THE BEHAVIORIAL ECOLOGY AND CONSERVATION OF AN AUSTRALIAN PASSERINE, THE BROWN TREECREEPER (*Climacteris picumnus*)

by

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ABSTRACT

This study addressed two aspects of ecological theory developed primarily in North America and examined these theories using an Australian passerine as a model species. The first theory concerns the mechanisms by which habitat fragmentation affects avian populations. I investigated the mechanisms causing the decline of the Brown Treecreeper (*Climacteris picumnus*) in fragmented habitat, and specifically considered the effects of isolation and habitat degradation, which are potentially important in Australian woodlands, and edge (patch size), which are important in North America. Brown Treecreeper groups were as productive in isolated patches as in connected patches of habitat regardless of patch size, yet unpaired males were common in isolated fragments of habitat. I conducted a field experiment that confirmed that female dispersal was disrupted among isolated fragments. Thus, my results suggested Brown Treecreepers were declining due to disruption of dispersal by habitat fragmentation rather than degradation or edge effects. I compared the results of an individual-based, spatially explicit simulation model to field observations and concluded that territory spatial arrangement and matrix composition altered dispersal success, recruitment, and subsequent population growth. With the aid of a geographic information system, I determined that both landscape factors (fragmentation patterns within 4.5-km) and habitat characteristics (cavity density) explained Brown Treecreeper presence and absence from random locations in woodland habitat. The birds appear to be absent from suitable habitat in unsuitable landscapes.

The second theory I addressed concerns the maintenance of avian cooperative breeding. The most widely accepted models to explain cooperative breeding suggest that individuals that delay dispersal obtain a payoff under conditions in which the quality of breeding positions varies greatly. These models arose chiefly from a few long-term studies in North American. This is an unfortunate bias because the occurrence of cooperative breeding among birds of Gondwanan origin is 22%, whereas the worldwide incidence is only 3%. I used demographic and habitat data to examine the influence of habitat and cooperative breeding on Brown Treecreeper fitness. Group size affected one component of fitness and habitat variables affected another. High cavity density may be favorable due to intense inter-specific competition for suitable cavities, which Brown

Treecreepers require for roosting and nesting. Low tree density may be advantageous by favoring ground foraging, in which Brown Treecreepers frequently engage. Experimental manipulations of important habitat variables are needed to determine whether variability in these ecological factors is critical in maintaining group formation in this species.

DEDICATION

To my parents, Barbara and Jerry Cooper, for never holding me back.

To my husband, Greg Sloan, for following me around the world.

To my daughter, Abby, for putting this in perspective.

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Chapter 1: INTRODUCTION

GENERAL OVERVIEW

This study addresses two aspects of ecological theory developed primarily in North America and examines these theories using an Australian passerine as a model species. Chapters 2-5 address the ecological basis of sensitivity to habitat fragmentation in the Brown Treecreeper (*Climacteris picumnus*). I use a variety of data including distribution, demographic, movement, habitat, and landscape data, to test hypotheses regarding the cause of Brown Treecreeper declines. In Chapter 2, I show that Brown Treecreeper groups are just as productive in isolated patches as in connected patches of habitat regardless of patch size. In Chapter 3, I provide experimental evidence that Brown Treecreepers are declining due to isolation effects of habitat fragmentation. In Chapter 4, I use a spatially realistic simulation to show that territory spatial arrangement and matrix composition can alter dispersal success and population growth. In Chapter 5, I use a geographic information system to examine the spatial scale at which Brown Treecreepers respond to landscape patterns and use landscape variables to improve a habitat model of Brown Treecreeper distribution. Chapter 6 addresses the maintenance of cooperative breeding, using the same Australian passerine, the Brown Treecreeper. I use demographic and habitat data to explore the constraints on independent reproduction. In Chapter 7, I summarize and synthesize the conclusions of this project, assess the limitations of the study, and make management recommendations for the conservation of woodland birds in the New England Tablelands.

STUDY SPECIES

There are six species of treecreepers in Australia, all belonging to the family Climacteridae within the Parvorder Corvida, a group of passerines that radiated in Australia. Treecreepers are ecologically equivalent to North American woodpeckers in that they (along with Sittellas (*Daphoenositta* spp.)) are the only specialized bark-climbing birds in the Australian-Papuan region (Noske 1986). Brown Treecreepers are insectivorous, though not entirely arboreal, spending approximately equal amounts of time foraging on the ground as on trees during the breeding season (Walters et al. 1999).

In the study area, Brown Treecreeper family groups defend territories averaging 4.5 ha, and ranging from 1.1 to 10.7 ha (this study). Brown Treecreepers in the study area generally begin breeding in late July or early August. Brown Treecreepers nest and roost in existing tree holes rather than excavating cavities. They nest in many types of cavities, including tree spouts created by hollow dead branches in live or dead trees, hollow fence posts, and tree-stump holes (Noske 1982a, b). Brown Treecreepers lay 2-3 eggs, which are incubated by the female for 16-17 days. Nestlings fledge after 25-26 days, similar to other cavity nesters (Noske 1982a).

The Brown Treecreeper is a cooperative breeder. Like most other avian cooperative breeders, male offspring generally become helpers while female offspring generally disperse. Male offspring that remain as helpers may either eventually inherit their natal territory after their father dies, effectively compete for a vacancy in a neighboring territory, or inherit a portion of their natal territory through a process termed territory budding (Woolfenden and Fitzpatrick 1978). Brown Treecreepers exhibit extra-group helping behavior, which primarily arises when males breeding on territories acquired through budding continue to attend the nest of their parents in addition to their own nest (Noske 1980, Walters et al. 1999, Doerr and Doerr 2001). As many as six birds have been observed feeding at one nest (Noske 1980). Females disperse 2-6 months after fledging and become either breeders or floaters (Noske 1980). Female offspring rarely remain on their natal territory as helpers.

Insectivorous birds that forage extensively on the ground appear to be especially sensitive to fragmentation and degradation in many parts of Australia (Recher and Lim 1990, Garnett 1992, Recher 1999). Cooperative breeders, which are numerous in Australia (Brown 1987, Russell 1989), may also be especially sensitive to habitat fragmentation because of the short-distance characteristics of their dispersal patterns (Walters 1998). Barrett et al. (1994) and Barrett (1995) documented the decline of the Brown Treecreeper in fragmented habitat in the New England Tablelands of northeastern New South Wales. Therefore, the Brown Treecreeper is a good model species to investigate how these life-history traits, the preference for ground foraging and cooperative breeding behavior, might be associated with population decline.

SENSITIVITY TO HABITAT FRAGMENTATION

Introduction to habitat fragmentation - The alarming loss of biological diversity is primarily attributed to the loss and fragmentation of natural habitats arising from those human activities (e.g., agriculture, human settlement, resource extraction) that convert portions of the natural landscape to different habitat types (Noss 1983, Wilcox & Murphy 1985, Rolstad 1991, Saunders et al. 1991). The mechanisms of habitat fragmentation have been a major focus of research and debate in conservation biology. Although habitat loss can occur without creating fragmentation, fragmentation is created by habitat loss (or, more precisely, creating one habitat in the place of another). Habitat loss alone obviously can directly limit the total number of organisms that can survive and reproduce in that habitat type and thereby cause a proportionate decrease in the density of a species under study. Conversely, fragmentation can cause a disproportionate decline in population density or reduction in fitness in remaining habitat. Typically, "fragmentation effects" go beyond the effects created by habitat loss and result from the spatial arrangement of the habitats that remain. Landscape spatial structure is an important factor influencing the persistence of populations (Fahrig and Merriam 1994).

Negative (or positive) effects to species persistence and population dynamics can arise in an altered landscape via two processes associated with fragmentation: (1) a corresponding increase in other habitats and (2) subdivision of the habitat of interest (Rolstad 1991). Each of these processes has important implications to species persistence and population dynamics. Process (1), the corresponding increase in other habitats, can cause an array of changes to the quality of the habitat of interest (edge and habitat degradation effects). Process (2), subdivision of the habitat of interest, can cause a myriad of isolation effects. Species vary greatly in their response to habitat fragmentation, from those species that exhibit population increases and range expansion with increasing fragmentation to those species that become extinct. The varying importance of edge, habitat degradation, and isolation effects to the viability of different species may explain this great variation in species' response to habitat fragmentation.

Edge effects - Forest fragmentation is hypothesized to be the primary cause of population declines of migratory passerines (Whitcomb et al.1981, Lord and Norton 1990). Migratory songbirds appear to be sensitive to fragmentation because of edge effects (Lovejoy et al. 1984, Lynch and Whigham 1984, Saunders et al. 1991). These effects operate by several mechanisms, including increased nest parasitism and predation. In certain landscapes in North America, habitat fragmentation increases the rates of both nest predation and nest parasitism by Brown-headed Cowbirds (*Molothrus ater*) (Gates and Gysel 1978, Wilcove 1985, Andren & Angelstam 1988, Temple and Cary 1988, Johnson and Temple 1990, Robinson 1992, Robinson et al. 1992, Robinson et al. 1995). Much of the research on the effects of edge on nest predation has been criticized because of the use of artificial nests (Paton 1994, Zanette and Jenkins 2000) and great variation in experimental designs (Simberloff et al. 1992). Nevertheless, recent well-designed field studies have found nest predation to decrease with increasing forest cover (e.g., Robinson et al. 1995).

Unfortunately, what has been learned from the studies of migratory birds in forest systems may not be applicable to the Brown Treecreeper, a non-migratory passerine in a woodland system. Although Brown Treecreeper population dynamics are affected by fragmentation, edge effects arising via nest parasites and nest predators appear to be absent in this system. Nest predation does not appear to have a greater impact on Australian passerines in small fragments compared to large ones, in edge compared to interior woodlands or near roads (Taylor and Ford 1998, Gardner 1998, Lindenmayer et al. 1999, Walters et al. 1999, Matthews et al. 1999, Zannette and Jenkins 2000). Although there are brood parasites (e.g., *Cuculidae*) in Australian woodlands, none achieve densities or impact other species in a way comparable to the way Brown-headed Cowbirds affect host populations in North America (Robinson et al. 1995, Ford et al. 2000).

Edge effects may also result from changes in physical or climatic factors that occur when fragmentation creates abrupt edges. For example, clear-cutting of rainforests creates edge effects by increasing sunlight and wind and reducing humidity at the boundary of habitats. Fluxes in radiation, wind, water, and nutrients may change in forest fragments. These factors can directly and indirectly affect both plants and animals (Franklin and Forman 1987, Chen and Franklin 1990). Woodlands are naturally more open than forests and there is little evidence that changes in radiation and wind have significant impacts in fragmented woodlands (Yates and Hobbs 1997). However, changes in water and nutrient fluxes are having effects in fragmented woodlands (Yates and Hobbs 1997). These impacts can penetrate further than the edge of a woodland patch and are better categorized as habitat degradation effects than edge effects. Habitat degradation is common in Australian woodlands and is discussed below.

Habitat degradation effects - Degradation may frequently accompany fragmentation, compounding the effects of habitat loss. However, habitat degradation may arise from associated lands uses, such as livestock grazing, rather than fragmentation per se. Degraded Australian woodlands are characterized by several events (Yates and Hobbs 1997): (1) the premature and relatively rapid death of trees (known as 'rural dieback' (reviewed by Landsberg and Wylie 1994); (2) lack of tree recruitment; (3) loss of original understory vegetation; (4) soil erosion and deterioration of soil structure; (5) invasion by exotic plant species; (6) increase in abundance of understory plant species that are unpalatable to livestock; (7) invasion by an aggressive avian species that excludes most other insectivorous and nectar-feeding birds, the Noisy Miner (*Manorina melanocephala*) (Dow 1977, Ford and Bell 1982, Grey et al. 1997, Grey et al. 1998); and (8) loss of mature trees, which produce the most nectar and contain the most cavities (Bennett et al. 1994).

Excessive livestock grazing and hazard-reduction burning are suspected as the primary causes of woodland degradation in Australia (Recher and Lim 1990, Landsberg et al. 1990). Woodlands heavily grazed by livestock experience more severe defoliation by insects and subsequent tree death. In addition, plant and avian diversity is generally lower in grazed stands (Ford and Bell 1982, Landsberg et al. 1990). Recher and Lim (1990) hypothesized that ground-foraging insectivores are sensitive to degradation because of the diversion of resources to livestock, trampling and destruction of the litter layer, and soil erosion, all of which could reduce invertebrate abundance. Also, the loss of low vegetation may increase predation risk to adults and low nests.

Isolation effects - Theoretical studies of the basis of bird species' sensitivity to fragmentation suggest that species may decline due to isolation effects that disrupt movements, such as natal dispersal (Askins et al. 1990, Harrison and Bruna 1999). For example, Doak et al. (1992) determined through simulation models that the disruption of movement can be influenced by the scale of fragmentation relative to the mobility of organisms. Also, fragmentation can lead to isolation effects even when a species can cross the intervening habitat if natural populations are normally clumped. In a simulation model of Red-cockaded Woodpecker (*Picoides borealis*) population dynamics, Letcher et al. (1998) demonstrated that territory aggregation was as critical to population persistence as initial population size.

Theoretical studies of isolation effects hinge on untested assumptions concerning dispersal behavior, including how barriers to dispersal vary among species. Although some researchers (e.g., Doak et al. 1992) think it is intuitive that habitat fragmentation can disrupt animal dispersal in general, others (e.g., Enemar 1959, Reed 1987, Raivio 1988) consider dispersal unproblematic for highly mobile species. Because birds are considered highly mobile organisms, it may seem counter-intuitive that bird movements could be disrupted by habitat fragmentation, but the scant empirical evidence available suggests otherwise. Landscape features affect movement patterns or behavior of migratory forest songbirds (Dunning et al. 1995, Desrochers and Hannon 1997), a variety of residents (St. Clair et al. 1998), and short-distance migrants (Haas 1995) in North America. More research investigating the effects of landscape structure on avian populations, dispersal behavior, and metapopulation dynamics is necessary to further avian conservation (Walters 1998).

Linking conservation research to management - Besides identifying the existence of fragmentation effects (positive or negative), it is also critical to identify the mechanism producing them (e.g., habitat degradation effects or isolation effects), because the conservation efforts employed to counteract each differ. Management to minimize species decline caused by habitat degradation effects includes methods to improve habitat quality, such as reducing the number of predators, eliminating exotics, restricting livestock grazing, and mimicing a natural fire regime. Management to minimize species decline caused by isolation effects includes establishing corridors between small refuges, translocating organisms between populations, and clustering habitat fragments. Determining which management activity will be most effective in alleviating the habitat degradation or isolation effects can be aided by understanding the mechanisms by which the effects operate on different species. For example, is the habitat degraded because of nest predators or reduced food abundance? Is dispersal unsuccessful because organisms do not enter intervening habitat or because they have a low probability of finding widely dispersed patches? Therefore, determining the relative importance of habitat degradation and isolation effects, as well as the behavioral mechanisms by which these effects act, is critical to improving wildlife conservation techniques.

While the effects of habitat degradation on avian communities have received little investigation, the effects of edge have been studied intensely. Conservation efforts to minimize edge effects have only come after considerable empirical evidence has demonstrated the importance of such effects. In contrast, the importance of isolation effects to population decline has been identified predominantly by theoretical endeavors, yet such theories have greatly influenced conservation decisions. Three prime examples of recently developed theory being hastily, and perhaps prematurely, applied to manage species threatened by extinction are the SLOSS debate (described below), corridor planning, and metapopulation dynamics. These examples illustrate the need for empirical studies that investigate the existence of isolation effects and the mechanisms by which they operate.

<u>Wildlife reserve design - the SLOSS debate</u>: Diamond (1975) and Wilson and Willis (1975) posed the question of whether the optimal reserve design was "single large or several small" reserves. This became known as the SLOSS debate. "Several small" has been favored for the benefit of maximizing species diversity (Simberloff and Abele 1976, 1982, Abele and Connor 1979, Gilpin and Diamond 1980, Higgs and Usher 1980, Higgs 1981, Järvinen 1982, Margules et al. 1982). Simberloff et al. (1992) noted that small, endemic populations on islands persist for millennia in the absence of humans and therefore concluded that rapid extinction of small populations is not automatic. Of course, populations suddenly restricted to "island" habitat patches may not have the same population dynamics as true island populations. Thus, "single large" has been favored for the benefit of minimizing extinction rates (e.g., Wilson and Willis 1975, Diamond 1975, 1976, Terborgh 1976, Fahrig and Merriam 1985). Part of the difference in conclusion lies in the difference in conservation goals (Burkey 1989). Burkey (1989) pointed out that an obvious problem with maximizing species richness is that the species that increase in edge habitat are not usually the focus of conservation efforts (Diamond 1976, Terborgh 1976, Whitcomb et al. 1976). Therefore, Burkey (1989) argued that minimizing

extinction after isolation should be the goal of reserve designers.

Corridors**:** Theory concerning isolation effects of fragmentation has led to widespread use by managers of movement corridors for wildlife. Wilson and Willis (1975) and Diamond (1975) were among the first to recommend corridors of similar habitat to facilitate migration between fragments. Wilson and Willis (1975) based their recommendation for corridors on the equilibrium theory of island biogeography (MacArthur & Wilson 1967). The corridor idea became widely accepted in the 1980s, but was followed by debate (Simberloff and Cox 1987, Noss 1987, Simberloff et al. 1992) that revealed the need for empirical studies. Most research has been theoretical (Burkey 1989, Merriam 1991), with a few exceptions (reviewed by Beier and Noss 1998). Finding evidence for the importance of corridors is not easy. As Simberloff et al. (1992) argued, just because "an animal uses corridors when these are present need not mean movement without them is impossible, or even less frequent."

Metapopulations**:** Ideas about isolation effects based on metapopulation theory have also been applied to management. One common basis of theories regarding isolation effects is that fragmentation disrupts the recolonization that follows natural extinctions in metapopulations. Therefore, even low rates of dispersal can be critical to population persistence. In a classic metapopulation (Levins 1969), extinctions of local populations are followed by the establishment of new populations by dispersers from remaining populations. Although the classic metapopulation described by Levins (1969) is probably very rare (Doak and Mills 1994), there is some evidence for metapopulations as more broadly defined by Hanki and Gilpin (1991). They defined a metapopulation as a "set of local populations which interact via individuals moving among populations." Rolstad (1991) cited four studies that demonstrate metapopulation dynamics in bird populations: (1) Spotted Owl (*Strix occidentalis caurina*)(Gutiérrez & Carey 1985, Thomas et al. 1990 and references therein); (2) Spruce grouse (*Dendragapus canadensis*) on the periphery of its range (Fritz 1979, 1985); (3) raptors in Java (Thiollay & Meyburg 1988); (4) Capercaillie grouse (*Tetrao urogallus*)(Rolstad & Wegge 1989). Also, Stacey and Taper (1992) found that populations of the Acorn Woodpecker were regularly rescued from extinction by very low levels of immigration from other, independently varying, populations. Their finding suggests that even though long-distance dispersal may be infrequent, it has a large influence on population persistence.

Aside from these few studies, most of what is known about metapopulations is derived from theory (Hastings 1990, Hastings 1991, Hastings and Wolin 1989, Hansson 1991, DeRoos et al. 1991, Verboom et al. 1991, Ray et al. 1991, Davis and Howe 1992, Doak and Mills 1994). There are a disquieting number of untested metapopulation models, yet the metapopulation paradigm has been used widely to support the need for corridors. However, even if metapopulations are common in nature, the models require movement, not corridors (Merriam 1991). Simberloff et al. (1992) cautioned that "there is now a tendency to take the metapopulation paradigm as broadly representative of nature, rather than as a new and untested hypothesis." Nevertheless, the metapopulation paradigm is a better framework for research than closed-population models, which are often insufficient to explain population dynamics within habitat fragments (Walters 1998).

Summary of habitat fragmentation research - Most studies of avian responses to fragmentation occurred in forest systems of the Northern Hemisphere. Although fragmentation effects appear to be a general phenomenon, the mechanisms underlying fragmentation effects appear to vary among species and ecosystems. Experimental research has revealed a wide range of species-specific responses to fragmentation (Debinski and Holt 2000).

The risk of extinction is the result of two opposing forces that arise from the subdivision of habitat. On the one hand, because fragmentation creates smaller populations within each patch, demographic stochasticity and loss of genetic variability may increase extinction risk. On the other hand, fragmentation may create collections of poorly linked subpopulations that have a lower overall risk of extinction from catastrophic events than does a single large population (Karieva 1990).

MAINTENANCE OF COOPERATIVE BREEDING

Introduction - Cooperative breeding systems are characterized by two behaviors: (1) natal philopatry in conjunction with delayed reproduction and (2) helping behavior, usually directed at younger siblings. Approximately 30% of the world's approximately 222 avian species that exhibit cooperative breeding occur in Australia (Dow 1980).

Moreover, the incidence of cooperative breeding among old endemic Australian passerines (i.e., species that originated from Gondwana rather than Larasia) is 22% according to Russell (1989), while the world-wide incidence is only 3%, according to Brown (1987). Given this geographic bias, we can learn about the generality of current hypotheses to explain cooperative breeding by testing models on an Australian cooperative breeder (Heinsohn et al. 1990).

Russell (1989) pointed out that cooperative breeding probably evolved during the initial radiation of passerines in Australia in an environment markedly different from today's. The suspected early origin of cooperative breeding has led some researchers to suggest that current environmental factors may not select for cooperative breeding, but instead cooperative breeding became "locked in" to the behavioral repertoire of a species (Dow 1980, Ford et al. 1988). It is possible that individuals accrue fitness advantages by helping in the context of a social system that is currently neutral or exaptive and that this system is maintained for reasons different from those that caused it's origin (Gould and Lewontin 1979, Gould and Vrba 1982, Zack and Ligon 1986), a condition described as phylogenetic inertia (Edwards and Naeem 1993).

Even though phylogenetic inertia might partly account for the prevalence of cooperative breeding in Australia, current ecological or social factors may still maintain components of cooperative breeding. Edwards and Naeem (1993) suggested that there may be a phylogenetic bias in factors that predispose juveniles to delay dispersal and that selection acts on these factors. An ecological factor may directly maintain cooperative breeding, or if cooperative breeding is not a derived character, it may act indirectly on behavioral, demographic, social, or physiological biases that predispose individuals to cooperative breeding. Edwards and Naeem (1993) gave several examples of "predisposing" behaviors that might be phylogenetically biased, such as reduced dispersal, "stimulus-response" behavior where the begging by young acts as a stimulus that causes any adult to respond by providing food (Jamieson and Craig 1987, Jamieson 1991), parental facilitation and tolerance of young, and the capacity for imitative learning (Wilson 1989).

According to the most widely accepted ecological model, here called the habitat-quality model, cooperative breeding is maintained by the same factors theorized to have caused its origin, i.e., the potential fitness gained from each life-history tactic is a function of the quality of breeding positions, which varies greatly due to differences in territory quality (Stacey and Ligon 1991, Walters et al. 1992a,b, Koenig et al. 1992). Some debate remains over the type and degree of variation. Disagreement is in part because interpretation depends on which territories are included in the analysis, i.e., which are considered unsuitable, and in part because territory quality has been hypothesized to vary in several ways, each described by variants to the habitat-quality model, e.g., the marginal-habitat model (Koenig and Pitelka 1981); the benefits-of-philopatry model (Stacey and Ligon 1987, 1991) (termed the habitat-variance model by Koenig et al. 1992); and the critical-resource model (Walters et al. 1992b).

Unfortunately, there is no model for how selection might maintain cooperative breeding in species where the behavior is ancestral. Once cooperative breeding is present in a lineage, very different selective forces than those proposed in the habitat-quality model may maintain delayed dispersal and helping.

Theoretical background - Although some research into cooperative breeding focuses on the evolution of helping behavior, emphasis has been on the evolution of delayed dispersal (see Koenig et al. 1992). The current paradigm developed to explain natal philopatry is an extension of two major lines of thought, the role of extrinsic constraints and the role of intrinsic benefits. Koenig et al. (1992) synthesized these ideas into a unified theory termed the delayed-dispersal threshold model that incorporated the wide variety of selective forces that have been postulated to act on cooperatively breeding birds. In their model, Koenig et al. (1992) identified five general demographic, ecological, and environmental factors affecting delayed dispersal: (1) relative population density; (2) fitness differential between early and delayed dispersal including (a) resource depressibility on territories, (b) group size and composition, (c) cost of dispersal, and (d) secondary benefits of delayed dispersal and helping; (3) fitness of floaters; (4) distribution of territory quality including (a) the marginal habitat hypothesis, (b) the variance hypothesis, and (c) sex ratio bias; and (5) environmental temporal variability.

Much of the debate and confusion over the evolution of cooperative breeding involved the use of the term habitat saturation (Koenig et al. 1992) and other semantic problems (Emlen 1994). Ecological constraints models emphasized extrinsic constraints that limit breeding opportunities for maturing offspring that disperse early in life. These constraints included: (a) a shortage of high quality breeding vacancies (territories), (b) a shortage of breeding partners, and (c) a low probability of reproductive success by inexperienced or unaided breeders (Emlen 1994).

Stacey and Ligon (1987, 1991) and Zack (1990) introduced models that emphasized the intrinsic benefits of group living. Benefits-of-philopatry models stressed the advantages gained by offspring that remain on their natal territory. These benefits included (a) enhanced survival from group living, (b) indirect fitness gains from helping parents or close relatives, (c) better opportunities to secure a high-quality nearby breeding vacancy in the future, (d) the chance to inherit the natal breeding location itself (Emlen 1994). Although some may view the benefits-of-philopatry models in opposition to models of ecological constraints, most researchers agree that all the models reduce to the same conclusions - - that variation in territory quality is a key factor in the evolution of cooperative breeding. As Emlen (1994) pointed out, there are likely to be no benefits to group living unless there is some kind of constraint on independent reproduction. Thus, the two factors are not exclusive or necessarily separable. Emlen (1994) suggested that it may be best to look at ecological factors giving rise to constraints and benefits and analyze if changes in these cause changes in the frequency of philopatry and dispersal in a population.

Empirical background - The current explanation of cooperative breeding was chiefly developed from and supported by long-term studies that have compared the fitness consequences of different dispersal options. Researchers have modeled the demographic conditions under which delayed dispersal can be favored by selection (Woolfenden and Fitzpatrick 1978, 1984, Powell 1989, Koenig et al. 1992) and have shown that the fitness of non-breeding helpers can equal or exceed that of dispersers (Stacey and Ligon 1987, Walters 1992a). The majority of support for the theory has been through testing the demographic predictions of the model rather than by identifying the actual ecological variation that is hypothesized to create the observed demographic conditions. For example, Stacey and Ligon (1991) claim support for the theory in the observation of higher among-territory variance in fitness in cooperatively breeding species than in non-cooperative species. Nevertheless, the premise of the habitat-quality model is that some ecological factor is the underlying selective force that maintains delayed dispersal, i.e., habitat quality must vary greatly among territories in order for there to be a payoff to delaying dispersal.

Only a few studies have identified an ecological basis of variation in territory quality and demonstrated how such variation is a cause of cooperative breeding. Walters et al. (1992b) experimentally identified variation in habitat quality dependent on the presence or absence of cavities as the ecological basis of group formation in Red-cockaded Woodpeckers. Red-cockaded Woodpeckers excavate cavities in living pines, which requires much time. Walters et al. (1992b) constructed artificial cavities in unoccupied habitat that appeared suitable except for the lack of cavities. Almost all of the unoccupied sites with artificial cavities became occupied, while control sites did not. Cooperative breeding in that species is probably a derived trait, and therefore the factors causing its origin and maintenance can be accounted for by current adaptive significance (Ligon 1993).

Komdeur (1992, 1996) provided extensive support for the synthesis of extrinsic constraints and intrinsic benefits through empirical and experimental research with the Seychelles warbler (*Acrocephalus sechellensis*). Komdeur (1992) developed an index of invertebrate prey availability as a measure of territory quality. After transferring warblers to unoccupied islands, Komdeur observed that cooperative breeding did not occur until all high-quality territories were occupied. In addition, birds born on high-quality territories stayed as helpers instead of breeding on low-quality territories (Komdeur 1992, 1996, Komdeur et al. 1995). Thus, extrinsic constraints played a role because in the absence of a shortage of good quality habitat (i.e., habitat saturation), cooperative breeding did not occur. Intrinsic benefits played a role as well, because each bird's decision to stay or disperse was influenced by the quality of its natal territory relative to potential breeding territories.

Identifying ecological sources of variation that account for the fitness payoff of delayed dispersal is crucial to acceptance of the habitat-quality model because factors other than territory quality could create observed variance in fitness among territories. For example, some have noted that group-size effects might magnify differences in territory quality (Wiley and Rabenold 1984, Zack and Rabenold 1989, Stacey and Ligon

1991). However, no one has investigated whether group-size effects, in the presence of a genetic basis (or phylogenetic bias) of delayed dispersal, can alone create variation in territory fitness.

Furthermore, the demographic conditions that characterize cooperative breeders may be a consequence, not a cause, of cooperative breeding, as has been argued to be the case for the demographic condition termed 'habitat saturation' (Stacey and Ligon 1987). Also, the current theory may be insufficient to explain cooperation in the Brown Treecreeper, where family groups appear to form clans and individuals often continue to help raise non-descendant kin even after obtaining a nearby breeding position. Because offspring of cooperative breeders inherit territories, theory that explains behaviors that increase the probability of family group survival and lineage survival may be needed (Woolfenden and Fitzpatrick 1978, Reed and Walters 1996). The implication of territory quality being the ecological basis of cooperative breeding is that different social systems can evolve in response to patterns of local variation in habitat quality (Powell 1989, Stacey and Ligon 1991).

Summary of cooperative breeding research - There remains only one basic explanation for the ecological basis of cooperative breeding, namely gradients in territory quality. The culmination of past research and debate suggests the sum of many factors result in the evolution of cooperative breeding. Even though current theory uses a framework that can incorporate multiple factors, the explanation for the ecological basis of cooperative breeding that has primacy is gradients in territory quality. However, this part of the theory has only been experimentally tested on two species. There is no theory that provides an alternative model for the maintenance of cooperative breeding among lineages where delayed dispersal and helping are ancestral. Given that cooperative breeding lineages have successfully diversified in Australia, current theory will be advanced by determining the relevance of habitat quality models to Australian cooperative breeders, such as the Brown Treecreeper. The challenge here is to identify the ecological basis of delayed dispersal and reproduction in Brown Treecreepers, in light of the fact that phylogenetic inertia might impinge upon the ecological basis, and to identify the type of habitat-quality model most appropriate to this species.

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CHAPTER 2. THE DEMOGRAPHY OF BROWN TREECREEPERS IN CONNECTED AND ISOLATED, LARGE AND SMALL, WOODLAND PATCHES

This chapter will be submitted for publication to Pacific Conservation Biology as:

Cooper, C. B., J. R. Walters, and H. A. Ford. The demography of Brown Treecreepers in connected and isolated, large and small, woodland patches.

ABSTRACT

I studied approximately fifty groups of the cooperatively breeding Brown Treecreeper in connected and isolated, unconnected woodland patches in the New England Tablelands of Northeastern New South Wales during 1996-1998. The occurrence of territories lacking females was higher in unconnected than connected habitat patches. Yet, nest success rate, fledgling productivity, and adult female survival did not differ among groups in unconnected and connected habitat patches. Because connectivity was partially correlated with patch size, I examined the demography of groups in small and large connected patches and small and large unconnected patches in order to examine area-sensitivity. Patch size did not influence group productivity. I hypothesize that patch connectivity influences Brown Treecreeper recruitment and dispersal.

INTRODUCTION

Forest-interior passerines are often considered “area-sensitive” because of their absence from or lower density in small habitat patches (e.g., Ambuel and Temple 1983, Blake and Karr 1984, Robbins et al.1989, Barrett 1995). However, it is well established that density is not always a good predictor of nesting success (Van Horne 1983). Therefore it is important that evaluations of area-sensitivity include measures of nesting success and survival (Winter and Faaborg 1999). Most suspected causes of area-sensitivity are related to edge effects as small patches contain a large percentage of edge and little interior habitat. Because a major consequence of habitat fragmentation is smaller habitat patches, area-sensitivity appears synonymous to sensitivity to habitat fragmentation.

However, species can also be sensitive to habitat fragmentation because of isolation of remnant patches. Barriers to dispersal vary among species and it is difficult to predict what constitutes a barrier for a particular one. Because birds are considered highly mobile organisms, it may seem counter-intuitive that bird movements could be disrupted by fragmentation. The scant evidence is inconclusive (Dunning et al. 1995, Haas 1995, Matthysen and Currie 1996, Desrochers and Hannon 1997, Matthysen and Adriaensen 1998). The importance of area- and isolation-related effects may vary with the behavior and ecology of a species as well as the nature of the landscape change (e.g., type of primary habitat, type of intervening habitat, the abruptness of the edge). Both sorts of variation may explain why species' respond differently to fragmentation, that is, why some species respond adversely while others do not (Walters 1998).

Brown Treecreepers are declining in the New England Tablelands and are sensitive to habitat fragmentation (Barrett 1995). The Brown Treecreeper is a cooperative breeder that forages on the trunks and limbs of trees and on the ground (Noske 1982a, b, 1986, 1991, Walters et al. 1999). Earlier work by Walters et al. (1999) showed that some fragments lacked female Brown Treecreepers, though foraging patterns and reproductive success did not differ among patches in more and less fragmented habitat. They suggest that sensitivity to fragmentation might be due to disrupted dispersal resulting from patch isolation, rather than effects of patch size. My objective is to more fully explore the relative influence of patch connectivity and patch size on the demography of Brown Treecreepers and expand and amplify the earlier findings by Walters et al. (1999). I use demographic data to examine pairing success, reproductive success, and female survival among groups in connected and unconnected patches, and among smaller and larger patches.

METHODS

Study area – The study site is a 1500 km^2 region surrounding the town of Armidale, in the New England Tablelands of northeastern New South Wales, Australia, (30^o 27’ S 151^o 13’ E) (Figure 2-1). The study area straddles the Great Dividing Range, with an elevation ranging from 730 to 1300 m. The climate is temperate with a mean annual rainfall of 789 mm. Coldest temperatures are usually in July when the average daily minimum temperature is 0.4°C. Warmest temperatures are usually in January when the average daily maximum is 27.2°C (Office of Bureau of Meteorology 2000). In the New England Tablelands, both woodlands and forests contain a variety of Eucalyptus of the subgenus Symphyomyrtus, which includes gums (Section Transversaria and Exsertaria), boxes and ironbarks (Section Adnataria), as well as some non-eucalyptus trees in the genus Angophora (Williams 1992). Open eucalyptus forests in the eastern portion of the study area are dominated by the stringybark, E. caliginosa, and others in the Subgenus Monocalyptus (Series Capitellatae). Rivers bordered by woodlands are generally dominated by River Sheoak (Casuarina sp.).

The New England Tablelands once were covered in nearly continuous *Eucalyptus* woodlands and forests. Temperate *Eucalyptus* woodland communities such as these are among the most poorly conserved ecosystems in Australia (Specht 1981, Yates and Hobbs 1996). Continent-wide, approximately 70-95% of various woodland types have been replaced by agriculture and pasture (Yates and Hobbs 1996). Those patches of woodland that remain are used for sheep and cattle grazing, and dead trees are removed for firewood. The current landscape of the New England Tablelands has been described as "variegated" (McIntyre and Barrett 1992) 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 densities ranging from completely cleared land to intact forest and woodland. With the aid of aerial photographs (1992, 1994) and topographic maps (each 1:25000), I used a geographic information system (ArcInfo) to digitize covertypes within the study area. I categorized the landscape covertypes by 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 (woodlands and forests).

Woodlands in the center 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) distributed across intervening habitat of mostly cleared land (44%) and sparse trees (35%). Three woodland fragments sampled in this area are adjacent to eucalpytus forests in steep gorges, a habitat unsuitable to Brown Treecreepers (Keast 1957, Noske 1980, 1982a,b, 1991). The western portion of the study area (approximately 104,000ha) contains more contiguous habitat with 20% woodlands (20,000ha) distributed in a matrix of sparse trees (48%), scattered trees (16%), and steep woodlands (10%).

Computing patch connectivity - Barrett et al. (1994) and Barrett (1995) found that the Brown Treecreeper occurred in woodland patches as small as 9 ha. For the purposes of this study, I used excluded woodland and forest patches less than 10 ha from the following analyses (Figure 2-1). I used ArcView to compute connected patch size, a measure of patch connectivity, for each patch. In one region of the study area the Brown Treecreeper territories occurred in patches that were close together, frequently separated by less than 200-m gaps. Connected patch size was measured as the total area of the set of patches with less than 200-m gaps among them that included the focal patch. A totally isolated patch had a connectivity size equal to its patch size, whereas highly connected patches had connected patch sizes uncorrelated with their individual patch size (Figure 2-2). I used this measure to divide the patches into two categories: connected (connected patch size $\geq$ 2, 000 ha) and unconnected (connected patch size $\leq$600 ha). I compared the demography of the birds in the two patch categories. Then I controlled for the effects of connectivity and compared the demography of the birds among patches of different sizes (< 300 ha and > 300 ha) within each patch category (Figure 2-2).

Demographic data - From 1996-1998, field assistants and I monitored approximately 50 groups in 19 locations in a total of 16 patches throughout the New England Tablelands. Some locations were comprised of groups that were the sole occupant of a patch and other locations contained numerous groups. Approximately 84% of adults and 85% of offspring were banded with unique color combinations and a metal band from the Australian Bird and Bat Banding Scheme. Each year, from late July to early December, we visited each territory at least once every 15 days. At each visit we identified each bird present to determine group size and followed females to determine whether a nest was present. Group members bringing nest material to a tree hole indicated nest building. A female being fed by group members and leaving a tree hole for periods no longer than 10 minutes indicated the presence of eggs. Group members bringing insects to and removing fecal sacs from a tree hole indicated the presence of nestlings. When nests were accessible (21% of all nests), nest status was determined by inspection of the nest. Offspring were counted after fledging during repeated and extensive visits to mist-net unbanded fledglings and to locate fledglings that were banded as nestlings. A group was considered successful in a given year if it produced at least one fledgling.

Statistical analyses - I used a Fisher's Exact test to determine whether the frequency of territories lacking females differed between connected and unconnected patches. I used logistic regression to model the frequency of nest failure versus nest success based on year (1996, 97, 98), group size (2,3,4,5), and connectivity (connected or unconnected). I also computed two measures of productivity. In order to control for yearly variation in reproductive success, I used the deviation from the mean number of fledglings produced by successful groups in that year as a measure of brood size. I used the deviation from the mean number of fledglings produced by all groups attempting nesting in that year as a measure of reproductive success per nesting group. I also computed deviation from the mean group size for all groups with a female. I compared these three variables between connected and unconnected patches using t-tests.

Survival of females was computed as the proportion of banded females present at the end of one breeding season that were still present at the end of the subsequent breeding season. If I did not locate the female or other members of her original group, then I considered the status of the female member of the missing group as unknown. I used logistic regression to model female breeder survival based on year (1997, 1998), and connectivity (connected or unconnected).

I used the statistical analyses of the previous paragraphs to compare the same variables between groups in (1) smaller versus larger connected patches and (2) smaller versus larger unconnected patches.

RESULTS

Natural history – During the breeding season, Brown Treecreepers resided on territories averaging 4.4 ha, ranging from approximately 1.1 to 10.7 ha. Even though territories in fragmented habitat often did not have immediate neighbors, they were not larger than in contiguous habitat (t-test, $P = 0.40$). I observed very little aggression among neighbors and adult males frequently foraged on neighboring territories. In areas where groups had many neighbors, it was common for birds (breeding males, breeding females, and helpers) to feed nestlings and fledglings on a neighbor's territory, particularly after their own nest failed.

Virtually all helpers were adult males (94% helped at their parent's nest), but two groups had female helpers and one group had a male fledgling that helped at a subsequent nest the same season he was born. On average, seven percent of helpers attempted to bud each year (i.e., breed independently on a portion of their parent's territory). In all cases, this followed or immediately preceded the death of the primary breeding female (presumably the helper's mother). Male courtship behaviors involved singing and visiting cavities, followed by carrying a large insect in the beak and walking in circles or figure-eights on a log or branch.

Almost half (48%) of all nest attempts were in live trees (usually in a limb), 23% were in cavities in low stumps, and 29% were in dead trees. Within each cavity, Brown Treecreepers built small nests of down, fur, grass, and pieces of snake skin. Juvenile and adult males brought similar materials to other cavities, either for prospective future nests or for roosting.

Demography in connected and unconnected patches – Of the groups studied from 1996-1998, 21 (18 of which had females attempt nesting at least one year) were classified as residing in 11 unconnected patches and 34 as residing in 5 connected patches.

The percent of territories that never lacked a female during this three-year study was greater in connected than unconnected patches (Fishers Exact, $P<0.0001$, df = 1, N=55) (Table 2-1). Logistic regression indicated that year (0.8, $P = 0.01$, df = 3, N = 109) and group size (-0.6, $P = 0.04$, df = 3, N = 109) had significant effects on the frequency of nest failure, but connectivity ($P = 0.50$, df = 3, N = 109) did not (Table 2-1). Among groups with a female present, mean group size, measured as average annual deviation from the mean, was larger in connected than unconnected patches (two-tailed t test, $P=0.01$, df=106, N=108). Brood size, measured as the average deviation from the annual mean number of fledglings produced from successful nests, was not different between connected and unconnected patches (two-tailed t test, $P = 0.2$, df = 76, N = 78)(Table 2-1). Fledgling production of all groups that attempted nesting, measured similarly, also did not differ (two-tailed t test, $P = 0.5$, df = 106, N = 108)(Table 2-1). Logistic regression indicated that year (-1.3, $P = 0.08$, df = 2, N = 62) had a marginally significant effect on adult female survival, while connectivity (P = 0.58, df = 2, N = 62) did not (Table 2-1).

Demography in small and large patches – There were 9 groups in 7 smaller unconnected patches (<300 ha) (6 of which had females attempt nesting) and 12 groups in 3 larger unconnected patches (>300 ha). There were 18 groups in 3 smaller connected patches and 16 groups in 2 larger connected patches.

The percent of territories that never lacked a female during this three-year study was greater in smaller than larger unconnected patches (Fishers Exact, P<0.002, df = 1, N=21) (Table 2-2). All territories in connected patches, large or small, always contained an adult female. Logistic regression indicated that the frequency of nest failure was not influenced by patch size among connected (P = 0.7) or unconnected (P = 0.5) patches. Year (P = 0.01), but not group size (P = 0.14), had a significant effect on the frequency of nest failure among connected patches (df = 3, N = 72). Neither group size (P = 0.14) nor year (P = 0.28) affected the frequency of nest failure among groups in unconnected patches (df = 3, N = 37). (Table 2-2).

Among groups with a female present, mean group size did not differ based on patch size among connected (P = 0.38) and unconnected (P = 0.19) patches. Among connected patches, both measures of group productivity, brood size (P = 0.14) and reproductive success per nesting group (P = 0.19) were not different between smaller and larger patches. The same was true for unconnected patches, (P = 0.77, P = 0.87, respectively) (Table 2-2).

Logistic regression indicated that patch size had significant effects on adult female survival among unconnected patches (2.5, P = 0.05), but not among connected patches (P = 0.23). Year was not related to adult female survival among unconnected (P = 0.93, df = 2, N = 22) or connected (P = 0.95, df = 2, N = 40) patches (Table 2-2).

DISCUSSION

Most of my findings are consistent with earlier work by Walters et al. (1999). A significantly higher proportion of groups in unconnected than connected patches lacked a female each year. The paucity of females in unconnected woodland fragments can not be attributed to either lower productivity or lower survival of females in fragments. Rather, in chapter 3, I found that female recruitment was much lower in unconnected habitat patches, and detected no movements between unconnected fragments. I hypothesize that juvenile females are unable or reluctant to disperse through a fragmented landscape to fill breeding vacancies. This is consistent with findings in central New South Wales where distance between patches explained Brown Treecreeper distribution. Brown Treecreepers were not found in patches more than 700 m from the next nearest patch (S. Briggs, personal communication). Alternatively, if isolated fragments are lower quality (see below), then juvenile females may respond to the lower quality of fragments by avoiding them. By each of these scenarios, highly philopatric males would remain unpaired in unconnected but not connected habitat. Experimental work is needed to distinguish these alternatives.

Winter and Faaborg (1999) showed that some species that did not appear area-sensitive based on census data were area-sensitive based on nest success data. They urged researchers to examine both census and nest success data before designating a species as sensitive to fragmentation. Our findings indicate that nest success data are not necessarily the most definitive information revealing sensitivity to fragmentation. I found that Brown Treecreepers are not area-sensitive even though they are sensitive to fragmentation. First, area effects on reproduction were not detected. Furthermore, contrary to most expectations of area-sensitivity, the (non-significant) trend was for groups in smaller connected patches to be more productive than groups in larger connected patches. Therefore, small patch size alone does not lower Brown Treecreeper productivity. Thus, some species whose reproduction and survival are not sensitive to fragment size may still be sensitive to habitat fragmentation due to decreased dispersal success. Brown Treecreepers may fall into this category, and be isolation-sensitive rather than area-sensitive.

Increased adult female mortality in unconnected, small patches might be interpreted as evidence of an area effect. However, higher adult female mortality rates in small, unconnected patches are consistent with the long-term effects of isolation as well as the immediate effects of area or habitat degradation. Although woodland loss and fragmentation in the region began with settlement of the area during the 1840s, the regrowth was probably cleared twice over the next 100 years (Davidson and Davidson

1992). Most clearing stopped in the 1940s, but grazing has increased and extensive dieback occurred during the 1970s (Davidson and Davidson 1992). Brown Treecreepers, like other cooperative breeders (Dow 1980), probably have long life spans. During this study, one male in an isolated fragment was at least 14 years old since he was banded as an adult in 1985. If isolation effects exist, the number of groups in unconnected patches will dwindle because some deceased female breeders are not replaced, especially in small patches, where within-patch recruitment is unlikely. In fact, all small, unconnected patches in this study contained only one group. Consequently, the remaining females in small, unconnected patches at the start of this study likely were older on average than females in other kinds of patches. Thus, if elderly females have higher mortality rates, isolation effects may explain the observed mortality pattern, and small, unconnected patches may not possess any quality that increases female mortality. Unfortunately, I can not distinguish these possibilities with the available mortality data. However, other results of this study are consistent with the hypothesis that the higher female mortality in small, unconnected patches is an artifact of the time-lagged response of the population to the effects of patch isolation due to woodland fragmentation.

High variation in Brown Treecreeper group productivity makes it statistically difficult to detect differences based on connectivity and patch size. There was a trend toward lower productivity in small, unconnected patches suggesting that patch connectivity and patch size may have a small impact on productivity in extreme cases. Other factors that may affect productivity are natural variation in habitat quality and habitat degradation. Natural variation in habitat quality is often quite high in cooperatively breeding species (Koenig et al. 1992). Alternatively, Brown Treecreepers might be particularly vulnerable to habitat degradation related to land use practices.

Recher and Lim (1990) and Recher (1999) argued that livestock grazing and altered fire regimes reduce ground vegetation, diminish resources, destroy the litter layer, and erode soil, thereby reducing food resources available to ground-foraging species in Australian woodlands. In a study of the Eastern Yellow Robin (*Eopsaltria australis*) in the New England Tablelands, Zanette et al. (2000) showed that food resources (insects) were lower in smaller than larger woodland patches. This relative food shortage affected the foraging time budgets and nestling weights, but not overall reproductive success of the Eastern Yellow Robin. Walters et al. (1999) found that foraging behavior of adult Brown Treecreepers did not differ among groups in more and less fragmented habitat, but did not measure food delivery to nests.

Habitat degradation may not be linked directly with patch connectivity or size, but rather with land use. Neither of the studies mentioned above compared patches of different land use types. Many woodland remnants in this study, irrespective of connectivity and size, were grazed by livestock and experienced fires. Many remnants showed signs of slight degradation, such as the presence of Noisy Miners (*Manorina melanocephala*) and invasion by mistletoe (Dow 1977, Ford and Bell 1982, Grey et al. 1997, 1998). Future research would profit from exploring the relationships between avian demography and land use activities such as grazing intensity or habitat variables directly related to degradation.

Conclusions: Data from our study indicate that establishing minimum-area requirements for this species based solely on the minimum area of occurrence would be inappropriate and ineffective at conserving Brown Treecreeper populations. Patch size did not have a large effect on survival or reproduction, and patch connectivity, not patch size, affected dispersal success. The appropriate management approach should reflect the underlying basis of sensitivity to habitat fragmentation, in this case disrupted dispersal due to patch isolation, or isolation-sensitivity, not sensitivity to patch size. I recommend that management practices include retaining connectivity among habitat patches and re-establishing connectivity between isolated patches. The only minimum-area requirement that might be appropriate for Brown Treecreepers is that based on home range size. Breeding season territory size to range from 1.1 to 10.7 ha and post-fledging home ranges were larger. Brown Treecreepers were not found in patches smaller than 9 ha in the New England Tablelands during surveys in the early 1990's (Barrett 1995) nor in patches smaller than 10 ha in central New South Wales (S. Briggs, personal communication). Thus, preserving patches smaller than 10 ha may be ineffective, regardless of their proximity to other patches.

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TABLES

Table 2-1. Demography of Brown Treecreepers in connected and unconnected habitat near Armidale, New South Wales, Australia. Means and percentages are 3-year averages.

	Unconnected	Connected
Number of Groups	21	34
Mean Group Size*	2.5	2.9
% Groups never lacking a female	52%	100%
% Groups (with female) attempting nest	96%	100%
% Groups nesting	88%	99%
% Groups with > 1 successful nest	61%	62%
Mean brood size	1.79	2.06
Mean # fledglings/breeding group	1.33	1.47
Mean adult female mortality	22%	18%

*Mean group size computed from groups with breeding female (N = 18, unconnected).

Table 2-2. Demography of Brown Treecreepers in small and large connected and small and large unconnected patches near Armidale, New South Wales, Australia. Means are 3-year averages.

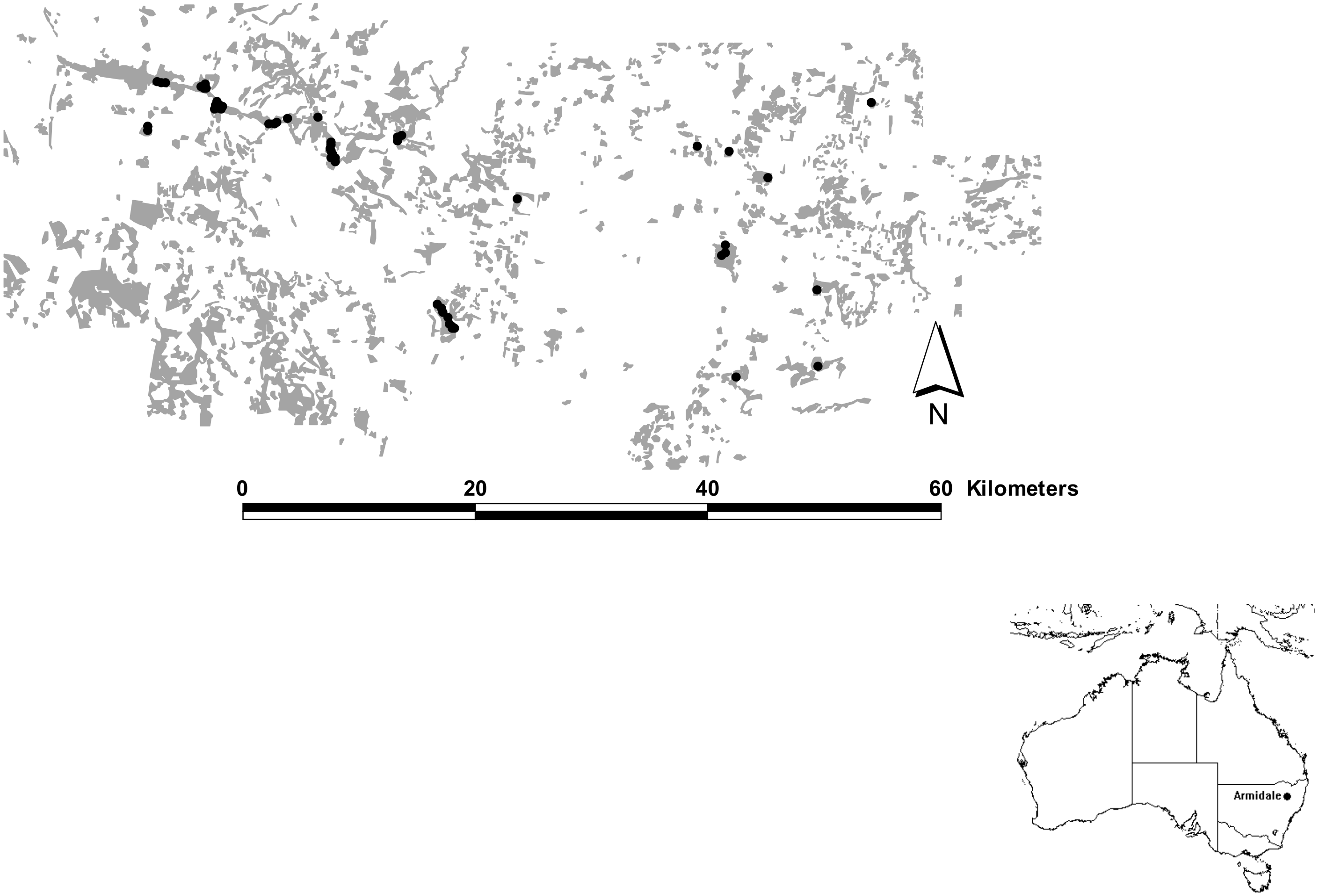
	Unconnected		Connected	
	Small	Large	Small	Large
Number of patches	9	3	2	2
Number of Groups	9	12	18	16
Mean Group Size*	2.17	2.53	3.04	2.84
% Groups never lacking a female	20%	83%	100%	100%
% Groups (with female) nesting	91%	100%	100%	100%
% Groups with > 1 successful nest	80%	71%	71%	61%
Mean brood size	1.71	1.80	2.26	1.81
Mean # fledglings/breeding group	1.14	1.29	1.64	1.28
Mean adult female mortality	42%	6%	27%	10%

*Mean group size computed from groups with breeding female (N = 6, small unconnected).

FIGURE CAPTIONS

Figure 2-1. The study area with woodland in gray, the location of all monitored groups indicated by black circles, and the town of Armidale indicated by a star. Inset shows location of Armidale in Australia.

Figure 2-2. The relationship of connected patch size to individual patch size for patches containing Brown Treecreepers that were monitored during 1996-1998. Connected patch size is the total area of the set of patches with less than 200-m gaps among them that included the focal patch. Patches with a connected patch size ≥ 2,000 ha were categorized as ‘connected’ and patches with a connected patch size ≤ 600 ha were categorized as ‘unconnected.’ The dashed line delineates patches classified as small (< 300 ha) and large (> 300 ha).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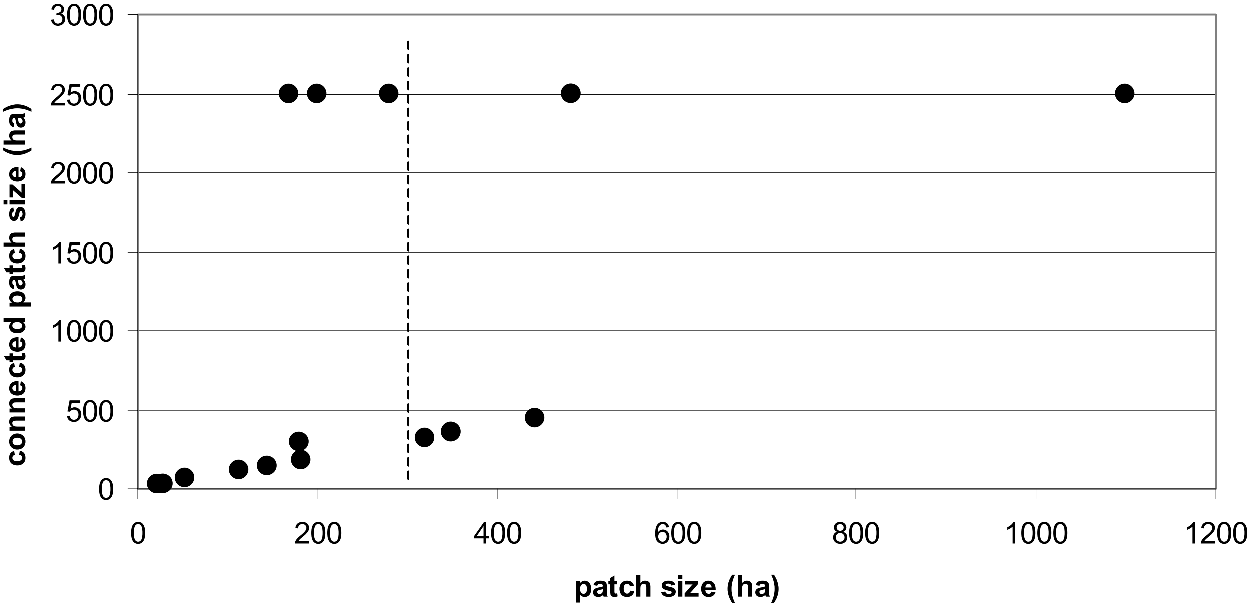
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200
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600
800
1000
1200
patch size (ha)

CHAPTER 3. EXPERIMENTAL EVIDENCE OF DISRUPTED DISPERSAL CAUSING DECLINE OF AN AUSTRALIAN PASSERINE IN FRAGMENTED HABITAT

This chapter was submitted to Conservation Biology on 27 July 2000 as:

Cooper, C. B. and J. R. Walters. Experimental Evidence of disrupted dispersal causing decline of an Australian passerine in fragmented habitat.

ABSTRACT

I evaluated two hypotheses to explain the decline of Brown Treecreepers (*Climacteris picumnus*) in fragmented habitat, habitat degradation and isolation. The frequency of territories lacking females was higher in fragmented than contiguous *Eucalyptus* woodlands in the New England Tablelands of Northeastern New South Wales during 1996-1998. I translocated 11 females to unpaired males in fragments and 5 females to unpaired males in contiguous habitat. I reasoned that females would reject territories with unpaired males in fragmented habitat if this habitat was degraded, but not if males were unpaired due to isolation. Females relocated to males in fragments generally paired, half attempted nesting, and some formed productive groups, while no female relocated to an unpaired male in contiguous habitat remained or paired. I reject habitat degradation as an explanation for the current decline of Brown Treecreepers, though degradation could have played a role in the past. Exceedingly low female recruitment within fragments and a lack of female dispersal between fragments provide additional evidence that dispersal into fragments rarely occurs naturally. I conclude that patch isolation is responsible for the lack of females in fragmented habitat.

INTRODUCTION

The reduction of biological diversity is attributed primarily to the loss and fragmentation of natural habitats by various human activities such as agriculture, urbanization, and resource extraction (Wilcox and 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). There are several mechanisms by which fragmentation can affect animal populations. These mechanisms may operate 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.

Two well-documented forms of edge effects, increased nest predation and brood parasitism, have been identified as primary causes of declines of some migratory passerines in parts of their breeding range in North America (Ambuel and Temple 1983, Brittingham and Temple 1983, Wilcove 1985, Robinson et al. 1995, Haskell 1995). Nevertheless, the importance of nest predation and brood parasitism in explaining adverse effects of habitat fragmentation may not be universal. These mechanisms do not appear to affect the Brown Treecreeper, an Australian passerine (Walters et al. 1999, Chapter 2). Although there are brood parasites (e.g., *Cuculidae*) in Australian woodlands, none achieve densities or impact other species in a way comparable to Brown-headed Cowbirds (*Molothrus ater*) in North America (Robinson et al. 1995, Ford et al. 2000). Nest predators may generally be expected to have a smaller effect on cavity-nesters, such as the Brown Treecreeper, than on cup-nesters (Matthysen and Adriaensen 1998). Furthermore, nest predators do not appear to have a greater impact on Australian open cup-nesting passerines in small fragments compared to large ones or in edge compared to interior woodlands (Taylor and Ford 1998, Zanette and Jenkins 2000), but more research is needed. Where patch edges border roads, mortality caused by motor vehicles has had a major impact on some species (e.g., Carnaby's Cockatoo (*Calyptorhyncus latirostris*) (Saunders 1982) and is suspected of causing declines of ground-foraging species and honeyeaters (Vestjens 1973, Disney and Fullagar 1978, Brown et al. 1986, Lepschi 1992).

In this system, impacts that alter habitat quality of a remnant are not confined to the patch edge and therefore are better categorized as habitat degradation effects than edge effects. Degraded *Eucalyptus* woodlands are characterized by a variety of features, including the premature and relatively rapid death of trees (known as 'rural dieback', Landsberg and 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 (Yates and Hobbs 1996). Lower avian diversity is found in woodlands suffering severe dieback (Ford and Bell 1982, Barrett 1995). Also, an aggressive avian species that excludes most other insectivorous and nectar-feeding birds, the Noisy Miner (*Manorina melanocephala*), is associated with fragmented and degraded habitat (Dow 1977, Ford and Bell 1982, Grey et al. 1997, 1998).

Understanding how avian dispersal patterns might be influenced by landscape structure is critical to testing theories regarding fragmentation effects. Barriers to dispersal vary among species and it is difficult to determine what constitutes a barrier for any species. Because birds are highly mobile organisms, it may seem counter-intuitive that movements of bird species could be disrupted by fragmentation, but the scant empirical evidence available suggests otherwise. Landscape features affect movement patterns or behavior of migratory forest songbirds (Dunning et al. 1995, Desrochers and Hannon 1997), a variety of residents (St. Clair et al. 1998), and short-distance migrants (Haas 1995) in North America.

Thus isolation effects and various forms of habitat degradation appear to be the most viable hypotheses to explain the sensitivity of some Australian birds to habitat fragmentation. Insectivorous birds that forage extensively on the ground appear to be especially sensitive to fragmentation and degradation in many parts of Australia (Recher and Lim 1990, Garnett 1992, Recher 1999). Recher and Lim (1990) and Recher (1999) argue that livestock grazing and altered fire regimes reduce ground vegetation, diminish resources, destroy the litter layer, and erode soil, thereby reducing food resources available to ground-foraging species. Zanette et al. (2000) found greater abundance of ground-dwelling insects in larger versus smaller woodlots, and this relative food shortage affected the foraging time budgets and nestling weight, but not overall reproductive success, of a ground-foraging insectivorous bird, the Eastern Yellow Robin (*Eopsaltria australis*). Cooperative breeders, which are numerous in Australia (Brown 1987, Russell 1989), may be especially sensitive to habitat fragmentation because of the short-distance characteristics of their dispersal patterns (Walters 1998). In this study, I examine the basis of sensitivity to fragmentation in the Brown Treecreeper, an insectivorous ground-foraging passerine that breeds cooperatively.

Brown Treecreepers 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, whereas most females disperse (Noske 1980, 1991). Barrett et al. (1994) and Barrett (1995) documented the decline of the Brown Treecreeper in fragmented habitat in 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 had reproductive success equal to those in large patches of contiguous habitat (Walters et al. 1999, Chapter 2).

Here I use a field experiment to test two hypotheses, habitat degradation and isolation, to explain the observed lack of females in fragmented woodlands. Distinguishing isolation and habitat degradation effects observationally is difficult. For example, Villard et al. (1993) found Ovenbird (*Seiurus aurocapillus*) pairing success decreased with isolation of forest fragments. However, because Ovenbirds are migratory and therefore perform some habitat selection process each year prior to breeding, Villard et al. (1993) could not determine whether fragmentation affected dispersal or habitat selection by females. Here I attempt to distinguish these hypotheses experimentally by translocating females to unpaired males in fragmented and contiguous habitat. Under the null hypothesis that habitat degradation accounts for the absence of females from territories in isolated fragments, I predict that translocated females should reject territories in fragments or exhibit poor reproduction and/or survival if they remain. Under the alternative hypothesis that isolation accounts for the absence of females in fragments, I predict that translocated females should remain in fragments, and reproduce and survive as well as birds in contiguous habitat (Figure 3-1). I also examined female recruitment and dispersal data to further test isolation as the basis of Brown Treecreeper sensitivity to fragmentation.

METHODS

Study area - The study site is comprised of *Eucalyptus* woodland and forest patches within a 1500 km^2 region surrounding the town of Armidale, in the New England

Tablelands of northeastern New South Wales, Australia, (30^o 27' S 151^o 13' E) (Figure 3-2). The study area straddles the Great Dividing Range, with an elevation ranging from 730 to 1300 m and is described in detail in Chapter 2.

Temperate *Eucalyptus* woodland communities are among the most poorly conserved ecosystems in Australia (Specht 1981, Yates and Hobbs 1996). Approximately 70-95% of various woodland types have been replaced by agriculture and pasture (Yates and Hobbs 1996). Furthermore, the woodlands on high quality soils have been preferentially cleared (Recher and Lim 1990, Hobbs et al. 1993, Robinson and 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 and Barrett 1992), 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 densities ranging from completely cleared land to forests. For the purposes of this study, I categorized the landscape by 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 (woodlands and forests).

In the study area, Brown Treecreeper family groups defend territories averaging 4.5 ha, and ranging from 1.1 to 10.7 ha (this study). The center 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%). Three woodland fragments sampled in this area are adjacent to *Eucalpytus* forests in steep gorges, a habitat unsuitable to Brown Treecreepers (Keast 1957, Noske 1982a,b). The western portion of the study area (approximately 104,000 ha) is predominantly contiguous habitat with 20% woodlands (20,000 ha) and an intervening habitat of sparse trees (48%), scattered trees (16%), and steep woodlands (10%). The monitored groups I consider as residing in contiguous habitat are in woodland patches connected to each other and to other patches through wooded corridors, with no gaps of cleared land greater than 200 m between patches. The monitored groups I refer to as residing in fragmented habitat are in woodland patches that are isolated from contiguous habitat by at least 2 km of mostly cleared land and sparse trees (Figure 3-2). Brown Treecreepers in contiguous habitat generally occurred in clusters of breeding groups with loosely spaced groups between clusters (Figure 3-2). In fragmented habitat, Brown Treecreepers were scarce and, through extensive surveying, I knew the locations of virtually all territories.

Group compositon and recruitment – Field assistants and I surveyed patches and monitored over 50 groups of Brown Treecreepers from 1996-1998 as detailed in Chapters 2 and 6. Monitoring involved color-banding of adults and offspring and repeated visits to census groups and collect reproductive 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-meters as the straight-line distance between initial banding location and resighting location.

Translocation experiment - We translocated females to unpaired males in fragmented and contiguous habitat at the conclusion of the 1996, 1997, and 1998 breeding seasons and prior to the 1998 and 1999 breeding seasons. Females selected to be translocated were found in contiguous habitat and ranged in age from 2 months post fledging (N = 8) to adult (N = 10). Unpaired males selected to receive females were either the sole occupant of a territory (N = 8), a male that shared a territory with another male (N = 2), or a helper that held a portion of his natal territory in the initial stages of budding (N = 6). Females were captured by mist-net in the morning, fitted with color bands if not already marked, and transported to their 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 locate translocated females the day after release, again within three weeks post-release, 2-3 months later, and during the following breeding season. If a female did not appear healthy upon release and subsequently disappeared, we moved a second female to that territory. This occurred once in fragmented habitat. If a translocated female appeared to survive translocation but not survive the winter, we moved a second female to that territory, if a male was still present. This occurred once in fragmented habitat.

Territory spatial distribution and dispersal predictions - I expected the distribution of observed dispersal movements to reflect the distribution of potential breeding vacancies. To determine the distribution of potential breeding vacancies, I computed the average number of known territories within successive distance intervals around all known territories. Specifically, I 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, I assumed that vacancies within a patch in fragmented habitat were only available to females originating in that patch. To calculate an expected distribution, I 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. The distributions differed considerably between the null and alternative hypotheses. I assumed all vacancies were available to females originating in contiguous habitat. Thus in contiguous habitat, the average number of territories in each distance interval was the same under both hypotheses.

To turn the distribution of potential breeding vacancies into the proportion of birds predicted to move each distance interval, I divided the average number of territories in each 500-m distance interval by the number of female fledglings banded in that population (i.e., fragmented or contiguous) (Figure 3-3). Under the null hypothesis, I expect dispersal distributions to be similar in fragmented and contiguous habitat. Under the alternative hypothesis, I expect the median of female dispersal distances to be higher and the maximum distance lower (i.e., a distribution with a truncated tail) in fragmented compared to contiguous habitat (Figure 3-3).

RESULTS

Group composition - The percent of territories that never lacked a female during this three-year study was greater in contiguous (100%) than fragmented (50%) habitat (Fishers Exact, $P<0.0001$, $df = 1$, $N=35$).

Translocation experiment - 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. Two of these females, both in fragmented habitat, were “follow-ups,” i.e., females moved to males after the first translocation attempt failed. In two fragmented sites, we moved males to the translocated females after the original receiving males disappeared. Two females that formed productive groups did so not at their release site, but with a different male in the same fragment. Seven females relocated to fragments paired and remained with the male occupant for at least one breeding season. Five of these females attempted nesting, 5 produced nestlings, and 3 produced fledglings. None of the females relocated to contiguous habitat paired and remained with the male for a breeding season. Translocated females were significantly more likely to pair with the males in fragmented habitat than in contiguous habitat (Fishers Exact Test, P = 0.005, df = 1, N = 16). I could not compare reproduction of translocated females between treatments since none of the females relocated to males in contiguous habitat paired. The nest success rate of translocated females (60%) was similar to the nest success rate of females in non-experimental groups in contiguous (62%) and fragmented (61%) habitat. The proportion of paired translocated females that attempted nests (71%) was low compared to paired females in other groups in contiguous (99%) and fragmented (96%) habitat (Chapter 2).

Movements in fragmented and contiguous habitat – Of 23 males that were banded as fledglings on their natal territory and resighted as adults, 19 were resighted on their natal territory, two successfully budded, one successfully dispersed to another territory, and one 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 I observed females (fledglings and adults of unknown age) to move was 1.14 ± 1.25 km (n=17) with a median distance of 0.77 km. The mean (±SD) was 0.72 ± 0.59 km in fragmented habitat (n=7) (median 0.88 km, maximum 1.4) and 1.39 ± 1.49 km in contiguous habitat (n=10)(median 0.69 km, maximum 4.5) (Figure 3-3). 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. The observed distribution of female movements in fragmented habitat was similar to the distribution predicted under the alternative hypothesis that fragmentation disrupts dispersal (Figure 3-3).

Recruitment in fragmented and contiguous habitat - Through surveying and data collection related to other work, field assistants and I determined that there were approximately 20 unmonitored groups within contiguous habitat and an additional 50 or more unmonitored groups outside the study area south of contiguous habitat. In 1992, and again in 1995-1998, J. Walters, field assistants, and I visited the majority of woodland remnants greater than 10 ha in fragmented habitat. I estimate that during the course of this study (1996-1998) there were approximately 13 unmonitored groups in fragmented habitat, most of which were in one large fragment that also contained 6 monitored groups. The relatively low proportion of groups monitored in contiguous habitat (approximately 28%) relative to fragmented habitat (approximately 58%) means that dispersal data from contiguous habitat are more strongly biased toward short-distance movements than data from fragmented habitat (see Koenig et al. 2000).

We detected 14 movements of juvenile females, 4 originating in fragments and 10 in contiguous habitat. Assuming half the juveniles we banded were female, and subtracting the 8 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. Recruitment of both unbanded and banded juvenile females into breeding vacancies was observed frequently in contiguous habitat, but only once in fragmented habitat (Table 3-1). The lone instance in fragmented habitat involved movement within a fragment: I observed no movement between or into fragments.

DISCUSSION

The results of this study suggest that Brown Treecreepers are declining in the New England Tablelands because of isolation arising from habitat loss and fragmentation. A significantly higher proportion of groups in fragmented than contiguous habitat lacked a female each year, no females were observed to disperse between fragments, and recruitment within fragments was very low. When females were translocated to these fragments, however, they usually paired and in some cases bred successfully.

Two earlier studies suggested that territories in fragmented habitat that still contained females were not degraded compared to territories in contiguous habitat (Walters et al. 1999, Chapter 2). This study suggests that many territories lacking females were not degraded because females remained and often bred on those territories after translocation. If females translocated to fragments had not remained, we would have been unable to distinguish between territory quality or mate quality as the cause of the high occurrence of unpaired males in fragments. However, because females paired with males after translocation, the lack of females in fragments appears unrelated to both habitat quality and mate quality. Thus, the translocation experiment allows us to eliminate habitat degradation as an explanation for the lack of females in fragmented habitat.

Furthermore, dispersal patterns matched those predicted under the isolation hypothesis, suggesting 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. Under the isolation hypothesis, the disruption of long-distance movements was predicted to create a shift toward more short-distance movements in fragmented habitat. This was not predicted for contiguous habitat. Yet, the observed within-patch movements of females in contiguous habitat were similar to within-patch movements in fragmented habitat. The apparent shift to more short-distance movements in contiguous habitat is attributable to a strong observational bias for short-distance movements because we monitored only a fraction of available territories in contiguous habitat. This bias is almost nonexistent in fragmented habitat because we monitored virtually all territories. The presence of more males than females in fragments is attributable to exceedingly high male philopatry, that is, males in fragments were probably on or adjacent to their natal territory. Thus the scale of male dispersal is too small to be disrupted by the scale of fragmentation in this study area.

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 better vacancy than the one at the release site. Another 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.

Few avian studies have attempted to measure habitat isolation and examine its role in species declines (e.g., Howe 1984, Brown and Dinsmore 1986, Blake and Karr 1987). Müller (1982) determined that the Middle Spotted Woodpecker (*Dendrocopus* *medius*) was sensitive to habitat isolation at a scale of > 9 km. In one of the few studies to directly examine dispersal in a fragmented landscape, Matthysen et al. (1995) concluded that while fragmentation caused an increase in the natal dispersal distance of Nuthatches (*Sitta europaea*), it did not alter the number of territories traversed by dispersers. In other words, fragmentation merely expanded the scale of dispersal, but did not appear to interrupt it. However, in later studies, Matthysen and Currie (1996) and Matthysen and Adriaensen (1998) inferred that Nuthatch survival during or shortly after dispersal must be low in fragmented habitat. Haas (1995) found that breeding dispersal of short-distance migrants that foraged in open habitat occurred predominantly through wooded corridors rather than across open habitat. Dunning et al. (1995) found that patch isolation disrupted or slowed colonization movements of Bachman's Sparrow (*Aimophila aestivalis*).

The data presented here suggest that the configuration of the landscape in the contiguous region currently permits the successful dispersal of Brown Treecreepers, while 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 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 possibly suitable for movement. In addition, unpaired males in these types of fragments were detected sporadically, suggesting they foray farther than males in fragments surrounded by cleared land. The poor success of translocations in contiguous habitat may also support this interpretation (see above). Other studies have shown that some birds will avoid crossing clear-cut gaps and rivers (Capparella 1992, Desrochers and Hannon 1997). 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, though how far they would 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. I observed a maximum movement of 1.2 km in fragmented habitat even though most patches were > 5 km apart. In contradiction to this possibility is the fact that dispersal observations are biased toward short-distance movements and it is not possible to correct biases in the right (i.e., long-distance) tail of the dispersal distribution (Koenig et al. 2000). Thus, it may be misleading to rely on observations of color-banded birds as an indicator of how far Brown Treecreepers are capable of moving. For example, in Red-cockaded Woodpeckers (*Picoides borealis*), the median dispersal distance of female fledglings is 3.2 km, but one female was observed to disperse 90 km (Walters et al. 1988).

A third possibility is that the high dispersion of territories in fragmented habitat may greatly reduce the probability of a female locating a territory. Several simulation models support the idea that clumped territories may promote successful dispersal, regardless of the intervening habitat (Doak et al. 1992, Letcher et al. 1998). In this species, territories exhibit a high degree of clumping because the dominant pathways for a male to acquire a breeding position are by territory budding and territory inheritance (personal observation, Noske 1980, 1991). Therefore, females must disperse out of their natal neighborhood to avoid related males, which may require leaving small fragments. In fragmented habitat, a wide search path or complex search pattern would be required to detect more than a handful of territories (Figure 3-2). Brown Treecreeper neighborhoods were more dense in contiguous habitat than fragmented habitat and birds moving through contiguous habitat encounter more groups per unit area, and therefore more potential breeding vacancies, than birds moving through fragmented habitat. In contiguous habitat, dispersers can travel from territory to territory on their dispersal journey. If dispersing birds use social cues more than habitat cues to find territories, dispersal is especially likely to be disrupted in fragmented habitat. Many species are known to require the presence of conspecifics as cues to selecting breeding sites (Reed et al. 1999).

Implications for management - There is considerable uncertainty about how fragmentation affects birds because both empirical evidence and the current conceptual framework are inadequate (Hunter 1991, Wiens 1995, Walters 1998). Currently most conservation plans simply aim to minimize fragmentation, connect patches with corridors, and control nest predators and parasites (Walters 1998). These practices are based on the perception that edge effects are of paramount importance and that corridors alleviate dispersal problems. Our findings suggest that edge effects are not important to all species or in all fragmented systems and that isolation rather than habitat degradation is the basis of adverse effects of fragmentation on this Australian species.

Lacking a general understanding of fragmentation effects, one is limited to making specific recommendations for the particular species and system studied, in this case Brown Treecreepers in the New England Tablelands. If cleared land is a "barrier" to the movement of Brown Treecreepers, then movement corridors would mitigate isolation effects. Conversely, if high territory dispersion is the cause of disrupted dispersal, then movement corridors will not alleviate the problem. Rather, connectivity must be in the form of occupied habitat, which provides social cues to facilitate movement and increase dispersal success. More research is needed on how Brown Treecreeper movements are altered by landscape features in order to determine what specific landscape features represent connectivity for this species. I observed that large patches (> 450 ha) or a series of well-connected patches (gaps ≤ 200 m between patches >100ha) appear to be necessary for the persistence of Brown Treecreeper populations. Isolated fragments of medium size (e.g., 350 ha) either did not contain Brown Treecreepers any longer or contained declining populatoins (i.e., contained few females). Because of the highly philopatric behavior of male Brown Treecreepers, this species can exist in a region for a long time after the population has become inviable. This supports the argument by Recher (1999) that the rate (or pattern) of species decline, not just local extinctions, should be considered when identifying the threatened status of a species.

Finally, the few translocations changed the proportion of groups with females and raised productivity in fragments considerably. Thus translocations might be effective in rescuing small isolated populations over the short term, while other efforts are made to re-establish habitat and/or connectivity among fragmented populations.

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TABLES

Table 3-1. Origin of females recruited into breeding vacancies in fragmented and contiguous habitat.

Type of Recruit	Fragmented	Contiguous
Unbanded immigrant	0%	44% (7)
Banded juvenile	13%(1)	56% (9)
Translocated female	87%(7)	0% (0)

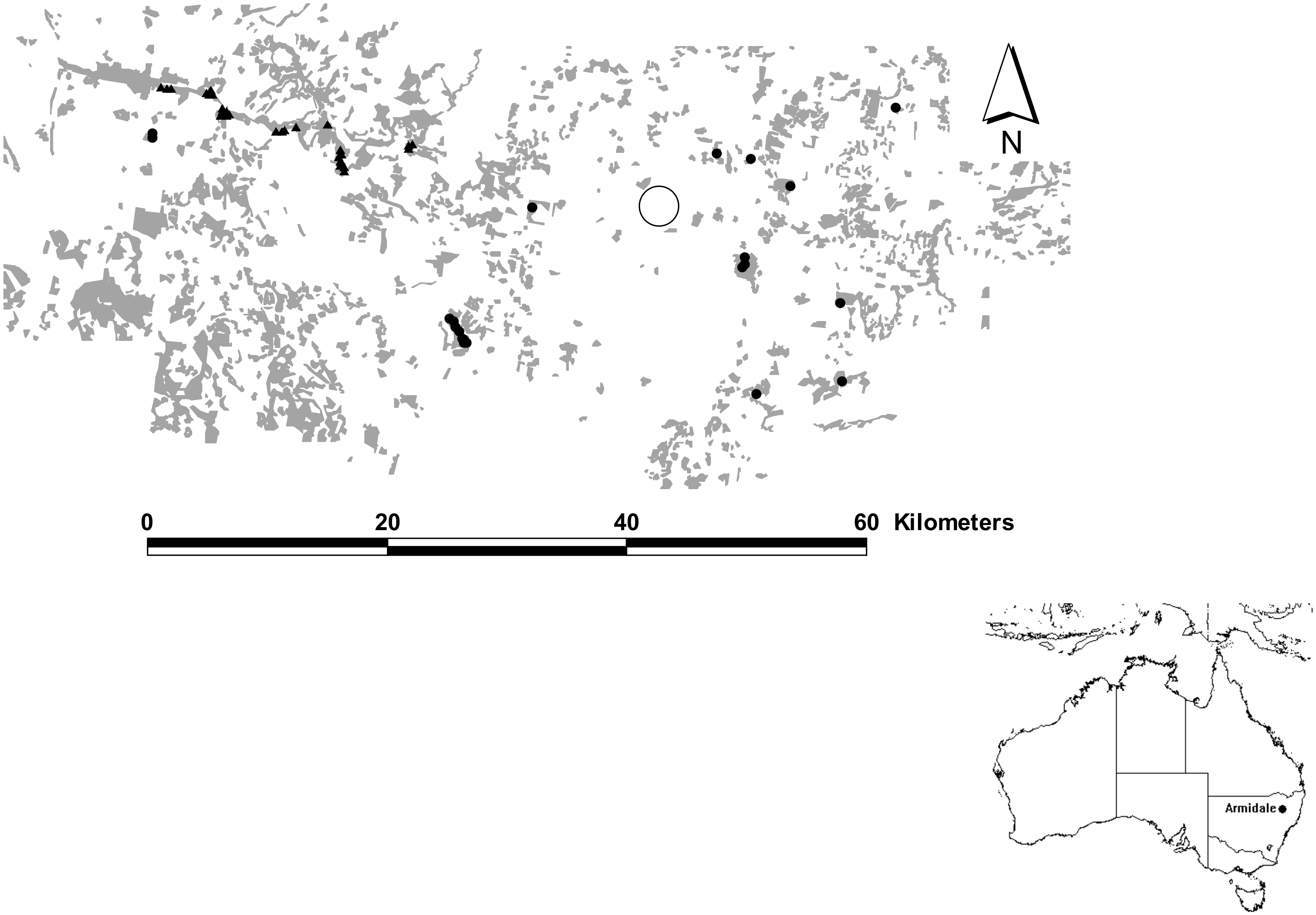
FIGURE CAPTIONS

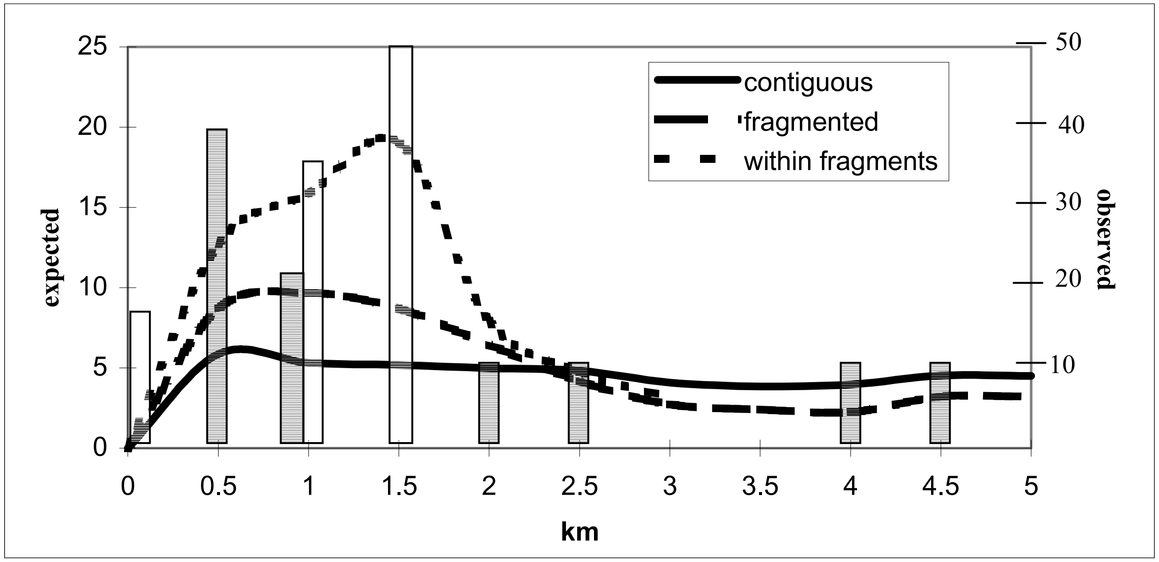
Figure 3-1. Four possible outcomes of translocations into contiguous and fragmented habitat, related to the two possible fragmentation effects (isolation, habitat degradation) hypothesized to cause the decline of Brown Treecreepers. If females translocated to solitary males do not remain in fragmented habitat, but do remain in contiguous habitat, then the habitat degradation hypothesis can not be rejected. If females translocated to solitary males form productive groups in fragmented habitat, then the habitat degradation hypothesis can be rejected, leaving the isolation hypothesis as the mostly likely explanation for Brown Treecreeper declines.

Figure 3-2. The study area with contiguous woodlands in gray. Monitored groups in contiguous habitat are designated by black triangles and groups in fragmented habitat are designated by black circles. The inset shows the location of Armidale in Australia.

Figure 3-3. Predicted distributions of female movements in fragmented habitat under the null hypothesis of no isolation effects (grey lines) and under the alternative hypothesis of isolation effects (dashed black line), and in contiguous habitat under both hypotheses (solid black line). To generate predicted distibutions, I assumed that observed dispersal movements reflect the distribution of potential breeding vacancies. Under the null hypothesis all known territories were potential breeding vacancies. Under the alternative hypothesis, all known territories were potential breeding vacancies for birds originating in contiguous habitat, but only vacancies within a patch in fragmented habitat were available to females originating in that patch. Predicted distributions were generated at 500-m distance intervals and resulting lines were smoothed for graphical purposes. I estimated movements by female Brown Treecreepers between the natal territory and the re-sight location to the nearest 100 m (bars).

		Contiguous Habitat	
		Female stays and breeds	Female disappears
Fragmented Habitat	Female stays and breeds	Isolation	Isolation
	Female disappears	Habitat degradation	Inconclusive


N
0
20
40
60 Kilometers
Armidale


expected
25
20
15
10
5
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observed
50
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1
1.5
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3
3.5
4
4.5
5
km
contiguous
fragmented
within fragments

CHAPTER 4. EFFECTS OF LANDSCAPE PATTERNS ON DISPERSAL SUCCESS: A SIMULATION OF BROWN TREECREEPER POPULATION DYNAMICS IN A SPATIALLY REALISTIC LANDSCAPE

ABSTRACT

I used a simulation model to examine the possible role of patch isolation in causing observed declines of Brown Treecreeper (*Climacteris picumnus*) in northern New South Wales, Australia. Using aerial photographs and a geographic information system, I created a spatially realistic landscape in which territories were constrained to woodlands and the matrix composition mimicked the actual landscape in the study area. I compared observed population behavior to the outcome of simulations based on two dispersal movement rules and three dispersal mortality rules. Under the first movement rule a dispersing bird's initial direction was selected at random (Random), and under the second a bird's initial direction was towards its nearest neighbor (Neighbor). The first mortality rule used a constant mortality rate for dispersing birds, while the second varied mortality rate dependent on habitat type. Under Random runs, populations in contiguous habitat were relatively stable while populations in fragmented habitat steadily declined due to low female recruitment, which is the same pattern observed in the real population. Populations in both contiguous and fragmented habitat increased under the Neighbor movement rule, suggesting that population dynamics were sensitive to dispersal search patterns. Habitat-based mortality rules had an effect on population behavior even though matrix composition affected long-distance dispersal, which was infrequent, rather than short-distance dispersal, which was exceedingly common. Thus, even for this cooperative breeder, where territories become clumped due to a high budding rate, long-distance dispersal influences overall population performance. The simulated population in fragmented habitat never decreased to within-patch densities as low as those observed in the field. It may be that variation in habitat quality in fragments is naturally high or recently degraded, or that kin discrimination reduces the effectiveness of dispersal within fragments.

INTRODUCTION

Habitat fragmentation can affect populations in several ways, including altering birth, death, and dispersal rates. Edge effects result in decreased reproduction or survival of birds near the edges of patches. Some well-documented examples include cowbird parasitism and nest predation of numerous species in North America (Robinson et al. 1995). Edge effects are influenced by the composition of the surrounding landscape as well as by patch size (Donovan et al. 1997). Isolation effects result in decreased dispersal among fragments. There is much theoretical support for the existence of isolation effects, but few empirical studies (Harrison and Bruna 1999).

How fragmentation patterns affect the vital rates of a population is the subject of continuing research, but the development of a unified theory has been hindered by theoretical (Caughley 1994, Walters 1998) and logistical obstacles (Harrison and Bruna 1999). One major obstacle is that many effects occur at large scales, which makes isolating effects of fragmentation from those of other confounding factors such as habitat loss and habitat degradation difficult. Large scales also make experimentation and replication difficult. There have been only a few large-scale forest studies that have temporally and spatially replicated fragments (e.g., the Biological Dynamics of Forest Fragments experiment in the Brazilian Amazon (Laurance and Bierregaard 1997)). Manipulative experiments are usually limited to non-forested landscapes, such as microlandscapes, experimental model systems, or fields (Wiens and Milne 1989, Wiens et al. 1993, Dooley and Bowers 1996, 1998, Gilbert et al. 1998). One approach has been to approximate a true experiment by selecting existing landscapes containing natural variation in fragmentation patterns as replicates (e.g., Villard et al. 1999, Tzcinski et al. 1999). Drawbacks to this approach include the frequent necessity to define fairly small landscapes in order to increase sample size (e.g., McGarigal and McComb 1995) and inability to collect detailed demographic data across replicates. An alternative approach has been to use spatially explicit models (e.g., McKelvey et al. 1993, Fahrig 1997, 1998).

Here I use an individual-based and spatially explicit simulation model to link individual behavior and life-history variation to population-level outcomes. Such a model enables one to predict emergent properties of a population based on the behavioral responses of individuals that comprise the population. Letcher et al. (1998) created an individual-based spatially explicit model of the population dynamics of the cooperatively breeding Red-cockaded Woodpecker (*Picoides borealis*). After adjusting the Letcher et al. (1998) model to match Brown Treecreeper life-histories, I simulate their population dynamics in a landscape developed with GIS software. Although similar models have been used to explore fragmentation effects (e.g., Doak et al. 1992, McKelvey et al. 1993, Liu et al. 1995), very few have addressed dispersal behavior and dispersal mortality, and even fewer have used real landscapes.

Previously, I found Brown Treecreepers in my study area were declining because isolation of woodland fragments disrupted dispersal, resulting in low recruitment (Chapter 3). Furthermore, Brown Treecreeper distribution within woodland patches was affected by the degree of fragmentation in the surrounding landscape (Chapter 5). The most commonly advocated management action to counter isolation of habitat patches is corridor development. The implicit assumptions for this action are that isolation arises from a lack of physical connectivity and that corridors can mitigate isolation by reestablishing connectivity. However, this reasoning has been criticized because it is movement, not necessarily a physical connection, that is required to mitigate isolation effects (Simberloff et al. 1992, With 1997). Furthermore, dispersal could be disrupted through a variety of mechanisms indirectly related to the larger gaps between habitat patches in fragmented landscapes, such as reduced clumping of patches or the presence of inhospitable or low quality habitat in gaps. Therefore, knowing that fragmentation is causing groups to be isolated is not sufficient information to make correct management decisions. Knowledge of the mechanisms underlying isolation effects is necessary. For example, if the matrix is a barrier to movement, then corridors of suitable habitat could be a viable management option. Yet if the matrix composition does not influence dispersal success relative to the influence of the dispersion of patches, then retaining or creating patch clumping is appropriate.

Here I ask the following questions: What is the relative importance of distance between territories and clumping of territories in Brown Treecreeper declines? Can matrix composition account for the pattern of Brown Treecreeper declines? I addressed the first question by comparing two movement rules. The first rule (Random) allowed each bird to go in a random direction and continue in a straight line. Thus, dispersing birds had to contend with the probability of selecting the “best” direction and with the distance to the nearest vacancy. The probability of selecting the “best” direction increases with territory clumping (Figure 4-1). The second rule (Neighbor) allowed each bird to go in the direction of its nearest neighbor and then continue in a straight line. Because territories were highly aggregated (because of high budding rate) and much of the contiguous habitat was linear, this rule maximized the probability of selecting the “best” direction, leaving birds to contend with the effects of distance. In other words, the Neighbor rule increased the searching efficiency of dispersers, thus allowing any effects of fragmentation to arise primarily through the distance between groups. I addressed the second question by comparing three mortality rules applied to dispersing birds. Under the first rule (Constant), each dispersing bird was subjected to a constant mortality rate. Under the second rule and third rules, disperser mortality rate was varied based on landscape composition according to two functions (Cubic 7 and Step 20) (see below).

METHODS

Field study - Study area: The study site is comprised of Eucalyptus woodland patches within a 1500 km^2 region surrounding the town of Armidale, in the New England Tablelands of northeastern New South Wales, Australia, (30^o 27’ S 151^o 13’ E) (Figure 4-2). The study area straddles the Great Dividing Range, with an elevation ranging from 730 to 1300 m and is described in detail in Chapter 2.

Temperate *Eucalyptus* woodland communities are among the most poorly conserved ecosystems in Australia with approximately 70-95% of various woodland types having been replaced by agriculture and pasture (Yates and Hobbs 1996). In the landscape of the New England Tablelands, there is a gradient of tree densities ranging from completely cleared land to forests. With the aid of aerial photographs (1992, 1994) and topographic maps (each 1:25000), I used a geographic information system (ArcInfo) to digitize covertypes within the study area. Barrett et al. (1994) and Barrett (1995) found that the Brown Treecreeper occurred in woodland patches as small as 9 ha. For the purposes of this study, we used a map of woodland and forest patches greater than 10 ha (Figure 4-2). I categorized the landscape covertypes by 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 (woodlands and forests). Urban areas, lakes, and surface mines were categorized as cleared land. Two other categories were based on slope: woodlands and forests on steep slopes and cliffs were classified as steep woodlands and forested gorges, respectively. Brown Treecreepers do not breed in steep woodlands and forested gorges (Keast 1957, Noske 1982a,b).

Patch connectivity: In a landscape with intact woodland patches of various sizes and locations in a complex matrix of pastures, how does one decide what is fragmented and what is not? I decided to distinguish fragmented habitat from contiguous habitat based on patch connectivity rather than patch size because earlier studies showed that Brown Treecreepers are isolation-sensitive rather than area-sensitive (Chapter 3). I used ArcView to compute connected patch size, a measure of patch connectivity, for each patch. Connected patch size was measured as the total area of the set of patches with less than 200m gaps between them that included the focal patch. A totally isolated patch had a connected size equal to its patch size, whereas highly connected patches had connected patch sizes uncorrelated with their individual patch size. I used this measure to divide the patches into two categories: contiguous or connected (connected patch size $\geq$ 2,000 ha) and fragmented or unconnected (connected patch size $\leq$ 600 ha).

Brown Treecreeper demographics: I used data from the population of Brown Treecreepers inhabiting the study area to estimate many of the parameters of the model. Research on this population began in 1992 (Walters et al. 1999), with some additional data collection in 1995 (J. Walters, personal communication), and continued from 1996-1998 (Chapter 2). Over 50 groups were monitored, and approximately 85% of adults and 84% of offspring were marked with unique color combinations and aluminum bands for the Australian Bird and Bat Banding Association. Further details of population monitoring can be found in Chapters 2 and 6. In the study area, Brown Treecreeper family groups defended territories averaging 4.5 ha, and ranging from 1.1 to 10.7 ha (Chapter 2).

The life history of the Brown Treecreeper is best modeled based on status classes of individuals with annual probabilities of transition between status classes. Female fledglings that survive usually disperse, and only rarely remain as helpers. Dispersers eventually find a breeding vacancy or die. Male fledglings that survive rarely disperse, instead they remain as helpers on their natal territory. Males may eventually obtain a breeding vacancy by either inheriting their natal territory or budding (Noske 1982a, Walters et al. 1999, Doerr and Doerr 2001). Generally, a breeder retains its status until death. Many males that become breeders through budding continue to help at their natal territory as well (Noske 1982a, Walters et al. 1999, Doerr and Doerr 2001). It is unknown how this affects group reproductive success, and this trait was not included in the model.

Previous research compared demography of groups in contiguous and fragmented habitat (Walters et al. 1999, Chapter 2)(Table 4-1). There was no difference in the average number of offspring produced per breeding group in fragmented and contiguous habitat or in adult female mortality rates. Yet, the number of female breeders in fragments decreased over time due to low female recruitment from within patches and between patches. Also, the maximum female dispersal distance was lower in fragmented habitat. Finally, there were no solitary males in contiguous habitat because breeding vacancies filled immediately, whereas in fragmented habitat many males remained solitary, failing to recruit females (except through experimental manipulation) for long periods.

Modeling - Model structure: the model was developed to simulate the population dynamics of Red-cockaded Woodpeckers and is described in detail in Letcher et al. 1998. The model is an individual-bases simulation because it tracks the life of each simulated bird as it interacts with other simulated birds and responds to the landscape. The model has a seasonal time step (3 months). Reproduction and mortality are based on age- and status-dependent relationships and specified transition probabilities (Figure 4-3) (see Brown Treecreeper Demographics above) (Table 4-2). During a time step, an individual can be either a fledgling, disperser, breeder, or (for males only), helpers or solitary depending on their age and whether they have found a breeding site (territory). Transistions between status classes depend on local availability of breeding vacancies and on competitive ability of individual birds. Male territory competition was based on two rules: closest male wins and if there is a tie, the older bird wins. Helpers always win over dispersing males. Competition for female vacancies followed the same rules, except that females did not fill a vacancy that contained her father or son.

The original model was modified by J. Priddy in several ways for application to Brown Treecreepers. First, the landscape was interfaced with a GIS map so that the initial territory distribution could be constrained by the distribution of woodland habitat. In this Brown Treecreeper model, territories are circles with fixed x-y coordinates assigned randomly to woodland habitat prior to the beginning of each run. The size of each territory depends on the proximity to surrounding territories with a pre-selected maximum of approximately 10 ha (175 m radius) and a minimum of approximately 5 ha (125 m radius). Also, when specified, the mortality rate of dispersing birds could change with landscape composition and new territory formation (described below) could be restricted to woodlands.

The model also was modified so that new territories could form though budding at a pre-selected rate. The budding process selects an occupied territory to bud, the potential bud is subjected to a habitat criterion (must fall within woodlands), then the oldest helper obtains the new budding territory with the status of solitary male. There are many emergent and stochastic factors that may result in a lower budding rate than specified.

The initial model had only one dispersal movement rule (Random), by which a random direction was selected for each dispersing bird, who continued in that direction until dying or successfully completing dispersal (i.e., becoming a breeder on a territory) (Figure 4-4). For this paper, a second movement rule was added by which dispersal begins by a bird moving in the direction of the closest neighboring territory and then continuing in that direction until death or successful dispersal. This movement rule, Neighbor, increases the searching efficiency of dispersers, thus allowing any effects of fragmentation to arise primarily through the distance between groups.

Finally, the initial model had one dispersal mortality rate for male dispersers and one mortality rate for female dispersers. For this paper, two more mortality rates for all dispersers were added to the model. The model has a seasonal time step (3 months) and each dispersing bird has a seasonal search range, within which a bird can compete for territory vacancies. Each habitat type in the GIS map of the study area has an assigned habitat value (Table 4-3). Each season the model computed the average habitat value in each bird's dispersal search range. I made dispersal mortality dependent on landscape composition by multiplying the baseline seasonal mortality rate by this value. Seasonal mortality rates were related to annual mortality rates by the following equation: seasonal mortality rate = 1 – [(1-annual mortality rate)^$^{1/4}$]. Mortality rate could vary with habitat types in an infinite number of ways. Under the Constant rule, the mortality rate was equal in all habitat types. To create two additional mortality rates, I selected two functions that link seasonal mortality rates with habitat type. Both functions had a flat section (multiplier 1) from 150 to 200 that represented the approximate habitat quality present where the original baseline mortality estimates were made (Figure 4-5). The Cubic7 function simulates a mild effect of landscape matrix on dispersal mortality by creating a slight decrease in mortality for extremely good habitat, and a fairly rapid increase in mortality as habitat gets worse, ending with a maximum multiplier of approximately 7 for 0% habitat quality. The Step20 function simulates a more severe matrix effect by imposing a mortality multiplier of 20 for all habitat less than optimal quality (i.e., < 150).

I used parameter estimates from Red-cockaded Woodpeckers (see Letcher et al. 1998) as a substitute for those that I could not estimate for Brown Treecreepers. Red-cockaded Woodpeckers and Brown Treecreepers have similar life-histories (e.g., they are both cooperative breeders, both insectivorous, both cavity nesters). The initial age distribution was based on woodpeckers for similar reasons. Letcher et al. (1998) report that the model is not sensitive to initial age distribution. Table 4-2 summarizes the input parameters. All input parameters were the same for birds in fragmented and contiguous habitat because, as mentioned above, reproduction and mortality rates did not differ between these populations in the field (Chapter 2). Demographic stochasticity was included in the model in order to create a variance around the number of fledglings produced from successful nests.

Model Runs: At the start of each model run, territories were placed randomly throughout woodlands until they covered approximately 10% of woodland area, creating a pattern similar to that observed in the field. Territory distribution changed over the duration of each run as territories went extinct (after being unoccupied for > 5 years) and as territories formed by budding from existing territories. The original model was not sensitive to initial conditions (Letcher et al. 1998). Therefore, I allowed all runs to begin with the same initial conditions, by which 90% of all territories were assigned a breeding male and female, 50% of breeding groups were assigned a helper, and 10% of territories were assigned solitary males.

I extracted several output variables from the simulation output for comparison of simulated contiguous and fragmented populations with field observations. Specifically, I examined population size, measured as number of breeding pairs, the population size at the end of each run, the maximum female dispersal distances, and the percentage of long-distance dispersal events (> 3.5 km). Also, I compared the proportion of solitary males that recruited a female before dying.

I present results from 7 sets of model runs, using 20 replicate runs for each model set, in order to explore model behavior and how territory spatial arrangement and matrix composition affect population dynamics in contiguous and fragmented habitat. Initially, the duration of all runs was 100 years. Because territory clumping gradually departed from initial conditions and became unrealistically high by 45 years, I examined output from the first 40 years of each run. Modeling short time periods often is preferable in order to minimize error propagation (Bessinger and Westphal 1998).

The first set of runs constituted a sensitivity analysis to determine which parts of the model had the largest effects on population behavior under nominal conditions. I evaluated the sensitivity of overall population growth rate (λ) to the input parameters. I varied 9 model parameters (see Table 4-2) by ±10% independently in separate runs, and ran 20 replicate simulations of each condition. The sensitivity of the model to changes in each parameter was calculated as $(y_+ — y_-)/(0.2 * y_o)$ where y_+ and y_- are the output values (λ) with parameters adjusted ±10%, respectively, and y_o is the mean output value using unadjusted parameters. Mean output values were computed as the average result of 20 baseline runs with the Random movement rule and the Constant mortality rule. Sensitivities greater than one or less than negative one indicate that changes in the parameter had greater than proportional effect on the outcome of the model.

The next 6 sets of runs comprised a factorial design with the two movement rules and three mortality rules: Random-Constant, Random-Cubic7, Random-Step20, Neighbor-Constant, Neighbor-Cubic7, and Neighbor-Step20. All output values were computed as the average (± SD) of 20 replicate runs. I used a three-factor ANOVA, with location (contiguous and fragmented), movement rule (Random and Neighbor), and matrix effect (Constant, Cubic 7, and Step 20) as factors to examine differences among sets of runs.

RESULTS

Proportional sensitivity analysis - The performance of the model was robust to changes in parameter vaules. Proportional sensitivities of (λ) were all less than 0.05 and greater than –0.25 (Figure 4-6). Female and male fledgling mortality, female breeder mortality and male solitary mortality had the largest (negative) sensitivities. Negative sensitivity means that an increase in the parameter results in a decrease in lambda.

Mean population size – Initial group size and group productivity did not differ between contiguous and fragmented habitat since the same model rules were applied to all territories, regardless of location. Nevertheless, populations in contiguous habitat remained relatively stable or increased relative to populations in fragmented habitat within each run (Figure 4-7). Populations in fragmented and contiguous habitat always did better under the Neighbor rule than the Random movement rule for each dispersal mortality rule, and worse under the Step20 mortality rule than the other mortality rules.

Mean population size at Y40 – Even though the number of breeding pairs in fragmented habitat always started out higher than the number in contiguous habitat due to the relative amount of habitat, the fragmented population always became smaller than the contiguous population by the end of runs (Figure 4-8). Population size after 40 years was lower in fragmented than contiguous habitat (Table 4-4, location effect), especially with the Neighbor movement rule (Table 4-4, location*move effect) and without any matrix effects (Table 4-4, location*matrix effect). Population size after 40 years was lower with the Random movement rule (Table 4-4, move effect), and lowest with the Step20 disperser mortality rate (Table 4-4, matrix effect).

Movement between fragmented and contiguous habitat – I defined contiguous and fragmented habitat based on connectivity, however a small percentage of birds (between 3-14%) successfully dispersed between contiguous and fragmented habitat during each run (Figure 4-9). When I restricted further analyses of dispersal events (i.e., female dispersal movements and long-distance movements) to only those dispersing birds that did not cross between contiguous and fragmented habitat, results did not differ. Therefore, I report results using all successful dispersal events in the following analyses.

Female dispersal distances - The average maximum dispersal distance of females did not differ between fragmented and contiguous habitat (Figure 4-10)(Table 4-4, location effect), yet was greater with the Neighbor movement rule (Table 4-4, move effect) and with Constant mortality rates (Table 4-4, matrix effect). Only runs with the most severe matrix effect (Step20) produced maximum dispersal distances as short as those observed in the field (Figure 4-10).

Long-distance dispersal events – Short-distance dispersal events were always more frequent than long-distance dispersal events. The proportion of long-distance movements was higher in fragmented habitat than in contiguous habitat (Table 4-4, location effect) (Figure 4-11). This difference was most apparent with the Random movement rule (Table 4-4, location*move effect) and the Constant dispersal mortality rate (Table 4-4, location*matrix effect), and least apparent with an extreme matrix effect (Step 20) (Figure 4-11).

Proportion of solitary males that recruit a female – Solitary males in contiguous habitat were always more likely to recruit a female breeder than solitary males in fragmented habitat (Figure 4-12)(Table 4-4, location effect). Solitary males were more successful in recruiting females when the Neighbor movement rule was in effect than when the rule was Random (Table 4-4, move effect), and without matrix effects than with matrix effects (Table 4-4, matrix effect) (Figure 4-12). Under the Random rule, between 45-60% of solitary males in fragmented habitat died without recruiting a female (Figure 4-12). Under the Neighbor rule, differences between fragmented and contiguous populations were less extreme (Table 4-4, location*move effect). Runs using the Random movement rule and the most severe matrix effect (Step20) created the largest differences between populations in fragmented and contiguous habitat, and most closely matched field observations.

DISCUSSION

My goal was to use a spatially explicit model to determine what movement patterns might account for the decline of Brown Treecreepers in the New England Tablelands. The size of the simulated population over time was highly sensitive to the dispersal movement rule and to the dispersal mortality rule. Furthermore, all differences in population size between fragmented and contiguous habitat were a direct result of differences in female dispersal success and recruitment, rather than birth and death rates. From this I draw several conclusions which I will discuss below. First, the Random rule better matched field observations, suggesting that the distribution of woodland habitat can severely restrict the search efficiency of Brown Treecreepers. Second, the severe matrix effect most closely matched field observations, suggesting that Brown Treecreepers may experience high mortality in non-woodland habitat. Third, the relative influence of dispersal on population size was dependent on territory spatial arrangement. Finally, more research is needed concerning movement patterns and dispersal decisions in order for model results to be meaningfully applied to conservation actions such as reserve design at a landscape scale.

Movement Rules - The importance of territory clumping in the model is ultimately linked to search strategies. Clumping of territories allows dispersal success and recruitment under simple search rules, whereas dispersal success among non-clumped territories requires complex search rules, such as Neighbor. Turner et al. (1993) reached similar conclusions in an analogous simulation of foraging of ungulates in Yellowstone National Park. They found that the arrangement of resources (clumped or random) mattered only when movement was limited. This matches intuitive expectations that searching for a resource (such as food or a territory) is easier when that resource is clumped. Yet, if an organism can employ an efficient or complex search strategy, the distribution of resources becomes less important.

Mortality Rules - In this model, matrix composition affected dispersal distances and success, leading to impacts on population persistence. Although long-distance dispersal events occurred at fairly low frequencies even among contiguous populations, matrix effects further decreased the frequency of long-distance movements and thus decreased female recruitment and population size. I only modeled two matrix effects and more extreme effects are possible. For example, cleared land may be a complete barrier to Brown Treecreeper movements, rather than a great risk. As a barrier, cleared land may affect even short-distance movements.

There is anecdotal evidence that non-forested habitat is a barrier to movement. In 1996, a field assistant and I fitted 2 helper males with radio-transmitters and moved them from their respective resident territory to territories 2 km away. One male was moved such that the straight-line distance between the two territories was composed of woodlands. The other male was moved such that the straight-line distance between the two territories was composed of sparse trees and cleared land, yet a circuitous return path though woodlands was possible. I anticipated that each bird would immediately return to its territory within hours. During forays, we observed Brown Treecreepers moving at least 500m in less than half an hour. Yet, neither bird was able to return home readily. In the first case, the male lost his radio-transmitter the day after release during a fight while intruding on another Brown Treecreeper territory. We detected the bird back on his territory 4 days after release. He was released in a narrow, linear habitat and therefore had an even chance of selecting the correct direction as a return path. In the second case, the bird forayed up to 1 km in every direction that was comprised of woodlands, but he never entered non-woodland habitat. On the fourth day after release, we could not locate the bird and he never returned to his original territory. These observations reveal the limited movement behavior of male Brown Treecreepers. Unfortunately, I can not determine whether this inference applies to females, whose dispersal behavior is more critical to population dynamics than that of males.

Dispersal success and population size - Other simulations (e.g., McKelvey et al. 1993, Letcher et al. 1998) also found that dispersed territories resulted in lower population growth than clumped territories due to more efficient searching by dispersers among clumped territories. These studies illustrated the importance of dispersal behavior to population dynamics. However, dispersal behavior is not always important to population persistence. South (1999) showed that errors in estimating dispersal success are not equivalent to errors in predicted population viability because dispersal success did not always have an effect on population persistence or patch occupancy. Pulliam et al.

(1992) and Liu et al. (1995) found dispersal to be less important to population viability than other demographic factors.

In Brown Treecreeper simulations, populations that increased quickly had a higher frequency of short-distance movements than populations that declined or increased slowly, under all movement rules, despite the fact that declining populations tended to have longer maximum dispersal distances. It appears that short-distance movements can have a greater effect on population behavior than long-distance movements. Ninety percent of movements were short-distance (< 3.5 km) and over 50% were < 1 km. Given this, it is surprising that matrix effects influenced population behavior because the matrix is more likely to affect long-distance movements than short-distance movements. In other words, I may have underestimated the importance of long-distance dispersal because the high clumping of territories creates a predominance of successful short-distance movements. If territories were less clumped, longer-distance movements would be more common, creating a situation where matrix elements could more strongly affect dispersal success. Under another scenario, if high stochasticity were to cause local population extinctions, long-distance movements would be necessary for regional population stability.

Search rules - My findings highlight the need for more research concerning movement patterns and dispersal decisions in order for model findings to be meaningfully applied to conservation. Most research concerning search paths has been on invertebrates (see Wiens and Milne 1989, Turchin 1998), but it is unclear how relevant or similar invertebrate movement rules are to vertebrates, particularly birds. Birds appear highly mobile under some circumstances, such as during migration, but even migrants appear constrained by some landscape features during short-distance movements (Desrochers and Hannon 1997, StClair et al. 1998). Without more information on how birds move through complex landscapes, the degree to which matrix composition contributes to isolation effects will remain uncertain.

Territory arrangement - This model, like most others, created isolation effects through a combination of movement rules and territory spacing. Therefore, the relevance of the results will depend not only on our knowledge of search patterns, but also on our knowledge of territory distribution, which has received little attention. In this model, territory spatial arrangement was not based on the actual coordinates of monitored territories, rather territory locations were determined by habitat fragmentation patterns as well as by behaviors associated with territory formation (i.e., budding).

Brown Treecreepers are highly clumped in contiguous habitat, and so the simulations presented here may be a good reflection of real dynamics in contiguous habitat. However, Brown Treecreepers were not clumped in fragmented habitat; instead most groups were the sole occupant in their patch. In order to match observed patterns, I would need to model fragmented patches as sparsely populated. During simulations, the population in fragmented habitat never decreased to within-patch densities as low as those observed in the field. To account for observed densities in fragmented habitat, habitat quality in fragments must be either highly variable naturally or recently degraded such that many areas in fragments are unsuitable woodlands. The fragmentation patterns that I mapped from aerial photographs may not be equivalent to the fragmentation patterns perceived by Brown Treecreepers due to habitat degradation or woodlands of low quality habitat. If so, then I may have underestimated habitat loss and fragmentation in the study area.

In summary, woodland fragmentation led to a non-clumped distribution of territories. Furthermore, a reduction in within-patch territory density for some other reason, such as degradation, could further reduce territory clumping. Once territories are far apart, more long-distance dispersal movements are necessary. High mortality in non-woodland habitat as well as low search efficiency when territories are not clumped result in a low frequency of long-distance dispersal and insufficient recruitment leading to population decline.

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TABLES

Table 4-1. Demographic patterns from field study (Chapter 2) and corresponding model output. Data are from 21 groups in fragmented habitat and 34 groups in contiguous habitat.

	Fragmented	**Contiguous**	**Quasi-Emergent Model Output**
Mean Group Size (no singles)	2.5	2.9	mean group size
Mean # fledglings/breeding group	1.33	1.47	mean fledglings
% Groups with > 1 successful nest	61%	62%	mean fledglings
Mean adult female mortality	22%	18%	adult female mortality
			Emergent Model Output
% Groups never lacking a female	52%	100%	% solitary males that recruit female
Max female dispersal distance	1.2	4.5	maximum female dispersal distance
% short-distance movements	100%	80%	% short-distance movements
% long-distance movments	0%	20%	% long-distance movements
% unbanded female recruits (i.e., immigrants)	0%	44%	Number breeding pairs
% banded female recruits	13%*	56%	Number of breeding pairs

*87% of breeding vacancies in fragmented habitat were filled by experimentally translocated females rather than natural dispersal

Table 4-2. Model parameters from orignial Red-cockaded Woodpecker model (Letcher et al. 1998) and Brown Treecreeper model. When possible, Treecreeper parameters were estimated from empirical data (Chapters 2 and 6). Asterisks indicate cases where Woodpecker parameters were used in the Treecreeper model. + indicates parameters included in the sensitivity analysis.

Parameter	Red-Cockaded Woodpecker	Brown Treecreeeper
Mortality		
$^{+}$Male fledgling annual mortality	0.50	*
$^{+}$Male disperser annual mortality	0.38	*
$^{+}$Male helper annual mortality	0.20	0.25
$^{+}$Male solitary annual mortality	0.34	*
$^{+}$Male breeder annual mortality	0.23	0.04
$^{+}$Female Fledgling annual mortality	0.58	0.60
$^{+}$Female disperser annual mortality	0.38	*, Figure 4-5
$^{+}$Female breeder annual mortality	0.29	0.15
Dispersal		
$^{+}$Prop. Of male fledglings dispersing	0.19	0.02
Male fledgling speed	5.1 km yr-1	*
Male disperser speed	2.3	*
Female fledgling speed	4.8	*
Female disperser speed	4.8	*
Male dispersing search range	3 km	1
Replace breeder search range	3 km	1
Female dispersing search range	3 km	1
Chance leaving in season 2	33%	*
Chance leaving in season 3	33%	*
Chance leaving in season 4	33%	*
Chance of solitary male leaving	0%	*
Male takes empty when no vacancy	100%	*
Dispersal direction	random	*, Neighbor

Table 4-2 continued.

Fecundity		
Nest failure model type	negative exponential	*
Nest failure model intercept	2.3404	0.916292
Nest failure model male's effect	-2.4295	0
Nest failure model female's effect	-1.1527	0
Nest failure model helper effect	-1.1012	0
Mean fledgling model type	negative exponential	*
Mean fledgling model intercept	2.06570	1.70575
Mean fledgling male effect	-1.18634	0
Mean fledgling female effect	-1.03431	0
Mean fledgling helper effect	0.28401	0.31901
Female nesting attempt parameter	1.14569	100
Renesting Probability	0.319	0
Initial Conditions		
%territory coverage	NA	10%
%male occupancy	100%	*
%solitary males	10%	*
%territories with helpers	50%	*
%breeding pair occupancy	90%	*
Age distribution	1990 RCW data	*
Landscape		
Scale	20 pixels per km	40 pixels per km
Size	32x24km	89.1x41.55km
Budding rate	1	7.5

Table 4-2 continued.

Miscellaneous		
Maximum bird age	15	*
Disuse time before territory removal	5	*
Emigration test forward angle	180o	*
Emigration test forward distance	100 km	*
Radial search resolution	10 per 3 km	10 per 1 km
Angular bird search resolution	21 per 360o	*

Table 4-3. Values assigned to each habitat category. Under 2 mortality rules (Cubic7 and Step20), dispersing birds sample the habitat within their season search radius. The relative (average) habitat value is used to determine seasonal mortality rate based on functions in Figure 4-5.

Habitat	Value
Woodland	255
Steep Woods	212
Scattered Trees	170
Forested Gorges	127
Sparse Vegetation	85
Cleared Land	42
Off Map Edge	0

Table 4-4. Three-factor ANOVA results based on model currencies in fragmented and contiguous habitat (location effect), under Random and Neighbor movement rules (move effect), and under Constant, Cubic7, and Step20 mortality rates (matrix effect). Bold letters indicate significant results.

Currency	**Effect**	**DF**	**F Value**	**Pr > F**
Mean population size at Y40				
	Location	1	262.44	<.0001
	Move	1	246.64	<.0001
	Matrix	2	38.76	<.0001
	Location*Move	1	30.99	<.0001
	Location*Matrix	2	5.97	0.0030
	Move*Matrix	2	11.52	<.0001
	Location*Move*Matrix	2	0.00	1.0000
Mean maximum distance				
	Location	1	0.45	0.5008
	Move	1	11.88	0.0007
	Matrix	2	455.69	<.0001
	Location*Move	1	1.52	0.2184
	Location*Matrix	2	12.54	<.0001
	Move*Matrix	2	0.68	0.5065
	Location*Move*Matrix	2	0.01	0.9862

Table 4-4 continued.

Currency	**Effect**	**DF**	**F Value**	**Pr > F**
% long-distance moves				
	Location	1	284.43	<.0001
	Move	1	132.80	<.0001
	Matrix	2	1020.12	<.0001
	Location*Move	1	64.01	<.0001
	Location*Matrix	2	60.06	<.0001
	Move*Matrix	2	22.10	<.0001
	Location*Move*Matrix	2	4.80	0.0091
% males that recruit a female				
	Location	1	392.48	<.0001
	Move	1	286.41	<.0001
	Matrix	2	53.14	<.0001
	Location*Move	1	21.30	<.0001
	Location*Matrix	2	3.92	0.0212
	Move*Matrix	2	2.20	0.1134
	Location*Move*Matrix	2	0.29	0.7458

FIGURE CAPTIONS

Figure 4-1. Schematic diagram illustrating the decreasing probability that a dispersing bird under the Random search rule will encounter a territory as territories become less clumped. In a series of time steps with a constant search radius (shaded circles in shaded rectangle), the fraction of a (dashed) circle covered by the search radius decreases as the circle size increases. Therefore, when territories are tightly clumped (within the small dashed line), a direction selected at random will likely lead to encountering another territory. When territories are not clumped (within the large dashed line), it becomes less likely that a direction selected at random will lead to encountering a territory.

Figure 4-2. Vegetation cover types in the study area. The habitat types are shown in gray scale with white representing cleared land with each darker shade representing higher tree densities: 0 trees/ha (cleared land), 1-10 trees/ha (sparse trees), 10-50 trees/ha (scattered trees), and > 50 trees/ha (woodlands and forests).

Figure 4-3. Model flowchart with annual transition probabilities for male (A) and female (B) Brown Treecreepers. Some transition probabilities were estimated from Brown Treecreeper data (Chapters 2 and 6) and Red-cockaded Woodpecker data (Letcher et al. 1998) (see Table 4-2). Other transitions do not occur at a specified rate, but emerge from the model based on local interactions and behavioral rules. Other transitions were constant during some runs and variable during other runs (see Figure 4-5).

Figure 4-4. Schematic diagram illustrating the Random search rule. Under the Random rule, a dispersing bird selects a direction at random (arrow) and continues in a straight line. Under the Neighbor rule, the initial direction of a dispersing bird is toward the closest territory (large circle). The season search radius is the cloud of black points. Habitat values are sampled at each point with the search radius and averaged to obtain a measure of relative habitat quality (see Figure 4-5).

Figure 4-5. Functions establishing relationship between relative habitat quality in a bird's dispersal search radius (see Table 4-4) and mortality multiplier. Cubic 7 follows a cubic function to a maximum multiplier of 7 (A). Therefore, when the habitat quality within a bird's seasonal search radius is 0, the bird will experience a mortality rate 7 times higher than baseline (Table 4-2). Step 20 assigns a multiplier of 20 to all dispersers in an average habitat quality below 150 (B). Under the Constant rule, the mortality multiplier is always 1.

Figure 4-6. Sensitivity of population growth (λ) to proportional changes in model parameters using the Random movement rule and the Constant habitat mortality rate (i.e., no matrix effect). F = female, M = male.

Figure 4-7. Number of breeding pairs (mean ± std of 20 runs) over 40 years in fragmented (black circles) and contiguous (white circles) habitat for each set of runs. N = neighbor, R = Random movement rules, Constant, Cubic7, Step20 = dispersal mortality rules (see text).

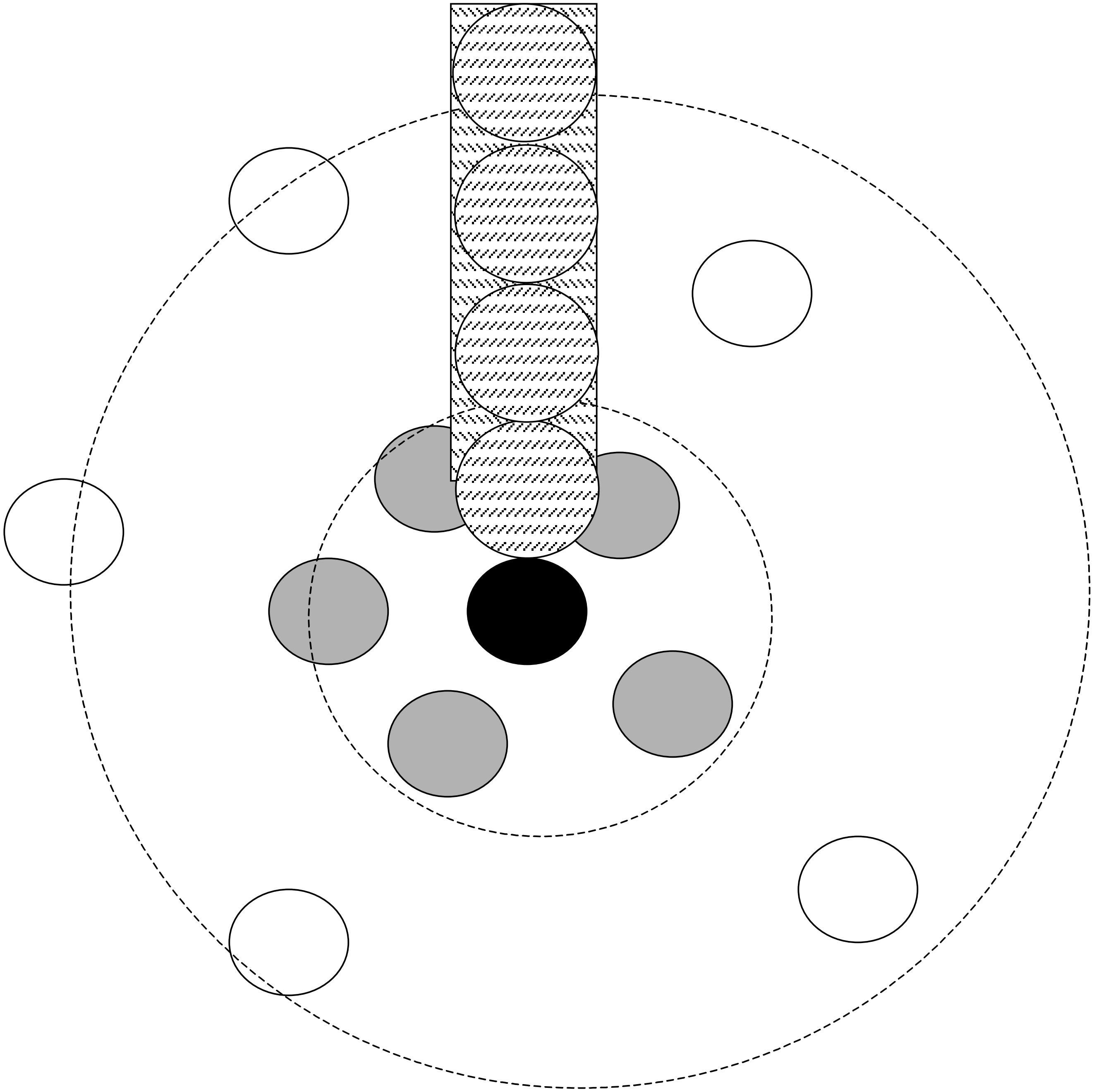
Figure 4-8. Mean number of breeding pairs (mean ± std of 20 runs) at 40 years in fragmented (black bars) and contiguous (white bars) habitat for each set of runs. N = neighbor, R = Random movement rules, Constant, Cubic7, Step20 = dispersal mortality rules (see text).

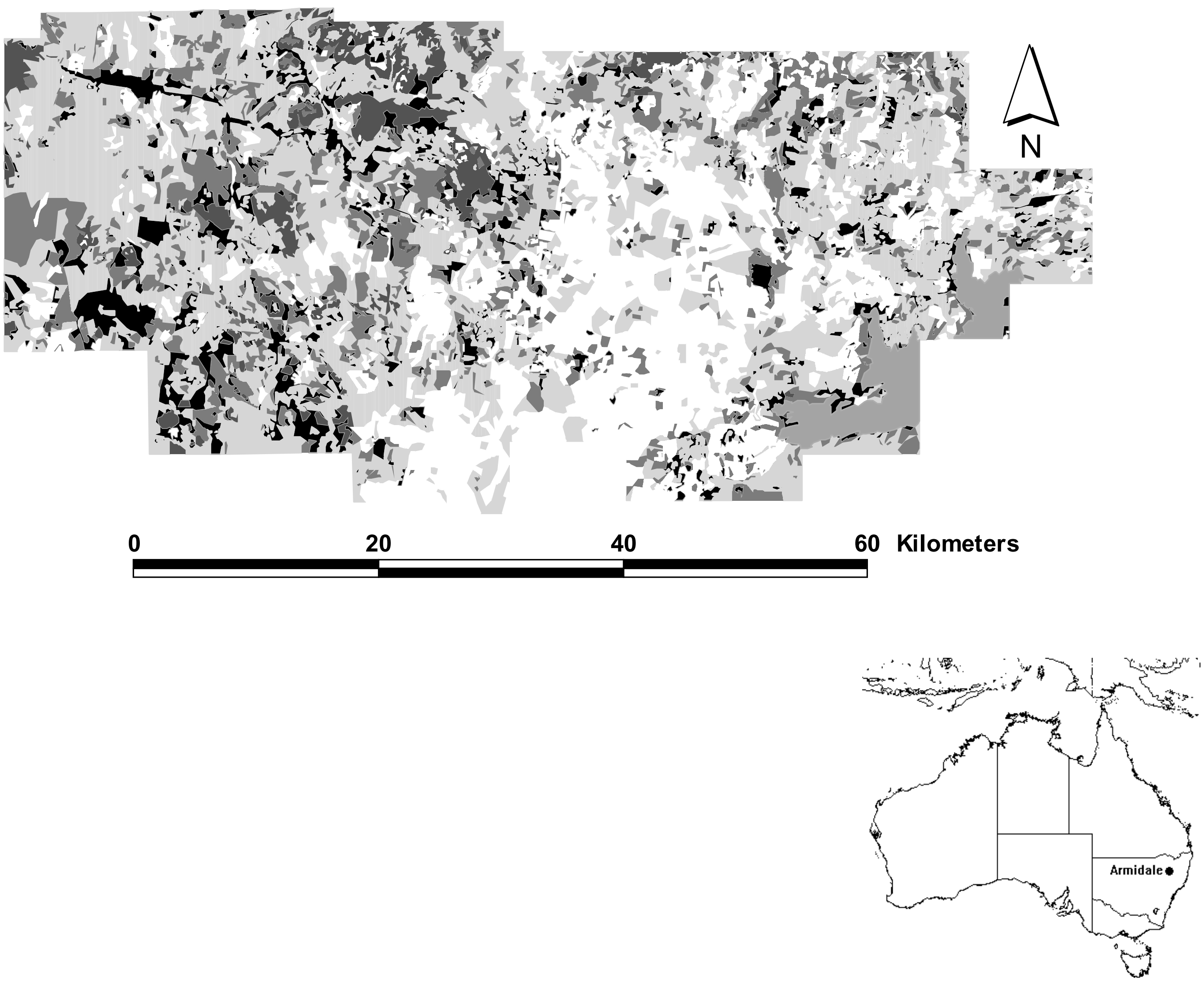
Figure 4-9. Mean percent of female dispersers (mean ± std of 20 runs) that crossed between contiguous and fragmented habitat. Cross-overs were either born in contiguous habitat and bred in fragmented habitat or born in fragmented habitat and bred in contiguous habitat. N = neighbor, R = Random movement rules, Constant, Cubic7, Step20 = dispersal mortality rules (see text).

Figure 4-10. Maximum female dispersal distance (mean ± std of 20 runs over 40 years) in fragmented (black bars) and contiguous (white bars) habitat for each set of runs. N = neighbor, R = Random movement rules, Constant, Cubic7, Step20 = dispersal mortality rules (see text).

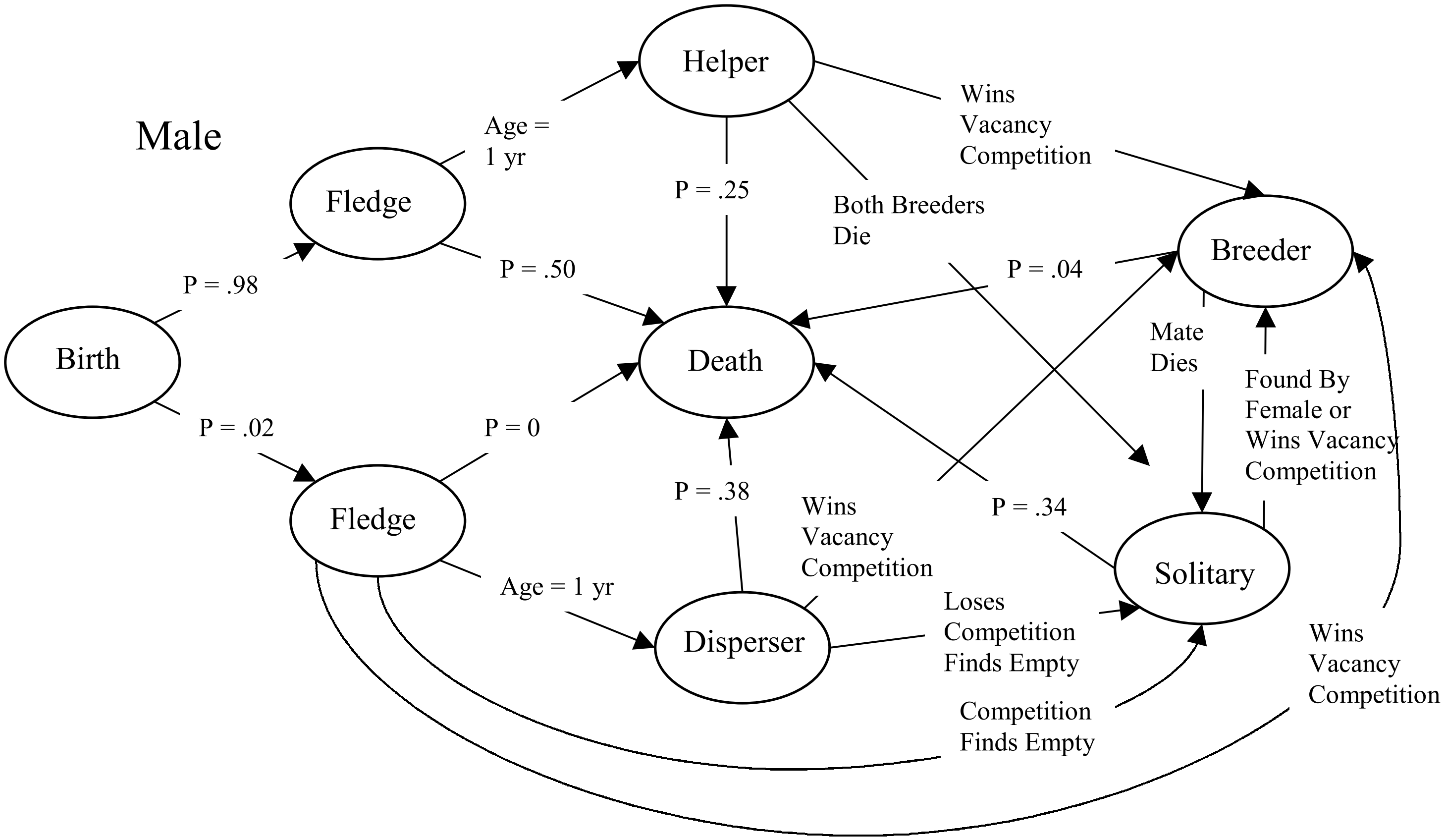
Figure 4-11. The proportion (mean ± std of 20 runs over 40 years) of long-distance (> 3.5 km) dispersal movements in fragmented (black bars) and contiguous (white bars) habitat for each set of runs. N = neighbor, R = Random movement rules, Constant, Cubic7, Step20 = dispersal mortality rules (see text).

Figure 4-12. The proportion (mean ± std of 20 run over 40 years) of solitary males that recruit a female in fragmented (black bars) and contiguous (white bars) habitat for each set of runs. N = neighbor, R = Random movement rules, Constant, Cubic7, Step20 = dispersal mortality rules (see text).

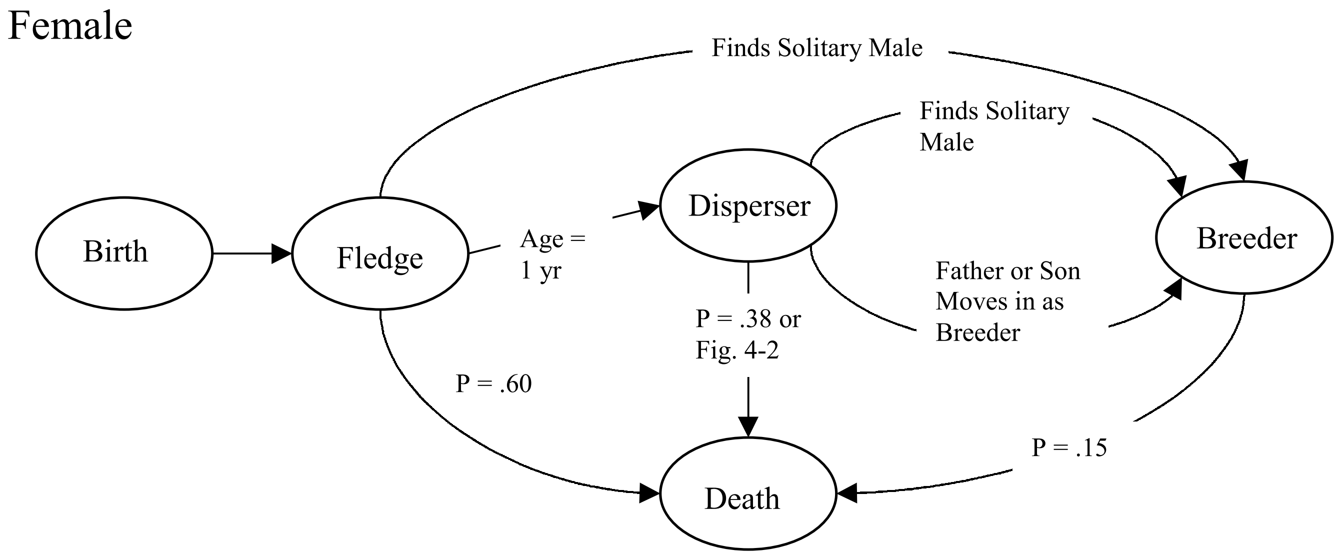


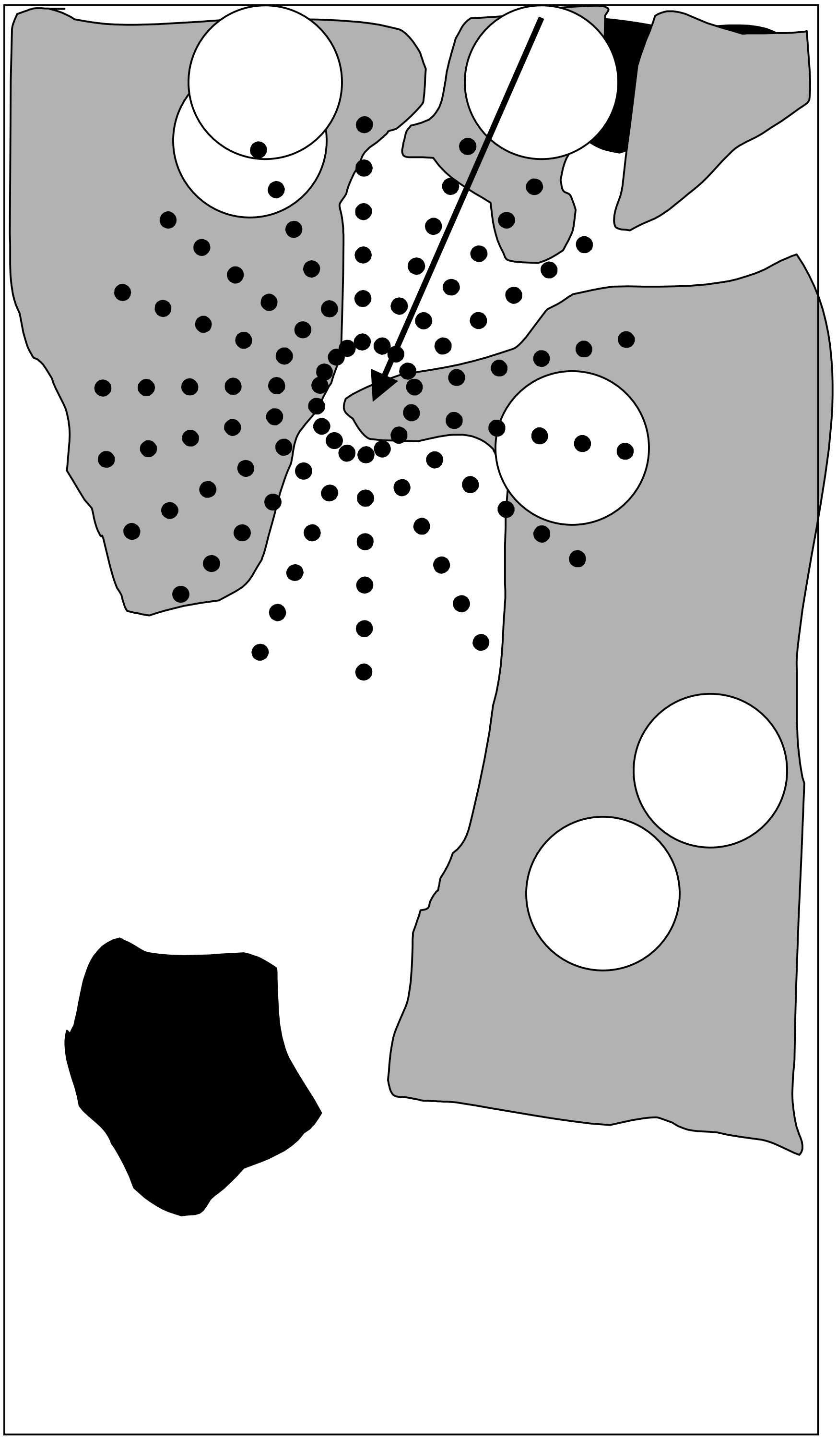

N
0
20
40
60 Kilometers
Armidale

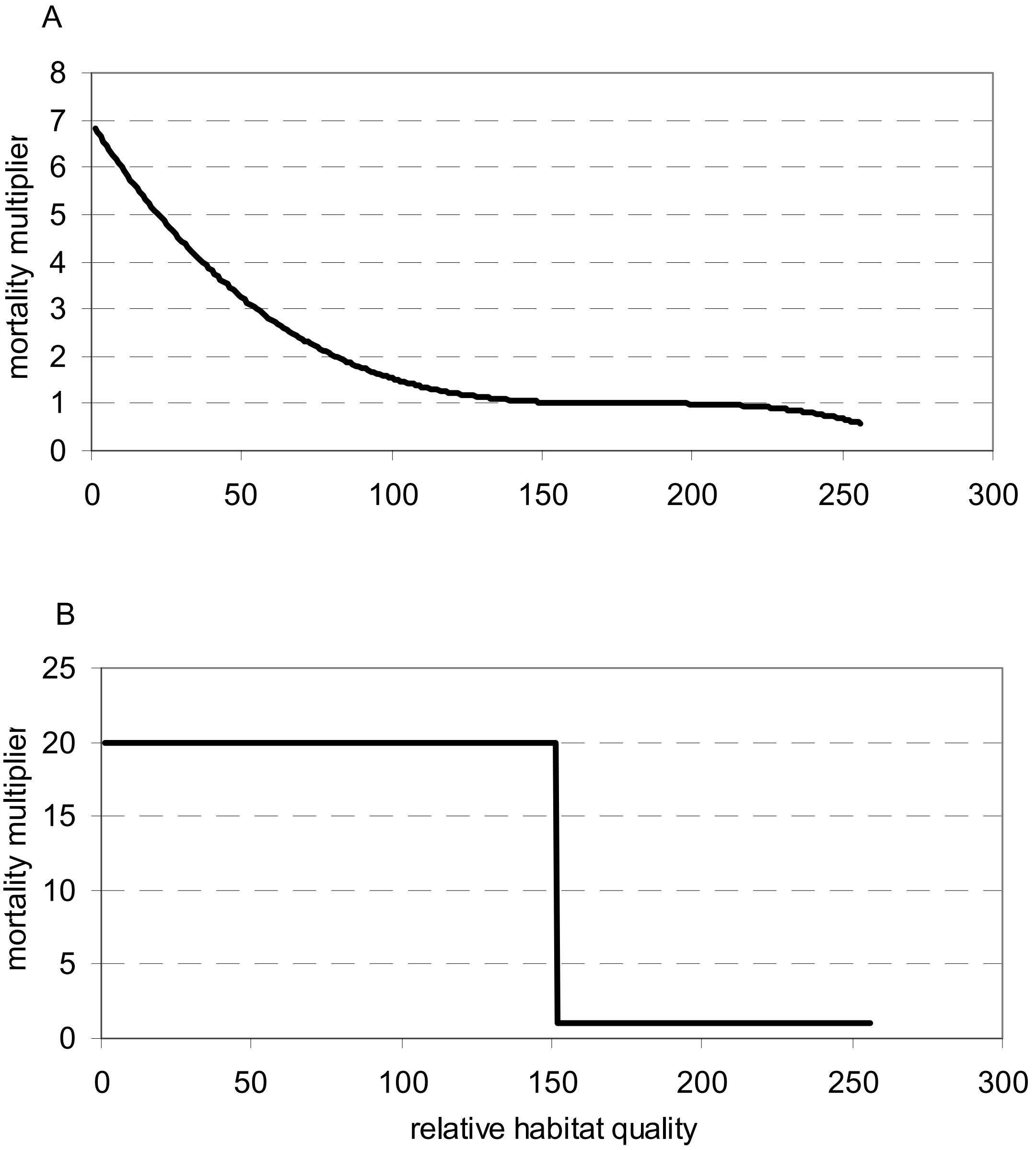
A

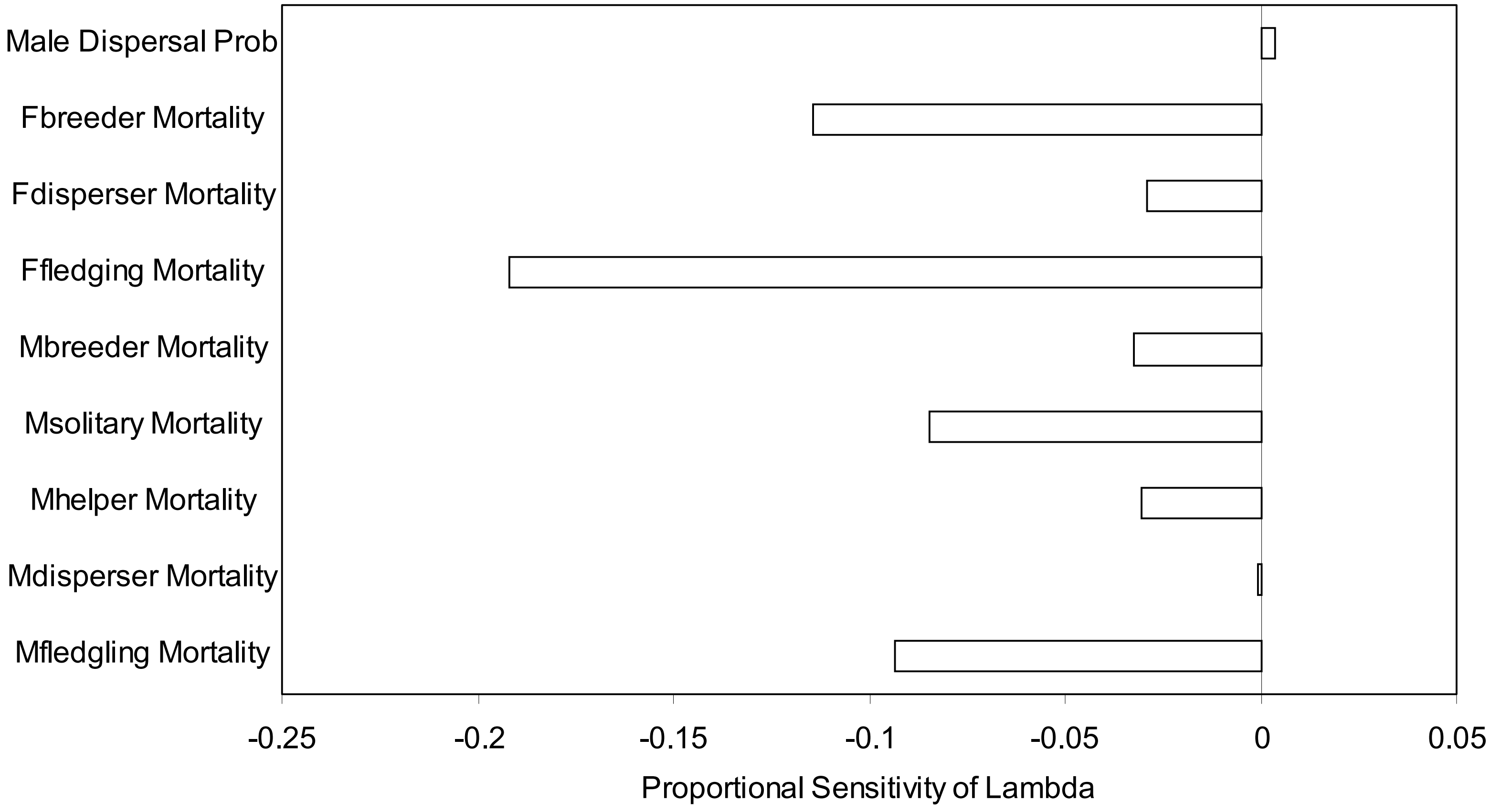

Male
Birth
P = .98
P = .02
Fledge
Fledge
Age =
1 yr
P = .50
P = 0
Age = 1 yr
Helper
Death
Disperser
P = .25
P = .38
Both Breeders
Die
Wins
Vacancy
Competition
Wins
Vacancy
Competition
P = .04
P = .34
Loses
Competition
Finds Empty
Competition
Finds Empty
Breeder
Solitary
Mate
Dies
Found By
Female or
Wins Vacancy
Competition
Wins
Vacancy
Competition

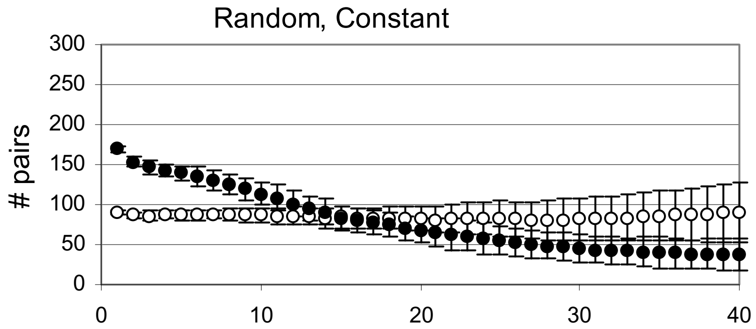
B

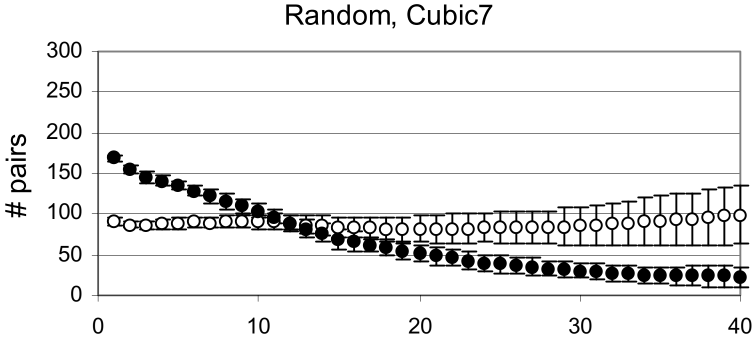

Female
Finds Solitary Male
Finds Solitary Male
Birth
Fledge
Age = 1 yr
Disperser
Breeder
Father or Son Moves in as Breeder
P = .38 or Fig. 4-2
P = .60
P = .15
Death

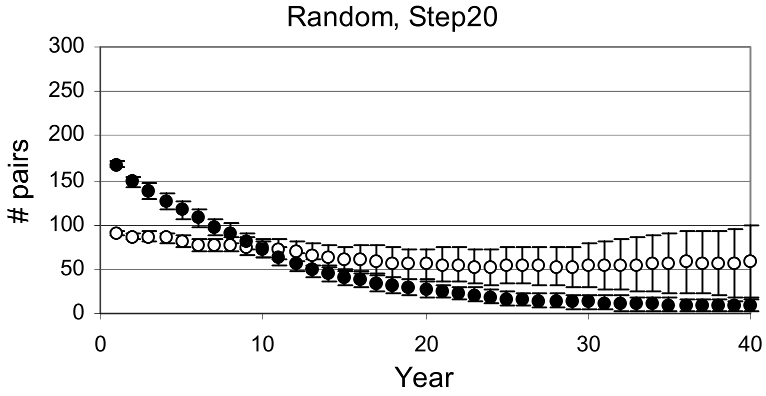


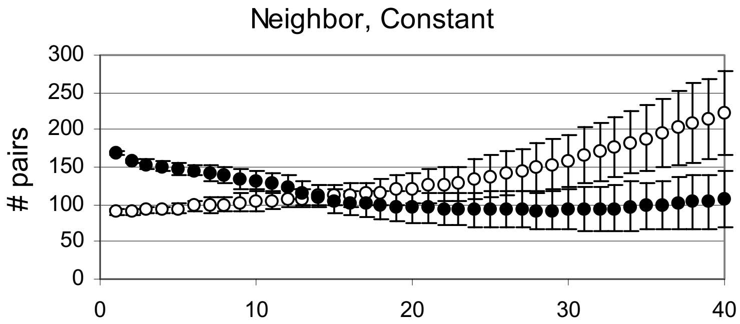

A
mortality multiplier
8
7
6
5
4
3
2
1
0
0
50
100
150
200
250
300
B
mortality multiplier
25
20
15
10
5
0
0
50
100
150
200
250
300
relative habitat quality

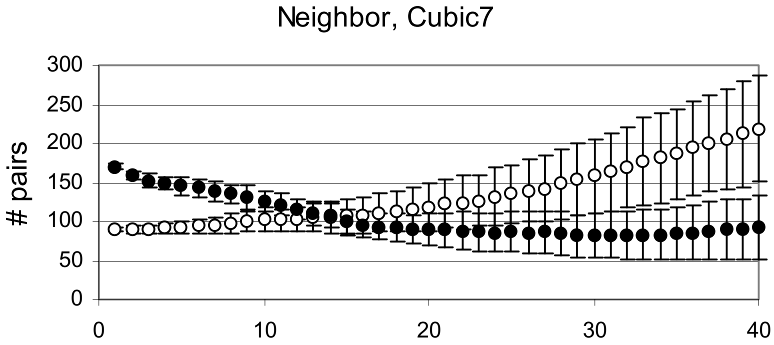

Male Dispersal Prob
Fbreeder Mortality
Fdisperser Mortality
Ffledging Mortality
Mbreeder Mortality
Msolitary Mortality
Mhelper Mortality
Mdisperser Mortality
Mfledgling Mortality
-0.25
-0.2
-0.15
-0.1
-0.05
0
0.05
Proportional Sensitivity of Lambda

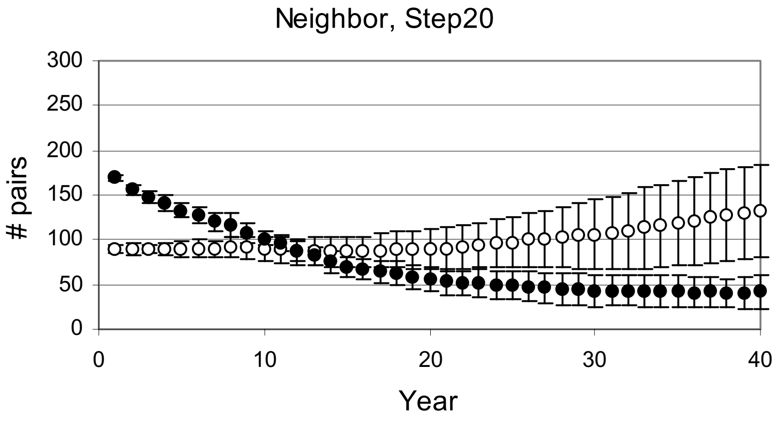

Random, Constant
pairs
300
250
200
150
100
50
0
0
10
20
30
40

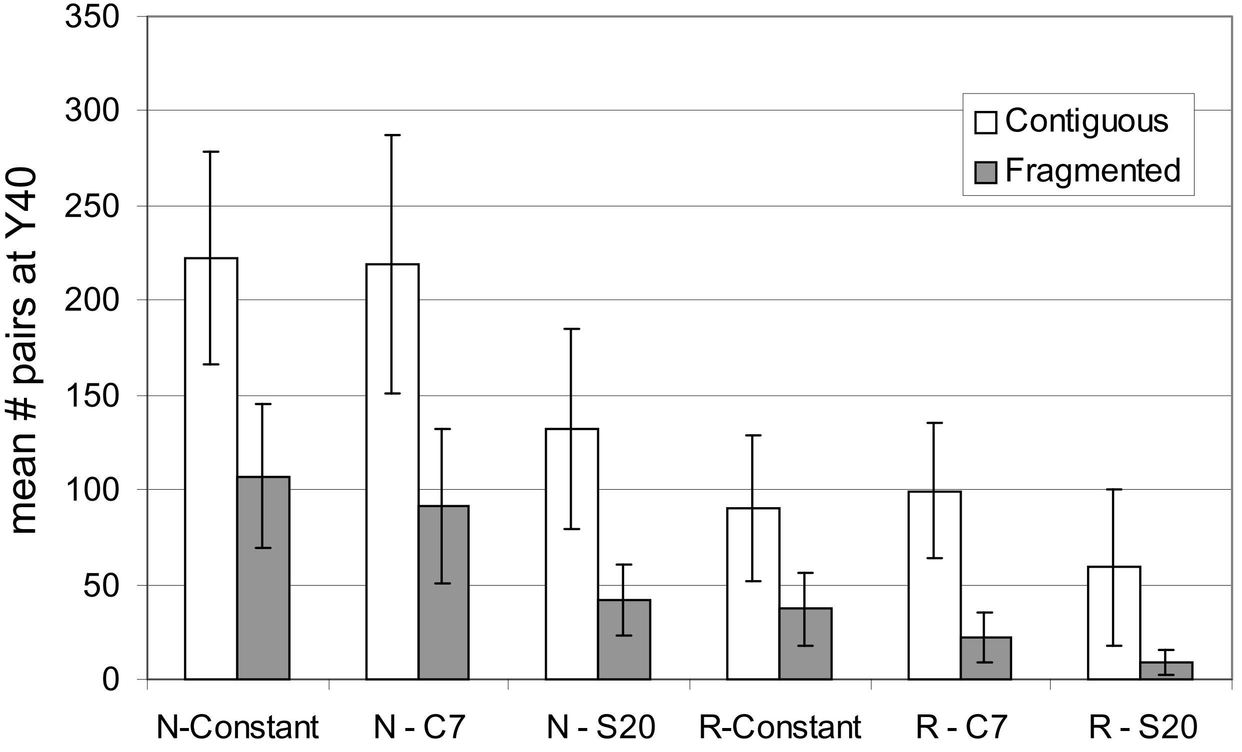

Random, Cubic7
pairs
300
250
200
150
100
50
0
0
10
20
30
40

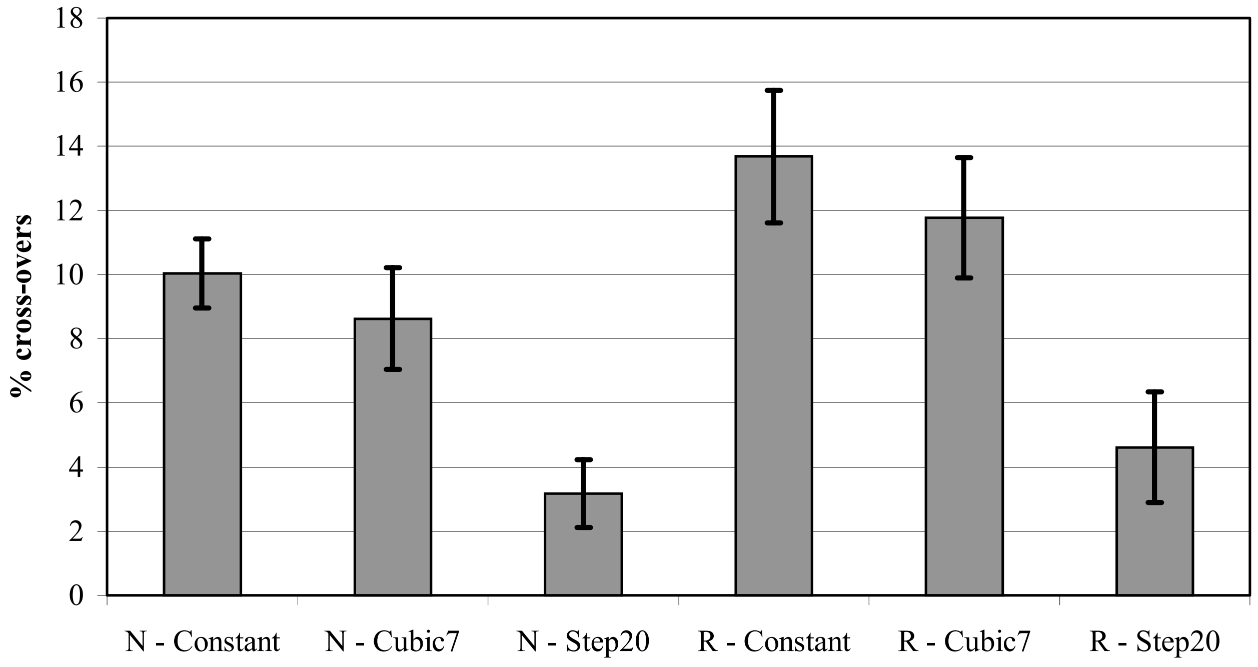

Random, Step20
pairs
300
250
200
150
100
50
0
0
10
20
30
40
Year

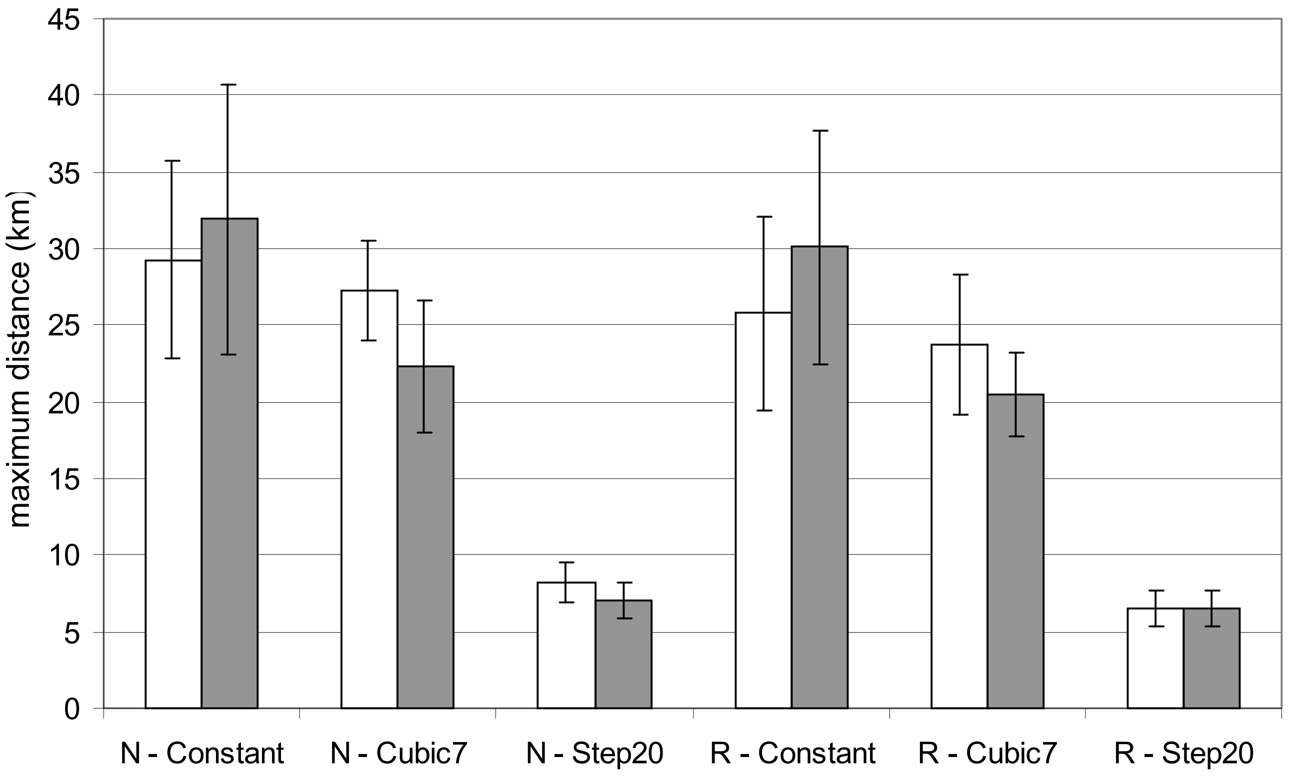

Neighbor, Constant


Neighbor, Cubic7

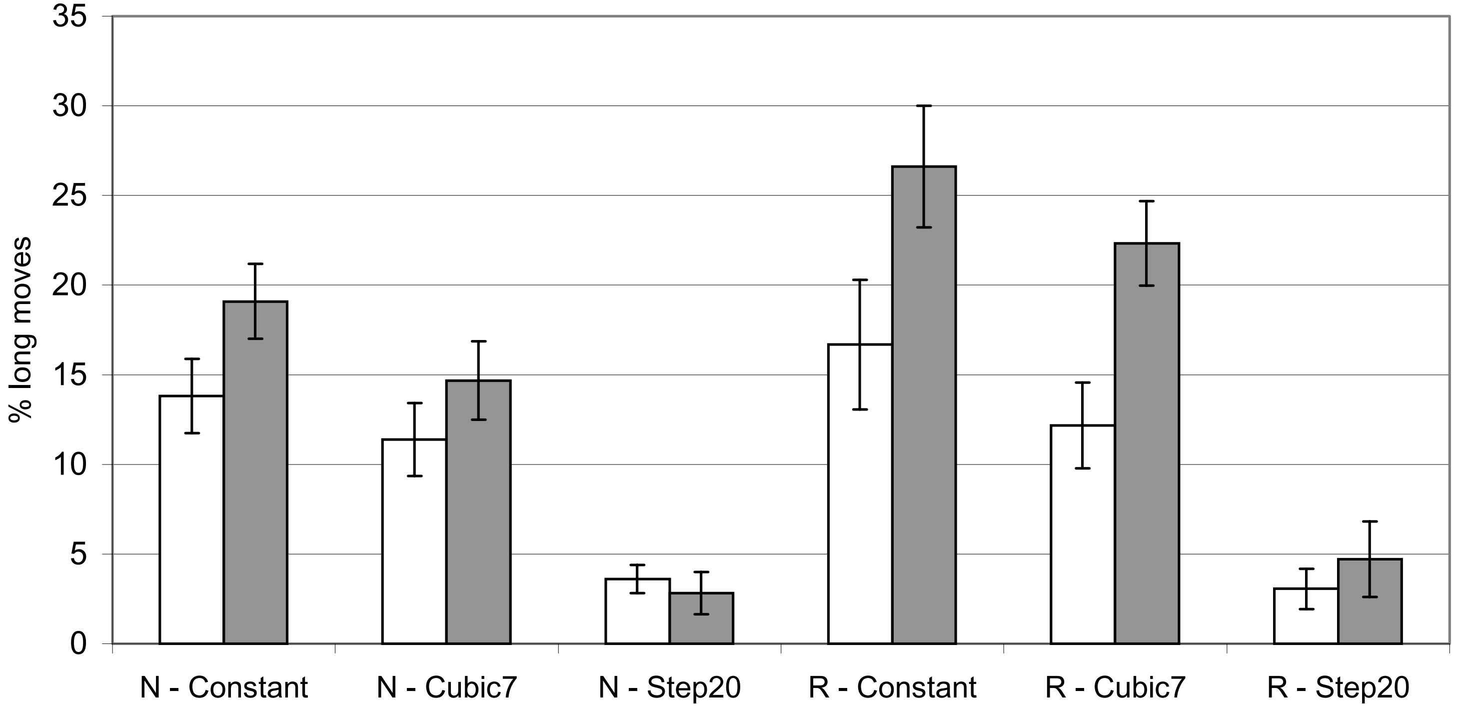

Neighbor, Step20

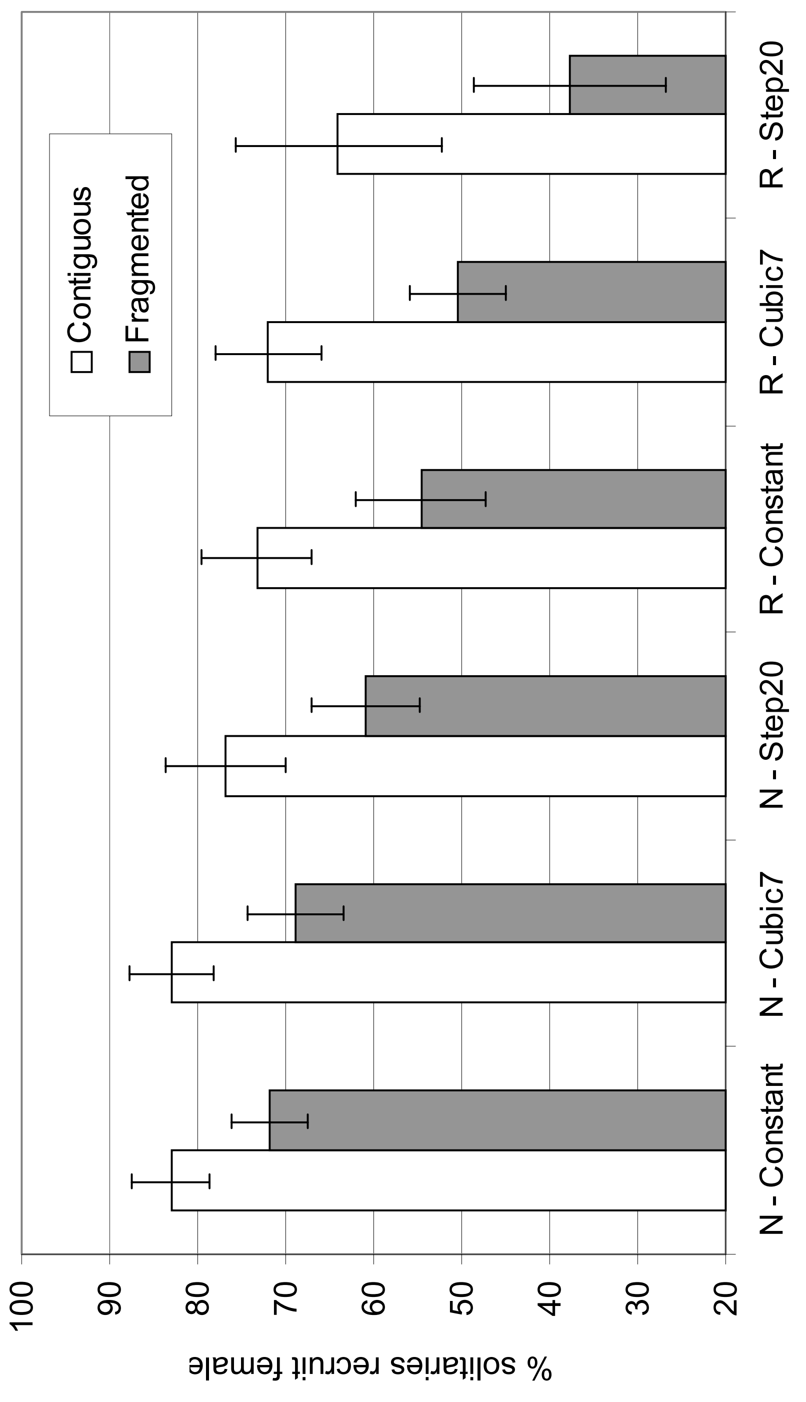

mean # pairs at Y40
350
300
250
200
150
100
50
0
N-Constant
N - C7
N - S20
R-Constant
R - C7
R - S20
☐ Contiguous
▨ Fragmented


% cross-overs
0
2
4
6
8
10
12
14
16
18
N - Constant
N - Cubic7
N - Step20
R - Constant
R - Cubic7
R - Step20



45
40
35
30
25
20
15
10
5
0
maximum distance (km)
N - Constant
N - Cubic7
N - Step20
R - Constant
R - Cubic7
R - Step20


35
30
25
20
15
10
5
0
% long moves
N - Constant
N - Cubic7
N - Step20
R - Constant
R - Cubic7
R - Step20


% solitaries recruit female
100
90
80
70
60
50
40
30
20
N - Constant
N - Cubic7
N - Step20
R - Constant
R - Cubic7
R - Step20
☐ Contiguous
▨ Fragmented

CHAPTER 5. HABITAT AND LANDSCAPE EFFECTS ON BROWN TREECREEPER DISTRIBUTION: INDEPENDENT EFFECTS OF WOODLAND LOSS AND FRAGMENTATION AT MULTIPLE SCALES

ABSTRACT

I examined the influence of local habitat features and features of the surrounding landscape at multiple scales on the distribution of Brown Treecreepers in a matrix of woodlands and pastures. The goals of this study were: (1) to determine the spatial scale at which landscape patterns influence Brown Treecreepers, (2) to determine the importance of the independent effects of woodland cover and fragmentation on the distribution of Brown Treecreepers, and (3) to employ landscape variables to improve models of Brown Treecreeper distribution based on local habitat features. Landscape patterns explained Brown Treecreeper distribution at large and small scales. Woodland fragmentation was important at a large scale while both woodland cover and fragmentation were important at a smaller scale. Excluding unoccupied sites in unsuitable landscapes (i.e., highly fragmented at a 4.5km-radius scale) 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 4.5km-radius scale may be a species-specific phenomenon in which landscape patterns affect dispersal success, or it may be an example of a general phenomenon arising from < 20% woodland cover at that scale. I conclude that understanding a time-lagged response to fragmentation requires more details than presence or absence, details such as pairing success, mortality rates, and reproductive rates. Also, as fragmentation increases, so does the need to incorporate landscape patterns into wildlife-habitat models.

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 influence wildlife population persistence and spatial distribution. Composition of avian communities has been shown to be influenced by landscape pattern (McGarigal and McComb 1995, Flather and Sauer 1996, Jokimaki and Huhta 1996, Bolger et al. 1997, Saab 1999). Fragmentation alters the distribution pattern (i.e., amount and configuration) of the habitat of interest and for this reason is expected to affect the distribution of avian species. However, most studies of habitat fragmentation occur at the scale of patches, rather than landscapes, with a few exceptions (Villard et al. 1999, Tzcersinki et al, 1999). It is unclear whether findings from patch studies can be extrapolated to the landscape level (Wiens et al.1993).

Landscape ecologist attempt to find links between landscape patterns and ecological processes (Forman and Godron 1986, Turner 1989). The demography of an avian population may respond to the pattern of habitat fragmentation via several ecological processes, including edge and isolation effects. In North America, many avian populations experience low reproductive success near forest edges (Robinson et al. 1995). Edge effects are influenced by local factors, such as predator density. However, the mechanisms responsible for edge effects are also influenced by the regional landscape composition (Donovan et al. 1997). Models of populations in fragmented landscapes generally predict that dispersal success will be affected by fragmentation (Doak et al. 1992). The logistical difficulties of studying dispersal have resulted in little empirical evidence in support of this prediction.

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. In Chapter 3, I found that unpaired males in fragmented woodland were not in poor quality habitat, rather recruitment of juvenile females into isolated fragments was disrupted. In Chapters 3 and 4, I concluded that the spatial distribution of fragmented habitat does not permit successful dispersal and recruitment, whereas the spatial distribution of contiguous habitat does. Brown Treecreepers in central New South Wales were not found in patches more than 700 m from the next nearest patch of 10 ha or larger (S. Briggs, personal communication). Therefore, Brown Treecreeper distribution appears to be influenced by landscape patterns.

Wildlife managers have focused not on effects of landscape patterns on animal distribution, but on modeling the relationship between animal abundance and local habitat features. The use of such models to correctly identify suitable habitat has been important for understanding animal ecology as well as for conservation. For example, the U.S. Endangered Species Act of 1976 is designed to protect critical habitat, even if the habitat is currently unoccupied (Schreiner 1976). Several U.S. government 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 more detailed understanding of the habitat requirements of Brown Treecreepers is needed to more effectively conserve this locally threatened species. In this case, however, an accurate habitat model can only be produced if landscape effects are considered as well. 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 confounding factor is the time delay in response of the population to landscape changes that 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).

Here I examine the distribution of Brown Treecreepers in relation to local habitat characteristics as well as to the independent effects of woodland cover and fragmentation. The goals of this study were: (1) to determine the scale at which landscape patterns influence Brown Treecreepers, (2) to determine the importance of the independent effects of woodland cover and fragmentation on the distribution of Brown Treecreepers, and (3) to use landscape variables to improve models of Brown Treecreeper distribution based on local habitat features.

METHODS

Study area and species - The study site is a 1500 km^2 region surrounding the town of Armidale, in the New England Tablelands of northeastern New South Wales, Australia, (30^o 27' S 151^o 13' E). The study area straddles the Great Dividing Range, with an elevation ranging from 730 to 1300 m. Additional details are provided in Chapter 2.

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). Brown Treecreepers are being considered for placement on threatened species lists in New South Wales and the Australian Capital Territory (H. Ford, personal communication).

Brown Treecreeper Distribution - To sample the distribution of Brown Treecreepers, 80 site locations were randomly chosen within the study area (Figure 5-1). I selected sites by superimposing a 500-m grid of points over topographic maps of the study area and randomly choosing a subset of points to become circular sample sites. Upon consulting aerial photographs and conducting ground-truthing, I excluded sites that were not in woodlands and I moved sites on the edge of woodlands so that the center of the site fell at least 150 m from the woodland 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, SD=2.5, range 1.1 – 10.7 ha, N=25) (Chapter 2).

Sites were sampled during the breeding season (1998) when Brown Treecreepers are quite vocal. A site was designated as unoccupied if Brown Treecreepers were not detected on or in the vicinity of the site. The size of Brown Treecreeper groups in occupied sites was determined while sampling habitat characteristics. Group size was recorded as one only after repeated visits verified the presence of only an unpaired male at the site.

I tested for habitat differences between sites that were occupied and unoccupied at three points in time. First, I was able to include data from the start of population monitoring, which began in 1992 (Walters et al. 1999). The second point in time included sites that were occupied and unoccupied at the end of this study in 1998. The third point in time was extrapolated based on sites that were occupied by ≥ 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 (Chapter 3). Therefore, sites with solitary birds would eventually become unoccupied and this last category represents an unspecified time in the future.

Habitat - Field assistants and I collected habitat data from 25 x25 m square plots in territories and at each randomly selected site. Randomly selected sites contained 4 plots, each 115 m in each cardinal direction from the center of the site (Figure 5-2). 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 all live trees greater than 15 cm dbh. Other studies of Australian bark-foraging passerines have profited by characterizing trees by their bark characteristics: Stringybarks (subgenus *Monocalyptus*, Series *Capitellatae*) possess a fibrous, furrowed bark; Gums (subgenus *Symphyomyrtus*, Section *Transversaria* and *Exsertaria*) shred their bark annually in long ribbons, revealing a smooth surface on which treecreepers can not easily forage; and Boxes and Ironbarks (both in subgenus *Symphyomyrtus*, Section *Adnataria*) typically possess a rough scaly bark on the trunk (Noske 1991; Stokes 1995). We classified each tree as one of the following types: Gum, Box, Stringybark, River Sheoak, Ironbark, Dead trees, and Other. River Sheoak (*Casuarina sp*.) occur in woodlands bordering rivers. For analyses, I 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 any 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, I used principal component analysis to reduce the data set 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 5-1). I used stepwise logistic regression, with significance levels of 0.5 for variable entry and 0.05 for variable retention, on the ground cover/midstory principle components, the tree principle components, and number of cavities to model Brown Treecreeper distribution (N = 80).

I 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 5-1). As above, I used stepwise logistic regression on these ground cover/midstory principle components, these tree principle components, and number of cavities to model Brown Treecreeper distribution in suitable landscapes (N = 43).

Principle 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 stringbarks. 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.

Landscape - With the aid of aerial photographs (1992, 1994) and topographic maps (each 1:25000), I used a geographic information system (ArcInfo) to create a digitized map of all woodlands in the study area. Woodlands were areas of *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. I 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 landscape buffers did not overlap more than 50% at the largest scale. I also excluded sites close to the map boundary (N = 2) so that no more than 20% of the largest buffer fell outside the map boundary. To increase sample size, I added to the randomly selected sites territories (N = 4) monitored during a related study (Chapters 2 and 6) that were not within 3.2 km of any randomly selected sites. The resulting sample for landscape analyses consisted of 44 sites (Figure 5-1). I computed Pearson's correlation coefficients for each landscape metric (*see below*) across scales. I 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 (Figure 5-2).

Trzcinski et al. (1999) showed that independent measures of cover and fragmentation can be derived from data on patch number, patch size, and amount of edge. I used Patch Analyst 2.1 (Elkie et al. 1999) to obtain measures of mean patch size, number of patches, total edge, and percentage woodland cover (%woods) within each landscape buffer around each site at each scale. Landscape metrics were highly correlated with one another (Table 5-2). I performed principle components analysis on correlation matrices of patch size, number, and edge, and used resulting factors with eigenvalues greater then 1.0 in analyses. At each scale, the first and second principle components together accounted for at least 90% of the variation in the data set (Table 5-3). At large and intermediate scales, the second principle component was highly correlated with %woods ($R^2 = 0.92$, $p < 0.0001$, $R^2 = 0.74$, $p < 0.0001$, respectively, Figure 5-3a, b), while the first principle component was not ($R^2 = 0.01$, $p = 0.48$, $R^2 =$

0.016, $p = 0.41$, respectively). Therefore, at these scales, the second principle component was equivalent to woodland cover.

At the large and intermediate scales, as the first principle 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, I computed a measure of fragmentation independent of woodland cover, namely the residuals from the (non-significant) correlation between the first principle component and woodland cover in simple linear regressions. At the smallest scale, both the first and second principle component were significantly correlated with woodland cover ($R^2 = 0.52$, $p < 0.0001$, $R^2 = 0.15$, $p < 0.0001$, respectively). At the smallest scale, as principle 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 principle component was more strongly correlated with woodland cover, I used the residuals from the correlation between the second principle component and woodland cover in a simple linear regression to create a measure of fragmentation. I performed stepwise logistic regression at each scale in independent analyses using %woods as a measure of cover and the residuals just described above as a measure of fragmentation.

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

RESULTS

Brown Treecreeper Distribution - The overall probability of a site being occupied by Brown Treecreepers was fairly low and exhibits a declining trend (Table 5-4).

Landscape Analyses – Landscapes around occupied sites tended to have fewer and larger woodland patches (Table 5-5). This is a pattern typical of less fragmented landscapes. In addition, landscapes around occupied sites tended to have more woodland cover (Table 5-5).

Depending on the analysis, woodland fragmentation at the 4.5 km-radius scale explained 21% - 33% of the variation in Brown Treecreeper distribution (Table 5-6). 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 5-6). At the 2.0 km-radius scale, only woodland cover explained a significant amount of the variation, and in only one of the 3 analyses.

Habitat Analyses – Before excluding unoccupied sites based on landscape characteristics, cavity density explained a low but marginally significant amount of variation in occupancy in 1992 ($R^2 = 0.06$, $p = 0.06$), occupancy in 1998 ($R^2 = 0.07$, $p = 0.04$), and occupancy by ≥ 2 birds in 1998 ($R^2 = 0.09$, $p = 0.03$) (Figure 5-4a) ($N = 80$). The best model of fragmentation effects on Brown Treecreeper distribution was occupancy by ≥ 2 birds in 1998 at the 4.5 km-radius scale. I included an unoccupied site in further habitat analyses if this fragmentation metric was greater than zero, corresponding to a $\geq 30\%$ probability of occupancy (Figure 5-5). I 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 was based on a residual value from a regression model using a principle component. Instead, I determined whether an unoccupied site shared a landscape similar to either a site occupied by ≥ 2 birds or a site in a suitable landscape as determined by the criterion. I 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 higher amount of the variation for occupancy in 1992 ($R^2 = 0.15$, $p = 0.02$), occupancy in 1998 ($R^2 = 0.15$, $p = 0.02$), and occupancy by ≥ 2 birds in 1998 (Figure 5-4b) ($R^2 = 0.19$, $p = 0.01$) ($N = 43$).

DISCUSSION

Scale - I 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. Bowers and Dooley (1999) suggested that fragmentation effects may be most evident at very small and very large scales, but obscured at intermediate scales. In their study of meadow voles (*Microtus pennsylvanicus*), the smallest "scale" was the individual organism, the intermediate scale was the patch, and the largest scale was the landscape in which the population resided. Also, in their system the population responded (positively) to edge habitat. 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 obscured at other scales requires more attention.

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 as Brown Treecreepers did not move among isolated fragments, and experimentally translocated females paired and bred successfully in isolated fragments that previously contained unpaired males (Chapter 3). 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 (Chapter 3). 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.

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. Andrén (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). I found that the degree of fragmentation that 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. When cover is low there is not enough area for patches to form convoluted shapes; instead patches are generally small and isolated.

Relative Effects of Habitat Loss and Fragmentation – Fragmentation effects independent of 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, Chapter 3). 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, Trzinski et al. 1999, Villard et al. 1999). However, only one scale was examined in each of the above studies. Trzinski 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 multiple spatial scales. For example, at a large scale, Bolger et al. (1997) found that the Rufous-sided Towhee (*Pipilo erythropthalmus*), 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 (Soule et al. 1988, Bolger et al. 1991).

Habitat – Removing sites in highly fragmented surroundings improved the Brown Treecreeper habitat model. Removing the single outlier (see Figure 5-3a) 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 will obscure wildlife-habitat relationships.

Management - Fahrig (1997) and Trzcinski et al. (1999) urged conservationists to acknowledge that the spatial arrangement of habitat can not mitigate the effects of habitat loss. Of course, the goals of reducing fragmentation and preserving cover are not necessarily incompatible since the most effective way to reduce fragmentation may often be to decrease habitat loss. However, increasing (or retaining) cover at one scale can also be accomplished by planning the spatial arrangement of patches at other scales. Because the effects of both cover and fragmentation change with scale, the argument that conservationists should choose to retain cover rather than consider the spatial arrangement of patches creates a false dichotomy.

Preserving or re-establishing cover is usually done at the scale of a management unit (e.g., private property, national forest, county), not necessarily at a scale encompassing a species' range or even a population. For example, several governmental and non-profit organizations in New South Wales (e.g., Greening Australia) have programs to encourage landowners to re-vegetate any part of their property. If landowners were coordinated to establish cover where properties have common borders, then fragmentation could be reduced while cover is increased. In this way, a consideration of the spatial arrangement of patches at a larger scale (i.e., several properties) can be as important to avian populations as increasing total woodland cover.

Limitations – Time-lagged responses to fragmentation and source-sink dynamics (Pulliam 1988, Pulliam and Danielson 1991) can confound analyses of the spatial distribution of a species. Landscape effects on Brown Treecreeper distribution became more evident as time passed. Presence/absence data taken soon after landscape alterations would be less reliable and should be used with caution. Presence/absence data will often be insufficient to draw conclusions and are no substitute for measurements of demographic or fitness parameters.

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TABLES

Table 5-1. Principle components (eigenvalue > 1) formed from habitat data.

	1st Habitat Analysis (N = 80)			2nd Habitat Analysis (N = 43)		
Tree Variables						
	PC1	PC2	PC3	PC1	PC2	PC3
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%
Ground Cover/Midstory Variables						
	PC1	PC2	PC3	PC1	PC2	PC3
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	-.03	-0.18
Variation explained	26%	23%	18%	28%	22%	21%

Table 5-2. Pearson correlation coefficients indicating the correlation between three landscape metrics at three scales ($N = 44$).

Metrics	Radius	Total Edge	Number Patches	%woods
	4.5km			
Mean Patch Size		0.22	-0.51**	0.83***
Total Edge			0.50**	0.67***
Number of Patches				-0.07
	2.0km			
Mean Patch Size		-0.11	-0.50**	0.65***
Ttotal Edge			0.57***	0.59**
Number of Patches				-0.18
	0.5km			
Mean Patch Size		0.30*	-0.59***	0.91***
Total Edge			0.13	0.45*
Number of Patches				-0.23

*$P <0.05$, **$P \leq 0.001$, ***$P < 0.0001$

Table 5-3. Principle component loading for the three metrics of landscape patterns at each scale.

	Scale					
	4.5km-radius		2.0km-radius		0.5km-radius	
Metrics	PC 1	PC 2	PC 1	PC 2	PC 1	PC2
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%

Table 5-4. Proportion of sample sites occupied by Brown Treecreepers.

Analysis	% Occupied Sites	number occupied	Total
1992	35%	28	80
1998	31%	25	80
by ≥ 2 birds, 1998	26%	21	80

Table 5-5. Summary of landscape metrics (N = 44) for occupied (1) and unoccupied (0) sites.

		Analysis					
Metric	Scale	1992		1998		by ≥ 2 birds, 1998	
	(radius)	1	0	1	0	1	0
	N	**22**	**22**	**20**	**24**	**17**	**27**
%wood	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	0.5(x1000)	3.6	2.9	3.6	2.9	3.7	3.0
	2.0(x1000)	23.2	21.5	22.6	22.1	31.0	20.2
	4.5(x1000)	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 5-6. Multiple logistic regression models for woodland cover and fragmentation from stepwise logistic regressions on Brown Treecreeper occupancy at multiple scales. N = 44 sites.

		Parameter Estimate			max-rescaled R^2
Radius	Analysis	Intercept	Cover[a]	Fragmentation[b]	
4.5km					
	by ≥ 2 birds, 1998	-0.74	-----	-1.22	0.33***
	1998	-0.27	-----	-0.86	0.23**
	1992	-0.04	-----	-0.77	0.21**
2.0km					
	by ≥ 2 birds, 1998	-2.0	0.06	-----	0.16**
	1998		-----	-----	-----
	1992		-----	-----	-----
0.5km					
	by ≥ 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**

*$P<0.05$, **$P < 0.01$, ***$P \leq 0.001$, using log-likelihood statistics

[a] measured as %woods

[b] measured as residual from regression of %woods on PC1

FIGURE CAPTIONS

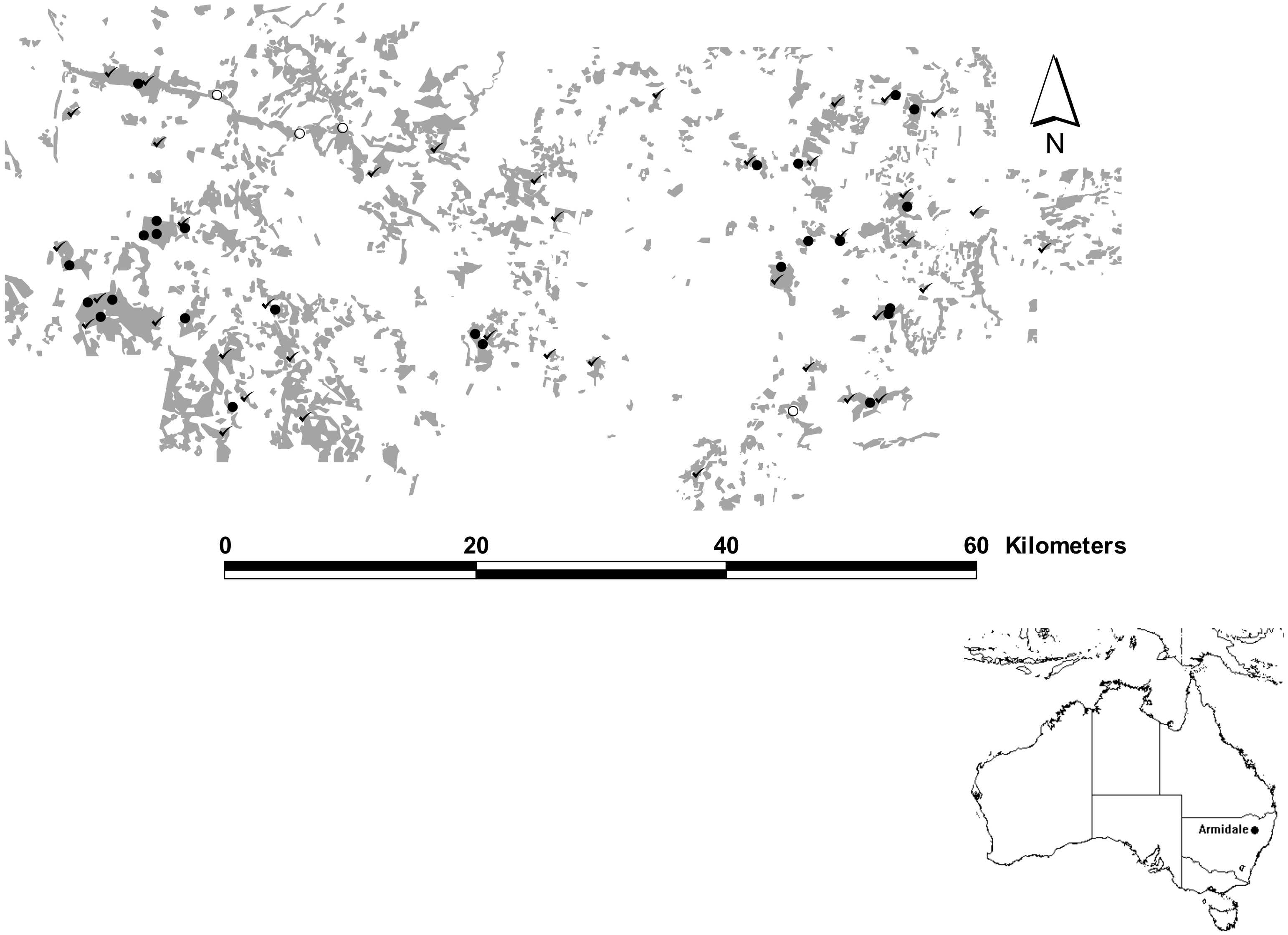
Figure 5-1. Study area and locations of randomly selected sites. Woodlands are in grey. Black circles represent randomly selected sites > 3.2 km apart (N=40), white circles represent territories included in landscape analyses (N = 4), and checks represent remaining sites used only in habitat analyses (N=40).

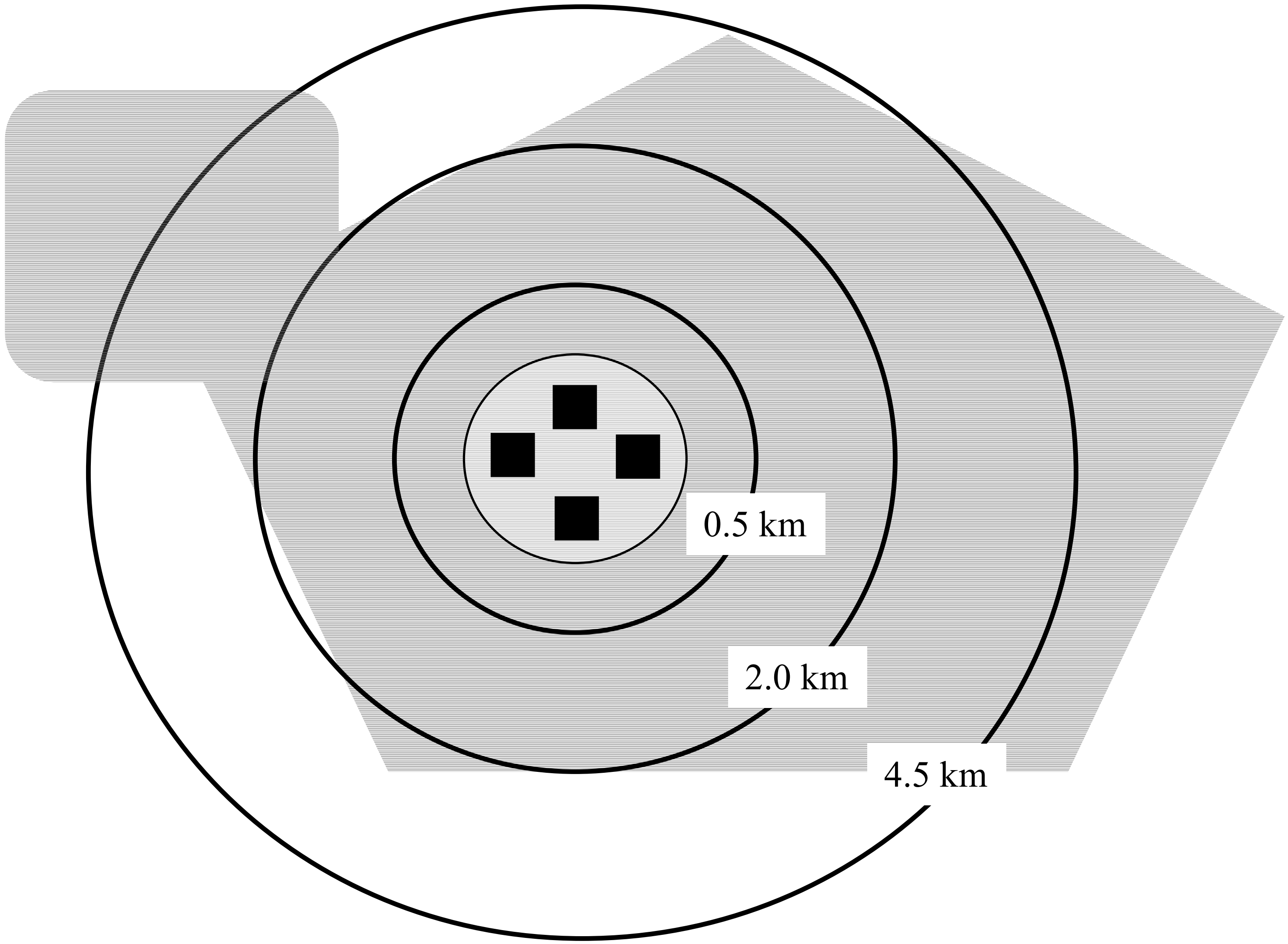
Figure 5-2. Schematic diagram illustrating one of the sites sampled for Brown Treecreeper presence or absence. Within a site, 4 plots (black squares) were used for sampling habitat. Surrounding a site, 3 concentric circles were used for collecting landscape data.

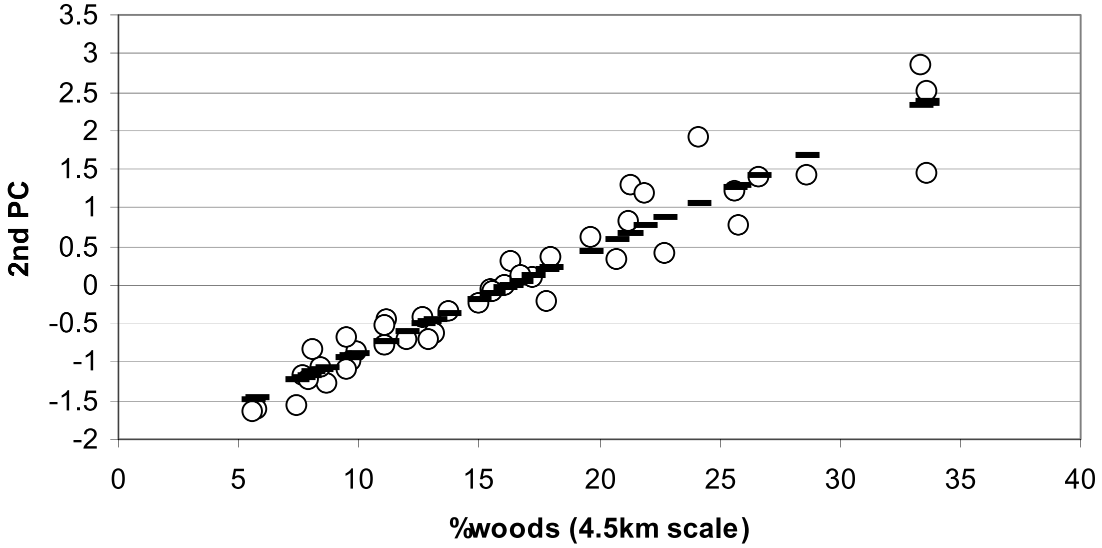
Figure 5-3. Relationships between the second principle component and percent woodland cover at (A) 4.5 km-radius and (B) 2.0km-radius scales ($n = 44$, $R^2 = .92$, $p < 0.0001$, $R^2 = .74$, $p < 0.0001$, respectively).

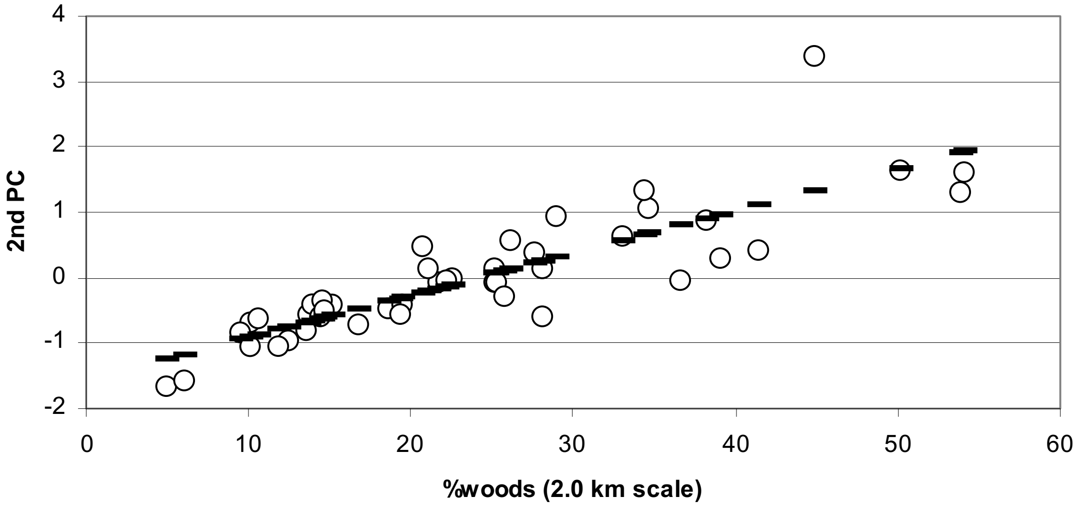
Figure 5-4. Logistic regression of occupancy by ≥ 2 birds in 1998 using (A) all randomly selected sites and (B) excluding unoccupied sites in unsuitable landscapes. Arrow indicates an outlier. Circles represent observed values. The dashed line represents the predicted values.

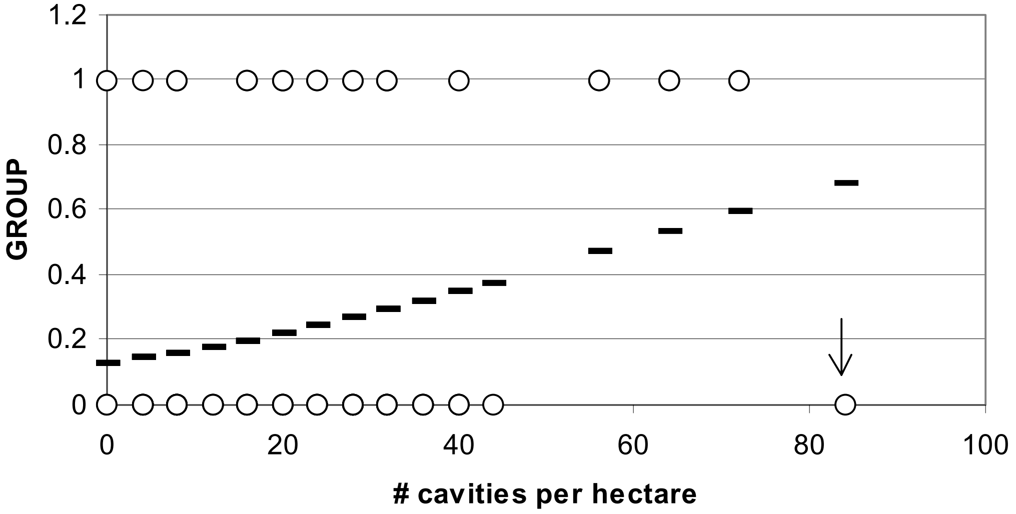
Figure 5-5. Logistic regression of area-independent measure of fragmentation at 4.5 km-radius scale (see text) on occupancy by ≥ 2 birds in 1998. Circles represent observed values. The dashed line represents the predicted values.

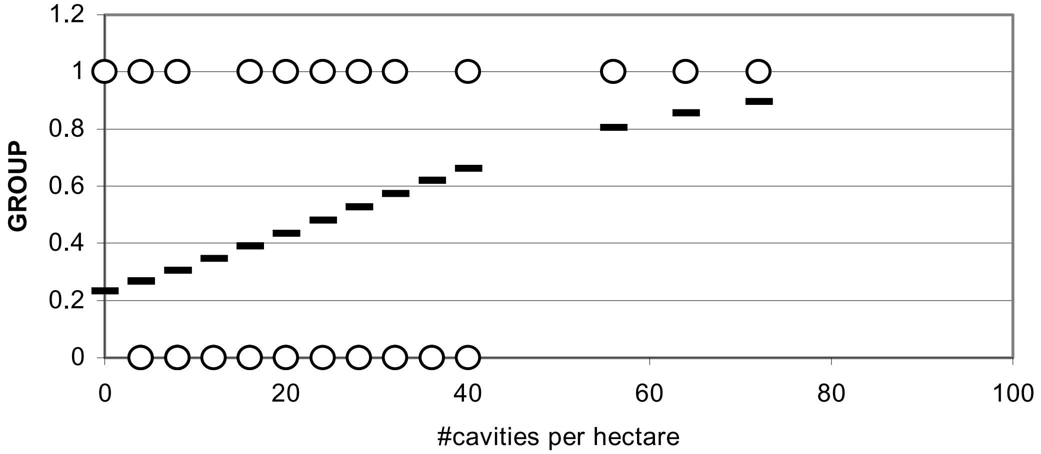

N
0
20
40
60 Kilometers
Armidale

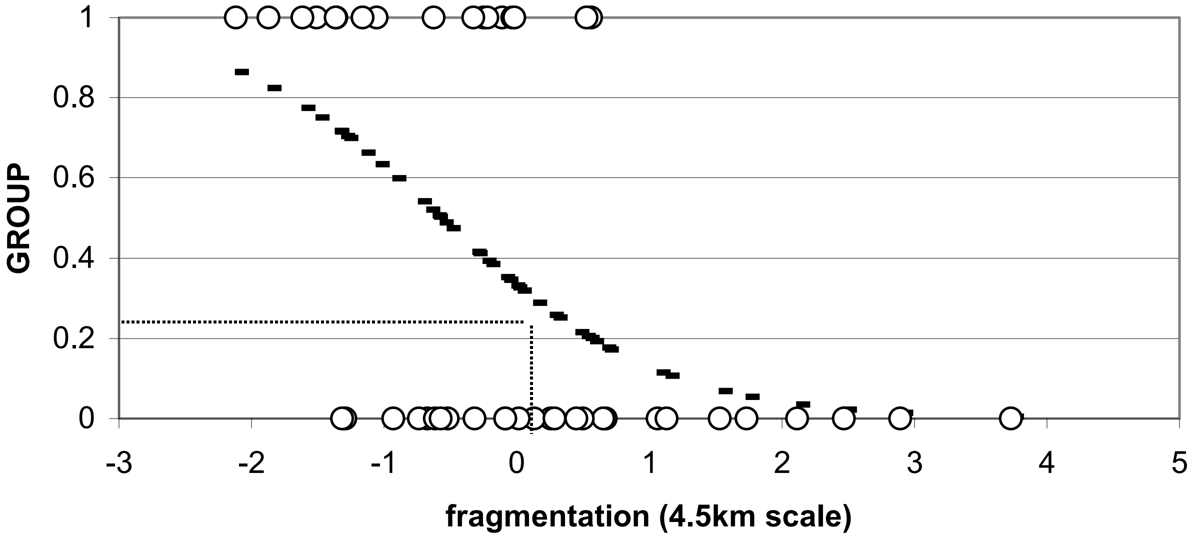

0.5 km
2.0 km
4.5 km


3.5
3
2.5
2
1.5
1
0.5
0
-0.5
-1
-1.5
-2
2nd PC
0
5
10
15
20
25
30
35
40
%woods (4.5km scale)


4
3
2
1
0
-1
-2
2nd PC
0
10
20
30
40
50
60
%woods (2.0 km scale)


1.2
1
0.8
0.6
0.4
0.2
0
GROUP
0
20
40
60
80
100
cavities per hectare


1.2
1
0.8
0.6
0.4
0.2
0
GROUP
0
20
40
60
80
100
#cavities per hectare


GROUP
1
0.8
0.6
0.4
0.2
0
-3
-2
-1
0
1
2
3
4
5
fragmentation (4.5km scale)

CHAPTER 6. HABITAT VARIATION AND COOPERATIVE BREEDING OF THE AUSTRALIAN BROWN TREECREEPER

ABSTRACT

Brown Treecreepers (*Climacteris picumnus*) breed cooperatively and occur in a variety of habitats throughout their range. In order to infer probable constraints on cooperative breeding in this species, I compared sources of ecological variation in predicting Brown Treecreeper group size and reproductive success in woodlands and forests near Armidale, New South Wales, Australia. Both group size and habitat variables explained variation in group reproductive success. Mean group size explained 36% of the variation in productivity, as measured by the mean number of fledglings produced per year. Tree and cavity density were related to one component of productivity, the number of fledglings produced from successful nests. High cavity density may be favorable due to intense inter-specific competition for suitable cavities, which Brown Treecreepers require for roosting as well as nesting. Low tree densities may be advantageous because such conditions favor the ground foraging in which Brown Treecreepers frequently engage. Experimental manipulations of important habitat variables are needed to determine whether these ecological factors are critical in maintaining group formation in this species.

INTRODUCTION

The Brown Treecreeper (*Climacteris picumnus*) is a cooperatively breeding, insectivorous passerine that nests and roosts in cavities. Brown Treecreepers inhabit eucalyptus woodlands and forests in eastern Australia, living in family groups usually consisting of a breeding pair and up to 4 male helpers (Noske 1980, 1991). This cooperative breeding system includes extra-group helping, whereby individuals frequently help raise young on neighboring territories in addition to their own (Noske 1980, Walters et al. 1999, Doerr and Doerr 2001).

By most community classification systems used in Australia, Brown Treecreepers are habitat generalists, although they do not occur in all available woodlands and forests. Therefore, superficially, this species does not appear to experience a shortage of unoccupied breeding habitat (a condition referred to as 'habitat saturation'), as many cooperative breeders do (Emlen 1982).

The concept of habitat saturation as a mechanism for family formation was the precursor to broader habitat-quality models of cooperative breeding (Stacey and Ligon 1991, Koenig et al. 1992, Walters et al. 1992). These widely accepted models provide an ecological explanation for cooperative breeding whereby individuals delaying dispersal obtain a payoff under circumstances in which the quality of breeding positions varies greatly. The generalized habitat-quality model arose chiefly from a few long-term studies on species in North America, such as the Acorn Woodpecker (*Melanerpes formicivorus*) (Stacey and Ligon 1987, Koenig and Mumme 1987, Stacey and Ligon 1991), Florida Scrub Jay (*Aphelocoma coerulescens*)(Wolfenden and Fitzpatrick 1984), and Red-cockaded Woodpecker (*Picoides borealis*)(Walters et al. 1992). This bias is problematic because roughly 30% of the world's approximately 222 avian species that exhibit cooperative breeding occur in Australia (Dow 1980). Moreover, the incidence of cooperative breeding among old endemic Australian passerines is 22% according to Russell (1989), whereas the worldwide incidence is only 3.2% according to Arnold and Owens (1998). Given this geographic bias, it is critical to determine the relevance of habitat quality models to Australian cooperative breeders.

Brown Treecreepers are part of a bark-foraging guild, though they spend almost half their foraging time on the ground. Australian woodlands and forests are distinguished primarily by percent canopy closure (10-30% for woodlands, 50-70% for forests; Specht 1981) and tree species, and can be associated with a variety of ground cover and shrub types. Other studies of Australian bark-foraging passerines have profited by characterizing trees by their bark characteristics: Stringybarks (subgenus *Monocalyptus*, Series *Capitellatae*) possess a fibrous, furrowed bark; Gums (subgenus *Symphyomyrtus*, Section *Transversaria* and *Exsertaria*) shred their bark annually in long ribbons, revealing a smooth surface on which treecreepers can not easily forage; and Boxes and Ironbarks (both in subgenus *Symphyomyrtus*, Section *Adnataria*) typically possess a rough scaly bark on the trunk (Noske 1991; Stokes 1995). In the New England Tablelands, Brown Treecreepers occupy areas dominated by Boxes, Ironbark, Gums, Stringybarks, and River Sheoak (*Casuarina* sp.). In other regions of New South Wales, Brown Treecreepers occupy coniferous (*Callitris* sp.) forests (personal observation).

Even though phylogenetic history might partly account for the prevalence of cooperative breeding in Australia, current ecological or social factors may still act to maintain components of cooperative breeding. As Koenig et al. (1992) pointed out, the relevance of phylogenetic history as an explanation for the high occurrence of cooperative breeding in Australia merely begs the question of why cooperative breeder lineages are so successful in Australia. Many field studies have focused on testing demographic predictions of the habitat-quality model, but few have identified ecological sources of variation, such as the hypothesized gradients in territory quality (Walters et al. 1992, Komdeur et al. 1995, Komdeur 1996). Debate continues over the type and degree of environmental variation, which may differ among species. Disagreement arises in part because interpretation of results depends on the identification of "breeding habitat," i.e., distinguishing suitable from unsuitable habitat. Disagreement also arises because territory quality has been hypothesized to vary in several ways, each described by variants of the habitat-quality model. For example, the marginal-habitat model (Koenig and Pitelka 1981) predicts a steeper gradient between poor or unoccupied habitat and territories than among territories, while the benefits-of-philopatry model (Stacey and Ligon 1987, 1991) (termed the habitat-variance model by Koenig et al. 1992) predicts a steep gradient in quality among territories. Finally, the critical-resource model (Walters et al. 1992) predicts that territory quality has a discontinuous distribution. In order to test these models on Brown Treecreepers, the first step is to examine fitness parameters in relation to environmental gradients across woodlands and forests.

Identifying ecological sources of variation that relate to fitness is crucial to acceptance of the habitat-quality model because factors other than territory quality could create any observed variance in fitness among territories. Furthermore, the demographic conditions consistent with the habitat-quality model may be a consequence, not a cause, of cooperative breeding, as has been argued to be the case for the demographic condition of 'habitat saturation' (Stacey and Ligon 1987). In this chapter, I examine relationships among group size, reproductive success, and ecological characteristics for a population of

Brown Treecreepers in order to determine how ecological conditions and cooperative breeding influence demography.

METHODS

Study area - The study site is a 1500 km2 region surrounding the town of Armidale, in the New England Tablelands of northeastern New South Wales, Australia, (30^{o} 27' S 151^{o} 13' E). The study area straddles the Great Dividing Range, with an elevation ranging from 730 to 1300 m. The climate is temperate with a mean annual rainfall of 789 mm. Coldest temperatures are usually in July when the average daily minimum temperature is 0.4^{o}C. Warmest temperatures are usually in January when the average daily maximum is 27.2^{o}C (Office of Bureau of Meteorology 2000).

Eucalyptus woodlands are generally described as communities where tree crowns are not in contact. In Australia, the most widely used system to classify vegetation communities is that of Specht (1981). According to this system of classification, the New England Tablelands contain *Eucalyptus* woodlands and forests.

Habitat Data Collection - Field assistants and I collected habitat data from 25 x 25 m square plots in Brown Treecreeper territories. Territories contained 2-6 plots, each selected by placing a 75-m grid over the territory and randomly selecting half the grid points.

Data included number and diameter at breast-height (dbh) of all trees greater than 15 cm dbh, recorded as one of the following tree types based on bark characteristics: Gum, Box, Ironbark, Stringybark, River Sheoak, Snags (i.e., dead trees), and Other. I dropped Ironbark, River Sheoak, and Other from analyses because they occurred at low frequencies among territories. Midstory vegetation was divided into two categories, tall shrub (>0.25 m and <2 m) and dwarf shrub (<0.25 m), and counted. Logs (fallen trunks or large branches > 1 m in length) were counted on each plot. We estimated ground cover composition in four categories (tall grass, low grass, rocks, 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 any live vegetation, though it may have fallen leaves and twigs. We also counted cavities (naturally occurring cavities in trees and stumps) in each plot (Table 6-1).

For all analyses of shrub and tree data, I used measures of basal area rather than stem density for several reasons. First, basal area was a better index of the amount of tree substrate available for foraging. Second, sites varied considerably in tree structure. In some areas, trees tended to fork two or more times just below breast height. As a result, stem density appears higher at these sites, even though the pattern of stem clumping results in canopy cover comparable to sites with lower stem density of trees with a single trunk. In addition, I wanted to assess the effects of habitat on fledgling productivity without masking effects from adjustments in territory size to accommodate nondepressible resources, such as tree cavities (see Koenig et al. 1992). Therefore, stepwise regressions for fitness analyses were also performed using habitat variables on a per capita basis. Results did not differ with the use of per capita habitat variables, so I only report methods and results from habitat variables measured on a per hectare basis.

Demographic Data – During 1996-1998, we monitored over 50 groups, 25 of which were monitored for all 3 years. Within these groups, approximately 84% of adults and 85% of offspring were banded with unique color combinations and a metal band from the Australian Bird and Bat Banding Scheme. Each year, from late July to early December, we visited each territory at least once every 15 days. At each visit we identified each bird present to determine group size and followed females to determine whether a nest was present. Group members bringing nest material to a cavity indicated nest building. A female being fed by group members and leaving a cavity for periods no longer than 10 minutes indicated the presence of eggs. Group members bringing insects to and removing fecal sacs from a cavity indicated the presence of nestlings. When nests were accessible (21% of all nests), nest status was determined by inspection of the nest. Offspring were counted after fledging during repeated and extensive visits to mist-net unbanded fledglings and to locate fledglings that were banded as nestlings.

Territory Boundaries and Size - I computed a single estimate of territory size by mapping territories on aerial photographs during the 1996 and 1997 breeding seasons. Territory boundaries were inferred from foraging patterns and occasional disputes with adjacent groups. When groups have a nest, adults exhibit central-place foraging behavior. After fledgling or several failures, groups tended to expand their foraging area, often overlapping with neighboring groups. Territory boundaries tended to shift slightly from year to year, particularly when birds shifted to different nest cavities. Even though foraging ranges of neighboring groups overlapped slightly, I mapped territory boundaries around non-disputed core areas. Mapped boundaries were used to select habitat-sampling points (see *Habitat Data Collection* above), to estimate territory size for computing per capita estimates of some habitat variables, and to estimate bird density per territory (see *Statistical Analyses*).

Statistical Analyses - I used linear regression to examine the general relationship between group size and Brown Treecreeper productivity using all monitored groups. In order to control for possible effects of yearly variation, I regressed group size on productivity using only the 25 territories monitored for 3 years. I also used these 25 territories in stepwise multiple regression models of habitat variables to model bird variables. The bird variables used in these analyses were the mean number of adults per social unit or group size (GS) for 1996-1998, the mean number of adults per hectare per territory (DENSITY) for 1996-1998, the mean number of fledglings produced from successful nests for 1996-1998 or brood size (BROOD), and the mean number of fledglings produced (FLEDGE) for 1996-1998 (Table 6-2).

I used principle component analysis to reduce the number of habitat variables included in multiple linear regression analyses. Previous work using a larger data set found the variables derived from the upper and lower vegetation strata were uncorrelated with each other, although some ground cover/midstory variables were correlated with one another and some tree variables were correlated with one another (Chapter 5). Therefore, PCA was performed separately on correlation matrices for 2 variable sets: (1) tree variables and (2) ground cover/midstory variables. Resulting factors with eigenvalues greater then 1.0 were used in the analysis. I used stepwise multiple linear regression, with significance levels of 0.5 for variable entry and 0.05 for variable retention, on principle components to model GS, DENSITY, BROOD, and FLEDGE. Specifically, I used stepwise multiple linear regression on the principle components from ground cover/midstory variables, the principle components from per hectare tree variables, and cavity density to model all bird variables.

Using variable set 1, PCA created 4 new ground cover/midstory variables (labeled PC–A through PC–D in order to distinguish these factors from variable sets 2) (Table 6-3). I interpreted PC-A to represent a gradient between low and tall grass. PC-B represents tall shrubs associated with rocks. I interpret PC-C as the absence of bare ground and the presence of logs. I interpret PC-D as a gradient between rocky ground and areas with dwarf shrubs and logs.

Using variable set 2, PCA created 3 new per hectare tree variables (Table 6-3). The first factor, PC1, represents a gradient between gums associated with snags and boxes. PC2 represents a gradient between areas with high tree density dominated by boxes and gums to areas with low tree density dominated by stringybarks. PC3 represents high tree density associated with high stringybark density.

RESULTS

Group Size and Productivity - Reproductive success, measured as mean brood size and measured as the number of fledglings produced per year, increased with mean group size (Figure 6-1, a & b). In Figure 6-1, the effects of year have not been taken into account. Controlling for yearly variation by using only those 25 groups monitored for 3 years, mean group size explained 24% of the variation in mean number of fledglings produced by groups (FLEDGE) (Figure 6-2). Mean group size did not explain variation in mean number of fledglings from successful nests (BROOD) ($P = 0.12$).

Habitat Quality and Productivity - None of the habitat variables explained variation in group size. Cavity density explained 22% of the variation in DENSITY (Table 6-4, Figure 6-3). BROOD had a positive relationship with number of cavities and a negative relationship with PC2, representing high basal area of trees and boxes and low basal area of stringybarks (Table 6-4, Figure 6-5a & 6-6a). No variables explained the number of fledglings from successful nests.

DISCUSSION

Group Size and Productivity – Initially, data suggest that each additional helper increased group reproductive success, except for the unusually large group of 6 adults. After controlling for the effect of year, the presence of helpers appears to increase group reproductive success measured as the number of fledglings produced, but does not explain variation in brood size. I could not control for the effects of territory quality or breeder age/experience, either of which could confound the effects of group size on productivity (Emlen and Wrege 1991, Magrath and Yezerinac 1997). That is, large groups may be the result of high quality habitat or high breeder quality, rather than a cause of high productivity. Therefore, it remains unclear whether helpers increase reproductive success of the breeding pair. Helper effects can arise in many ways and a detailed analysis of these possibilities is outside the scope of this chapter.

Nevertheless, one possible way helpers could affect the number of fledglings produced is by reducing nest failures. The overall nest failure rate (36%, N=122), which was similar to those recorded for other secondary cavity nesters (Odum 1941, Ricklefs 1969, Martin and Li 1992), was influenced by abandonment, conflicts with interspecific cavity competitors, and predation. Half of all failures occurred in one year (1998), and of these, 40% occurred during the nestling stage, a pattern suggestive of predation. Yet, during the other two years of this study, 80% of nest failures occurred during incubation, a pattern that suggests desertion as the most common cause of nest failure (Ricklefs 1969). Brown Treecreeper helpers feed the incubating female, perhaps decreasing nest desertion rates.

Another way helpers could affect the number of fledglings produced is by reducing breeder workload and thereby increasing the probability of renesting after failure. Although I did not measure the feeding rates of breeders and helpers, I observed that larger groups had a higher probability of renesting after failure (logistic regression, $R^2 = 0.43$, $P = 0.004$). Some studies of cooperative breeders have found that helpers reduce breeder workload (e.g., Red-cockaded Woodpeckers, Khan 1999), while others have found that breeders do not decrease their workload in the presence of helpers (e.g., White-browed Scrubwrens (*Sericornis frontalis*), Magrath and Yezernac 1997).

Territory Quality and Productivity – Several habitat gradients were associated with brood size and I use these gradients to define habitat quality. Specifically, the important characteristics of high quality territories were low tree density with a high number of cavities per adult group member. Medium quality territories lack some of these habitat characteristics, while low quality territories have the opposite composition.

In Chapter 5, I found that unoccupied habitat varied greatly in cavity density but sites with < 40 cavities per hectare had a low probability of occupancy. The most productive territories in this study had > 40 cavities per hectare, but surprisingly, most territories had < 40 cavities per hectare (Figure 6-5), suggesting they were low quality with respect to cavity availability.

Some of the properties of high quality territories may be associated with increased food abundance. Since Brown Treecreepers forage on all types of trees and occurred in sites regardless of tree type, it seems likely that the variation in foraging quality among tree species is small or unimportant to fitness. We expected variation related to ground cover to be of greater importance because Brown Treecreepers spend over half their foraging time on the ground (Walters et al. 1999). The influence of tree density on habitat quality can not be explained by a shading effect on ground cover, because canopy density does not appear to influence composition of the lower strata (e.g., habitat variables of the upper and lower strata were not correlated). Perhaps tree density causes variation in the spatial distribution of ground cover components. For example, bare ground isolated from tall grass may have a different value to Brown Treecreepers than bare ground evenly interspersed with tall grass or interspersed with short grass. Also, bark insects might be more concentrated on tree bark when tree density is lower, especially if they originate from the ground. Although Brown Treecreeper fitness increased as tree density decreased, this relationship can not be exptrapolated beyond woodlands. Brown Treecreepers do not inhabit areas where tree density is extremely low, such as sparsely vegetated pastures.

Brown Treecreepers require naturally occurring cavities for roosting and nesting (Noske 1982). Yet, there are no primary excavators in Australian woodlands and forests. Instead, cavities occur naturally in decaying stumps, spouts formed from broken tree branches, and under loose bark. There is growing evidence that suitable cavities are or will soon be a limiting factor for cavity-nesting animals in all Australian woodlands and forests (Bennett et al. 1994). Even though only 7 passerines in Australia are obligate cavity nesters, there is intense competition for cavities with other fauna. For example, 75% of arboreal mammals in Australia use tree hollows (Smith and Lindenmayer 1988). In Western Australia, 47% of cavities suitable for cockatoos (Psitaciformes) were occupied (Saunders et al. 1982). In the New England Tablelands, I saw nesting Brown Treecreepers fight with and lose nest cavities to parrots.

Why are Brown Treecreepers Cooperative? – The habitat-quality model is the only existing theory that attempts to account for the ecological basis of cooperative breeding behavior. One common theme of cooperative breeding research is the presence of a critical resource, such as cavities. Walters et al. (1992) identified variation in habitat quality dependent on the presence or absence of cavities as the ecological basis of group formation in Red-cockaded Woodpeckers, a species in which cooperative breeding is probably a derived trait (Ligon 1993). Prior to the experimental work by Walters et al. (1992), cavities had long been suspected of being the basis of cooperative breeding in Red Cockaded Woodpeckers because Red Cockaded Woodpeckers excavate cavities in living pine trees which requires a large energy and time investment (Ligon 1970, Lennartz et al. 1987). Ligon et al. (1988) showed that Green Woodhoopoes (*Phoeniculus purpureus*) were limited by the availability of roost cavities and suggested that roost site limitation was a selective force for cooperative breeding in that species. The dependence of Green Woodhoopoes on cavities for roosting was related to a physiological inability to withstand low nighttime temperatures. Noske (1991) suggested that the use of cavities for roosting and nesting by Brown Treecreepers may be a selective force for cooperative breeding and noted that the sympatric White-throated Treecreeper, a non-cooperative breeder, does not roost in cavities.

The presence (Chapter 5), fitness (BROOD), and density of Brown Treecreepers in an area (DENSITY) were influenced by the density of cavities in that area. Can we therefore expect that cavity density is the underlying selective force for cooperative breeding in this species? If so, we might expect the Brown Treecreeper to fit the critical resource model. This is possible because sites with very low cavity density appeared unsuitable (Chapter 5), potentially creating a discontinuous gradient between high and low (i.e., unsuitable) quality territories (Figure 6-6). However, the Brown Treecreeper could potentially fit other models. Cavity density could fit the habitat-variance model if productivity increased steeply and monotonically with increases in cavity density, thereby creating a steady gradient in quality across territories (Figure 6-6). This is possible since brood size increased linearly with cavity density. Under the marginal-habitat model, a gradient between high and low quality habitats can be created by the percentage of habitat that is suitable relative to the percentage that is unsuitable (Koenig and Pitelka 1981) (Figure 6-6). However, because differences between these possibilities are relative rather than absolute, without experiments or comparisons with non-cooperative species in similar habitat, it is difficult to identify which model fits the Brown Treecreeper.

Under each of the models mentioned above, it is unclear why adult birds could not split a given area of high quality into more territories. As Langen and Vehrencamp (1998) phrased the cooperative breeding question: why don't we see a higher density of territories for the same density of birds? They responded to this question with regard to White-throated Magpie-jays (*Calocitta formosa*) by suggesting that the area required for breeding may be greater than the area required for each individual to meet its own foraging demands. This explanation could also be true with regard to Brown Treecreepers. Another possible explanation is that the number of territories in an area depends on the spatial distribution of available cavities, which in turn is influenced by whatever factors cause cavities to form naturally and/or by the density of cavity competitors. As mentioned above, cavities are a critical resource responsible for group formation in Red-cockaded Woodpeckers. Yet, an unemphasized characteristic of these cavities is that they generally occur in clusters, making it difficult for territories to be divided into smaller territories with the same bird density.

An alternative possibility is that Brown Treecreepers do split territories into more breeding groups but are restricted by social rather than habitat factors. This seems a likely scenario because budding is the most common avenue to a breeding position in this population, occurring at a high rate of approximately 7% per territory per year. Budding and independent reproduction may be limited by the availability of females (Koenig et al. 1992). Reproductive skew theory suggests that dominants (in this case parents) could limit the sharing of breeding opportunities (in this case budding by male offspring)(Emlen 1995). Therefore, social factors in addition to habitat limitations may be required to fully explain cooperative breeding in this species.

Conclusion - Here I identify a possible gradient in quality of Brown Treecreeper habitat, whose relationship to fitness can be tested experimentally. An appropriate test for Brown Treecreepers could involve adding tree cavities to unoccupied, but otherwise suitable areas, followed by an examination of impacts on territory occupancy. If such alterations resulted in helpers becoming independent breeders (i.e., increased male dispersal), then this would reveal that the amount of high quality habitat is a constraint on cooperative breeding in this species. If such alterations did not result in the formation of new groups, then this would suggest that cooperative breeding in this species is driven by factors other than cavities. Another prediction of the model is that, all else being equal, birds on high quality territories should become helpers. Therefore, another test could involve adding tree cavities to poor quality territories. If such alterations resulted in the formation of larger groups (i.e., less male dispersal), then this too would reveal that the amount of high quality habitat is fundamental to cooperative breeding in this species.

Unfortunately, there is no model for how selection might act to maintain cooperative breeding in species where the behavior is ancestral. Once cooperative breeding is present in a lineage, very different selective forces may act to maintain delayed dispersal and helping than those proposed to be responsible for their origin under the habitat-quality model. The frequency of male Brown Treecreeper dispersal was very low in this population (2% - see Chapter 3). It is unknown whether the exceedingly high frequency of male philopatry is related directly to habitat quality or influenced by population density or recent landscape changes. A Brown Treecreeper population in southern New South Wales also exhibits a low frequency of male dispersal (estimated 3%) and a high degree of budding (Doerr, V., personal communication). High stability in the rate of helping and dispersal may indicate phylogenetic inertia and primacy of social factors over habitat factors in maintaining cooperative breeding.

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TABLES

Table 6-1. Sets of habitat variables related to Brown Treecreeper demography in stepwise multiple linear regression analyses. Each variable is a mean from 2-6 random plots from each territory (see *Habitat Data Collection*).

Variable	Mean (Sdev)
a) Ground and Shrub Layer	
%low grasses	38 (20)
%tall grasses	48 (21)
%bare ground	8 (12)
%rocky surface	6 (9)
# logs >1 m in length	59 (47)
Low shrubs (#shrub stems <0.25 m)	75 (49)
Tall shrubs (#shrub stems >0.25 m and <2 m)	128 (105)
b) Per Hectare measures (# trees (m2) per hectare)	
Boxes	5 (6)
Gums	5 (6)
Stringybarks	2 (4)
Live trees	16 (9)
Snags	2 (3)
Cavities	25 (21)

Table 6-2. Definition and basic statistics of bird variables used in stepwise multiple linear regression analysis. All means are from data from 1996-1998.

Variable	Definition	Mean	SD	CV	Min	Max	N
GS	mean no. adult birds in the social group	2.8	0.63	22	2	4	25
DENSITY	number of adult birds per hectare on a territory	0.92	0.66	72	0.25	3	25
BROOD	mean no. fledglings produced per successful nest per season	2.0	0.73	37	1.0	4.0	24
FLEDGE	mean no. fledglings produced per season	1.4	0.73	53	0	3	25

Table 6-3. Principle components of habitat variables used in regression analyses. Variable set 1 contains ground cover/midstory factors. Variable set 2 includes per hectare tree factors. All factors were generated by principal components analysis (N = 25). Only factors with eigenvalues >1.0 are shown. Variables are defined in Table 6-1.

	Variable set 1			
	PC-A	PC-B	PC-C	PC-D
Eigenvalue	2.1	1.5	1.3	1.1
Proportion of	0.30	0.22	0.19	0.15
Variable				
Bare ground	-0.07	0.27	**-0.77**	0.24
Low grass	**-0.65**	-0.002	0.14	-0.22
Tall grass	**0.55**	-0.33	0.23	0.33
Rocks	0.25	**0.45**	0.25	**-0.63**
Logs	-0.14	0.34	**0.46**	**0.44**
Dwarf shrub	-0.25	0.33	0.21	**0.44**
Tall shrub	0.35	**0.63**	-0.09	0.05

	Variable set 2		
	PC1	PC2	PC3
Eigenvalue	1.5	1.3	1.0
Proportion	0.30	0.26	0.20
Variable			
Live trees	-0.7	**0.66**	**0.56**
Boxes	**-0.49**	**0.54**	-0.27
Gums	**0.60**	0.33	0.26
Snags	**0.56**	-0.15	-0.07
Stringybarks	-0.29	**-0.42**	**0.74**

Table 6-4. Linear models created by stepwise multiple regressions of bird variables (Table 6-2) on variable set 1 and 2 (Table 6-3). Linear models created by stepwise multiple regressions of DENSITY and BROOD on variable set 1 and 2 (Table 6-3). No habitat variables explained variation in group size or FLEDGE.

Response	Regressor	Estimate (±SE)	F	adjR2	P > T
Variable Set 1 & 2 (per hectare estimates)					
DENSITY	CAV	0.02 (0.01)	7.96	0.22	0.01
BROOD	CAV	0.02 (0.01)	8.97	0.43	0.003
	PC2	-0.37 (0.11)	11.53		

FIGURE CAPTIONS

Figure 6-1. The relationship between group size and reproductive success from 53 territories, (A) measured as the number of fledglings produced per year and (B) measured as the number of fledglings from successful nests per year. Black circles indicate the mean and vertical lines indicate ± 1 standard deviation.

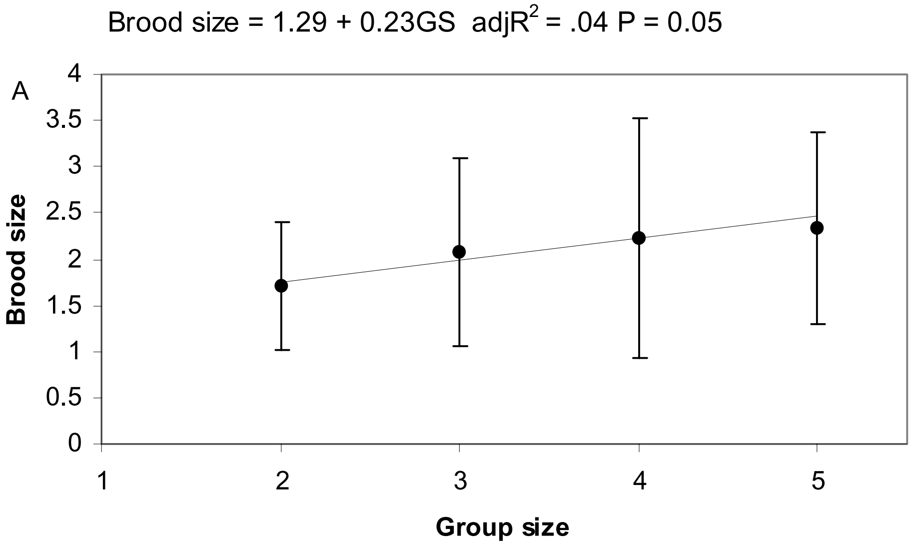
Figure 6-2. Simple linear regression of group size on reproductive success after controlling for yearly variation (N = 25 territories). Reproductive success is measured as the number of fledglings produced.

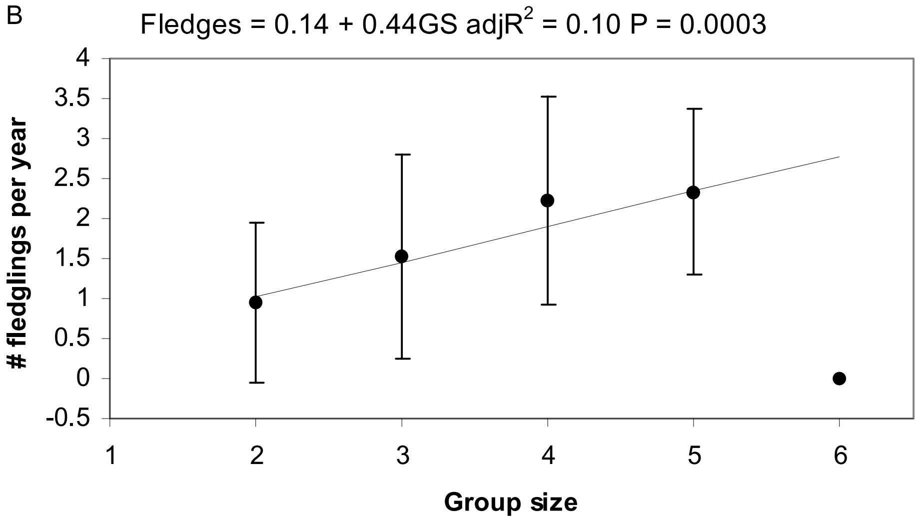
Figure 6-3. Simple linear regression of DENSITY (group size independent of territory size) on cavity density (N = 25).

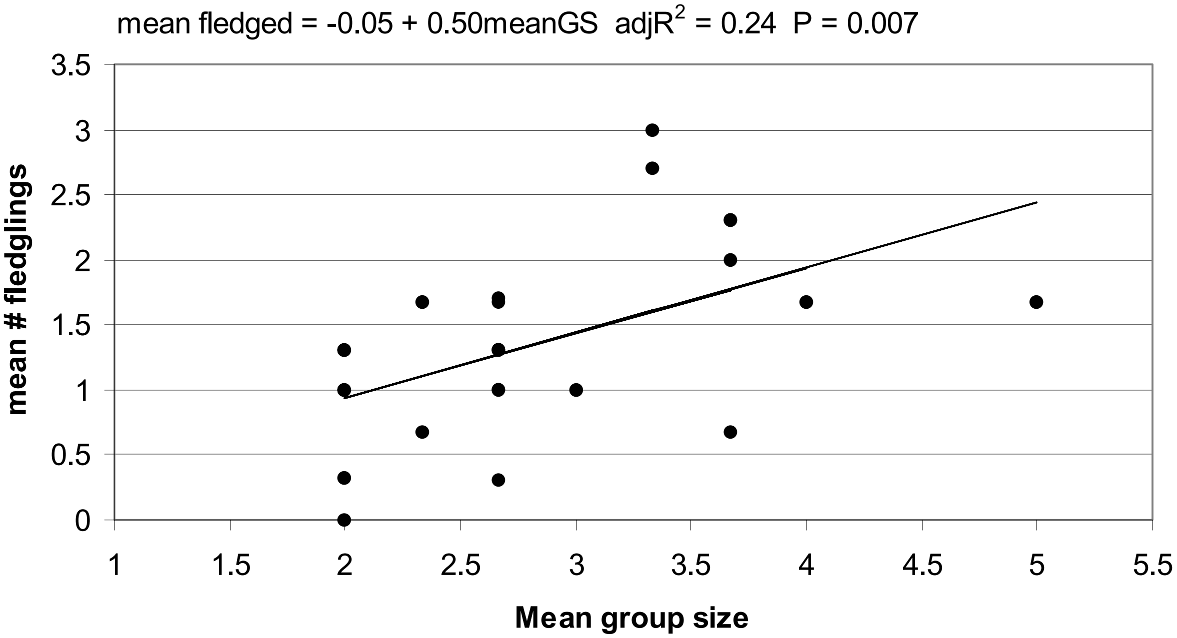
Figure 6-4. Scatter plots of BROOD against cavities per hectare (N = 25).

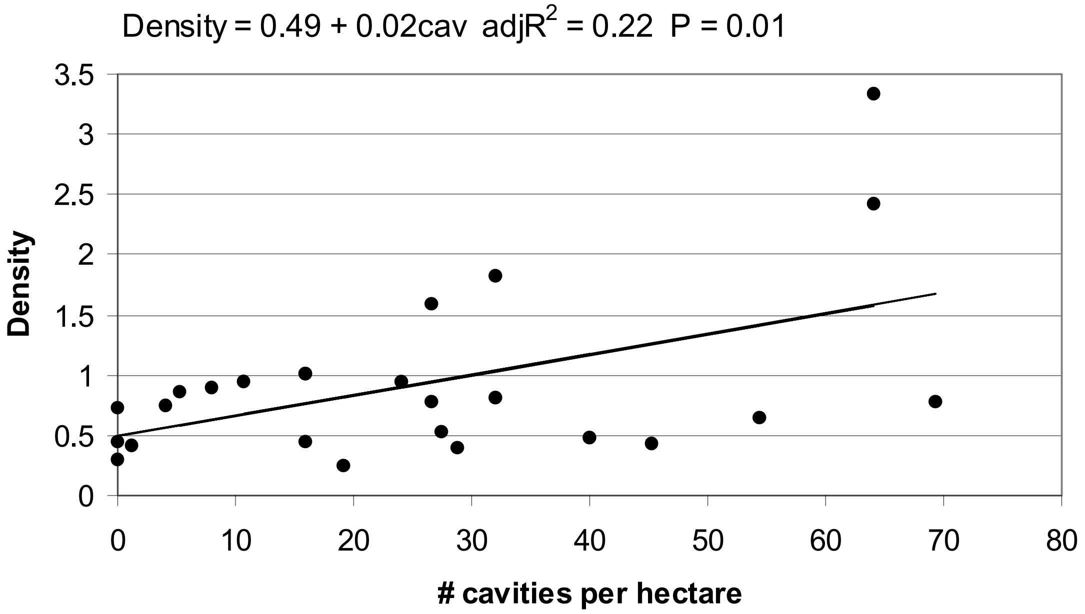
Figure 6-5. Scatter plot of BROOD against basal area of trees per hectare (N = 25).

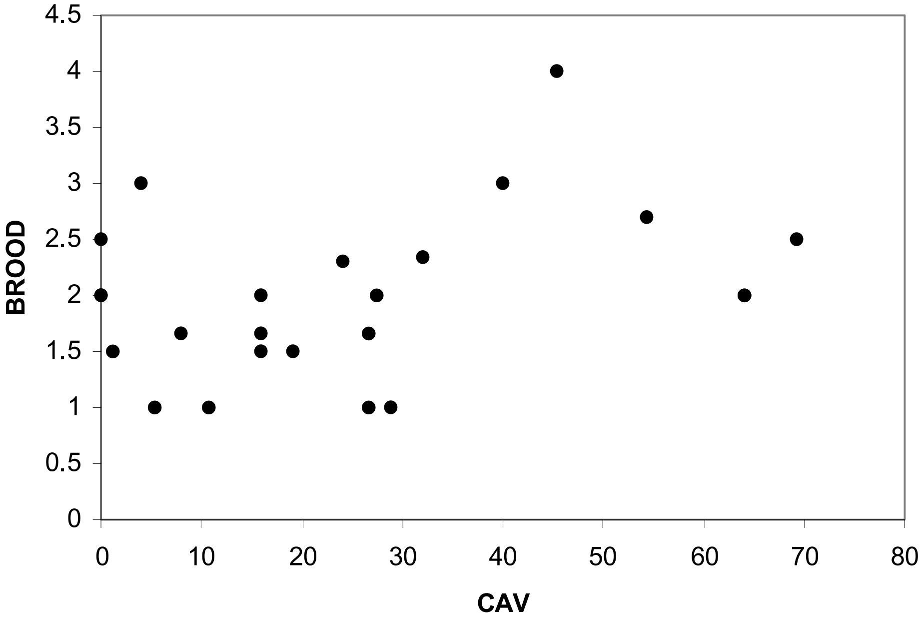
Figure 6-6. The hypothetical distribution of cavity density and fitness under (A) the critical-resource model, (B) the variance model, and (C) the marginal-habitat model.

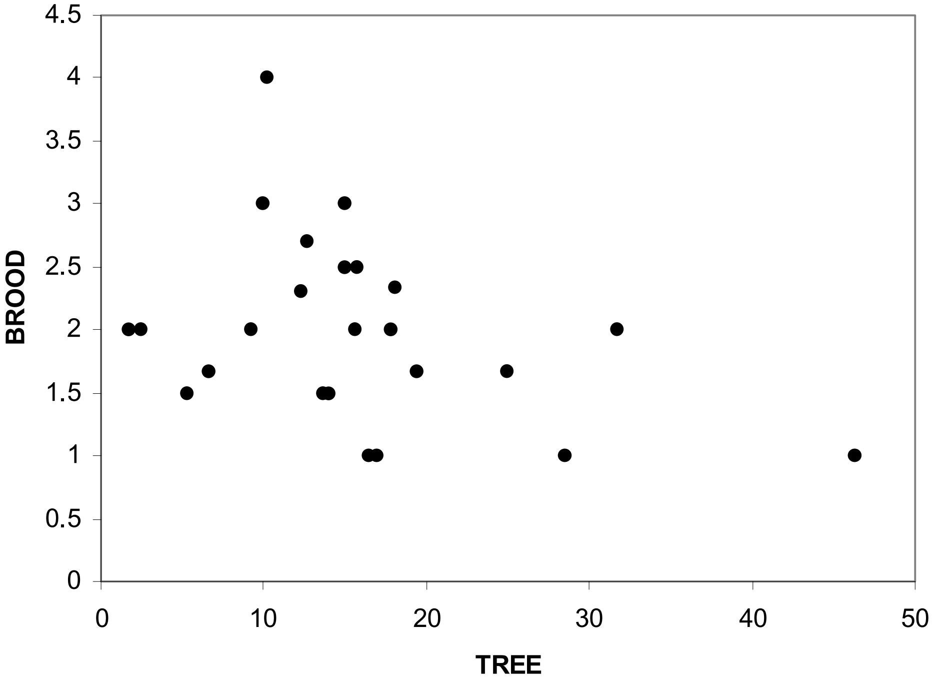

Brood size = 1.29 + 0.23GS adjR^2 = .04 P = 0.05
A
Brood size
4
3.5
3
2.5
2
1.5
1
0.5
0
1
2
3
4
5
Group size

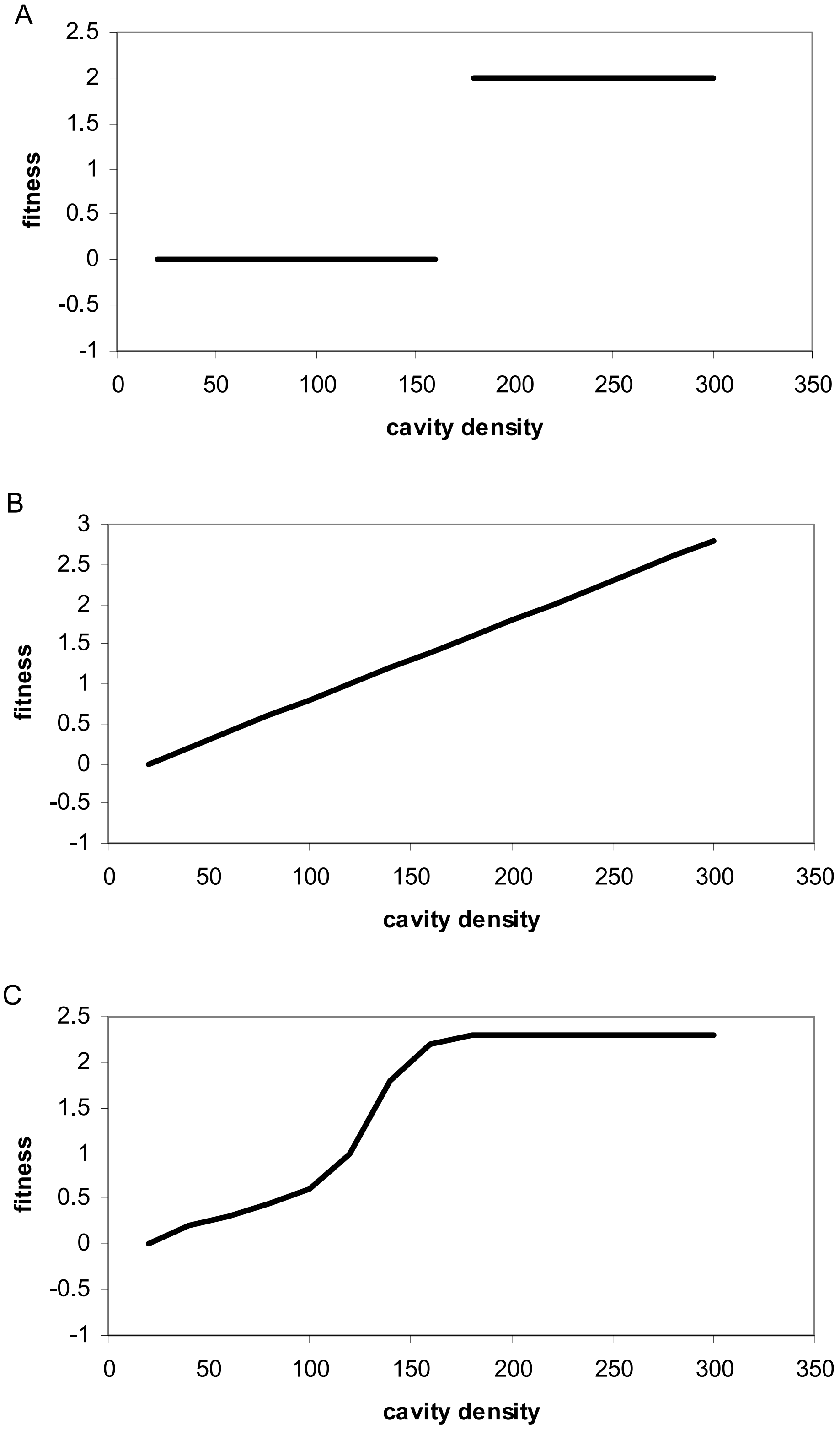

B
Fledges = 0.14 + 0.44GS adjR^2 = 0.10 P = 0.0003
# fledglings per year
4
3.5
3
2.5
2
1.5
1
0.5
0
-0.5
1
2
3
4
5
6
Group size


mean fledged = -0.05 + 0.50meanGS adjR^2 = 0.24 P = 0.007
mean # fledglings
Mean group size
0
0.5
1
1.5
2
2.5
3
3.5
1
1.5
2
2.5
3
3.5
4
4.5
5
5.5


Density = 0.49 + 0.02cav adjR2 = 0.22 P = 0.01
Density
3.5
3
2.5
2
1.5
1
0.5
0
0
10
20
30
40
50
60
70
80
cavities per hectare


4.5
4
3.5
3
2.5
2
1.5
1
0.5
0
BROOD
0
10
20
30
40
50
60
70
80
CAV


BROOD
4.5
4
3.5
3
2.5
2
1.5
1
0.5
0
0
10
20
30
40
50
TREE


A
2.5
2
1.5
1
0.5
0
-0.5
-1
fitness
0
50
100
150
200
250
300
350
cavity density
B
3
2.5
2
1.5
1
0.5
0
-0.5
-1
fitness
0
50
100
150
200
250
300
350
cavity density
C
2.5
2
1.5
1
0.5
0
-0.5
-1
fitness
0
50
100
150
200
250
300
350
cavity density

CHAPTER 7. CONCLUSIONS

SYNTHESIS

Brown Treecreepers are declining in the New England Tablelands of New South Wales, Australia in response to loss and fragmentation of their woodland habitat. The demographic evidence I presented here suggested that Brown Treecreepers are sensitive to patch isolation rather than patch size (Chapter 2). Many isolated fragments lacked breeding females because they were either isolated or degraded. Experimentally moving females to unpaired males in fragmented and contiguous habitat indicated that patches were not degraded, rather isolation was disrupting female dispersal among fragments (Chapter 3). Woodland fragmentation led to a non-clumped distribution of territories and this was the most likely mechanism by which dispersal and recruitment were affected (Chapter 4). Finally, Brown Treecreeper presence and absence from sites within woodland patches was best explained by fragmentation patterns within a 4.5-km radius surrounding sites. This may be a species-specific phenomenon in which fragmentation patterns at that scale affect female dispersal success, or it may be an example of a general phenomenon arising from < 20% woodland cover at that scale (Chapter 5).

Brown Treecreepers are cooperative breeders in a lineage in which delayed dispersal and helping are ancestral behaviors. I identified gradients in cavity and tree density related to Brown Treecreeper fitness (Chapter 6). Cavity density was also related to Brown Treecreeper distribution, after controlling for the effects of fragmentation (Chapter 5). More research is needed to distinguish the role of habitat and social factors in maintaining cooperative breeding among Australian passerines.

A strength of this research was the use of a field experiment to distinguish between isolation and habitat degradation effects. Another strength was the multi-faceted approach that included the analysis of distribution data, detailed demographic data, and model simulations to investigate the mechanism by which isolation effects occurred. One limitation of this research was a lack of information about habitat degradation in the field.

FUTURE RESEARCH

Although I found that the isolation of patches and subsequent isolation of territories in fragmented habitat were the current cause of Brown Treecreeper population declines, habitat degradation was present and may influence population viability. This research did not rule out the possibility that unoccupied patches were comprised of degraded, unsuitable habitat. Also, isolation effects (i.e., disrupted dispersal among patches) may only be important after there has been a reduction in within-patch territory density for some other reason, and degradation is the most likely such reason. Finally, highly degraded habitat is equivalent to no habitat from the perspective of Brown Treecreepers. Yet census methods used to tally woodland cover (e.g., ground surveys or the interpretation of aerial photographs) generally do not distinguish between healthy woodlands and degraded woodlands. Therefore, degradation may bias conservation and research concerning Brown Treecreeper declines by causing an underestimate of habitat loss and fragmentation.

The relationship between dispersal success and population dynamics may vary with the frequency of long- and short-distance dispersal, which, in turn, may reflect territory spatial distribution. Thus isolation effects may be highly dependent upon territory spatial arrangement, which may be determined by fragmentation patterns, natural habitat quality gradients, or breeding behavior. In the case of Brown Treecreepers, a clumped distribution of territories may increase the frequency of short-distance dispersal events and thus minimize the influence of the matrix on dispersal mortality. Without more information on how birds actually move through complex landscapes and about the link between territory distribution and dispersal patterns, it will be difficult to predict when matrix composition may become important to isolation effects.

Conservation and management as well as ecological and behavioral research frequently requires the identification of suitable habitat. Fragmentation confounds such analyses. For example, excluding unoccupied sites in unsuitable landscapes improved the ability of local habitat features to explain Brown Treecreeper distribution. This information was important in examining factors affecting the maintenance of cooperative breeding in Brown Treecreepers.

AVIAN MANAGEMENT IN THE NEW ENDLAND TABLELANDS

In North America, where forest edge can decrease the viability of passerine populations, management has focused on creating suitable landscapes that retain large forest patches. In Australian woodlands, edge effects are less of a problem than in North America. Instead habitat degradation and patch isolation are the most likely mechanism by which fragmentation might affect Australian passerines in woodlands.

The Brown Treecreeper may serve as a model species for other passerines with similar life-histories, such as cooperative breeders, cavity nesters, or ground-foragers. Nevertheless, the relative importance of woodland loss, degradation, and isolation to declines in other avian species in the Tablelands may vary considerably among species. All woodland species would benefit from an increase in woodland acreage. One way to increase woodland acreage is reforestation by tree planting. In the Tablelands, many woodland patches contain low bird diversity because they are degraded and/or isolated. Therefore, the management priority should be to increase the amount of *suitable* woodland acreage. Suitable woodlands are woodland patches that are not degraded and that exist in contiguous landscapes. Thus, a second way to increase the amount of woodlands available to Brown Treecreepers and similar avian species is to rehabilitate degraded woodlands by returning to natural fire regimes and decreasing livestock grazing.

The suitability of woodlands was influenced by cavity density. Thus, a third way to increase the amount of woodlands available to Brown Treecreepers is to increase cavity density within woodlands. Half of all Brown Treecreepers nests in this study were in live trees. Cavities appeared to be more common in the limbs of box and gum trees than in stringybark trees. Future research and management could involve adding cavites, by drilling holes in stumps or limbs or placing artificial nest boxes on trees, and evaluating the response of Brown Treecreepers at an individual and population level as well as consequences to animal diversity.

A fourth way to increase the amount of available woodlands is by providing connectivity among patches. Although other thresholds of isolation might exist, I observed that large patches (> 450 ha) or a series of well-connected patches (gaps $\leq$ 200 m between patches >100ha) appeared to be necessary for the persistence of Brown

Treecreeper populations. There exist many potential ways connectivity, or movement between patches, can occur, such as through small gaps between patches, a matrix of habitat that is safe for movement, corridors of breeding habitat, or corridors of habitat that is safe for movement.

A management strategy to create landscapes that benefit the maximum number of woodland bird species will increase woodland cover and decrease woodland fragmentation simultaneously. Given the potential importance of territory clumping, and the lack of knowledge concerning dispersal search strategies and matrix effects, management at the landscape scale directed at clustering remnant habitat is as promising an option as corridor development. However, preserving or re-establishing cover is usually done at the scale of a management unit (e.g., a single private property, national forest, county), not necessarily at a scale encompassing a species range or even a population. Therefore, managing woodland clumping at a landscape scale must take into account land ownership. Several governmental and non-profit organizations in New South Wales (e.g., Soil and Land Conservation Council, Greening Australia) already have programs to encourage landowners to re-vegetate any part of their property. Avian communities would benefit if landowners established woodlands where properties have common borders, because both woodland loss and fragmentation could be reduced simultaneously.

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The influence of timber harvest patterns on biodiversity using a simulation model.

Graduate Research Associate, Department of Biology, Virginia Polytechnic Institute & State University, VA 1995-2000

Designed and carried out research on Brown Treereepers. Field work included banding adults after capture in mist nests, banding nestlings, observing group interactions, monitoring nest success, measuring habitat variables, and supervising field assistants. Used MSExcel, SAS, and ArcView to organize and analyze data. Used ArcInfo to digitize landscape covertypes. Used Visual Basic to run simulation model of Brown Treecreeper population dynamics.

Research Associate, University of Idaho, ID 1994

Conducted pilot study investigating foraging locations of Tundra Swans at a migration stop-over site in Northern Idaho with lead contamination.

Graduate Research Associate, Department of Zoology and Physiology, 1991-1993
University of Wyoming, WY
Designed and carried out research on the use of constructed wetlands by dabbling ducks. Field work included sampling submergent vegetation, recording detailed foraging observations, surveying for ducks, and supervising field assistants. Used MSExcel, SAS, and Fortran to organize and analyze data.

Field Research Experience

Research Technician, Smithsonian Conservation and Research Center, VA 1991
Searched for Kentucky warblers, read color bands, searched for nests, captured adults in mist-nets, and banded nestling.

Research Technician, Smithsonian Conservation and Research Center, VA 1990
Assisted in research that applied behavioral conditioning treatments prior to release in the wild of Siberian polecats as a model for black-footed ferret reintroduction. Duties included caring for captive polecats while implementing pre-release training such as chasing polecats with a dog and owl, feeding polecats live prairie dogs, and dead prairie dogs.

Field Technician, US Fish and Wildlife Service, Puerto Rico 1990
Conducted dawn to dusk observations of nesting Puerto Rican Parrots.

Field Technician, NSCU, Department of Zoology, NC 1989
Trapped, tagged, and radio-tracked black bears in mountainous terrain during summer. Located dens in winter.

Intern, Student Conservation Association, Puerto Rico 1989
Conducted dawn to dusk observations of nesting Puerto Rican Parrots.

Field Technician, US Forest Service, Klamath National Forest, CA 1988
Conducted dawn to dusk observations of foraging Swainson's hawks. Trapped hawks in mist-nests for banding and radio-tagging.

Undergraduate Intern, NSCU, Department of Forestry, NC 1987
Conducted bird counts by sight and sound in cypress-tupelo swamp in Alabama. Sampled vegetation in cut and uncut forest.

Hack Site Attendant, NC Wildlife Resources Commission, NC 1986
Fed and observed young Peregrine Falcons prior to and after their release. Protected the site from intruders.

Undergraduate Intern, NCSU, Department of Zoology, NC 1985

Trapped, tagged, and radio-tracked black bears in mountainous terrain during summer. Located bear dens in winter. Supervised Earthwatch volunteers. Sampled vegetation.

Work-Study Intern, NCSU, Department of Zoology, NC 1984

Tended greenhouse grasses. Searched cattails for grasshopper eggs. Measured, marked, and determined the sex of grasshoppers after each molt.

Volunteer, Duke Primate Center, NC 1984

Fed and observed the behavior of captive lemurs.

Laboratory Experience

Research Technician, Smithsonian Conservation and Research Center, VA 1991

Drew blood samples from captive White-cheeked Pintail ducks and recorded plumage characteristics. Assisted with column chromatography to separate steroid hormones (testosterone, dihydrotestosterone, luteinizing hormone, and corticosterone). Assisted in the measurement of hormone concentrations by radioimmunoassay.

Teaching Experience

Teaching Assistant, Virginia Tech, VA 1998

Taught 2 laboratory sections of ornithology. Took students on field trips and reviewed museum specimens. Prepared and graded laboratory practical exams. Graded writing assignments.

Associate Naturalist, The Conservancy, FL 1990-1991

Took 4th and 6th grader on field trips to beach and upland habitats as well as to a laboratory at The Conservancy. Guided bird watching canoe trips for adults to rookery islands and throughout mangrove swamps. Guided outings in boat trips to barrier islands. Taught preschool programs with injured wildlife from rehabilitation center.

Volunteer Naturalist, Western North Carolina Nature Center, NC 1989

Taught 3rd grade program in the fall about apples. Provided demonstrations to general public about bees, turtles, and amphibians at Center.

Environmental Policy Experience

Research Fellow, Tip of the Mitt Watershed Council, MI 1995

Developed cumulative impact assessment protocol for wetland permit review by the Department of Natural Resources. Commented on dredge-and-fill permit applications.

Other Experience

GIS Analyst, The Nature Conservancy, RI 2000

Computed landscape metrics surrounding bird count stations using ArcView

Research Grants and Awards

National Science Foundation, Dissertation Improvement Grant, 1998-2000

Graduate Research and Development Award of the Graduate Student Assembly, Virginia Tech, 1997

Sigma Xi Graduate Student Research Award, 1997

Lloyd T. Weeks Endowment Scholarship (Undergraduate), 1985

Publications

Walters, J. R., H. A. Ford, and C. B. Cooper. 1999. Ecological basis of Brown Treecreeper sensitivity to habitat fragmentation: a preliminary assessment. *Biological Conservation*: 90:13-20.

Cooper, C. B. and S. H. Anderson. 1996. Use of constructed wetlands by dabbling ducks on the National Elk Refuge, WY. *Wetlands* 16: 557-563.

Publications In Review

Cooper, C. B. and J. R. Walters. Experimental evidence of disrupted dispersal causing decline of an Australian passerine in fragmented habitat. *Conservation Biology*. In Review.

Cooper, C. B., J. R. Walters, H. A. Ford. The demography of Brown Treecreepers in connected and isolated, large and small, woodland patches. *Emu*. Submission pending.

Publications In Preparation

Cooper, C. B. and J. R. Walters. Habitat and landscape effects on Brown Treecreeper distribution: independent effects of woodland loss and fragmentation at multiple scales.

Cooper, C. B., J. Priddy, and J. R. Walters. Effects of landscape patterns on dispersal success: a simulation of Brown Treecreeper population dynamics in a spatially realistic landscape.

Cooper, C. B. and J. R. Walters. Habitat variation and cooperative breeding of the Australian Brown Treecreeper.

Reports

Cooper, C. B. and J. W. Cwikiel. 1995. Cumulative Impact Assessment in Michigan's Wetland Permit Program: Definitions, Literature Review, and Recommendations. Michigan Department of Natural Resources, Lansing, MI.

Cooper, C. B. 1994. Cumulative impact assessment: who's doing what? *Great Lakes Wetlands* 5(4):7-8.

Cooper, C. B. and J. T. Ratti. 1994. Preliminary analysis of Tundra swan habitat use associated with Northern Idaho mining and techniques for minimizing exposure to environmental toxicity. Water Resources Research Institute, University of Idaho, Moscow, ID, 84pp.

Abstracts

Cooper, C. B. and J. R. Walters. 1999. Presentation: Why are Brown Treecreepers Sensitive to Habitat Fragmentation? American Ornithologist's Union Meeting, Ithaca, NY.

Cooper, C. B., J. R. Walters, and H. A. Ford. 1997. Poster: The Basis of Brown Treecreeper Sensitivity to Fragmentation. Australasian Wildlife Management Society Meeting, Armidale, NSW, Australia.

Cooper, C. B. and S. H. Anderson. 1994. Poster: Use of constructed wetlands by dabbling ducks. North American Ornithological Conference, Missoula, MT.