

# Independent effects of woodland loss and fragmentation on Brown Treecreeper distribution

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## Abstract

We examined the influence of local habitat and the surrounding landscape on the distribution of Brown Treecreepers in a matrix of woodlands and pastures. Our goals were to: (1) determine the importance and scale of the independent effects of woodland cover and fragmentation on treecreeper distribution, and (2) employ landscape variables to improve models of treecreeper distribution based on local habitat features. Woodland fragmentation was important at a large scale while both woodland cover and fragmentation were important at a smaller scale. Excluding unoccupied sites in highly fragmented landscapes improved the ability of local habitat features to explain Brown Treecreeper distribution, which appeared to be constrained by cavity density. Brown Treecreepers' response to fragmentation at the larger scale may occur because fragmentation disrupts dispersal. Alternatively, their response may be an example of a general phenomenon of fragmentation effects only arising when < 20% of woodland cover remains at a given scale. As fragmentation increases, so does the need to incorporate landscape patterns into wildlife-habitat models. © 2002 Elsevier Science Ltd. All rights reserved.

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## 1. Introduction

The theory of island biogeography (MacArthur and Wilson, 1967) and principles of metapopulation dynamics (Hanski and Gilpin, 1991) suggest that the amount and spatial configuration of habitats in the landscape will influence persistence and spatial distribution of wildlife. Composition of avian communities is influenced by the amount and configuration of natural and human-dominated patches in the landscape (McGarigal and McComb, 1995; Flather and Sauer 1996, Jokimaki and Huhta, 1996; Bolger et al., 1997; Saab, 1999). Habitat fragmentation alters the amount, configuration, and sometimes the quality, of habitat and is therefore expected to affect bird distribution. However, most studies of habitat fragmentation and birds occur at the scale of single patches, rather than landscapes, with a few exceptions (Trzcinski et al., 1999; Villard et al., 1999). It is unclear whether findings from

patch studies can be extrapolated to the landscape level (Wiens et al., 1993).

Barrett et al. (1994) and Barrett (1995) documented the decline of the Brown Treecreeper (*Climacteris picumnus*) in fragmented habitat in the New England Tablelands of northeastern New South Wales. Walters et al. (1999) found the pattern of decline was characterized by the presence of unpaired males in fragmented habitat. Cooper and Walters (2002) demonstrated experimentally that unpaired males in fragmented woodland were not in poor quality habitat; rather, recruitment of juvenile females into isolated fragments was disrupted. They found that spatial distribution of highly fragmented habitat did not permit successful dispersal and recruitment, which occurred in more contiguous habitat. Brown Treecreepers in central New South Wales are not found in patches more than 700 m from the next nearest patch of 10 ha or larger (S. Briggs, personal communication). Thus, distribution of Brown Treecreepers appears to be influenced by landscape patterns.

Wildlife managers have focused on modelling the relationship between animal abundance and local habitat features, rather than the effects of distribution of habitats across a landscape. Using models to correctly

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identify suitable habitat is critical to conservation. For example, the US Endangered Species Act of 1976 is designed to protect critical habitat, even if the habitat is currently unoccupied (Schreiner, 1976). Several US governmental agencies responsible for managing wildlife use habitat models built from distribution data, such as habitat suitability index models and habitat-capacity models (Anderson and Gutzwiller, 1994). Wildlife managers also use models of wildlife–habitat relationships to make predictions about species distribution patterns at regional scales (e.g. GAP analysis project; Scott et al., 1993; Edwards et al., 1996).

A detailed understanding of the habitat requirements of Brown Treecreepers is needed to effectively conserve this locally threatened species. In this case, however, an accurate habitat model must include landscape effects. If landscape patterns strongly influence distribution patterns, the identification of critical habitat features can be confounded by a lack of individuals in good quality habitat in unsuitable landscapes. Similarly, if habitat features strongly influence distribution patterns, the identification of critical landscape patterns can be confounded by a lack of individuals in poor quality patches in suitable landscapes. Another difficulty is the time delay in response of the population to landscape changes, which can result in the continued presence of individuals in unsuitable landscapes. All species are patchily distributed at some scale and patterns of aggregation can become exaggerated by habitat loss and fragmentation (Simberloff, 1995). Brown Treecreepers are naturally patchily distributed because they are cooperative breeders that exhibit a high frequency of territorial budding, resulting in clusters of groups or clans (Noske, 1982a; Walters et al., 1999). In addition, they avoid degraded woodlands and forested areas on steep rocky hills and gorges (Noske, 1982a,b).

We examined the distribution of Brown Treecreepers in relation to local habitat characteristics as well as landscape characteristics, specifically, the independent effects of woodland cover (cover = the total amount of a specified habitat) and fragmentation (fragmentation = the spatial arrangement of a specified habitat in the landscape). Measures of cover and fragmentation can vary considerably as the size of the landscape examined changes. Therefore, we analyze the effects of cover and fragmentation at multiple scales or landscape sizes. Fragmentation can also affect habitat quality through edge effects, but this study does not address edge effects, because other research showed their influence on Brown Treecreeper ecology to be minimal (Cooper and Walters, 2001). Our goals were to: (1) determine the scale and importance of the independent effects of woodland cover and fragmentation on the distribution of Brown Treecreepers, and (2) use landscape variables to improve models of Brown Treecreeper distribution based on local habitat features.

## 2. Methods

### 2.1. Study area and species

The study site is a 1500 km<sup>2</sup> region surrounding the town of Armidale, in the New England Tablelands of northeastern New South Wales, Australia, (30° 27' S 151° 13' E). The study area straddles the Great Dividing Range, with an elevation ranging from 730 to 1300 m. Additional details are in Cooper et al. (2001).

The Brown Treecreeper is a cooperatively breeding passerine endemic to Australia. These birds are insectivorous and forage both on tree surfaces and on the ground. They live in *Eucalyptus* woodlands, nesting and roosting in naturally occurring cavities (Noske, 1982a). The subspecies of Brown Treecreepers in the Tablelands was recently designated as Near Threatened in the latest Action Plan for Australian Birds (Garnett and Crowley, 2000).

### 2.2. Brown Treecreeper distribution

To sample the distribution of Brown Treecreepers, we selected sites within the study area (Fig. 1) by superimposing a 500-m grid of points over topographic maps and randomly choosing a subset of 80 points. After consulting aerial photographs and conducting ground-truthing, we excluded points that were not in woodlands and moved points on the edge of woodlands to at least 150 m from the edge. Each site had a radius of 135 m, and was 5.7 ha, which is slightly larger than the mean territory size (mean = 4.4 ha, S.D. = 2.5, range 1.1–10.7 ha,  $N=25$ ) (Cooper et al., 2001).

Sites were sampled during the breeding season, when Brown Treecreepers are vocal. A site was designated as unoccupied if Brown Treecreepers were not detected on or in the vicinity of the site. Sites were visited for approximately 1 hour, during which time we determined the size of Brown Treecreeper groups and sampled habitat characteristics. Group size was recorded as one only after repeated visits verified that no additional birds were present. Plumage indicated that lone birds were always male.

We tested for habitat differences between sites that were occupied and unoccupied. We did this at three points in time. The first point was at the start of population monitoring in 1992 (Walters et al., 1999), and the second was at the end of this study in 1998. The third point was extrapolated based on sites that were occupied by  $\geq 2$  birds or  $< 2$  birds in 1998. Other research revealed that if a bird remained solitary for more than a few days, it was highly unlikely to ever recruit a mate (Cooper and Walters, 2002). Therefore, sites with solitary birds would eventually become unoccupied and this last point represents an unspecified time in the future.

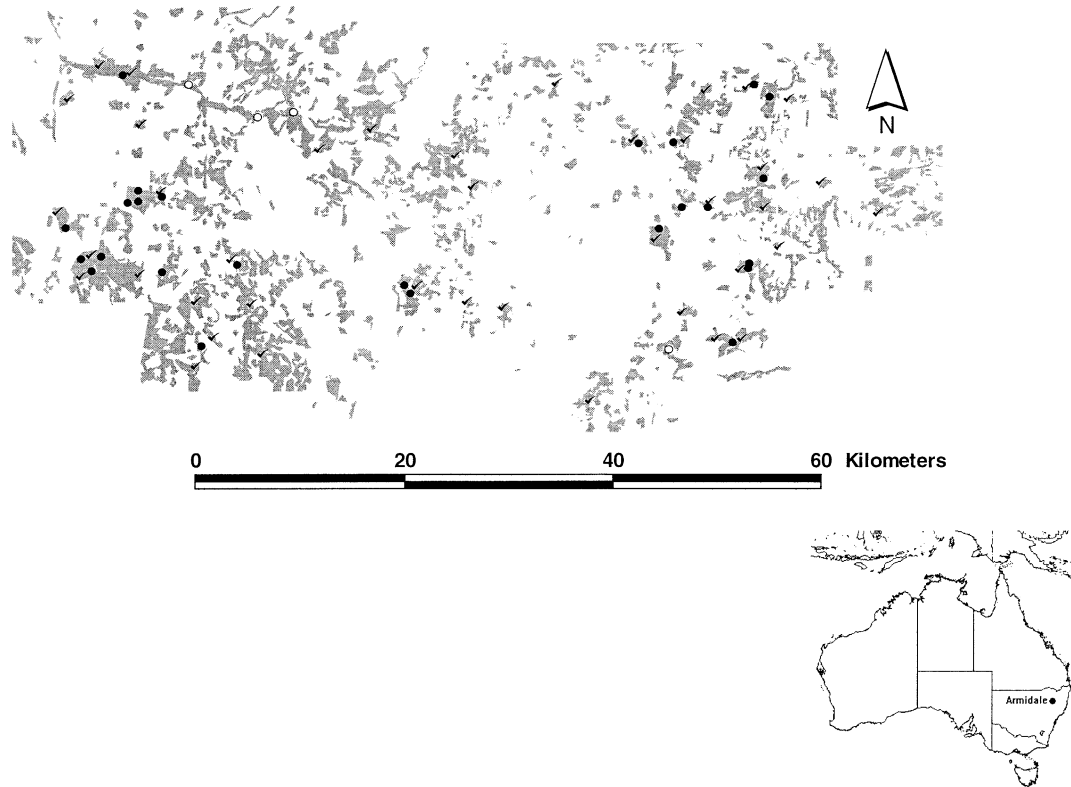


Fig. 1. Study area and locations of randomly selected sites. Woodlands are in grey. Black circles represent randomly selected sites  $> 3.2$  km apart ( $N=40$ ), white circles represent territories included in landscape analyses ( $N=4$ ), and checks represent remaining sites used only in habitat analyses ( $N=40$ ). Inset shows location of study area (Armidale) in Australia.

### 2.3. Habitat

With field assistants, we collected habitat data from  $25 \times 25$  m square plots in territories and at each randomly selected site. Randomly selected sites contained four plots, each 115 m in each cardinal direction from the center of the site. Territories contained 2–6 plots. Territory plots were selected by placing a 75-m grid over each territory and randomly selecting half the grid points as plot centers. We tallied the number and diameter at breast-height (dbh) of trees greater than 15 cm dbh on each plot. Other studies of Australian bark-foraging passerines have profited by characterizing trees by their bark characteristics (Noske, 1991; Stokes, 1995). Accordingly, we classified each tree as one of the following types: Gum (*Eucalyptus*, subgenus *Symphyomyrtus*, Section *Transversaria* and *Exsertaria*), Box (*Eucalyptus*, subgenus *Symphyomyrtus*, Section *Adnataria*), Stringybark (*Eucalyptus*, subgenus *Monocalyptus*, Series *Capitellatae*), River Sheoak (*Casuarina* spp.), Ironbark (*Eucalyptus*, subgenus *Symphyomyrtus*, Section *Adnataria*), Dead trees, and Other. For analyses, we excluded those categories that occurred at low frequencies, namely River Sheoak, Ironbark, and Other. We divided midstory vegetation into two categories, tall shrub ( $> 0.25$  m and  $< 2$  m) and dwarf shrub ( $< 0.25$

m), and counted the number of stems of each. We counted logs (fallen trunks or large branches  $> 1$  m in length) on each plot and estimated ground cover composition in four categories, tall grass, low grass, rocks, and bare ground. The distinction between tall and low grass was made not only by the height of grasses and forbes, but also by the form (e.g. clump grasses generally grew tall). Bare ground was ground without live vegetation, though it may have fallen leaves and twigs. We also counted cavities (naturally occurring cavities in trees and stumps) in each plot.

The variables derived from the upper (i.e. tree) and lower vegetation strata were uncorrelated with each other (i.e. all Pearson's correlation coefficients  $< 0.4$ ). However, some ground cover/midstory variables were slightly correlated with one another and some tree variables were correlated with one another (Pearson's correlation coefficients  $> 0.4$ ). Therefore, we used principal component analysis (PCA) to reduce the data sets to uncorrelated variables. PCA was performed separately on correlation matrices for tree variables and for ground cover/midstory variables, and resulting factors with eigenvalues greater than 1.0 were used in subsequent analyses (Table 1). We used forward stepwise logistic regression, with significance levels of 0.5 for variable entry and 0.05 for variable retention, on the

ground cover/midstory principal components, the tree principal components, and number of cavities to model Brown Treecreeper distribution ( $N=80$ ).

We later used landscape variables to exclude sites in unsuitable landscapes, and again performed PCA separately on correlation matrices for tree variables and for ground cover/midstory variables, and used resulting factors with eigenvalues greater than 1.0 to generate a new habitat model (Table 1). As above, we used forward stepwise logistic regression on these ground cover/midstory principal components, tree principal components, and number of cavities to model Brown Treecreeper distribution in suitable landscapes ( $N=43$ ).

Principal components for each of the above analyses were similar. PC1 derived from tree variables represents a gradient from a low tree density dominated by gums to a high tree density dominated by stringybarks. PC2 derived from tree variables represents a gradient from boxes to stringybarks. PC3 derived from tree variables represents a gradient from snags to gums in the first analysis and in number of gums in the second analysis. PC1 derived from ground cover/midstory variables represents a gradient of low grass and shrubs without rocks to tall grass with rocks. PC2 derived from ground cover/midstory variables represents a gradient from high to low bare ground and logs. PC3 derived from ground cover/midstory variables represents a gradient from tall grass and shrubs to low grass in the first analysis and a gradient from bare ground and tall shrubs to low grass in the second analysis.

Table 1  
Principal components (eigenvalue > 1) formed from habitat data

	$N=80^a$			$N=43^b$		
	PC1	PC2	PC3	PC1	PC2	PC3
<i>Tree variables</i>						
Gums	-0.34	0.48	-0.49	-0.33	0.12	0.86
Boxes	0.25	0.69	0.19	0.31	0.79	-0.15
Live Trees	0.63	0.37	-0.18	0.59	0.03	0.47
Stringybarks	0.65	-0.34	-0.01	0.56	-0.55	0.04
Snags	-0.11	0.20	0.83	-0.36	-0.24	-0.11
Variation explained	35%	25%	20%	38%	22%	20%
<i>Ground cover/midstory variables</i>						
Bare ground	0.01	0.73	0.001	-0.12	-0.34	0.68
Low grass	0.57	-0.37	-0.37	0.51	-0.34	-0.45
Tall grass	-0.48	-0.24	0.54	-0.28	0.69	-0.01
Dwarf shrub	0.43	0.02	0.48	0.51	0.30	0.19
Tall shrub	0.37	0.24	0.47	0.41	0.29	0.44
Logs	-0.07	0.47	-0.29	-0.19	-0.35	0.27
Rocks	-0.35	-0.06	-0.20	-0.44	-0.03	-0.18
Variation explained	26%	23%	18%	28%	22%	21%

<sup>a</sup> First habitat analysis.

<sup>b</sup> Second habitat analysis.

## 2.4. Landscape

With the aid of aerial photographs (1992, 1994) and topographic maps (each 1:25 000), we used a geographic information system (ArcInfo) to create a digitized map of all woodlands in the study area. Woodlands were areas dominated by *Eucalyptus* trees with distinct boundaries and densities of approximately 50–200 trees/ha.

Landscape attributes (see below) were computed within 0.5, 1, 1.5, 2, 2.5, 3, 3.5, 4, and 4.5 km radii of each site. We excluded from landscape analyses the minimum number of sites necessary such that the remaining sites were > 3.2 km apart. Removing sites closer than 3.2 km was necessary to ensure that landscapes did not overlap more than 50% at the largest scale. We also excluded sites close to the map boundary ( $N=2$ ) so that no more than 20% of the landscape at the largest scale fell outside the map boundary. To increase sample size, we included territories ( $N=4$ ) monitored during a related study (Walters et al., 1999; Cooper and Walters, 2002) that were not within 3.2 km of any randomly selected sites. The resulting sample for landscape analyses consisted of 44 sites (Fig. 1). We computed Pearson's correlation coefficients for each landscape metric (see below) across scales. We removed from analyses scales that were highly correlated ( $r > 0.8$ ) with other scales, leaving one small (0.5), medium (2.0) and large (4.5) scale (Fig. 2).

Trzcinski et al. (1999) showed that independent measures of habitat loss (e.g. woodland cover) and fragmentation can be derived using three metrics: patch number, patch size, and amount of edge. The first step of the technique involves deriving two principal com-

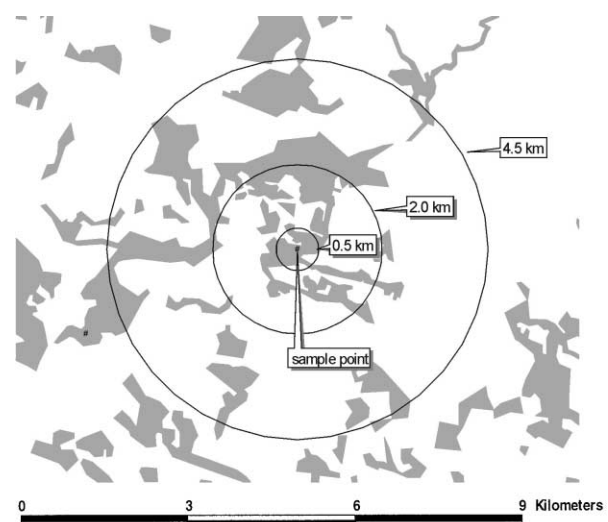


Fig. 2. Schematic diagram illustrating one of the sites (sample point) surveyed for Brown Treecreeper presence or absence. Habitat was sampled within each sample point in four plots (25×25 m each). Surrounding each sample point, three concentric circles (radii specified in diagram) were used for collecting landscape data.

ponents from the three metrics, one of which accounts for the effects of woodland loss. The residuals from a regression of the remaining PC on percentage woodland cover is used as a measure of habitat fragmentation.

To implement this technique, we used Patch Analyst 2.1 (Elkie et al., 1999) to obtain measures of landscape metrics (mean patch size, number of patches, total edge) and percentage woodland cover (%woods) within each landscape radius (i.e. scale) around each site. Landscape metrics were correlated with one another (Table 2). We performed principal components analysis on correlation matrices of patch size, number, and edge, and used resulting factors with eigenvalues greater than 1.0 in analyses. At each scale, the first and second principal components together accounted for at least 90% of the variation in the data (Table 3). At large and intermediate scales, the second principal component was highly correlated with %woods ( $R^2=0.92$ ,  $P<0.0001$ ,  $R^2=0.74$ ,  $P<0.0001$ , respectively,  $N=44$ ; Fig. 3), while the first principal component was not ( $R^2=0.01$ ,  $P=0.48$ ,  $R^2=0.016$ ,  $P=0.41$ , respectively). Therefore, at these scales, the second principal component accounts for the effects of woodland loss.

At the large and intermediate scales, as the first principal component increased, mean woodland patch size decreased while the number of woodland patches and woodland edge increased, as expected from a measure of fragmentation. Following the methods of Trzcinski et al. (1999), for the large and intermediate scales, we computed a measure of fragmentation independent of woodland cover, namely the residuals from the (non-significant) correlation between the first principal component and %woods in simple linear regressions. At the smallest scale, both the first and second principal component were significantly correlated with %woods ( $R^2=0.52$ ,  $P<0.0001$ ,  $R^2=0.15$ ,  $P<0.0001$ , respectively). At the smallest scale, as principal component two increased, total woodland edge, number of woodland patches, and mean patch size increased. Mean patch size is not expected to increase with fragmentation. Nevertheless, since the first principal component

was more strongly correlated (than the first PC) with %woods, we used the residuals from the correlation between the second principal component and %woods in a simple linear regression to create a measure of fragmentation. We performed forward stepwise logistic regression to model the distribution of treecreepers in relation to landscape features at each scale in independent analyses using %woods as a measure of cover and the residuals just described above as a measure of fragmentation.

### 2.5. Identification of unoccupied sites in suitable landscapes

We used the best logistic regression model from landscape analyses to create a criterion to delineate sites with >30% probability of occupancy given fragmentation patterns. We then repeated the habitat analysis, but excluded unoccupied sites that did not meet the suitable landscape criterion.

## 3. Results

### 3.1. Brown Treecreeper distribution

The proportion of sites occupied by Brown Treecreepers declined from 35% at the first point in time (1992) to 26% at the last (>2 birds in 1998) (Table 4).

### 3.2. Landscape analyses

Landscapes around occupied sites tended to have fewer and larger woodland patches (Table 5), a pattern typical of less fragmented landscapes. In addition, landscapes around occupied sites tended to have more woodland cover (Table 5). Depending on the analysis, woodland fragmentation at the 4.5 km-radius scale explained 21–33% of the variation in Brown Treecreeper distribution (Table 6). The amount of variation explained by fragmentation is increasing with time. Both woodland cover and fragmentation at the smallest scale had significant effects on Brown Treecreeper distribution (Table 6). At the 2.0 km-radius scale, only

Table 2  
Pearson correlation coefficients indicating the correlation between three landscape metrics (mean patch size, total edge, number of patches) at three scales (4.5 km, 2 km, 0.5 km) ( $N=44$ )

Radius	Metric	Total edge	Number patches
4.5	Mean patch size	0.22	-0.51**
	Total edge		0.50**
2	Mean patch size	-0.11	-0.50**
	Total edge		0.57***
0.5	Mean patch size	0.30*	-0.59***
	Total edge		0.13

\*  $P<0.05$ .

\*\*  $P<0.001$ .

\*\*\*  $P<0.0001$ .

Table 3  
Principal component loading for the three landscape metrics at each scale

Metrics	Scale					
	4.5 km-radius		2.0 km-radius		0.5 km-radius	
	PC 1	PC 2	PC 1	PC 2	PC 1	PC 2
Mean patch size	-0.47	0.70	-0.49	0.75	0.73	0.22
Total edge	0.45	0.71	0.54	0.66	0.12	0.89
Number of patches	0.76	0.01	0.68	0.02	-0.67	0.40
Variation explained	54%	41%	61%	30%	53%	39%

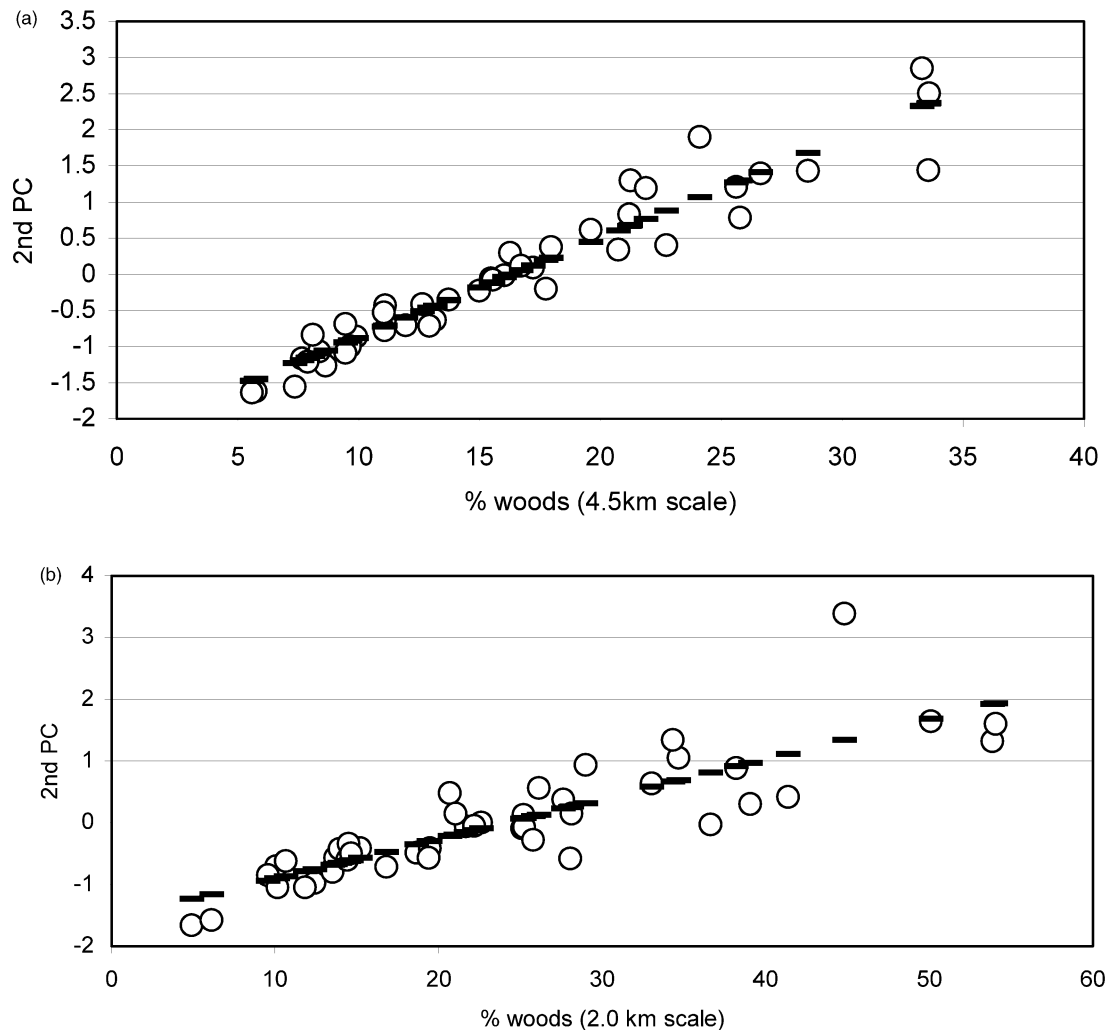


Fig. 3. Relationships between the second principal component and percent woodland cover at (a) 4.5 km-radius and (b) 2.0 km-radius scales.

woodland cover explained a significant amount of the variation, and in only one of the three analyses.

### 3.3. Habitat analyses

Before excluding unoccupied sites based on landscape characteristics, cavity density explained a small but marginally significant amount of variation in occupancy in 1992 ( $R^2=0.06$ ,  $P=0.06$ ), in 1998 ( $R^2=0.07$ ,  $P=0.04$ ), and by  $\geq 2$  birds in 1998 ( $R^2=0.09$ ,  $P=0.03$ ) (Fig. 4a) ( $N=80$ ). The best model of effects of fragmentation on Brown Treecreeper distribution was

occupancy by  $\geq 2$  birds in 1998 at the 4.5 km-radius scale. We included an unoccupied site in further habitat analyses if this fragmentation metric was greater than zero, corresponding to a  $\geq 30\%$  probability of occupancy (Fig. 5). We could not directly apply the criterion developed from the logistic regression model to sites not included in the landscape analysis (i.e. those that were  $< 3.2$  km from another site) because the criterion (i.e.  $\geq 30\%$  probability of occupancy) was based on a residual value from a regression model using a principal component. In order to include these sites in habitat analyses, we determined whether an unoccupied site shared a landscape similar to either a site occupied by  $\geq 2$  birds or a site that had  $\geq 30\%$  probability of occupancy. We considered two landscapes at the 4.5 km-radius scale to be similar if the sites were  $< 2$  km apart, which creates  $> 70\%$  overlap. After removing unoccupied sites in unsuitable landscapes from the analysis, cavity density explained a significant and larger amount of the variation for occupancy in 1992 ( $R^2=0.15$ ,  $P=0.02$ ), occupancy in 1998 ( $R^2=0.15$ ,

Table 4  
Proportion of sample sites occupied by Brown Treecreepers

Analysis	% Occupied sites	Number occupied	Total
1992	35	28	80
1998	31	25	80
by $\geq 2$ birds, 1998	26	21	80

$P=0.02$ ), and occupancy by  $\geq 2$  birds in 1998 (Fig. 4b) ( $R^2=0.19$ ,  $P=0.01$ ) ( $N=43$ ).

## 4. Discussion

### 4.1. Spatial scale

We observed clearer effects of landscape patterns on Brown Treecreeper distribution at the smallest and largest scales used in this study, than at an intermediate scale. Other studies found effects at the patch scale, but not at larger landscape scales (see Bolger et al., 1991). Why effects are evident at particular scales and not at others might be explained in several ways. Brown Treecreepers' response to the landscape may reflect effects of fragmentation on a single ecological process manifested

at several scales. For example, a high degree of fragmentation (i.e. many small isolated patches) could disrupt dispersal if individuals were unable or unwilling to cross non-woodland habitats. Previous research found that isolation rather than edge influenced Brown Treecreeper population dynamics. Treecreepers did not move among isolated fragments, and experimentally translocated females paired and bred successfully in isolated fragments that previously contained unpaired males (Cooper and Walters, 2002). Brown Treecreeper dispersal distances in the study area ranged from 0.2 km to at least 4.5 km, with males moving no farther than a neighbor's territory and females moving over larger distances (Cooper and Walters, 2002). Landscape patterns at the intermediate scale of 2 km-radius may not capture the features affecting the short-distance movements of males or the long-distance movements of females.

Table 5  
Summary of landscape metrics and %woods ( $N=44$ ) for occupied (1) and unoccupied (0) sites

Metric	Scale (radius, km)	Analysis					
		1992		1998		By $\geq 2$ birds, 1998	
		1	0	1	0	1	0
$N$		22	22	20	24	17	27
%woods	0.5	66	50	66	51	69	51
	2.0	27	21	27	21	30	21
	4.5	17	16	18	16	19	15
Mean patch size	0.5	47	36	48	36	51	36
	2.0	90	49	95	48	108	45
	4.5	62	40	64	40	71	38
Total edge ( $\times 1000$ )	0.5	3.6	2.9	3.6	2.9	3.7	3.0
	2.0	23.2	21.5	22.6	22.1	31.0	20.2
	4.5	78.0	84.6	77.2	84.7	78.0	83.7
Number of patches	0.5	1.2	1.2	1.2	1.2	1.2	1.2
	2.0	6.2	8.4	6.0	8.5	5.2	8.6
	4.5	19.9	29.5	19.4	29.1	17.5	29.2

Table 6  
Multiple logistic regression models for woodland cover and fragmentation from stepwise logistic regressions on Brown Treecreeper occupancy at multiple scales ( $N=44$  sites)<sup>a</sup>

Radius (km)	Analysis	Parameter estimate			
		Intercept	Cover <sup>b</sup>	Fragmentation <sup>c</sup>	Max-rescaled ( $R^2$ ) <sup>d</sup>
4.5	By $\geq 2$ birds, 1998	-0.74	-	-1.22	0.33***
	1998	-0.27	-	-0.86	0.23**
	1992	-0.04	-	-0.77	0.21**
2.0	By $\geq 2$ birds, 1998	-2.0	0.06	-	0.16**
	1998	-	-	-	-
	1992	-	-	-	-
0.5	By $\geq 2$ birds, 1998	-10.2	0.16	-0.12	0.37***
	1998	-8.39	0.14	-0.11	0.30**
	1992	-2.41	0.04	-	0.19**

<sup>a</sup> Dashed lines indicated variables were not included in model ( $P>0.05$ ).

<sup>b</sup> Measured as %woods.

<sup>c</sup> Measured as residual from regression of %woods on PC 1.

<sup>d</sup>  $P<0.05$ , \*\* $P<0.01$ , \*\*\* $P\leq 0.001$ , using log-likelihood statistics.

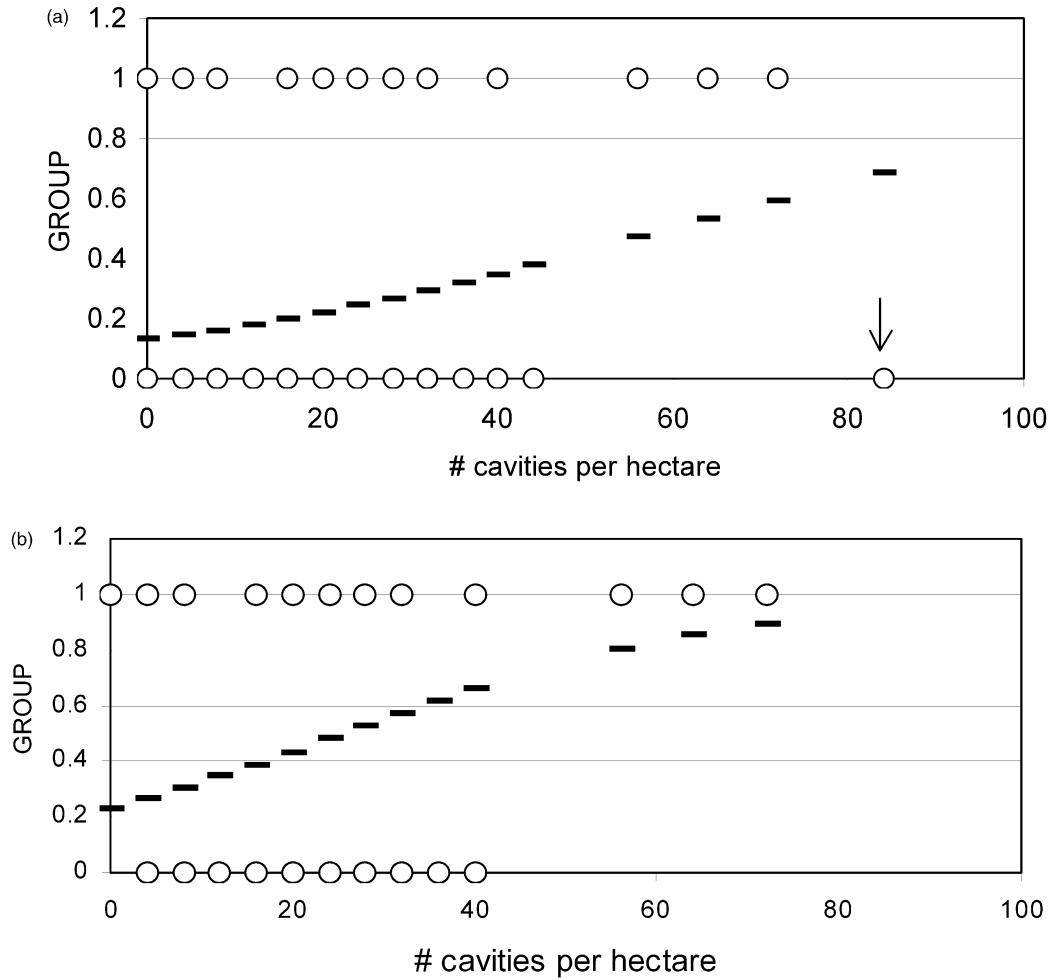


Fig. 4. Logistic regression of occupancy by  $\geq 2$  birds in 1998 (GROUP) as a function of cavity density using (a) all randomly selected sites and (b) excluding unoccupied sites in unsuitable landscapes. Arrow indicates an outlier. Circles represent observed values. The dashed line represents the predicted values.

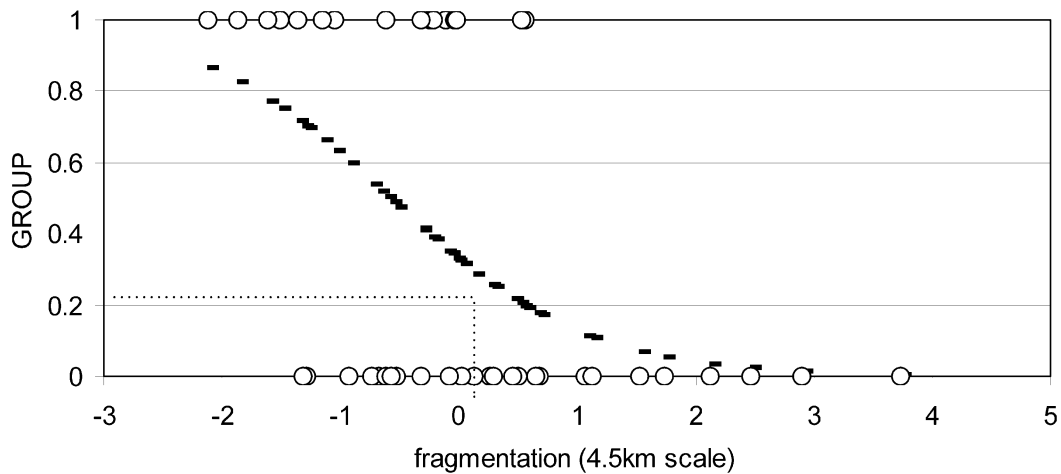


Fig. 5. Logistic regression of area-independent measure of fragmentation at 4.5 km-radius scale (see text) on occupancy by  $\geq 2$  birds in 1998 (GROUP). Circles represent observed values. The dashed line represents the predicted values. Dots are used to show that a score of 0 corresponds to a 30% probability of occupancy. This is the occupancy criterion used in habitat analysis (see text).



Alternatively, Brown Treecreepers' response to several landscape scales may reflect the various scales at which different ecological processes occur. For example, woodland area and fragmentation at the 0.5 km-radius scale might influence foraging habitat availability and restrict the home range size of Brown Treecreeper groups, while fragmentation at the 4.5 km-radius scale may influence dispersal. Brown Treecreepers were not found in patches smaller than 9 ha (Barrett, 1995) and 10 ha (S. Briggs, personal communication) regardless of distance to another woodland patch. If Brown Treecreepers do not expand their home ranges to include several patches when necessary, then landscape patterns at a small scale might be very important.

Perhaps the response of Brown Treecreepers to fragmentation at the 4.5 km-radius scale is unrelated to any species-specific behavior, but exemplifies a general fragmentation effect. Andr en (1994) and Fahrig (1997) suggested that fragmentation is only important to population persistence when habitat cover is <20% of the landscape. The amount of cover is dependent on the scale of the landscape considered. In this study, at the 0.5 km-radius scale, landscapes averaged 58% cover, while at 2.0 and 4.5 km-radii scales, woodland cover was much lower (21 and 17%, respectively). We found that the degree to which fragmentation could be separated from measures of landscape cover was dependent on the landscape scale, probably in relation to the amount of cover at each scale.

#### 4.2. Time scale

Time-lagged responses to fragmentation can confound analyses of the spatial distribution of a species. Landscape effects on Brown Treecreeper distribution became more evident as time passed, even though most of the habitat loss in the region occurred decades ago (Hobbs and Yates, 2000). Occupancy data taken soon after landscape alterations would be less reliable and should be used with caution. Occupancy data will often be insufficient to draw conclusions and are no substitute for measurements of demographic or fitness parameters.

#### 4.3. Relative effects of habitat loss and fragmentation

Fragmentation effects independent of habitat area were important to this species' distribution. This is consistent with other evidence implicating isolation effects as responsible for declines of Brown Treecreepers (Walters et al., 1999; Cooper and Walters, 2001; Cooper et al., 2001). Other studies examining the influence of landscape patterns on avian distributions found responses were species-specific, and more species responded to area than to fragmentation (McGarigal and McComb, 1995; Trzcinski et al., 1999; Villard et al., 1999). However, only one scale was examined in each of

the above studies. Trzcinski et al. (1999) and Villard et al. (1999) both used a 10x10 km scale, while McGarigal and McComb (1995) examined avian distributions at a small scale of 250–300 ha areas. The relationship of the distribution of Brown Treecreepers to landscape patterns varied with the scale of analysis. If other avian species show similar patterns, then it would be premature to conclude that Brown Treecreepers are one of the few species to respond to fragmentation independent of area until other studies are conducted at additional spatial scales. For example, at a large scale, Bolger et al. (1997) found that the Rufous-sided Towhee (*Pipilo erythrophthalmus*), California Thrasher (*Toxostoma redivivum*), California Quail (*Callipepla californica*), Bewick's Wren (*Thyomanes bewickii*) and Wrentit (*Chamaea fasciata*) did not respond to landscape patterns. Yet, studies at a smaller spatial scale found that these same species did respond to some landscape patterns such as patch size and time since isolation (Soul e et al., 1988; Bolger et al., 1991).

#### 4.4. Habitat

Removing sites in highly fragmented surroundings improved the Brown Treecreeper habitat model. Removing the single outlier (see Fig. 3a) accounted for more than half of the improvement in the model ( $R^2=0.12$ ). However, without landscape considerations the removal of the outlier would be difficult to justify. This emphasizes the need for landscape patterns to be incorporated into wildlife–habitat models. Bolger et al. (1997) found that habitat models for most species in their study were improved by including landscape variables. As habitat fragmentation becomes a more predominant feature of landscapes, it will become more common for species to be absent from good habitat due to landscape effects. Including such sites in habitat modeling will obscure wildlife–habitat relationships.

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