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Importance of nest attributes in the conservation of endemic birds of the Juan Fernández Archipelago, Chile

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Summary

Understanding the particular nesting ecology of island endemic species represents the first step in identifying suitable micro-habitats and establishing efficient management programmes. This could become even more important when island bird assemblages are prone to invasion by ecologically similar species that may eventually cause niche compression or the extirpation of species already present on the island. In this study we describe the nesting ecology of both native and introduced landbird species of the Juan Fernández Islands and determine the extent to which native species could be negatively affected by alien competitors. A total of 119 nests belonging to the 11 resident landbird species were analysed. Landbirds exhibited a wide range of nesting habitat preferences on the different islands, covering different vegetation types, altitudes and ecosystems. By means of a cluster analysis we determined that competition between alien and endemic species apparently does not represent an important factor affecting resource use by endemic birds. Endemic landbirds preferred sites comparatively higher above the ground, with a greater slope and a larger level of shelter, than alien species. The introduced hummingbird, the Green-backed Firecrown *Sephanoides sephaniodes*, had different nesting preferences to the endemic Juan Fernandez Firecrown *S. fernandensis*, whereas the House Sparrow *Passer domesticus* selected nest sites located in populated areas, suggesting that both alien species may not be competing with endemic passerines for nest sites. However, urgent measures are necessary to reduce the potential predation risk on Juan Fernandez Firecrown nests by the alien Austral Thrush *Turdus falcklandii*.

Resumen

Comprender la particular ecología de nidificación de las especies endémicas sobre islas representa el primer paso para identificar micro-hábitats que son adecuados para estas especies y establecer programas de manejo eficaces. Esto podría ser aún más importante cuando los ensambles de aves son propensos a la invasión de otras especies ecológicamente similares que eventualmente puede causar la compresión del nicho o la extirpación de las especies ya presentes en la isla. En este estudio se describe la ecología de anidación de especies de aves terrestres nativas e introducidas de las Islas de Juan Fernández y el grado en que las especies nativas podrían verse afectadas negativamente por los competidores introducidos. Un total de 119 nidos pertenecientes a las 11 especies de aves terrestres fueron analizados. Estas especies mostraron una amplia gama de preferencias de hábitat de anidación en las diferentes islas, abarcando diferentes tipos de vegetación, altitudes y ecosistemas. Por medio de un análisis de conglomerados se determinó que la competencia entre especies exóticas y endémicas, aparentemente no representa un factor importante afectando el uso de recursos por las aves endémicas. Las aves terrestres endémicas prefirieron sitios comparativamente más altos por encima del suelo, con una pendiente mayor y un mayor nivel de cobertura, que las especies exóticas. El colibrí introducido *Sephaniodes* *sephanoides* no tienen las mismas preferencias de nidificación que el colibrí endémico de Juan Fernández *Sephaniodes fernandensis*, mientras que el Gorrión Común *Passer domesticus* seleccionó nidos ubicados en las zonas pobladas, lo que sugiere que ambas especies exóticas no compiten con las especies endémicas. Sin embargo, urgentes medidas son necesarias para reducir el riesgo de depredación potencial de los nidos del colibrí endémico por el Zorzal *Turdus falcklandii*.

Introduction

Oceanic island biodiversity is decreasing at an alarming rate due to current human disturbances, such as habitat loss and invasion by non-native species (Sax and Gaines 2008). Natural catastrophes, such as weather or geological events rarely represent the sole reason for island population extinctions (e.g. Steadman 2006). Consequently, conservation of island species requires an understanding of how susceptible native species are to anthropogenic changes and to what extent island species are negatively affected by alien species.

Endemic bird species are prone to high extinction rates on oceanic islands (Sax *et al.* 2002). Several such extinctions have been attributed to decreasing nesting success due to human-induced ecological changes, such as the invasion of nest predators, habitat destruction or elevated levels of competition with alien species (Medina and Nogales 2009, Ha *et al.* 2010). However, island bird species could also be intrinsically more vulnerable than mainland birds to these negative anthropogenic effects as a result of evolutionary processes. A significant similarity in breeding requirements could be considered an indicator of competition between species, given that nesting structures are usually scarce on small islands and because alien species can contribute to increases in nesting density in some habitats, hence attracting nest predators (e.g. Gates and Gysel 1978). Furthermore, natural inter-specific competition and predation tend to be lower on islands than on the mainland, causing a high degree of differentiation in nest site choice (Wright 1980, Blondel 2000, Blumstein 2002). Nesting location patterns of island birds, therefore, should result in unsaturated species assemblages prone to invasion by ecologically similar species that may eventually cause niche compression or the extirpation of a species already present (Stachowicz 1999, Zabin 2009).

In this study we assessed the nesting ecology of landbirds of the Juan Fernandez Archipelago where three endemic species and three endemic subspecies can be found. Two landbird species have been intentionally introduced: the House Sparrow *Passer domesticus* and the Rock Dove *Columba livia*. Another two species were able to establish populations probably only after anthropogenic disturbances following the discovery of the islands, the mainland Green-backed Firecrown *Sephanoides sephaniodes* and the Austral Thrush *Turdus falcklandii magellanicus*. Recent human colonisation and introduction of herbivores have caused even more severe habitat degradation (Cuevas and van Leersum 2001, Ricci 2006). In addition, introduced mammals, like cats, dogs, rats *Rattus* spp. and Coatis *Nasua nasua* act as important nest predators of local avifauna (e.g. Moors 1985, Bourne *et al.* 1992, Hahn and Römer 2002). Although most Juan Fernandez bird species are endangered, few studies have researched their nesting requirements and little is known about the potential harmful effects of alien bird species and nest predators. For example, only three nest records of the Juan Fernandez Firecrown *Sephanoides fernandensis* have been published (Lönnberg 1921) and only four nests of the Masafuera Rayadito *Aphrastura masafuerae* have ever been described (Hahn *et al.* 2004). However, the latter two species show a severe population decline and now represent Chile's only 'Critically Endangered' bird species (IUCN 2009). Furthermore, for another two endemics, the Masafuera Hawk *Buteo polyosoma exsul* and the Juan Fernandez Kestrel *Falco sparverius fernandensis*, which also show small sized populations (c.250 and 55 individuals respectively), no nests have been described. This study aimed to establish conservation guidelines for Juan Fernandez landbirds. To achieve this goal we describe the nesting ecology of endemic birds and determine overlap in nesting resource use between endemic and alien species.

Methods

Study area

The Juan Fernández Islands are of volcanic origin and situated in the south-east Pacific Ocean, off Chile. They stretch from 33°28′ to 33°47′ S and 78°47′ to 80°47′ W, and consist of the islands of Robinson Crusoe (formerly Másatierra), Alejandro Selkirk (formerly Másafuera), Santa Clara, and ten rock islets around them (morros) (Figure 1). The easternmost island, Robinson Crusoe (47.11 km^2, 915 m asl) is 587 km distant from the South American continent. The westernmost, Alejandro Selkirk (44.46 km^2, 1,320 m) is located another 167 km west of Robinson Crusoe. The smaller Santa Clara (2.23 km^2, 375 m) is only 1.5 km south-west of Robinson Crusoe.

The archipelago is characterised by a high number and proportion of endemic plants (Skottsberg 1956, Stuessy and Ono 1998) and animal species (Kuschel 1963, Castilla 1987). Amongst the 310 breeding bird species of Chile (Araya *et al.* 1995) only 15 are endemic, but five of them, and another three endemic subspecies, are limited to this archipelago (i.e., a total of eight endemic taxa). The entire archipelago, with exception of the settlement on Robinson Crusoe (c.800 inhabitants), has been a Chilean national park since 1935 and a UNESCO biosphere reserve since 1977. Therefore, it is not only of major importance for the endemic avifauna of Chile, but also of international interest as an Endemic Bird Area (EBA) (Wege and Long 1995, Stattersfield *et al.* 1998).

Juan Fernández Islands were once covered by continuous native vegetation composed of several endemic tree and shrub species (Skottsberg 1956, Stuessy and Ono 1998). Starting with human colonisation during the second half of the 1700s, anthropogenic activities have resulted in an extensive loss and degradation of the original native forests, resulting in 11 different habitat types which differ markedly in their structure, composition and extent within islands (Figure 1).

Nesting data

We measured three types of variables describing the nesting ecology of landbird species of Juan Fernández Islands:

1) Qualitative nest attributes: a set of variables describing overall habitat types, nest sites and nest attributes. Qualitative nest attributes were obtained from published information and data collected by ourselves, including data from Hahn 2006, Hahn *et al.* 2004, 2010; see below). Literature data were collected from Reed (1874), Schalow (1899), Lönnberg (1921), Brooke (1987) and Johow (2002).
2) Quantitative nest attributes: a set of variables quantifying the nest geometry (e.g. nest diameter) egg dimensions, and egg colour. This information was collected only for nests that were found during the laying stage (see below).
3) Quantitative nesting microhabitat attributes: a set of variables describing the micro-habitat attributes around the nests. This information was used for posterior comparative analysis between species (Table 1, and see the data analysis section, below).

We sampled nests of landbird species of Juan Fernandez Islands during the 1992, 1993, 1994, 1995, 2001, 2002 and 2009 breeding seasons (October to February), totalling 315 sampling days. Nests were sampled using a stratified design, which involved determining key habitat types for each landbird species (Hahn *et al.* 2005, 2006). Thus, in each habitat type, nests were searched for systematically and/or opportunistically along 300-m transects. We established 1–4 transects per habitat type, allocated proportionally to the area of habitat in each island. We used different cues for locating nests, including flushing an adult from the nest and watching parental behaviour (e.g. carrying nest material or food; Martin 1992, Rodewald 2004). During nest searches, we used appropriate camouflage clothing because most species showed shy and cryptic behaviour during the breeding season. In addition, birds were acoustically identified after learning the bird vocalisations from observation and taping with a DAT-Recorder (Sony, HD-S100). Only nests of Rock Doves, Juan Fernandez Tit-tyrants *Anairetes fernandezianus*, Juan Fernandez Firecrowns,

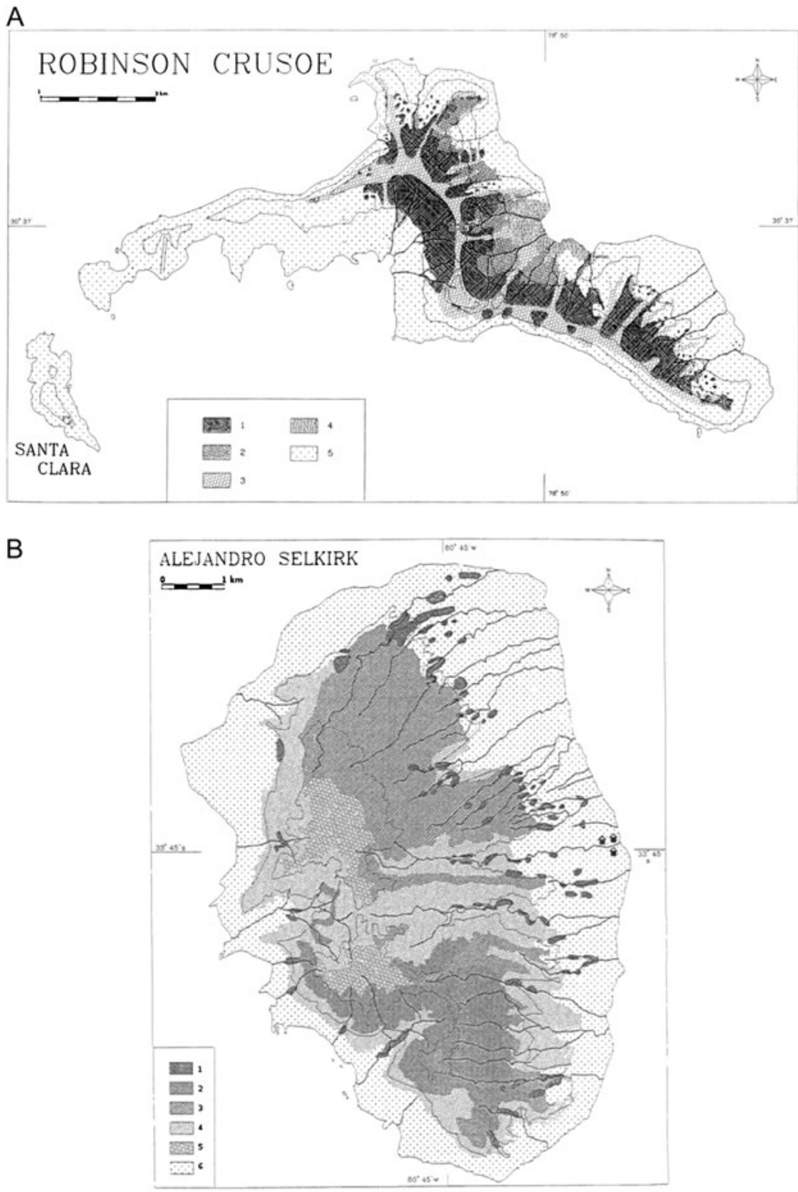

Figure 1. Habitat types on the Juan Fernández Islands and their distribution. (a) Habitat type codes for Robinson Crusoe (4711 ha) and Santa Clara (223 ha) are: 1 = Native montane forest (990 ha); 2 = Non-native lowland scrub (290 ha); 3 = Semi-native ridge scrub (599 ha); 4 = Non-native settlement area (109 ha); 5 = Non-native basal grassland (2946 ha). (b) Alejandro Selkirk (4446 ha): 1 = Native montane forest (194 ha); 2 = Native sub-alpine tree-ferns (445 ha); 3 = Non-native sub-alpine vegetation (792 ha); 4 = Native rock carpets (998 ha); 5 = Semi-native alpine ferns (187 ha); 6 = Non-native basal grassland (1830 ha).

Table 1. Description of quantitative nesting microhabitat attributes of Juan Fernández landbirds used in Principal Component Analysis (see text).

Variable	Description
Relief incline	Slope (degree) measured in 1 m distance upward and downward (m) using a clinometer.
Nest height	Height above the ground (m) measured vertically using a measuring tape.
Plant cover	Total plant cover (%) (including canopy and understorey vegetation) within a circular 25 m^2 plot surrounding the nest site.
Nest shelter	Vegetational cover (%) directly on the nest, measured at 1-m in height and at a radial distance of 1 m.
Biotic richness	Number of plant species (n) within a circular 25 m^2 plot surrounding the nest site.
Vegetation height	Average height (m) of upper tree storey within a circular 25 m^2 plot surrounding the nest site, estimated using a hypsometer.
Nest material diversity	Number of plant species (*n*) in the nest materials, measured using a magnifying glass.

Green-backed Firecrowns and Austral Thrushes were found during the egg-laying or incubation periods. Nest attributes could differ between nests found during the incubation and nestling periods (due to the loss of nests in sites exposed to predators). However, we did not detect any differences in microhabitat attributes at least between incubation and nestling nests of the Juan Fernandez Tit-tyrant (e.g. differences in nest height: 1.97 ± 0.52 m vs. 1.96 ± 1.71 m for nestling and incubation nests, respectively; differences in nest shelter: 6.21 ± 2.59% vs. 4.35 ± 4.05% for nestling and incubation nests, respectively) and the Austral Thrush (differences in nest height: 2.01 ± 1.22 m vs. 1.91 ± 1.71 m for nestling and incubation nests, respectively; differences in nest shelter: 5.94 ± 2.03% vs. 9.83 ± 3.98% for nestling and incubation nests, respectively).

Data analysis

Quantitative nesting microhabitat attributes per bird species were organised into a resource utilisation matrix (Table 1). We used principal component analysis (PCA) and cluster analysis (CA) in order to sort the nesting variables and landbird species, respectively. PCA permitted the reduction of several standardised nesting variables to a small set of uncorrelated factors. Factors with an eigenvalue greater than unity we considered as significant. We classified factor loadings as "strong to moderate" if the loading values were > 0.4 (e.g. Pizarro *et al.* 2010). In order to examine the sharing of nesting resources between alien and endemic species, as well as to compare the nesting ecology between both islands and between passerine and non-passerine species, multivariate cluster analysis (Q-cluster analysis) was applied to classify these bird species based on each significant factor obtained by PCA. We used a neutral modelling approach to test the null hypothesis that no difference exists between the actual assemblage and randomly reorganised assemblies based on resource utilisation (Caswell 1977, Joern and Lawlor 1980). For this analysis, we bootstrapped the original resource utilisation matrix 100 times in order to obtain new random PCA factors, over which we determined Euclidean distances of PCA scores between species. By means of this procedure we determined whether observed species similarities were larger than those expected by chance (Joern and Lawlor 1980). Finally, a Linear Discriminant Analysis (LDA) was performed to determine whether endemic and passerine bird species could be distinguished from non-endemics and non-passerine species, respectively, based on their quantitative nesting microhabitat attributes.

Results

Nesting attributes

We compiled a total of 119 nest records of 11 different landbird taxa on the Juan Fernandez Islands, 43 of them recorded by this study and the rest ($n = 76$) drawn from literature (Table 2, Table 3). Across all the data sources considered, the species with the highest number of recorded nests were the two firecrown species on Robinson Crusoe, the Juan Fernandez Firecrown and the Green-backed Firecrown (Table 4). These are very similar in shape, size, placement, and material, but the Juan Fernandez Firecrown can be distinguished by a) the greater height above ground (3.5 m vs. 2.5 m; $n = 2$ and $n = 2$, respectively) and b) the use of small white spider cocoons and webs by the Juan Fernandez Firecrown (Table 2, Table 3, Table 4). Both firecrown species have been detected in areas well-protected from wind and weather.

On Alejandro Selkirk, Masafuera Hawks and Masafuera Cinclodes *Cinclodes oustaleti baeckstroemii* were found in all geographical areas and altitudes (Table 2). The breeding range of Masafuera Rayaditos, however, was limited to one fifth of the island, namely the northern and southern upland of sub-alpine and alpine zones. On Robinson Crusoe several species, including Juan Fernandez Firecrowns, Green-backed Firecrowns, Austral Thrushes, and Juan Fernandez Tit-tyrants, mainly inhabit forested habitats and they may nest from sea level up to 900 m.

The height of Juan Fernandez Tit-tyrant nests showed a great deal of variation in height and were located mostly on the endemic laurel trees *Myrceugenia fernandeziana* and attached to peripheral twigs (Table 4). As these twigs are more resistant to the wind than those used for firecrown nests, the Juan Fernandez Tit-tyrant is able to breed also in forests exposed to the wind, where no firecrown nests were found. Besides their placement, Juan Fernandez Tit-tyrant nests were also distinguishable from firecrown nests by their slightly larger dimensions (diameter, depth) and frequent integration of grass in the nest materials (Table 2, Table 3).

The Austral Thrush shows the largest nesting distribution range on the islands (Table 2). On Robinson Crusoe, Austral Thrushes build nests mainly in native forests and typically place them in a fork between the stem and a branch (Table 4). On Alejandro Selkirk Island a thrush nest was found at 800 m, hidden inside a solitary patch of the fern *Lophosoria quadripinnata* (c.0.5 m height) surrounded by grassland (Table 2). Masafuera Rayaditos and Masafuera Cinclodes are the only species nesting in small natural cavities of rock walls and tower rocks, making use of lava bubbles or niches created by erosion and micro-geological shift in-between two rock layers (Table 2). Nest holes of both were placed well above the ground in steep natural walls, hardly in reach of any non-flying predator. However, cavities used by cinclodes had larger dimensions than those used by rayaditos (Table 3).

Nest sites of Masafuera Hawks were detected in half-open positions on rock walls and in the *Pinus radiata* tree of settled areas (Table 2). These nests were constructed of twigs and had been used for several years. The introduced Rock Dove frequented inaccessible rock niches distant from Robinson Crusoe's settlement (Table 2). Although House Sparrow nests have been previously observed on Alejandro Selkirk, we did not detect the presence of breeding House Sparrows in this island, while on Robinson Crusoe, sparrow nests were placed in exotic *Araucaria* trees and in crevices of nearby house roofs (Table 2). A Juan Fernandez Kestrel nest was observed on a cliff at 300 m, whereas a Short-eared Owl *Asio flammeus suinda* nest was observed on a rock wall (Table 2).

Nesting microhabitat attributes

Two significant factors (i.e. eigenvalue > 1) were extracted by PCA, which explain 75.6% of the total variation in the standardised nesting variables (Table 5). According to its load values, the first factor (PC1), which accounts for 52.3% of the total variance, had a "strong to moderate" loading on relief inclination, plant cover and nest material diversity (Table 5). The second factor (PC2) accounts for 23.3% of the total variance and had a "strong to moderate" loading on nest height, nest shelter and vegetation height (Table 5).

Table 2. Descriptive nesting attributes of resident landbird species of the Juan Fernández Islands, Chile. Data come from our findings and published information. Sources used were: a) Brooke (1987), b) Lönnberg (1921), c) Johow (2002), d) Schalow (1899), e) Reed (1874).

Nesting attribute	Species										
	Juan Fernandez Kestrel	Short-eared Owl	Rock Dove	House Sparrow	Juan Fernandez Tit-tyrant	Juan Fernandez Firecrown	Green-backed Firecrown	Austral Thrush	Masafuera Hawk	Masafuera Rayadito	Masafuera Cinclodes
Total Number of nests	1	2	2	1	9	28	46	17	3	4	7
Number of nests previously reported	0	1(e)	1(d)	0	0	26 (23c; 3b)	44 (43c; 1a)	3 (2d; 1a)	0	0	1 (a)
Breeding / nesting season	Oct to Dec	Oct to Dec	Nov to Feb	Nov to Jan	early Nov to late Jan	Sep to mid Nov	Oct to mid Feb	Oct to Jan	Nov to Feb	late Nov to early Feb	mid Nov to early Feb
Altitude (m.asl)	380	350	10–400	11	185–400	120–660	60–550	220–800	23–110	1206–1245	61–1259
Habitat	Open habitats; sometimes perching on trees	Open habitats; sometimes perching on trees	Open habitats; foraging between herbs / grasses	Mosaic of open / rich-structured habitat types	Diverse structured vegetation stands as laurel forests	Diverse structured vegetation as forests and plantations	Diverse structured vegetation as forests, shrubs, plantations	Diverse structured vegetation as forests, shrubs, plantations	Open habitats; perching on top of plants	sub-alpine tree-fern - and alpine fern stands	Moist / shady habitats with few / low vegetation

Table 2. Continued.

Nesting attribute	Species										
	Juan Fernandez Kestrel	Short-eared Owl	Rock Dove	House Sparrow	Juan Fernandez Tit-tyrant	Juan Fernandez Firecrown	Green-backed Firecrown	Austral Thrush	Masafuera Hawk	Masafuera Rayadito	Masafuera Cinclodes
General type of nest	Open breeder: seen high up in cliff niche near shore	Open breeder: nest in rock wall niche	Open breeder: poor nest in niche of steep rock wall / cliff	Crevice breeder: closed nest attached to trunk and branches	Open breeder: cup-shaped nest periphery attached to laurel twig	Open breeder: cup-shaped nest attached to thin (laurel) twig tip	Open breeder: cup-shaped nests attached to thin (laurel) twig tip	Open breeder: large open nest in trunk fork (RC) or ferns (AS)	Open breeder: huge perennial eyrie in tree canopy or cliff niche	Hole-breeder: small natural hole in rock walls / tower rocks	Hole-breeder: natural hole in steep rock wall or slope / ridge
Hosting plant	Nest directly on bare rocky ground	Nest directly on bare ground	Nest directly on bare ground of eroded basaltic lava	In mature *Araucaria araucana*	100% *Myrceugenia fernandeziana*	78% *Myrceugenia*; 11% *Cupressus*; 11% *Blechnum*	67% *Myrceugenia*; 33% *Pinus, Acacia, Maitenus, Cupressus, Rubus, Aristotelia*	6% *Cupressus*, 6% *Rubus* 88% *Myrceugenia and Lophosoria*	*Pinus radiata* (*Myrceugenia*: pers. com. Schiller 2002) or at rock walls / cliffs	Basaltic rocks: hole origin from lava bubbles / micro-geological shift	Basaltic rocks: hole origin from lava bubbles / micro-geological shift
Materials of nest	no nest materials	no nest materials	Constructed with few culms laid above each other	Grasses and herb culms	50–80% grass, 0–15% moss, 5–45% *Aristotelia*, 0-5% spid. webs	*Lophosoria* trichomes, mosses (*Weymouthia*), spider cocoons/ webs	Fern (*Lophosoria*) trichomes, mosses (*Weymouthia*), fibril	Grasses; leaves: *Myrceug., Aristotelia, Cupressus*; loam	Thin twigs 2–5 mm thick, collected from shrubs and sea-shore	Hole mainly rock framed; 10–70% mosses/ lichens	Hole mainly rock framed; 10–70% mosses /lichens

Table 3. Quantitative nest attributes of resident landbird species of the Juan Fernández Islands, Chile. Symbols: - = no available data; (*n*) = number of nests sampled

Nesting attribute	Species							
	Rock Dove	Juan Fernandez Tit-tyrant	Juan Fernandez Firecrown	Green-backed Firecrown	Austral Thrush	Masafuera Hawk	Masafuera Rayadito	Masafuera Cinclodes
Exterior nest diameter (min-max) cm	-	7.4 (6.9-7.9) (*n*=5)	6.5 (5.5-7.5) (*n*=2)	5.8 (5.5-6.0) (*n*=2)	19.4 (14.0-24.0) (*n*=4)	90 (50-180) (*n*=2)	3 x 5.5 (*n*=4)	5.5 x 20 (*n*=6)
Interior nest diameter (min-max) cm	-	3.8 (3.2-4.9) (*n*=5)	3.0 (2.3-3.2) (*n*=2)	2.8 (2.4-3.0) (*n*=2)	7.3 (6.0-8.5) (*n*=4)	-	-	-
Nest depth (min-max) cm	-	5.0 (3.8-5.6) (*n*=5)	2.8 (2.0-3.0) (*n*=2)	2.3 (2.0-2.5) (*n*=2)	6.5 (4.5–7.5 (*n*=4)	-	-	-
Colour of eggs (%)	-	100% glossy white	100% white	100% white	70% turq. 30% brown	-	-	-
Egg length; average (min-max) mm	39.0 (39.0-39.0) (*n*=2)	17.4 (17.1-17.8) (*n*=5)	18.0 (18.0-18.0) (*n*=2)	14.1 (13.8-14.4) (*n*=2)	27.4 (27.0-27.7) (*n*=2)	-	-	-
Egg breadth; average (min-max) mm	27.3 (27.5-27.0) (*n*=2)	13.1 (12.8-13.2) (*n*=5)	11.0 (11.0-11.0) (*n*=2)	9.7 (9.3-10.1) (*n*=2)	21.15 (21.3-21.0) (*n*=2)	-	-	-

Table 4. Mean values of seven quantitative nesting microhabitat attributes of 11 landbird species of the Juan Fernández Islands. Standard errors are presented only for samples where $n > 3$.

Species	Relief inclination	Nest height	Plant cover	Nest shelter	Biotic richness	Vegetation height	Nest material diversity	*n*
Juan Fernandez Kestrel	45.0	13.5	6.2	12.9	2.0	1.40	1	1
Short-eared Owl	45.6	16.1	7.0	12.8	2.0	1.30	1	1
Rock Dove	49.5	13.6	5.9	23.9	1.0	1.10	1	1
House Sparrow	5.2	2.1	24.3	54.2	3.0	17.48	9	1
Juan Fernandez Tit-tyrant	12.2 ± 7.6	1.97 ± 0.8	45.6 ± 32.5	5.8 ± 2.3	2.1 ± 1.1	2.8 ± 0.8	4.3 ± 3.3	9
Juan Fernandez Firecrown	12.1	4.1	51.2	6.8	5	5.76	4	2
Green-backed Firecrown	10.1	2.0	106.7	6.5	9	5.79	4	1
Austral Thrush	11.5 ± 3.6	2.0 ± 1.1	84.9 ± 31.4	6.5 ± 2.8	5.2 ± 2.2	6.03 ± 2.8	3.9 ± 1.5	14
Masafuera Hawk	23.7	7.3	6.0	11.3	5	2.58	4	3
Masafuera Rayadito	84.2 ± 52.1	3.7 ± 1.6	27.3 ± 13.1	90.3 ± 10.8	1.1 ± 1.5	1.0 ± 0.9	1.5 ± 1.8	4
Masafuera Cinclodes	47.6 ± 30.8	2.0 ± 1.3	13.1 ± 9.7	87.7 ± 11.9	1.2 ± 0.6	0.9 ± 0.7	1.6 ± 1.1	6

Based on the scores of each PCA, two different dendrograms were built (Fig. 2). For the first factor (PC1), the 11 land bird species were divided into three distinguished multi-specific groups by multivariate cluster analysis (Figure 2). The first group includes the endemic Juan Fernandez Tit-tyrant, Juan Fernandez Firecrown and Masafuera Hawk. The nests of the endemic Juan Fernandez Tit-tyrant and Juan Fernandez Firecrown are relatively similar in their relief incline (relatively flat nest sites) and are located in sites with high plant cover (Table 4). The latter two species had a similar material diversity to the nests of the Masafuera Hawk (medium diversity in nest materials) (Figure 2, Table 4). The second group includes three alien species, the House Sparrow, the Green-backed Firecrown and the Austral Thrush, whose nests are built in sites with a small slope (Figure 2, Table 4). The third group includes five species of which only one, the Rock Dove, is not native. All species in the third group nest in sites with a relatively large relief incline and low plant cover, and their nests are made with a reduced diversity of materials (Figure 2, Table 4). As part of this group, the Masafuera Rayadito is the species using the steepest nesting sites of all landbird species (Table 4).

Table 5. Rotated component matrix for the significant factors (PC), including load values for each nesting variable and variance explained (%) by each component. Bold values indicate factors having "strong to moderate" loading.

Variable	PC1 (52.3%)	PC2 (23.3%)
Relief incline	**−0.46**	0.13
Nest height	−0.33	**−0.40**
Plant cover	**0.40**	−0.17
Nest shelter	−0.24	**0.61**
Biotic richness	0.38	−0.37
Vegetation height	0.33	**0.45**
Nest material diversity	**0.46**	0.29

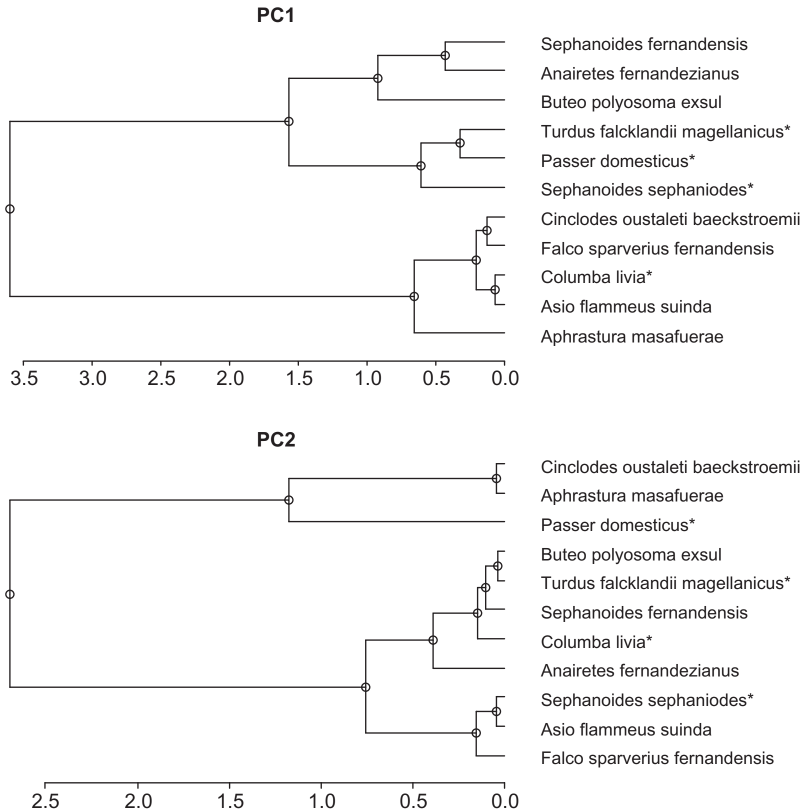

Figure 2. Dendrograms derived from two significant Principal Component factors (Table 3) ordering landbird species of the Juan Fernández Islands according to seven different quantitative nesting attributes presented in Tables 2 and 4. Vertical dashed lines represent the threshold distance (similarity = 69%) over which the similarities between species in nest attributes are not different than that expected by chance. Species with an asterisk denote alien landbird species.

For the second factor (PC2), the 11 land bird species were divided into three multi-specific groups and one monospecific group by multivariate cluster analysis (Figure 2). The first multi-specific group includes the endemics Masafuera Rayaditos and Masafuera Cinclodes which nest at a low height and use sites with low vegetation and poor cover (Figure 2, Table 4). The second multi-specific group includes three endemics and two alien species: Masafuera Hawk, Juan Fernandez Tit-tyrant, Juan Fernandez Firecrown, Austral Thrush, and Rock Dove, whose nest sites mostly have poor shelter (Figure 2, Table 4). Of these species, the nests of Juan Fernandez Tit-tyrants, Juan Fernandez Firecrowns and Austral Thrushes are located at a low height above the ground (Table 4). According to the third multi-specific group, Juan Fernandez Kestrels, Short-eared Owls, and Green-backed Firecrowns tend to nest in poorly sheltered sites with low vegetation (Figure 2, Table 4). Finally, the House Sparrow was the species whose nest sites had the greatest vegetation height (Figure 2, Table 4).

LDA resulted in a function that correctly classified 100% of landbird species (n = 11) as passerine and non-passerine species (Table 6). Quantitative nesting microhabitat attributes that presented the highest loadings within this discriminant function were nest height and nest shelter (for both variables $r > 0.6$, $n = 11$, Fig. 3). Nests of passerine species were located lower than

Table 6. Results of two Linear Discriminant Analyses classifying landbird species of Juan Fernández Islands based on quantitative nesting microhabitat attributes. Correlation coefficients with discriminant function scores are shown for each microhabitat attribute.

Variable	Passerine vs. non-passerine	Endemic vs. non-endemics
Relief incline	−0.06	−0.32
Nest height	0.70*	0.15
Plant cover	− 0.21	0.37
Nest shelter	− 0.60*	− 0.31
Biotic richness	0.39	0.3
Vegetation height	− 0.33	0.45*
Nest material diversity	− 0.30	0.27
Correctly classified (%)	100.0	90.9
Eigenvalue	7.61	5.95
P-value	0.018	0.032

*Indicates the largest absolute correlations between a microhabitat attribute and the discriminant function.

nests of non passerines, whereas nest shelter was larger in passerine than non passerine species (Fig. 3). LDA also resulted in a function that correctly classified 90.9% of the landbird species as endemic and non-endemics ($n = 11$) (Table 6). Vegetation height was the quantitative nesting microhabitat attribute presenting the highest loadings within this discriminant function ($r = 0.45$, $n = 11$).

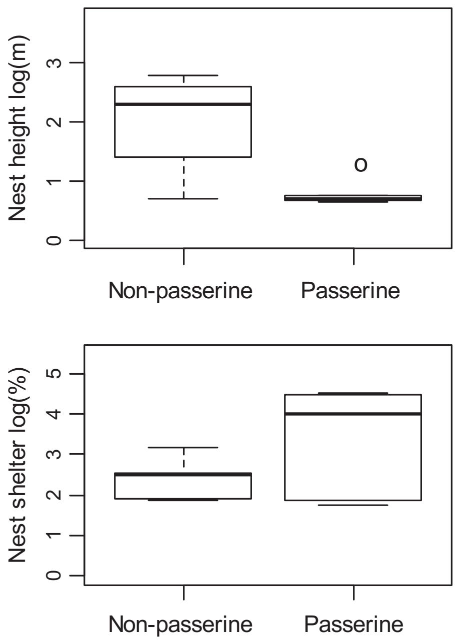

Figure 3. Box-and-whisker plots showing differences in two nesting microhabitat attributes (nest height and nest shelter) which were used in a LDA for classifying between passerine and non-passerine landbird species of the Juan Fernández Islands (see text). These plots show the median (black line) and the 25% and 75% quartiles (box) of the nesting microhabitat attributes whereas whiskers extend up to 1.5 times the inter-quartile range of the box.

Discussion

Understanding the particular nesting ecology of each endemic species on the Juan Fernández Archipelago represents the first practical step in the conservation of these species, since this background information is needed to identify suitable micro-habitats and to establish efficient management programmes. From our results, and previous studies in the Juan Fernández Islands, is possible to deduce that landbirds exhibit a wide range of nesting habitat preferences on the different islands, covering different vegetation types, altitudes and ecosystems. The high degree of differentiation in the nest site preferences of native birds could correspond to low levels of natural inter-specific competition on islands (e.g. Blondel 2000).

Cluster analysis revealed that the Juan Fernandez bird assemblage is functionally structured in clusters of species (usually called "guilds") using nesting resources in a similar way (i.e. they are significantly different from random expectations). Three nesting variables, relief incline, plant cover, and nest material diversity, can be interpreted as representing the same niche axis (PC1 in our analyses). Through this axis, species use different combinations of these three nesting variables. Thus, for example, the endemics Juan Fernandez Tit-tyrant and Juan Fernandez Firecrown build nests in native forests located on relatively flat terrain, a habitat that has been widely degraded and destroyed by human activities. Moreover, the Masafuera Rayadito shows only low nesting diversity and uses steep hillside sites. However, a nest predator, such as the Masafuera Hawk, could be an important natural factor contributing to the distribution and use of micro-habitat of Juan Fernandez landbirds (Hahn *et al.* 2005, 2006).

Cluster analysis allowed us to identify suitable micro-habitat conditions for endemic species. We were also able to use it to determine the extent of competition among alien landbirds for nest resources. This analysis suggests that current competition levels between alien and endemic species apparently do not represent an important factor affecting resource use by endemic birds, with the exception of the Austral Thrush whose effect is discussed below. This conclusion is based on the following reasons: 1) alien species tend to use different nesting resources to endemic birds; 2) alien species tend to use the same nesting resources as endemic, but not taxonomically related, species.

An important problem for the conservation of the endemic Juan Fernandez Firecrown has been to determine to what extent this species competes by recourses with the introduced Green-backed Firecrown. In this study we have shown that the Green-backed Firecrown has different nesting preferences to the Juan Fernandez Firecrown, preferring sites with denser vegetation and higher plant species diversity and located at a lower height from the ground. Since mainland Green-backed Firecrowns fit into the range of island nest heights of this species, it is probable that it has not undergone relevant filtering effects of selective factors on the islands, thus maintaining its preference for nest sites. These findings suggest that the Green-backed Firecrown would not constrain the nesting habitat use of the Juan Fernandez Firecrown, considering that the former species is more aggressive and agile than the latter. However, our results are not conclusive in explaining whether the actual choice of nest sites of the Juan Fernandez Firecrown may be the result of competitive-displacement by the Green-backed Firecrown in the early stages of its invasion of the islands. We might only reveal the pattern of nest site selection of the endemic Juan Fernandez Firecrown through experimental studies.

The widely common House Sparrow selected nest sites with the greatest vegetation height, nesting preferably on exotic trees, such as *Araucaria* spp., that grow in areas where humans have settled. Therefore, House Sparrows might neither be directly competing with endemic passerines for nest sites nor contributing to increases in nest density in the same habitats used by endemic birds. However, low competition levels for nest sites between House Sparrows and native species may be an artefact of the low availability of food on the islands, resulting in small populations of sparrows spatially constrained to areas of human settlement.

Although endemic landbirds might not be negatively affected by alien landbirds via competition (see above), the ecological effects of Austral Thrushes in the bird assemblage of Juan Fernandez could go further than competition by nest sites. As our results suggest, thrushes use similar habitat and nesting resources to the smaller endemics, Juan Fernandez Firecrowns and Juan Fernandez Tit-tyrants on Robinson Crusoe Island (i.e. sites with poor shelter and at a low height above the ground). The fact that these species overlap in their habitat utilisation implies that they could interact in a variety of ways, not only through competition for nesting recourses. We have observed nest predation events of an adult Austral Thrush on a Juan Fernandez Firecrown nest and we have further confirmed this observation with information from local people. Given the size difference between the species, it is probable that similar predation events could affect nests of Juan Fernandez Tit-tyrants. Similarly, the mainland Austral Thrush is a predator of smaller passerine species (pers. obs). Given that such predation strategies of Austral Thrushes are part of their general behaviour, it may be necessary to reduce their potential predation risk on Juan Fernandez Firecrown nests. However, before applying such management activities it is necessary to assess the magnitude of and the ecological factors responsible for the predatory responses of this species.

The most threatened species on the islands is Masafuera Rayadito with a total population of about 140 individuals. Although Rayaditos occupy well-protected nests in small natural holes in steep rock walls, it is likely that predation by rats, and probably hawks, on broods is important (Hahn *et al.* 2004). The Masafuera Cinclodes, which also selects well-protected nest holes for breeding, is not currently classified as endangered due to its population size (c.1,500 birds). The endemic species most exposed to nest predation are probably Juan Fernandez Firecrowns and Juan Fernandez Tit-tyrants. However, the latter is presently not highly threatened (c.2,500 individuals), but the Juan Fernandez Firecrown is classified as 'Critically Endangered' (IUCN 2009), with an estimated population size of c.1,100 individuals (Hahn *et al.* 2006, 2009). Although this estimate is much higher than that of the Masafuera Rayadito, the Juan Fernandez Firecrown population is additionally threatened by having an unequal sex ratio (Roy *et al.* 1999, pers. obs.) and by having nest sites often reachable by rats and cats. As hummingbirds are highly immobile during nocturnal torpor, they are especially vulnerable to predation by small omnivorous mammals including rats and mice, which are both present on the islands in high numbers. In fact, rat predation on the Juan Fernandez Firecrown has already been reported Busse (1971).

In order to confirm our findings and to provide a sufficient background for conservation management, more systematic nest data need to be collected for all endemic landbirds. Knowledge of reproductive success will be essential to uncover the true threats and to identify the reasons for low population sizes. Experiments with artificial nests and artificial eggs may help to estimate the impact of predation by introduced mammals on bird reproduction. Eradication programmes have to include all introduced mammal species (Bourne *et al.* 1992, Hahn and Römer 2002), starting with cats in the Robinson Crusoe settlement and goats on Alejandro Selkirk. However, conservation priority should be given to programmes to establish mammal-safe nest boxes for cavity nesters, habitat restoration by reducing herbivore impacts (eradication of goats, rabbits, cows) and controlling alien seed dispersal, such as by thrushes.

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