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DISTRIBUTION, HABITAT USE, AND ABUNDANCE PATTERNS OF LANDBIRD COMMUNITIES ON THE JUAN FERNÁNDEZ ISLANDS, CHILE

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Resumen. – Distribución, uso del hábitat y abundancia relativa en comunidades de aves terrestres en las Islas Juan Fernández, Chile. - La superficie total de las Islas Juan Fernández (~ 95 km²) (Chile) fue cartografiada en relación a los hábitat de aves. Doce tipos principales de hábitat fueron descritos. Una comparación de la reconstrucción avifaunística conocida con nuestros resultados indica que el número de especies de aves terrestres regularmente anidando en las islas subió de 7 a 11 desde el descubrimiento de las islas en 1574. Seis de las siete taxa de aves terrestres nativas son endémicas, cada una restringida a una sola isla. Presentamos la distribución y abundancia relativa para todas las especies de aves terrestres y todos los tipos de hábitat. Las especies endémicas generalmente prefieren hábitat dominados por plantas autóctonas. Las especies non endémicas ocupan un espectro de hábitat más amplio que las endémicas. Adicionalmente, las especies non endémicas tienen su mayor densidad o abundancia relativa en hábitat donde plantas introducidas son dominantes. Las especies endémicas ocupan menos tipos de hábitat, tienen una área de distribución mas pequeña, y su abundancias relativa es en general mas baja. Al agrupar las aves en gremios con respecto a los tipos de hábitat se crean cuadro grupos principales. Los componentes importantes que permiten la diferenciación de estos gremios de aves insulares se identifican por 1) la distancia entre las islas, 2) la estructura de la vegetación (paisaje abierto o vegetación densa), y 3) la interacción y competencia entre las especies. Aunque ninguna de las especies de aves terrestres endémicas se ha extinguido, aproximadamente tres cuartos de sus hábitat autóctonos ya han sidos destruidos y todas las especies de aves endémicas están amenazadas. El manejo de conservación debe concentrarse sobre los dos gremios de aves todavía presentes en áreas con vegetación nativa, y debe incluir un programa de erradicación de mamíferos exóticos. Estos últimos son predadores sobre aves o modifican la vegetación existente.

Abstract. – The entire surface area of the Juan Fernández Islands (~ 95 km²) (Chile) was mapped according to bird habitats. Twelve principal habitat types were described. Comparisons of an avifaunal reconstruction with our recent findings show that the number of regularly breeding terrestrial bird species increased from 7 to 11 since the discovery of the islands in 1574 until today. Six out of the seven native landbird species are endemic, each being restricted to a single island. Distribution and abundance patterns are given for all landbird species and habitat types. Endemics generally show preference for habitat types dominated by native plants. Although non endemic birds have invaded such habitats also, they prefer habitats with introduced plants. Non endemic species were found in a broader range of habitat types than

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native species. In addition, non endemics reached the highest relative abundance in habitats dominated by introduced plants. Endemics are more specialized, occupy fewer habitat types, have small distribution areas, and low relative abundance. Clustering of bird communities according to their occurrence in habitat types leads to four main groups. Important components that help explain the differentiation of these island bird clusters are identified to be 1) the distance between the islands, 2) the vegetation structure (open vs. dense growth), and 3) the interaction/competition of species. Although none of the endemic landbird species has become extinct, they have lost about three quarters of their native habitats, and all six are threatened. Conservation management should focus on two bird clusters that persist in relict areas of native vegetation, and must include a program to eradicate alien mammals, which are either predators on birds or modifiers of vegetation. *Accepted 8 April 2005*.

Key words: Juan Fernández, Chile, Robinson Crusoe Islands, landbirds, habitats, communities, biogeography, endemism, introductions, conservation.

INTRODUCTION

Most oceanic islands occur far away from large land masses and often have small surface area. This combination of factors has led to biogeographical isolation, which in turn is expressed in low immigration rates but high extinction rates, and hence reduced species richness. Through separation over long time periods, often millions of years, islands have become centers of species differentiation, where endemic species evolved (Johnson & Stattersfield 1990, overview in Whittaker 1998). Although islands cover only about 2% of the terrestrial surface of the globe, an important part of the world's biodiversity is found on them. For instance, 14% of all mammal species (Alcover et al. 1998) and more than 30% of the species of several bird families (Dickinson 2003) are island dwellers. This is also true for plants (Stuessy & Ono 1998), which represent key organisms for the formation of bird habitats.

After their discovery and settlement by man, severe changes in the native communities of oceanic islands took place. Many species of animals and plants were introduced, and others were eradicated, and so the remaining endemics had to share their island with invaders (Long 1981, Sanders *et al.* 1982, Ebenhardt 1988, Stuessy *et al.*

1996, Greimler et al. 2002b, Haberle 2003). Depending on the intensity of human impact, the consequences of introductions and eradications on bird communities has been quite varied. On some islands, the total number of bird species was reduced after large-scale or even entire destruction of native habitats (e.g., King 1985, 1978); on others, that number increased as a partial consequence of the creation of new habitat types (Sax et al. 2002). Therefore, a comparison of avian communities between the time of first discovery and the present may provide information of the development of the biota of a given island group and suggest ways to preserve remnants of native communities.

On the Juan Fernández Islands, human impact started on 22 November 1574 with the discovery by the Portuguese captain Juan Fernández. This archipelago consists of two main islands, Robinson Crusoe (until 1966 Másatierra) and Alejandro Selkirk (until 1966 Másafuera), the smaller island Santa Clara (or Goat Island), and some ten rock islets around them (Morros). The easternmost island is Robinson Crusoe (47.11 km², 915 m elevation). The westernmost island Alejandro Selkirk (44.64 km², 1320 m) is 167 km west of Robinson Crusoe. Santa Clara (2.23 km², 375 m) is only 1.5 km south-west of Robinson Crusoe. The volcanic Juan Fernández archipelago is located 587 km west off the Chilean mainland in the south-east Pacific Ocean (33°28'48" S to 33°47'57" S and 78° 47'12"W to 80°47'44"W). It is geographically quite isolated as there are no other islands within a 500 km-zone around it. The cool Humboldt Current additionally provides a maritime barrier that separates it from the continent. The whole archipelago, except for the settlement of San Juan Bautista on Robinson Crusoe, is a Chilean national park founded in 1935 and a UNESCO Biosphere Reserve founded in 1977. More detailed geographical descriptions can be found in Castilla (1987) and Skottsberg (1920–1956).

The islands had neither been reached by Polynesians, like Easter Island in the West, nor by Native Americans, like the South American mainland in the East. They belong to the few islands in the Pacific Ocean which have been discovered by Europeans, not by Polynesians. Therefore their natural history has been comparatively well recorded and can be traced in the logbooks of various sailors (overview in Wester 1991). The Juan Fernández Islands, which represent less than 1% of the surface of Chile, presently are home to more than 30% of that county's endemic bird taxa (evaluation based on Araya et al. 1995; for biogeography and endemism see also Blake & Atwood 1942, Stuessy et al. 1992, Wege & Long 1995, Stattersfield et al. 1998, Morrone 2000). However, a study of bird diversity in the Juan Fernández Islands must also take into account the non endemics that have presumably immigrated there during the last few centuries. A comparison of the habitat types occupied by endemics versus non endemics might show whether endemic or non endemic species possess different distribution and abundance patterns, and to what extent they are associated with each other in communities.

Such a comparison has not been possible until now, as no analysis of habitat occupation of the Juan Fernández Islands' birds had been carried out [for botanical information see Skottsberg (1953) and Greimler et al. (2002a)]. In this paper we provide, for the first time, such a quantitative comparison. We discuss recent species richness [see also Schlatter (1987) and Brooke (1987)], geographical distribution, relative abundance patterns, and community composition of the endemic and non endemic landbird taxa. In particular, we want to answer the questions: (1) what landbird species regularly breed on the islands today, (2) how different is today's bird fauna to the one that existed there in 1574, (3) how are endemic and non endemic birds distributed across gradients of habitat types and what are their abundance patterns, and (4) what communities can be identified within each habitat type.

The results of such an analysis might also be of relevance to conservation and to future ecosystem management (Moors 1985). This is urgent as all six endemic landbird species of the archipelago are threatened and appear in red lists (Glade 1993, Stattersfield & Capper 2000, BirdLife International 2004). Several species have reached critically low population numbers and are under immediate threat of extinction (Bourne et al. 1992, Roy et al. 1999b, Hahn & Römer 2002). Even though the remarkably uniqueness of the biota of the Juan Fernández Islands has been known for a long time (e.g., Lönnberg 1921, Skottsberg 1920-1956), little information exists about plant-bird mutualism (e.g., Bernardello et al. 2001, Colwell 1989) in comparison with the situation on the mainland of southern Chile (e.g., Vuilleumier 1985, Armesto et al. 1996). Less is known about habitat preferences and the composition of communities. Thus, the present report attempts to fill a significant gap in the knowledge of an important component of the birdlife of Chile and its offshore islands.

TABLE 1. Nativity codes, altitudinal range, and area of habitat types of the Juan Fernández Islands (Chile). Nativity code (NC): u = predominantly native; l = predominantly non native; h = about 50% of each. Absolute and percent values for surface area of habitat types based on a quantitative analysis of vegetation maps (Hahn unpubl.).

No.	Habitat types	NC	Range (m)	Area (ha)	%
R. Crusoe			0-915	4711	100
1	Montane forest	u	220-650	990	21
2	Low elevation scrub	1	100-360	290	6
3	Mountain ridge scrub	h	150-915	599	13
4	Cultivated land of settlement area	1	0-100	39	1
5	Lowland forest culture near settlement	1	70-170	70	1
6	Grasslands and erosion terrain of lowlands	1	0-400	2723	58
S. Clara			0-375	223	100
7	Grasslands and erosion terrain of lowlands	1	0-375	223	100
A. Selkirk			0-1320	4446	100
8	Montane forest	u	350-750	194	4
9a	Sub-alpine tree-fern stands	u	550-1100	445	10
9b	Sub-alpine vegetation complex	1	550-1100	792	18
10	Vegetation of rock walls and canyon sides	h	200-1300	998	22
11a	Alpine summit fern stands	u	1100-1320	67	2
11b	Alpine region vegetation complex	1	1100-1250	120	3
12	Grasslands and erosion terrain of lowlands	1	0-550	1830	41

METHODS

We carried out field studies on all three islands during a total of 299 days (24 November 1992 to 2 February 1993, 24 March to 13 April 1994, 22 October 1994 to 13 February 1995, 9 November 2001 to 11 February 2002). Habitat types based on surveys of vegetation and analyses of vegetation structure were characterized following the methodology of Braun-Blanquet (1964) and Korpel (1995). Vegetation sample-plots varied from 25 to 100 m² and covered all main habitat types. Data in Skottsberg (1953), gathered with phyto-cenological methods following the Swedish school (four storey classes), and of Greimler et al. (2002a) by mapping habitats mainly based on dominant plant species, were compared to our system of vegetation maps to control geographical conformity and temporal changes. Mapping results were digitalized and transferred to topographic maps using a Geo-Information System (program AutoCAD). To measure the surface area of habitat types (Table 1), distribution maps were printed on thick cardboard, and then manually cut into pieces. The components of every habitat type were separately weighed (OHAUS balance accurate to ± 0.001 g). The obtained proportions of cardboard pieces were set in relation to the total island area and calculated for each type in hectare. Habitat lines are blurred and not sharp like in the maps, and thus the calculation of surface area is based on a two-dimensional view from above and not on a three-dimensional relief. True surface values are up to 10% higher depending on the relief of individual habitats.

Birds were identified visually by using Araya *et al.* (1992, see also Jaramillo 2003) and

TABLE 2. Resident landbird species of the Juan Fernández Islands (Chile). X = abundant in most areas of a given habitat type, S = rare and/or occurs only occasionally, T = occurs locally in given habitat type, blank = no record. Bold-faced type indicates a comparatively high population density in occupied areas (see text). Population sizes (total number of individuals) are estimates based on line transect census counts carried out in 2001/02 (Hahn unpubl.). Nomenclature follows Dickinson (2003).

		Rob	inso	n Cr	usoe		Santa		1	Aleja	ndro	Selki	rk		Total
Bird taxa							Clara								popu.
	1	2	3	4	5	6	7	8	9a	9b	10	11a	11b	12	
Asio flammeus suinda			Т			Х	Х								50
Columba livia f. domestica					Т	Х	Х								1000
Falco sparverius fernandensis				S	S	Х	Х								55
Passer domesticus				Х											80
Anairetes fernandezianus	Х	Х		S	S										2500
Sephanoides fernandensis	Х	S		Х	Х										1100
Sephanoides sephaniodes	Х	Х	Х	Х	Х						S				4500
Turdus falcklandii magellanicus	Х	Х	Х	Х	Х			Х	Х	Х	Х	S	S		4000
Buteo polyosoma exsul								Х	Х	Х	Х	Х	Х	Х	250
Cinclodes oustaleti baeckstroemii										Т	Х	Т	Х	Т	1500
Aphrastura masafuerae									Т		Т	Х			140

species descriptions in the original literature. Acoustical identification was possible after learning vocalizations from observation and taping with a DAT-Recorder (Sony, HD-S100) (Hahn & Mattes 2000). Numerous methods have been used during past decades (e.g., Ralph & Scott 1981, Mühlenberg 1993, Bibby et al. 2000) to estimate the size of bird populations. In order to compare our data with those of others, we chose the line transect method (Emlen 1971, 1977, Bibby et al. 2000). A total of 111 line transects were carried out lasting 2195 min and covering an area of 2228 ha. We made 2496 contacts of individual birds during these counts. The original data of population estimates will be presented elsewhere, but the total individual numbers for each species are given in this survey (Table 2). The method of WARD was used for clustering the data with the computer program S-PLUS (for multivariable statistics see Sachs 1997, Steinhausen & Langer 1977). For the relative abundances, data were classified in five categories from rare to very abundant (see Mattes 1988). Then the distances of the cluster analysis (measurable on the heterogeneity scale) were calculated and illustrated. For the qualitative data, only two classes of equal weight had to be calculated (presence and absence of a bird species in a certain habitat type).

RESULTS

Habitat types. The island Santa Clara is covered by non native grassland and rocks. Its native vegetation was entirely destroyed (Skottsberg 1953) following the introduction of sheep, goats, and rabbits. Its habitats closely resemble those of the lower elevation of nearby Robinson Crusoe. The latter and Alejandro Selkirk, the two main islands, share several geographic characters and habitat features including latitude, geological substrate, numerous plant taxa, and similar human impact. Their surface areas are very similar and so are the proportion of native ($\sim 27\%$) and non native (~73%) habitats. However, differences exist and include the higher elevation of Alejandro Selkirk (up to sub-alpine and alpine levels) and the more intensive

human influence on Robinson Crusoe (settlement since 1850; presently about 600 inhabitants). Table 1 summarizes the habitat survey and provides areal values based on vegetation maps of all three islands.

Bird distribution. Eleven landbird species are presently resident and regularly breed on the three islands of the Juan Fernández Archipelago. Eight (73%) of these breed on Robinson Crusoe, three (27%) on Santa Clara, and four (36%) on Alejandro Selkirk. Six out of the eleven (55%) are endemic taxa (three subspecies and three species). We consider the Short-eared Owl (Asio flammeus suinda) as a native species on Robinson Crusoe and Santa Clara. According to historical sources and present data, no endemic or native landbird species of the archipelago became extinct. The Austral Thrush (Turdus falcklandii magellanicus) and the Green-backed Firecrown (Sephanoides sephaniodes) probably reached the islands before 1830 (see Audouin 1830), where they were able to found permanent populations on base of new habitats created through early human impact. Both species also occur on the Chilean mainland where they are common and widespread. It is not clear whether they reached the islands by their own means or have been brought by man (intentionally or accidentally by following ships). Two species, the House Sparrow (Passer domesticus) and the Feral Pigeon (Columba livia), were brought to Robinson Crusoe intentionally and are now free ranging. Feral Pigeons escaped from the settlement area and readapted themselves to the wild like their European ancestors. Thus, the number of resident landbird species has increased in historical times from 7 to 11 (Table 2).

The three species breeding on Santa Clara, the Juan Fernández Kestrel (*Falco sparverius fernandensis*), the Short-eared Owl and the Feral Pigeon, are also found on Robinson Crusoe. The diversity of habitats they occupy on both islands is limited and they depend on open terrain. Falco and Asio species have large territories and therefore need much space, but on the islands open habitats have increased during the last few centuries as a result of the impact of introduced herbivores (goats, sheep, cattle, rabbits). Open habitats now cover an area of more than 3000 ha. Introduced House Sparrows are restricted to the settlement and therefore occupy only a very small area. Juan Fernández Tit-Tyrants (Anairetes fernandezianus) and Juan Fernández Firecrowns (Sephanoides fernandensis) live sympatrically in the same four partially native and partially non native habitat types. However, although their presence in non native habitats is worthy of note, the total distribution area of these two species is less than 1400 ha. Austral Thrushes and Green-backed Firecrowns occupy the broadest range of habitats (and in greatest abundance) on Robinson Crusoe, being absent only in open landscapes. The Green-backed Firecrowns that are occasionally seen on Alejandro Selkirk have not managed to establish a permanent population there. The Austral Thrush is the only landbird species regularly breeding on both major islands, Robinson Crusoe and Alejandro Selkirk.

The Másafuera Hawk (Buteo polyosoma exsul), an endemic subspecies (Salvin 1875, Lönnberg 1921, Johnson 1965), is reported from all areas and habitats of Alejandro Selkirk, and thus is the landbird species that occupies the broadest range of habitats and the broadest distribution (4446 ha) on this island. Several Másafuera Hawks were introduced to Robinson Crusoe in the 1980s by the National Park Service for reducing rabbit numbers, but hawks did not breed there. The Másafuera Cinclodes (Cinclodes oustaleti baeckstroemii), an endemic subspecies (Lönnberg 1921, Johnson 1967), occurs in habitat mosaics made up of patches of low vegeta-

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FIG. 1: Grouping of terrestrial bird species of the Juan Fernández Islands according to their presence in given habitat types. Main groups are identified by Roman numbers. The Heterogeneity scale indicates the degree differentiation between bird species.

tion, rocks, and small brooks. Although some landscapes are not inhabited, for example stands of dense vegetation, the Másafuera Cinclodes is found in a number of habitats from the lowlands up to alpine level on Alejandro Selkirk where its distributional area covers about 2000 ha. The Másafuera Ravadito (Aphrastura masafuerae), an endemic species (Philippi & Landbeck 1866, Johnson 1967), is the landbird species occupying the smallest range of habitats on Alejandro Selkirk, and indeed on the whole archipelago. It is confined to two sub-alpine habitat types and to the small alpine summit region of higher altitude. It regularly occurs in fully intact and native vegetation, but is absent from stands broken up by feral goat grazing. Its distribution area does not exceed 1000 ha.

Bird-habitat clusters. Clustering of landbird species of the Juan Fernández Archipelago according to their occurrence in given habitat types leads to four main groups (Fig. 1). The first main group (I = endemics present in distinctly structured habitats of Alejandro Selkirk) exclusively includes the three endemic taxa of Alejandro Selkirk: Másafuera Hawk, Másafuera Cinclodes, and Másafuera Rayadito. This contributes to the high differentiation (integration level) from the other bird species of the archipelago. The medium scale level of 0.3 to nearly 0.4 between these three species indicates different habitat requirements within the island. The main groups II to IV are separated from the first, and are similar to each other by containing mainly birds restricted to Robinson Crusoe and Santa



FIG. 2: Grouping of terrestrial bird species of the Juan Fernández Islands according to semi-quantitative abundance in habitat types. Groups are identified by Roman numbers. The Heterogeneity scale indicates the degree differentiation between bird species.

Clara. Not vegetation structure, but interisland distance is the decisive factor for the out-grouping of Selkirk species.

The second main group (II = species present in a broad habitat range of dense vegetation structure) includes Austral Thrush and Green-backed Firecrown, which occur in nearly all habitat types of Robinson Crusoe and in some of Alejandro Selkirk. The third main group (III = open country species of the eastern islands) contains the typical open country representatives of Robinson Crusoe and Santa Clara. Only the Juan Fernández Kestrel, an endemic subspecies, is found in the settlement area as well, thus segregated from Short-eared Owl and Feral Pigeon.

The fourth main group (IV = species of settlement area and native forest of Robinson

Crusoe) contains, besides the non native House Sparrow, two endemic species, the Juan Fernández Firecrown and the Juan Fernández Tit-Tyrant. These endemics predominantly occur in/near the non native vegetation of the settlement areas and in the native forests, but are rarely or not at all seen in other habitat types characterized as non native.

Based on landbird abundances, the House Sparrow and the Feral Pigeon are separated from their previous qualitative groups (Fig. 2). The Feral Pigeon forms the mono species open country group IIIa (partly numerous open country species of the eastern islands). This separation is the result of the high pigeon numbers on Santa Clara. Short-eared Owls and Juan Fernández Kestrels are gathered in the open country group IIIb and are nowhere numerous. In the quantitative analysis, the House Sparrow appears close to this group (IIIb) which results from the sympatric occurrence of the Juan Fernández Kestrel and the House Sparrow in the agrosystems and gardens of the settlement area. The relatively low integration level of groups IVa / IIIa to the main group I is based on similar abundances rather than similar habitat preferences.

The Juan Fernández Firecrown and the Juan Fernández Tit-Tyrant constitute the group IVb, now separated from the House Sparrow. They possess by far the largest part of their total population in the natively dominated montane forest, but occur in several non native habitat types in smaller numbers. In the quantitative analysis, group II is the most isolated of all. Although the Austral Thrush and the Green-backed Firecrown do not occur in the same habitat types on Alejandro Selkirk, they are found in the same environments on Robinson Crusoe: both are very abundant in the non native lowland scrubs and occur with similar abundance in the other habitat types of the island.

DISCUSSION

The lack of extinctions and the increase of resident landbird species from 7 to 11 are related to processes of habitat development. Although a large part of the original vegetation has been destroyed by introduced herbivores, fires, and logging, relict stands of all major vegetation types are persisting in about one fourth of the total area. Thus, native birds possessed a refuge area, while they were able to inhabit non native habitats at the same time. In turn, non native habitats were the base on which four bird species managed to immigrate and establish a population. Austral Thrushes and Green-backed Firecrowns especially benefited from new habitats dominated by plants they already had lived with on the

Chilean mainland (Aristotelia chilensis, Ugni molinae, Fuchsia spp.). Broader habitat range and higher overall abundance of non native landbirds are reflected by the large surface area (three quarters) covered with non native vegetation. Distribution ranges and population sizes of almost all native species probably have strongly decreased since human impact started on the islands some 430 years ago (Audouin 1830, Sclater 1871, Salvin 1875, Schalow 1899, Lönnberg 1921). The Másafuera Rayadito for example is highly threatened (Hahn et al. 2004; see also Remsen 2003, Stattersfield et al. in prep.), now surviving on one fifth of the island range with a total population of only about 140 individuals.

Endemic landbirds of the Juan Fernández Archipelago generally show a high preference for native habitat types. Non endemics invaded such habitats also, but generally prefer non native ones. Non endemics are clearly more abundant on Robinson Crusoe than on Alejandro Selkirk. Table 2 shows that the species-rich habitats on Robinson Crusoe are in and around the settlement area. This fact may be explained by the diversity of plant species and diversity of vegetation structures. There is also a mosaic of small plantations, gardens, thickets, and exotic plants of high feeding potential for birds. High overall bird density is found in the lowland shrub vegetation where Austral Thrushes and Green-backed Firecrowns find plenty of berries and flowers (e.g., of Aristotelia, Ugni, and Rubus). Reciprocally, these species help maintaining these non native plants by pollination and seed dispersal. On Alejandro Selkirk, species richness and total bird abundance are generally lower; the habitat types most frequented by birds are dominated by native plants. Non native plants have spread out predominantly on Robinson Crusoe through more ship landings and harboring of a settlement since about 150 years, whereas Alejandro Selkirk remained comparatively more isolated (e.g., MacLiesh & Krieger

1962, Walter 1974, Wester 1991). The montane forests of these two islands also show a well-marked difference: on Robinson Crusoe, four bird species are regularly found (one even abundant), on Alejandro Selkirk only two species occur, both being rather rare. This can not be better explained by the rarity of flower/fruit-bearing plants on Selkirk than by differences in arthropod prey (we carried out a comparative census using standardized beating-stick method).

A comparison of the island birds with their allies on the South American mainland shows that most insular populations inhabit environments of similar structure. American Kestrel and Short-eared Owl predominantly live in open areas on the mainland, but cover a broader range of habitats (see Johnson 1965, Yañez et al. 1980, Rau et al. 1992). Mainland pigeons might be found at few arid sites along the Pacific coast, but often occur in and around human settlements. Tufted Tit-Tyrants (Anairetes parulus) (Roy et al. 1999a), Austral Thrushes and Green-backed Firecrowns predominantly occur in high and dense vegetation. The latter two species also use a wide habitat range on the mainland: i.e., they live in urban areas as well as in native forests (Barros 1958, Smith-Ramirez 1993, Jiménez 2000, Reid et al. 2002, pers. observ.). Phylogenetically, the Green-backed Firecrown and the Juan Fernández Firecrown, are sister species. Although both have become morphologically quite distinct from each other during the past 600,000 years (Stiles 1987, Colwell 1989, Roy et al. 1998), they have occurred sympatrically on Robinson Crusoe for more than 175 years (Audouin 1830) but probably less than 430 years. Now they are competing for the same food resources (nectar flowers and small insects). The mainland Red-backed Hawk (Buteo p. polyosoma) is a generalist and opportunistic forager, like the Másafuera Hawk, but has a much broader prey and habitat range at its disposal (Housse

1939, Johnson 1965, Schlatter et al. 1980, Jiménez & Jaksic 1991, Fuentes et al. 1993, Jiménez 1995). The Grey-flanked Cinclodes (Cinclodes o. oustaleti) occupies similar habitats like its island counterpart (brooks, moist upland), but has opportunity to use a larger altitudinal range (up to 4200 m a.s.l.; see Johnson 1967, Remsen 2003). However, the Thorn-tailed Rayadito (Aphrastura spinicauda) makes a clear difference to its island sister species: it is predominantly a forest bird (Finckh 1996, Estades & Temple 1999). Contrarily, the Másafuera Rayadito lives in low stands of Lophosoria ferns and Dicksonia treeferns, but is generally absent from the island's Myrceugenia forests (Hahn & Römer 1996, Hahn et al. 2004).

Qualitative grouping of landbirds according to their occurrence in habitat types leads to four well defined clusters. Two principal factors seem to be decisive for this pattern. First, the significant geographic distance between the major islands results in a low exchange rate. However, this is not sufficient to explain the high differentiation of the two avian communities, as some of the species have been recorded on the other island, but did not manage to survive there. These island ecosystems are composed of very specific species assemblages, showing exclusion (island effect). For example the Másafuera Hawk is supposed to have a regulating impact on several prey species (Fuentes et al. 1993): House Sparrows, Feral Pigeons and even rabbits, which were introduced to Alejandro Selkirk by fisherman, but, contrarily to Robinson Crusoe, disappeared shortly after arrival (for similar effects of island predators on prey, see Whittaker 1998). Short-eared Owl and American Kestrel were recorded on Alejandro Selkirk (V. Camacho pers. com.), but they may have been attacked relatively soon. Másafuera Hawks were observed hunting even on juvenile goats (pers. observ. 1995). Thus, besides pure distance, the specific species composi-

tion also needs to be taken into account when analyzing any island bird community. Second, the grouping was influenced by a basic difference in environment structure: bird species either occurred in open habitat or in dense vegetation. The quantitative analysis splits the four main groups into smaller units and calls the attention off the central issue of bird-habitat relationships, as some species with similar environmental demands are separated (Mattes 1988). However, the quantitative grouping also provides useful and interesting knowledge on the ecological differentiation of some species. For example, the introduced House Sparrows and Feral Pigeons are separated from the main groups and therefore are distinguished from native elements on the abundance level.

Conservation management should focus on bird-habitat clusters rather than on single species (see also Gerss 1990). On the Juan Fernández Archipelago, the main groups I and IV are of primary concern for conservation activity. These represent the rare endemic landbirds and, by that, also the remaining native habitat types. Threat and red-listing of practically all the endemics are related to the loss of habitat and reduction of distribution range. However, introduction of alien predators puts additional pressure on them: dogs, cats, coatis, Norway and ship rats were recorded (Hahn & Römer 2002) and are amongst the worst known set of aliens to imagine on remote islands. Prime conservation aim has to be the eradication of all introduced mammal species, both habitat modifiers and predators. Eradication campaigns should start as soon as possible with goats on Alejandro Selkirk, rabbits on Santa Clara, and cats in the settlement of Robinson Crusoe. On Santa Clara, all introduced species may be wiped out quickly because of the island's smaller size. Then it may be used as a natural refuge for some endangered species.

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APPENDIX 1. Breeding landbirds of the Juan Fernandez Islands (Chile). Nomenclature follows Dickinson (2003).

	Species	Sources	
*	Falco sparverius fernandensis	Chapman (1915)	
*	Buteo polyosoma exsul	Salvin (1875)	
	Columba livia	Gmelin (1789)	
	Asio flammeus suinda	Vieillot (1817)	
* *	Sephanoides fernandensis	King (1830)	
	Sephanoides sephaniodes	Lesson & Garnot (1817)	
*	Cinclodes oustaleti baeckstroemii	Lönnberg (1921)	
* *	Aphrastura masafuerae	Philippi & Landbeck (1866)	
* *	Anairetes fernandezianus	Philippi (1857)	
	Turdus falcklandii magellanicus	King (1851)	
	Passer domesticus	Linnaeus (1758)	

* = endemic subspecies, ** = endemic species

APPENDIX 2. Recent and older names of islands in the Juan Fernandez Archipelago. Sources: Castilla (1987), Skottsberg (1920–1956). The new names were implemented by the Chilean government in 1966.

Old names	New names
Más Afuera (or Másafuera)	Alejandro Selkirk
Más a Tierra (or Másatierra) *	Robinson Crusoe
Santa Clara (or Goat Island)	Santa Clara

* = In some sources the archipelago name "Juan Fernandez" was also used for Robinson Crusoe alone.