

# Mating success of the endemic Des Murs' Wiretail (*Sylviorthorhynchus desmursii*, Furnariidae) in fragmented Chilean rainforests

IVÁN A. DÍAZ,<sup>1,3\*</sup> JUAN J. ARMESTO<sup>1</sup> AND MARY F. WILLSON<sup>2</sup>

<sup>1</sup>Center for Advanced Studies in Ecology and Biodiversity (CASEB), Catholic University of Chile, Casilla 114-D, Santiago, Chile and Fundación 'Senda Darwin', Santiago, Chile (Email: diazi@ufl.edu); <sup>2</sup>5230 Terrace Place, Juneau, Alaska and <sup>3</sup>Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, Florida, USA

**Abstract:** We studied the effects of fragment size, vegetation structure and presence of habitat corridors on the reproductive success of the Des Murs' Wiretail (*Sylviorthorhynchus desmursii* Des Murs, Furnariidae), a small (10 g) understory bird, endemic to South American forests. In a rural landscape of Chiloé Island, southern Chile (42°S; 70°W), we determined the mating and nesting success of wiretails in 28 territories distributed in seven small (1–20 ha) and two large (>300 ha) forest fragments during the 1997–1998 breeding season. Wiretails inhabited dense bamboo thickets in the understory of forest patches, dense shrublands covering old fields, and dense early successional forest vegetation. Wiretails avoided open pastures. Reproductive success depended solely on the probability of finding mates, and the main factor affecting mating success was the presence of corridors. Mated individuals occupied 72% of the territories in forest patches <20 ha connected by corridors, 73% of the territories in large (>300 ha) fragments, but only 20% of territories in isolated fragments surrounded by pastures. Because of the rapid expansion of pastures in southern Chile, the conservation of wiretails and other understory birds will depend on the maintenance of travel corridors with dense understory vegetation between forest fragments.

**Key words:** bird conservation, bird habitat use, Chilean southern temperate rainforest, habitat corridor, *Sylviorthorhynchus desmursii*, understory bird.

## INTRODUCTION

Land cover change due to human activities is one of the major threats to forest biodiversity (Meffe & Carroll 1997). In human-dominated landscapes, forest patch size, isolation, edge effects and habitat degradation may increase the extinction rates of forest birds because of reduced population sizes, lower chances of dispersal and successful mating, loss of resources for successful breeding, increased predation risk along edges and higher susceptibility to environmental or population fluctuations (Wilcove 1985, 1986; Lovejoy *et al.* 1986; Lande 1988; Simberloff 1988; Saunders *et al.* 1991; Wenny *et al.* 1993; Meffe & Carroll 1997; Burke & Nol 1998; Dale 2001).

Habitat corridors inter-connecting remnant forest patches can lessen the negative effects of habitat fragmentation, particularly the effects of fragment size and isolation. Corridors are defined as strips of suitable habitat that serve as passageways between fragments

(Rosenberg *et al.* 1997), thus increasing the probability of dispersal, finding suitable territories and mating (Opdam 1991; Taylor *et al.* 1993; Rosenberg *et al.* 1997; Beier & Noss 1998). Although theoretical analyses support the importance of corridors for reducing the negative effects of habitat isolation (Fahrig & Merriam 1985; Fahrig & Paloheimo 1988; Andrén 1994), empirical evidence remains controversial (Simberloff *et al.* 1992; Rosenberg *et al.* 1997; Beier & Noss 1998; Haddad 1999a,b; Mech & Hallett 2001). In addition, associated effects of fragmentation other than edge effect or isolation, such as reduction in habitat quality have been little explored (see Burke & Nol 1998).

South American temperate rainforests (37–55°S) are recognized as a hotspot of endemic species and represent a globally threatened ecosystem (Armesto *et al.* 1998; Olson & Dinerstein 1998; Myers *et al.* 2000). In the past 100 years, forest cover has decreased dramatically due to extensive logging, burning and conversion to pastures, arable fields and commercial plantations of exotic trees (Lara *et al.* 1996; Bustamante & Castor 1998). Now, the countryside consists of a mosaic of forest fragments of

\*Corresponding author.

Accepted for publication June 2005.

different sizes in an agricultural matrix dominated by pastures.

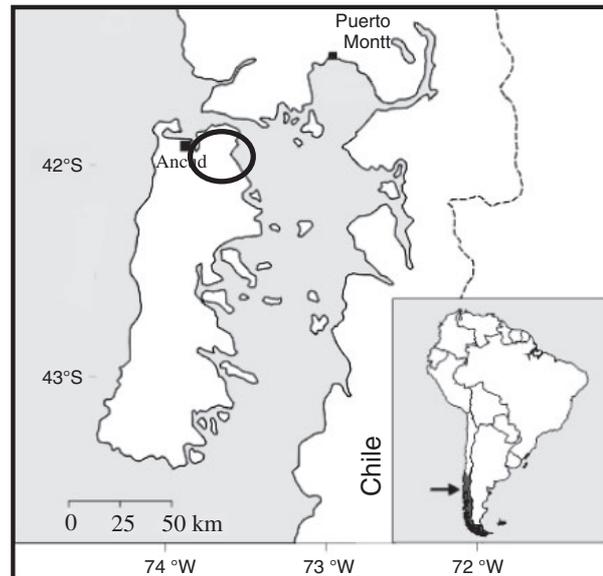
Forests of southern Chile are inhabited by five endemic understory bird species characterized by their limited flying capacity, reluctance to cross open areas (Sieving *et al.* 1996, 2000), and reduced abundance in small forest fragments (Willson *et al.* 1994). One of these birds, the Des Murs' Wiretail (*Sylviothorhynchus desmursii*; Furnariidae; hereafter wiretail), is a small (10 g), territorial, insectivorous bird endemic to temperate rainforests of South America (Goodall *et al.* 1946; Vuilleumier 1985; Fjeldsá & Krabbe 1990). Reproductive success of this species may be affected by isolation and degradation of forest fragments, but no current studies have examined these effects. Willson *et al.* (2001) compared predation on artificial wiretail nests between forest interior and edges, finding low predation rates (<10% of all nests) along forest edges.

In this article, we documented the habitat use of wiretails in a rural landscape of Chiloé Island, southern Chile, to define what elements of the landscape could function as corridors connecting forest fragments. We also analysed the effects of forest patch size and the presence or absence of corridors on mating and nesting success of wiretails in this landscape. We tested two predictions about the reproduction of wiretails in fragmented forest habitats of northern Chiloé Island: (i) reproductive success of wiretails is greater in larger fragments; and (ii) for fragments of similar size, reproductive success increases with fragment connectivity (by habitat corridors). In addition, we explored the effect of habitat quality, assessed by density of understory vegetation, on the reproductive success of wiretails.

## METHODS

### Study site

The study was conducted about 15 km north-east of Ancud, northern Chiloé Island, in the rural landscape surrounding Senda Darwin Biological Station (SDBS) (Fig. 1). This landscape is composed of a mosaic of small and medium sized (<15 ha) remnant fragments of forest immersed in a matrix of pastures and shrublands (Willson *et al.* 1994; Willson & Armesto 1996). The climate is wet-temperate, with a strong oceanic influence. Average annual rainfall at SDBS (4-year record) is 1906 mm with 70% of the precipitation occurring from April to September. Mean annual temperature is 11°C, with maximum monthly temperatures (January) of 24°C and minimum monthly temperatures (June–July) of 2.5°C.



**Fig. 1.** Location of the study area in the vicinity of Senda Darwin Biological Station (circle), Chiloé Island, southern Chile. Inset = geographical range of temperate rainforests in southern South America (shaded).

Forests in the area belong to a mosaic of Valdivian and North-Patagonian rainforest types (Veblen *et al.* 1996), with a 20- to 25-m high canopy dominated by mostly broad-leaved evergreen tree species, such as *Amomyrtus luma* (Myrtaceae), *Amomyrtus meli* (Myrtaceae), *Drimys winteri* (Winteraceae), *Podocarpus nubigena* (Podocarpaceae) and *Laureliopsis philippiana* (Monimiaceae). Occasional emergent species include *Nothofagus nitida* (Nothofagaceae) and *Eucryphia cordifolia* (Eucryphiaceae), especially in the less disturbed fragments. Dense thickets of the native bamboo *Chusquea quila* (Gramineae), especially in tree-fall gaps, and woody seedlings of Myrtaceae and Podocarpaceae trees compose the understory (Armesto & Figueroa 1987).

Since the early 1900s, forests have been converted to pastures, through both logging and burning. Deforested areas that were abandoned (because of low productivity due to poor drainage) are now covered by dense shrublands composed mainly of *Baccharis patagonica* (Asteraceae), *Gaultheria mucronata* (Ericaceae), *Berberis darwinii* and *Berberis buxifolia* (Berberidaceae). On higher and drier ground, second-growth areas are covered by a 6- to 10-m tall canopy composed mainly of *A. meli*, *A. luma*, *Gevuina avelana* (Proteaceae), *D. winteri* and *Luma apiculata* (Myrtaceae), occasionally mixed with *Berberis* spp. and *Rhaphithamnus spinosus* (Verbenaceae) along forest edges. Narrow strips of forest often remain along riparian corridors and fencerows. Cleared areas around forest fragments and houses are predominantly pastures for cattle.

### Forest fragments studied

We selected for study, two 'large' forest fragments >300 ha in size and seven small forest fragments between 1 and 20 ha, all within a 15 km radius of SDBS. We also conducted observations of corridor vegetation use by wiretails in two additional small forest fragments located near SDBS.

### Bird surveys

Observations of birds were conducted daily from 7.00 hours to 18.00 hours, from mid-October 1997 to mid-February 1998, during the austral spring and summer. Data were recorded through one complete reproductive season, from the establishment of wiretail territories and selection of mates to the time when fledglings left the parental nests. Observers wore cryptic clothing to minimize disturbance to bird activity. Each site was surveyed regardless of weather, as the birds were active most of the time. Overall, we accumulated over 750 h of observations.

### Assessment of territory sizes

This species is a territorial, year-round resident that normally lives in pairs, with both members actively defending their territory. Wiretails responded to song playbacks by aggressively approaching the speakers and emitting their own territorial defence songs. In each forest fragment, we first identified territories by playing the territorial call using song playbacks (Marion *et al.* 1981; Sieving *et al.* 1996). The vocal responses of wiretails were recorded on a map. To define territorial boundaries, each wiretail was induced to move in different directions, progressively away from the initial location, until the bird ceased to respond. At this point, we assumed that the speaker was outside the territory.

For each target bird or pair, assays were repeated on a minimum of 12 days over a period of three months. Territorial boundaries generally corresponded to forest edges with open fields, or to a border with a conspecific territory, where we observed frequent fights among birds. Those fights represented additional evidence for territorial boundaries. Additionally, we conducted passive observations of target wiretails to determine their movements and habitat usage, without playback stimulation.

The area of each forest fragment in which we measured territories was obtained from direct measurements on aerial photos (IGM, Chile; scale 1 : 20 000). All wiretail territories present in small forest fragments were identified and measured, but in large fragments we mapped territories in a subsample of about 5 ha

within each fragment. We used the Minimum Convex Polygon (MCP) method to estimate the size of wiretail territories, by mapping the locations where each wiretail was observed, and connecting the points on the map. The MCP method has been used for radiotelemetry studies of animals with large home ranges, and is frequently subjected to corrections such as discounting 5% of the calculated area (Aebischer *et al.* 1993; Powell 2000). Several limitations have been recognized in this method, such as the lack of information on preferred habitat and the inclusion of unused areas as part of the territory (Powell 2000). However, we were able to detect territory owners, their neighbours, and the unused areas because home ranges of wiretails are small. Consequently, we considered it unnecessary to make corrections to our estimates of territory size.

### Habitat characterization

Wiretails restricted their activity to the forest understorey layer (<3 m from the ground). They did not use the canopy layer or open areas such as pastures or agricultural fields (Goodall *et al.* 1946; Sieving *et al.* 1996, 2000). To determine the foliage density and floristic composition of vegetation in habitats used by wiretails, we laid down a 50-m-long transect within each mapped territory. For every metre along the transect line, we visually counted the number of branches present at 1-m intervals along a 3-m vertical pole, identifying each plant species. When we had doubts, we collected samples for identification in the laboratory of SDBS. Results of foliage density were expressed as the number of contacts (NC) by vegetation intercepting the pole for each vertical metre up to 3 m. We also made visual estimates of the percent canopy cover (>15 m) directly above each sampling point (0%, <25%, 25–50%, 50–75% and >75% cover).

We considered the NC as an indirect measure of food availability for wiretails, because studies conducted in the same area suggested a positive relationship between the number of branches and the abundance of foliage arthropods, irrespective of plant species composition (Reid *et al.* 2004). Therefore, NC weighted by territory size can be an indirect measure of the quality of each territory.

### Barriers to movement and travel corridors

To identify potential travel corridors and barriers for wiretail dispersal, we used song playbacks to induce eight wiretail pairs to move along narrow strips of tree and shrub vegetation surrounded by pastures. In three cases the strips of vegetation followed fencerows, and one strip was along a small ravine. One pair was stim-

ulated to enter a shrubland along a forest edge, and two pairs were stimulated to cross small distances of open pastures or roads. Finally, one pair was stimulated to move from sites with a dense understorey to contiguous sites where the understorey was cleared, as the result of forest management practices. All of these observations were conducted during three non-consecutive mornings.

### Fragment connectivity

After identifying potential travel corridors for wiretails, we defined whether the forest fragments studied were isolated or connected to other fragments by one or more travel corridors. For this analysis, forest fragments connected by a travel corridor to at least one other fragment were given a connectivity value of 1, while forest fragments without travel corridors and separated by at least 50 m of open pastures from the nearest fragment were given a connectivity value of 0.

### Mating and nesting success

Successful reproduction of birds was determined by the probability of finding a mate (mating success)  $\times$  the probability of a pair nesting and leaving descendants (nesting success). We calculated these two components separately. For a given habitat fragment, the probability of mating success was estimated as:  $P(\text{mating}) = \text{Number of territories occupied by pairs} / \text{Total number of territories (pairs + unmated adults)}$  in that fragment. Likewise, the probability of a pair leaving descendants for a given habitat fragment was estimated as:  $P(\text{nesting}) = \text{Number of pairs with fledglings} / \text{Total number of pairs in the fragment}$ .

To determine the proportion of territories occupied either by single adults or by nesting pairs, we periodically monitored all the territories in the forest fragments studied during the entire breeding season. Nesting territories were recognizable because both members of the pair moved and foraged together and responded together to song playbacks. In contrast, in territories defended by single individuals, aggressive responses to playbacks were less intense and birds were always observed alone. Because this species is not sexually dimorphic, we could not determine whether single individuals were male or female. Finding wiretail nests is difficult, so nesting success per territory was defined as 0 or 1, depending on whether fledglings were observed at some time during the breeding season. After fledglings abandoned the parental nest, they usually remained within the parental territory for around 2 weeks, allowing sufficient time for identification of successful nesters. When we defined nesting pairs as successful, we usually observed two nestlings,

which is in agreement with Goodall *et al.* (1946), who described the wiretail brood size as 2–3 nestlings.

### Data analyses

We analysed the effects of forest fragment size, habitat quality (density of understorey) and between-fragment connectivity on wiretail reproductive success using a General Linear Model (GLM), considering the binary variable connectivity as a random factor, and the continuous variables as covariates. Territory quality was calculated as the logarithm of the product of the number of branch contacts with a 3-m pole (NC) by territory size (ha). We evaluated normality of the data by the Kolmogorov-Smirnov test, and by examination of the residuals (Zar 1996). Data were normalized with Log ( $X + 1$ ) transformation.

To characterize the habitats used by wiretails, we performed a Cluster Analysis with Ward's linkage method on the data on floristic composition for the 28 wiretail territories studied, with the relative abundance of each plant species in the columns and each wiretail territory in the rows. Groups were determined by a minimum of 5% of dissimilitude. Finally, we compared the effect of the forest edge (<10 m from the edge) *versus* interior (>100 m from the nearest edge) on wiretail reproductive success using a Logistic Regression. For this analysis, we considered only territories located in the two larger fragments ( $n = 8$  territories) to avoid the effect of patch area and isolation. We included the territory size multiplied by the NC as a covariate, to control for habitat quality (see above). All data analyses were computed using SPSS (SPSS Inc. Chicago, IL, USA).

## RESULTS

### Wiretail territories and habitat characterization

We located 28 territories defended by wiretails in the nine forest fragments studied (Table 1). Unmated individuals occupied 15 territories, and nesting pairs occupied 13 territories. The size of territories varied from 0.1 to 3.5 ha. There were significant differences in territory size among forest fragments of different size, but not among territories occupied by single individuals or by nesting pairs (Table 2).

Cluster Analysis of the vegetation features of wiretail territories showed four main habitat types: (i) dense thickets of the native bamboo *C. quila* in the understorey of canopy gaps within old-growth forest fragments; (ii) early successional forests dominated by high densities of shade-tolerant myrtle trees (<5 m tall), such as *A. luma*, *A. meli* and *Myrceugenia planipes*, with

**Table 1.** Forest patch areas, number of territories, territory sizes and mating success of Des Murs' Wiretail (*Sylvioorthorhynchus desmursii*, Furnariidae) in a rural landscape of northern Chiloé Island, southern Chile

Study sites	<i>n</i>	Mean fragment area (ha)	No. of territories	Wiretail territory size (ha)	Mating success/fragment
Small fragments	7	5.2 ± 3.2	20	0.57 ± 0.2	0.42 ± 0.14
Large fragments	2	>300	8	0.83 ± 0.17	0.74 ± 0.09

Values are means ± 1 SE.

**Table 2.** ANOVA assessing the effect of forest fragment size and mating status (singles or pairs) on territory size of wiretails

Source	Mean square	Error	d.f.	<i>F</i>	<i>P</i>
Fragment size	1.727	0.165	7	10.46	0.025
Mating status	0.624	0.163	1	3.82	0.122
Fragment size × mating status	0.164	0.136	4	1.20	0.360

**Table 3.** Number of contacts (mean ± 1 SE) of understorey vegetation in the first 3 m above the ground level

Study site	First metre	Second metre	Third metre	Total (sum of three intervals)	Canopy cover (%)
Small fragments	6.7 ± 0.7	6.4 ± 0.5	5.0 ± 0.5	18.0 ± 1.0	<50
Large fragments	8.7 ± 1.2	6.3 ± 1.1	3.6 ± 1.3	18.6 ± 1.5	<50

Canopy cover (%) of the tree layer (>10 m tall) in all the territories occupied by wiretails is also shown.

abundant foliage below 3 m; (iii) dense shrublands adjacent to forest fragments, composed mainly of *B. patagonica* with dense foliage up to 1.5 m; and (iv) dense shrublands adjacent to forest fragments composed of *Berberis* spp., *Chusquea* spp., *Gaultheria* spp., *Aristolelia* sp., ferns (*Blechnum* sp.) with scattered *Rhaphithamnus* sp. and regeneration of Myrtaceae. During the study period, birds were occasionally observed moving in tall sedge vegetation in riparian habitats adjacent to forest fragments and in dense patches of the exotic *Ulex europaeus* (Papilionaceae), mixed with native shrubs and tree regeneration, along forest edges. Wiretails were also occasionally observed nesting in tall ferns (*Blechnum* sp.) and in sawgrass (*Cyperus* spp.).

The density of the understorey in the first 3 m of the vertical profile averaged 18 NC for large and small fragments (Table 3). In all territories foliage was denser in the first metre above the ground than in the second or third metre (Table 3). Moreover, in two territories there was no understorey present in the third metre, but there was a dense understorey in the first metre (10.8 and 13.0 NC) that decreased in the second metre (3.7 and 3.6 NC). These results suggest that wiretails inhabit areas with a dense vegetation layer in the first metre above the ground.

None of the five wiretails in the forest interior that were stimulated using song playbacks moved through open understorey areas with a fairly closed canopy

(>75%). Individuals defending territories that extended to the forest edge (*n* = 16) responded to playbacks by moving to the shrub-dominated vegetation adjacent to forest edges, but none of these birds ventured into open pastures. However, at two occupied shrubland sites adjacent to a road, we often observed pairs flying across an 8 m wide road between shrubs located on each side.

In summary, wiretails established territories in the forest understorey entangled by native bamboos or with high densities of Myrtaceae saplings and sparse (<50%) tree canopy cover, but also inhabited dense shrubland habitat along forest edges. They did not use areas without dense vegetation in the first metre above the ground.

### Corridors

Wiretails moved quickly through dense vegetation, such as forest understorey and vegetation strips in fencerows. The narrowest fencerow used by wiretails was 3 m wide and 100 m long. It contained 1–2 m tall shrubs and small trees of *A. luma*, *B. darwinii* and *R. spinosus*, including tangles of the vine *Mitraria coccinea*, with NC = 16.4 ± 1.0 (mean ± 1 SE), similar to values recorded in wiretail territories (Table 3). Another strip of vegetation about 200 m long, 3 m wide, with stems 2–3 m high and NC = 21.4 ± 1.2 was

regularly used by one pair of wiretails as a part of their nesting territory.

Based on these results, we define ‘corridors’ for wiretails as any strip of vegetation including shrubs or small trees (2–3 m high) with a width of at least 3 m, a canopy cover < 50% above 10 m, and a mean NC > 13.0 for the first three metres. This NC value corresponded to the lower limit recorded for wiretail territories in the forest fragments studied.

Two forest fragments studied were ‘connected’ if (i) they were separated by < 10 m of open areas (road or pasture), or (ii) they were joined by a vegetation strip or patch with the characteristics of a corridor defined above. Following these criteria, four small fragments were considered isolated, while three other small fragments were connected with neighbouring forest fragments. The 5-ha area studied within each large fragment was connected to the rest of the patch forming a large continuous forest area.

#### Effect of patch size, habitat quality and corridors on reproductive success

In isolated forest fragments less than 20 ha in size, only 20% of the territories were defended by pairs, while in connected forest fragments less than 20 ha, 72% of the territories were occupied by pairs (Fig. 2). The proportion of territories occupied by wiretail pairs in large fragments (>300 ha) was 73% (Fig. 2).

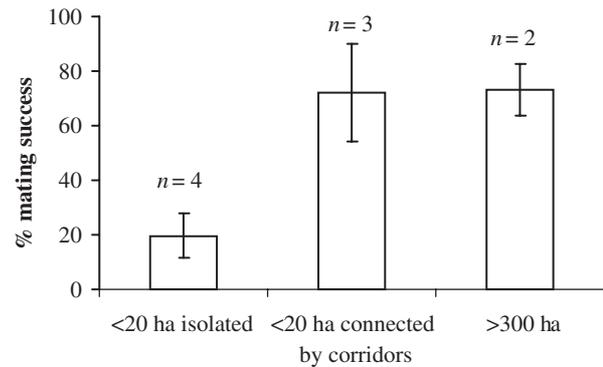
All 13 monitored pairs successfully nested, giving a probability of nesting success equal to 1 for all couples formed. Consequently, wiretail reproduction depended exclusively on the probability of mating. That is, the difficulty of finding a mate limited the reproductive success of this species. Considering only the size of the forest fragment, the reproductive success of wiretails was greater in large fragments (0.74) than in small fragments (0.42) (*T*-test for samples with unequal variances  $P = 0.03$ , Table 1). However, considering the combined effects of fragment size, habitat quality (NC multiplied by territory size), and presence or absence of habitat corridors, the main factor accounting for the variation in wiretail mating success was the presence of a habitat corridor, while the other

variables had no significant effects (Table 4). Additional variables, such as the location of the territory (edge *vs.* forest interior) had no effect on mating or nesting success (Logistic Regression  $B = -1.07^{0.34}$ ,  $P = 0.99$ ).

## DISCUSSION

### Habitat use by wiretails

Wiretails use only the dense shrubby understorey vegetation of forest patches, regardless of the presence or absence of canopy trees. In fact, we observed wiretail territories in sites characterized by the absence of trees, such as tree-fall gaps and edges, but possessing understorey dominated by dense bamboo or shrubs such as *B. patagonica* with patchy bamboo. Therefore, from the point of view of wiretails, habitat fragmentation should be understood as understorey fragmentation, as a result of conversion to open areas (such as pastures), and not necessarily forest canopy fragmentation.



**Fig. 2.** Percentage of territories in each forest fragment type that were occupied by mating pairs of wiretails. Isolated forest fragments < 20 ha had a lower proportion of mated individuals than connected fragments < 20 ha or large fragments > 300 ha (ANOVA  $F_{1,5} = 12.9$ ,  $P = 0.01$ ; Bonferroni *post hoc* test,  $P < 0.04$ ). This also reflected the percentage of territories that showed reproductive success, because all pairs produced fledglings.  $n$  = total number forest fragments used in this analysis. Values are means  $\pm$  1 SE.

**Table 4.** General Linear Model analysis to assess the effects of forest patch area, habitat quality (NC of understorey vegetation multiplied by territory size) and the presence or absence of travel corridors on mating success of wiretails (Zar 1996)

Source	Mean square	Error	d.f.	<i>F</i>	<i>P</i>	Power
Intercept	15.8	232.4	1	0.07	0.805	0.055
Patch area	210.1	170.2	1	1.23	0.329	0.139
Habitat quality	315.6	170.2	1	1.85	0.245	0.185
Presence of corridors	1985.1	170.2	1	11.66	0.027	0.725

For the general model presented  $R^2 = 0.783$  (ANOVA  $F_{2,6} = 10.82$   $P < 0.01$ ).

### Effects of fragment size and habitat corridors

Our results supported our predictions that wiretail reproductive success increases with increased connectivity for forest patches of similar size. Habitat corridors, with dense understorey vegetation, facilitated the dispersal of wiretails between small (<20 ha) forest fragments, increasing their probability of finding mates, thus resulting in a similar reproductive success in small and large fragments. By interconnecting small forest fragments, habitat corridors may increase the amount of habitat accessible to each wiretail, hence decreasing the negative effects of isolation, such as inbreeding and demographic or environmental fluctuations (Lande 1988; Simberloff 1988; Meffe & Carroll 1997).

For two other endemic understorey birds, the Ochre-flanked Tapaculo (*Eugralla paradoxa*) and the Chucao Tapaculo (*Scelorchilus rubecula*), dispersal through habitat corridors seems to be the most important factor that accounts for occupancy and mating success in isolated forest fragments in the same study area (McPherson 1999; Willson 2004). These two species are also reluctant to disperse across open pastures (Sieving *et al.* 1996, 2000), which indicates that decreased mating success would be a general effect of forest fragmentation for understorey birds in this rural landscape.

The effect of habitat fragmentation on nesting success and survival probabilities of birds are well studied in conservation biology, but mating success has received little attention (Dale 2001). Therefore, the reported increase in mating success related to the presence of travel corridors between small patches is our most novel result. The high proportion of unmated individuals in isolated fragments could be due to a biased sex ratio as a result of female-biased dispersal (Dale 2001). Because most of the single individuals observed in this study were vocalizing their territorial call, we suspect that they were mostly males. However, the effect of fragmentation on sex-biased dispersal of wiretails should not be ruled out until further study.

### Alternative explanations

Alternative explanations for the reduced reproduction of insectivorous understorey birds in small, isolated forest fragments include a possible increase in nest predation along edges (Wilcove 1985; Robinson *et al.* 1995) and a decrease in habitat quality associated with fragment or territory size (Canaday 1996; Zquette *et al.* 2000; Sekercioglu *et al.* 2002). In the same study area, Willson *et al.* (2001) showed very low rates of predation (<10%) on artificial wiretail nests located in forest edges and marginal differences in the rate of predation between edges and interior ( $P = 0.08$ ). They also found that concealed nests (such as wiretail nests)

were less susceptible to predation. DeSanto *et al.* (2002) monitored real nests of cavity nesters in the same area, finding no increase in nest predation along edges. In summary, the evidence indicates that nest predation along forest edges does not greatly affect wiretail reproductive success.

A decrease in habitat quality (density of understorey vegetation) may also decrease the density of understorey birds in fragmented forests (Burke & Nol 1998; Zquette *et al.* 2000). In our study area, Reid *et al.* (2004) showed that arthropod abundance increases as a function of understorey foliage density. Territories with less dense vegetation or small territories may support a smaller stock of arthropods, thereby limiting wiretail nesting success. However, all of the wiretail pairs studied nested successfully, independent of vegetation structure or territory size (Tables 1,3), suggesting that wiretails in fragmented forests would not be limited by food resources.

The availability of sufficient food resources to ensure survival and reproduction of wiretails even in small territories could be explained by a hypothesis proposed by MacLean and Seastedt (1979). They predicted that above a threshold territory size, food resources are permanently available for a territorial animal, despite seasonal variation in the amount of food resources (MacLean & Seastedt 1979; Sherman & Eason 1998). For wiretails, we hypothesize that small territories occupied by pairs were still larger than the threshold size that would restrict the food availability for these birds, allowing wiretails to breed successfully.

Several additional studies, in other regions, suggest that the main effect of forest fragmentation on reproductive success of birds is a decrease in mating success, which results from disruption of the dispersal of birds among fragments. For instance, Sekercioglu *et al.* (2002) evaluated the habitat quality hypothesis for an insectivorous bird community in Costa Rica, finding that food resources did not differ between continuous and fragmented forests. They concluded that disruption of dispersal would be the main factor causing the loss of insectivorous species. Similar conclusions were obtained by Walters *et al.* (1999) for the Brown Treecreeper (*Climacteris picumnus*, Climacteridae) in fragmented forests in Australia, where disruption of dispersal decreased mating success, but neither edge effects nor habitat quality were related to reproductive success. For wiretails, as well as for other insectivorous understorey birds, facilitating dispersal by habitat corridors may increase mating success, thereby increasing long-term population viability.

### Effectiveness of habitat corridors

The effectiveness of habitat corridors in conservation biology is still controversial because several studies

have shown ambiguous effects of corridors on animal dispersal across the matrix (LaPolla & Barret 1993; Crome 1997; Rosenberg *et al.* 1997; Mech & Hallett 2001). The unclear results could be due in part to an ambiguous definition of habitat corridor. Morrison *et al.* (1992) and Corsi *et al.* (2000) attributed this ambiguity to confusion between two definitions of habitat: one from a human point of view (e.g. forests, woodlands, shrublands) and the other from a species-specific point of view. For example, from the perspective of an individual animal, a heterogeneous landscape would not necessarily be perceived as fragmented. Suitable habitat elements may still remain in the matrix after human disturbance (McIntyre & Hobbs 1999). In this study, we defined wiretail habitat as dense understorey, independent of the presence or absence of overstorey trees. Wiretail habitat corridors are strips of understorey vegetation.

In the rural landscape of Chiloé Island, corridors of understorey vegetation could represent an important conservation tool, facilitating the dispersal of wiretails between fragments. Native bamboo thickets under tree-fall gaps and second-growth vegetation along edges are very important for the conservation of this and for other endemic understorey birds. The potential risk of reduced mating success for these birds should increase over time as native vegetation becomes further fragmented due to human activities. While keeping the present patterns of land use, farmers should be encouraged to maintain forest remnants and strips of second-growth forest or shrublands composed of native vegetation as connecting habitat. This practice would make it possible for wiretails and other endemic understorey birds to use the rural mosaic of forest fragments and pastures as a continuous habitat, thereby increasing their chances for survival in human-dominated landscapes.

#### ACKNOWLEDGEMENTS

We are grateful to F. Díaz, N. Romero, K. Sieving, P. Feinsinger, J. C. Torres-Mura, M. Canals, R. Bustamante, A. Grez, J. Morrison, J. Sanderson, S. McGehee, J. Arnett, M. Bruscia, L. Phillips, L. McDonnell, E. Arizmendi, J. Figueroa, S. Castro, the late L. Cavieres, M. Soto, R. Nespolo, L. Rojas, E. Elgueta, C. Papic, F. Pérez, A. Maldonado, M. Serrano, S. Hetrick and M. Speirs for support and assistance, to A. Muñoz, J. M. Davis, G. Luck, C. H. Sekercioglu, M. Craig and M. Bull for comments on the manuscript, and to the landowners for allowing us to conduct this study. This work was funded by grants from the American Bird Conservancy, William Belton Grants Program (project PMAY00797), fellowship PG/027/97 from Departamento de Postgrado y Postítulo, Universidad de Chile, and an endowed

Presidential Chair in Science to J. J. Armesto. Writing was supported by MCEB, Grant P99-103 F ICM and by FONDAP-FONDECYT Grant 1501-0001 to the Center for Advanced Studies in Ecology and Biodiversity. This is a contribution of the research program of Senda Darwin Biological Station, Ancud, Chiloé.

#### REFERENCES

- Aebischer N. J., Robertson P. A. & Kenward R. E. (1993) Compositional analysis of habitat use from animal radio-tracking data. *Ecology* **74**, 1313–25.
- Andrén H. (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* **71**, 355–66.
- Armesto J. J. & Figueroa J. (1987) Stand structure and dynamics in the rain forests of Chiloé Archipiélago, Chile. *J. Biogeogr.* **14**, 367–76.
- Armesto J. J., Rozzi R., Smith-Ramírez C. & Arroyo M. T. K. (1998) Conservation targets in South American temperate forests. *Science* **282**, 1271–2.
- Beier P. & Noss R. F. (1998) Do habitat corridors provide connectivity? *Conserv. Biol.* **12**, 1241–52.
- Burke D. M. & Nol E. (1998) Influence of food abundance, nesting-site habitat, and forest fragmentation on breeding ovenbirds. *Auk* **115**, 96–104.
- Bustamante R. O. & Castor C. (1998) The decline of an endangered temperate ecosystem: the Ruil (*Nothofagus alessandrii*) forest in central Chile. *Biodivers. Conserv.* **7**, 1607–26.
- Canaday C. (1996) Loss of insectivorous birds along a gradient of human impact in Amazonia. *Biol. Conserv.* **77**, 63–77.
- Corsi F., de Leeuw J. & Skidmore A. (2000) Modeling species distribution with GIS. In: *Research Techniques in Animal Ecology* (eds L. Boitani & T. K. Fuller) pp. 389–434. Columbia University Press, New York.
- Crome F. H. J. (1997) Researching tropical forest fragmentation: Shall we keep on doing what we are doing?. In: *Tropical Forest Remnants: Ecology, Management and Conservation of Fragmented Communities* (eds W. F. Laurance & R. O. Bierregaard Jr) pp. 485–501. University of Chicago Press, Chicago.
- Dale S. (2001) Female-biased dispersal, low female recruitment, unpaired males, and the extinction of small and isolated bird populations. *Oikos* **92**, 344–56.
- DeSanto T., Willson M. F., Sieving K. E. & Armesto J. J. (2002) Nesting success of Tapaculos (Family Rhinocryptidae) in South-temperate rainforests of Chile. *Condor* **104**, 482–95.
- Fahrig L. & Merriam G. (1985) Habitat fragment connectivity and population survival. *Ecology* **66**, 1762–8.
- Fahrig L. & Paloheimo J. (1988) Effect of spatial arrangement of habitat fragments on local population size. *Ecology* **69**, 468–75.
- Fjeldså J. & Krabbe N. (1990) *Birds of the High Andes*. Zoological museum, University of Copenhagen and Apollo Books, Svendborg.
- Goodall J. D., Johnson A. W. & Philippi R. A. (1946) *Las aves de Chile, su conocimiento y sus costumbres*. Platt Establecimientos Gráficos S.A., Buenos Aires.
- Haddad N. M. (1999a) Corridor use predicted from behaviors at habitat boundaries. *Am. Nat.* **153**, 215–27.
- Haddad N. M. (1999b) Corridor and distance effects on inter-fragment movements: a landscape experiment with butterflies. *Ecol. Appl.* **9**, 612–22.

- Lande R. (1988) Genetics and demography in biological conservation. *Science* **241**, 1455–60.
- LaPolla V. N. & Barret G. W. (1993) Effects of corridors width and presence on the population dynamics of the meadow vole (*Microtus pennsylvanicus*). *Landscape Ecol.* **8**, 25–37.
- Lara A., Donoso C. & Aravena J. C. (1996) La conservación del bosque nativo en Chile: Problemas y desafíos. In: *Ecología de los bosques nativos de Chile* (eds J. J. Armesto, C. Villagrán & M. T. K. Arroyo) pp. 335–62. Editorial Universitaria, Santiago.
- Lovejoy T. E., Bierregard R. O., Rylands A. B. *et al.* (1986) Edge and other effects of isolation on Amazon forest fragments. In: *Conservation Biology, the Science of the Scarcity and Diversity* (ed. M. Soulé) pp. 257–85. Sinauer, Sunderland.
- McIntyre S. & Hobbs R. (1999) A framework for conceptualizing human effects on landscapes and its relevance to management and research models. *Conserv. Biol.* **13**, 1282–92.
- MacLean S. F. & Seastedt T. R. (1979) Avian territoriality: sufficient resources or interference competition. *Am. Nat.* **114**, 308–12.
- McPherson H. (1999) Landscape effects on the distribution of an endemic rhinocryptid, the Ochre-flanked Tapaculo, *Eugralla paradoxa*, in fragmented south-temperate rainforest (MSc Thesis). University of Florida, Gainesville.
- Marion R. W., O'Meara T. E. & Maher D. S. (1981) Use of playback recordings in sampling elusive or secretive birds. *Studies Avian Biol.* **6**, 81–5.
- Mech S. G. & Hallett J. G. (2001) Evaluating the effectiveness of corridors: a genetic approach. *Conserv. Biol.* **15**, 467–74.
- Meffe G. K. & Carroll C. R. (1997) *Principles of Conservation Biology*. Sinauer Associates, Inc, Sunderland, MA.
- Morrison M. L., Marcot B. G. & Mannan W. (1992) *Wildlife-Habitat Relationship: Concepts and Applications*. The University of Wisconsin Press, Madison, WI.
- Myers N., Mittermeier R. A., Mittermeier C. G., Da Fonseca G. & Kent J. (2000) Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–8.
- Olson D. M. & Dinerstein E. (1998) The global 200: a representation approach to conserving the earth's most biologically valuable ecoregions. *Conserv. Biol.* **12**, 502–15.
- Opdam P. (1991) Dispersal in fragmented populations: the key to survival. In: *Species Dispersal in Agricultural Habitats* (eds R. G. H. Bunce & D. C. Howard) pp. 3–10. Belhaven Press, London.
- Powell R. A. (2000) Animal home ranges and territories and home range estimators. In: *Research Techniques in Animal Ecology* (eds L. Boitani & T. K. Fuller) pp. 65–110. Columbia University Press, New York.
- Reid S., Díaz I. A., Armesto J. J. & Willson M. F. (2004) The importance of native bamboo for understory birds in Chilean temperate forests. *Auk* **121**, 515–25.
- Robinson S. K., Thompson F. R. III, Donovan T. M., Whitehead D. R. & Faaborg J. (1995) Regional forest fragmentation and the nesting success of migratory birds. *Science* **267**, 1987–90.
- Rosenberg D. K., Noon B. R. & Meslow E. C. (1997) Biological corridors: form, function, and efficacy. *Bioscience* **67**, 677–87.
- Saunders D. A., Hobbs R. J. & Margules C. R. (1991) Biological consequences of ecosystem fragmentation: a review. *Conserv. Biol.* **5**, 18–29.
- Sekercioglu C. H., Ehrlich P. R., Daily G. C., Aygen D., Goehring D. & Sandí R. F. (2002) Disappearance of insectivorous birds from tropical forest fragments. *Proc. Natl. Acad. Sci. USA* **99**, 263–7.
- Sherman P. T. & Eason P. K. (1998) Size determinants in territories with inflexible boundaries: manipulation experiments on White-Winged Trumpeters' territories. *Ecology* **79**, 1147–59.
- Sieving K. E., Willson M. F. & De Santo T. L. (1996) Habitat barriers to movement of understory birds in south-temperate rainforest. *Auk* **113**, 944–9.
- Sieving K. E., Willson M. F. & De Santo T. L. (2000) Defining corridors for endemic birds in fragmented south-temperate rainforest. *Conserv. Biol.* **14**, 1120–32.
- Simberloff D. (1988) The contribution of population and community biology to conservation science. *Annu. Rev. Ecol. Syst.* **19**, 473–511.
- Simberloff D., Farr J. A., Cox J. & Mehlman D. W. (1992) Movement corridors: conservation bargains or poor investments? *Conserv. Biol.* **6**, 493–504.
- Taylor P. D., Farhig L., Henein K. & Merriam G. (1993) Connectivity is a vital element of landscape structure. *Oikos* **68**, 571–3.
- Veblen T. T., Kitzberger T., Burns B. R. & Rebertus A. J. (1996) Perturbaciones y dinámica de regeneración en bosques andinos del sur de Chile y Argentina. In: *Ecología de Los Bosques Nativos de Chile* (eds J. J. Armesto, C. Villagrán & M. T. K. Arroyo) pp. 169–98. Editorial Universitaria, Santiago.
- Vuilleumier F. (1985) Forest birds of Patagonia: ecological geography, speciation, endemism, and faunal history. *Ornithol Monogr.* **36**, 254–304.
- Walters J. R., Ford H. A. & Cooper C. B. (1999) The ecological basis of sensitivity of brown treecreepers to habitat fragmentation: a preliminary assessment. *Biol. Conserv.* **90**, 13–20.
- Wenny D. G., Clawson R. L., Faborg J. & Sheriff S. L. (1993) Population-density, habitat selection and minimum area requirements of 3 forest-interior warblers in central Missouri. *Condor* **95**, 968–79.
- Wilcove D. S. (1985) Nest predation in forest tracts and the decline of migratory songbirds. *Ecology* **66**, 1211–14.
- Wilcove D. S., McLellan C. H. & Dobson P. (1986) Habitat fragmentation in the temperate zone. In: *Conservation Biology, the Science of the Scarcity and Diversity* (ed. M. Soulé) pp. 237–56. Sinauer, Sunderland.
- Willson M. F. (2004) Loss of habitat connectivity hinders pair formation and juvenile dispersal of chucaco tapaculos in Chilean rainforests. *Condor* **106**, 166–71.
- Willson M. F. & Armesto J. J. (1996) The natural history of Chiloé: on Darwin's trail. *Rev. Chil. Hist. Nat.* **69**, 149–61.
- Willson M. F., De Santo T. L., Sabag C. & Armesto J. J. (1994) Avian communities of fragmented south temperate rainforest in Chile. *Conserv. Biol.* **8**, 508–20.
- Willson M. F., Morrison J. L., Sieving K., De Santo T. L., Santisteban L. & Díaz I. (2001) Patterns of predation risk and survival of bird nests in a Chilean agricultural landscape. *Conserv. Biol.* **15**, 447–56.
- Zanette L., Doyle P. & Trémont S. M. (2000) Food storage in small fragments: evidence from an area-sensitive passerine. *Ecology* **81**, 1654–66.
- Zar J. H. (1996) *Biostatistical Analysis*. Prentice Hall, New Jersey.