Experimental Evidence of Disrupted Dispersal Causing Decline of an Australian Passerine in Fragmented Habitat

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Abstract: We evaluated two hypothetical explanations for the decline of the cooperatively breeding Brown Treecreeper (Climacteris picumnus) in fragmented habitat: habitat degradation and isolation. We monitored the reproductive performance of approximately 50 breeding groups in Eucalyptus woodlands in the New England tablelands of northeastern New South Wales during 1996-1998. In addition, we translocated females to contiguous woodland and woodland fragments with unpaired males. We predicted that experimentally relocated females would reject territories with unpaired males in fragments if the habitat was degraded but not if males were unpaired due to isolation. We moved 11 females to fragments with unpaired males and 5 females to contiguous habitat with unpaired males. Nine females remained with males in fragments. Five of these females attempted nesting and 3 produced fledglings. No female relocated to contiguous habitat with an unpaired male remained or paired. We rejected habitat degradation as an explanation for the current decline of Brown Treecreepers within remnants, although degradation likely played a role in the past at a regional scale. Exceedingly low female recruitment within fragments and a lack of female dispersal between fragments provide additional evidence that female dispersal into territories in fragments rarely occurs naturally. We conclude that patch isolation is responsible for the high proportion of unpaired males in fragmented habitat.

Evidencia Experimental de la Disrupción de la Dispersión que Ocasiona la Pérdida de una Especie Paserina Australiana en un Hábitat Fragmentado

Resumen: Evaluamos dos hipótesis para explicar la disminución del sube palos cañacho (Climacteris picumnus) en hábitat fragmentado: degradación y aislamiento del hábitat. Monitoreamos el rendimiento reproductivo de aproximadamente 50 grupos de reproductores en bosques de Eucalyptus en el altiplano de Nueva Inglaterra al Noroeste de New South Wales durante 1996-1998. Aunado a esto, trasladamos hembras a bosques contiguos y a fragmentos de bosque con machos sin pareja. Pronosticamos que las hembras experimentales reubicadas rechazarían territorios con machos sin pareja en aquellos fragmentos donde el hábitat estuviera degradado, pero no habría rechazo si los machos no tuvieran pareja debido al aislamiento. Movimos 11 hembras a fragmentos con machos sin pareja y 5 hembras a hábitats contiguos con machos sin pareja. Nueve de las hembras permanecieron con los machos en los fragmentos. Cinco de estas hembras intentaron anidar y 3 produjeron polluelos. Ninguna de las hembras reubicadas en hábitats contiguos con un macho sin pareja permaneció en el sitio ni formó pareja. Rechazamos la degradación del hábitat como una explicación para la disminución actual del sube palos cañacho dentro de los remanentes. Sin embargo, la degradación seguramente ha jugado un papel en el pasado a escala regional. El reclutamiento extremadamente bajo de hembras dentro de los fragmentos y la carencia de dispersión de hembras entre fragmentos provee una evidencia adicional de que la dispersión de las hembras hacia territorios en fragmentos raramente ocurre de manera natural. Concluímos que el aislamiento de los pares es responsable de la alta proporción de machos sin pareja en hábitats fragmentados.

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Introduction

The reduction of biological diversity is attributed primarily to the loss and fragmentation of natural habitats as a result of human activities such as agriculture, urbanization, and resource extraction (Wilcox & Murphy 1985; Rolstad 1991; Saunders et al. 1991). A species sensitive to fragmentation numerically declines or experiences reduced fitness in a habitat segment as the landscape surrounding that segment is altered (Walters 1998). Fragmentation can affect animal populations via changes in the periphery of remnant patches (edge effects), increased distance between remnant patches (isolation), or processes concurrent with fragmentation that change the habitat quality of remnant patches (habitat degradation). Edge effects and habitat degradation can affect population dynamics by altering birth and death rates, whereas isolation can affect populations by altering dispersal patterns.

Elevated nest predation and brood parasitism cause declines in some passerines in woodland fragments in North America (Ambuel & Temple 1983; Brittingham & Temple 1983; Wilcove 1985; Robinson et al. 1995; Haskell 1995). In Australian woodlands, however, brood parasites and nest predators do not appear to have a greater effect on open cup-nesting passerines in small fragments than in large fragments, or in edge than in interior woodlands (Taylor & Ford 1998; Ford et al. 2001; Zanette & Jenkins 2000). Instead, habitat degradation and patch isolation seem the most likely explanations of declines of Australian birds in fragmented woodlands. We attempted to distinguish between these possibilities in the case of the Brown Treecreeper (Climacteris picumnus).

Degraded Eucalyptus woodlands are characterized by a variety of features, including the premature and relatively rapid death of trees (“rural dieback”; Landsberg & Wylie 1994), a lack of tree recruitment, loss of the original understory vegetation, soil erosion, deterioration of soil structure, and invasion by exotic plant species (Hobbs & Yates 2000). Lower avian diversity is found in woodlands suffering severe dieback (Ford & Bell 1982; Barrett 1995), frequently with only one aggressive avian species remaining (Dow 1977; Grey et al. 1997, 1998). At the landscape scale, severe degradation ultimately eliminates woodlands and thus, along with clearing, produces fragmentation. Here we considered mild degradation within woodland remnants. Mild degradation is hypothesized to lower reproduction and/or increase mortality in ground-foraging birds in many parts of Australia, perhaps because degradation reduces available food resources or eliminates refuges from predators (Recher & Lim 1990; Garnett 1992; Saunders & Ingram 1995; Recher 1999; Zanette et al. 2000).

Understanding how avian dispersal patterns might be influenced by landscape structure is critical to testing theories regarding fragmentation effects. Birds are highly mobile organisms, yet landscape features affect the movement patterns or behavior of migratory forest songbirds (Dunning et al. 1995; Desrochers & Hannin 1997), a variety of residents (St. Clair et al. 1998), and short-distance migrants (Haas 1995) in North America and of land birds in Western Australia (Saunders & deRebeira 1985). Cooperative breeders, which are numerous in Australia (Brown 1987; Russell 1989), may be especially sensitive to isolation effects because of the short-distance characteristics of their dispersal patterns (Walters 1998).

Brown Treecreepers are cooperative breeders that inhabit temperate Eucalyptus woodlands and forests, nesting and roosting in naturally occurring tree cavities. They spend approximately half their foraging time on the ground (Walters et al. 1999). Helpers are generally male, and most acquire breeding positions through territorial budding—expanding territory size followed by splitting the territory in two (Woolfenden & Fitzpatrick 1978)—whereas most females disperse (Neske 1980, 1991). Barrett et al. (1994) and Barrett (1995) documented the decline of the Brown Treecreeper in fragmented habitat on the New England Tablelands of northeastern New South Wales. Walters et al. (1999) found that many Brown Treecreeper groups in fragments in this region lack females. Yet among groups with a female, those in small fragments have reproductive success equal to groups in large patches of contiguous habitat (Walters et al. 1999; Cooper 2000).

To explain the observed lack of females in fragmented woodlands, we attempted to experimentally distinguish between habitat degradation and isolation by translocating females to unpaired males in fragmented and contiguous habitat. Under the hypothesis that isolation accounts for the absence of females in fragments, we predicted that translocated females would remain in fragments, reproduce, and survive as well as birds in contiguous habitat (Table 1). We also expected lower (natural) female recruitment, fewer long-distance movements, and fewer movements among remnants in fragmented than in contiguous habitat (Table 1). If translocated females reject territories in fragments or exhibit poor reproduction and/or survival when they remain, then we can reject isolation effects as the reason for males being unpaired in fragments. In this case, alternative hypotheses such as habitat degradation or inferior male quality are favored as explanations of the high proportion of solitary males. Using data on natural dispersal and reproduction (Table 1), we attempted to further distinguish between isolation and habitat degradation.

Methods

Study Area

The study site was composed of Eucalyptus woodland and forest patches within a 1500 km² region surrounding the town of Armidale, on the New England Table-
Table 1. Predictions deduced from the isolation and habitat-degradation hypotheses for Brown Treecreepers in fragmented habitat of New South Wales.

<table>
<thead>
<tr>
<th>Hypothesis</th>
<th>Predicted</th>
<th>Observed</th>
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<tbody>
<tr>
<td>Isolation</td>
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<tr>
<td>proportion of solitary males</td>
<td>$F &gt; C$</td>
<td>yes</td>
</tr>
<tr>
<td>reproductive performance</td>
<td>$F = C$</td>
<td>yes</td>
</tr>
<tr>
<td>(natural) recruitment of juvenile females</td>
<td>$F &lt; C$</td>
<td>yes</td>
</tr>
<tr>
<td>proportion of translocated females that remain and breed</td>
<td>$F &gt; C$</td>
<td>yes</td>
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<tr>
<td>long-distance movements of females</td>
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<td>yes</td>
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<tr>
<td>frequency of female movements between patches</td>
<td>$F &lt; C$</td>
<td>yes</td>
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<tr>
<td>Habitat degradation</td>
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<tr>
<td>proportion of solitary males</td>
<td>$F &gt; C$</td>
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*aAbbreviations: F, fragmented habitat; C, contiguous habitat.  
*bThere is a high proportion of unpaired male Brown Treecreepers in fragmented habitat because female dispersal is disrupted among fragments.  
*cPredictions are the same for both hypotheses.  
*dThere is a high proportion of unpaired male Brown Treecreepers in fragmented habitat because fragments are degraded and therefore contain low-quality habitat and/or males of inferior quality.

lands of northeastern New South Wales, Australia (lat. 30°27’S, long. 151°13’E) (Fig. 1). The study area straddled the Great Dividing Range, with elevation ranging from 730 to 1300 m, and is described by detail by Cooper (2000).

Temperate *Eucalyptus* woodland communities are among the most poorly conserved ecosystems in Australia (Specht 1981; Sivertsen & Clarke 2000; Yates & Hobbs 2000). Approximately 70–95% of various woodland types have been replaced by agriculture and pasture (Yates & Hobbs 2000). Furthermore, the woodlands on high-quality soils have been preferentially cleared (Recher & Lim 1990; Hobbs et al. 1993; Robinson & Traill 1996). Patches of woodland that remain are used for sheep and cattle grazing, and dead trees are removed for firewood. The landscape of the New England Tablelands has been described as “variegated” (McIntyre & Barrett 1992; McIntyre & Hobbs 1999), rather than fragmented into discrete “islands” in a “sea” of completely cleared land. In the variegated landscape of the New England Tablelands, there is a gradient of tree density ranging from completely cleared land to forest. Cooper (2000) digitized the land-cover types in the study area according to the following tree densities: 0 trees/ha, cleared land; 1–10 trees/ha, sparse trees; 10–50 trees/ha, scattered trees; and >50 trees/ha, woodland and forest (Fig. 1).

In the study area, Brown Treecreeper family groups defend territories averaging 4.5 ha and ranging from 1.1 to 10.7 ha in size. The central and eastern portions of the study area (approximately 237,000 ha) are highly fragmented, with only 7% of the landscape in woodlands (16,000 ha), which are distributed across intervening habitat of mostly cleared land (44%) and sparse trees (35%) (Cooper 2000). Three woodland fragments we sampled in this area were adjacent to *Eucalyptus* forests in steep gorges, a habitat unsuitable to Brown Treecreepers (Keast 1957; Noske 1982a, 1982b). The western portion of the study area (approximately 104,000 ha) was predominantly contiguous habitat, with 20% woodlands (20,000 ha) and an intervening habitat of sparse trees (48%), scattered trees (16%), and steep woodlands (10%) (Cooper 2000). The monitored groups we considered as residing in contiguous habitat were in woodland patches connected to one another and to other patches through wooded corridors with no gaps of cleared land larger than 200 m between patches. The monitored groups we refer to as residing in fragmented habitat were in woodland patches isolated from contiguous habitat by at least 2 km of mostly cleared land and sparse trees (Fig. 1). Brown Treecreepers in contiguous habitat generally occurred in clusters of breeding groups with loosely spaced groups between clusters (Fig. 1). In fragmented habitat, Brown Treecreepers were scarce; through extensive surveying, we determined the locations of virtually all territories.

Translocation Experiment

We translocated females to fragmented and contiguous habitat with unpaired males at the conclusion of the 1996, 1997, and 1998 breeding seasons and prior to the 1998 and 1999 breeding seasons. Females selected for translocation were captured in contiguous habitat and ranged in age from 2 months post-fledging ($n = 8$) to adult ($n = 10$). Females were released on territories which an unpaired male either was occupied alone ($n = 8$), shared with another male ($n = 2$), or occupied as a helper that held a portion of his natal territory in the initial stages of budding ($n = 6$).
Females were captured with a mist net in the morning, fitted with colored bands if not already marked, and transported to a new location within 3 hours. After release, females were observed until they contacted the resident unpaired male or for 1 hour, whichever came first. We attempted to find translocated females the day after release, within 3 weeks after release, 2-3 months later, and during the following breeding season. If a female did not appear healthy upon release and subsequently disappeared, or appeared to survive translocation but not the winter, we then moved a second female to that territory if a male was still present. This occurred twice in fragmented habitat.

We moved 18 females to unpaired males on 16 territories, 13 females to 11 territories in fragmented habitat and 5 to 5 territories in contiguous habitat. In two fragmented sites, we moved males to the translocated females after the original receiving males disappeared.

Spatial Distribution of Territory and Dispersal Predictions

We surveyed patches and monitored over 50 groups of Brown Treecreepers from 1996 to 1998, as detailed by Cooper (2000). Monitoring involved color-banding of adults and offspring and repeated visits at least every 14 days to survey groups to collect data during the breeding season (late July through December) each year. We monitored groups with translocated females in an identical manner. When dispersal was detected, movements were measured to the nearest 100 m as the straight-line distance between initial banding location and resighting location.

We expected the distribution of observed dispersal movements to reflect the distribution of potential breeding vacancies. To determine the distribution of potential breeding vacancies, we computed the average number of known territories within successive distance intervals around all known territories. Specifically, we tallied the number of known territories within over 100 concentric circles, each at 500-m intervals (500 m–65 km), surrounding each territory where offspring were banded. Under the alternative hypothesis that dispersal is disrupted by fragmentation, we assumed that vacancies within a patch in fragmented habitat were available only to females originating in that patch. To calculate an expected distribution, we determined for all known territories the distances to all other territories in the same patch and then computed the average number of such territories in each distance interval in fragmented habitat. We assumed that all vacancies were available to females originating in

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Figure 1. Study area, with monitored groups designated by black circles and unmonitored groups by open triangles. Woodlands are in gray; white is a matrix of scattered trees, light vegetation, and cleared land. Universal transverse mercator (UTM) units are shown at corners.
Contiguous habitat. Thus, in contiguous habitat, the average number of territories in each distance interval were the same under both hypotheses. To turn the distribution of potential breeding vacancies into the proportion of birds predicted to move each distance interval, we divided the average number of territories in each distance interval by the number of female fledglings banded in that population (i.e., fragmented or contiguous).

Results

Group Composition and Translocation Experiment

The percentage of territories that lacked a female was 0% in contiguous habitat and 50% in fragmented habitat (Fisher's exact, \( p < 0.0001, df = 1, n = 35 \)). None of the females relocated to contiguous habitat paired and remained with the male for a breeding season. Seven females that were relocated to fragments paired and remained with the male occupant for at least one breeding season. Five of these females attempted nesting, five of which produced nestlings and three of which produced fledglings. Translocated females were significantly more likely to pair with the males in fragmented habitat than with those in contiguous habitat (Fisher's exact test, \( p = 0.005, df = 1, n = 16 \)). We could not compare the reproduction of translocated females between treatments because none of the relocated females paired with males in contiguous habitat. The nest-success rate of translocated females in fragments (60%) was similar to the nest-success rate of females in nonexperimental groups in contiguous (62%) and fragmented (61%) habitat. The proportion of paired relocated females that attempted nests (71%) was low compared with that of paired females in other groups in contiguous (99%) and fragmented (96%) habitat.

Movements in Fragmented and Contiguous Habitat

Of 23 males banded as fledglings on their natal territory and resighted as adults, 19 were resighted on their natal territory, 2 successfully budded, 1 successfully dispersed to another territory, and 1 helped on both his natal territory and on a neighbor's territory simultaneously. The mean (± SD) distance moved between banding and resighting was 0.06 ± 0.19 km (\( n = 23 \)), with a median distance of 0.

The mean (± SD) distance that we observed females (fledglings and adults of unknown age) move was 1.14 ± 1.25 km (\( n = 17 \)), with a median distance of 0.77 km and a maximum distance of 4.5 km. The mean (± SD) was 0.72 ± 0.59 km in fragmented habitat (\( n = 7 \), median 0.88 km, maximum 1.4 km) and 1.39 ± 1.49 km in contiguous habitat (\( n = 10 \), median 0.69 km, maximum 4.5 km) (Fig. 2). All movements observed in fragmented habitat were within patches. In contiguous habitat, the two longest movements observed (4 and 4.5 km) were between patches.

Recruitment in Fragmented and Contiguous Habitat

We detected 14 movements of juvenile females, 4 originating in fragments and 10 in contiguous habitat. Assuming that half the juveniles we banded were female, and subtracting the eight juvenile females used in the translocation experiment, the observed movements account for 44% of the juvenile females banded in fragmented habitat and 29% of those banded in contiguous habitat. Other observed movements were of birds of unknown age. All breeding vacancies in contiguous habitat were filled quickly, 44% by unbanded female immigrants and 56% by banded juvenile females. In contrast, only one female (banded) was recruited into a breeding vacancy in fragmented habitat (13%), and there were no immigrants. The lone instance in fragmented habitat involved movement within a fragment: we observed no movement between or into fragments. The remaining female recruits in fragmented habitat (87%) were those experimentally relocated.

Discussion

Our results suggest that Brown Treecreepers are declining in the New England Tablelands because of isolation, rather than degradation of remnant habitat (Table 1). A significantly higher proportion of groups in fragmented than contiguous habitat lacked a female each year, no females were observed to disperse between fragments or otherwise move long distances from fragments, and recruitment within fragments was low. When females were translocated to these fragments, they usually paired and in some cases bred successfully.

The results of two earlier studies suggest that reproduction and foraging behaviors are similar among territories with females in fragmented and contiguous habitat, suggesting that fragments were not degraded (Walters et al. 1999; Cooper 2000). In the current study, none of the predictions derived from the habitat-degradation hypothesis we tested were supported, except for those common to the isolation hypothesis (Table 1). Thus, we reject habitat degradation as an explanation of the continuing decline of Brown Treecreepers in woodland fragments in the study area. This conclusion pertains to the current effects of mild degradation on remnants still occupied by Brown Treecreepers and not to factors influencing the current regional distribution of the species, which may have been influenced by severe habitat degradation. Although we suspect that degradation played a role in rendering many areas unsuitable for occupancy by Brown Treecreepers (Cooper 2000), we conclude that degradation is not the direct cause of the
high proportion of solitary males in currently occupied fragments.

Under the null hypothesis of no isolation, we expected the distribution of dispersal distances to be similar in fragmented and contiguous habitat. Under the alternative hypothesis of isolation effects, we expected the median female dispersal distance to be higher and the maximum distance lower (i.e., a distribution with a truncated tail) in fragmented than in contiguous habitat (Fig. 2). The observed distribution of female movements in fragmented habitat was similar to that predicted from isolation effects (Fig. 2). We monitored a much lower proportion of the occupied contiguous habitat (approximately 28%) than occupied fragmented habitat (approximately 58%) in the study area. Thus, dispersal data from contiguous habitat were more strongly biased toward short-distance movements than data from fragmented habitat (Koenig et al. 2000). The observed dispersal patterns in contiguous habitat were in fact skewed farther left (toward short distances) than predicted, whereas the observed patterns in fragmented habitat closely matched predictions for isolation effects (Fig. 2).

Our results suggest that the paucity of females in fragmented habitat is due to the inability or reluctance of females to disperse through a fragmented landscape to fill breeding vacancies. The presence of more males than females in fragments is attributable to high male philopatry. That is, males in fragments were probably on or adjacent to their natal territory, because the dominant pathways for a male to acquire a breeding position are by territory budding and territory inheritance (Noske 1980, 1991; C.B.C., personal observation). Thus, the scale of male dispersal was too small to be disrupted by the scale of fragmentation in our study area. In contrast, females must disperse from their natal neighborhood to avoid mating with related males, which may require leaving small fragments.

One puzzling result was that translocations in contiguous habitat were uniformly unsuccessful. Perhaps females relocated to males in contiguous habitat were able to move easily to a vacancy other than the one at the release site. Alternatively, unpaired males in contiguous habitat may occupy low-quality habitat. We think this unlikely, because these males typically obtained mates in future years. A more likely possibility is that the unpaired males in contiguous habitat were not sufficiently advanced in the budding process to form a pair bond. Those that were, in this scenario, already had a mate.

Our data suggest that the configuration of the landscape in the contiguous region permits the successful dispersal of Brown Treecreepers, whereas the configuration in the fragmented region does not. Connectivity, essentially a quantification of ease of dispersal (Schumaker 1996), represents a species-specific "perception" of fragmentation. Potential sources of connectivity suggest three possible mechanisms by which female dispersal and re-
recruitment might be disrupted in fragmented habitat but not in contiguous habitat. One possibility is that cleared land, and even sparse tree cover, is perceived by Brown Treecreepers as a barrier to movement. Support for this possibility comes from the observation that the only translocated females to disappear from fragments soon after release were those moved to fragments bordered in part by steep wooded gorges rather than solely by cleared land. These wooded gorges are unsuitable for breeding but are probably suitable for movement. In contradiction to this possibility is the observation that large portions of some Brown Treecreeper home ranges are composed of sparsely wooded pasture. Brown Treecreepers often forage in treeless areas, although how far they venture into such areas is unknown.

A second possibility is that the distance between groups in remaining fragments may be greater than Brown Treecreepers are capable of traveling during dispersal. Support for this possibility comes from the observation that, like other cooperative breeders, most Brown Treecreepers travel short distances during dispersal. We observed a maximum movement of 1.2 km in fragmented habitat, even though most patches were >5 km apart. A third possibility is that the high dispersion of territories among fragments, regardless of the intervening habitat, may reduce the probability of a female locating a territory (Doak et al. 1992; Letcher et al. 1998). In fragmented habitat, a wide search path or complex search pattern would be required to detect more than a handful of territories (Fig. 1), whereas birds moving through contiguous habitat encounter more groups per unit area because territories occur at high densities.

The extent to which our findings might apply to other species, in Australia and elsewhere, is unclear. Certainly isolation merits more attention as a cause of population declines in fragmented habitat.

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Literature Cited


