LOSS OF HABITAT CONNECTIVITY HINDERS PAIR FORMATION AND JUVENILE DISPERAL OF CHUCAO TAPACULOS IN CHILEAN RAINFOREST

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Abstract. Loss of connectivity among forest fragments of south-temperate rainforest in Chile reduced mating success of male Chucao Tapaculos (Scelorchilus rubecula) and the probability of juvenile dispersal. Of 159 chicks banded in 2000 and 2001, 19 of 91 (21%) in poorly connected fragments stayed in their natal fragments, overall, compared to only 2 of 68 (3%) in well-connected fragments. The frequency of unmated males was consistently higher in poorly connected fragments (12 of 65 males, or 18%) compared to well-connected fragments (1 of 82 males, or 1%). Chucao populations could be maintained most readily in this increasingly agricultural matrix by a network of woodlots with dense understory, connected by wooded corridors.

Key words: Chile, Chucao Tapaculo, connectivity, forest fragmentation, Scelorchilus rubecula, south-temperate rainforest.

La Pérdida de Conectividad de Hábitat Impide la Formación de Parejas y la Dispersión de Juveniles de Scelorchilus rubecula en la Selva Lluviosa de Chile

Resumen. La pérdida de conectividad entre fragmentos de bosque de la selva lluviosa austral templada en Chile redujo el éxito de apareamiento de los machos y la probabilidad de dispersión de los juveniles en el tapaculo Scelorchilus rubecula. De 159 pichones anillados en 2000 y 2001, 19 de 91 (21%) individuos presentes en fragmentos poco conectados permanecieron en sus fragmentos natales, comparado con sólo 2 de 68 (3%) individuos que permanecieron en fragmentos bien conectados. La frecuencia de machos sin pareja fue consistentemente mayor en fragmentos poco conectados (12 de 65 machos, 18%) comparada con fragmentos bien conectados (1 de 82 machos, 1%). Las poblaciones de S. rubecula podrían ser mantenidas de modo más eficiente en esta matriz creciente de agricultura mediante una red de bosques con sotobosque denso, conectados por corredores de bosque.

A major consequence of forest fragmentation is loss of connectivity among residual forest patches. Although the value of travel corridors for wildlife populations has been debated (Beier and Noss 1998), and the value of corridors certainly varies among species (Haas 1995, Hannon and Schmiegelow 2002), connectivity of habitat patches is often thought to be important in maintaining well-distributed bird populations and metapopulation structure (Siegling et al. 2000, Lens et al. 2002) and therefore is often an essential component of avian conservation planning. Nowhere is this truer than in the south-temperate rainforests of Chile, where deforestation continues to destroy forest-bird habitat and increase isolation of remnant forest fragments (Willson and Armesto 1996). Fragment connectivity is especially critical for birds with poor capacities for dispersal (Lens et al. 2002), either for morphological (e.g., poor flight ability) or behavioral (e.g., avoidance of certain vegetation configurations) reasons.

Chucao Tapaculos (Scelorchilus rubecula, family Rhinocryptidae) are nonmigratory, endemic to the south-temperate rainforest (Fjelldå and Krabbe 1990), and dependent on dense understory vegetation (De Sauto et al. 2002). They forage for invertebrates on the forest floor, use dense thickets to conceal recent fledglings, and usually nest in cavities in the understory but show unusual variability in nest sites (De Sauto et al. 2002). Chucaos have short wings and seldom fly more than a few meters. They are extremely reluctant to emerge from dense forest cover into open fields (Siegling et al. 1996) but readily use densely vegetated corridors or shrubby second-growth to move among remnant forest patches in the increasingly agricultural landscape (Siegling et al. 2000; T. M. Darnell, unpubl. data). Chucaos are of conservation concern because of their endemic status and small geographic range, dramatic loss of habitat to deforestation, and apparent dependence on habitat connectivity to move among remnant forest patches.

In the absence of logging and trampling by domestic animals, chucaos can nest fairly successfully in forest fragments (De Sauto et al. 2002), but the consequences of fragment isolation are just beginning to be examined. Here I document the effects of reduced habitat connectivity on the likelihood of juvenile dispersal from the natal patches and on the success of territorial chucao males in obtaining mates.

METHODS
STUDY AREA
This study was done in northeastern Isla Grande de Chiloé, a continental island close to the mainland, in
south-central Chile (42°S, 74°W). The forest is a diverse mix of Valdivian and North Patagonian rainforests, consisting of broadleaf, mostly evergreen trees and some southern conifers (Armento and Figueroa 1987, Veblen et al. 1996, Armento et al. 1997). The understory consists largely of saplings and a native bamboo (*Chusquea quila*) that grows densely, particularly in treefall gaps, and dies back rather synchronously on an approximately 20-year cycle. Although this island was once largely covered by forest, the northern part of the island is now severely deforested, leaving a network of forest fragments in a matrix of early second growth and pasture. Most of the forest remnants are still interconnected via wooded stream courses and ravines, but some have become totally isolated by pastures or only tenuously connected by tiny, poorly vegetated stream courses that provide little cover.

All forest fragments (*n* = 11) I studied were located in a roughly 200-km² section of northeastern Chilió, between the settlements of Chacao, Manaio, Linao, and Cruce San Juan (De Santo et al. 2002). The distribution of study fragments was determined chiefly by existing patterns of land-clearing, with little difference in elevation (<100 m) among fragments. At least 1 km (straight-line distance) separated all study fragments from each other, except one pair of fragments separated by about 300 m. These two fragments were well connected to other fragments but not to each other.

I chose six focal fragments (all separated by about 3 km or more, straight-line distance) to examine juvenile dispersal and mating status of males in some detail. All fragments provided good habitat for chucos, with well-developed understory, numerous logs and snags, and small streams or low-lying damp spots often used for foraging. Three sites were well connected to other fragments by broad, wooded ravines and three were poorly connected by single, narrow, interrupted strips of vegetation. Previous field experiments in this region showed that tapaculos prefer travel corridors with dense vegetation for movement at the local scale (less than about 200 m; Sieving et al. 2000). Therefore, for purposes of this study, well-connected fragments are defined as having at least one broad (>20 m), densely wooded corridor leading from that fragment to other habitat fragments or as portions of very large, undisturbed forest stands. In all cases in this study the connection itself was occupied by territorial pairs, indicating that the habitat was suitable for the species. Poorly connected fragments had only one long (>400 m), narrow (<5 m), poorly vegetated corridor linking them to other habitable fragments; these skimmly strips of vegetation were frequently interrupted by open gaps up to 20 m in width. They were unsuitable as living habitat (and no chucos lived there) and inadequate as travel corridors (Sieving et al. 2000). Poorly connected fragments tended to occur in inland areas, simply because ravines there are commonly shallower than in coastal areas, and farmers more often cut the timber therein.

To augment the sample for estimating the frequency of unmated males, several other, ancillary fragments of differing connectivity were surveyed once during the nesting season. These "snapshot" surveys were included because, if fragment isolation indeed hinders pair formation, then the probability of finding unmated males in isolated fragments should be higher, as a rule, than in well-connected fragments. One additional fragment, containing apparently good habitat for several pairs of chucos, was completely isolated from all other forests by barren pasture >100 m wide and held no chucos at all.

**FIELD SURVEYS**

In the six focal fragments, my field crews and I mapped territories, searched for nests, banded chicks, and determined mating status of males in the austral spring (October 2000 to January 2001, September–December 2001). Previous work showed that chicks can be banded at about 14 days of age, when the legs have hardened sufficiently that the bands do no damage, but attempts to band chicks after age 16–17 days often leads to premature fledging. To each banded bird (at about 14 age days) we applied one numbered aluminum band and three plastic color bands in individually distinctive combinations. In all, we banded 159 chicks in 2000 and 2001 and resighted 13% in the year following band placement.

To resight banded birds in subsequent years and assess natal dispersal, we visited each focal fragment and neighboring forest fragments. Without radio-tracking, it is not feasible to search large areas for banded birds, so the searches were area-restricted and undoubtedly missed some birds that successfully dispersed over relatively long distances. Searches for resightings consisted of repeated visits (at least three) to a fragment using song playbacks to attract birds. Chucos are usually very responsive to playbacks (Sieving et al. 1996, 2000) and commonly approach the speaker closely enough for observers to read their band combinations. Searches worked in teams of 3–6, to improve the efficiency of resighting in dense vegetation. Use of playbacks is more effective with male than with female chucos, so resightings potentially have some bias toward males.

To establish mated status, the sexes were distinguished by behavior, because there is little morphological difference between male and female chucos. We followed males and classified them as mated if we saw them accompanying a female or fledglings, or carrying food or nesting material. In contrast, unmated males were not seen with females, chicks, food, or nest material over several hours of observation, and they sang and patrolled their territories almost constantly.

Mann-Whitney *U*-tests were used to compare the frequencies of nondispersing juveniles and unmated males in isolated and connected fragments. Sex ratios of nondispersing juveniles were examined with a binomial test. Statistical significance was accepted at *P* < 0.05.

**RESULTS**

**JUVENILE RETENTION IN NATAL FRAGMENTS**

The proportion of banded juveniles that remained in their natal fragments as adults was consistently higher in the poorly connected fragments than in better-connected fragments (Table 1). In all cases in these two years, juveniles remaining in their natal patches settled
TABLE 1. Frequency of juvenile Chucao Tapaculos retained in natal forest fragments differing in degree of habitat isolation of Chiloé Island, Chile. The numerator is the number of retained juveniles, and the denominator is the number of chicks banded in each focal fragment. Data from both years are presented, to show that results were consistent across years. There was no overlap in overall frequencies in the two types of fragments (two-tailed Mann-Whitney U-test, \( P = 0.10 \)). If data for each year are considered to be independent, there is still no overlap in frequencies, and the increased sample size yields \( P < 0.01 \).

<table>
<thead>
<tr>
<th>Well-connected fragments</th>
<th>Poorly connected fragments</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Site</strong></td>
<td><strong>Year 1</strong></td>
</tr>
<tr>
<td>C-R</td>
<td>0/10</td>
</tr>
<tr>
<td>Kes</td>
<td>1/10</td>
</tr>
<tr>
<td>Zuñi</td>
<td>0/3</td>
</tr>
<tr>
<td>Total</td>
<td>1/23</td>
</tr>
</tbody>
</table>

on territories different from their natal territory. Despite the isolation of poorly connected fragments, two males banded as juveniles were later resighted, holding territories, outside their natal fragment (one in a broad riparian corridor, one in a small, disturbed fragment). No birds from well-connected fragments were resighted outside their natal fragments during the years of this study, but three males banded in previous years were later found in fragments as much as 5 km from their natal area.

The sex ratio of banded chicks that were resighted as adults in natal fragments was 8 males:13 females, not significantly different from 1:1 (binomial test, \( P = 0.38 \)). There was no evident relationship between the number of territorial males in a fragment and the number of juvenile males that remained or the number of unmated males and the number of juvenile females that remained, but the sample sizes for these comparisons are small.

FREQUENCY OF UNMATED MALES

Males in poorly connected fragments were more likely to be unmated than males in better-connected fragments, in both focal and ancillary fragments (Table 2). Some males in poorly connected focal fragments were never observed with a mate for the duration of two potential brood-rearing periods (over three months). In contrast, males in well-connected focal fragments were seldom unmated for more than two weeks. However, in one case a male whose mate was killed (on the nest) by a predator disappeared himself after a few days. There was no association of unmated status with evidence of logging or livestock activity in the fragments. Some unmated males eventually acquired mates and often nested successfully, suggesting that pair formation was limited by the availability of suitable females. After a release (by another investigator) of a banded adult female chucao near one of the poorly connected focal fragments, this female cruised about the fragment and eventually nested with a previously unmated male. Although this female changed mates the following year, the male on the territory where she first settled was mated again in the second year. Two other long-unmated males found mates after several months, and owners of those territories were paired for the rest of that breeding season and in the following year.

DISCUSSION

JUVENILE RETENTION

Retention of juveniles was higher in poorly connected fragments, and isolation of the fragment is the most

TABLE 2. Frequency of unmated male Chucao Tapaculos in forest fragments of differing connectivity, Chiloé Island, Chile. The numerator is the number of unmated males and the denominator is the number of males surveyed. Data for both years are presented, to show that results were consistent across years. There was no overlap in the overall frequencies in the two types of fragments (two-tailed Mann-Whitney U-test, \( P < 0.01 \)).

<table>
<thead>
<tr>
<th>Well-connected fragments</th>
<th>Poorly connected fragments</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Site</strong></td>
<td><strong>Area (ha)</strong></td>
</tr>
<tr>
<td>C-R</td>
<td>8</td>
</tr>
<tr>
<td>Kes</td>
<td>&gt;22</td>
</tr>
<tr>
<td>Zuñi</td>
<td>4</td>
</tr>
<tr>
<td>Koc</td>
<td>&gt;1000</td>
</tr>
<tr>
<td>R-Pab</td>
<td>&gt;100</td>
</tr>
<tr>
<td>Wop</td>
<td>9</td>
</tr>
<tr>
<td>Total</td>
<td>1/82</td>
</tr>
</tbody>
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\( a \) Only a small fraction of the entire fragment was surveyed.

\( b \) Ancillary fragments surveyed once.
likely explanation for this pattern. An alternative explanation is a density-dependent response, with lower dispersal at lower densities. However, two observations suggest that density is not a primary factor determining juvenile retention in natal fragments, at least for males. (1) Estimated territory density in poorly connected and well-connected fragments was similar (median = 0.8 ha⁻¹ in both cases). (2) The pattern of low retention of juvenile males in well-connected fragments and higher retention in poorly connected fragments was consistent, even though territory density varied annually (by as much as 50% in a given fragment; Table 2).

FREQUENCY OF UNMATED MALES

The territories of long-unmated chucos were similar in size, location, and vegetation structure to territories occupied by pairs, and habitat quality is very unlikely to explain the failure of certain males to obtain mates. Over the past 10 years, I have observed that chucos in these forest fragments occupy territories that vary in vegetation structure, ranging from primary forest devoid of disturbance from logging or livestock, with extensive dense understory and wet swales or small drainage systems; to secondary forest lacking large trees, with disturbance from livestock and selective logging, less extensive dense understory, and few damp areas for foraging; to coastal scrub. Males with mates and successful nests are found on territories along this entire gradient. The unmated males reported in this study were, in general, found in locations not disturbed by logging or livestock, with plenty of understory, logs and snags, and wet drainage. There was no evidence of poor habitat quality in places occupied by unmated males.

Forest edge did not explain unmated status of males either, because most chucos territories (of both mated and unmated males) in the smaller fragments abut an edge, and there is no evidence that chucos avoid forest edges in any case (De Santo et al. 2002). Similarly, it is hard to argue that nest sites per se limit the probability of females settling on the territories of unmated males. Chucos nest in a great variety of widely available cavities or semi-enclosed niches, but they also sometimes build domed or even open-cup nests on the ground or in small trees, sometimes in territories known to offer cavities and niches used for nesting at other times. Finally, several chucos territories with long-unmated males in poorly connected patches eventually held paired males and successful nests, suggesting that at least some of these territories were suitable, and that the principal factor limiting mate-finding was the availability of females.

Several other studies have reported effects of habitat connectivity specifically on female birds. Like the chucos, territorial males of the Ochre-flanked Tapaculo (Euprattus paradoxa) and Des Murs' Wiretail (Sylviparus thorhynchi desmursii) often lacked mates in isolated habitat patches in Chilean rainforest (McPherson 1999, I. Díaz, pers. comm.). Natal dispersal of female White-browed Babblers (Pomatoschistus superciliosus) in Australia was enhanced by patch connectivity (Cale 2002). Experimental translocations of female Brown Treecreepers (Climacteris picumnus) to forest fragments in eastern Australia suggested that low female recruitment in fragments and lack of female dispersal between fragments determined the low mating success of males in fragments (Cooper and Walters 2002). Fragmentation impaired dispersal and delayed female recruitment in the Red-Cockaded Woodpecker (Picoides borealis; Schiegg et al. 2002). Other studies estimated connectivity at the landscape level (Gibbs and Faaborg 1990, Van Horn et al. 1995, Bayne and Hosson 2001) or judged relative isolation on the basis of location within the geographic range (Dale 2001), without assessing corridors per se. Pairing success in such studies commonly decreased with decreasing estimates of connectivity, but with some variation among species.

Other studies have reported that fragment size affects pairing success (e.g., Dale 2001, Zanette 2001), but habitat quality and male turnover are among the potentially confounding variables (e.g., Sabine et al. 1996, Burke and Nol 1998, Zanette 2001). Small fragment size was not a significant contributor to the results reported here, because the smallest focal fragments were better connected than many of the larger ones and did not differ in frequency of unmated males (Table 2).

The high frequency of unmated males in poorly connected fragments in Chiloé and the failure of nondispersing females to pair with them remain something of a mystery, in the absence of detailed information on differential mortality, dispersal distances, or initial sex ratios. Several possibilities, including the following, might be considered. (1) The sex ratio of chucos is biased in favor of males. However, rapid mate replacement in well-connected patches indicates the existence of a population of female "floaters" and does not suggest a severely biased sex ratio of mating-age individuals there. (2) Dispersal of chucos is biased in favor of females. A review of sex biases in avian dispersal showed that, for most passerines, natal dispersal is either female-biased or shows no gender bias (Clarke et al. 1997). Female-biased dispersal can lead to high frequencies of unmated males in fragmented habitats, if females have a limited time to search for available males but their dispersal movements often take them to unsuitable habitats, so that many females fail to find a mate in the available time (Dale 2001). However, female chucos have up to about eight months to search for mates (the time from the independence of first-brood chicks to the time of clutch initiation the following season), so it is not clear that time is the limiting factor in this case. (3) Either the unpaired males or the nondispersing females are inferior in some way, possibly related to the risk of inbreeding. High levels of juvenile retention indicate an increased risk of inbreeding, but the seriousness of that problem depends on undetermined levels of gene flow and on environmental conditions (Couvet 2002, Keller et al. 2002). Some of the males in this study eventually nested successfully; this delay could have been due to inferiority of either males or available females, but it also suggests that the males were acceptable mates. (4) Dispersal costs (Waser et al. 1994, Weatherhead and Forbes 1994) from poorly connected fragments are particularly high, because of predation risks in open habitats, particularly from avian predators such as
hawks and caracaras (pers. obs.). Female chucaos might disperse farther, if not more often, than males or suffer greater mortality, particularly when emigrating from poorly connected fragments.

CONSERVATION OF CHUCAOS

Habitat connectivity can prevent at least some of the negative effects of habitat fragmentation. Conservation of chucaos in the increasingly fragmented habitats in Chiloé would benefit from a program that fostered the maintenance or restoration of wooded corridors connecting forest patches. Many Chilote landowners retain woodlots as winter shelter for livestock, and they often leave forest vegetation in steep-walled ravines and gulies. Such drainages commonly reach the seacoast, where steep but densely vegetated seaciffs offer both habitat and travel corridors among fragments. A good conservation plan for this region would include a network of woodlots, wooded ravines, and seaciffs, allowing chucaos, other tapaculos, and perhaps small mammals and amphibians, to move around the landscape to occupy available habitats. It is clear that existing protected areas in Chile are insufficient to preserve native biodiversity (Pauchard and Villarroel 2002), and the increasing press of humankind makes it necessary to find ways for humans and native wildlife to coexist on the landscape.

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