

---

# An Experimental Test of Matrix Permeability and Corridor Use by an Endemic Understory Bird

TRACI D. CASTELLÓN\* AND KATHRYN E. SIEVING

Department of Wildlife Ecology and Conservation, 303 Newins-Ziegler Hall, University of Florida, Gainesville, FL 32611-0430, U.S.A.

---

**Abstract:** *Because of widespread habitat fragmentation, maintenance of landscape connectivity has become a major focus of conservation planning, but empirical tests of animal movement in fragmented landscapes remain scarce. We conducted a translocation experiment to test the relative permeability of three landscape elements (open habitat, shrubby secondary vegetation, and wooded corridors) to movement by the Chucaco Tapaculo (Scelorchilus rubecula), a forest understory bird endemic to South American temperate rainforest. Forty-one radio-tagged subjects were translocated (individually) to three landscape treatments consisting of small release patches that were either entirely surrounded by open habitat (pasture), entirely surrounded by dense shrubs, or linked to other patches by wooded corridors that were otherwise surrounded by open matrix. The number of days subjects remained in release patches before dispersal (a measure of habitat resistance) was significantly longer for patches surrounded by open habitat than for patches adjoining corridors or surrounded by dense shrubs. These results indicate that open habitat significantly constrains Chucaco dispersal, in accord with expectation, but dispersal occurs equally well through wooded corridors and shrub-dominated matrix. Thus, corridor protection or restoration and management of vegetation in the matrix (to encourage animal movement) may be equally feasible alternatives for maintaining connectivity.*

**Key Words:** corridors, dispersal, forest fragmentation, gap crossing, matrix, Rhinocryptidae

Una Prueba Experimental de la Permeabilidad de la Matriz y el Uso de Corredores por una Especie de Sotobosque Endémica

**Resumen:** *Debido a la fragmentación de hábitat generalizada, el mantenimiento de la conectividad en el paisaje se ha convertido en un aspecto principal de la planificación de conservación, pero las pruebas empíricas del movimiento de animales en paisajes fragmentados son escasas. Realizamos un experimento de translocación para probar la permeabilidad relativa de tres elementos del paisaje (hábitat abierto, vegetación secundaria arbustiva y corredores arbolados) al movimiento del Tapaculo de Chucaco (Scelorchilus rubecula), una especie de ave de sotobosque endémica al bosque lluvioso templado de América del Sur. Translocamos (individualmente) a 41 aves con radio transmisores a tres paisajes-tratamiento consistentes en pequeños parches de liberación que estaban completamente rodeados de hábitats abiertos (pastizales), completamente rodeados de arbustos densos o unidos a otros parches por medio de corredores arbolados que a su vez estaban rodeados por matriz abierta. El número de días en que los sujetos permanecieron en los parches de liberación antes de dispersarse (una medida de la resistencia al hábitat) fue significativamente mayor para parches rodeados por hábitat abierto que para parches contiguos a corredores o rodeados por arbustos densos. Estos resultados indican que la dispersión de Chucaco es inhibida significativamente por el hábitat abierto, de acuerdo con lo esperado, pero ocurre igualmente bien a través de corredores arbolados y matriz arbustiva. Por lo tanto, la protección o restauración de corredores y el manejo de la vegetación en la matriz (para estimular el movimiento de animales) pueden ser alternativas igualmente viables para mantener la conectividad.*

**Palabras Clave:** corredores, cruce de claros, dispersión, fragmentación de bosques, matriz, Rhinocryptidae

---

\*email tdarnell@ufl.edu

Paper submitted February 15, 2005; revised manuscript accepted April 27, 2005.

## Introduction

To offset effects of habitat fragmentation, maintaining landscape connectivity has become a major focus of conservation planning, and providing movement corridors is currently a favored approach (e.g., Desrochers & Hannon 1997; Haddad 1999; Berggren et al. 2002). Research, however, has largely ignored the degree to which animals move through the nonhabitat matrix (Beier & Noss 1998; Ricketts 2001; Hudgens & Haddad 2003). For many species the matrix constitutes unsuitable and potentially hostile habitat (Arendt 2004), but it is rarely a complete barrier to dispersal. In some cases, movement through the matrix may be sufficient for immigration to offset extinction in local (sub)populations (Witt & Huntly 2001; Hudgens & Haddad 2003), and distinct habitat types within the matrix (defined by vegetative and other structural features) may be differentially permeable to a variety of species (Ricketts 2001; Ries & Debinski 2001; Rodríguez et al. 2001). Understanding how habitat structure in the matrix influences permeability to animal movement is key to managing complex landscapes for conservation (Turchin 1998; Ricketts 2001; Vandermeer & Carvajal 2001).

Experimental methods are the most efficient means for identifying causal mechanisms, but most experimental studies examining animal movement have used invertebrate subjects, often in highly artificial experimental landscapes (e.g., Berggren et al. 2002; Hein et al. 2003). To date, experimental methods applied to vertebrate subjects include using tape-recorded songs to provide a stimulus for forest birds to enter wooded corridors or cross open habitat gaps (e.g., Sieving et al. 1996; St. Clair et al. 1998; Bélisle & Desrochers 2002), and translocating small mammals and birds to assess gap-crossing decisions (Bright 1998; Bowman & Fahrig 2002) and movement paths in the context of homing behavior (Bright 1998; Bélisle & St. Clair 2001; Bakker & Van Vuren 2004). Translocation has also been used to assess migration rates among patches with and without corridors, relative to a single high-contrast matrix type (Bowne et al. 1999), and to assess homing time in landscapes with differing percentages of open matrix (Bélisle et al. 2001; Gobeil & Villard 2002). From these studies we know that a variety of forest vertebrates are clearly averse to entering open habitat, that wooded corridors most likely facilitate movement for some species, and that homing behavior may be impeded in landscapes dominated by open matrix.

Although these studies have contributed greatly to development of the dispersal barriers and landscape connectivity concepts, they fail to distinguish the relative importance of corridors versus alternative matrix types and many rely on assumptions that hinder applicability to natural dispersal. Playback experiments, for example, can yield detailed observations on specific movement choices, but they may have little relevance to dispersal

because movement in response to perceived territorial intruders or predators may differ from dispersal. Similarly, homing behavior of subjects translocated short distances misrepresents dispersal in that the landscape near a subject's home range is familiar, whereas dispersing individuals must respond to novel landscape mosaics and unfamiliar risk environments (Yoder et al. 2004). In contrast, long-range homing studies may generate excellent approximations of dispersal but often lack the level of observational detail to detect specific movement choices (e.g., the decision to cross an area of matrix or detour through a corridor or alternative habitat type). Thus, direct comparisons of movement by dispersing individuals through corridors with alternative matrix habitats are still needed (Nicholls & Margules 1991; Inglis & Underwood 1992; Simberloff et al. 1992).

We used radiotelemetry to monitor movements of translocated Chucao Tapaculos (*Scelorchilus rubecula*) to compare the permeability of wooded corridors relative to two common matrix habitat types (open pasture and shrubby secondary vegetation). The experimental design avoided pitfalls associated with passive observation, including lack of control over landscape composition and lack of detail regarding specific movement choices. Yet empirical realism remained high because subjects were wild-caught individuals released into very small patches (inadequate for breeding), stimulating dispersal typical of birds searching for new territories (Ims 1995). Furthermore, we translocated subjects far enough (5–9 km) from their capture sites to prevent homing and eliminate bias due to previous knowledge of the landscape (Yoder et al. 2004). To our knowledge, this is the first study to experimentally test permeability of matrix types differing in vegetation structure relative to movement corridors using a vertebrate subject.

## Methods

### Study System

South American temperate rainforest occupies a narrow zone between 35°S and 55°S in Chile and western Argentina and is considered a global hotspot for endemic species loss (Balmford & Long 1994; Davis et al. 1997; Stattersfield 1998). Among forest birds, endemic understory insectivores in the family Rhinocryptidae (tapaculos) are among the most sensitive to fragmentation in the biome (Willson et al. 1994). Tapaculos are primarily terrestrial species that are poor flyers and strongly associated with dense forest understory (Reid et al. 2004). Although reluctant to enter open habitat, they will use narrow wooded strips for movement among forest patches (Sieving et al. 1996, 2000). This sensitivity to dispersal habitat makes the group potentially valuable as focal species for planning the connectivity component of landscape design

because a landscape that provides functional connectivity for the group would probably meet the dispersal requirements of many forest species.

We selected the Chucao Tapaculo for study because it is locally abundant and intermediate in size and vagility among the four tapaculos (Sieving et al. 2000). Chucaos are year-round residents that are strongly territorial and usually retain the same breeding territory year after year (De Santo et al. 2002; M. Willson, unpublished data). They are poor flyers and move (even during dispersal) by walking, hopping, and flying short distances (no more than a few meters), usually within or near dense vegetative cover.

The study was conducted in a fragmented agricultural landscape on northern Chiloé Island, Chile (41°55'S, 73°35'W). Pastures and abandoned agricultural fields dominate the landscape, with wooded habitat covering approximately 35% of the total study area (approx. 300 km<sup>2</sup>). At present, many forest patches remain interconnected by linear vegetated strips, including fencerows, riparian draws, and ravines. Dominant trees are broad-leaved evergreens and a few conifers (*Nothofagus nitida* [Phil.] Krasser, *Drimys winteri* J. R. et G. Forster, *Eucryphia cordifolia* Cav., and *Podocarpus nubigena* Lindl.), with understory composed principally of bamboo (*Chusquea valdiviensis* Phil.) and saplings (Donoso 1993). Secondary vegetation in many abandoned agricultural fields is dominated by *Baccharis magellanica* (Lam.) Pers., a persistent shrubby invader of poorly drained soils, with thick mats of *Sphagnum* spp. moss covering the ground.

### Experimental Design

Subjects were captured in large forest tracts, fitted with radio transmitters and released individually (each subject tested once) into small wooded patches at the centers of experimental landscapes. Release patches were unoccupied by conspecifics and large enough to meet the subjects' immediate requirements for food and shelter, but too small (<0.30 ha) to serve as adequate breeding territories ( $\geq 1$  ha; De Santo et al. 2002). This approach provided a standardized stimulus for rapid dispersal from release patches, allowing direct observation of movement paths. We interpreted delayed dispersal of a subject from the release patch as a measure of behavioral resistance to entering and moving through the matrix elements presented.

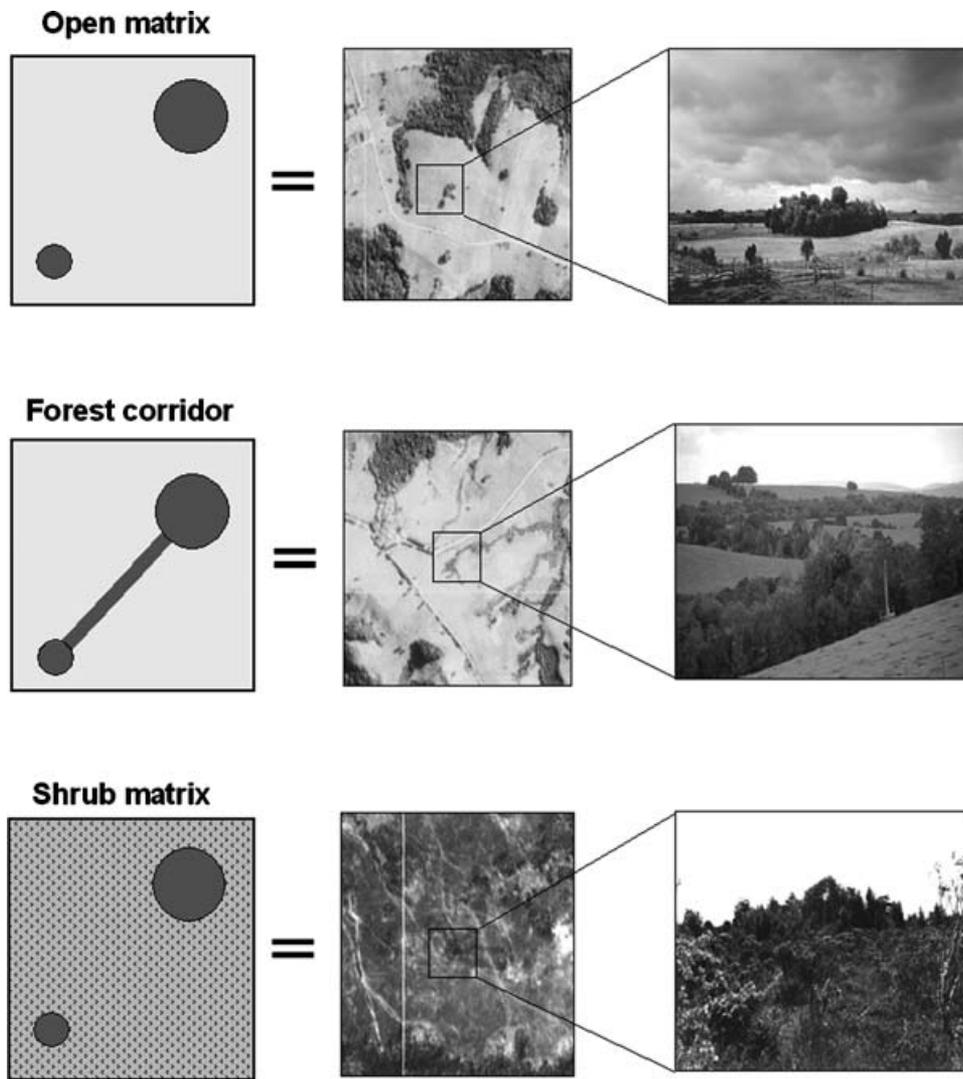
The experimental treatments consisted of release patches that were entirely surrounded by open habitat, entirely surrounded by dense shrubs, or linked to other patches by wooded corridors embedded in open matrix (Fig. 1) but were within 150 m of at least one suitable habitat patch. The fourth block of the experimental design, forest patches with wooded corridors embedded in

a shrub matrix, was not included because this configuration did not exist in the study landscape. The "open" and "shrub" matrix types consisted, respectively, of pastures and shrubby vegetation dominated by *B. magellanica* (1- to 2-m tall). Wooded corridors adjoining release patches in the corridor treatment were either continuous or had breaks in the vegetation of  $\leq 2$  m and were otherwise surrounded by open pasture. Each corridor was approximately 10 m wide, but margins were not perfectly linear and some corridors narrowed or expanded within a range of 2-15 m at various points. Lengths of corridors (to the nearest adjoining patch) varied from 60 to 500 m. In general, corridor vegetation consisted of 2- to 3-m-tall native trees, with occasional sections of lower stature vegetation, and understory dominated by saplings and bamboo. Corridors of these dimensions were expected to function only as conduits for movement rather than as habitat for long-term survival or breeding (Sieving et al. 2000).

### Selection of Release Sites

Replicate release sites used in each treatment were chosen from the existing landscape through assessment of aerial photographs and site visits. We standardized replicates as much as possible with regard to release patch area, habitat quality, and landscape context. Each release patch was surrounded by only one matrix type, with similar ranges among treatments for potentially important landscape-context factors (distance to the nearest patch large enough to support a breeding territory [ $\geq 1$  ha], distance to the nearest patch of any size, and the percentage of wooded habitat within a 100-m buffer). We used a total of 25 sites (8-9 replicates per treatment), with a maximum of two trials conducted at each site. Repeated use of sites was necessary because of scarcity of locations with appropriate characteristics. Sites were never reused, however, until we were certain the previous subject was no longer present. Although release patches were free of conspecifics, all but the most isolated patches  $\geq 3$  ha in the surrounding landscape were occupied (T.M.C., unpublished data).

Despite our best efforts to minimize differences among release patches, the corridor sites available in the study landscape tended to be less disturbed than open- and shrub-matrix sites. Therefore, some release patches in the corridor treatment were slightly larger and of better quality than those in other treatments. Conversely, release patches in the open matrix (pasture) treatment were of lowest quality because of effects of livestock. Because we expected the stimulus for dispersal to be strongest when habitat quality was low (e.g., Buddle & Rypstra 2003), using lower quality release patches (stimulating quicker dispersal) in the open matrix treatment made our analysis conservative with regard to the a priori expectation of longer dispersal delays for this group.



*Figure 1. Schematic representation of the three landscape treatments (release patches surrounded by open matrix, adjoining a wooded corridor, or surrounded by a matrix of dense shrubs), along with aerial photographs (1:10,000) of corresponding translocation sites for each treatment (one replicate each shown) and photographs of the sites taken in the field. Test subjects were released (individually) into a small wooded patch at the center of each replicate.*

### Capture and Handling

Chucaos were captured during the breeding seasons (2000–2002) with walk-in traps baited with earthworms. We marked each subject with colored plastic leg bands and a small radio transmitter (1.3–1.7 g, approximately 3–4% of adult body mass). We attached transmitters with a skin-safe epoxy (ARC 5; Composite Technology, Stonham, Massachusetts), formulated to cure rapidly under low temperature, high humidity conditions. The transmitters were bonded to the tops of tail feathers (rectrices), at the base of the feathers near the quills, positioned to avoid contact with the uropygial gland. Because Chucaos do not use long-distance flight for travel, foraging, or predator avoidance, mounting transmitters onto tail feathers was appropriate.

We captured subjects between sunrise and 1100 hours and held them a maximum of 2.5 hours from the time of capture to release. Each subject was transported individually in an opaque container that prevented visual assessment of the surroundings. To minimize the influence of

stress from handling and transport on movement behavior, each subject was left undisturbed inside the container (provisioned with earthworms as food) at the release site for 15 minutes. Additionally, the observer conducted the release from a concealed location by pulling a long string to remove a section of the container's lid. Subjects exited in an upward direction, preventing bias in the postrelease movement path. Once the subject exited the container, the observer left the area as quickly and quietly as possible. To prevent temporal bias among treatments, a release was conducted in one replicate of each treatment before conducting a subsequent release in any of the treatments.

It was not possible to standardize for sex or age among subjects because data on plumage characteristics are not available to readily distinguish sexes (laparoscopy was deemed too invasive) or between older juveniles and adults. This lack of standardization made our study conservative because juvenile and female birds are typically more dispersive than adults and males (Greenwood & Harvey 1982; Johnson & Gaines 1990). We were also unable to standardize among subjects that were territory holders

versus floaters at the time of capture. Nonetheless, we expect that all subjects, regardless of their territorial status, were strongly motivated to disperse from the unsuitably small release patches.

### Monitoring Dispersal Movements

Each corridor adjoining a release patch was monitored continuously (during daylight hours) by a telemetry operator stationed in a nearby concealed location or by an automated receiver and data logger (models R2100 and DCC D5041, Advanced Telemetry Systems, Isanti, Minnesota). We placed a 25-cm omnidirectional antenna at the center of each corridor (at the midpoint lengthwise) and set the telemetry reception range to the corridor width by adjusting the receiver gain. This configuration ensured that presence of the subject would be recorded only when it passed through the corridor. If the subject dispersed from the release patch but was never recorded inside the telemetry reception area, it was assumed that dispersal occurred through the open matrix in which the release patch and corridor were embedded. This design was an improvement over many previous studies that assumed corridor use without addressing the potential for dispersal through the matrix (Simberloff et al. 1992; Beier & Noss 1998).

In addition to continuous monitoring of corridors, an observer on foot located each subject once daily with a hand-held receiver and directional antenna. To avoid disturbance to subjects, the observer approached only close enough to identify the occupied habitat patch and then left the area. If no movement was observed over a 3-day period, the observer approached close enough to obtain visual confirmation that the transmitter was attached and the subject was alive. Dispersal was defined functionally as movement from an occupied patch to any other landscape element (usually another wooded patch, but movements into the shrub matrix were observed). Because release patches in noncorridor treatments were each surrounded by only one matrix type (either open habitat or shrubs), we assumed that any subject found outside the release patch must have crossed the associated matrix, moving a distance equal to or greater than the minimum distance to the nearest neighbor patch (not necessarily the patch occupied at the time of observation). No assumptions could be made about the actual travel path in the matrix, however, because any number of routes could have been followed to reach the observed location.

We used data from continuous monitoring of corridors only to document corridor use, whereas the number of days each subject remained in the release patch was determined from daily telemetry surveys. This distinction was important because some subjects made excursions into a corridor (detected via continuous monitoring) but returned to the release patch before being observed outside the patch during the daily survey. Under these circum-

stances, using data from corridor monitoring to establish time to dispersal would have been inappropriate because noncorridor treatments were not monitored with equal intensity, and similar exploratory movements into the matrix may have been undetected. Therefore, using these data would have biased dispersal-time estimates, making it appear that dispersal occurred more quickly in the corridor treatment.

Once subjects dispersed outside the experimental areas (each with only one matrix type), we had no control over the landscape conditions they encountered, and there were many factors we could not monitor that potentially influenced movement decisions, including intraspecific interactions, territory vacancies, and habitat quality. Thus, monitoring of dispersal movements outside experimental areas was entirely descriptive and interpretation was necessarily conservative. Given an observed movement from one documented location to another, our qualitative analysis addressed only the following measures: minimum distance across the matrix the subject must have moved to reach the new location (i.e., minimum distance from the occupied patch to the nearest-neighbor patch, making no assumptions about the actual travel path); area of each visited patch; number of times each patch was visited by the same subject; and linear distances between observed locations. Although these measures are basic, they nonetheless provided previously unavailable anecdotal information with potential value for conservation planning.

As constraints permitted, monitoring of each subject continued until the transmitter failed ( $\leq 30$  days) or detached, or until a subject settled in a new patch for  $\geq 2$  weeks. On a few occasions monitoring was terminated early for subjects that dispersed into large roadless areas, where tracking was impractical. Some signals were permanently lost for unknown reasons. When this occurred, we searched intensively by driving and walking within a search radius of several kilometers from the last known location. We made attempts to locate the lost subject for 3 days, then searched opportunistically as time permitted.

### Measurement of Landscape Metrics

We used remote sensing and geographic information system (GIS) analysis to quantify landscape metrics. Scanned panchromatic orthophotographs (1:20,000), taken in January 1993, were georeferenced and joined to create a single digital orthophotomosaic with 2-m<sup>2</sup> pixel resolution. We hand digitized wooded habitat cover (old growth and secondary combined) at a minimum mapping unit of 10 m<sup>2</sup> in ArcView 3.2 (ESRI 1999). We groundtruthed photo-interpretation extensively in the field during site visits for telemetry monitoring and corrected significant changes in land cover since acquisition of the photographic data on the digital maps.

We plotted radiotelemetry location data on the digital map and estimated dispersal distances by measuring the minimum straight-line distances between daily locations for each subject and the maximum displacement of each subject from its release patch. In addition, we measured the orientation angle of each subject's movement path (from the release patch to the last recorded location) relative to the center of its capture site. Landscape context metrics were calculated using ArcView and FRAGSTATS (version 3.3; McGarigal et al. 2002). These included release patch area, distance to the nearest neighbor patch (of any size and  $\geq 1$  ha), percentage of wooded habitat within a 100-m buffer, and area of each visited patch. The 100-m buffer radius was selected because the hypothesized relationship between landscape context and a subject's decision to disperse presumed that the subject was capable of evaluating the surrounding landscape. Because we had no independent data on Chucao perceptual range (Lima & Zollner 1996), we conducted a preliminary analysis of patch occupancy data (T.M.C., unpublished data) and selected the smaller of the two buffer distances (100 and 300 m) wherein landscape context variables were identified as significant predictors of Chucao occupancy.

### Data Analysis

The translocation experiment assessed the number of days birds remained in release patches before dispersal, which was interpreted as a measure of subjects' reluctance to disperse and conversely resistance of the presented landscape elements to movement. We used Cox regression to compare this response among treatments. Cox regression compares survival curves (survival = time elapsed before occurrence of a terminal event) among treatment groups. In this experiment, dispersal of a subject from the release patch was treated as the terminal event, whereas remaining in the patch was analogous to survival. Survival analysis was appropriate because it permitted use of censored (i.e., incomplete) data collected on subjects that died or lost their transmitters before dispersal. Predictor variables included the landscape treatment (corridor, open matrix, and shrub-matrix treatments) and the set of landscape context variables described in the previous paragraph. We included the interaction term (treatment \* distance to the nearest patch  $\geq 1$  ha) because a more pronounced effect was expected for the open matrix treatment, which was presumed most resistant to movement.

Model fitting was conducted using forward-stepwise likelihood-ratio estimation (Harrell 2001). At each step of model building, we added the variable that produced the most significant ( $p \leq 0.05$ ) change in the model chi-square (equal to the difference between the  $-2$  log-likelihood of the model at the previous step and the current step). Then, to arrive at the most parsimonious set of predictors, we independently removed variables already

in the model and calculated the change in the chi-square. If the change was not significant ( $p \geq 0.10$ ), we removed the specified variable. This iterative process was continued until no more variables could be added or removed. We determined significance of differences among treatments with linear contrasts. Alternative model-building approaches (backward-stepwise and single-step entry of all variables) were also tested to ensure that conclusions were not dependent on the model selection procedure.

To assess potential loss of data independence caused by repeated use of some release sites, we conducted a preliminary analysis of data from those sites in which site identity was entered as a categorical factor. Because site identity was not a significant predictor of days to dispersal and each individual subject was tested only once, each trial was treated as an independent statistical unit in the final analysis. Before analysis we calculated Pearson correlation coefficients for pair-wise comparisons among landscape variables to ensure that none were strongly correlated (i.e.,  $r > 0.7$ ). Finally, to identify any potential influence of homing behavior on movement direction, we assessed the orientation angles of movement paths relative to subjects' capture sites with a *V* test (Batschelet 1981). All statistical tests were performed at a 95% confidence interval in SPSS 11.0.1 (SPSS 2001) and Oriana 2.01c (for circular statistics; Kovach Computing Services 2004).

### Results

Forty-one Chucaos were translocated and 558 locations were obtained during daily telemetry surveys. Thirteen subjects were released into replicates of the corridor treatment, and 14 subjects each were released into the open and shrub-matrix treatments. Of the 41 subjects, 33 (78%) dispersed successfully from release sites, including all subjects in the shrub-matrix treatment and 11 subjects in the corridor treatment (Table 1). Data for the two remaining subjects in the corridor treatment were censored (7–8 days after release). Results for the open-matrix treatment were more variable. Of the 14 subjects, 7 dispersed successfully, 4 were censored (within 5–7 days), and 3 remained in the release patch for the duration of the 30-day monitoring period.

Landscape treatment was the only significant (Wald<sub>2</sub> = 7.55,  $p = 0.02$ ) factor predicting time to dispersal in the forward-stepwise Cox regression (model fit;  $\chi^2_2 = 8.30$ ,  $p = 0.02$ ), and treatment was consistently identified as the most important factor in the backward (Wald<sub>2</sub> = 8.02,  $p = 0.02$ ) and full model (Wald<sub>2</sub> = 8.47,  $p = 0.01$ ) analyses. Thus, we discuss only results for the forward-stepwise method. Mean ( $\pm$ SD) time to dispersal was significantly longer for subjects in the open matrix treatment (10.29 days  $\pm$  11.23, Fig. 2) than for those in the corridor (3.38 days  $\pm$  2.93, Wald<sub>1</sub> = 3.75,  $p = 0.05$ ) and shrub matrix

**Table 1.** Summary of radiotelemetry results for translocated Chucao Tapaculos (each located once daily) and landscape characteristics of experimental sites where birds were released.\*

Site/subject	Days in patch	Days total	Disposition	Patch area (ha)	N-N $\geq 1$ ha (m)	N-N (m)	Wooded%
C1a	1	9	lost transmitter	0.19	340	20	7.53
C1b	3	6	death				
C2	8	8	lost transmitter	0.30	50	50	13.58
C3	2	30	completed	0.12	380	50	6.92
C4a	2	23	death	0.20	590	60	12.14
C4b	1	30	completed				
C5a	1	30	completed	0.16	280	20	12.15
C5b	7	25	completed				
C6a	8	30	completed	0.21	180	30	6.79
C6b	2	30	completed				
C7a	1	3	lost transmitter	0.13	300	50	11.18
C7b	1	30	completed				
C8	7	7	lost transmitter	0.12	280	130	3.95
O1a	6	6	death	0.09	130	70	3.98
O1b	30	30	completed				
O2a	30	30	completed	0.14	120	120	3.15
O2b	30	30	completed				
O3a	1	30	completed	0.07	90	80	2.94
O3b	5	5	lost transmitter				
O4a	15	25	lost transmitter	0.23	280	60	5.71
O4b	5	30	completed				
O5	6	6	death	0.20	90	40	3.48
O6a	2	17	death	0.05	30	30	12.65
O6b	1	30	completed				
O7a	2	30	completed	0.04	60	30	3.44
O7b	7	7	death				
O8	3	30	completed	0.03	101	100	1.11
S1	18	24	lost transmitter	0.10	280	50	12.24
S2a	2	30	completed	0.30	220	100	4.23
S2b	5	9	lost transmitter				
S3a	1	6	roadless	0.25	140	60	4.44
S3b	2	30	completed				
S4	4	10	death	0.09	130	90	1.80
S5a	1	16	unknown	0.02	60	60	9.15
S5b	1	23	completed				
S6	2	6	lost transmitter	0.04	120	10	3.10
S7a	1	6	roadless	0.05	190	90	1.09
S7b	1	2	lost transmitter				
S8	1	2	roadless	0.09	60	60	2.05
S9a	1	5	lost transmitter	0.05	120	120	0.88
S9b	1	30	completed				

\*The site/subject code indicates the treatment group (C, corridor; O, open; S, shrubs) and the replicate-site number. Codes ending in a or b indicate sequential releases conducted in the specified site. Days in patch is the number of days the subject remained in the release patch prior to dispersal, death, or transmitter loss. Days total is the duration of monitoring, and disposition indicates the conditions under which monitoring was terminated. These included completion of monitoring, death, transmitter loss, dispersal into roadless areas, or signal loss for unknown reasons. Release-site characteristics included the release patch area, distance from the release patch to the nearest-neighbor (N-N) patch  $\geq 1$  ha, distance to the N-N patch of any size, and the percentage of wooded habitat (wooded%) within a 100-m buffer centered on the release patch.

(2.93 days  $\pm$  4.51, Wald<sub>1</sub> = 7.59,  $p$  = 0.01) treatments, whereas time to dispersal was similarly short in the latter two treatments (Wald<sub>1</sub> = 0.67,  $p$  = 0.41). Travel paths were not biased toward the initial capture sites ( $V$  test,  $u_{30}$  = 1.40,  $p$  = 0.08).

For illustrative purposes Fig. 3 presents the dispersal path of subject C1a, and results for the remaining subjects are summarized in the following paragraphs. Subject C1a, released at location (loc.) 1, dispersed via the corri-

dor (loc. 2) to a 0.5-ha patch (loc. 3) the day following release. The linear distance to loc. 3 and the distance via the corridor were approximately 90 m each. The following morning the subject returned to the corridor (loc. 4) but was found later the same day in a 2-ha patch (loc. 5) that adjoined the corridor. Locations 4 and 5 were 360 m apart, but the route via the corridor was approximately 460 m. Subsequently, the subject returned to the corridor (loc. 6) but was found again the following day in the

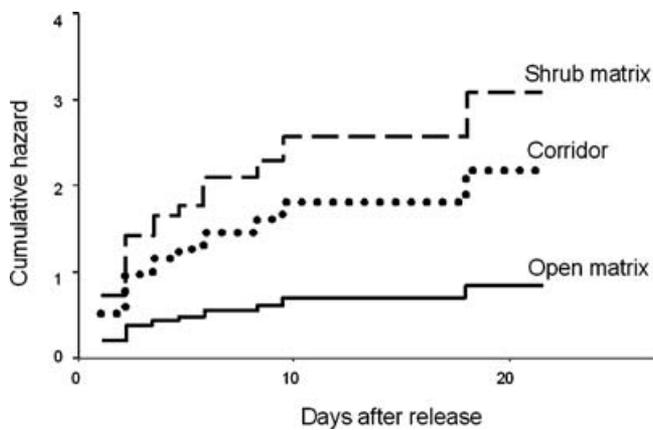


Figure 2. Hazard function showing likelihood (not scaled to 100 because of censored data) of dispersal by translocated *Chucaos* from release patches as a function of time (days).

2-ha patch (loc. 7), where it remained for 3 days. It made a 1-day excursion to a small (<0.5-ha) linear patch (loc. 8), crossing a 20-m open-matrix gap, and then returned to the 2-ha patch (loc. 9). Next it was found in the corridor (loc. 10) about 200 m from the previous location, which was a 230-m path via the corridor route. Finally, on the tenth day, the detached transmitter was found in the 0.5-ha patch (loc. 11) that was first visited the day after release. Based on these data it cannot be definitively concluded that the corridor was always used as a travel route among the adjoining patches. The subject was never observed outside wooded habitat, however, and it was repeatedly detected inside the corridor during periods

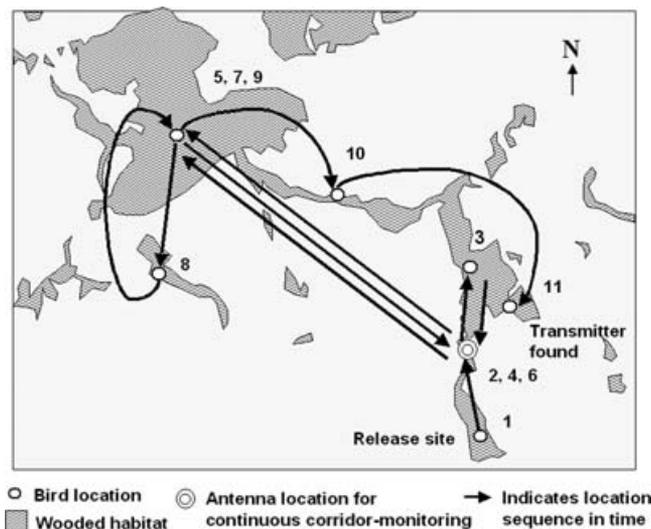


Figure 3. Map (1:2000) of wooded habitat patches embedded in a matrix of open pasture. Numbers (1-11) are locations of a translocated subject (C1a) recorded over a 10-day period.

between observations in patches. Therefore we assume that the majority of movements occurred via the corridor, although the subject made two documented moves  $\geq 20$  m across the open matrix.

Eleven of the 13 subjects in the corridor treatment dispersed from the release patches via corridor routes. One of the remaining subjects (C4b) moved partially down the corridor, within range of the receiver, then took a shortcut across the open matrix to reach the second patch. The minimum distance of the shortcut was approximately 50 m, whereas the corridor route was approximately 150 m. Subject C6b also dispersed 25 m across the open matrix instead of using the 185-m corridor but moved into the corridor from the second patch later the same day.

The mean confirmed distance traveled ( $\pm$ SD) by subjects through corridors was 351 m ( $\pm$ 236), which ranged from 1 to 9 times the lengths of the noncorridor routes. The mean corridor-to-linear distance ratio was 2.66 ( $\pm$ 2.22) times longer for corridor routes. Data on dispersal distances across the open and shrub matrix were more uncertain because the matrix could not be monitored continuously, and any number of paths could have been taken. Thus, we could only measure minimum distances across the matrix that we knew subjects must have crossed to reach the observed locations. Mean distances were 56 m ( $\pm$ 27) for the open matrix and 100 m ( $\pm$ 45) for the shrub matrix, although many travel paths were probably considerably longer.

Regardless of intervening habitat, the mean linear distance traveled within a 24-hour period was 170 m ( $\pm$ 225) and the maximum distance was 1400 m. For subjects tracked >20 days, the mean displacement distance from the release patch was 674 m ( $\pm$ 606), and the maximum displacement was 2200 m. Finally, the mean size of wooded patches that subjects were known to have visited was 20.94 ha ( $\pm$ 77.00), whereas the mean patch size for the study area as a whole was 5.85 ha ( $\pm$ 103.15). Subjects dispersing across the matrix frequently moved among small stepping stone patches, sometimes making repeated return visits. Thirty-six percent of dispersing subjects visited at least one small patch (<1 ha), and 45% returned at least once to a previously visited patch.

In some cases, subjects dispersing through both open and shrub matrix failed to orient toward suitable habitat at relatively short distances (<150 m). For example, subject O8 failed to orient toward a 13.5-ha patch located 85 m across the open matrix, moving instead to a tiny (<0.1-ha) patch located 95 m across the open matrix in the opposite direction. The subject ultimately settled on a territory in the 13.5-ha patch, after traveling a long circuitous route to reach the patch it initially ignored. Likewise, in the shrub matrix, subject S4 wandered seemingly at random for 7 days before dying, apparently of starvation. This subject failed to orient toward several wooded patches on the periphery of the shrub field that were  $\geq 130$  m from the release patch. Necropsy results showed no signs of injury

or illness, but the digestive tract was empty at the time of death. All other subjects that died during experimental trials (Table 1) were found either partially consumed or with wounds consistent with predation.

## Discussion

### Corridor versus Matrix Dispersal

Wooded corridors and shrubby vegetation functioned similarly as movement habitat for dispersing Chucaos. Thus, these elements may be similarly viable for use in landscape management to enhance connectivity. As expected, open habitat constrained Chucao movement but did not entirely prevent it. Open habitat gaps  $\leq 20$  m were crossed routinely, but subjects appeared reluctant to cross gaps  $\geq 60$  m and few crossed gaps  $\geq 80$  m. Although the release of subjects into such unsuitable patches undoubtedly provided a strong stimulus for dispersal, the fact that some individuals remained in the tiny release patches  $\geq 30$  days (rather than crossing 120–130 m of open matrix) demonstrates the strength of their resistance to dispersing in the open. This constraint may reduce immigration into isolated forest patches, potentially influencing patch occupancy patterns at the landscape scale. Census data confirm that Chucaos are frequently absent from isolated patches, suggesting population-level effects of dispersal limitation. In contrast to open habitat, subjects regularly traveled distances  $\leq 300$  m in narrow wooded corridors and easily crossed distances  $\geq 100$  m in shrub-dominated matrix. Regular use of small stepping-stone patches indicates that such patches may be important for movement in fragmented landscapes.

### Generality of Results

Among forest bird species understory insectivores have been identified repeatedly as highly sensitive to fragmentation (e.g., Lovejoy et al. 1986; Recher & Serventy 1991; Sieving & Karr 1997). In South American temperate rainforest, this group includes the endemic tapaculos, which are among the most sensitive to fragmentation in the biome (Willson et al. 1994). Four species occur in the region—the Chucao, Ochre-flanked Tapaculo (*Eugralla paradoxa*), Magellanic Tapaculo (*Scytalopus magellanicus*), and Black-throated Huet-huet (*Pterotochos tarnii*). These species are reluctant to enter open habitat (pasture), but edge permeability generally increases with increasing density of vegetation in the matrix (Sieving et al. 1996). Song playback can draw respondents ( $\geq 40\%$ ) into narrow ( $\leq 10$  m) wooded corridors (Sieving et al. 2000).

Only the smallest species, the Magellanic Tapaculo ( $\sim 11$  g), readily enters sparsely vegetated matrix. This species occupies the widest variety of habitat types, has the largest geographic range (Sibley & Monroe 1990; Ridgely & Tudor 1994), and is arguably the strongest flyer

(T.M.C. & K.E.S., personal observations) among the four species. The Ochre-flanked and Chucao Tapaculos have intermediate body mass (25 g and 40 g, respectively) and very small geographic ranges, whereas the largest species, the Huet-huet (ca. 150 g), has a range that is intermediate in size (Sibley & Monroe 1990; Ridgely & Tudor 1994). Although the Chucao and Huet-huet respond similarly to habitat boundaries, the Ochre-flanked Tapaculo, the rarest and most patchily distributed of the species, appears most reluctant to enter the matrix (Sieving et al. 1996).

Similar reluctance among tapaculos (except the more dispersive Magellanic Tapaculo) to enter open or sparsely vegetated matrix indicates that results obtained for the Chucao, which is intermediate in size, vagility, and habitat specificity, may be generally applicable for planning conservation action to support the entire group. Although maximum travel distances will likely differ among species, these differences may be predictable based on differences in body mass and territory sizes (Sutherland et al. 2000; Bowman 2003). Planners should be cognizant of autecological differences among species (e.g., bamboo specialization of the Ochre-flanked Tapaculo [Sieving et al. 2000], and nest-site specificity and larger home-range sizes for the Huet-huet [De Santo et al. 2002]), however, to ensure that habitat networks meet the requirements of the entire species suite. Our results may also be generally applicable for understory and shrub requiring birds elsewhere (e.g., Sieving & Karr 1997) and, because tapaculos are essentially terrestrial, their responses may be indicative of many nonvolant species (e.g., Bakker & Van Vuren 2004).

### Conservation Implications

For species such as tapaculos, which are poor flyers and cannot use sudden flight or other aerial escape tactics for predator avoidance, behavioral resistance to entering open areas may be due to lack of escape cover (Lima 1993; Rodríguez et al. 2001; Sieving et al. 2004). Thus, it may be possible to encourage movement through the matrix by managing vegetation to increase cover and, in some cases, fully restoring forested habitats or corridors may not be required to restore connectivity. Chucao movement was facilitated by shrubby vegetation in the matrix, and anecdotal observations (dispersal through both low-stature secondary forest and shrub fields dominated by invasive *B. magellanica*) indicate that cover provided by the vegetation rather than species composition was the relevant factor.

Availability of such alternative management strategies (i.e., management of matrix vegetation structure rather than corridor protection/restoration) is useful because it allows planners to optimize conservation efforts in response to local constraints (Arendt 2004). For example, it may be advantageous to protect or restore wooded

corridors in regions where land area is at a premium for economic uses (because corridors require minimal area), whereas natural regeneration of secondary vegetation (requiring little economic investment) may be adequate in regions where land use is less intensive. Natural regeneration of permeable vegetation in the matrix as an alternative to corridor restoration may be especially beneficial where local ecological constraints inhibit forest regeneration, for example, in Chiloé, where waterlogged soils are invaded by persistent hydrophytic assemblages (i.e., *Sphagnum* spp. and *B. magellanica*; Van Breemen 1995) that are nonetheless permeable to Chucaco movement (this study).

Our results clearly demonstrate that treating all nonforest habitats as homogeneous and impermeable could lead to omission of potentially useful alternatives for conservation planning. Providing travel habitat in the form of corridors or permeable matrix, however, should not be viewed as a feasible alternative to protecting large tracts of primary forest needed for breeding and long-term survival (Rosenberg et al. 1997). Census data show that Chucacos and other endemic tapaculos rarely forage or defend territories in wooded corridors <25 m wide (Sieving et al. 2000) and are virtually never observed in fields dominated by *B. magellanica* (T.M.C. & K.E.S., personal observations). Predatory risk also appears greater in small patches and corridors (where six subjects were lost to predation) than in more extensive forested areas (see also Willson et al. 2001). Further, the fact that some subjects had difficulty orienting toward suitable forest patches while dispersing through shrubs (i.e., indicative of a restricted perceptual range in this habitat type; Zollner & Lima 1997), one apparently dying of starvation, indicates that excessively large areas of shrub land could represent a form of dispersal trap (Schlaepfer et al. 2002). Nonetheless, our results are encouraging in that they support two feasible alternatives for maintaining functional landscape connections that may allow managers to optimize conservation efforts at local and regional scales.

## Acknowledgments

We sincerely thank H. Jañez, D. Smith, M. Willson, M. Binford, A. Wursten, N. Haynes, J. Davis, M. Milleson, M. Reetz, I. Díaz, T. Contreras, N. Seavy, M. Machicote, G. Jones, G. Cumming, C. Smith, J. Armesto, D. Levey, and all those who reviewed earlier drafts of the manuscript. We also thank the Chiloé landowners who graciously provided access to their farms where all our fieldwork was conducted. Partial funding was provided by the Disney Conservation Fund. In-kind support was provided by Fundación Senda Darwin, the University of Florida Map and Image Library, Geoplan Center, Geography Department, Land Use and Environmental Change Institute, and the Department of Wildlife Ecology and Conservation.

## Literature Cited

- Arendt, R. 2004. Linked landscapes—Creating greenway corridors through conservation subdivision design strategies in the north-eastern and central United States. *Landscape and Urban Planning* **68**:241–269.
- Bakker, V. J., and D. H. Van Vuren. 2004. Gap-crossing decisions by the red squirrel, a forest-dependent small mammal. *Conservation Biology* **18**:689–697.
- Balmford, A., and A. Long. 1994. Avian endemism and forest loss. *Nature* **372**:623–624.
- Batschelet, E. 1981. *Circular statistics in biology*. Academic Press, New York.
- Beier, P., and R. F. Noss. 1998. Do habitat corridors provide connectivity? *Conservation Biology* **12**:1241–1252.
- Bélisle, M., and A. Desrochers. 2002. Gap-crossing decisions by forest birds: an empirical basis for parameterizing spatially-explicit, individual-based models. *Landscape Ecology* **17**:219–231.
- Bélisle, M., and C. St. Clair. 2001. Cumulative effects of barriers on the movements of forest birds. *Conservation Ecology* **5**(2):9.
- Bélisle, M., A. Desrochers, and M. J. Fortin. 2001. Influence of forest cover on the movements of forest birds: a homing experiment. *Ecology* **82**:1893–1904.
- Berggren, A., B. Birath, and O. Kindvall. 2002. Effect of corridors and habitat edges on dispersal behavior, movement rates, and movement angles in Roesel's Bush-Cricket (*Metrioptera roeselii*). *Conservation Biology* **16**:1562–1569.
- Bowman, J. 2003. Is dispersal distance of birds proportional to territory size? *Canadian Journal of Zoology* **81**:195–202.
- Bowman, J., and L. Fahrig. 2002. Gap crossing by chipmunks: an experimental test of landscape connectivity. *Canadian Journal of Zoology* **80**:1556–1561.
- Bowne, D. R., J. D. Peles, and G. W. Barrett. 1999. Effects of landscape spatial structure on movement patterns of the hispid cotton rat (*Sigmodon hispidus*). *Landscape Ecology* **14**:53–65.
- Bright, P. W. 1998. Behavior of specialist species in habitat corridors: arboreal dormice avoid corridor gaps. *Animal Behaviour* **56**:1485–1490.
- Buddle, C. N., and A. L. Rypstra. 2003. Factors influencing emigration of two wolf spider species (Araneae: Lycosidae) in an agroecosystem. *Environmental Entomology* **32**:88–95.
- Davis, S. D., V. H. Heywood, O. Herrera-MacBryde, J. Villa-Lobos, and A. C. Hamilton, editors. 1997. *Centers of plant diversity: a guide and strategy for their conservation*; Vol. 3, the Americas. World Wildlife Fund for Nature and the World Conservation Union of Nature, Cambridge, United Kingdom.
- De Santo, T. L., M. F. Willson, K. E. Sieving, and J. J. Armesto. 2002. Nesting biology of tapaculos (family Rhinocryptidae) in fragmented south-temperate rainforests of Chile. *Condor* **104**:482–495.
- Desrochers, A., and S. J. Hannon. 1997. Gap crossing decisions by forest songbirds during the post-fledging period. *Conservation Biology* **11**:1204–1210.
- Donoso, C. 1993. *Bosques templados de Chile y Argentina: variación, estructura, y dinámica*. Editorial Universitaria, Santiago (in Spanish).
- ESRI (Environmental Systems Research Institute). 1999. *ArcView 3.2: Geographic information system software*. ESRI, Redlands, California.
- Gobeil, J.-E., and M.-A. Villard. 2002. Permeability of three boreal forest landscape types to bird movements as determined from experimental translocations. *Oikos* **98**:447–458.
- Greenwood, P. J., and P. H. Harvey. 1982. The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics* **13**:1–21.
- Haddad, N. M. 1999. Corridor and distance effects on interpatch movements: a landscape experiment with butterflies. *Ecological Applications* **9**:612–622.
- Harrell, F. E. 2001. *Regression modeling strategies: with applications to linear models, logistic regression, and survival analysis*. Springer-Verlag, New York.

- Hein, S., J. Gombert, T. Hovestadt, and H. J. Poethke. 2003. Movement patterns of the bush cricket *Platypleis albopunctata* in different types of habitat: matrix is not always matrix. *Ecological Entomology* **28**:432–438.
- Hudgens, B. R., and N. M. Haddad. 2003. Predicting which species will benefit from corridors in fragmented landscapes from population growth models. *The American Naturalist* **161**:808–820.
- Ims, R. A. 1995. Movement patterns related to spatial structures. Pages 85–109 in L. Hansson, L. Fahrig, and G. Merriam, editors. *Mosaic landscapes and ecological processes*. Chapman & Hall, London, United Kingdom.
- Inglis, G., and A. J. Underwood. 1992. Comments on some designs proposed for experiments on the biological importance of corridors. *Conservation Biology* **6**:581–586.
- Johnson, M. L., and M. S. Gaines. 1990. Evolution of dispersal: theoretical models and empirical tests using birds and mammals. *Animal Behaviour* **28**:1140–1162.
- Kovach Computing Services. 2004. Oriana circular statistics software version 2.01c. Kovach Computing Services, Pentraeth, United Kingdom.
- Lima, S. L. 1993. Ecological and evolutionary perspectives on escape from predatory attack: a survey of North American birds. *Wilson Bulletin* **105**:1–47.
- Lima, S. L., and P. A. Zollner. 1996. Towards a behavioral ecology of ecological landscapes. *Trends in Ecology & Evolution* **11**:131–134.
- Lovejoy, T. E., et al. 1986. Edge and other effects of isolation on Amazon forest fragments. Pages 257–285 in M. E. Soulé, editor. *Conservation biology: the science of scarcity and diversity*. Sinauer Associates, Sunderland, Massachusetts.
- McGarigal, K., S. A. Cushman, M. C. Neel, and E. Ene. 2002. FRAGSTATS: spatial pattern analysis program for categorical maps. University of Massachusetts, Amherst. Available from [www.umass.edu/landeco/research/fragstats/fragstats](http://www.umass.edu/landeco/research/fragstats/fragstats) (accessed July 2004).
- Nicholls, A. O., and C. R. Margules. 1991. The design of studies to demonstrate the biological importance of corridors. Pages 49–61 in D. A. Saunders and R. J. Hobbs, editors. *Nature conservation 2: the role of corridors*. Surrey Beatty, Chipping Norton, New South Wales, Australia.
- Recher, H. F., and D. L. Serventy. 1991. Long term changes in relative abundances of birds in King's Park, Perth, western Australia. *Conservation Biology* **5**:90–102.
- Reid, S., I. A. Diaz, J. J. Armesto, and M. F. Willson. 2004. Importance of native bamboo for understory birds in Chilean temperate forests. *Auk* **121**:515–525.
- Ricketts, T. H. 2001. The matrix matters: effective isolation in fragmented landscapes. *The American Naturalist* **158**:87–99.
- Ridgely, R. S., and G. Tudor. 1994. *The birds of South America; vol. II, the suboscine passerines*. University of Texas Press, Austin.
- Ries, L., and D. M. Debinski. 2001. Butterfly responses to habitat edges in the highly fragmented prairies of central Iowa. *Journal of Animal Ecology* **70**:840–852.
- Rodríguez, A., J. Andrén, and G. Jansson. 2001. Habitat-mediated predation risk and decision making of small birds at forest edges. *Oikos* **95**:383–396.
- Rosenberg, D. K., B. R. Noon, and E. C. Meslow. 1997. Biological corridors: form, function, and efficacy. *Bioscience* **47**:677–687.
- Schlaepfer, M. A., M. C. Runge, and P. W. Sherman. 2002. Ecological and evolutionary traps. *Trends in Ecology & Evolution* **17**:474–480.
- Sibley, C. G., and B. L. Monroe Jr. 1990. *Distribution and taxonomy of birds of the world*. Yale University Press, New Haven, Connecticut.
- Sieving, K. E., and J. R. Karr. 1997. Avian extinction and persistence mechanisms in lowland Panama. Pages 156–170 in W. F. Laurance and R. O. Bierregaard Jr., editors. *Tropical forest remnants: ecology, management, and conservation of fragmented communities*. University of Chicago Press, Chicago.
- Sieving, K. E., T. A. Contreras, and K. L. Maute. 2004. Heterospecific facilitation of forest-boundary crossing by mobbing understory birds in north-central Florida. *Auk* **121**:738–751.
- Sieving, K. E., M. F. Willson, and T. L. De Santo. 1996. Habitat barriers to movement of understory birds in fragmented south-temperate rainforest. *Auk* **113**:944–949.
- Sieving, K. E., M. F. Willson, and T. L. De Santo. 2000. Defining corridor functions for endemic birds in fragmented south-temperate rainforest. *Conservation Biology* **14**:1120–1132.
- Simberloff, D. S., J. A. Farr, J. Cox, and D. W. Mehlman. 1992. Movement corridors: conservation bargains or poor investments? *Conservation Biology* **6**:493–504.
- SPSS. 2001. SPSS advanced statistics software, version 11.0.1. SPSS, Chicago.
- Stattersfield, A. J. 1998. Endemic bird areas of the world: priorities for biodiversity conservation. *Birdlife Conservation Series no. 7*. Birdlife International, Cambridge, United Kingdom.
- St. Clair, C. C., M. Bélisle, A. Desrochers, and S. J. Hannon. 1998. Winter responses of forest birds to habitat corridors and gaps. *Conservation Ecology* **2**(12): [www.consecol.org/vol12/iss12/art13](http://www.consecol.org/vol12/iss12/art13).
- Sutherland, G. D., A. S. Harestad, K. Price, and K. P. Lertzman. 2000. Scaling of natal dispersal in terrestrial birds and mammals. *Conservation Ecology* **4**(1):16.
- Turchin, P. B. 1998. *Quantitative analysis of movement*. Sinauer Associates, Sunderland, Massachusetts.
- Van Breemen, N. 1995. How *Sphagnum* bogs down other plants. *Trends in Ecology & Evolution* **10**:270–275.
- Vandermeer, J., and R. Carvajal. 2001. Metapopulation dynamics and the quality of the matrix. *The American Naturalist* **158**:211–220.
- Willson, M. F., T. L. De Santo, C. Sabag, and J. J. Armesto. 1994. Avian communities in fragmented south-temperate rainforest in Chile. *Conservation Biology* **8**:508–520.
- Willson, M. F., J. L. Morrison, K. E. Sieving, T. L. De Santo, L. Santisteban, and I. Diaz. 2001. Patterns of predation risk and survival of bird nests in a Chilean agricultural landscape. *Conservation Biology* **15**:447–456.
- Witt, W. C., and N. Huntly. 2001. Effects of isolation on red-backed voles (*Clethrionomys gapperi*) and deer mice (*Peromyscus maniculatus*) in a sage-steppe matrix. *Canadian Journal of Zoology* **79**:1597–1603.
- Yoder, J. M., E. A. Marschall, and D. A. Swanson. 2004. The cost of dispersal: predation as a function of movement and site familiarity in ruffed grouse. *Behavioral Ecology* **15**:469–476.
- Zollner, P. A., and S. L. Lima. 1997. Landscape-level perceptual abilities in white-footed mice: perceptual range and the detection of forested habitat. *Oikos* **80**:51–60.