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# Defining Corridor Functions for Endemic Birds in Fragmented South-Temperate Rainforest

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**Abstract:** For five species of endemic understory birds (families Rhinocryptidae, Furnariidae) inhabiting fragmented temperate rainforest in southcentral Chile, we distinguished between vegetated corridors functioning as living space and those potentially suitable for short-distance movements only. In the first phase of the study, we surveyed 24 forested corridors  $\leq 50$  m wide using passive and song-playback censuses. Corridor width determined species presence or absence, whereas the number of individuals increased with width and understory vegetation density. Birds were infrequently encountered in corridors  $\leq 10$  m wide but were always present in corridors 25–50 m wide. Birds present in intermediate-width (11–24 m) corridors were detected significantly less often during passive than playback census, suggesting that these birds exhibited conspicuous territorial display less frequently than those present in wider corridors, where passive and playback census yielded similar detection rates. Corridors approximately 10–25 m wide, therefore, may be transitional between corridors too narrow for most regular uses and those sufficiently wide for birds to establish territories. Also, bird abundance decreased as the ratio of corridor length to width (L/W) increased. Almost no birds were detected in corridors with  $L/W \geq 10$ , suggesting the existence of a threshold value for the influence of L/W on corridor use. In the second phase of the study, taped-song playback experiments in corridors  $\leq 10$  m wide showed that all five species traveled in them for short distances: 52% of respondents moved up to 50 m from forest patches into narrow corridors. Availability of dense understory vegetation was the primary predictor of birds' responses to playback and may determine their willingness to use minimal corridors for short movements. We suggest that corridors for endemic rainforest-understory birds living in agricultural landscapes of southern Chile can be designed to fulfill distinct functions.

Definición de las Funciones de un Corredor para Especies de Aves Endémicas en un Bosque Lluvioso Templado del Sur Fragmentado.

**Resumen:** En este trabajo establecimos distinciones entre corredores con vegetación que funcionan como espacio para vivir y corredores potencialmente aptos únicamente para movimientos de distancias cortas, para cinco especies de aves de sotobosque endémicas (Familias Rhinocryptidae, Furnariidae) que habitan un bosque lluvioso templado fragmentado en la región central del sur de Chile. En la primera fase del estudio, evaluamos 24 corredores con vegetación  $\leq 50$  m de ancho usando censos pasivos y con cantos grabados. La amplitud del corredor determinó la presencia/ausencia de especies, mientras que el número de individuos incrementó con la amplitud y densidad de la vegetación del sotobosque. Las aves fueron poco frecuentes en corredores  $\leq 10$  m de ancho, pero estuvieron siempre presentes en corredores de 25–50 m de ancho. Las aves presentes en corredores de amplitud intermedia (11–24 m) fueron detectadas menos frecuentemente durante los censos pasivos que durante los censos con grabaciones, lo que sugiere que estas aves exhibieron menos despliegues territoriales visibles que aquéllas presentes en corredores más amplios donde los censos pasivos y con grabación resultaron en tasas de detección similares. Los corredores de aproximadamente 10–25 m de ancho, pueden, por lo tanto, ser transitorios entre corredores que son demasiado angostos para la mayoría de los usos regulares y corredores lo suficientemente amplios como para establecer territorios. Adicionalmente, la abundancia de aves disminuyó cuando la proporción entre el largo y el ancho del corredor (L/W)

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*incrementó. Casi no se detectaron aves en corredores con  $L/W \geq 10$ , lo cual sugiere la existencia de un valor límite para la influencia de  $L/W$  en el uso del corredor. En la segunda fase del estudio, experimentos con cantos grabados en corredores  $\leq 10$  m de ancho mostraron que las cinco especies viajaron en los corredores por distancias cortas: el 52% de las aves que respondieron se movieron hasta 50 m de los parches de bosque hacia corredores angostos. La disponibilidad de vegetación densa de sotobosque fue el principal predictor de las respuestas de las aves a las grabaciones y podría determinar la disposición de las aves a usar corredores mínimos para movimientos cortos. Sugerimos que los corredores para aves endémicas de bosques lluviosos que viven en paisajes agrícolas del sur de Chile pueden ser diseñados para cumplir diversas funciones.*

## Introduction

Linear forest remnants in landscapes where human activity has fragmented once-continuous forest ecosystems may serve forest animals in two ways: as suitable habitat (survival and reproduction functions) and as travel routes between suitable habitat patches (travel function) (Haas 1995; Rosenberg et al. 1997). If used for either purpose by animals, linear habitat remnants are called wildlife corridors. In human-dominated landscapes where fragmented ecosystems embedded in a hostile matrix create unnatural metapopulations (Noss & Cooperrider 1994), corridors are often promoted for provision of connectivity among semi-isolated subpopulations (Noss 1987; Hansson 1991; Harris & Scheck 1991; Saunders & Hobbs 1991). Despite the conceptual popularity of corridors in conservation research (Harrison & Bruna 1999), functional designs are scarce because little is known about which physical characteristics of corridors influence animals' perceptions and differential use of them across scales (Simberloff et al. 1992; Soulé & Gilpin 1991; Ims 1995).

Theory predicts that aspects of corridor shape will be important determinants of animal use (Soulé & Gilpin 1991). For small animals (snails, mice, beetles, butterflies), width emerges repeatedly as a determinant of dispersal success through corridors embedded in a hostile matrix (Baur & Baur 1992; Rosenberg et al. 1997; Tischendorf & Wissel 1997; but see Rufenacht & Knight 1995). Likewise, travel of large animals through linear corridors is affected by width, modified by continuity of vegetative cover (Beier 1993, 1995). Corridors can be too narrow or too wide for efficient short-distance dispersal; if too narrow, animals may be reluctant to enter, and if too wide, animals make cross-directional movements that reduce dispersal efficiency and success (Soulé & Gilpin 1991; Andreassen et al. 1996; Rosenberg et al. 1998). Wide corridors are more likely to function as habitat, however, supporting breeding activity and richer, more complete faunas in general (Keller et al. 1993; Spackman & Hughes 1995; Hodges & Krementz 1996). Quantifying influences of other critical corridor features on animal use, particularly length, has been nearly impossible in field studies (but see Haddad 1999a). Moreover, a test of

the central assumption of nearly all corridor studies—that corridor features encouraging use by animals also enable *successful* use (i.e., true functionality)—has not been accomplished in a real landscape for forest-requiring species (Beier & Noss 1998). But despite a dearth of causal inference in the literature (Nicholls & Margules 1991), the weight of confirmatory evidence suggests that forest-requiring animals frequently elect to enter, travel through, and live in forested corridors with apparent success. As a first step toward understanding how corridors might aid in conservation of a guild of understory bird species globally endangered by habitat loss and fragmentation, we identify specific features of corridors influencing the birds' use of them for travel versus habitat functions.

South-temperate rainforest in Chile (for ecological description see Donoso 1993; Armesto et al. 1995; Veblen et al. 1996) is rapidly disappearing, and what remains is increasingly fragmented by agriculture, logging, and pine and eucalyptus plantations (Carte 1994; Estades & Temple 1999). Because of this deforestation, endemic birds of south-temperate rainforest are declining and globally endangered (Glade 1988; Collar et al. 1992; Balmford & Long 1994). Among the species most sensitive to rainforest fragmentation are members of the family Rhinocryptidae (Willson et al. 1994), commonly known as tapaculos. We have documented that four rhinocryptids and one furnariid endemic to southcentral Chile seldom emerge from cover and are extremely reluctant to enter open fields (Sieving et al. 1996). We presume, therefore, that functioning ecological connections between habitable patches are necessary for sustaining metapopulations of the birds in an agriculture-dominated region where the structural contrast between remnants of native rainforest and uninhabitable matrix is extreme. Furthermore, we address corridor features promoting their use under the assumption that the endeavor is relevant for conservation—that sufficient habitat currently exists in the region to maintain bird populations above extinction thresholds (With & King 1998; Harrison & Bruna 1999).

In a landscape dominated by cattle pasture in southern Chile, we tested the hypothesis that width is the principal feature determining use of forest corridors as habitat versus potential travel-only paths by five study species. Because vegetation structure and composition

within corridors (Sustek 1992; Lindenmayer & Nix 1993; Beier 1995; Rosenberg et al. 1998) and aspects of shape other than width (e.g., length and length-to-width ratio; Soulé & Gilpin 1991; Harrison 1992; Bennett et al. 1994; Haddad 1999a) might also influence use, we quantified vegetative and physical features of forested corridors as predictors of bird abundance, species composition, and different types of use. We also identified specific features of potential travel-only corridors (the narrowest vegetated strips in the landscape) which influenced birds' decisions to enter and move short distances within them.

## Methods

Our study encompassed two phases: an initial descriptive survey of species occurrence and bird abundance in 24 forested corridors in 1995–1996, followed by experimental tests of features influencing the probability that birds would use the narrowest strips (1996–1997). Characteristics of potential travel corridors used in the second phase were suggested by results of the initial survey. We utilized taped-song playbacks (Falls 1981; McGregor 1992) in both parts of the study, first to enhance detection rates and address questions of differential use of forested corridors during the initial survey and, in the second phase, to test the willingness of individuals to enter narrow (potential travel-only) corridors and make short-distance movements within them.

## Study Species and Sites

Five bird species that are permanent residents of rainforest in southern Chile were the focus of our study (Table 1). Among the least vagile of birds in the region, they pointedly avoid open pasture, which probably constitutes a barrier to their movement between patches of suitable habitat (Sieving et al. 1996; Estades & Temple 1999). Low vagility in open habitat, in turn, probably explains their sensitivity to forest fragmentation in agricultural landscapes (Willson et al. 1994; Díaz 1999; McPherson 1999; Cornelius et al. 2000). All species are classified as narrow endemics in the rainforest of south-

ern Chile and westernmost Argentina (Vuilleumier 1985; Fjeldså & Krabbe 1990; Stattersfield et al. 1998) and are associated with forest understory (Johnson 1967; Araya & Chester 1993). Defense of breeding territories is vigorous: song, plumage displays, and physical aggression are used to confront intraspecific intruders (K.E.S., M.F.W., T.L.D., personal observations). Territories are not completely exclusive areas, however, because we observed individual territory holders leaving their own core areas and moving through areas defended by other individuals. Furthermore, territory sizes of the study species are variable, accommodating various features of habitat and landscape configuration. For example, density estimates in 10 forest patches and 5 unfragmented forest sites (Table 1) indicate that space requirements change with degree of deforestation and understory disturbance (see also Estades & Temple 1999).

All our work was conducted in the middle of the birds' breeding season, which extends from October to March. All species are multibrooded, and fledglings are commonly encountered on natal territories beginning in late November. Dispersing juveniles are increasingly encountered during December–January, and attempts to claim breeding territories by young of the year are readily observed by mid-February. Both phases of this study were conducted between November and January, when taped-song playback elicits aggressive approaches by territory owners and is likely to attract curious fledglings still on their natal territories, dispersing adults, and post-fledgling juveniles (K.E.S., M.F.W., T.L.D., personal observations).

We conducted this work on Isla Grande de Chiloé (Region X, southcentral Chile) in privately owned corridors in the northeastern sector of the island, primarily south of Route 5 between the towns of Ancud and Chacao (lat 41°55'S, long 73°35'W). The rural landscape is increasingly dominated by cattle pasture, hayfields, orchards, and subsistence cultivation of potato. Forest patch size varies from several thousand hectares (only one of these remains in northeastern Chiloé and it is shrinking) to <1 ha (Willson et al. 1994). Most forest patches, which are maintained and used by landowners for wood extraction and livestock shelter, are interconnected by linear vegetated strips, including shrubby fencerows, uncleared upland for-

**Table 1.** List of English common, Chilean common, scientific, and family names; mean body mass; and estimated range of population density of the study species.

<i>Common name</i>	<i>Chilean name</i>	<i>Scientific name</i>	<i>Family</i>	<i>Body mass (g)</i>	<i>Population density*</i>
Chucao Tapaculo	Chucao	<i>Scelorchilus rubecula</i>	Rhinocryptidae	40	3.1 - 6.15
Black-throated Huet-Huet	Huet-Huet	<i>Pteroptochos tarnii</i>	Rhinocryptidae	150	0.47 - 3.28
Ochre-flanked Tapaculo	Churrín de la Mocha	<i>Eugralla paradoxa</i>	Rhinocryptidae	25	0.0 - 1.25
Magellanic Tapaculo	Churrín Magellanica	<i>Scytalopus m. magellanicus</i>	Rhinocryptidae	11	0.94 - 1.56
Des Mur's Wiretail	Colilarga	<i>Sylvioorthorhynchus desmursii</i>	Furnariidae	10	0.47 - 1.00

\*Expressed as the estimated number of pairs per 5 ha (minimum - maximum) based on fixed-width transect sampling (K. E. S., unpublished data); n = 15 sites for each range given.

est, and riparian ravines. Forest patches and potential corridors used in this study were composed primarily of native plant species, including *Drimys winteri*, *Nothofagus dombeyi*, and several myrtaceous species in the canopy, and principally *Chusquea* spp. (bamboo) and sapling trees in the understory (Hoffmann 1995; Veblen et al. 1996).

### Phase One: Initial Survey of Forested Corridors

We selected 24 forested corridors  $\leq 50$  m wide for the initial survey because wider strips were generally always occupied by the study species and therefore were unlikely to be perceived as distinct from patches of potential habitat. All corridors with the proper characteristics were included in the study as we found them and obtained permission from landowners. We did not select our sites randomly but included representative corridors throughout our study area (approximately 250 km<sup>2</sup>). Focal corridors used in phase one had nearly continuous native tree canopy and understory cover throughout their length (no gaps of  $>5$  m), were bordered by open pasture, and were connected to two patches of forest  $\geq 5$  ha in area, one at either end, that could serve as potential sources of resident or dispersing birds (Table 2; for minimum patch size requirements of the study species see Willson et al. 1994). In one case, three different corridors connected the same two patches. In another case, two different corridors extended from one part of a large patch through fields to another part of the same forest patch, and, in two cases, two corridors connected one patch to two separate patches. In all cases, the junctures between corridors attached to the same patches were far enough apart ( $>100$  m) that it is unlikely that the same individuals were detected in more than one corridor. We censused the 24 corridors and their associated forest patches using both passive and taped-song playback counting techniques (Falls 1981; Marion et al. 1981; Parker 1991; Bibby et al. 1992; Sliwa & Sherry 1992). Comparison of detections made by playback and passive counts allowed us to interpret how birds were using the corridors.

Near dawn on a morning with no rain or strong wind, a passive census was initiated with a 5-minute point count at the juncture of the corridor with one of the two forest patches. The purpose of the point counts was to establish presence or absence of birds in the vicinity of the corridor entrances. In small patches, point count areas were defined by patch size (individuals seen at the juncture or heard anywhere in the patch were recorded) and in larger patches ( $>10$  ha) by bird detection distances. Because we only used corridors bordered by open pasture, no birds were ever detected anywhere but in patches or corridors. After the initial point count, the observer walked the length of the corridor at a rate of 10 m/minute, counting birds. The census pace was necessarily slow to accommodate slow singing rates of the study species. Two of the corridors were steep-walled ravines; these were censused along one side from the top and others were censused from the center. At the end of each corridor, another 5-minute point count was conducted in the second forest patch. If the passive census was completed before 0900 hours, then a playback census was conducted immediately; otherwise, a playback census was done on another day.

To initiate a playback census, territorial song sequences of the study species were broadcast for 10 minutes at the juncture between the corridor and the forest patch; individuals detected in the patch were recorded. These initial playbacks served the same purpose as the passive point counts. Song sequences, recorded with a Marantz cassette recorder with directional microphone, were broadcast by means of inexpensive cassette players attached to portable stereo speakers with volume boosters. Following the initial broadcast, the observer moved into the corridor and played all song sequences again at 33%, 50%, and 67% of the length of the corridor (unless the corridor was  $<50$  m long, in which case songs were broadcast in the middle only) and recorded all individuals detected by sight or sound within the corridor. Finally, we completed the playback census by broadcasting songs in the second forest patch. Song broadcasts were followed by at least 5 minutes of silent

**Table 2. Descriptive statistics for independent variables used in regression analyses of habitat features affecting bird numbers in phase one (initial survey of forested corridors) and phase two (playback experiments at potential travel corridors) of the study.**

Variable <sup>a</sup>	Phase one, initial survey (n = 24)			Phase two, playback experiments (n = 52)		
	minimum	$\bar{x}$	maximum	minimum	$\bar{x}$	maximum
Width (m)	2.5	22.9	50.0	1.7	6.3	10.0
Length (m)	55.0	138.0	380.0	15.0	65.2	450.0
Riparian code	1	—	2	1	—	2
MVD (number of hits)	3.1	7.3	11.8	1.9	7.0	15.0
MQD (number of hits)	0.0	1.5	7.7	0.0	1.3	8.2
Canopy proportion <sup>b</sup>	0.3	0.9	1.4	0.0	0.5	1.6

<sup>a</sup>Riparian code: 1, dry or standing water; 2, moving water. MVD, mean vegetation density; MQD, mean quila density (see methods).

<sup>b</sup>Proportions are angular transformed.

observation to detect cryptic individuals. Given the small number of detections in each corridor, we avoided double counting individuals by noting approach directions and monitoring individual locations and activities.

Sometimes species were absent from patches adjacent to corridors (no registrations in patches during passive and playback point counts) and had no access to a corridor being censused. In such cases, those combinations of species and sites were not included in analysis. Of 120 possible data points (24 corridors  $\times$  5 species), we eliminated 15 from analyses (11 patches or corridors lacking Ochre-flanked Tapaculos and 4 without Huet-Huets).

Avian abundance was indexed by the maximum number of individuals of each species recorded during either passive or playback census. Individuals defending a corridor (via song) would be readily detected during passive or playback census, whereas individuals either traveling through (e.g., floaters) or foraging outside their normal territories may not be conspicuous during a passive census but would approach a playback. Certain individuals, however, might avoid a playback and the perceived conflict with a territory owner (e.g., juveniles; Woolfenden & Fitzpatrick 1984). All types of individuals (territorial adults, dispersing or floating juveniles, etc.) were likely to be encountered by us during sampling. Therefore, to maximize the probability that we would include birds exhibiting any of the above behaviors, we used the maximum number of individuals detected during either census type as the abundance estimate. We did not use density as the response variable because we did not have all possible combinations of length versus width of corridors (wide and long ones were lacking). Maximum width was constrained to 50 m but length was unconstrained, and area was more highly correlated with length than width (which were uncorrelated). Therefore, if bird density is used as the response variable, regression analyses would be biased against the influence of corridor width when both length and width are used as independent predictor variables.

We used logistic and multiple linear regression analyses to identify relationships between descriptive corridor features (Table 2) and response variables (species presence and abundance of individuals in corridors, respectively). In cases where no model was obtained with forward or stepwise selection, we applied backward elimination methods (Weisberg 1985; Norusis 1993). In multiple linear regression, residual analyses were used to identify model specification and nonconstant variance. Transformations were used where appropriate. No models obtained violated multicollinearity assumptions: all had condition indices of  $<10.0$  (Weisberg 1985).

To explore the influence of corridor shape—defined as the ratio of length (L) to width (W) [L/W]—on bird numbers, we applied curve-fitting procedures (SPSS, version 8.0 for Windows) to census data plotted against L/W. Because corridor width was fixed at  $\leq 50$  m—to represent

the local scale at which the space requirements of the study species were defined—this analysis allowed us to assess the relative importance of corridor length to bird use. Corridor length was not constrained when we selected sites, and it varied over a much greater range than width; so, L/W was also quite variable.

### Phase Two: Playback Experiments at Potential Travel-Only Corridors

Results of the initial survey indicated that strips narrower than 10 m generally were not used as habitat, but that birds occasionally occurred in them. Therefore, in the year after phase one, we conducted playback experiments to identify features of narrow strips determining birds' willingness to move into them and potentially use them as travel paths. As before, we used nonrandom but representative sites throughout the study area as we encountered them and obtained permission. We included only narrow strips of forest and/or shrubs  $\leq 10$  m wide that were bounded by pasture. Most strips connected forest patches of various size, but we also used vegetated peninsulas extending into pasture, including shrubby fencerows (Table 2). Corridor requirements for inclusion in phase two experiments included conjunction with at least one forest patch  $\geq 5$  ha in size, a lack of gaps  $>5$  m wide in the vegetative cover (canopy tree cover not required), and at least one responding individual of the study species in the adjacent patch (all birds present at each juncture were tested).

Following Sieving et al. (1996), we utilized taped-song playback to motivate our study animals to make a choice either to enter a potential corridor or not (the single-measure approach; McGregor 1992). When a species' song is played near a territory boundary, it elicits an aggressive response from the territory holder(s), including close approach and loud and frequent singing. Given that strict territorial boundaries are not observed by these species, particularly during playback, a responsive individual's willingness to move into a corridor during playback is most likely determined by the characteristics of the corridor and the individual's motivational state rather than territorial limits. Whereas birds censused in phase one probably included a few juveniles, all individuals tested in phase two experiments were likely territorial adults—those responsive enough to approach a playback and engage in persistent vocal and visual display.

To initiate a playback experiment, several sequences of the study species' territorial songs were broadcast at the juncture between the strip and the forest patch for up to 10 minutes. If an individual responded to the tape (i.e., called or moved toward the speaker), the event was included in analysis. Once a bird responded, the researcher moved the speaker several meters into the strip and concealed herself in vegetation. The responding species' song was played for 5 minutes or until the re-

spondent left the patch and entered the corridor. If the individual entered the corridor, the speaker was moved further out and the tape was played again. If a bird did not leave the patch within the first 5 minutes but did move to the juncture where it could see the corridor, or if the bird came out <5 m and then retreated (three occasions), the event was recorded as a negative (unwilling) response. If a respondent traveled >5 m into the corridor, it was recorded as a positive response (willing to enter). At each site, we tested all individuals present and responsive at the juncture. Willing respondents were drawn as far into the corridor as they would go, or up to 50 m if the corridor was longer. We sampled until we had a minimum of 10 respondents of each species, and this determined how many sites were tested. We used logistic regression analysis (Norusis 1993) to identify the features of potential travel corridors (Table 2) that influenced willingness of the focal species to move into them.

### Physical and Vegetative Descriptors of Corridors

We quantified the following six variables in corridors used in the study and incorporated them as independent variables in regression analyses (Table 2). For corridor (1) length and (2) width, we paced the length directly and calculated the mean width from three measures taken in the middle and near each end.

We assigned a (3) riparian code score of 1 if a corridor was dry or had standing water or a score of 2 if moving water was present. As a categorical variable, riparian code was used only in logistic regression models.

We used (4) mean vegetation density (MVD) to quantify density of understory vegetation relevant to the terrestrial study species. We developed an index similar in concept to a "density board" (Bibby et al. 1992). Standing a 3-m pole (2-cm diameter) perpendicular to the ground at randomly determined points within each corridor, we counted the number of leaf-bearing branches touching the pole in all 3 m to obtain the number of

"hits." The MVD in the lowest 3 m of the understory was determined by averaging the number of hits per point over all random points in each corridor. In phase one the number of points used varied with the area of the corridor, from a minimum of 50 for corridors  $\leq 1500 \text{ m}^2$  in size to a maximum of 100 for those  $\geq 4000 \text{ m}^2$  in size. In phase two we used 50 points in all potential travel-only corridors because most were relatively small.

We calculated (5) mean density of quila (MQD) as a subset of MVD. Known locally as quila, bamboo (*Chusquea* spp.) is a common component of understory vegetation and appears to provide good cover and foraging habitat for the study species; therefore, we distinguished quila from all other leaf-bearing stems.

As a measure of (6) percent canopy cover, we used the proportion of sampling points in each corridor that had canopy tree foliage above the vegetation pole. The proportions were angular-transformed for analysis.

## Results

### Phase One: Initial Corridor Survey

Logistic regression revealed that corridor width was the primary predictor of species presence in corridors (pooled, Huet-Huet, and Magellanic Tapaculo models; Table 3). Chucao presence was strongly associated with canopy cover and weakly negatively influenced by increasing corridor length. No model was obtained for Ochre-flanked Tapaculo, but for the Des Mur's Wiretail, backward selection retained a weak association with quila density.

We obtained a robust model with multiple regression for all species combined, and we identified corridor width and quila density as predictors of bird abundance, explaining about two-thirds of the variance (Table 4). Models for individual species varied from good (Magellanic Tapaculo; explaining 58% of the variation) to poor (wiretail; 33%). Huet-Huet, Magellanic, and Chucao Tapaculos increased

**Table 3.** Logistic regression results from the initial survey of forested corridors showing likelihood of bird species presence in relation to six independent variables.<sup>a</sup>

Species	n <sup>b</sup>	Model selected <sup>c</sup>	Coefficients	-2 LLR <sup>d</sup>	$\chi^2$	p
Five species pooled	24	C + width	0.08	118.1	27.4	<0.0001
Chucao Tapaculo	24	C + canopy - length	11.40, -0.02	13.6	19.5	0.0001
Black-throated Huet-Huet	20	C + width	0.11	19.5	8.3	0.0040
Magellanic Tapaculo	24	C + width	0.22	15.6	17.0	<0.0001
Ochre-flanked Tapaculo	13	C	— <sup>e</sup>	— <sup>e</sup>	— <sup>e</sup>	— <sup>e</sup>
Des Mur's Wiretail	24	C + MQD <sup>f</sup>	0.37	28.8	3.0	0.083

<sup>a</sup>Independent variables are listed in Table 2 (see methods).

<sup>b</sup>Sample sizes differ because Black-throated Huet-Huet and Ochre-flanked Tapaculo were not present in all locations (see text).

<sup>c</sup>C is a constant.

<sup>d</sup>-2 log-likelihood ratio.

<sup>e</sup>No predictors were selected.

<sup>f</sup>Model obtained via backward selection; MQD, mean quila density.

**Table 4.** Multiple regression models that identify predictors of bird abundance in initial surveys of 24 forested corridors.

Species	n <sup>a</sup>	Model selected <sup>b</sup>	Beta coefficients <sup>c</sup>	r <sup>2</sup>	Adjusted r <sup>2</sup>	F	p
Five species pooled	24	C + width + MQD	0.58, 0.35	0.66	0.63	20.8	<0.001
Chucaos Tapaculo	24	C + width	0.67	0.45	0.43	18.1	<0.001
Chucaos Tapaculo <sup>d,e</sup>	24	C + canopy	0.72	0.52	0.50	24.2	<0.001
Black-throated Huet-Huet	20	C + width	0.69	0.48	0.45	16.7	0.001
Magellanic Tapaculo <sup>d</sup>	24	C + width	0.76	0.58	0.56	30.0	<0.001
Ochre-flanked Tapaculo	13	C + MQD – canopy	0.99, –0.53	0.66	0.59	9.6	0.005
Des Mur's Wiretail	24	C + MQD – canopy	0.61, –0.45	0.33	0.27	5.2	0.015

<sup>a</sup>Sample sizes differ because Black-throated Huet-Huet and Ochre-flanked Tapaculo were not present in all locations (see text).

<sup>b</sup>C is a constant; MQD, mean quila density. Five independent variables were used (see methods).

<sup>c</sup>Standardized coefficients that account for different units of measure (z score; Norusis 1993).

<sup>d</sup>Square-root transformation of the response variable was used to correct for unequal variances (Weisberg 1985).

<sup>e</sup>Square-root transformation of the response variable altered the model for this species without correcting the unequal variances, but the model was improved so we include it.

in number with corridor width (Fig. 1). Chucaos were more abundant under closed canopy, whereas Ochre-flanked Tapaculos and wiretails were more numerous where quila was dense and canopy was sparse (Table 4); corridor width was unimportant for the latter two species (Fig. 1).

When birds were present in corridors, playback detected more individuals than passive census (14 of 17 nonzero cases;  $t = 5.0$ ,  $df = 16$ ,  $p < 0.001$ ; Table 5; Fig. 2). Playbacks significantly increased the detectability of four of the five species (Wilcoxon matched-pairs signed-ranks test on numbers of birds detected by playback versus passive census, given that a bird was known to be present: Chucaos Tapaculo, 30:23, not significant; Black-throated Huet-Huet, 16:4,  $z = -2.1$ ,  $p = 0.04$ ; Magellanic Tapaculo, 19:8,  $z = -2.23$ ,  $p = 0.03$ ; Des Mur's Wiretail, 16:3,  $z = -2.74$ ,  $p = 0.006$ ; Ochre-flanked Tapaculo, 8:2,  $z = -1.89$ ,  $p = 0.059$ ).

Examination of passive versus playback census data in relation to corridor width revealed three natural groupings of points (Fig. 2). In corridors narrower than 10 m, birds were generally not present (five of six corridors). In the eight intermediate-width corridors (11–23 m), birds were generally present but most were detected only via playback, whereas some birds were always detected in the 10 widest corridors with either census type. The difference in response to playback versus passive censuses was greatest in the medium-width corridors (circled area, Fig. 2). Playbacks detected 767% more birds than passive census in those corridors (compared with only a 67% increase in detection in the widest corridors), and the proportion of birds present but detected only by playback was significantly higher in intermediate-width corridors than wider ones ( $F = 7.1$ ,  $p = 0.029$ ,  $df = 1$ ; Table 5). Birds present in the widest corridors were generally more conspicuous than birds in intermediate-width corridors, and this differential between the two techniques provided a means to infer width-related variation in corridor use.

### Corridor Shape and Bird Abundance

The distribution of the maximum number of birds detected in relation to corridor length-to-width ratios (L/W) fit logarithmic ( $r^2 = 0.39$ ,  $F = 13.9$ ,  $p = 0.001$ ), linear ( $r^2 = 0.259$ ,  $F = 7.7$ ,  $p = 0.011$ ), and inverse ( $r^2 = 0.304$ ,  $F = 9.62$ ,  $p = 0.005$ ) functions; bird numbers clearly decreased with increasing L/W (Fig. 3). The distribution of the data, however, suggests a discontinuous threshold value for L/W between 10–15. No birds were found in corridors with higher L/W values, and below the threshold, bird abundance varied widely without relation to L/W (no significant models—linear, logarithmic, or inverse—were obtained for L/W values <15). Six of the eight highest L/W values were for narrow corridors <10 m wide, so, our data do not allow independent assessment of very narrow versus very long corridor configurations.

### Phase Two: Willingness to Enter Potential Travel-Only Corridors

We tested 103 individuals in 52 different potential travel corridors that responded to playback tapes, and 54 (52%) entered narrow strips with the following frequencies: Chucaos Tapaculo (18 of 30 tested), Black-throated Huet-Huet (6/14), Ochre-flanked Tapaculo (4/10), Magellanic Tapaculo (13/25), and Des Mur's Wiretail (13/24). Combined responses of all five species were related to quila density and the presence of streams (Table 6). The chucaos, in particular, was most likely to enter corridors with streams. We noticed during experiments that, unlike other species, responding chucaos often walked in shallow water. Wiretails and Magellanic Tapaculos could be drawn into strips with higher quila density where canopy cover was reduced. No predictors were identified for Ochre-flanked Tapaculo and Black-throated Huet-Huet responses by either forward or backward stepwise methods (Table 6).

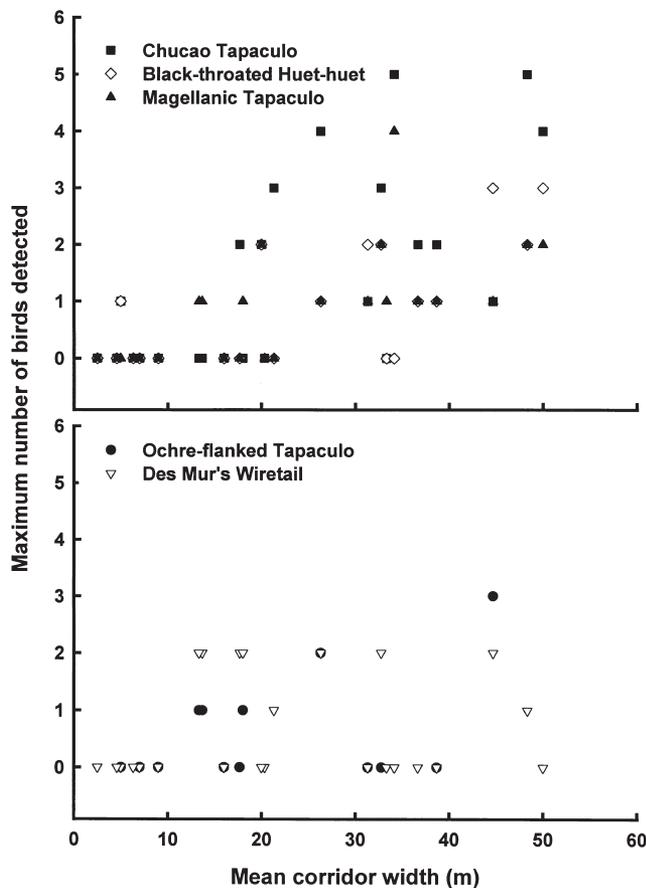


Figure 1. Maximum number of birds of each species detected on either passive or playback censuses in the initial survey of 24 forested corridors. Corridor width is an important predictor of abundance for three species (top panel) but not for the other two (bottom panel).

## Discussion

### Determinants of Corridor Function

For at least three of the study species (Black-throated Huet-Huet, Magellanic, and Chucaco Tapaculos), corridor width was a strong predictor of species presence and abundance in the initial survey, given favorable vegetative structure (Tables 3 & 4; Fig. 1). With more data, Ochre-flanked Tapaculo abundance might be linked to corridor width (Fig. 1), but our analysis suggested that both this species and the wiretail have a strong affinity for dense vegetation, including bamboo (Tables 3 & 4; Fig. 1; see also Díaz 1999; Estades & Temple 1999; McPherson 1999), which outweighs other corridor characteristics. Our results are consistent with other empirical studies that support the theoretical positive relationship between corridor width and animal use (i.e., greater species richness and abundance; Friend 1991; Rosenberg et al. 1997; Beier & Noss 1998). In seeming contradiction, Lindenmayer and Nix (1993) discounted

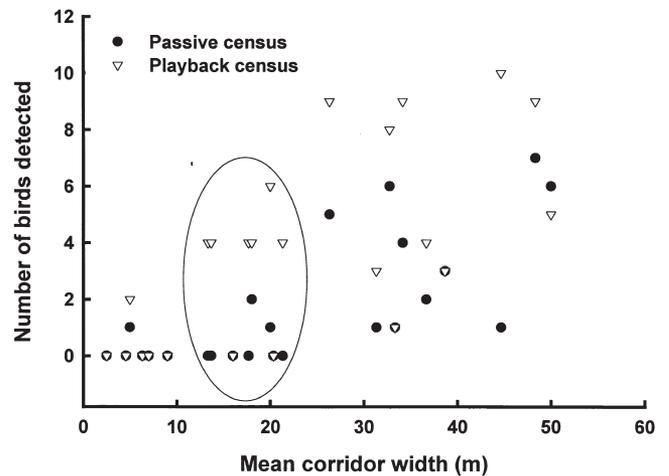


Figure 2. Comparison of maximum number of individuals detected via passive and playback census (five species pooled) during phase-one surveys. Circled area highlights the contrast between passive and playback census results in corridors 10–22 m wide; birds present in these intermediate-width corridors were less detectable via passive census than birds present in wider corridors.

any effect of corridor width on mammalian use of forest corridors in Australia; but the narrowest corridors they surveyed were 30 m wide. Because some of their study species were similar in body size to ours, perhaps with similar space requirements, it is possible they did not include corridors narrow enough to discourage regular use and thus detected no effect of width.

We used differences in bird detections between passive and playback census to suggest how corridor width might influence use. That birds were present but less detectable via passive census in corridors of intermediate width suggests that they were singing less and behaving more cryptically (Parker 1991) than birds in wider corridors. During censusing in narrow and intermediate-width corridors, the entire width of each corridor was usually visible, but this was not necessarily true in the widest corridors. If bird behavior was invariant, therefore, a greater proportion of birds present in the intermediate-width and narrow corridors during passive censuses should have been detected than in the widest corridors. But this was not the case, especially for chucaos: they were equally detectable by the two census types in the widest corridors but relatively undetectable via passive censusing in corridors 11–23 m wide (Table 5). Therefore, corridors in this width range are probably transitional for chucaos: wide enough to be used in some ways—supplemental foraging, daily movements between close patches, dispersal—but too narrow to support core territory establishment. In contrast, huet-huets were not easily detectable via passive censusing in

**Table 5.** Number of birds detected in passive versus playback censuses, respectively, in corridors of different widths ( $n = 8$  corridors for each column) in phase one of the study.

Species	Corridor			Total
	narrowest (2–14 m)	intermediate (15–31 m)	widest (32–50 m)	
Chucaos Tapaculo	1 / 1	3 / 11	19 / 18	23 / 30
Black-throated Huet-Huet	0 / 1	1 / 4	3 / 11	4 / 16
Magellanic Tapaculo	0 / 2	1 / 5	7 / 12	8 / 19
Ochre-flanked Tapaculo	0 / 2	2 / 3	0 / 3	2 / 8
Des Mur's Wiretail	0 / 4	2 / 7	1 / 5	3 / 16
Total	1 / 10	9 / 30	30 / 49	40 / 89

any corridor (on average, 70–100% of individuals present were only detected via playback), suggesting that even the widest corridors we surveyed might not reliably encourage territory establishment (and conspicuous defense) by these larger-bodied birds (Table 1).

Our analysis suggests that the significant negative relationship between bird abundance and corridor length-to-width ratio may be described by a threshold effect. The study species rarely occurred in corridors where the ratio of length to width exceeded 10, suggesting that relatively long corridors (those beyond the threshold, or >500 m long) are not useful for birds seeking either living and foraging space or travel paths. Chucaos may even avoid longer corridors (Table 3). Although our data set does not allow us to discern the independent effects of narrow width versus excessive length, it supports speculations and empirical findings that relatively long corridors have reduced utility for animals living in fragmented habitat mosaics (Harris 1984; Noss & Cooper-rider 1994; Rosenberg et al. 1997; Beier & Noss 1998; Haddad 1999a).

#### Willingness to Enter Potential Travel Corridors: the Primacy of Cover

This study, the birds' avoidance of open fields (Sieving et al. 1996; Estades & Temple 1999), and our observations all indicate that these understory birds tend to stay in cover. Understandably, quila emerged as an important predictor of positive responses to playback in marginal corridors because it provides dense foliage that all the study species regularly or habitually use on Chiloé. In addition, small streams with banks—favored by chucaos responding to playbacks (Table 6)—also provide low-light pathways that might reduce mortality risks from known predators, including carnivorous birds and the native forest cat (*Oncifelis guíña*). Plumage colors of the study species range from orange and browns to grays and black, and in rainforest understory these tones are relatively inconspicuous to human eyes against the backgrounds of leaf litter, mud, fallen trees, and mosses. Other birds select particular light environments for

courtship displays and protection (Endler 1997), and these understory species probably have similar abilities for discriminating among potential travel paths with different cover characteristics.

We recognize, however, that the birds' discrimination among potential travel paths must be interpreted with care, given the methodology we used to manipulate their behavior. Taped-song playback is increasingly utilized in landscape ecological studies of birds, but cautious interpretations of results are warranted because both the birds' behavioral states and their risk environments are altered during playback. Birds responding to conspecific song are in heightened states of excitement (Zimmer 1982; Diehl & Helb 1992) and aggression (Prescott 1987), and playback-elicited territorial or mobbing displays can increase birds' conspicuousness and risk of predation. For example, we observed attacks on our study species by Bicolored Hawks (*Accipitor bicolor*) and Austral Pygmy Owls (*Glaucidium brasilianum*) during playbacks. Thus, if respondents experienced high risk of predation while in a heightened state of aggression, we cannot be certain whether they were more or less cautious during playback than when alone. Moreover, it is difficult to know how the behavior of territorial adults during playbacks may reflect the behavior of dispersing (juvenile) birds.

Based on our knowledge, we suggest the following. First, it does not appear that birds responding to playback were desensitized to predation risk or that they behaved differently than free-ranging animals. Two birds were attacked by raptors during trials but readily escaped into nearby cover; aggression did not push them beyond ready access to refuge. Moreover, once pulled into corridors, respondents took much longer to return to the forest patches and many continued to sing (at a slower rate) and forage for food as they retreated. Apparently, the birds' decision to enter the corridors during playback was not dissociated from their willingness to use them for short-distance moves and maintenance activities. Similarly, in an experimental study of two butterfly species allowed to range freely in experimental plots, Haddad (1999b) found a robust correlation between the

**Table 6.** Logistic regression results for taped-song playback experiments at potential travel-only corridors (phase two of the study), indicating the likelihood that respondents were willing to enter corridors in relation to six independent variables.

Species	n	Model selected <sup>a</sup>	Coefficients	-2 LLR <sup>b</sup>	$\chi^2$	p
All five species	103	C + MQD - rip (1)	0.47, -1.41	116.0	26.5	<0.001
Chucao Tapaculo	30	C - rip (1)	-2.90	28.8	11.6	0.0007
Black-throated Huet-Huet	14	C	— <sup>c</sup>	— <sup>c</sup>	— <sup>c</sup>	— <sup>c</sup>
Magellanic Tapaculo	25	C + MQD	0.52	30.0	4.7	0.0301
Ochre-flanked Tapaculo	10	C	— <sup>c</sup>	— <sup>c</sup>	— <sup>c</sup>	— <sup>c</sup>
Des Mur's Wiretail	24	C + MQD	0.91	27.8	5.3	0.0212

<sup>a</sup>C is a constant; MQD, mean quilla density; - rip (1), coefficient for riparian score 1 (dry or standing water) is negative, meaning birds favored corridors with running water.

<sup>b</sup>-2 log-likelihood ratio.

<sup>c</sup>No predictors were selected.

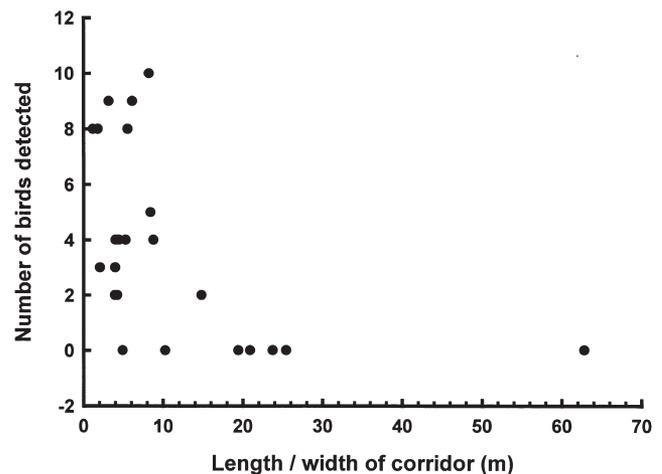
behaviors of entering and subsequently moving into or through habitat corridors embedded in nonhabitat matrix. Thus, we have no clear evidence that birds were more or less vulnerable to predation during experiments or that playbacks caused them to make decisions uncharacteristic of free-ranging animals.

Second, we suspect that territorial adults are less likely to enter marginal corridors with poor cover than dispersing juvenile birds and, therefore, that our playback experiments were conservative assessments of the species' willingness to enter narrow corridors. Juveniles appear to be more adventurous than breeding adults. For example, we saw hatch-year huet-huets in narrow road hedges >0.5 km from forest, passing through large shrub fields with only scattered trees and moving readily through a narrow corridor near an observer while an accompanying adult refused to follow. In addition, aggressive attacks by parents (K.E.S., M.F.W., T.L.D., personal observations) provide motivation for juveniles to move out into the landscape once they have attained the age of independence. If juveniles are more dispersive in marginal cover than adults, as we suspect they are, then our experimental tests of adults' willingness to select and enter narrow corridors are conservative and likely to identify potential travel paths that dispersing juveniles would readily enter and use.

### Corridor Efficacy for Endemic Understory Birds

Over half the birds we tested chose to enter and move short distances in narrow (travel-only) corridors, but path selection and use is only a partial realization of corridor efficacy (Rosenberg et al. 1997). To provide connectivity in a landscape dominated by a hostile matrix, corridors must reliably support successful trips. Distance is hypothesized to be the most important determinant of successful interpatch dispersal (at any temporal or spatial scale; Haddad 1999a; Zollner & Lima 1999). Important interpatch movements made by the study species include natal and breeding dispersal and daily home-range activities, and most of these occur at a relatively small scale. During a companion study, we documented

five successful natal dispersal events by color-banded chucaos within forest patches, all <300 m long. Even assuming possible constraints imposed by forest patch size, mean natal dispersal distances of these species are likely to be at the bottom end of the known range for passerines (range 350–1700 m; Barrowclough 1980). Therefore, restoration and maintenance of biologically relevant connectivity for these birds will clearly involve short interpatch distances (at the scale of hundreds of meters or less) when travel-only corridors are being considered. Also, because greater width can reduce the velocity of animal movement through corridors (Rosenberg et al. 1998), there may be functional niches for short but narrow corridors in conservation plans. For example, most Chilote landowners operate small farms with small but habitable forest patches within 100–200 m of each other. Narrow corridors with dense cover might efficiently shunt dispersing birds between close patches and would be easier for farmers to manage and use as natural stock fences or windbreaks than wide corridors that might slow the birds' passage, exposing them to



**Figure 3.** Maximum number of birds (species pooled) detected via either passive or playback census versus the shape (ratio of length to width, L/W) of corridors censused in phase one of the study.

greater risk (Zollner & Lima 1999). Of course, rigorous definition of optimum lengths and other features for successful travel-only corridors will require radiotelemetry studies of free-ranging birds that have different kinds of corridors available to them (Beier & Noss 1998).

Assessing the efficacy of wider corridors as functional habitat requires survival and reproductive information from residents of both corridors and unfragmented forest for comparative, long-term study. In a companion study, we found that rhinocryptids often fledge young from nests in corridors. In fact, rhinocryptid reproductive success in fragmented forest is nearly as high on average as in unfragmented rainforest. In contrast, it appears that other understory birds with open-cup nests (rhinocryptids nest primarily inside trees, stumps, and banks) suffer elevated losses in forest fragments, and artificial open-cup nests placed in corridors are attacked significantly more often than those in forest patches (T.L.D., M.F.W., K.E.S., and J.L. Morrison, unpublished data). Even though the rhinocryptids appear to reproduce successfully in corridors, elevated nest predation pressures may signify greater fledgling and adult mortality for all species. Thus, testing the assumption that corridor use is equivalent to long-term functionality is a priority for this system.

## Conclusions

This study was one step in an effort to understand the design of agricultural landscapes that will sustain viable populations of endemic rainforest birds. Our conclusions cannot be used directly as management guidelines, but they represent normative hypotheses for studies of functional corridor designs. Our study also provides the means to visualize what connectivity for rhinocryptids looks like and facilitates analysis of landscape-level distributional constraints (With & King 1998; Brooker et al. 1999). Given suitable vegetation characteristics and conjunction with habitable forest patches, we hypothesize that (1) to fulfill both habitat and travel functions, corridors that are 50 m wide should be less (potentially much less) than 500 m long ( $L/W \leq 10$ ) if they are to be inhabited or used regularly, and narrower corridors should be scaled down in length accordingly; (2) habitat functions can be provided for the smaller species in corridors at least 25 m wide, although territory establishment and defense by huet-huets may not occur regularly at the narrow end of this range; (3) regular nonterritorial use (e.g., foraging, traveling) may be supported by corridors at least 10 or 11 m wide; (4) all five species can probably use narrow corridors for short-term (within a day) and short-distance (<100 m) travel if sufficient understory cover is available; and (5) if wide enough, riparian corridors with canopy cover should invite use by chucaos.

These hypotheses are relevant for the landscape of northeastern Chiloé, where agriculture relies primarily on animal power and most nonagricultural landcover is comprised of native vegetation. Mainland Chile and Argentina, encompassing the majority of the rainforest bioregion, is dominated by industrialized agriculture where exotic and invasive plant species are widespread, vegetative heterogeneity is low, and native forest cover per unit landscape area is lower overall. Therefore, responses of the study species to corridors in mainland landscapes may be distinct from what we have documented for northeastern Chiloé (Estades & Temple 1999).

Concepts of corridors and landscape designs for conservation are decades old (Shelford 1933; Croker 1991). Recent thinking and empirical work increasingly refines the scientific approach to testing their utility (Ims 1995; Beier & Noss 1998; Brooker et al. 1999), and our work is part of that trend. Using direct behavioral responses to landscape elements to identify their potential functions for target species is a relatively new approach (Lima & Zollner 1996), and song-playback experiments have provided a means of accomplishing this for forest birds (Sieving et al. 1996; Desrochers & Hannon 1997; Rail et al. 1997). These methods will likely apply to forest understory and shrub-requiring birds elsewhere (e.g., Danks 1991; Sieving & Karr 1997; Brooker et al. 1999).

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