

docarpus National Park in southern Ecuador (ca. 100 km north of Angashcola), where recent records of *S. cinctus* derive (Bloch et al. 1991), and the Reserva del Alto Quindío Acaime/Los Nevados National Park/Ucumari Regional Park complex in Colombia. Other potentially viable populations of *S. cinctus* in Ecuador probably occur within Sangay National Park (Chimborazo/Morona-Santiago) and the Cayambe/Coca Ecological Reserve (R. S. Ridgely pers. comm.). Stringent protection of these areas should be strongly supported.

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## Habitat Barriers to Movement of Understory Birds in Fragmented South-Temperate Rainforest

KATHRYN E. SIEVING,<sup>1,3</sup> MARY F. WILLSON,<sup>2</sup> AND TONI L. DE SANTO<sup>2</sup>

<sup>1</sup>Department of Wildlife Ecology and Conservation, University of Florida,  
303 Newins-Ziegler Hall, Gainesville, Florida 32611, USA; and

<sup>2</sup>Pacific Northwest Research Station, Forestry Sciences Laboratory,  
2770 Sherwood Lane, Suite 2A, Juneau, Alaska 99801, USA

The temperate rainforests in South America are restricted to southern Chile and adjacent southwestern Argentina (Vuilleumier 1985). Home to a number of endemic bird species, some that are listed as endangered or threatened (Glade 1988, Collar et al. 1992), this forest biome is rapidly being harvested for timber

and fragmented by agricultural expansion. Habitat fragmentation has detrimental effects on forest bird populations (Wilcove et al. 1984, Lovejoy et al. 1986, Hagan and Johnston 1992, Donovan et al. 1995, Robinson et al. 1995). Among forest bird species, terrestrial or understory insectivores repeatedly have been identified as highly sensitive to forest fragmentation, particularly in the tropics (Leck 1979, Willis 1979, Karr 1982, Lovejoy et al. 1986, Sieving and Karr 1997)

<sup>3</sup> E-mail: kes@gnv.ifas.ufl.edu

but also in temperate regions (Recher and Serventy 1991, Willson et al. 1994).

One potential cause of bird population declines in fragmented natural habitats is isolation by expansion of altered human habitats, which may restrict dispersal movements between fragments (Opdam et al. 1985, Dunning et al. 1995). As a preliminary step to assessing avian use of forested corridors between fragments (Simberloff et al. 1992), we examined three habitats that may serve as movement barriers in a temperate rainforest landscape in southern Chile. Using song playback experiments (McGregor 1992a), we quantified the willingness of five understory species to enter previously cleared areas between forest fragments.

*Study site and species.*—Isla Grande de Chiloé (41°55'S, 73°35'W) is a large continental island less than 10 km offshore; it has been isolated from mainland Chile for approximately 10,000 years (Willson and Armesto 1996). Agriculture is the dominant land-use pattern in the northern, eastern, and southern portions of Chiloé. Farmers of Chiloé use animal power to clear their land. Thus, the process of pasture creation is slow and the landscape is still diverse; fields with intermediate vegetative cover are interspersed among completely cleared fields and forest fragments. Forested areas are maintained by farmers for wood extraction and winter livestock shelter. Our study sites were located adjacent to forest patches, ranging in size from less than one to several hundred hectares, on private farms in northeastern Chiloé. In our experiment, potential barrier habitats were divided into three categories: (1) open pasture, with short (<5 cm tall) grass offering no cover to forest birds; (2) scattered cover, where stumps, sparse shrubs, fern clusters, piles of cut branches, and a few regenerating saplings were interspersed with patches of grass; and (3) dense cover, comprised of older clearings with continuous cover of bamboo (*Chusquea* sp.), ferns, saplings, and brush piles.

We selected five understory species (four rhinocryptids and one furnariid) that persist in fragmented forests of Chiloé (Willson et al. 1994). All are endemic to the south-temperate rainforest of southern Chile and Argentina, but their geographic ranges vary in size. The smallest of the rhinocryptids is the Magellanic Tapaculo (*Scytalopus m. magellanicus*; ca. 11 g), which also has the widest geographic distribution (Sibley and Monroe 1990, Ridgely and Tudor 1994). The Ochre-flanked Tapaculo (*Eugralla paradoxa*; ca. 25 g) and the Chucao Tapaculo (*Scelorchilus rubecula*; ca. 40 g) have very small geographic ranges. The Black-throated Huet-huet (*Pterotochos tarnii*) is the largest of the four rhinocryptids (ca. 150 g) and has an intermediate geographic range. Des Murs' Wiretail (*Sylviorthorhynchus desmursii*; ca. 10 g), the one furnariid, has a geographic range larger than the Black-throated Huet-huet but smaller than the Magellanic Tapaculo (Meyer de Schauensee 1970, Ridgely and Tudor 1994).

All five species are permanent residents, strongly territorial (pers. obs.), and feed primarily on invertebrates gleaned from leaf litter and low foliage (Johnson 1965, pers. obs.).

*Experimental method.*—We used taped song playbacks (Falls 1981, McGregor 1992a) to determine whether birds were willing to cross non-forested habitats between forest patches where test animals held territories. Territorial songs of each species were recorded from commercial and field recordings and played from speakers in a standardized manner (described below) to individuals holding territories near edges of forest fragments. Our playbacks simulated a potential territorial invasion and elicited agonistic approaches by target birds (Falls 1981, Becker 1982, Colgan 1989). During preliminary trials in the forest, all five species responded strongly to playbacks in and near their territories, making close approaches to the speaker while displaying aggressive behaviors.

Playback experiments were conducted during daily singing/activity peaks for all species (0600–1000 and 1600–1830 h, local time) during two breeding seasons (January, and November to December of 1994). All five species were engaged in nesting activities during these times (Johnson 1965, Sieving et al. unpubl. data), although actual stage of the nesting cycle varied among individuals. We used the following protocol. A 6-watt portable speaker (Sony SRS-58) attached to a handheld tape player by a 10-m cord was set 15 to 20 m from the forest edge. Up to four observers, including the tape player operator, were stationed 20 to 40 m apart on either side of the speaker. Thus, approximately 60 m of forest edge could be observed on either side of the speaker. After all observers were in place for 2 min, the target species' song sequence was played from the speaker. Songs were played for varying amounts of time depending upon the behavior of subjects. A response was defined as a bird moving (while seen or heard singing by any observer) to the forest edge and in the direction of the speaker after the playback began. If no subject responded by approaching the forest edge and speaker from the forest interior after 5–10 min, the playback was terminated and not used. Once a subject had responded, however, the tape was played until the subject either left the forest edge and moved back to forest interior, clearly refusing to enter the test habitat after at least 10 min of active response (singing and/or pacing and perching at the edge), or until it entered the test habitat and approached the speaker. The latter behavior was recorded as a barrier entry that indicated the respondent was willing to enter the test habitat. Our experimental design is described by McGregor (1992b) as the single-measure approach to quantifying playback responses.

We were conspicuous when conducting experiments in habitats with little cover (especially open pasture). Although our presence might have deterred approach by the birds, several factors suggest that this

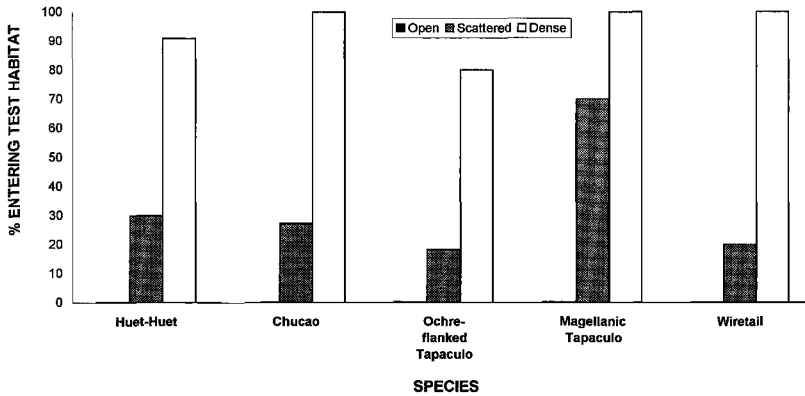


FIG. 1. Responses of endemic forest birds to song playbacks at boundaries in three types of non-forest habitat (potential movement barriers). Values are percentages of individuals moving from forest to non-forest with open, scattered, or dense cover. The number of individuals responding to playbacks (in open pasture, scattered cover, and dense cover, respectively) were: Black-throated Huet-huet: 10, 10, 11; Chucao Tapaculo: 10, 11, 12; Ochre-flanked Tapaculo: 10, 11, 10; Magellanic Tapaculo: 12, 10, 12; and Des Murs' Wiretail: 10, 10, 10.

was not the case. First, all five species are uncommonly tame around people observing nests at close range. For example, Chucaos have frequently approached us and have hopped on boots, laps, and hand-held equipment. When encountered in the forest, all species merely make small (<5 m) detours around humans in their path, whether or not they give vocal alarms. Thus, a minimum distance of 10 m between the speaker and the nearest observer should have been sufficient to elicit an unbiased response. For additional security, however, observers wore camouflage drapes in open habitats to reduce their conspicuity. Therefore, we are confident that a bird's hesitation to cross a habitat boundary was, in all experiments, primarily a response to the lack of cover at the speaker and not to the presence of observers.

Playbacks were conducted until at least 10 responses for each species in each habitat category were obtained. To avoid pseudoreplication, no individual bird was tested more than once (McGregor 1992b). Data were tabulated in a 3-factor contingency table and submitted to log-linear analysis with likelihood ratio chi-square tests on the model specifying all two-way interactions. The three factors were habitat (open, scattered, dense), bird species, and response (crossed into test habitat vs. stayed in forest). We re-fit the model without each of the 3 two-way interactions, in turn, to assess the importance of each. The difference in test statistics between the more- and less-saturated models was used to indicate the importance of the terms that were left out (Wilkinson et al. 1992). Finally, because the species-by-response interaction term was significant, the analysis was run again with data for one species, the Magellanic Tapaculo, excluded. This analysis allowed us to assess whether this spe-

cies' response was significantly different from the others.

*Results.*—A total of 159 subjects responded. No individuals entered open pastures (0 of 52), less than one-third entered scattered cover (17 of 52), and most entered dense cover (52 of 55; Fig. 1). The three-way interaction term (species  $\times$  habitat  $\times$  response) was not significant ( $\chi^2 = 3.71$ ,  $df = 3$ ,  $P = 0.3$ ). Habitat significantly influenced all species' responses ( $\chi^2 = 136$ ,  $df = 7$ ,  $P < 0.001$ ) in consistent order across species (habitat  $\times$  species term not significant;  $\chi^2 = 7.3$ ,  $df = 8$ ,  $P > 0.5$ ). The species  $\times$  response interaction was significant ( $\chi^2 = 10.8$ ,  $df = 4$ ,  $P < 0.05$ ), indicating that at least one species responded differently than the others. Magellanic Tapaculos appeared to enter scattered cover much more frequently than the others (Fig. 1), so we excluded data for this species and re-fit the models that included and excluded the species  $\times$  response interaction term. This time the difference was not significant ( $\chi^2 = 2.1$ ,  $df = 3$ ,  $P > 0.5$ ), indicating that Magellanic Tapaculos responded differently than the other species. Generally, as cover increased, the extent to which test habitats served as barriers to boundary crossings declined.

Our playbacks elicited vigorous aggressive responses. In most cases, responding individuals of all species came to the forest edge, as close to the speaker as possible, regardless of whether they entered the test habitat. Most respondents sang with full intensity (volume and frequency), or elevated intensity compared with pre-playback singing effort. Chucaos, huet-huets, and Magellanic Tapaculos that responded without entering test habitats perched in exposed sites and moved back and forth along the edge while singing. Des Murs' Wiretails and Ochre-flanked Tapaculos that responded without crossing into the test habitats

were less likely to perch in exposed sites at the edge. Individuals gathering food to feed nestlings even ceased foraging to approach the speaker and sing while holding food in their bills. Individuals of all species that entered test habitats either came to the speaker, or circled it completely (2 to 10 m away). Following termination of playbacks, respondents generally stopped or slowed the rate of singing and moved back into the forest.

*Discussion*—We conclude that open pasture is a “hard” barrier to territorial individuals of our study species, whereas scattered cover is a “soft” barrier, at least to most of the species (*sensu* Stamps et al. 1987). Responding individuals exhibited consistent reluctance to enter open pastures despite strong stimulation to do so. Respondents behaved similarly to individuals we have observed in more than 10 aggressive encounters between neighboring territory holders (primarily of Chucaos), where countersinging, close approach, and displays from low perches often were followed by physical attacks (*pers. obs.*). Behavioral patterns exhibited by respondents in our experiments were typical of territorial birds motivated to search out and face potential intruders (Falls 1981, Colgan 1989). Although we do not claim that the species we studied never enter open pasture, we are confident that they are reluctant to do so.

Proximity of the respondents’ territory borders to the test habitats could have influenced responses if the birds do not customarily cross territory borders. However, we have observed color-banded Chucaos making foraging forays into core areas of other pairs’ territories. Additionally, during border disputes among Chucaos, fights often carry far over into the interior of one of the territories. These observations indicate that, while borders are recognized by neighbors, territorial individuals will venture outside their own boundaries when appropriately motivated. Furthermore, the distances moved off-territory easily exceeded the distances from forest edge to speaker in our experiments (15–20 m). Given the short distances involved, we are confident that we tested response to cover and not to territory configuration. One way to improve the strength of our experiment, however, would be to use interactive playbacks (Dabelsteen 1992). By using context-dependent songs to enhance the motivation level of respondents, response intensity could be maximized.

The Magellanic Tapaculo was the only species we tested that entered stumpy pastures, which comprised the sparse end of the gradient of “scattered cover.” Individuals flew rapidly, in a zig-zag approach, from stump to stump out to the speaker and foraged near the speaker for up to 20 min after termination of a playback. This comparatively bold behavior is not surprising given that the Magellanic Tapaculo occupies the widest variety of habitat types of the five species. It nests not only in forest, but also in shrubby bogs, along cart tracks and streams, forest edges, in

fields with slash piles (*unpubl. data*), and even in rocky grasslands (Fjeldså and Krabbe 1990). It also is found on distant offshore islands where the other species do not occur (Ridgely and Tudor 1994, Venegas 1994). That it readily entered nearly cleared habitats in this study is consistent with its broad habitat requirements and perhaps with its larger geographic range.

In contrast, the Ochre-flanked Tapaculo is described as very secretive (Ridgely and Tudor 1994) and is the rarest and seemingly most patchily distributed in our fragmented study areas, where it is often associated with dense bamboo. For these reasons, we suspect that its slight reluctance to enter scattered and dense cover habitats outside forest (Fig. 1) reflected a real interspecific difference. This species may have perceived some of our dense-cover sites as unsuitable, based on subtle differences in vegetation structure. For conservation planning, further investigation of interspecific differences in landscape use by these endemic species is warranted (Opdam et al. 1995).

Our study demonstrates that cleared fields are less permeable to the study species than are successional habitats that offer more cover. Furthermore, playback experiments could be designed to determine what types and configurations of successional habitats can minimize barriers to bird movement among forest fragments. Fortunately, current agricultural practices on Chiloé Island maintain substantial brushy habitat interspersed with sizeable forest patches and fields, and this probably contributes to the persistence of forest endemics in the landscape, despite a considerable reduction in the amount of forest cover.

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## Time Of Departure by Summer Tanagers (*Piranga rubra*) from a Stopover Site Following Spring Trans-Gulf Migration

FRANK R. MOORE<sup>1</sup> AND DAVID A. ABORN

*Department of Biological Sciences, University of Southern Mississippi, Hattiesburg, Mississippi 39406, USA*

Nocturnal passerine migration typically commences within an hour of sunset (Drury and Nisbet 1964, Casement 1966, Cochran et al. 1967, Parslow 1968, Gauthreaux 1971, Hebrard 1971, Åkesson et al. 1996), and the bulk of migrants depart before the end of nautical twilight (which ends when the sun is 12° below the horizon or almost an hour after sunset). This "window" of nightly departure is probably tied to the availability of directional information from a wide array of environmental cues (Emlen 1980, Moore 1987, Piersma et al. 1990) as well as to the onset of atmospheric conditions favorable for migratory flight (Kerlinger and Moore 1989).

Although several orientation studies have quantified the cage activity of migrants during this "window" of time (see Moore 1987), species-specific departure of free-ranging passerines has been reported in only a few species (Cochran et al. 1967, Åkesson et al. 1996). Discounting birds artificially stimulated to initiate flight, 7 of 12 radio-tagged *Catharus* thrushes that departed under clear skies during spring migration through Illinois did so within an hour of sunset, while greater variation occurred when birds ( $n = 6$ ) departed on overcast evenings (Cochran et al. 1967). Åkesson et al. (1996) found that half of the 10 radio-tagged Song Thrushes (*Turdus philomelos*) that stopped over on the island of Öland, Sweden, initiated migration before the end of nautical twilight or within about 90 min of sunset, whereas the others departed much later in the night and possibly the next morning. We report the time of departures of Summer Tanagers (*Piranga rubra*) from a stopover site along the northern coast of the Gulf of Mexico following trans-Gulf migration and consider several factors (e.g. fat loads) that might explain observed variation.

*Methods.*—Observations were made on Horn Island (30°14'N, 88°40'W), a barrier island located 20 km off the Mississippi Gulf coast, during the spring migrations of 1992–94. Summer Tanagers were caught shortly after arrival on the island using mist nets, and 24 birds were fitted with radio transmitters (Custom Telemetry and Consulting, Inc., Watkinsville, Georgia) to study movement in relation to habitat during stopover. Transmitters were attached to the base of the rectrices using cyanoacrylate glue and a small cable tie. Each transmitter weighed 1.3–1.4 g and had a range of 1 km and a lifespan of seven days.

After release at their place of capture, birds were tracked using a hand-held, 2-element Yagi antenna. Tracking continued until the bird left the island (i.e. continued migration) or the transmitter failed. Although continuous daily tracking stopped at approximately 1800 CST, the signal was monitored hourly after dark. Some birds roosted close enough to our living quarters that the signal could be detected at night using the Yagi antenna. If a bird's signal could not be detected using the hand-held antenna, the receiver was connected to a Yagi antenna attached halfway up a 66-m radio tower, which was centrally located on the 22-km-long island. Signals were not monitored after 2300. If a signal was not received at sunrise the following day, and there was no indication of impending transmitter failure the previous night, we assumed the bird had migrated. Birds whose signals were lost prior to 2300 were considered to have migrated between the time the signal was last received and the time when the signal was no longer received. Although it is possible that a bird moved out of receiving range during the night, this explanation is unlikely. The five radio-tagged tanagers that stayed on the island beyond the day of capture did not change locations during the night. Moreover, birds did not make any long-distance movements during the day, and there was no reason to expect they would do so at night unless they were initiating migration.

<sup>1</sup> E-mail: fmoore@whale.st.usm.edu