecrown <i>Sephanoides sephaniodes</i> ^h	GBFI	1	Nect	Resident
Piciformes, Picidae				
Chilean Flicker <i>Colaptes pitius</i>	CHFL	2	Insect	Resident ⁱ
Striped Woodpecker <i>Veniliornis lignarius</i>	STWO	1	Insect	Resident
Passeriformes, Tyrannidae				
Great Shrike-Tyrant <i>Agriornis lividus</i>	GSTY	1	Carn	Resident
Tufted Tit-Tyrant <i>Anairetes parulus</i>	TTYT	1	Insect	Resident
Patagonian Tyrant <i>Colorhamphus parvirostris</i>	TATY	?	Insect	Winter visitor (uncommon)
White-crested Elaenia <i>Elaenia albiceps</i>	WCEL	1	Insect	Summer visitor
Dark-faced Ground-Tyrant <i>Muscisaxicola maclovianus</i>	DFGT	2	Insect	Winter visitor
Fire-eyed Diucon <i>Xolmis pyrope</i>	FEDI	1	Insect	Resident
Passeriformes, Cotingidae				
Rufous-tailed Plantcutter <i>Phytotoma rara</i>	RTPL	1	Foliv	Transient
Passeriformes, Furnariidae				
Dusky-tailed Canastero <i>Pseudasthenes humicola</i>	DTCA	1	Insect	Resident
Common Miner <i>Geositta cunicularia</i>	COMI	1	Insect ^j	Resident
Rufous-banded Miner <i>Geositta rufipennis</i>	TBMI	2	Insect ^j	Occasional

(Continued)

TABLE 1. Continued

Species	Abbreviation	Category	Diet ^a	Status
Plain-mantled Tit-Spinetail <i>Leptasthenura aegithaloides</i>	PMTS	1	Insect	Resident
Scale-throated Earthcreeper <i>Upucerthia dumetaria</i>	STEA	1	Insect	Winter visitor
Passeriformes, Rhinocryptidae				
Moustached Turca <i>Pterotochos megapodius</i>	MOTU	1	Insect	Resident
White-throated Tapaculo <i>Scelorchilus albicollis</i>	WTTA	1	Insect	Resident
Dusky Tapaculo <i>Scytalopus fuscus</i>	DUTA	1	Insect	Resident
Passeriformes, Hirundinidae				
Chilean Swallow <i>Tachycineta meyeni</i>	CHSW	1	Insect	Resident
Passeriformes, Troglodytidae				
Chilean House Wren <i>Troglodytes aedon chilensis</i>	SHWR	1	Insect	Resident
Passeriformes, Mimidae				
Chilean Mockingbird <i>Mimus thenca</i>	CHMO	1	Omn	Resident
Passeriformes, Turdidae				
Austral Thrush <i>Turdus falcklandii</i>	AUTH	1	Omn	Resident
Passeriformes, Emberizidae				
Common Diuca-Finch <i>Diuca diuca</i>	CDFI	1	Gran	Resident
Gray-hooded Sierra-Finch <i>Phrygilus gayi</i>	GHSF	1	Gran	Resident
Mourning Sierra-Finch <i>Phrygilus fruticeti</i>	MOSF	1	Gran	Resident
Band-tailed Sierra-Finch <i>Phrygilus alaudinus</i>	BTSF	1	Gran	Resident
Grassland Yellow-Finch <i>Sicalis luteola</i>	GYFI	1	Gran	Resident
Rufous-collared Sparrow <i>Zonotrichia capensis</i>	RCSP	1	Gran	Resident
Passeriformes, Icteridae				
Austral Blackbird <i>Curaeus curaeus</i>	AUBL	1	Omn	Resident
Shiny Cowbird <i>Molothrus bonariensis</i>	SHBL	2	Omn ^k	Occasional
Long-tailed Meadowlark <i>Sturnella loyca</i>	LTME	1	Omn	Resident
Passeriformes, Fringillidae				
Black-chinned Siskin <i>Sporagra barbata</i>	BCSI	1	Gran	Resident

^aYáñez et al. (1980).^bEstades (1997), Morrison and Phillips (2000).^cRomano et al. (2005).^dEstades (1997).^eCommon outside park but habitat inside park includes dense vegetation it does not favor.^fCommon outside of park in agricultural regions.^gAppears to be colonizing this region of Chile from the north.^h*S. sephaniodes* is referred to by many authors as *S. sephanioides*. The taxonomic history of this specific epithet is complicated, as both names were published within one year by Lesson and by Lesson and Garnot. We thank J. V. Remsen (Louisiana State University) and Edward Dickinson for their detective work on this issue.ⁱCommon in bosques but only occasionally descends to matorral.^jHellmayr (1932), Ridgley and Tudor (1994).^kLowther and Post (1999).

hypothesis that avian community composition was similar in different seasons. MRPP is a nonparametric procedure so has limited assumptions concerning the distribution of data (McCune et al. 2002).

RESULTS

Rainfall at our site fluctuated moderately over the period of study, but this fluctuation was minor in comparison to those caused by ENSO over the 20-year duration of our research program (Fig. 1). Consequently, our analyses are largely limited to comparisons across seasons and over a relatively xeric 6-year period similar to the dry period reported on by Jakšić

and Lazo (1999; e.g., 1993–96). We recorded 56 bird species in 4608 minutes of point counts.

GENERAL PATTERNS IN ABUNDANCE

The avifauna of Fray Jorge thorn scrub was strongly influenced by insectivores ($S = 20$ species) and granivores ($S = 13$), but it also included a large carnivore guild ($S = 14$) (Table 1). Four of the latter were observed only once in our surveys, however, and represent transient or uncommon species (Black-faced Ibis, *Theristicus melanopis*; Peregrine Falcon, *Falco peregrinus*; Cinereous Harrier, *Circus cinereus*) or otherwise nocturnal species (Short-eared Owl, *Asio flammeus*). The single piscivore observed (Peruvian Booby, *Sula variegata*)

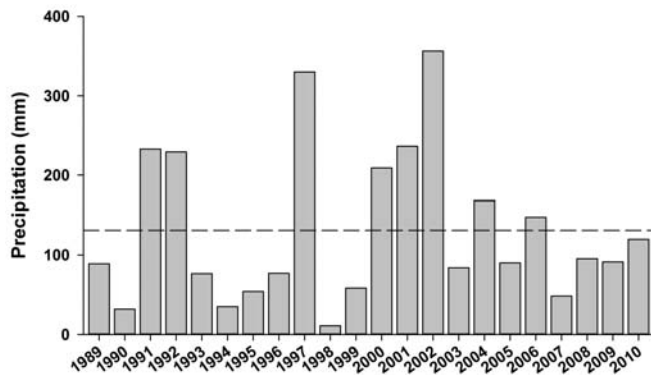


FIGURE 1. Annual precipitation over the 20 years of our research at Bosque Fray Jorge National Park, emphasizing the variation in rainfall by year. Data reported here were recorded from 2004 through 2010.

is a marine forager and is not a typical element of this fauna. In contrast, only two of the granivores and four of the insectivores were observed in only one session. Our surveys include one folivore (Rufous-tailed Plantcutter, *Phytotoma rara*), which was encountered infrequently on visual surveys but was netted frequently during separate banding efforts, particularly during spring migration, indicating it may be a common transient. Two nectarivores (Green-backed Firecrown, *Sebanoides sebanoides*; Giant Hummingbird, *Patagona gigas*) remained predictable throughout the study period, however, and a third (Oasis Hummingbird, *Rhodopis vesper*) was observed during one session but not on point counts. The last species is resident in valleys much farther to the north in Arica, and our records are the first we know of for this region (Region IV or Coquimbo) of Chile. Four of five omnivorous species (Chilean Mockingbird, *Mimus thenca*; Austral Thrush, *Turdus falklandii*; Austral Blackbird, *Curaeus curaeus*; Long-tailed Meadowlark, *Sturnella loyca*) were observed in most sessions; only the Shiny Cowbird (*Molothrus bonariensis*) was relatively unexpected in any given survey.

A coarse perspective on temporal patterns may be extracted from the number of individuals observed (including fly-bys and flyovers) per survey. Of 56 species documented, 12 were observed in a single survey, three in just two surveys, and one in only three surveys. These 16 species were not regularly observed and are treated cautiously in analyses. In contrast, 15 species were present in all surveys, and three more were present in 17. Thus 34 of 56 species (61%) were either rarely observed (three or fewer surveys) or were highly predictable in their occurrence (16 or more surveys); the remaining 22 species were observed fairly consistently in any given season.

Highly predictable resident species include the highly terrestrial rhinocryptids (Dusky Tapaculo, *Scytalopus fuscus*; White-throated Tapaculo, *Scelorchilus albicollis*; Moustached Turca, *Pterotochos megapodius*) and the ground-nesting Chilean Tinamou (*Nothoprocta perdicaria*) and introduced

California Quail (*Callipepla californica*), as well as the granivorous Common Diuca Finch (*Diuca diuca*), insectivorous Tufted Tit-Tyrant (*Anairetes parulus*), Dusky-tailed Canastero (*Asthenes humicola*), Striped Woodpecker (*Picoides lignarius*), and Plain-mantled Tit-Spinetail (*Leptasthenura aegithaloides*), and the omnivorous Chilean Mockingbird. Additionally, sparsely distributed carnivores such as the Black-chested Buzzard-Eagle (*Geranoaetus melanoleucus*), Harris's Hawk (*Parabuteo unicinctus*), and Great Shrike-Tyrant (*Agriornis lividus*) were observed in all survey periods but they were not detected on point counts in four or five seasons. Two nectarivores (both hummingbirds) and the insectivorous Chilean House Wren (*Troglodytes aedon chilensis*) were predictable residents, although their detectability varied seasonally. The avifauna of our study area fluctuated greatly through the year (Fig. 2), primarily because of the seasonal (winter to spring) influx of migratory granivores such as the Band-tailed Sierra-Finch (*Phrygilus alaudinus*), Mourning Sierra-Finch (*P. fruticeti*), Black-chinned Siskin (*Sporagra barbata*), and, to a lesser extent, Grassland Yellow-Finch (*Sicalis luteola*) and Chilean Pigeon (*Patagioenas araucana*) and migratory insectivores such as the Fire-eyed Diucon (*Xolmis pyrope*) and White-crested Elaenia (*Elaenia albiceps*). The Patagonian Forest Earthcreeper (*Upucerthia saturator*) and Common Miner (*Geositta cunicularia*) were never abundant; the former species migrates to the region most winters, but the latter is a common resident outside the park in fallow agricultural lands.

In spite of marked variation in the abundance and composition of species at our study site, neither species richness (S) nor assemblage evenness (E) varied seasonally (S : $\bar{X} = 30.67$ species, range 24–36; $F_{2,15} = 0.52$, $P = 0.61$; E : $\bar{X} = 0.80$, range 0.77–0.84, $F_{2,15} = 2.07$, $P = 0.16$). In contrast, species diversity (H') was greater in winter and the breeding season than in summer ($H' = 2.77$ and 2.79 vs. 2.67 ; $F_{2,15} = 8.27$, $P = 0.004$), reflecting an influx of seasonal migrants.

TROPHIC STRUCTURE

In general, our data do not support a hypothesis of strong seasonality in trophic structure (Fig. 3). When species were allocated to trophic groups, ANOVA on number of species observed per season demonstrated significant seasonal variation on the first two axes of a PCA (PC 1, $\lambda = 1.64$, $F_{2,14} = 8.80$, $P = 0.003$; PC 2, $\lambda = 1.37$, $F_{2,14} = 8.58$, $P = 0.004$). When subsequent ANOVAs were Bonferroni-adjusted, however, only insectivores' species richness varied seasonally, with more species present in winter than in summer and the breeding season ($F_{2,14} = 7.55$, $P = 0.006$). Granivores tended to be more speciose in the breeding season, and omnivores less speciose in summer, but these trends are not statistically defensible (granivores; $P = 0.026$, Bonferroni-adjusted critical value = 0.012; omnivores, $P = 0.039$, Bonferroni-adjusted critical value = 0.017).

Population densities also varied significantly by season, although only on the second PC axis (PC 1, $\lambda = 2.2$, $F_{2,14} = 0.01$,

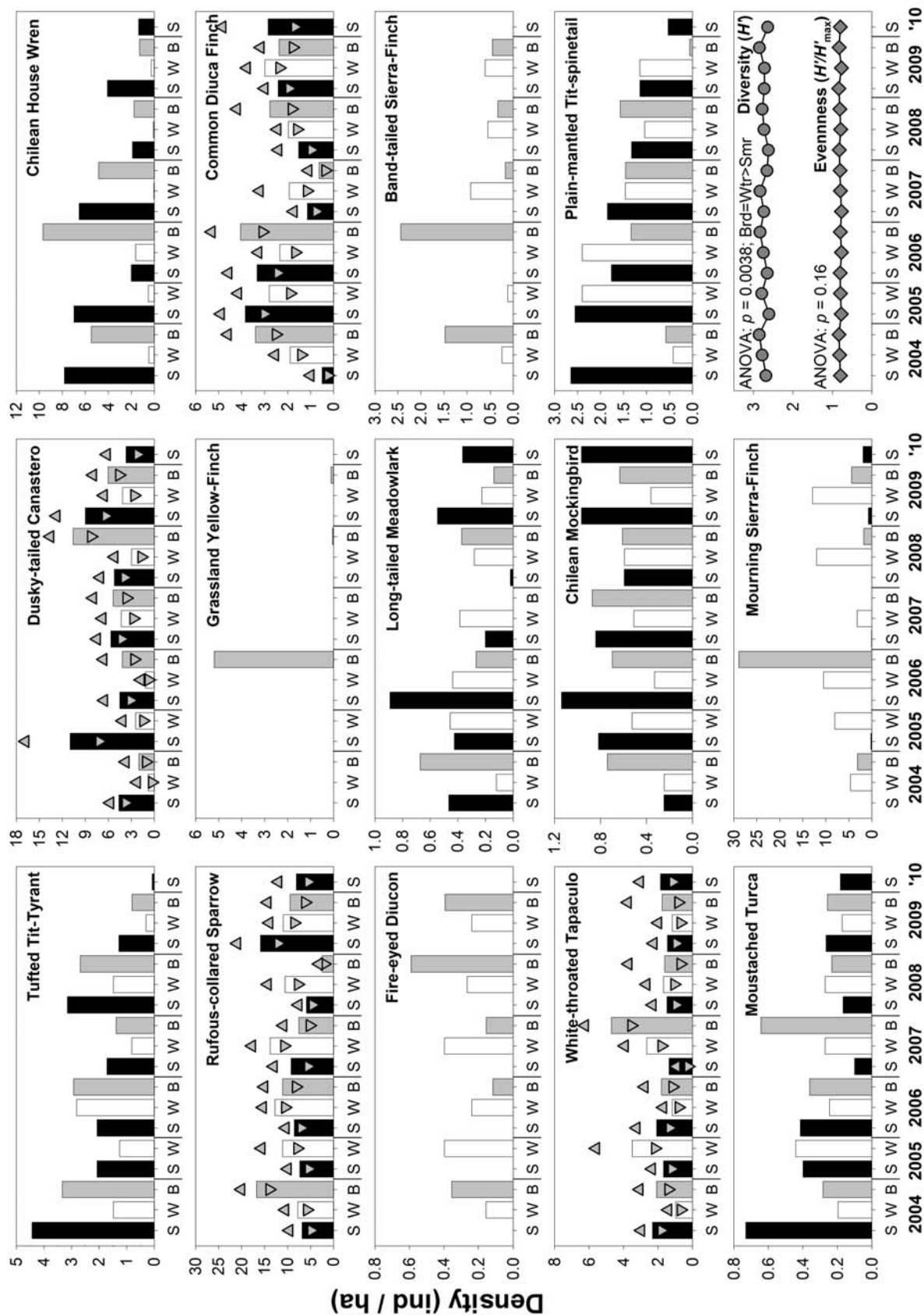


FIGURE 2. Temporal patterns in some species at Fray Jorge. Presented are mean values across replicate point counts; upper and lower 95% confidence limits are presented for category 1 species (see text). Lower right panel shows temporal patterns in two community metrics, Shannon–Wiener species diversity (H') and evenness (H'/H'_{\max}).

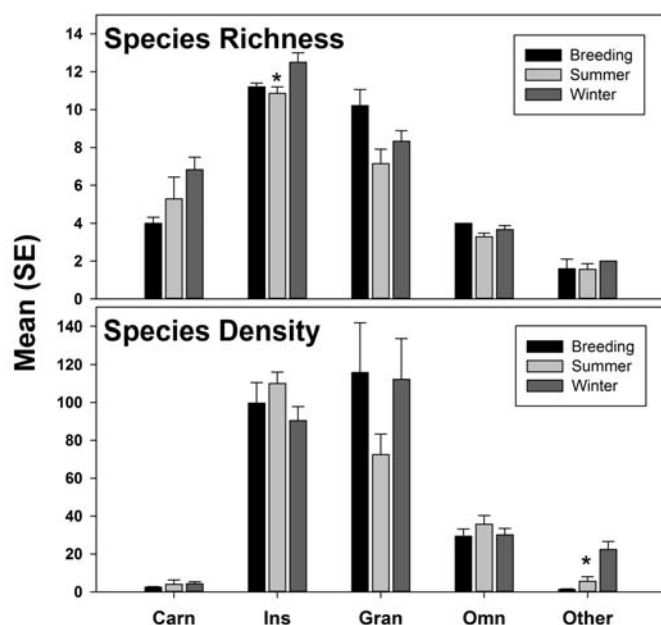


FIGURE 3. Seasonal patterns in species richness (upper panel) and bird density (individuals ha^{-1} ; bottom panel) at Fray Jorge, separated by foraging guild. “Other” includes two species of nectarivore, one folivore, and one piscivore. Asterisks indicate seasonal comparisons different after Bonferroni adjustment of critical values.

$P = 0.989$; PC 2, $\lambda = 1.208$, $F_{2,14} = 12.88$, $P < 0.001$). The only trophic group to vary seasonally in density was the nectarivores (comprising only two common species), which were more abundant in winter than in summer or during the breeding season ($F_{1,14} = 15.75$, $P < 0.001$; Fig. 3).

NESTEDNESS

Across all surveys and including all 56 species, the species \times session matrix was 40% filled (from the NTC) and had a matrix temperature of 29.57° (the NTC calculated a higher value of 32.21°). The probability of this matrix structure occurring by random reshuffling of these data was low ($P < 0.00001$). On the basis of only those species present in three or more surveys ($S = 41$ species), matrix fill was 58% (from the NTC), temperature was 31.35° (34.74° by the NTC), and the probability of this occurring at random was low ($P < 0.00001$). Hence, we reject the hypothesis that the avifauna at our site was a random association of species; rather, certain species constitute core elements of this avifauna and are highly predictable, while other species enter or leave the assemblage in a predictable manner.

NONMETRIC MULTIDIMENSIONAL SCALING

The best ordination included three dimensions, in which stress was significantly lower than when randomized data were used ($P = 0.004$). The resulting axes explained 12.0%, 11.5%, and 68.9% of the variance in the ordination (Fig. 4). Winter assemblages were distinct from those of both summer

(MRPP; $t_1 = -5.34$, $A = 0.22$, $P < 0.001$) and breeding season ($t_1 = -2.48$, $A = 0.11$, $P = 0.02$), whereas summer and breeding-season assemblages were similar ($t_1 = -1.06$, $A = 0.04$, $P = 0.14$). This is most clearly visible in bivariate space comprised of axes 1 and 3, which explain just over 80% of the variance in the ordination. When species are overlaid upon the NMS axes (Fig. 5), it is clear that winter surveys are strongly influenced by the Grassland Yellow-Finch, Mourning Sierra-Finch, Green-backed Firecrown, Gray-hooded Sierra-Finch (*Phrygilus gayi*), and Black-faced Ibis, whereas summer surveys were dominated by the Black-chested Buzzard-Eagle, Harris's Hawk, Variable Hawk, and to a lesser extent Great Shrike-Tyrant, Chilean Swallow (*Tachycineta meyeni*), and Dusky-tailed Canastero.

The lack of segregation between summer and the breeding season evidently was caused by the otherwise unique position of data for the breeding season of 2007, which clustered in ordination space with those for summer 2004. In fact, 2007 was the driest year in this 6-year study period (48.4 mm precipitation), and if this single data point is removed, then all three seasons become distinct in ordination space (summer–winter, $t = -5.37$, $A = 0.22$, $P < 0.001$; summer–breeding, $t = -3.69$, $A = 0.15$, $P = 0.003$; winter–breeding, $t = -3.01$, $A = 0.17$, $P = 0.01$).

DISCUSSION

The avifauna of our study site in north-central Chile is moderately diverse and varies greatly by both season and year. In spite of variation in species composition over time, however, total species richness and species diversity appear to hold fairly constant, suggesting the presence of compensatory dynamics.

At a site in the foothills of the Andes near Aucó, Jaksic and Lazo (1999) recorded 61 species. Although we documented only 56 species on our transects, incidental (off-transect) records at the site bring the sum to 74 species. In many cases, a species at Fray Jorge was replaced by a relative at Aucó, such as the Dusky-tailed Canastero (Fray Jorge) vs. Cordilleran Canastero (*A. modesta*; Aucó), Dusky Tapaculo (Fray Jorge) vs. Magellanic Tapaculo (*S. magellanicus*; Aucó), and Picui Ground-Dove (*Columbina picui*; Fray Jorge) vs. Black-winged Ground-Dove (*Metriopelia melanoptera*; Aucó). Or, one site added a second closely related species, such as the Pacific Dove (*Zenaida meloda*; Fray Jorge) with the Eared Dove (Fray Jorge and Aucó), the Straight-billed Earthcreeper (*Ochetorhynchus ruficaudus*; Aucó) with the Patagonian Earthcreeper (Fray Jorge and Aucó), the Common Miner (Fray Jorge) with the Rufous-banded Miner (*Geositta rufipennis*; Fray Jorge and Aucó), and the Yellow-rumped Siskin (*Sporagra uropygialis*; Aucó) with the Black-chinned Siskin (Fray Jorge and Aucó). Other species at Aucó were widespread (e.g., Andean Condor, *Vultur gryphus*) or characteristic of more mesic or anthropogenically altered habitats (e.g., House

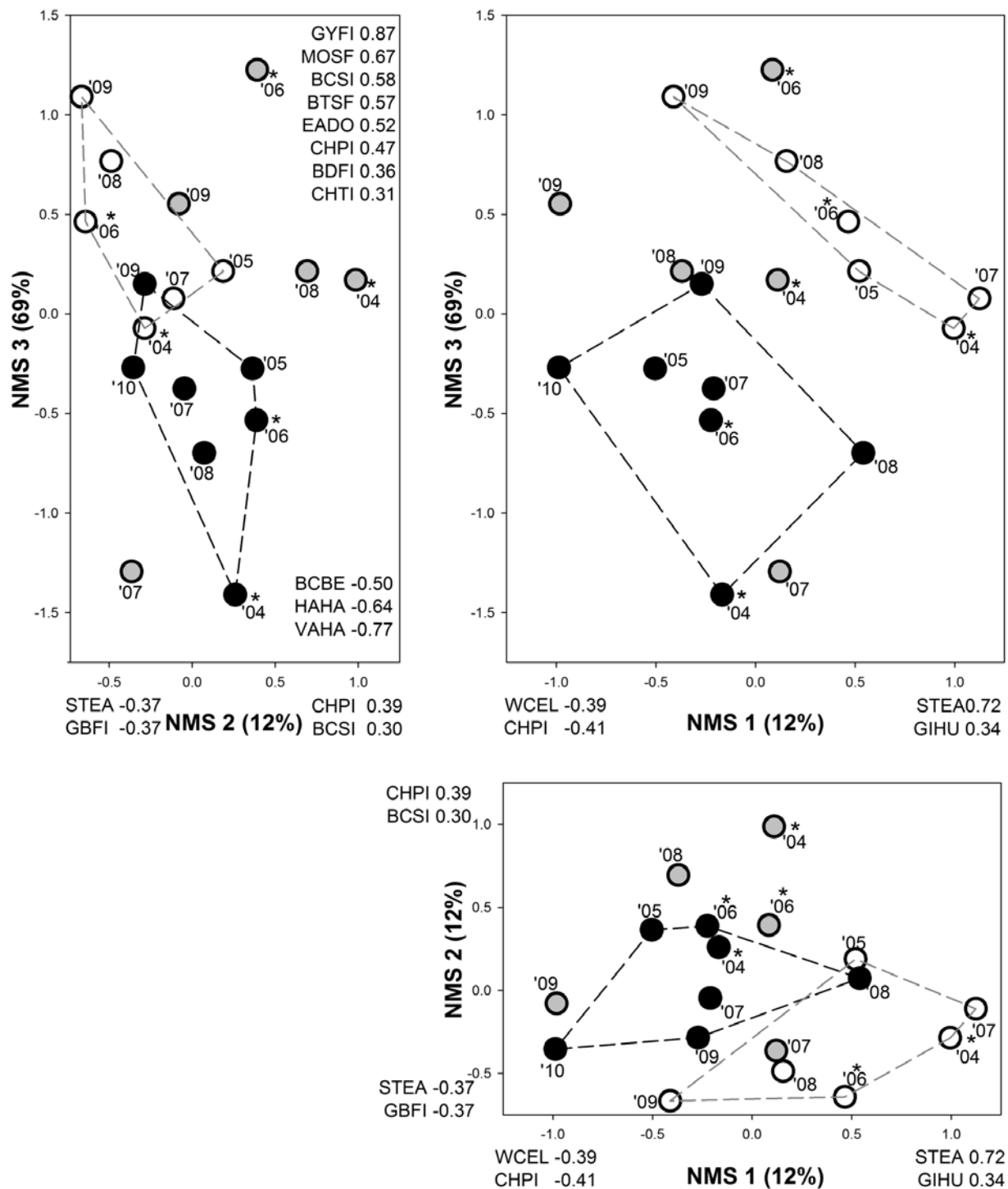


FIGURE 4. Results of nonmetric multidimensional scaling of the avian assemblages at Fray Jorge over 6 years. The three possible bivariate plots for these axes are presented with loadings by key species indicated for each axis and seasons indicated by shading (black = summer, white = winter, gray = breeding). Asterisks indicate two particularly wet years during this period. Species scores are provided for each axis; see Table 1 for four-letter abbreviations for species.

Sparrow, *Passer domesticus*). Presence of the last species at Aucó suggests that this site is less isolated from anthropogenic disturbances than is Fray Jorge. Trophic groups at Fray Jorge

were dominated by insectivores (36%), carnivores (25%), and granivores (23%), accounting for 84% of the local assemblage, proportions similar to those at Aucó (insectivores 34%,

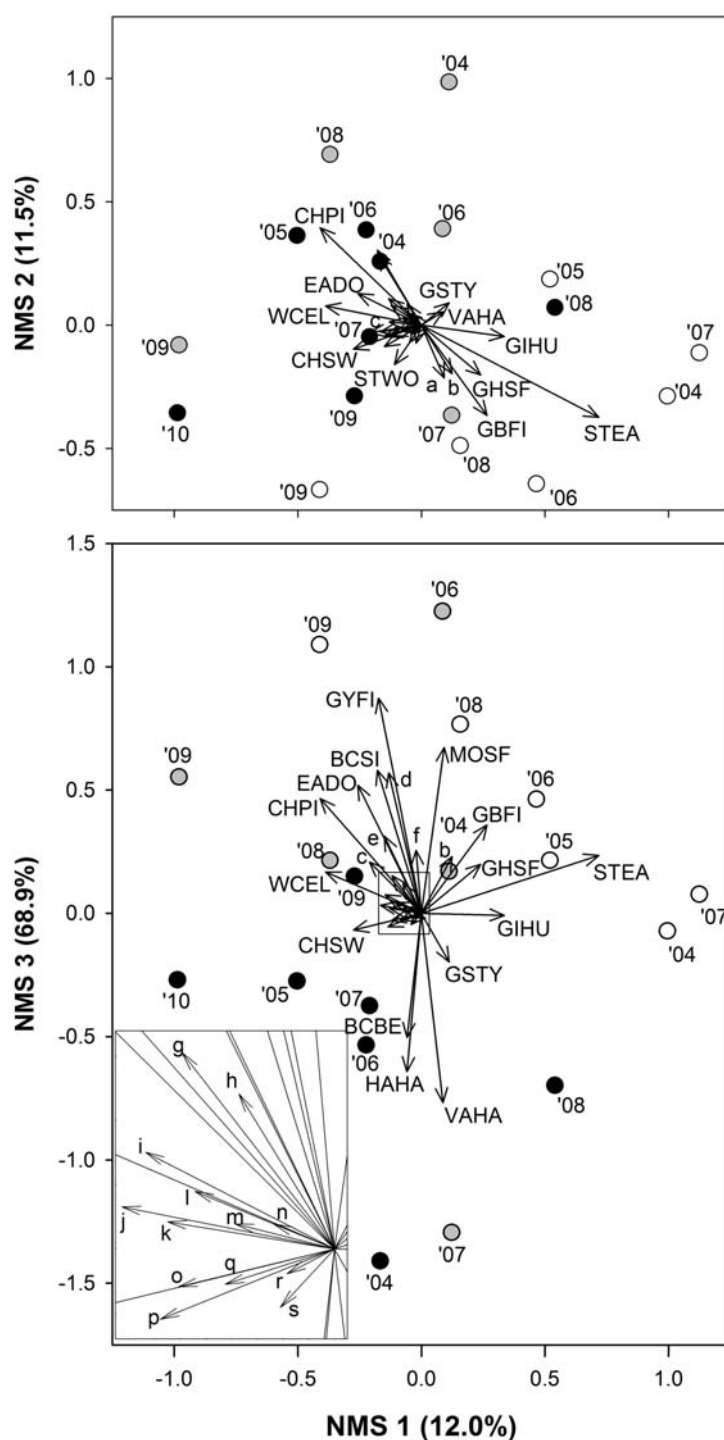


FIGURE 5. Detail of nonmetric multidimensional scaling of avian assemblages at Fray Jorge. Presented are centroids for each survey (shading as in Fig. 4) in the first and second ordination axes (upper panel) and the first and third ordination axes (bottom panel). Vectors indicate the magnitude and directionality of influence by constituent species. Inset highlights vectors for species with lower influence on these axes. Species designations: a = Mourning Sierra-Finch, b = Austral Thrush, BCBE = Black-chested Buzzard-Eagle, BCSI = Black-chinned Siskin, c = Common Duet-Finch, CHPI = Chilean Pigeon, CHSW = Chilean Swallow, d = Band-tailed Sierra-Finch, e = Chilean Tinamou, EADO = Eared Dove, f = Fire-eyed Duet, g = Austral Blackbird, GBFI = Green-backed Firecrown, GHSF = Gray-hooded Sierra-Finch, GIHU = Giant Hummingbird, GSTY = Great Shrike-Tyrant, GYFI = Grassland Yellow-Finch, h = Rufous-collared Sparrow, HAHA = Harris's Hawk, i = Long-tailed Meadowlark, j = California Quail, k = Dusky Tapaculo, l = Striped Woodpecker, m = White-throated Tapaculo, MOSF = Mourning Sierra-Finch, n = Moustached Turca, o = Chilean House Wren, p = Dusky-tailed Canastero, q = Chilean Mockingbird, r = Tufted Tit-Tyrant, s = Plain-mantled Tit-Spinetail, STWO = Striped Woodpecker, STEA = Scale-throated Earthcreeper, VAHA = Variable Hawk, WCEL = White-crested Elaenia.

carnivores 28%, and granivores 25%) (Jaksić and Lazo 1999). Marone (1992) reported on a subset of the avifauna at Ñacuñan, focusing on the eight most common species, and on the guild structure of 40 species excluding raptors. He reported higher numbers of insectivores (60%) and fewer granivores (25%) and folivores (15%). When we subsample our data to be comparable (e.g., excluding hawks, owls, caracaras, and the single piscivore that was observed one time), our results converge only partially on those from Argentina; of the remaining 41 species in this fauna, insectivores increase in prominence (46%), but granivores remain more speciose (32%), and we have only a single folivore (2%). Thus Ñacuñan has a higher proportion of insectivores and especially folivores but fewer granivores. There are more species recorded for Monte, Argentina (88), than for the two Chilean sites, and seasonal movements of insectivorous birds may account for the higher diversity of insectivores and overall. Further research on the relative roles of local influences (habitat, productivity, etc.) and regional factors (regional species pool, role of migration, etc.) in structuring these faunas would be productive.

We expected to document seasonal variation in trophic structure, but results for this were not compelling. Although insectivores and, to a much lesser extent, granivores and omnivores exhibited seasonal patterns in species richness, population densities of these guilds were temporally relatively invariant. In contrast, the depauperate guild of nectarivores (Giant Hummingbird and Green-backed Firecrown) was much more abundant in winter, reflecting a seasonal influx of the smaller of these species.

We were not surprised that the avifauna at Fray Jorge is temporally nested. We documented 18 core species that were observed in at least 17 of our 18 surveys. These were complemented by another dozen species that were present in 10 or more surveys. In contrast, fully a dozen species were documented only one time on surveys, and another three only twice. We suspect that temporal time series such as those analyzed here should typically be nested, and that this reflects the predictability with which species return seasonally to complement the core constituents of the local avifauna (Hanski 1982, Gibson et al. 1999, Elmendorf and Harrison 2009); additionally, less abundant species would, all else being equal, be expected to be the first to be absent in a given year as a simple function of species-abundance distributions (Magurran 2007). Nonetheless, the role of seasonality in producing the observed nested structure is somewhat unclear. Of the 11 species observed in two to six surveys, four were observed only in winter (Scale-throated Earthcreeper, Common Miner, Peregrine Falcon, Patagonian Tyrant [*Colorhamphus parvirostris*]), one only during the breeding season (Rufous-tailed Plantcutter), and two more predominantly in the breeding season (Chilean Pigeon, White-crested Elaenia). Seven of 12 species observed once were observed in summer, three in only winter, and two species were observed only in a single

breeding-season survey. However, of 14 species observed in 7 to 15 surveys, there was little indication of seasonally nested structure (although these species were highly nested, with a matrix temperature of 32.12°, $P < 0.00001$). Hence, nestedness in this system appears to reflect dynamics within a season more than just seasonal presence vs. absence.

The nonmetric multidimensional analysis was particularly informative for this fauna. The second and third axes of this analysis clearly illustrate the distinctiveness of summer and winter faunas, and that breeding-season faunas generally grouped closer to winter than to summer faunas. A single exception was the breeding season of 2007 (Fig. 4) and likely illustrates the importance of timing of rainfall at this semiarid site. This year (2007) was the driest in the 6-year time series analyzed (Fig. 1). The breeding season either was abbreviated or curtailed in this year; by November, when we conducted our “breeding-season” surveys, the avifauna at Fray Jorge was more characteristic of a summer fauna than either a winter or a breeding-season fauna, and in ordination space this grouped with other summer surveys. It is worth pointing out that the segregation of data points in Figures 4 and 5 reflects strictly seasonal membership in this fauna; the habitats are not changing other than in response to seasonal patterns of rainfall and temperature. These findings are similar to those from similar semiarid habitats in Baja California (26° N), where initiation of breeding of several species of birds is strongly correlated with rainfall and temperature, with earlier onset during wet periods (George 1987). Reporting similar results from southern California, Unitt (2004:31–32) suggested that drought conditions do not only shift the timing of avian breeding but rather delay the onset and hasten the termination of the breeding season.

What is clear from our data is that the avifauna includes a number of nomadic or migratory species. Among species that were present in four or more surveys, two of three granivores (Band-tailed Sierra-Finch, Mourning Sierra-Finch) were highly seasonal, with the former most abundant during breeding surveys and the latter during winter surveys. Another, the Gray-hooded Sierra-Finch, generally was uncommon but was three times more abundant in winter than in either summer or the breeding season. Whereas the former two species routinely breed at Fray Jorge, the latter appears to be a winter migrant, although some birds may linger to nest, particularly during wetter springs. The Green-backed Firecrown was four times more abundant in winter than summer, and although the Giant Hummingbird was never common, it was 4.7 and 5.1 times more common in the breeding season and winter than in summer. Both species of hummingbirds begin nesting in the park in late July and August (austral winter) and generally are among the first species in Fray Jorge to begin breeding (A. Engilis Jr., pers. obs.), paralleling the timing of nesting of Allen’s (*Selasphorus sasin*) and Costa’s (*Calypte costae*) Hummingbirds in coastal and desert scrub at similar latitude in North America (George 1987, Mitchell 2000). The Austral Thrush was less abundant

than the Giant Hummingbird but followed a similar seasonal pattern, being 10.8 and 12 times more abundant in the breeding season and winter than during summer. This last species may still be present in summer but is far less vocal and therefore harder to locate from point counts. Several species that were present in relatively few surveys were nonetheless highly seasonal. The Common Miner and Scale-throated Earthcreeper were documented in only four and five surveys, respectively, but all occurred in winter. The Black-chinned Siskin, White-crested Elaenia, and Grassland Yellow-Finch were observed in eight, six, and five surveys but were 18–121 times more abundant in the breeding season than in summer; two of these were 4–36 times more abundant in the breeding season than in winter, whereas the third (White-crested Elaenia) migrates to tropical regions and consequently is never observed in winter.

Although we have documented that many species are seasonally abundant, what is not clear is whether these species are nomadic or truly migratory, and where they go when they leave the park. It is likely that most migratory species here are members of the South American cold-temperate group (Joseph 1997) and that the South American temperate–tropical group is less strongly represented. Migration is not as prominent in South America as it is in North America, in part because of the relatively smaller area of temperate habitat (Elphick 2007), but many species in Chile move latitudinally, altitudinally, or across the Andes with the seasons. It is likely that birds at Fray Jorge employ a mixture of altitudinal and latitudinal migration. Some Giant Hummingbirds, for example, migrate between Chile and Argentina (Fjeldsø and Krabbe 1990), as do earthcreepers (Areta and Pearman 2009). White-crested Elaenias follow a similar route, but (as noted above) evidently continue north to the Amazon Basin (Fjeldsø and Krabbe 1990, Schulenberg 2009). Yellow-finches and siskins may be more nomadic than migratory.

Resolution of migratory patterns within South America's southern cone should be a priority for research, as it has implications for conservation and management. Recent efforts based on tracking banded birds in Argentina (Capllonch and Lobo 2005, Capllonch and Zelaya 2006, Capllonch 2007, Capllonch et al. 2009) provide an excellent beginning toward this objective, as does the comprehensive avian research underway at Ñacuñan Biosphere Reserve (Cueto et al. 2008, Lopez de Casenave et al. 2008). The recent creation of a national banding office within Chile's national agricultural agency, the Servicio Agrícola y Ganadero (<http://www.sag.gob.cl>) is likely to further foster such efforts (Estades 2004). Efforts to resight banded birds have an inherently low probability of success, however, and application of indirect methods such as stable isotopes and related geochemical markers promises to continue to move this field forward (Rubenstein et al. 2002, Hobson 2005, Kelly 2006, Paxton et al. 2007).

The avifauna of semiarid habitats in northern Mediterranean Chile is diverse (Araya and Bernal 1995, Jaramillo et al. 2003, Jakšić et al. 2004) but surprisingly poorly studied

(e.g., Jakšić and Lazo 1999, Engilis and Kelt 2009, 2011). This region's annual rainfall varies dramatically in response to ENSO (Jakšić 2001), followed by equally dramatic changes in vegetative ground cover, population densities of small mammals (Meserve et al. 2003, 2009, 2011, Gutiérrez et al. 2010), and, in turn, by vertebrate predators (Jakšić et al. 1997). We have integrated triennial avian surveys into our long-term research program at Fray Jorge, and in the coming years we anticipate clarifying the extent to which birds respond demographically and energetically in a manner similar to that of mammals in this region.

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LITERATURE CITED

- ARAYA, B., AND M. BERNAL. 1995. Aves, p. 350–360. *In* J. A. Simonetti, M. T. K. Arroyo, A. E. Spotorno and E. Lozada [EDS.], *Diversidad biológica de Chile. Comité Nacional de Diversidad Biológica, Comisión Nacional de Investigación Científica y Tecnológica (CONICYT)*, Santiago, Chile.
- ARETA, J. I., AND M. PEARMAN. 2009. Natural history, morphology, evolution, and taxonomic status of the earthcreeper *Upucerthia saturator* (Furnariidae) from the Patagonian forests of South America. *Condor* 111:135–149.
- ATMAR, W., AND B. D. PATTERSON. 1993. The measure of order and disorder in the distribution of species in fragmented habitat. *Oecologia* 96:373–382.
- BAHRE, C. J. 1979. *Destruction of the natural vegetation of north-central Chile*. University of California Press, Berkeley.
- BEALS, E. W. 1984. Bray–Curtis ordination: an effective strategy for analysis of multivariate ecological data. *Advances in Ecological Research* 14:1–55.
- BERTHOLD, P., E. GWINNER, AND E. SONNENSCHNEIN. 2003. *Avian migration*. Springer, Berlin.
- BIBBY, C. J., N. D. BURGESS, D. A. HILL, AND S. H. MUSTOE. 2000. *Bird census techniques*. Academic Press, San Diego.
- BOLGER, D. T., M. A. PATTEN, AND D. C. BOSTOCK. 2005. Avian reproductive failure in response to an extreme climatic event. *Oecologia* 142:398–406.
- BROWN, J. H. 1986. The roles of vertebrates in desert ecosystems, p. 51–71. *In* W. G. Whitford [ED.], *Pattern and process in desert ecosystems*. University of New Mexico Press, Albuquerque.
- BUCKLAND, S. T., D. R. ANDERSON, K. P. BURNHAM, J. L. LAAKE, D. L. BORCHERS, AND L. THOMAS. 2001. *Introduction to distance sampling: estimating abundance of biological populations*. Oxford University Press, Oxford, England.

- BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York.
- CAPLLONCH, P., AND R. LOBO. 2005. Contribución al conocimiento de la migración de tres especies de *Elaenia* de Argentina. *Ornitología Neotropical* 16:145–161.
- CAPLLONCH, P., AND P. ZELAYA. 2006. Sobre la distribución y migración de la mosqueta parda (*Lathrotriccus euleri argentinus*) en Sudamérica. *Ornitología Neotropical* 17:501–513.
- CAPLLONCH, P. 2007. Migraciones de especies de Tyrannidae de la Argentina: parte 1. *Acta Zoológica Lilloana* 51:151–160.
- CAPLLONCH, P., D. ORTIZ, AND K. SORIA. 2009. Migraciones de especies de Tyrannidae de la Argentina: parte 2. *Acta Zoológica Lilloana* 53:77–97.
- CHESSER, R. T. 1994. Migration in South America: an overview of the austral system. *Bird Conservation International* 4:91–107.
- COTTON, P. A. 2003. Avian migration phenology and global climate change. *Proceedings of the National Academy of Sciences U.S.A.* 100:12219–12222.
- CUETO, V. R., J. L. DE CASENAVE, AND L. MARONE. 2008. Neotropical austral migrant landbirds: population trends and habitat use in the central Monte desert, Argentina. *Condor* 110:70–79.
- DEAN, W. R. J. 2004. Nomadic desert birds. Springer, Berlin.
- DEL-VAL, E., J. J. ARMESTO, O. BARBOSA, D. A. CHRISTIE, A. G. GUTIÉRREZ, C. G. JONES, P. A. MARQUET, AND K. C. WEATHERS. 2006. Rain forest islands in the Chilean semiarid region: fog-dependency, ecosystem persistence and tree regeneration. *Ecosystems* 9:598–608.
- ELMENDORF, S. C., AND S. P. HARRISON. 2009. Temporal variability and nestedness in California grassland species composition. *Ecology* 90:1492–1497.
- ELPHICK, J. 2007. The atlas of bird migration: tracing the great journeys of the world's birds. Natural History Museum, London.
- ENGILIS, A. JR., AND D. A. KELT. 2009. Foraging behavior of Tufted Tit-Tyrants (*Anairetes parulus*) in semiarid northcentral Chile. *Wilson Journal of Ornithology* 121:585–592.
- ENGILIS, A. JR., AND D. A. KELT. 2011. Foraging behavior of Plain-mantled Tit-Spintail (*Leptasthenura aegithaloides*) in semiarid scrublands, north-central Chile. *Ornitología Neotropical* 22:247–256.
- ESTADES, C. F. 1997. Bird–habitat relationships in a vegetational gradient in the Andes of central Chile. *Condor* 99:719–727.
- ESTADES, C. F. [ED.]. 2004. Estrategia nacional para la conservación de aves 2004. Unión de Ornítólogos de Chile and Programa Interdisciplinario de Estudios en Biodiversidad of the Universidad de Chile, Santiago, Chile.
- FAABORG, J., R. T. HOLMES, A. D. ANDERS, K. L. BILDSTEIN, K. M. DUGGER, S. A. GAUTHREAUX, P. HEGGLUND, K. A. HOBSON, A. E. JAHN, D. H. JOHNSON, S. C. LATTI, D. J. LEVEY, P. P. MARRA, C. L. MERKORD, E. NOL, S. I. ROTHSTEIN, T. W. SHERRY, T. S. SILLETT, F. R. THOMPSON, AND N. WARNOCK. 2010. Recent advances in understanding migration systems of New World land birds. *Ecological Monographs* 80:3–48.
- FJELDSÅ, J., AND N. KRABBE. 1990. Birds of the high Andes. Zoological Museum, University of Copenhagen, Copenhagen.
- GAJARDO, R. 1994. La vegetación natural de Chile: clasificación y distribución geográfica. Editorial Universitaria, Santiago, Chile.
- GARCIA, L. V. 2003. Controlling the false discovery rate in ecological research. *Trends in Ecology & Evolution* 18:553–554.
- GEORGE, T. L. 1987. Nesting phenology of landbirds in Baja California. *Condor* 89:920–923.
- GIBSON, D. J., J. S. ELY, AND S. L. COLLINS. 1999. The core–satellite species hypothesis provides a theoretical basis for Grime's classification of dominant, subordinate, and transient species. *Journal of Ecology* 87:1064–1067.
- GUTIÉRREZ, J. R., P. L. MESERVE, D. A. KELT, A. ENGILIS JR., M. A. PREVITALI, W. B. MILSTEAD, AND F. M. JAKSIĆ. 2010. Long-term research in Bosque Fray Jorge National Park: twenty years studying the role of biotic and abiotic factors in a Chilean semiarid scrubland. *Revista Chilena de Historia Natural* 83:69–98.
- HANSKI, I. 1982. Dynamics of regional distribution: the core and satellite species hypothesis. *Oikos* 38:210–221.
- HELLMAYR, C. E. 1932. The birds of Chile. Field Museum of Natural History Zoological Series 19, Publication 308.
- HOBSON, K. A. 2005. Using stable isotopes to trace long-distance dispersal in birds and other taxa. *Diversity and Distributions* 11:157–164.
- HOLM, S. 1979. A simple sequentially rejectable multiple test procedure. *Scandinavian Journal of Statistics* 6:65–70.
- JAKSIĆ, F. J., E. SILVA-ARANGUIZ, AND S. I. SILVA. 2004. Fauna del Parque Nacional Bosque Fray Jorge: una revisión bibliográfica, p. 93–114. *In* F. A. Squeo, J. R. Gutiérrez and I. R. Hernández [EDS.], Historia Natural del Parque Nacional Bosque Fray Jorge. Ediciones Universidad de La Serena, La Serena, Chile.
- JAKSIĆ, F. M., S. I. SILVA, P. L. MESERVE, AND J. R. GUTIÉRREZ. 1997. A long-term study of vertebrate predator responses to an El Niño (ENSO) disturbance in western South America. *Oikos* 78:341–354.
- JAKSIĆ, 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.
- JAKSIĆ, F. M. 2001. Ecological effects of El Niño in terrestrial ecosystems of western South America. *Ecography* 24:241–250.
- JAMES, F. C., AND C. E. MCCULLOCH. 1990. Multivariate analysis in ecology and systematics: Panacea or Pandora's box? *Annual Review of Ecology and Systematics* 21:129–166.
- JARAMILLO, A., P. BURKE, AND D. BEADLE. 2003. Birds of Chile. Princeton University Press, Princeton, NJ.
- JOSEPH, L. 1997. Towards a broader view of neotropical migrants: consequences of a re-examination of austral migration. *Ornitología Neotropical* 8:31–36.
- KEAST, A. 1959. Australian birds: their zoogeography and adaptations to an arid continent. *In* A. Keast, R. L. Crocker and C. S. Christian [EDS.], Biogeography and ecology in Australia. W. Junk, the Hague.
- KELLY, J. F. 2006. Stable isotope evidence links breeding geography and migration timing in wood warblers (Parulidae). *Auk* 123:431–437.
- KELT, D. A., P. L. MESERVE, M. L. FORISTER, L. K. NABORS, AND J. R. GUTIÉRREZ. 2004a. Seed predation by birds and small mammals in semiarid Chile. *Oikos* 104:133–141.
- KELT, D. A., P. L. MESERVE, AND J. R. GUTIÉRREZ. 2004b. Seed removal by small mammals, birds and ants in semi-arid Chile, and comparison with other systems. *Journal of Biogeography* 31:931–942.
- LOPEZ DE CASENAVE, J., V. R. CUETO, AND L. MARONE. 1998. Granivory in the Monte desert, Argentina: is it less intense than in other arid zones of the world? *Global Ecology and Biogeography Letters* 7:197–204.
- 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.
- LOWTHER, P., AND W. POST. 1999. Shiny Cowbird (*Molothrus bonariensis*), no. 399. *In* A. Poole and F. Gill [EDS.], The birds of North America. Birds of North America, Inc., Philadelphia.
- MAGURRAN, A. E. 2007. Species abundance distributions over time. *Ecology Letters* 10:347–354.
- MARONE, L., J. LOPEZ DE CASENAVE, AND V. R. CUETO. 2000. Granivory in southern South American deserts: conceptual issues and current evidence. *BioScience* 50:123–132.

- MARONE, L., J. LOPEZ DE CASENAVE, F. A. MILESI, AND V. R. CUETO. 2008. Can seed-eating birds exert top-down effects on grasses of the Monte desert? *Oikos* 117:611–619.
- MCCUNE, B., J. B. GRACE, AND D. L. URBAN. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, OR.
- MCCUNE, B., AND M. J. MEFFORD. 2006. PC-ORD. Multivariate analysis of ecological data. version 5.32. MjM Software, Gleneden Beach, OR.
- MESERVE, P. L., D. A. KELT, W. B. MILSTEAD, AND J. R. GUTIÉRREZ. 2003. Thirteen years of shifting top-down and bottom-up control. *BioScience* 53:633–646.
- MESERVE, P. L., J. R. GUTIÉRREZ, D. A. KELT, M. A. PREVITALI, A. ENGLISH JR., AND W. B. MILSTEAD. 2009. Global climate change and biotic–abiotic interactions in the northern Chilean semiarid zone: potential long-term consequences of increased El Niños, p. 139–162. *In* J. A. Long and D. S. Wells [EDS.], *Ocean circulation and El Niño: new research*. Nova Science, New York.
- MESERVE, P. L., D. A. KELT, M. A. PREVITALI, W. B. MILSTEAD, AND J. R. GUTIÉRREZ. 2011. Global climate change and small mammal populations in north-central Chile. *Journal of Mammalogy* 92:1223–1235.
- MITCHELL, D. E. 2000. Allen's Hummingbird (*Selasphorus sasin*), no. 501. *In* A. Poole and F. Gill [EDS.], *The birds of North America*. Birds of North America, Inc., Philadelphia.
- MÖLLER, A. P. 2011. When climate change affects where birds sing. *Behavioral Ecology* 22:212–217.
- MORAN, M. D. 2003. Arguments for rejecting the sequential Bonferroni in ecological studies. *Oikos* 100:403–405.
- MORRISON, J. L., AND L. M. PHILLIPS. 2000. Nesting habitat and success of the Chimango Caracara in southern Chile. *Wilson Bulletin* 112:225–232.
- MYERS, N., R. A. MITTERMEIER, C. G. MITTERMEIER, G. A. B. DA FONSECA, AND J. KENT. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403:853–858.
- PATTERSON, B. D., AND W. ATMAR. 1986. Nested subsets and the structure of insular mammalian faunas and archipelagos. *Biological Journal of the Linnean Society* 28:65–82.
- PAXTON, K. L., C. VAN RIPER, T. C. THEIMER, AND E. H. PAXTON. 2007. Spatial and temporal migration patterns of Wilson's Warbler (*Wilsonia pusilla*) in the Southwest as revealed by stable isotopes. *Auk* 124:162–175.
- PRENTICE, I. C. 1977. Non-metric ordination methods in ecology. *Journal of Ecology* 65:85–94.
- REMSEN, J. V., C. D. CADENA, A. JARAMILLO, M. NORES, J. F. PACHECO, J. PÉREZ-EMÁN, M. B. ROBBINS, F. G. STILES, D. F. STOTZ, AND K. J. ZIMMER [ONLINE]. 2011. A classification of the bird species of South America, version 14 November 2011. <<http://www.museum.lsu.edu/~Remsen/SACCBaseline.html>>.
- RICE, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43:223–225.
- RIDGELY, R. S., AND G. TUDOR. 1994. *The birds of South America*, vol. 2, the suboscine passerines. University of Texas Press, Austin, TX.
- RODRÍGUEZ-GIRONÉS, M. A., AND L. SANTAMARIA. 2006. A new algorithm to calculate the nestedness temperature of presence–absence matrices. *Journal of Biogeography* 33:924–935.
- ROMANO, M., I. BARBERIS, F. PAGANO, AND J. MAIDAGAN. 2005. Seasonal and interannual variation in waterbird abundance and species composition in the Melincue saline lake, Argentina. *European Journal of Wildlife Research* 51:1–13.
- RUBENSTEIN, D. R., C. P. CHAMBERLAIN, R. T. HOLMES, M. P. AYRES, J. R. WALDBAUER, G. R. GRAVES, AND N. C. TUROSS. 2002. Linking breeding and wintering ranges of a migratory songbird using stable isotopes. *Science* 295:1062–1065.
- SAINO, N., R. AMBROSINI, D. RUBOLINI, J. VON HARDENBERG, A. PROVENZALE, K. HUEPPOP, O. HUEPPOP, A. LEHIKONEN, E. LEHIKONEN, K. RAINIO, M. ROMANO, AND L. SOKOLOV. 2011. Climate warming, ecological mismatch at arrival and population decline in migratory birds. *Proceedings of the Royal Society B* 278:835–842.
- SCHULENBERG, T. S. [ONLINE]. 2009. White-crested Elaenia (*Elaenia albiceps*). <http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=30734> (27 November 2010).
- SPIEGEL, C. S., P. J. HART, B. L. WOODWORTH, E. J. TWEED, AND J. J. LEBRUN. 2006. Distribution and abundance of forest birds in low-altitude habitat on Hawai'i Island: evidence for range expansion of native species. *Bird Conservation International* 16:175–185.
- SQUEO, F. A., J. R. GUTIÉRREZ, AND I. R. HERNÁNDEZ. 2004. *Historia Natural del Parque Nacional Bosque Fray Jorge*. Ediciones Universidad de La Serena, La Serena, Chile.
- SQUEO, F. A., R. ARAVENA, E. AGUIRRE, A. POLLASTRI, C. B. JORQUERA, AND J. R. EHRLINGER. 2006. Groundwater dynamics in a coastal aquifer in north-central Chile: implications for groundwater recharge in an arid ecosystem. *Journal of Arid Environments* 67:240–254.
- STUTCHBURY, B. J. M., J. R. HILL III, P. M. KRAMER, S. A. RUSH, AND S. A. TAROF. 2009. Sex and age-specific annual survival in a neotropical migratory songbird, the Purple Martin (*Progne subis*). *Auk* 126:278–287.
- STYRSKY, J. N., AND J. D. BRAUN. 2011. Annual fecundity of a neotropical bird during years of high and low rainfall. *Condor* 113:194–199.
- THOMAS, L., J. L. LAAKE, E. REXSTAD, S. STRINDBERG, F. F. C. MARQUES, S. T. BUCKLAND, D. L. BORCHERS, D. R. ANDERSON, K. P. BURNHAM, M. L. BURT, S. L. HEDLEY, J. H. POLLARD, J. R. B. BISHOP, AND T. A. MARQUES. 2009. Distance 6.0, release 2. Research Unit for Wildlife Population Assessment, University of St. Andrews, St. Andrews, Scotland.
- THOMAS, L., S. T. BUCKLAND, E. A. REXSTAD, J. L. LAAKE, S. STRINDBERG, S. L. HEDLEY, J. R. B. BISHOP, T. A. MARQUES, AND K. P. BURNHAM. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology* 47:5–14.
- UNITT, P. 2004. San Diego County bird atlas. San Diego Society of Natural History Proceeding 39.
- ULRICH, W., M. ALMEIDA, AND N. J. GOTELLI. 2009. A consumer's guide to nestedness analysis. *Oikos* 118:3–17.
- WIENS, J. A. 1991. The ecology of desert birds, p. 278–310. *In* G. A. Polis [ED.], *The ecology of desert communities*. University of Arizona Press, Tucson, AZ.
- YÁÑEZ, J. L., H. NÚÑEZ, R. P. SCHLATTER, AND F. M. JAKSIĆ. 1980. Diet and weight of American Kestrels in central Chile. *Auk* 97:629–631.