

Rarity in Chilean forest birds: which ecological and life-history traits matter?

Hernán L. Cofre^{1*†}, Katrin Böhning-Gaese² and Pablo A. Marquet^{1,3}

¹Center for Advanced Studies in Ecology and Biodiversity and Departamento de Ecología, Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile, ²Institut für Zoologie, Johannes Gutenberg-Universität Mainz, Becherweg 13 D-55099, Mainz, Germany and ³Instituto de Ecología y Biodiversidad, Casilla 653, Santiago, Chile

*Correspondence: Hernán L. Cofre, Escuela de Medicina Veterinaria, Facultad de Ecología y Recursos Naturales, Universidad Nacional Andrés Bello, Santiago, Chile.

E-mail: h.cofre@uandresbello.edu

†Present address: Escuela de Medicina

Veterinaria, Facultad de Ecología y Recursos Naturales, Universidad Nacional Andrés Bello, Santiago, Chile.

ABSTRACT

While it is a truism that species rarity is non-randomly distributed across regions, habitats, and taxa, there is little consensus on which factors are the best predictors of low abundances and restricted geographical ranges. In this study, we evaluate the effects of ecological and life-history traits, as well as phylogeny, on rarity in the abundance and distribution of land birds inhabiting forest habitats in the Mediterranean and temperate regions of Chile. We use data on abundance collected at 16 sites and data on latitudinal distribution obtained from a literature compilation. Statistical analyses were based on multiple regression and multivariate models. We used Signed Mantel test to analyse the relationship between species ecological and life-history traits and rarity, taking into account the effect of phylogenetic relatedness. We found that rarity, in terms of distribution, is associated with a low investment in reproduction, non-migratory status, and degree of habitat specialization. These ecological and life-history traits, in association with forest loss due to climatic changes and human impacts, may explain the narrow distribution of most endemic forest birds species. Rarity in abundance, on the other hand, is more difficult to explain. However, the fact that large species with an insectivorous diet showed low density in the assemblages studied suggests that abundance is mostly regulated by energy (resource) requirements and availability. Finally, our study shows that there is no phylogenetic influence in the observed patterns.

Keywords

Chile, density, forest birds, latitudinal range, macroecology, rarity.

INTRODUCTION

Since the beginning of ecology as a discipline, species with low abundance and/or small geographical range have been recognized as rare (Darwin, 1859; Preston, 1948; Rabinowitz *et al.*, 1986). There are two main reasons for studying patterns of abundance and distribution of rare species. First, it is known that species with small population size are more threatened with extinction than abundant species (Pimm *et al.*, 1988; Goerck, 1997; Purvis *et al.*, 2000; Manne & Pimm, 2001). Second, most species in local communities are rare, whereas few are exceptionally abundant (e.g. Fisher *et al.*, 1943; Preston, 1948; Hubbell, 2001). Despite this, most ecological studies and most ecological generalizations have been based on more common species (Kunin & Gaston, 1993; Cotgreave & Pagel, 1997). Therefore, there is an urgent need to understand how well current ecological theory applies to the majority of our biotic diversity (Gaston, 1994; Kunin & Gaston, 1997).

Many ecological and life-history attributes have been suggested as good correlates of rarity (see Gaston, 1994; Kunin & Gaston, 1997; Murray *et al.*, 2002; for review). However, at present there

is little consensus on which factors are the best predictors of abundance and range size of species. In birds, for instance, many ecological and life-history traits have been shown to be correlated with rarity. Some of them are: body size (Karr, 1977; Terborgh *et al.*, 1990; Cotgreave & Harvey, 1992; Gillespie, 2000), dispersal ability (Goerck, 1997; Duncan *et al.*, 1999; Böhning-Gaese *et al.*, 2006), reproductive traits (Blackburn *et al.*, 1996; Gaston & Blackburn, 1996; Cotgreave & Pagel, 1997; Duncan *et al.*, 1999; Böhning-Gaese & Oberrath, 2001), habitat specificity or niche breadth (Kattan, 1992; Goerck, 1997; Mace & Kershaw, 1997; Brändle & Brandl, 2001; Gillespie, 2002), niche position or type of habitat used (Gregory & Gaston, 2000; Böhning-Gaese & Oberrath, 2001; Marsden & Whiffin, 2003), diet (Kattan, 1992; Goerck, 1997; Gillespie, 2002), and migratory status (Cotgreave, 1994; Böhning-Gaese & Oberrath, 2001).

In this scenario, the main objective of this study is to analyse the relationship between rarity and some life-history and ecological traits of birds inhabiting forest habitats in Chile with the aim of answering the following questions: Which are the ecological and life-history correlates of rarity in these species? Are phylogenetic effects important in accounting for bird species rarity? This is the

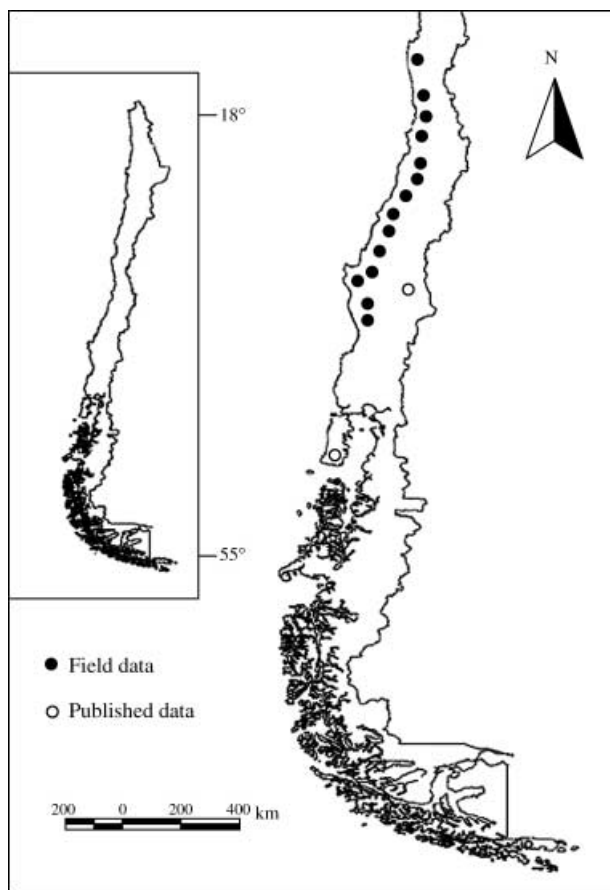


Figure 1 Location of sites surveyed in this study (14) and obtained from the literature (2).

first assessment of rarity correlates in a southern temperate avifauna. The few studies made in the Neotropics had been done in tropical habitats (e.g. Kattan, 1992; Goerck, 1997; Poulsen & Krabbe, 1997; Gillespie, 2000; Marsden & Whiffin, 2003). Furthermore, by analysing the strength of the phylogenetic relatedness of species on these patterns, we provide a test of the generality of phylogenetic effects on rarity in a South American bird species assemblage dominated by a large number of endemics. At the same time, our study will shed light on the robustness of the results from studies on bird rarity in South America that have not assessed phylogenetic effects (e.g. Goerck, 1997; Poulsen & Krabbe, 1997; Gillespie, 2000, 2002).

METHODS

Study area

This study was carried out in forest habitats within Mediterranean and temperate Chile (Armesto *et al.*, 1996a), at southern South America. This area includes the only region of Mediterranean climate in the Neotropics (Fig. 1). Forests in the study area occur mainly in coastal regions and inland creeks and ravines. Within the area of Mediterranean climate, mean total annual rainfall varies between 200 mm and 1000 mm depending on latitude,

and occurs mostly in winter. The average annual maximum temperature varies between 12–16 °C, and the minimum is rarely below 0 °C. The temperate area included in our analysis is characterized by a mean total annual rainfall that varies between 800 mm and 2000 mm. Here, the average annual maximum temperature varies between 10–14 °C (Di Castri & Hajek, 1976; Amigo & Ramírez, 1998).

The avifauna of Mediterranean and temperate Chile is not very diverse (less than 200 terrestrial species), but it is of great biogeographical interest because of the high number of endemic species. At least 50 species are known to breed or forage in forest habitats, of which 30% are endemic to these forests (Vuilleumier, 1985; Rozzi *et al.*, 1996a). Birdlife International has recognized a total of 12 restricted-range species in Mediterranean and temperate Chile in its recent global analysis of Endemic Bird Areas (Stattersfield *et al.*, 1998).

Field methods and data

We studied the avifauna inhabiting undisturbed forests within the Mediterranean and temperate regions of Central Chile at 14 sites (Fig. 1) between 30°–43° S. All censuses were done during the breeding season, between October 2001 and January 2002 and between October 2002 and January 2003. Our study was restricted to the terrestrial bird assemblage, excluding raptors and nocturnal species. This assemblage included 33 forest species (Table 1). We used the ‘distance sampling’ point count methodology (see Bibby *et al.*, 1992; Ralph *et al.*, 1996), specifically, the modified variable-circular plot technique (Reynolds *et al.*, 1980), which had been used before in Chilean rainforests (Jiménez, 2000). Following Willson *et al.* (1994), Estades & Temple (1999), and Jiménez (2000), we use a plot size of 50 m, a counting time of 8 min, a minimum distance from the edge of 150 m, and a minimum distance between two points of 200 m. At all sites, 10 point counts were conducted between 07:00 and 10:30 h for 5 or 6 days distributed over the whole area to cover the various vegetation types present at the site (Poulsen & Krabbe, 1997; Jiménez, 2000). It is known that an effort of this magnitude is enough to detect most species in temperate rain forests (Willson *et al.*, 1994; Rozzi *et al.*, 1996a,b; Jiménez, 2000; Díaz *et al.*, 2005; see also Poulsen & Krabbe, 1997).

In addition, the point-count data were supplemented with active searching for less conspicuous species within an area of 1 km² using playback calls (Poulsen & Krabbe, 1997). All species that were registered using this method, and that were not detected by the point counts, were classified as ‘singletons’ (*sensu* Colwell & Coddington, 1994), i.e. the density of these species was defined as 1 individual per 10 point counts. In addition, we used density data from two additional sites that used a similar methodology (Estades, 1997; Jiménez, 2000).

Rarity and species attributes

In this study, rarity was assessed by considering regional abundance and latitudinal geographical range (Gaston, 1994). Regional abundance of each species was defined as the mean

Table 1 Ecological and life-history traits of 33 non-raptor terrestrial bird species inhabiting forest habitats in Mediterranean and temperate Chile

Family	Species	Type of forest	Habitat specificity	Diet	Migratory status	Brood size	Body mass (g)	Regional abundance	Latitudinal range
Columbidae	<i>Columba araucana</i> *	MF/TF	G	H	m	1	200	1.04	18.5
Trochilidae	<i>Patagona gigas</i>	MF/TF	G	O	M	1–2	18.20	0.37	42
	<i>Sephanoides sephanoides</i>	MF/TF	G	O	M	2	5.60	2.72	26.5
Picidae	<i>Colaptes pitius</i>	MF/TF	G	O	R	4–6	125	0.25	24.5
	<i>Picoides lignarius</i>	MF/TF	G	I	R	3–5	39.97	0.45	22
	<i>Campephilus magellanicus</i>	MF/TF	S	I	R	2–3	260	0.10	20
Psittacidae	<i>Enicognathus leptorhynchus</i> *	TF	S	H	R	4–6	250	—	12.5
	<i>Enicognathus ferrugineus</i>	MF/TF	S	H	m	4–6	200	0.61	20.5
Furnariidae	<i>Sylviorthorhynchus desmursii</i>	MF/TF	G	I	R	3	10.50	0.51	20.75
	<i>Aphrastura spinicauda</i>	MF/TF	S	I	m	3–5	10.57	3.78	24.5
	<i>Leptasthenura aegithaloides</i>	MF	G	I	m	4	9.10	0.70	36.5
	<i>Asthenes humicola</i> *	MF	G	I	R	3–4	22.50	0.66	11
Rhinocryptidae	<i>Pygarrhichas albogularis</i>	MF/TF	S	I	R	3	13.00	1.01	23.75
	<i>Pteroptochos tarnii</i> *	TF	S	O	R	2	144.33	0.64	11.5
	<i>Pteroptochos castaneus</i> *	MF	S	O	R	2–3	130	0.45	2.5
	<i>Eugralla paradoxa</i> *	MF/TF	S	O	R	2–3	34.50	0.28	8
	<i>Scelorchilus albicollis</i> *	MF	G	I	R	2–3	41.00	0.90	10
	<i>Scelorchilus rubecula</i> *	TF	S	O	R	2.32	40.35	1.33	14
	<i>Scytalopus magellanicus</i>	MF/TF	G	I	R	3	11.93	0.35	27.5
Tyrannidae	<i>Xolmis pyrope</i>	MF/TF	G	O	m	2–3	30.45	0.44	28.5
	<i>Phytotoma rara</i>	MF/TF	G	H	m	2–4	52.36	0.17	23.5
	<i>Elaenia albiceps</i>	MF/TF	G	O	M	3	15.60	5.05	58
	<i>Anairetes parulus</i>	MF/TF	G	I	R	3	7.20	1.31	27.5
	<i>Coloramphus parvirostris</i>	MF/TF	G	I	M	3	9.55	0.34	25
Hirundinidae	<i>Tachycineta meyeni</i>	MF/TF	G	I	M	4–6	15.35	1.05	28.67
	<i>Pygochelidon cyanoleuca</i>	TF	G	I	M	3–5	11.85	0.20	65
Certiidae	<i>Troglodytes aedon</i>	MF/TF	G	I	M	4–7	9.47	1.89	111
Muscicapidae	<i>Turdus falcklandii</i>	MF/TF	G	O	R	2–3	86.27	0.88	29.75
Fringillidae	<i>Zonotrichia capensis</i>	MF/TF	G	H	M	3–4	20.75	0.76	66
Fringillidae	<i>Curaeus curaeus</i>	MF/TF	G	H	R	4–5	90.00	0.64	26
	<i>Phrygilus gayi</i>	MF	G	H	M	2–5	21.00	1.87	30
	<i>Phrygilus patagonicus</i>	MF/TF	G	H	M	2–4	20.13	1.16	23.5
	<i>Carduelis barbata</i>	MF/TF	G	H	M	3–6	22.30	0.78	27.5

MF, Mediterranean forest; TF, temperate forest; G, generalist; S, specialist; H, herbivorous; O, omnivorous; I, insectivorous; M, long-distance migrant; m, short-distance migrant; R, resident. *Endemic species.

density of species, taking into account only the sites where the species was registered. The geographical range of each species was obtained from published data (e.g. Fjeldsa & Krabbe, 1990; Anderson & Rozzi, 2000; Cornelius *et al.*, 2000; Reid *et al.*, 2002; Jaramillo, 2003) and was defined as the latitudinal extent (*sensu* Gaston, 1994; see also Gillespie, 2002). Data about the life-history and the ecology of species were obtained from an exhaustive review of the literature (e.g. Johnson, 1965, 1967; Ralph, 1985; Vuilleumier, 1985; Jaksic & Feisinger, 1991; Armesto *et al.*, 1996b; Rozzi *et al.*, 1996a,b; Sieving *et al.*, 1996, 2000; Willson *et al.*, 1996, 2001; De Santo *et al.*, 2002; Díaz *et al.*, 2005). We considered five species attributes as independent variables in our analysis of rarity: (1) habitat specificity, (2) migratory status, (3) diet, (4) body mass, and (5) clutch size (see Table 1). In order to test for the effect of some of these variables on rarity, the species were classified in the following categories: (a) *Habitat specificity*: According to its

dependence of forest habitats species were assigned to one of two categories: (0) generalist (species that use another kind of habitat in addition to forests, and (1) specialist (species that only breed and forage in forest habitat) (Kattan, 1992; Goerck, 1997; Gillespie, 2002); (b) *Migratory status*: (0) resident, and (1) short- or long-distance migrant (including species that perform short-distance movements within Chile, and long-distance migratory species, that move between the tropical and temperate zones in South America); (c) *Diet*: The species were assigned to one of following three categories depending on the main type of food: primarily plants (seeds, fruits, and other plants tissues), plants, and invertebrates (omnivorous species), and primarily invertebrates (insects, spiders, and other animal tissues). To analyse these attributes, two dummy variables were created (Draper & Smith, 1998) herbivory and insectivory. Thus, if a species was an herbivore, then it was classified as herbivory = 1 and insectivory = 0. If a

species was an omnivore, it was classified as herbivory = 1 and insectivory = 1. If a species was an insectivore, it was classified as herbivory = 0 and insectivory = 1.

Mean body size (g), latitudinal range size, and clutch size (number of eggs per brood) were \log_{10} transformed for all statistical analyses. Regional abundance was expressed as \log_{10} (mean regional density + 1).

Non-phylogenetic statistical analyses

We used a multiple regression analysis with backward elimination and a stepwise forward selection method to examine the extent to which the observed variance in regional abundance and latitudinal range may be explained by a combination of species attributes. Model selection was based on the Akaike Information Criterion (AIC) (Akaike, 1973). Because multiple regressions may fail to identify significant independent variables when multicollinearity is present, we examined the tolerance values in this procedure. Tolerance is computed as $1 - R^2$ for a regression between a given independent variable and all other independent variables (Draper & Smith, 1998; Legendre & Legendre, 1998). As a rule of thumb, multicollinearity is indicated by tolerance values < 0.20. In this study, all tolerance values were > 0.5; therefore all variables had a small redundancy or large contribution to the regression. All regular statistical methods were implemented with the use of STATISTICA 5.1 for Windows (StatSoft Inc., Tulsa, OK, USA) and the R statistical software (R Development Core Team 2005).

Phylogenetic statistical analyses

Because our analysis involves comparisons across different species, it is possible that species can share traits because of shared ancestry (Felsenstein, 1985; Harvey & Pagel, 1991). In order to assess the contribution of phylogenetic relatedness on traits potentially associated to rarity, we used an extension of the Mantel test (Mantel, 1967; Smouse *et al.*, 1986; Legendre & Legendre, 1998), the Signed Mantel test (Böhning-Gaese *et al.*, 2000; Böhning-Gaese & Oberrath, 2001; Oberrath & Böhning-Gaese, 2001), to assess the effect phylogenetic relatedness in the models identified through multiple regression. The Mantel test is concerned with assessing the correlation between the elements of two distance matrices (Manly, 1986). To construct each matrix, species are compared with all the other species. Thus, for each variable (dependent and independent variables), the distance data on N sampling units (birds species) are represented by an $N \times N$ matrix with $N(N - 1)/2$ different paired distances. In this study, we constructed two Y matrices that described the dissimilarity (distance) in regional abundance and latitudinal range, respectively, a X_1 matrix with phylogenetic distance among species, and X_2, \dots, X_n matrices that represented the dissimilarities in the other attributes among the species. In Mantel tests, the regression of the individual values in the matrices yields the partial regression coefficients $b_1, b_2 \dots b_n$, and the respective t -values (Smouse *et al.*, 1986). A valid significance level for each X -variable (the Mantel significance level) is then derived by comparing the original

Table 2 Results of multiple regression analyses explaining regional abundance and latitudinal range of species

Variable	Coefficients	<i>P</i> -values
Regional abundance model		
\log_{10} body size	-0.42	0.004
Herbivory	0.25	0.05
Adjusted R^2	0.21	
Akaike Information Criterion	25.8	
Latitudinal range model		
Habitat specificity	-0.30	0.01
Migratory status	0.14	0.12
\log_{10} clutch size	0.49	0.09
Adjusted R^2	0.35	
Akaike Information Criterion	4.98	

t -value with a null distribution of t -values constructed by Monte Carlo randomization. To construct the null distribution of t -values we used 2000 randomizations.

The phylogenetic distance between each pair of species was defined as their genetic distance $\Delta T_{50} H$ according to the molecular phylogeny of Sibley & Ahlquist (1990), which is a resolved phylogeny based on DNA–DNA hybridization, with $\Delta T_{50} H$ being the temperature when 50% of hybridizable DNA has melted. The $\Delta T_{50} H$ values were classified in discrete classes following Sibley & Ahlquist (1990), and Sibley & Monroe (1990). Sibley and Ahlquist's (1990) phylogeny has been widely applied in the comparative analyses of ecological and evolutionary patterns of birds (e.g. Nee *et al.*, 1991; Blackburn *et al.*, 1996; Blackburn & Ruggiero, 2001). To construct the dissimilarity matrix for the rest of the variables, a trait dissimilarity index was calculated by subtracting the trait value of one species from the value of the other species (Oberrath & Böhning-Gaese, 2001).

RESULTS

The multiple regression analysis of factors affecting abundance and latitudinal range identified two different models (Table 2). For regional abundance, the variables that entered the model were body size and herbivory (best model with lowest AIC). The relationship between body size and abundance was negative, and herbivorous species were more abundant than non-herbivorous species. In contrast, the latitudinal range of species was best predicted by habitat specificity, migratory status, and clutch size. Forest specialists had narrower geographical ranges than generalist species (Fig. 2a). There was a positive relationship between clutch size and geographical range, and resident species had narrower geographical ranges than migrants (Fig. 2b). Although migratory status was not significant in this model, it was so in the Signed Mantel test not including phylogenetic effects (Table 3).

When we take into account the phylogenetic relatedness among species, using a multivariate Mantel test (Table 3), the results did not change. Diet as well as body size maintained their

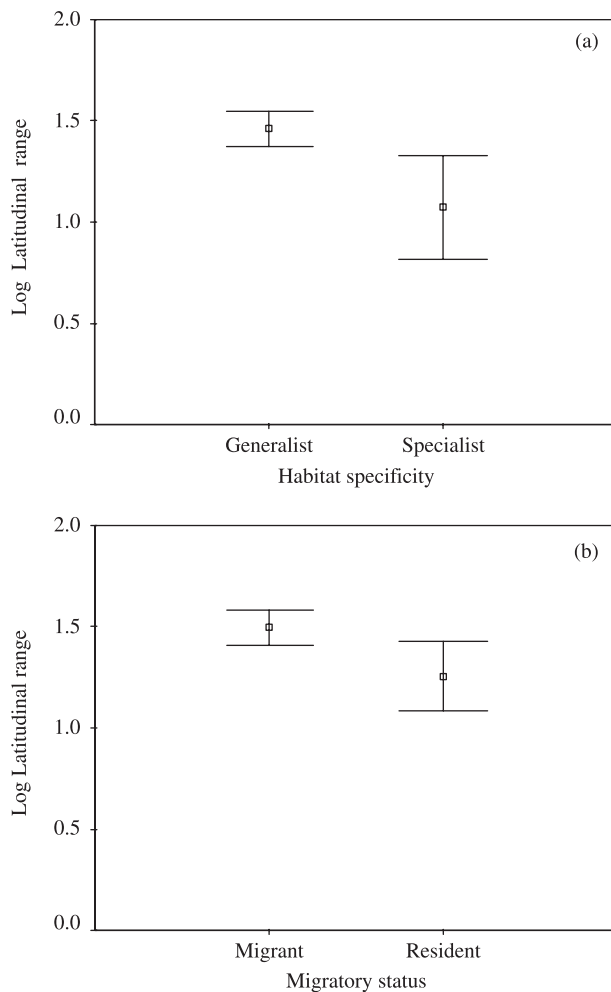


Figure 2 Influence of (a) habitat specificity on latitudinal range (b) migratory status on latitudinal range. Displayed are least squares means (± 1 SE).

strong effects on regional abundance, and habitat specificity, clutch size, and migratory status maintained their effects on latitudinal range (Table 3). Phylogeny was not significant in any of the models selected using multiple regression procedures.

DISCUSSION

We found that nearly 40% of the variance in range size of forest birds in central Chile may be explained by migratory status, clutch size, and habitat specificity. For regional abundance, only 20% of variance can be explained by body size and diet. These results are very similar to those reported for well-studied European bird assemblages (e.g. Blackburn *et al.*, 1996; Böhning-Gaese & Oberrath, 2001) or well-known taxonomic groups such as Anseriformes (Gaston & Blackburn, 1996).

We found that habitat specificity was strongly related to latitudinal range but not to abundance. The fact that this result only partially agrees with Brown's (1984, 1995) niche breath hypothesis, which predicts that both distribution and abundance should be affected in similar ways by degree of specialization in ecological requirements, suggests that other factors might be important (e.g. Gaston *et al.*, 1997). In our case, the observed positive relationship between latitudinal range and habitat specificity is likely the result of the long and narrow shape of ecoregions present in Chile, which causes that birds that inhabit only forest habitats in central Chile had a significantly smaller latitudinal extent than birds that occurred in many more kind of habitats. However, the fact that similar results have been found for South American birds in tropical ecoregions (Kattan, 1992; Goerck, 1997; Gillespie, 2002), not necessarily narrow in shape, suggests that other ecological factors are important. This is particularly likely in the case of forest endemic species. Most endemic forest specialists in our analysis, such as the Magellanic woodpecker (*Campephilus magellanicus*), Austral parakeet (*Enicognathus ferrugineus*), and most of species in the family Rhinocryptidae are large sized and have been described as sensitive to forest fragmentation and as strongly dependent on forest sites for nesting and feeding (Rozzi *et al.*, 1996a; Cofré, 1999; Estades & Temple, 1999; De Santo *et al.*, 2002; Reid *et al.*, 2002; Díaz *et al.*, 2005). Therefore, we hypothesize that endemic forest birds in Chile are limited in their distribution primarily by the latitudinal distribution of their habitat and secondarily by particular components of the forest habitat, including food type (Ralph, 1985; Estades, 1997) and availability of nest sites (De Santo *et al.*, 2002; Cofré, 2004).

Table 3 Results of multivariate Mantel test including and not including phylogenetic distance, testing the influence of species attributes on regional abundance and latitudinal range. Numbers in table are *t*-values. *P*-values based on 2000 permutations

Species traits	Regional abundance		Latitudinal range	
	Not including phylogenetic distance	Including phylogenetic distance	Not including phylogenetic distance	Including phylogenetic distance
Phylogeny	—	-1.94	—	-2.74
Log ₁₀ body size	-7.49***	-7.77***	—	—
Habitat specificity	—	—	-6.84***	-7.11***
Herbivory	4.65*	5.04**	—	—
Migratory status	—	—	4.6**	4.71**
Log ₁₀ clutch size	—	—	5.54*	5.62*

P* < 0.05, *P* < 0.01, ****P* < 0.001.

It has been reported that rare species tend to have lower reproductive investment than common ones (e.g. Kunin & Gaston, 1993, 1997; Blackburn *et al.*, 1996; Duncan *et al.*, 1999; Gaston, 2003). Here, we found evidence of a positive relationship between clutch size (an indirect measurement of reproductive investment) and latitudinal geographical range. Indeed, most endemic species have a small brood size (\leq three eggs) such as the ochre-flanked tapaculo (*Eugralla paradoxa*), black-throated huet-huet (*Pteroptochos tarnii*), chestnut-throated huet-huet (*Pteroptochos castaneus*), Magellanic woodpecker, and Chilean pigeon (*Columba araucana*) (Johnson, 1967; De Santo *et al.*, 2002). This result is consistent with other studies in birds. For example, Brown (1995) showed a similar positive relationship between brood size and geographical range in North American and Australian birds, Cotgreave & Pagel (1997) found the same relationship for terrestrial birds of Australia, and Duncan *et al.* (1999) found a positive relationship between the range size and life-history traits related to high population growth rates (many broods per year and short fledging time) of bird species introduced to New Zealand (from the UK). Furthermore, traits associated with fast offspring production (e.g. egg size, incubation, and fledging time) have been showed to be correlated with abundance and geographical range for Central European birds species (Böhning-Gaese & Oberrath, 2001), British birds (Blackburn *et al.*, 1996), and Anseriformes (Gaston & Blackburn, 1996).

There are a number of studies that support a positive relationship between dispersal ability and range size for terrestrial and aquatic animals (reviewed in Gaston, 1994, 2003). Our study lends support to this conclusion, as most of the restricted range species are resident understorey birds of the family Rhinocryptidae and Furnariidae (e.g. *S. desmursii*, *P. albogularis*) that have been described to be among the most sensitive to habitat fragmentation in southern Chilean temperate forests, due to their poor dispersal ability to cross non-forest habitats (Willson *et al.*, 1994; Sieving *et al.*, 1996, 2000). Because of strong evidence of a negative relationship between dispersal ability and extinction probability in terrestrial birds (e.g. Willson *et al.*, 1994; Sieving *et al.*, 1996), a possible explanation for the small geographical ranges of these species is associated to a historical reduction in forest habitat caused by the progressive aridity during the Early to Mid-Holocene in central Chile (e.g. Villa-Martínez *et al.*, 2003), compounded with a recent history of forest loss due to human impacts in the last 500 years (Fuentes & Muñoz, 1995). This is consistent with the explanation of why forest endemics with restricted dispersal ability, especially those in the family Rhinocryptidae, are not presently found in temperate forest relicts in semiarid Chile (Cornelius *et al.*, 2000; Reid *et al.*, 2002).

The observed negative correlation between body size and abundance and the positive effect of herbivory on abundance suggests that abundance rarity might be related to energetic limitation (Blackburn *et al.*, 1993; Gaston, 1994; Blackburn & Gaston, 1997). In fact, energy availability has emerged as the most likely mechanism constraining maximum abundance (e.g. Savage *et al.*, 2004; Marquet *et al.*, 2005). Studies in birds have shown that the relationship between body mass and population density, although usually negative, can be highly variable (e.g.

Cotgreave & Harvey, 1992; Blackburn *et al.*, 1993; Blackburn & Gaston, 1997), such that it tend to be polygonal (e.g. Nee *et al.*, 1991). Our analysis shows large variability in this relationship in agreement with most studies performed at local scales (Blackburn & Gaston, 1997). In addition, we found that herbivore species eating plants tissues, such as seeds and fruits, are more abundant than insectivorous and omnivorous species, after controlling for body size. This evidence suggests that abundance rarity of large insectivorous species might be related to energetic limitations. Arita (1993) reported a similar pattern for bats, where species that feed on plant parts or products (fruit, nectar, and pollen) were more abundant than insectivores. Similarly, Goerck (1997) suggests that large insectivorous birds may be rare because of the seasonal variability of their resources.

Finally, in agreement with most studies on bird species, phylogenetic relatedness does not have any effect on the relationship between rarity and ecological traits (e.g. Blackburn *et al.*, 1996; Gaston & Blackburn, 1996; Blackburn & Ruggiero, 2001; Oberrath & Böhning-Gaese, 2001; but see Nee *et al.*, 1991).

CONSERVATION IMPLICATIONS

According to Manne & Pimm (2001), scarce and restricted species in the Neotropical avifauna are also the most threatened, a result consistent with the notion that they face the double jeopardy of extinction associated to low abundance and restricted range (Johnson, 1998). In this study we identified several species that face this double jeopardy in Mediterranean and temperate forest ecosystems of Chile. Some of them are ochre-flanked tapaculo, chestnut-throated huet-huet, Magellanic woodpecker, and Patagonian tyrant (*Coloramphus parvirostris*). All these species have been previously identified as very sensitive to fragmentation (Willson *et al.*, 1994; Estades & Temple, 1999; Cornelius *et al.*, 2000); however, they have not been granted with national (only the Magellanic woodpecker), or international (e.g. Stattersfield *et al.*, 1998), conservation status. Our data reinforce the notion that the status of these should be revisited (see also Cofré, 1999) as their persistence is of concern given that they inhabit an area heavily impacted by human activities associated with urban and agricultural expansion, exotic species, forestry, and human-induced fires (Lara *et al.*, 1996; Armesto *et al.*, 1998; Arroyo *et al.*, 1999, 2004; Echeverría *et al.*, 2006; Pauchard *et al.*, 2006). This area encompasses Mediterranean-type ecosystems (31° S to 36°30' S), which are well known for harbouring a large proportion of earth biodiversity (Cowling *et al.*, 1996). In continental Chile, the area between 25° S to 47° S and a narrow coastal strip between 19° to 25° S are part of the Chilean winter rainfall-Valdivian forest hotspot (Arroyo *et al.*, 1999, 2004; Myers *et al.*, 2000), characterized by a large number of endemic animal and plant species. The identification of species potentially at risk in this area requires urgent action, specially considering the low percentage (less than 3%) of protected areas herein located (Armesto *et al.*, 1998; Cofré & Marquet, 1999), the current rates of human encroachment (Echeverría *et al.*, 2006; Pauchard *et al.*, 2006), and its vulnerability to future land use changes (Wilson *et al.*, 2005).

Future studies on this avifauna should focus in assessing abundance and distribution patterns of species in forest that have been poorly studied (e.g. forest between 43° and 52° S). Moreover, autoecological and population studies of the rarest species should be carried out in order to identify their threat status and vulnerability to habitat fragmentation.

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