Responses in the abundance of generalist birds to environmental gradients: The rufous-collared sparrow (*Zonotrichia capensis*) in the southern Neotropics[1]

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Abstract: Bird species are adapted to certain ranges of physical conditions and will respond to environmental heterogeneity depending on their ability to exploit a broad range of resources and their tolerance to new environmental conditions. We used the rufous-collared sparrow as a model to explore how the abundance of generalist passerine birds may vary along environmental gradients in the southern Neotropics. We analyzed variations in the abundance along 6 gradients expressing variations in climate, productivity, the proportion of native forest in the landscape, the proportion of vegetation types through the transition between regions, and the intensity of human activities (agriculture, urbanization). The rufous-collared sparrow was most abundant in seasonal and semi-arid climates. Thermal amplitude was the best climatic predictor of the species abundance at the large scale. Within regions where climatic conditions are relatively homogeneous, land use better predicted abundance patterns. The species responded positively to increasing primary productivity, agricultural intensity, and native forest degradation and conversion and negatively to increasing urbanization. The rufous-collared sparrow adapts successfully to new environments created by human activities such as agriculture, ranching, forestry, and urbanization. Some native species may be tolerant to certain types and intensity of human activities, and knowledge of how they respond to both natural and human-created environments may help efforts to anticipate the impact of human activities on native birds in a changing world.

Keywords: abundance, generalist species, human-modified habitats, Neotropical birds, spatial patterns, rufous-collared sparrow.

Résumé : Les espèces d'oiseaux sont adaptées à un certain éventail de conditions physiques et répondent à l'hétérogénéité environnementale en fonction de leur capacité à exploiter une vaste gamme de ressources et de leur tolérance à de nouvelles conditions environnementales. Nous avons utilisé le bruant chingolo comme modèle pour explorer comment l'abondance de passereaux généralistes varie le long de gradients environnementaux dans le sud des néotropiques. Nous avons analysé les variations d'abondance le long de six gradients reflétant des variations du climat, de la productivité végétale, de la proportion de forêts naturelles dans le paysage, de la proportion des types de végétation dans les zones de transition entre des régions, et de l'intensité des activités humaines (agriculture, urbanisation). Le bruant chingolo était plus abondant dans les climats saisonniers et semi-arides. L'amplitude thermique était la variable climatique qui prédisait le mieux l'abondance de l'espèce à grande échelle. Dans les régions où les conditions climatiques sont relativement homogènes, l'utilisation du territoire était la variable qui prédisait le mieux les patrons d'abondance. L'espèce répondait positivement à l'augmentation de la productivité primaire, de l'intensité de l'agriculture, de la dégradation et de la conversion des forêts naturelles, et négativement à l'augmentation des aires urbanisées. Le bruant chingolo s'adapte avec succès aux nouveaux environnements créés par les activités humaines comme l'agriculture, l'élevage, la foresterie et l'urbanisation. Certaines espèces indigènes peuvent être tolérantes à certains types et degrés d'intensité d'activités humaines et la connaissance de leurs réponses aux environnements tant naturels qu'anthropiques aide à prévoir l'impact des activités humaines sur les oiseaux indigènes dans un contexte de changement.

Mots-clés : abondance, bruant chingolo, espèce généraliste, habitats modifiés par les humains, oiseaux néotropicaux, patrons spatiaux.

Nomenclature: Reitz & Klein, 1966; Ridgely & Tudor, 1989.

Introduction

Many bird species are expected to respond to changes in environmental conditions caused by factors operating on both evolutionary and ecological time scales. Evolution has been a major force driving species distribution. Distributional ranges at the large scale or presence/absence at a given site are determined primarily by each species' niche requirements. Climatic variations occur along latitudinal and elevational gradients (Willig, Kaufman & Stevens, 2003), and species are adapted to certain ranges of physical conditions. Climate also determines major vegetation types where bird species are adapted to exploit a range of resources.

Human activities modify natural environments and therefore habitat suitability for birds (Petit & Petit, 2003), constantly testing species' capacity to survive in new environments. The responses of bird species to environmental changes caused by human activities depend on their ability to exploit a broad range of resources and plasticity in adapting to new environmental conditions caused by both abiotic factors and interspecific interactions. Alterations in environmental conditions may affect survival and reproduction, which will be reflected in the species' abundance and, in extreme situations, distributional range.

Extinctions caused by human activities are not a random process (Smart et al., 2006), and affect mainly specialist species, as predicted by the niche evolutionary theory (Julliard, Jiguet & Couvet, 2004). Habitat loss, fragmentation, degradation, and replacement are expected to negatively affect specialist bird species through a reduction in the quantity and quality of available habitat (Julliard et al., 2006; Devictor, Julliard & Jiguet, 2008). In contrast, it is expected that human activities may affect generalist species in either a negative or a positive way. Those species capable of adapting to widespread human activities such as agriculture, forestry, and urbanization are the winners in the process of biotic homogenization (McKinney & Lockwood, 1999; Olden, 2006). When assessing consequences of habitat change in biological communities, it is necessary to consider both positive and negative responses of species (Devictor, Julliard & Jiguet, 2008); for this reason, we decided to examine how generalist birds respond to environmental gradients.

Little is known about the responses of Neotropical birds to spatial variations in environmental conditions and habitat type. The rufous-collared sparrow (*Zonotrichia capensis*) is a widespread Neotropical species that can be used as a model to explore how the abundance of generalist passerine birds may change along natural and human-created environmental gradients. Here, we used a multi-model inference process to define the relative importance of each predictor variable in explaining responses in the abundance of rufous-collared sparrows along gradients expressing variations in climate, productivity, the proportion of native forest in the landscape, the proportion of vegetation types through the transition between regions (ecotone), and the intensity of human activities (agriculture, urbanization) in the southern Neotropics.

Methods

STUDY DESIGN, GRADIENTS, AND REGIONS

Birds were surveyed along environmental gradients in the southern Neotropics, in the context of 3 research projects that generated 6 bird and environmental data sets. Different sets of candidate variables were chosen to describe each gradient to maximize variations in the selected factors (*e.g.*, primary productivity, urbanization). When selecting the environmental variables, we also considered that climatic variations occur at larger geographical scales than variations in habitat types. Along each gradient, the abundance of rufous-collared sparrows (the response variable) and environmental variables (independent variables) were estimated for each experimental unit. According to the sampling design used in the study of each particular gradient, the experimental unit was a point count, a transect, or a landscape (Table I).

We examined 6 environmental gradients (Figure 1; Table I):

Gradient 1 is a latitudinal and climatic gradient. It is the longest of the study gradients, covering 1700 km through 5 biogeographic regions (Table I) from 27° s to 42° s in central Argentina. Mean annual temperature varies from 21 °C in the North to 9 °C in the South (range 12 °C), and annual rainfall varies from 850 mm to 140 mm (range 710 mm) (Table II).

Gradient 2 is a productivity gradient that extends from 37° s, 63° w to 37° s, 58° w in the southern Pampean region, where primary productivity increases from West to East in a matrix of mixed croplands and pastoral farming. Both latitude and altitude are similar along the gradient; thus, mean annual temperature remained approximately constant at about 16 °C. Rainfall is evenly distributed throughout the year, decreasing from East (1100 mm·y^{-1}) to West (600 mm·y^{-1}).

Gradient 3 is the ecotone between 2 biogeographic regions (Table I); it covers the transition from savanna woodlands in the North (29° s, 61° w) to grasslands in the South (34° s, 61° w). The main human activities in both regions are pastoral farming and crop production (for more details on the gradient see Filloy & Bellocq, 2006).

Gradient 4 is a forest cover gradient comprising areas varying in proportion of native subtropical forest in the Interior Atlantic Forest of Argentina and Paraguay. A 4400 km^2 area was divided into 10- ×10-km UTM (Universal Transverse Mercator) cells (landscapes), and a total of 41 cells (landscapes) were selected to provide a range from 20% to 100% native forest cover (for more details on the gradient see Zurita & Bellocq, 2009). A decreasing proportion of native forest cover in the landscape is associated with a complementary increase in the proportion of human-modified habitats (including annual and perennial crops, ranching, and tree plantations).

Gradient 5 is an agricultural gradient extended along 300 km from pure croplands (mainly soy, corn, wheat, sunflower) in the North (34° s, 60° w) through mixed farming to pure pastoral farming (cattle raising) in the South (36° s, 59° w). Differences in land use are the result of

geomorphological characteristics rather than climatic variations (see Filloy & Bellocq, 2007). In the Pampean region where the gradient was established, the land is almost completely devoted to either crop production or pastoral farming; thus, an increasing proportion of croplands in the landscape is associated with a complementary decline in the proportion of pastoral lands (Filloy & Bellocq, 2007).

Gradient 6 is an urban–rural gradient extending from the core urban area of Mercedes city (Pampean region, 29° 12' s, 58° 05' w, 62 500 inhabitants) to the rural zone (Garaffa, Filloy & Bellocq, 2009).

Regions covered by at least 1 gradient were the Atlantic Forest, Chaco, Espinal, Pampa, Monte, and Patagonia (see Cabrera & Willink, 1980 for a full description of the regions) (Figure 1). The Interior Atlantic Forest is a semi-deciduous forest: it has a subtropical climate with a cold season during June–August and no dry season; vegetation is highly stratified (3 to 5 arboreal strata) and diverse; the understory is composed of ferns, bamboos, and herbs); and the main human activities in the region include pastoral farming, forestry, and agriculture. In the Chaco region, the climate is warm and dry; the xerophilous forest and savannas that characterize the region are dominated by *Schinopsis* trees; and the natural forests have for the most part been converted to savannas or steppes due to fires and wood extraction. In the Espinal region, the climate is warm and wet in the North and temperate and dry in the West. The savannas and xerophilous forest, lower than those from Chaco, are dominated by *Prosopis* spp. The climate in the Pampean region is temperate-warm, with rainfall occurring all year round. Grasses of the Poaceae family dominate the community. The natural grassland underwent rapid transformation and intense degradation due to agriculture during the 20th century (Soriano, 1992). In the Monte region the climate is cool and dry. Vegetation is dominated by *Larrea* shrubs about 1–2 m in height. The climate in Patagonia is cold and dry, with snow and freezing temperatures occurring almost all year round. The steppe is dominated by grasses of the genus *Stipa*.

BIRD SURVEYS

All bird surveys were conducted using the point count technique (Bibby, Jones & Marsden, 1998) during the breeding season in the spring. We used a fix radius when detection capability was either limited (subtropical forest) or strongly variable within the gradient (urban–rural gradient) (Table I). Point counts were located along transects except for those in the Atlantic forest, which were distributed throughout a 4400-km² area (Table I). Transects were established on secondary roads that were mostly unpaved. Each gradient was surveyed once (except Gradient 2) by the same 2 observers for 4 h after sunrise. Recording time per sampling point was 5 minutes. The experimental unit (transect, landscape, or point count), the number of experimental units, and the number of point counts per experimental unit varied according to gradient nature and extension (Table I). Abundance of rufous-collared sparrows was estimated as the number of individuals per experimental unit. Hence, abundance was estimated as the number of rufous-collared sparrows heard or seen per transect in Gradients 1, 2, 3,

and 5; per landscape in Gradient 4; and per point count in Gradient 6.

In each of the 41 landscapes composing Gradient 4 (20% to 100% of native forest cover), we established 20 bird point counts (for a total of 820 point counts). The locations of the point counts were assigned proportionally to the area covered by native forest and human modified habitats; for example, in a landscape with 60% forest cover, 12 bird point counts were located in native forest and 8 in human-modified habitats. We estimated the abundance of the rufous-collared sparrow per landscape as the total
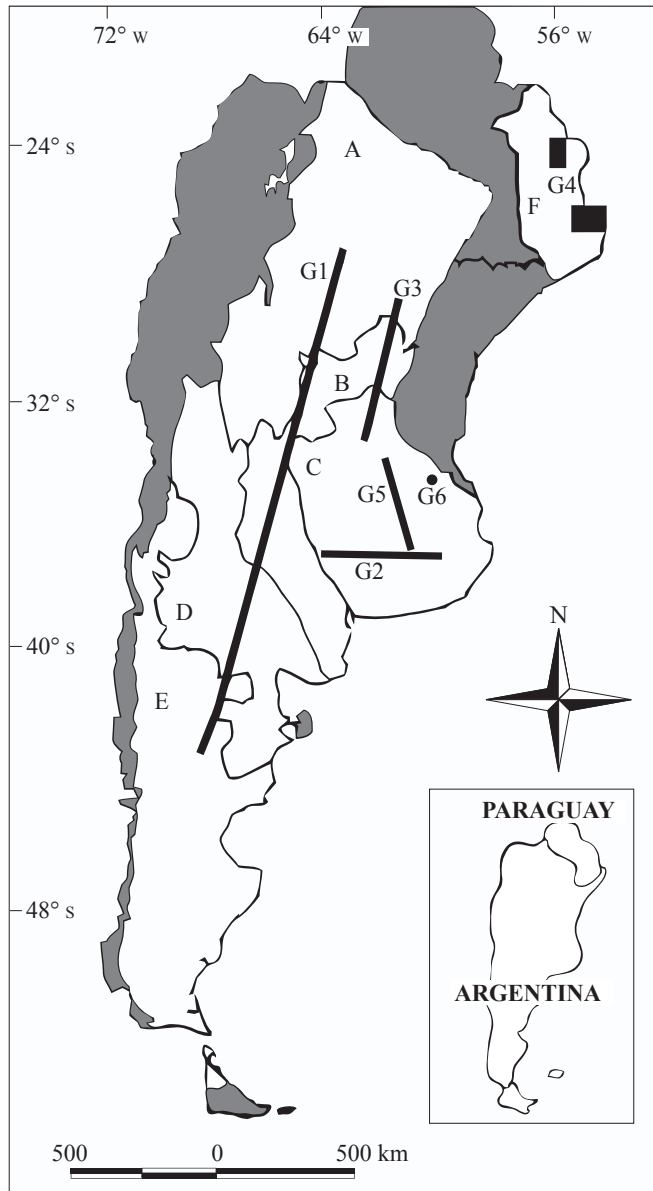

FIGURE 1. Geographical location of study gradients in Argentina and Paraguay (G1 to G6, see methods for details). The work covered 6 regions (A: Chaco, B: Espinal, C: Pampean, D: Monte, E: Patagonia, F: Atlantic Forest). Grey areas represent other Argentinean and Paraguayan regions excluded from the work. G1: latitudinal and climatic gradient; G2: productivity gradient; G3: transition between savanna woodlands and grasslands; G4: gradient of subtropical forest cover; G5: agricultural gradient; G6: urban–rural gradient.

number of individuals recorded in the 20 bird point counts of that cell (for more details see Zurita & Bellocq, 2009).

ENVIRONMENTAL VARIABLES

Along gradients, environmental variables were estimated at each experimental unit (Table II). The range of values covered by the environmental variables in each gradient is provided in Table II. Unlike habitat type, climatic factors are expected to vary at large geographical scales rather than within biogeographic regions in most situations

(Currie, 1991). Thus, values of climatic variables were obtained for transects in Gradient 1 and 3 from a database for all localities of Argentina (De Fina, 1992) (Table II). We selected climate data from localities no more than 5 km away from transects.

To explore the productivity gradient (Gradient 2), we worked with the 3 most commonly used estimators of net primary productivity: normalized difference vegetation index (NDVI), actual evapotranspiration (AET) (Evans, Warren & Gaston, 2005), and mean annual rainfall

TABLE I. Gradient type, biogeographic regions covered by the gradient, extent of the gradient, experimental unit (EU), number of point counts (PC) per experimental unit, distance between point counts, and number of visits at each point count.

Gradient type	Regions covered[1]	Extent	Bird survey technique	Experimental unit	Number of EU	Number of PC per EU	Distance between PC (km)	Number of visits per PC
1. Climate	Chaco Espinal Pampean Monte Patagonia	1700 km	Point count, unlimited radius	25-km transect	22	26	1	1
2. Productivity	Pampean	500 km	Point count, 200-m fixed radius	10-km transect	12	11	1	2
3. Regional ecotone	Espinal Pampean	500 km	Point count, unlimited radius	25-km transect	16	26	1	1
4. Native forest	Atlantic Forest	4400 km^2	Point count, 50-m fixed radius	10 × 10-km landscape	41	20	≥ 0.5	1
5. Agriculture	Pampean	300 km	Point count, unlimited radius	25-km transect	18	26	1	1
6. Urbanization	Pampean	3.4 km	Point count, 50-m radius	Point count	17	-	0.2	1

[1] Following Cabrera and Willink (1980).

TABLE II. Proportion of the variation in rufous-collared sparrow abundance (R^2) explained by environmental variables along 6 gradients in the southern Neotropics. Terms in bold indicate the best explanatory variable (obtained by the multi-model inference process) for each gradient.

Gradients	Response variables	Range covered	R^2	F (P)
1. Climate	January mean temperature (Ja)	17.7–27.9 °C	0.02	0.31 (0.5863)
	July mean temperature (Ju)	0.9–14.3 °C	0.11	2.50 (0.1295)
	Mean annual temperature	9.3–21.1 °C	0.06	1.30 (0.2669)
	Annual thermal amplitude (Ja–Ju)	**13.6–17.4 °C**	**0.35**	**10.77 (0.0037)**
	Total annual rainfall	135–848 mm	0.11	2.52 (0.1278)
	Winter rainfall (Wp)	26–68 mm	0.16	3.93 (0.0612)
	Summer rainfall (Sp)	22–309 mm	0.01	0.15 (0.6998)
	Rainfall seasonality │Sp – Wp│	2–264 mm	0.19	4.61 (0.0441)
2. Productivity	Summer rainfall	128–225 mm	0.62	16.65 (0.0022)
	Actual evapotranspiration	**2.42–3.86 mm·d^{-1}**	**0.67**	**20.43 (0.0011)**
	Normalize difference vegetation index	99.34–198.95	0.23	3.00 (0.1139)
3. Regional ecotone	Mean annual temperature	16.6–20.05 °C	0.55	12.22 (0.0058)
	Annual thermal amplitude (Ja–Ju)	13.4–14.5 °C	0.08	0.85 (0.3777)
	Total annual rainfall	768–957 mm	0.14	1.65 (0.2280)
	Rainfall seasonality │Sp – Wp│	200–281 mm	0.05	0.54 (0.4809)
	% cover woodlands	0–92%	0.24	3.16 (0.1058)
	% cover croplands	**0–94.4%**	**0.85**	**82.44 (< 0.001)**
	% cover cattle pastures	5.6–73%	0.03	0.35 (0.5669)
4. Native forest	% cover native forest	28.2–100%	0.41	27.46 (< 0.001)
5. Agriculture	% cover croplands	6.2–87.4%	0.38	7.81 (0.013)
6. Urbanization	**% cover constructed area**	**0–87.5%**	**0.45**	**12.45 (0.003)**
	% canopy cover	7.5–32.1%	0.03	0.48 (0.5003)
	% cover green areas	0–62%	0.01	0.12 (0.7209)
	% cover rural areas	0–92.5%	0.44	12.18 (0.0033)

(Sala *et al.*, 1988). For each transect, the NDVI was estimated using Landsat 5 TM satellite images from the last 5 y. From a database of daily AET maps available for central and eastern Argentina (INTA, 2008), we obtained AET values for each transect and season for the last 5 y and estimated a daily AET average value. The mean annual rainfall was obtained from a climatic database showing 50-y averages for many localities of Argentina (De Fina, 1992); rainfall values for localities lacking climatic data were estimated by taking into account the physiography of the region and the available values of mean annual rainfall from nearby localities provided by the National Weather Service.

The percentage covered by different habitat types was estimated along each transect in Gradients 3 and 5 (Table II). We recorded the distance covered by each habitat type along both sides of the road transect and then calculated the percentage occupied by each type (see Filloy & Bellocq, 2007).

We used classified Landsat TM images from the same period of field sampling to estimate the percentage coverage of native forests on each of the 41 landscapes used in Gradient 4 (see Zurita & Bellocq, 2009).

Along the urban–rural gradient (Gradient 6), we measured 4 local land-cover variables using IKONOS satellite images: constructed area (includes buildings, houses, and paved roads), tree cover, open green areas (includes managed and unmanaged vegetation such as parks and gardens), and rural areas with either pasturelands or crop fields. To quantify land cover along the gradient, we established an area of 75 m radius centred on each bird point count (see Garaffa, Filloy & Bellocq, 2009).

DATA ANALYSES

We collected data on several candidate variables, and thus several candidate models, along the 6 gradients to explain the rufous-collared sparrow abundance. We first followed a multi-model inference process, running all possible models containing from a single to all explanatory variables (including square components to include non-linear relationships). This enabled us to evaluate their relative contribution in explaining bird abundance (Rangel, Diniz-Filho & Bini, 2010). Thus, we were able to select the single variable most strongly related to the rufous-collared sparrow abundance for each gradient. Then, since we were especially interested in analyzing the response model for each particular variable, single regression analyses were run to explore the response of bird abundance to the selected environmental variables for each gradient. Our approach enabled us to identify the best environmental predictors (from the sets of candidate variables) of the rufous-collared sparrow abundance along each environmental gradient. Finally, we explored whether explanatory variables accounted for the spatial structure of the abundance data; we performed partial regressions considering the geographical coordinates of the sample units to identify the proportion of the spatial variation in bird abundance that could be accounted for by the explanatory variables (Legendre & Legendre, 1998). By partialling out the relative contribution of explanatory variables on the variation in bird abundance, the partial regression analysis enabled an accurate quantification of species–environment interactions and opened the possibility of inferring which processes shape the environment and could in turn shape bird abundance through space (Borcard, Legendre & Drapeau, 1992). All analyses were performed using the software Spatial Analysis in Macroecology v.4 (SAM; Rangel, Diniz-Filho & Bini, 2010).

Results

Abundance of sparrows changed along the 1700-km climatic gradient in the southern Neotropics (Gradient 1). Abundance increased initially from low to high latitudes, reaching a maximum at about 36° s and then declining (Figure 2a). At that large geographical scale, thermal amplitude was the best climatic variable in predicting species abundance (Table II). Abundance of rufous-collared sparrows linearly increased with increasing annual thermal amplitude (Figure 2b). Rainfall seasonality also showed a significant relationship to bird abundance (Table II).
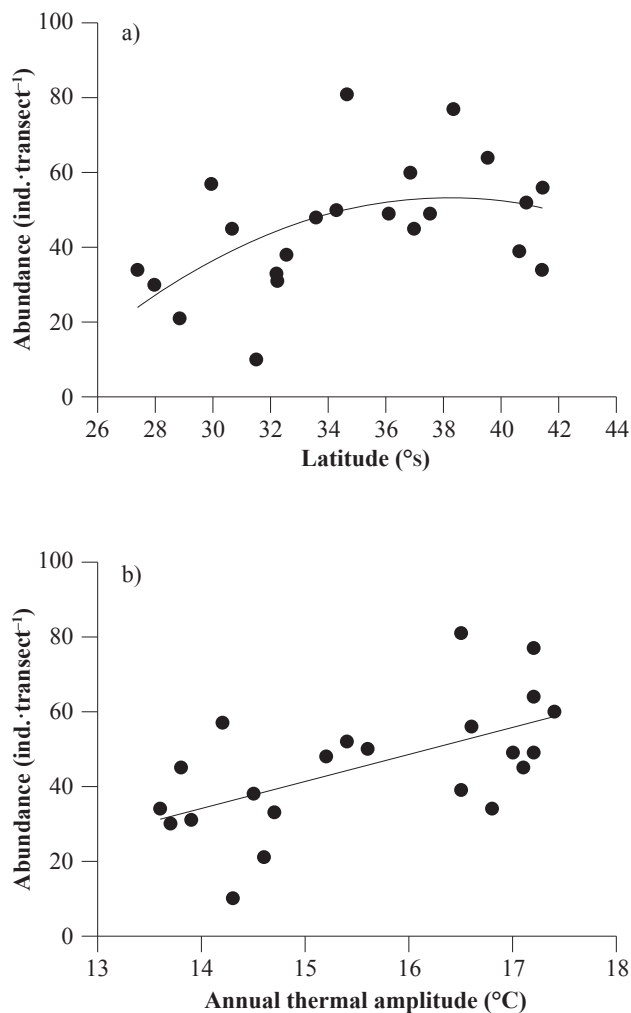

FIGURE 2. Relationship between abundance of the rufous-collared sparrow and (a) latitude, (b) annual thermal amplitude, along a 1700-km latitudinal gradient (G1) covering 5 biogeographic regions in the southern Neotropics.

Both the AET and summer rainfall were related to bird abundance along the productivity gradient within the Pampean region (Gradient 2), but the AET showed the highest coefficient of determination (Table II). Abundance increased linearly with the AET (Figure 3).

The percentage of land covered by crop fields explained 85% of the variation in the species abundance along a gradient covering 2 regions from savannas to grasslands (Gradient 3) (Table II; Figure 4). Abundance increased as more land was devoted to agricultural practices (crops such as corn, soy, wheat, sunflower), in detriment of the percent covered by semi-natural habitats (degraded savannas). Mean annual temperature also had a significant relationship to bird abundance (Table II).

In the Atlantic Forest, the rufous-collared sparrow responded positively to decreasing cover of native forest in the landscape (Gradient 4), with the decrease explaining 41% of the variation in bird abundance (Table II; Figure 5). The species was not recorded in landscapes with 100%

cover of natural subtropical forests (it was first recorded at 80% natural forest cover). Abundance increased faster when decreased less than 50% proportions of native forest in the landscape (Figure 5). It was found in all major human-modified habitats, including annual and perennial crops, cattle pastures, and native (*Araucaria angustifolia*) and exotic (*Eucalyptus* sp. and *Pinus* sp.) tree plantations.

In the Pampean region, the abundance of rufous-collared sparrows increased with agricultural intensity (Gradient 5, after Filloy & Bellocq, 2007) from pure pastoral farming to pure croplands (Table II; Figure 6).

Abundance of the rufous-collared sparrow declined from the rural zone to the core urban area in Mercedes city. Cover of constructed areas explained 45% of the variation in the sparrow abundance (Figure 7). Percent cover of rural areas was also related to bird abundance (Table II).

The partial regression analyses separated the relative contributions of environment and space on the
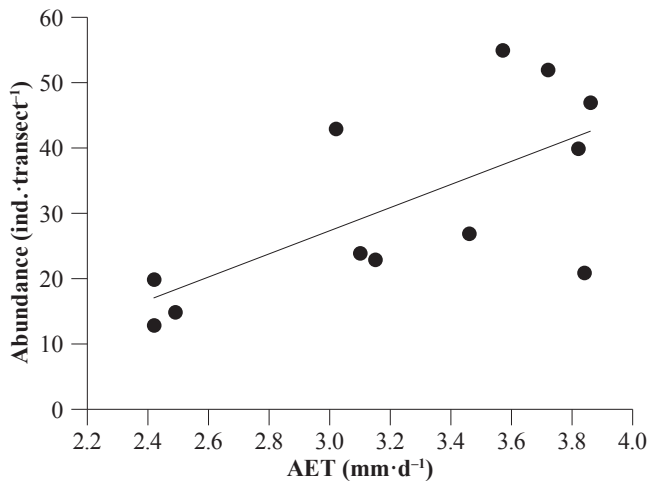

FIGURE 3. Variations in the abundance of rufous-collared sparrows along a 500-km gradient of increasing actual evapotranspiration (AET; G2) (or its surrogate primary productivity) in the Pampean region.

FIGURE 5. Relationship between the abundance of rufous-collared sparrows and the proportion of natural subtropical forest in the landscape (G4).
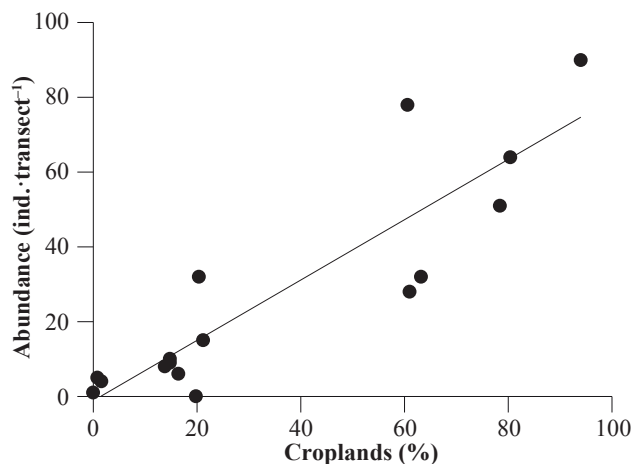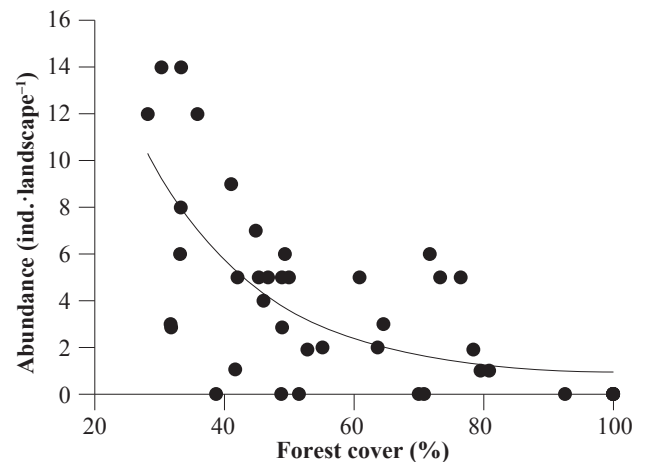

FIGURE 4. Relationship between the abundance of rufous-collared sparrows and the percentage of land covered by crop fields along a 500-km gradient from savannas to grasslands (G3).
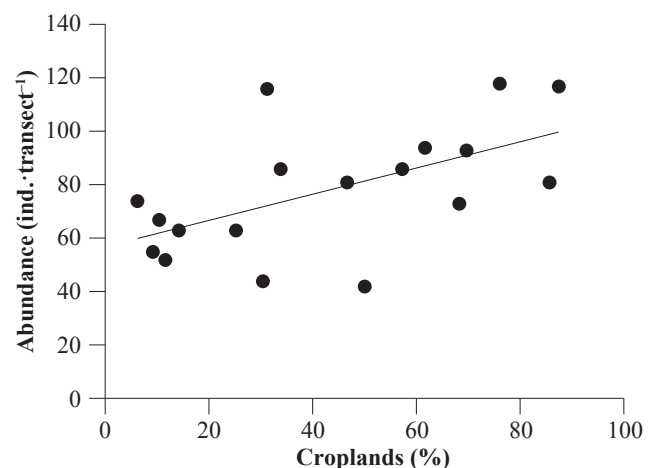

FIGURE 6. Abundance of rufous-collared sparrows along an agricultural gradient (G5) in the Pampean region. Modified from Filloy and Bellocq (2007).

rufous-collared sparrow abundance. The method also separated the total contribution of space into 2 classes: variation in bird abundance shared by space and environment and variation due to pure space. We found that the selected explanatory variables accounted for the spatial variation of the sparrow abundance, since, for most gradients, almost all variation due to space was shared with the independent factor (Table III). The proportion of variance explained by pure space that could not be accounted by the explanatory variables was low (< 10%) for most gradients. Gradients 4 and 5 showed low and negligible total space effect, respectively; in those cases, a spatial structure due to an environment–species relationship cannot be inferred.

Discussion

GENERAL PATTERNS OF ABUNDANCE

We identified 4 main patterns of abundance emerging from the overall results. First, species abundance varied along both natural and human-created environmental gradients. Abundance of rufous-collared sparrows changed with variations in climatic variables, habitat, and intensity of human activities. Second, the species could be found in most semi-natural and human-modified habitats in the southern Neotropics, but some human activities (such as
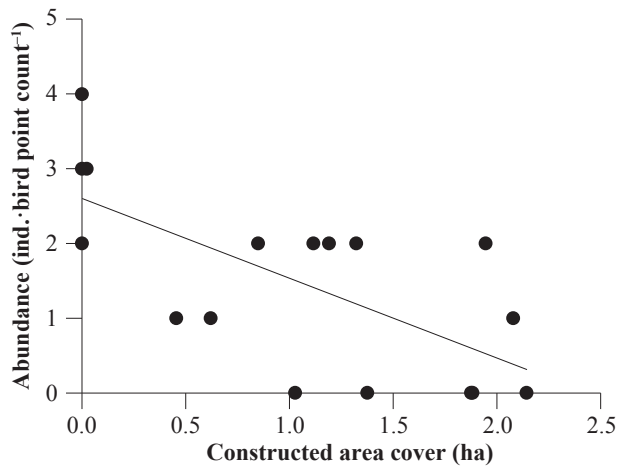

FIGURE 7. Response in the abundance of rufous-collared sparrows to changes in constructed areas along the urban–rural gradient (G6) of a Pampean city.

TABLE III. Spatial structure in the abundance of rufous-collared sparrow obtained from partial regression analyses. The difference between total space and space and environment indicates the remaining spatial variation (pure space) that could not be accounted for by the explanatory variable.

	% variance explained by	
	Total space	Space and environment
Gradient 1	25.5	23.3
Gradient 2	63.8	61.1
Gradiant 3	75.6	73.3
Gradient 4	20.8	9.7
Gradient 5	9.8	-
Gradient 6	36.7	33.7

agriculture or logging) seem to be more favourable than others (such as urbanization). Third, responses of abundance to spatial environmental variations were gradual, and no threshold values were found. Fourth, spatial variations in the abundance of the rufous-collared sparrow can be satisfactorily accounted for, and thus predicted, by a single factor.

LARGE-SCALE RESPONSES TO CLIMATIC FACTORS

Relationships between abundance and climatic variables across a species' geographic range reflect the optimum values for those niche dimensions. It is expected that a species' reproductive performance and survival will be the best at the core area of its distributional range, which will be reflected in higher abundance in that area (Brown, 1984; Gaston, 1990). Declining abundance from the core to the range borders may be explained by ecological or physiological limitations (e.g., Redpath et al., 2002). Our results revealed that abundance increased with annual thermal amplitude, suggesting that the species may be better adjusted to temperate and semi-arid climates than to tropical climates.

Our productivity gradient occurred along 500 km of relatively constant temperature, elevation, and land use. According to the productivity hypothesis, increasing productivity indicates increasing availability of food resources, such as plant or arthropod biomass (Mittelbach et al., 2001; Hawkins et al., 2003). As expected for a generalist species able to feed on both seeds and arthropods (Novoa, Bozinovic & Rosenmann, 1990), abundance of rufous-collared sparrows increased with increasing AET, indicating that highly productive environments can support larger populations than less productive environments.

Given that rainfall seasonality in Gradient 1 and AET and summer rainfall in Gradient 2 were highly associated to the species abundance, it is expected that predicted climatic changes will influence the abundance (and eventually the distribution) of the rufous-collared sparrow. Simulations of climatic change under different scenarios in South America have predicted changes in rainfall seasonality in subtropical and temperate climates of northern and central Argentina, with increased rainfall in the summer and the fall and decreased rainfall in the winter and the spring (Nuñez, Solman & Cabré, 2009). These changes in the seasonal distribution of rainfall may affect productivity, especially if a decrease in rainfall occurs during the breeding season (spring) in temperate and semi-arid climates.

RESPONSES TO HABITAT TYPE AND LAND USE

Although the species was not recorded at survey points located in native subtropical forests, it was found in mature pine (exotic species) and araucaria (native species) plantations (Zurita et al., 2006), indicating that not only habitat openness but also vegetation structural complexity influences the abundance and distribution of the rufous-collared sparrow. At the landscape level, however, the species is tolerant to high proportions of subtropical forests. The negative exponential relationship between bird abundance

and the proportion of native forest showed that a decline in forest cover produces a larger increase in bird populations at low than at high values of native forest cover. This habitat-generalist species seems to benefit from habitat conversion, expanding its range into former tropical and subtropical forests. Species responding positively to habitat replacement have been largely discussed in the context of "winners" in the process of biotic homogenization (McKinney & Lockwood, 1999). Widespread species such as the rufous-collared sparrow are probably pre-adapted to exploit a variety of different habitats, while species with restricted geographic distributions are more dependent on a limited number of habitat types (Feeley *et al.*, 2007). A positive response to native forest loss and fragmentation has been previously recorded for many species in several studies (Fahrig, 2003). For the rufous-collared sparrow, the creation of suitable habitat associated to forest loss allows the species to exploit areas that were previously unsuitable and to increase population size.

Our results showed that croplands may offer a better scenario than pastoral farming for the species' population growth. The rufous-collared sparrow is not only tolerant to intensive agriculture, it seems to be a crop exploiter as well. Crop production is more intense and intrusive than pastoral farming. Typically, intensive agriculture may have indirect negative effects on bird populations by reducing the quality and availability of food supplies and nesting sites (Verhulst, Baldi & Kleijn, 2004). Yet, it has been documented that some bird species adapt successfully to high-intensity farming systems (Bucher & Nores, 1988; O'Connor *et al.*, 1999). Unlike most passerine birds in the Pampean region (Filloy & Bellocq, 2007), the rufous-collared sparrow has responded positively in terms of abundance to increasing croplands in the landscape. It seems that croplands offer resources that the bird is able to exploit, such as seeds.

Although the rufous-collared sparrow is tolerant to and even favoured by some human activities, such as agriculture, it responded negatively to increasing urbanization. Abundance decreased as human development increased from the rural zone to the core urban area. The species can be classified as an urban adapter according to Blair (1996), because it is relatively common in residential and suburban areas but rare or absent in core urban areas.

Finally, we demonstrated an approach to analyzing the responses of generalist birds to environmental changes. While a general pattern cannot be extrapolated from a single species, the responses of the rufous-collared sparrow to 6 different environmental gradients represent an example of spatial patterns in the abundance of a generalist bird at different gradient types, geographical scales, and biogeographic regions. Many native species may be tolerant to or even benefit from changing and new environments, and knowledge of how they respond to both natural and human-created environmental gradients at different geographical scales may help efforts to anticipate the impact of human activities on native birds in a changing world.

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