

EFFECTS OF GRASSLAND FRAGMENTATION ON INSECT SPECIES LOSS, COLONIZATION, AND MOVEMENT PATTERNS

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Abstract. Ecological theory predicts that isolated habitat patches will experience greater rates of species loss and lower rates of recolonization compared to less isolated habitats. As a corollary, corridors of suitable habitat should reduce patch isolation, thereby decreasing species loss and enhancing colonization. Little ecological evidence exists, however, to compare species loss and colonization in habitat patches with and without corridors under field conditions. Using insects in a native grassland habitat, I performed a three-year field experiment that varied fragment size and connectivity to test the hypotheses that corridors influence patterns of insect species loss, rates of recolonization, and insect movement among habitat fragments. I detected few effects of corridors consistent with theoretical predictions. First, corridors generally failed to reduce insect species loss from otherwise isolated grassland patches, except for subtle effects in medium-sized patches. Species richness was slightly higher in medium patches with corridors than in medium isolated patches when averaged over the three years of the study. I observed the strongest positive effect of corridors in the third and driest year of the study. Second, corridors did not significantly influence overall rate of patch colonization, but slightly increased the probability of colonization by less vagile species. Interestingly, corridors did not affect recolonization by rare species, which are often the subject of conservation concern. Third, I characterized individual movement pathways of three insect species in plots with and without corridors. One of the three species significantly preferred corridors, while the other two species moved independently of corridors. Taken together, these results suggest that corridors have the potential to promote movement of organisms among habitat patches, but that their function may depend upon species characteristics, landscape context, patch size, and environmental variation.

Key words: *animal movement; colonization; corridors; field experiment; grasslands; habitat fragmentation; insect diversity; species loss; species richness.*

INTRODUCTION

Ecologists have long recognized that many organisms exhibit patchy distribution patterns, usually in response to spatial variation in environmental conditions or resource distribution (Watt 1947, Wiens 1976, Tilman and Kareiva 1997). The rapid pace of landscape modification by humans over the past half century has introduced novel spatial patterns of organisms and resources. Human activities often sever connections between once-continuous expanses of native habitat (Harris 1984, Wilcox and Murphy 1985, Saunders et al. 1991, Forman 1995), resulting in native habitat patches interspersed with areas of degraded habitat. Native habitat loss and isolation are extremely widespread, both geographically and among habitat types, and pose perhaps the most serious threat to the earth's biological diversity (Soulé 1986, Kareiva et al. 1993, Edwards et al. 1994, Laurance and Bierregaard 1997).

Disruptions to continuous habitats may alter many ecological processes, including nutrient and sediment flow in riparian ecosystems (Binford and Buchenau 1993, Naiman et al. 1993), plant dispersal (Robinson et al. 1992, DeFerrari and Naiman 1994), plant community dynamics (Laurance et al. 1998), plant and animal reproduction (Dooley and Bowers 1998, Jules 1998), and animal movement patterns (Kareiva 1987, Henein and Merriam 1990, Ims 1995, Andreassen et al. 1998). Shifts in animal movement patterns may produce particularly severe consequences. For example, behavioral avoidance of or higher predation rates in modified habitats may reduce movement rates between native habitat fragments, resulting in higher probabilities of species extinction and lower rates of colonization relative to continuous habitats (Wilcove et al. 1986, Laurance and Bierregaard 1997).

One means proposed for moderating the negative effects of habitat isolation on animal movement and species persistence is the preservation of native habitat corridors that structurally link otherwise isolated habitat remnants (Diamond 1975, Wilson and Willis 1975, Forman and Godron 1981, Harris and Scheck 1991, Lindenmayer and Nix 1993, Noss and Cooperrider 1994, Forman 1995). Corridors are supposed to in-

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crease landscape connectivity by facilitating movement of organisms between habitat fragments (Burkey 1989, Saunders and Hobbs 1991, Harris and Silva-Lopez 1992, Fahrig and Merriam 1994), thereby reducing rates of species loss and enhancing probabilities of colonization. Biological conservation efforts aimed at preservation of plant and animal diversity in fragmented landscapes have considered the inclusion of corridors an important strategy in ameliorating the effects of human disturbance (Beier 1993, Arnold 1995, Bueno et al. 1995, Shafer 1997).

Ecological evidence to support the functional importance of corridors for species persistence is scarce, however. Most ecological information on habitat corridors consists of documentation of animal presence and movement in corridors (Wegner and Merriam 1979, Bennett 1990, Bennett et al. 1994, Petit 1994, Haas 1995). Such evidence is necessary, but not sufficient to show that in the absence of corridors, population extinction would occur. A few controlled experiments that have directly examined corridor presence on population persistence have shown positive effects of corridors on persistence for some species (La Polla and Barrett 1993, Gilbert et al. 1998), but not others (Forney and Gilpin 1989). Few experimental field studies, however, have directly compared the combined processes of species loss, recolonization, and animal movement in the presence and absence of corridors. Such information is critical in understanding whether corridors in fragmented landscapes function to reduce habitat and population isolation and thereby contribute significantly to the persistence of native plants and animals (Brown and Kodric-Brown 1977, Lindenmayer 1994).

Theoretical background

The ecological theories of island biogeography (MacArthur and Wilson 1967) and metapopulation dynamics (Levins 1969) provide the conceptual framework for predictions regarding the role of habitat corridors in species persistence. Island biogeography theory has prompted research focused on the influences of fragment size and isolation on species composition, while metapopulation theory has centered attention on persistence of spatially distributed populations (Fahrig et al. 1983, Fahrig and Merriam 1985, Lankester et al. 1991, Harrison 1993, Hanski et al. 1995, Harrison and Taylor 1997).

In relation to habitat corridors, the key prediction from island biogeography theory is that immigration rates should vary inversely with the distance of a fragment from a source of colonists. For terrestrial habitat fragments, such a colonist source could be a continuous expanse of native habitat. Brown and Kodric-Brown (1977) added to the theory by suggesting that island distance may influence extinction rates via this effect on immigration. Specifically, in insular habitats or closely spaced resource patches, immigration rates may

be very high relative to extinction rates, shifting the balance of these two rates in favor of immigration (Brown and Kodric-Brown 1977). These high rates of immigration may effectively decrease the probability of extinction by "rescuing" populations before they reach precariously small sizes, which Brown and Kodric-Brown referred to as the "rescue effect" (Brown and Kodric-Brown 1977: 445). If corridors reduce the effective distance between patches, then they should enhance colonization rates and facilitate the rescue effect.

Metapopulation theory also suggests that corridors can modify species persistence (Hanski and Gilpin 1991, Doak and Mills 1994, McCullough 1996). In metapopulation dynamics, local populations of organisms occur in spatially discrete patches where they undergo periodic colonization and extinction (Levins 1969). Despite the extinction of local populations, the metapopulation can persist indefinitely. Failed colonization of empty patches may occur because of patch isolation (Hansson 1991, Fahrig and Merriam 1994), and the persistence of the metapopulation depends upon recolonization following extinction ("non-equilibrium metapopulation," Harrison and Taylor 1997). Metapopulation theory applied to the dynamics of species in human-induced habitat fragments (Dunning et al. 1995, Harrison and Fahrig 1995, McCullough 1996) suggests that corridors between fragments should increase regional persistence of native species by reducing isolation effects and increasing colonization probability.

To summarize, ecological theory predicts that any mechanism that reduces isolation among habitat patches should also expedite movement of organisms between patches, thereby reducing rates of species loss and enhancing the probability of fragment recolonization. If corridors successfully reduce isolation, then habitat fragments connected by corridors should support more stable populations and perhaps a higher number of species than completely isolated fragments of equal size (Brown and Kodric-Brown 1977, Simberloff and Cox 1987, Bennett 1990).

Current evidence

Consistent with predictions from island biogeography theory, field experiments with insects recolonizing isolated habitat patches (Simberloff and Wilson 1969, Brown and Kodric-Brown 1977, Kruess and Tschamke 1994) have shown that increased distance decreases patch colonization rates and increases extinction probability. The key issue in the present discussion is whether corridors linking habitat fragments functionally reduce habitat isolation sufficiently to prevent population extinction.

Three lines of empirical and modeling evidence suggest the potential for corridors to reduce habitat isolation and modify individual movement behavior, as well as population and community dynamics. First, cor-

ridors can function as movement pathways for animals of various taxa (Merriam and Lanoue 1990, Saunders and Hobbs 1991, Lindenmayer and Nix 1993, Borgella 1995). For example, chipmunks and white-footed mice in an agricultural landscape used wooded fencerows to travel between forest patches (Wegner and Merriam 1979, Henein and Merriam 1990, Merriam and Lanoue 1990, Bennett et al. 1994). Second, simulation models and laboratory and field experiments have shown that populations may persist longer or species richness may be slightly higher in habitat patches connected by corridors than in isolated patches (Fahrig and Merriam 1985, Forney and Gilpin 1989, La Polla and Barrett 1993, Holyoak and Lawler 1996, Schmiegelow et al. 1997, Gilbert et al. 1998, Gonzalez et al. 1998). Third, there is limited evidence that corridors may influence recolonization of habitat patches. Henderson et al. (1985) found that two deciduous forest patches connected by fencerows were recolonized by chipmunks following experimental removal of resident individuals. There were no comparisons of recolonization in forest patches without corridors, however, so it was not possible to assess the relative effect of corridors on recolonization from their study.

In contrast to the evidence cited above, some ecologists have suggested that corridors may have neutral or even negative effects on individual movement and species persistence (Simberloff and Cox 1987, Simberloff et al. 1992, Lindenmayer et al. 1993, Schultz 1998). First, not all species may perceive and use linear strips of vegetation as movement pathways. For example, Hill (1995) frequently found two of four lowland rain forest insect species in forest corridors, but rarely found the two other species there. Because corridors are narrow, linear habitat strips, interior habitat species may perceive them as edge habitat and avoid them (Andreassen et al. 1996, Collinge 1996, Lidicker and Koenig 1996). Second, the narrow, linear shape of corridors may make them difficult for animals to perceive, depending upon an organism's behavior (Tilman et al. 1997). In other words, the likelihood of finding corridors may be minimal for some species. Third, corridors may have negative effects, such as facilitating propagation of disturbance or disease (Simberloff and Cox 1987, Simberloff et al. 1992, Hess 1996). Perhaps most importantly, the lack of ecological field data on the contribution of corridors to population persistence has generated much controversy concerning their implementation as a primary emphasis of conservation plans (Simberloff and Cox 1987, Hobbs 1992, Mann and Plummer 1995). Given the uncertainties regarding corridor effectiveness, some have argued that maintaining or enhancing large blocks of habitat will contribute much more significantly to species persistence than preserving narrow corridors can (Simberloff et al. 1992, Mann and Plummer 1995).

Given the paucity of experimental evidence on the functional importance of habitat corridors, I conducted

a field experiment to directly test specific hypotheses regarding corridors. I studied natural populations of insects in a native, grassland habitat for several important reasons. First, by using an experimental approach, I could assess species composition of study plots before, as well as after, habitat manipulation. Second, I could readily alter the spatial structure of the grassland habitat by mowing specified areas of grassland vegetation. Third, insects are excellent indicators of habitat degradation (Klein 1989, Kim 1993) and strongly influence the distribution and abundance of organisms both at higher and lower trophic levels (Louda 1984, Miller 1993). Finally, the native prairie habitats of North America have suffered loss and isolation to a similar extent as many forested ecosystems (Herkert 1994, Samson and Knopf 1994, Robertson et al. 1997) but have received comparatively little attention in studies of habitat fragmentation.

By manipulating grassland fragment size and corridor presence, this experiment addressed the following questions: (1) Do corridors reduce rates of species loss from grassland fragments? (2) Does this effect depend upon fragment size? (3) Do corridors enhance the rate of insect colonization of grassland fragments? (4) Do corridors affect insect species differentially in the recolonization process? (5) Do certain insect species use corridors as movement pathways? Based on ecological theory and prior empirical evidence, I predicted these outcomes: (1) that insect species loss would be highest in the most isolated grassland fragments, (2) that the benefits of corridors would be most evident for the smallest fragments, (3) that insects would recolonize fragments with corridors faster than isolated fragments, so fragments with corridors would have a higher number of individuals and species earlier in the recolonization process than isolated fragments, (4) that isolated fragments would be mainly recolonized by the most vagile and common species, while fragments with corridors would be colonized by a random subset of all species, and (5) that insects would prefer corridors as movement pathways.

METHODS

Study site

I conducted my field research in the plains of the Front Range of north-central Colorado, USA, ~12 km southeast of Boulder (39°44'58" N, 104°59'22" W; 1740 m [5800'] elevation) during the 1992–1994 growing seasons (June–October). The study area was a native, mixed-grass prairie community located on a 100-ha property managed by the City of Boulder Open Space Department. The approximately 3-ha research site was located on cobbly clay loam soil with north facing, 5–25% slopes. Common grasses present in the study area were western wheatgrass (*Agropyron smithii*), blue grama (*Bouteloua gracilis*), side-oats grama (*Bouteloua curtipendula*), buffalo grass (*Buchloe dactylo-*

ides), and Canada blue-grass (*Poa compressa*), interspersed with the common herbaceous perennials aster (*Virgilus falcatus*), snakeweed (*Gutierrezia sarothrae*), blazing star (*Liatrus punctata*), prairie cone-flower (*Ratibida columnifera*), orange arnica (*Arnica fulgens*), and a sedge species (*Carex pennsylvanica*). I recorded 84 plant species (89%) native to the region and 10 exotic species (11%). I deposited voucher specimens of all plant species observed in study plots in the University of Colorado Herbarium, Boulder, Colorado.

I collected over 300 insect species in the study area over the three growing seasons, with representatives in all of the major insect orders: Coleoptera, Diptera, Hemiptera, Homoptera, Hymenoptera, Lepidoptera, Odonata, and Orthoptera. Voucher specimens of all insect species were deposited in the Entomology Collection of the University of Colorado Museum, Boulder, Colorado, as well as in the Museum of Comparative Zoology at Harvard University, Cambridge, Massachusetts.

Experimental design

In the summer of 1992, I established a three-year field experiment designed to evaluate the influence of grassland fragmentation on insect species loss, colonization, and individual movement patterns. In each of the three years of the study, 1992, 1993, and 1994, I manipulated grassland fragment size and connectivity by mowing specified areas of grassland vegetation. The experimental design included three connectivity treatments and three plot size treatments, arranged in six blocks (Fig. 1). Treatments were arranged in blocks to account for any systematic variation in environmental conditions from north to south across the study area (Sokal and Rohlf 1995). Because the location of the unmowed control plots could not be randomized within blocks, the experimental design was effectively a split-split-plot design, with blocks as the whole plot factor, connectivity as the split-plot factor, and size as the split-split-plot factor (Fig. 1; Nicholls and Margules 1991, Manly 1992). The assignment of treatments in every other block was reversed in orientation to account for any systematic variation in environmental conditions from east to west across the study area. Fragment connectivity ranged from complete connectivity ("control" plots surrounded by unmowed vegetation), to partial connectivity ("corridor" plots surrounded by mowed vegetation except for a 1×10 m strip of unmowed vegetation connecting the fragment to the unmowed grassland), to complete isolation ("isolated" plots surrounded by mowed vegetation). Thus, corridors were linear strips of unmowed vegetation that connected the unmowed grassland fragments to continuous grassland vegetation. Within each connectivity treatment I randomly applied three plot size treatments, spanning three orders of magnitude; 1 m^2 ("small"), 10 m^2 ("medium"), and 100 m^2 ("large"). Each plot was separated from adjacent plots by a distance of 10

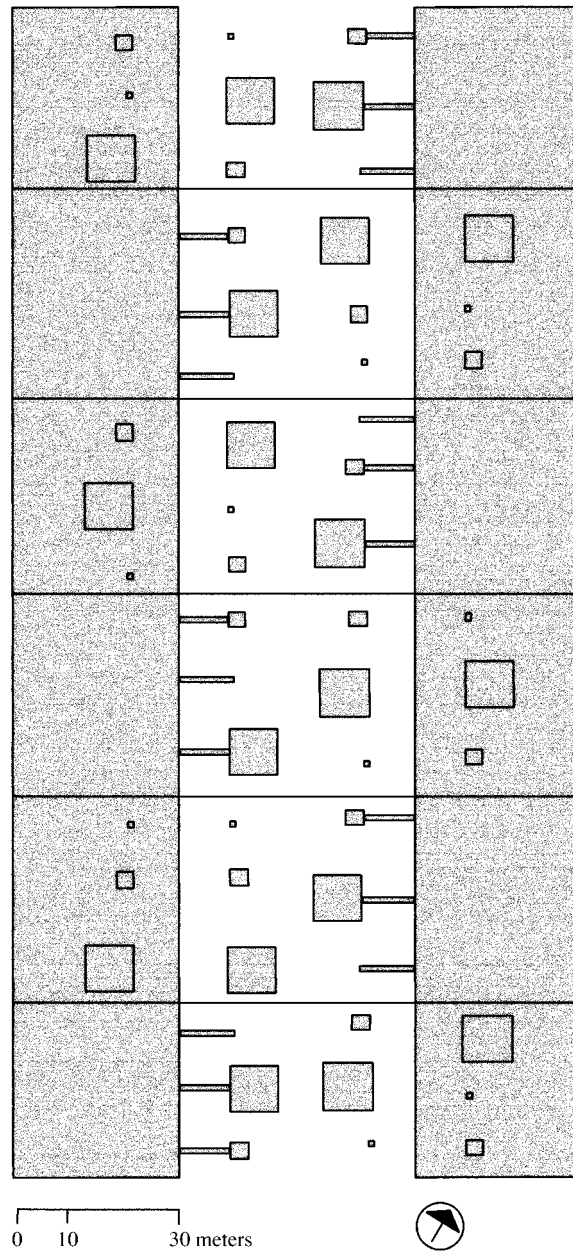


FIG. 1. Split-split-plot experimental design of the field study on insect response to habitat fragmentation. Shaded areas represent unmowed grassland vegetation; white areas represent mowed grassland. Three plot sizes (1 m^2 , 10 m^2 , and 100 m^2) were randomly established in the context of three connectivity treatments (control, corridor, and isolated). Horizontal lines denote whole plot boundaries ($N = 6$). Each plot is separated from adjacent plots by 10 m. The entire study area shown in diagram is ~ 3 ha. The arrow indicates magnetic north.

m. The plot sizes represented the range of those used in other studies of herbaceous plant and insect diversity (Kareiva 1987, Bach 1988, Robinson and Quinn 1988). Each block contained nine treatments (3 connectivity treatments \times 3 sizes) and was replicated six times over

the study site (9 treatments \times 6 replicates/treatment = 54 plots total).

I established the 54 plots at the study site in mid-July 1992 using compass readings, tape measures, and surveyors' flags. Because plant diversity is known to influence insect diversity (Strong et al. 1984), I recorded initial plant species composition in each study plot on 28–31 July 1992. I determined the number of plant species in each plot by first walking the perimeter of each plot and identifying and recording all plant species observed. I then established two transects down the center of each plot, one from the north to south edge, and one from the east to west edge. I identified and recorded all plant species present in 10 \times 10 cm squares located every other 10 cm along each transect.

I imposed the fragment size and connectivity treatments by mowing specified areas of grassland vegetation, according to the experimental design. Mowing was completed on 4 August 1992, 22 June 1993, and 15 June 1994 using gasoline-powered weed eaters as well as a tractor with an \sim 3 m wide "brush-hog" attachment. Mowing reduced the height of the grassland vegetation by 65%, from a mean of 22.27 cm (1 SE = 2.34, N = 20) to 8.96 cm (1 SE = 0.99, N = 20), and removed flowering stalks from grasses and herbs. Grass clippings were scattered over the study area during mowing by the action of the weed eaters, and the relatively constant winds at the study site blew the clippings from the area. Due to the generally dry weather, very little vegetative regrowth occurred in the mowed areas for the two or three months following the mowing treatment. It was necessary once in 1993 (12 August) and once in 1994 (9 August) to trim all vegetation in the mowed areas using gasoline-powered weed eaters several weeks after the initial mowing to ensure that vegetation surrounding the corridor and isolated treatment plots remained short and uniform in height.

Insect species loss

To estimate insect species loss in response to plot size and connectivity, I intensively sampled insect species composition in 1992 and 1993 before and on several dates after mowing. In 1994, I sampled only the 18 10-m² ("medium") plots in conjunction with the recolonization experiment (see *Methods: Recolonization*). I determined insect species composition by sweeping each plot a specified number of times with a 38-cm diameter sweep net over a specified area (Southwood 1978, Evans 1984). In small plots, I swept the entire 1-m² area of the plot (4 sweeps). In medium plots, I swept the entire 10-m² area, using the same number of net sweeps per area as in the small plots (4 sweeps/m² = 40 sweeps). In large plots, I subsampled a 10-m² area of the plot (40 sweeps) as described for medium plots. I then swept the remainder of the area in each large plot and reserved the net contents as a separate sample. This ensured that the entire area of every plot was swept by the net, thus avoiding any differences in

subsequent species composition due to unequal removal of insects in plots of different sizes. I defined species loss as the disappearance of a species from a plot subsequent to mowing. All insect samples were collected between 1100 and 1500 on warm, sunny days in order to standardize sampling conditions.

I conducted pretreatment insect sampling in each plot on 31 July 1992 and 15 June 1993. Post-treatment insect sampling was conducted at \sim 4-wk intervals during 1992 and 1993 following the mowing treatment. Sampling dates were 27 August, 23 September, and 24 October 1992, and 13 July, 10 August, 9 September, and 5 October 1993. In addition to sampling in each study plot, on all post-treatment sampling dates I also collected from areas that had been mowed. For mowed samples, I conducted 40 sweeps over a 10-m² area in the central mowed area (Fig. 1), at least 10 m from the closest unmowed plot edge. Insects were transferred from sweep nets to labeled plastic bags, frozen, and sorted to morphospecies. Insect species identifications were determined with the assistance of the insect collections and curatorial staff at the University of Colorado and Colorado State University, or insects were sent to entomological specialists for determination (see Collinge 1995 for a complete list of all insects recorded during the study).

Recolonization

To assess insect recolonization of habitat fragments with and without corridors, I conducted a second experiment in 1994 within the context of the main field experiment described above. For this recolonization experiment, I used only the 18 medium-sized (10-m²) plots of the three connectivity treatments: control, corridor, and isolated (N = 6 plots/treatment) (Fig. 1). The experiment involved reducing insect abundance in medium-sized plots, followed by measurement of recolonization. On 11 August 1994, \sim 8 wk after the mowing treatment, I sampled insect species composition by sweeping the entire area of each 10-m² plot (40 sweeps) as described in *Methods: Insect species loss*. A pilot study completed in early August indicated that after 400 continuous sweeps in a 10-m² area, the number of insects sampled decreased from 30–40 individuals per plot to 4–6 individuals (S. Collinge and C. Buehning, *personal observation*). Therefore, to simulate local extinction, I reduced insect abundance in each plot by following the initial 40 sweeps described above with 360 more sweeps. The contents of the first 40 sweeps were kept as a record of initial conditions and the final 40 sweeps were kept as a record of species composition at the plot "depletion" stage. The insects captured in the remaining 320 sweeps were released in grassland habitat \sim 800 m from the study area.

To compare recolonization of the control, corridor, and isolated plots, I sampled insect species composition in each plot 1 h, 1 d, 2 d, 8 d, and 14 d following plot depletion. I defined recolonization operationally as the

arrival of an individual insect in a plot subsequent to plot depletion. Over the two-week period of this recolonization experiment 150 insect species were collected.

Insect movement

To assess behavioral responses of individual insects to corridors, I characterized movement patterns for three species of insects in the context of the main field experiment in June and July of 1994. The three species, *Eleodes extricata* Say (Coleoptera: Tenebrionidae), *Phyllophaga lanceolata* Say (Coleoptera: Scarabidae), and *Gryllus* sp. (Orthoptera: Gryllidae) were chosen to represent different insect orders and varied in body size, primary movement mode, and use of food resources.

Eleodes extricata is a widespread, grassland darkling beetle (W. Steiner, *personal communication*) classified as a scavenger, feeding primarily on decaying vegetation, fungi, and seeds (Borror and White 1970). *E. extricata* has a streamlined body shape and appeared to be more mobile on foot than the June beetle, *Phyllophaga lanceolata*. *P. lanceolata* occurs widely throughout the Great Plains of North America (Luginbill and Painter 1953). Larvae feed in the soil on roots of grasses and other plants, while adults feed above ground, mainly on flowers and foliage (Borror and White 1970). Adults appear from late April to mid-July in Colorado and were found most commonly on stems of herbs or grasses at the study site. June beetle adults are heavy-bodied and are relatively poor fliers, so their movement is primarily on foot (Luginbill and Painter 1953). The field cricket, *Gryllus* sp. has a relatively large body, with chewing mouthparts for feeding primarily on vegetation (Helfer 1987). Its flying ability is poorly developed and so it moves by a combination of walking and short jumps.

I conducted all direct observations of individual movement on warm, sunny days from 28 June to 20 July 1994 between 0730 and 1300. For these observations, I collected individual insects from outside the study area and marked them on the thorax with a spot of brightly colored paint (Bach 1984). I released the marked insects adjacent to the medium-sized (10-m²) study plots of the corridor and isolated treatments (Fig. 1). For the corridor treatment, I released insects in one of three locations within the unmowed corridor, while for the isolated treatment, I released insects in analogous locations relative to the isolated plots. Most releases ($N = 23$, 66%) were made equally distant from the fragment edge and the start of the unmowed area, and centered with respect to the plot edge. Other insects were released at the edge of the fragments ($N = 4$, 11%) or at the edge of the unmowed grassland ($N = 8$, 23%). Approximately equal numbers of individuals of each of the three species were released in corridor and isolated treatments (*Eleodes*, $N = 7$ corridor, $N = 8$ isolated; *Phyllophaga*, $N = 4$ corridor, $N = 6$ isolated;

Gryllus $N = 5$ corridor, $N = 5$ isolated). After release, I observed each insect for a standardized 30-min period from a distance of 2 m to avoid modifying their behavior. Every 30 s during the observation period, I recorded the location of the insect using a numbered bamboo skewer (method modified from Wiens and Milne 1989, Wiens et al. 1993, With 1994). At the end of the thirty-minute period, I reconstructed and recorded the insect's movement pathway.

Data analyses

Insect species loss.—I used the 1992 insect samples to assess the effectiveness of mowing as a means of isolating grassland plots by comparing the number of insect species (species richness) observed in unmowed and mowed areas. Because my overall sampling effort in unmowed areas was much greater than in mowed areas ($N = 216$ unmowed samples, $N = 18$ mowed samples), I compared insect species richness in unmowed and mowed areas for an equal sampling effort. For this comparison, I generated species accumulation curves using 18 samples each from the unmowed control area, large fragments, medium fragments, small fragments, and mowed area (fragments = isolated plots; $N = 6$ replicates \times 3 dates = 18 samples of each). Samples from the control area, large and medium fragments, and mowed area were directly comparable to each other because they each represented 40 net sweeps over a 10-m² area. Small fragments represented four net sweeps over a 1-m² area.

Plant species richness was estimated in 1992 only as the total number of plant species observed per plot. I used linear regression to estimate the relationship between plant species richness and plot area, as well as insect species richness and plot area at the start of the experiment. To evaluate the association between plant and insect species richness, I conducted two correlation analyses: for the first analysis, I combined the data for the three plot sizes, and in the second, I analyzed the data for each plot size separately.

To compare insect species richness among the nine treatments over the two-season sampling period of July 1992 to October 1993, I performed within-subjects analysis of variance (ANOVA) according to the split-split-plot experimental design. For these analyses, the six blocks (Fig. 1) were treated as the subjects in which insect species richness was sampled at each level of connectivity (factor A, three levels), plot size (factor B, three levels), and time (factor C, seven levels) (Keppel 1982). Because of variation in environmental conditions among blocks, I assumed block \times treatment interactions, and therefore examined the effect of each factor in the ANOVA using the block \times factor interaction as the error term (Keppel 1982, Newman et al. 1997). I interpreted the sphericity test on orthogonally transformed variables to determine the covariance structure of the data set, and used the results to deter-

mine whether to interpret unadjusted univariate results or MANOVA results (SAS Institute 1990).

For each within-subjects ANOVA, I performed three a priori orthogonal comparisons to test hypotheses regarding relationships among the three connectivity treatments (SAS Institute 1990, Sokal and Rohlf 1995). The first comparison tested the hypothesis that corridors effectively reduced plot isolation; it compared control and corridor plots to isolated plots. The second comparison tested the hypothesis that corridors did not reduce the effects of isolation, so I compared control plots to corridor and isolated plots. The third tested the hypothesis that the partial connectivity afforded by corridors partially ameliorated the negative effects of isolation, so I examined the linear effect of the connectivity treatments. In other words, this third comparison tested the hypothesis that corridor plots were intermediate to control and isolated plots. For all linear contrasts, I used the block \times connectivity interaction as the error term (Newman et al. 1997). Because of differences in sampling effort among plot sizes, I also compared insect species richness among connectivity treatments for each plot size separately. For the seven dates in 1992 and 1993, I performed within-subjects ANOVA, followed by the planned comparisons described above.

For medium plots I gathered insect species richness data for all three years of the study: 1992, 1993, and again in 1994, in conjunction with the recolonization experiment. I compared samples taken 8 wk after the fragmentation treatment was imposed in each year (23 September 1992, 10 August 1993, and 11 August 1994) using within-subjects ANOVA and the three planned comparisons described above. All statistical analyses were conducted with SAS (SAS Institute 1990) or JMP (SAS Institute 1997) and all P values were deemed significant using $\alpha = 0.05$.

Recolonization.—Insect species composition in each of the 10-m² study plots before and during recolonization was quantified and described in several ways. For each sampling time (initial, immediately following depletion, 1 h, 1 d, 2 d, 8 d, and 14 d following depletion), I recorded insect abundance as the total number of individual insects observed in each 10-m² plot. I also determined insect species richness for the set of samples described above. In addition, the 150 insect species observed in this experiment were categorized according to three attributes; body size, commonness, and movement mode; to determine if these characteristics explained significant variation among species in their pattern of recolonization of grassland fragments (Laurance 1991, Brown et al. 1993). Body size was characterized as large (≥ 7 mm in length) or small (≤ 2 mm in length). “Common” species were those for which 20 or more individuals were sampled during the two-week period, and “rare” species were those for which two or fewer individuals were sampled over the same period. For movement mode, I placed insects into

three categories: crawl with short flights, fly, and jump. I determined the number of species in body-size classes and movement modes for a subset of the samples (1 h, 1 d, and 14 d). I calculated the abundance (number of individuals) of rare and common species for the same three samples (1 h, 1 d, and 14 d) for statistical analyses.

I compared insect abundance, overall species richness, and abundance or richness of the particular species groups described above for each connectivity treatment over the two-week recolonization period using within-subjects ANOVA for a split-plot design, followed by the three a priori comparisons described above. All analyses were conducted with SAS (SAS Institute 1990) and JMP (SAS Institute 1997).

Insect movement.—For each observed insect movement pathway, I calculated the total distance traveled, which was the total path length taken during the observation period, and the rate of movement, which was the total distance traveled by an individual insect divided by the number of minutes observed. Some insects left the plot or were lost during the 30-min observation period. Because truncated observation periods may bias downward estimates of total distance traveled (Johnson et al. 1992), I performed univariate ANOVA using only those data for insects observed for the entire 30-min period ($N = 3$ for all species and treatments except for *Gryllus* sp. in the corridor treatment, where $N = 2$). Additionally, to assess whether individual insects showed an affinity for the corridors, I compared the number of observations recorded in the corridors versus outside the corridors using a chi-square analysis. For insects released in corridor plots, I tabulated the number of observation points in the unmowed corridor and the number outside the corridor. For insects released near isolated plots, I recorded the number of observation points in a 1 \times 10 m mowed area, directly analogous to the location of the unmowed corridor, and the number outside this area. These totals were compared for each species separately using 2 \times 2 contingency table analyses (Zar 1996), which tested the null hypothesis that the number of observation points inside versus outside the corridor area was not associated with corridor presence.

RESULTS

Insect species loss

Effectiveness of mowing treatment.—Mowing was an effective means of isolating grassland fragments, as it significantly decreased the suitability of the grassland habitat for the majority of insect species observed in this study. Seventy-two percent (221/305) of the insect species collected at the study site were never found in the mowed areas (Collinge 1995). For an equal sampling effort ($N = 18$ samples) in unmowed control areas, large and medium fragments, and mowed areas, the unmowed plots accumulated many more insect spe-

TABLE 1. Results of within-subjects ANOVA (F ratios) on insect species loss from study plots.

Source	1992 and 1993					1992–1994	
	df	All plot sizes combined	Large	Medium	Small	df	Medium plots
Connectivity	2, 10	0.56	1.14	0.43	1.11	2, 10	3.51
Size	2, 10	259.24***					
Time	6, 30	59.79***	51.50***	60.84***	9.22***	2, 10	24.78***
Connectivity \times size	4, 20	1.24					
Connectivity \times time	12, 60	22.58***	0.39	1.55	0.90	4, 20	1.15
Size \times time	12, 60	19.54***					
Connectivity \times size \times time	24, 118	0.86					
Contrasts							
Corridors effective	1, 10	0.65	0.03	0.79	1.64	1, 10	5.61
Corridors ineffective	1, 10	1.14	1.92	0.05	0.51	1, 10	0.02
Corridors intermediate	1, 10	1.17	0.81	0.40	1.34	1, 10	2.12

Notes: For these analyses, blocks were subjects ($N = 6$), and within-subjects effects were connectivity, size, and time. All effects were tested using the effect \times block interaction as the error term.

*** $P < 0.001$.

cies (115) than the mowed areas (70). Large fragments were essentially equal to the control area in cumulative species richness, while medium fragments were slightly lower. Small fragments contained the fewest species, but this also represented the fewest number of net sweeps (4 sweeps vs. 40 for all other samples). The species accumulation curves reached asymptotes by samples 13–16 (out of 18 samples), suggesting that few additional species would have been collected with additional sampling.

Correlation between plant and insect species richness.—Plant and insect species richness both increased with plot area, and they correlated significantly with one another when data for the three plot sizes were combined (Pearson's $r = 0.805$, $N = 54$, $P < 0.001$). Within each plot size, plant and insect species richness were not highly correlated, although large plots tended toward a positive association (large, Pearson's $r = 0.405$, $N = 18$, $P = 0.095$; medium, $r = 0.329$, $N = 18$, $P = 0.183$; small, $r = -0.030$, $N = 18$, $P = 0.908$). Because plant species richness did not significantly correlate with insect species richness for each plot size, it was not used as a covariate in further analyses of insect species richness.

Insect community response.—Not surprisingly, large plots maintained higher insect species richness than small plots throughout the study (size effect; Table 1, Fig. 2), but contrary to prediction, connectivity treatments did not vary significantly in species richness (connectivity effect; Table 1). Insect species richness varied significantly among the seven sampling dates in 1992 and 1993 (Table 1; time effect, $P < 0.001$), with highest values in June and July of both years in all plots, declining in September and October (Fig. 2). Further examination of connectivity treatment effects via the three planned comparisons described above yielded no statistically significant results ($P > 0.05$ for

all comparisons), thus corridors did not prevent species loss over the 1992–1993 study duration.

I obtained similar results when I performed analyses of insect species richness for each plot size separately for 1992 and 1993. Insect species richness declined seasonally in all plots (Table 1, time effect: large, medium, and small; all $P < 0.001$), but connectivity treatments did not vary significantly in species richness (connectivity effect, $P > 0.05$ for all plot sizes). When I examined insect species richness in medium plots for all three years of the study, I observed a marginal, positive effect of corridors on species richness (Table 1; contrast “corridors effective,” $F_{1,10} = 5.61$, $P = 0.069$; Fig. 3).

Recolonization

The number of individual insects per plot (insect abundance) and insect species richness both increased in all plots during the two-week recolonization period (Table 2, time effect, $P < 0.05$ for both abundance and richness; Fig. 4). Neither abundance nor species richness differed significantly among connectivity treatments, however (Table 2). Connectivity treatments were similar in their pattern of change in insect abundance and species richness over the 14-d recolonization period (nonsignificant connectivity \times time interaction; Table 2).

One hour after depletion, the increase in insect abundance in isolated plots (Fig. 4) was due to rapid movement into these plots by a large number of individuals of two very common species, an ant, *Leptothorax tricaratus* (Emery) (Hymenoptera: Formicidae), and a leafhopper, *Cuerna striata* (Walker) (Homoptera: Cicadellidae). There was a general trend for fewer insects to colonize isolated plots than control and corridor plots following depletion (Fig. 4), although this effect was highly variable and not statistically significant (Table 2).

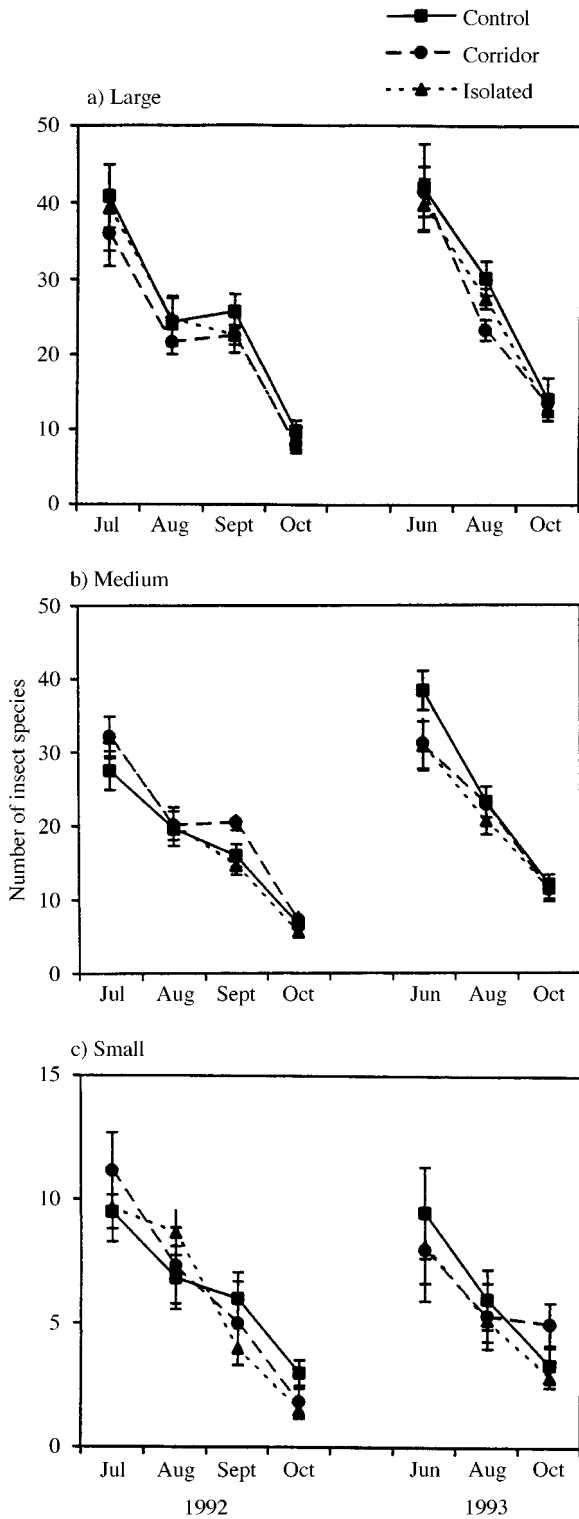


FIG. 2. Number of insect species (species richness) in (a) large, (b) medium, and (c) small plots for three connectivity treatments on four dates in 1992 and three dates in 1993. The July 1992 sample and June 1993 sample were taken prior to the mowing treatment, while the rest of the samples were taken after the mowing treatment. Means ± 1 SE are presented.

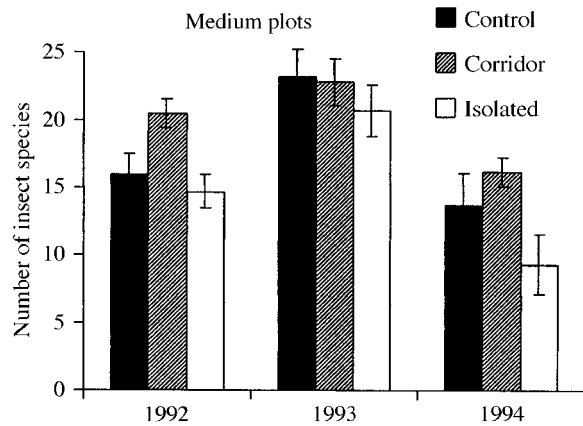


FIG. 3. Number of insect species (species richness) in 10-m² control, corridor, and isolated grassland plots in 1992, 1993, and 1994. Samples were collected eight weeks after the fragmentation treatments were established in each year: 23 September 1992, 10 August 1993, and 11 August 1994. Means ± 1 SE are presented.

Corridors did not differentially affect colonization of study plots by insect species grouped according to movement mode, rarity, or body size (Table 3). One exception to this general pattern was that there was a marginal, positive effect of corridors on colonization by less mobile insects, those that move primarily by crawling, with occasional short flights (e.g. beetles and true bugs), (Table 3; corridors effective, $F_{1,10} = 6.27$, $P = 0.067$). Highly mobile insects (flying and jumping) colonized connected and isolated plots equally (Table 3; no significant connectivity effect or time \times connectivity interaction). Corridors did not differentially affect colonization by large and small species, nor by rare and common species (Table 3, no significant connectivity effects).

Insect movement

Insect movement rate and distance traveled by the three species observed did not vary among connectivity

TABLE 2. Results of within-subjects ANOVA (F ratios) on insect abundance and insect species richness on five sampling dates (1–14 d) during the recolonization period.

Source	df	Insect abundance	Species richness
Connectivity	2, 10	1.58	1.26
Time	4, 20	5.98**	3.36*
Connectivity \times time	8, 40	0.55	0.71
Contrasts			
Corridors effective	1, 10	2.09	2.29
Corridors ineffective	1, 10	0.03	0.12
Corridors intermediate	1, 10	0.54	1.15

Notes: For this analysis, blocks were subjects ($N = 6$), with connectivity and time as within-subjects effects. All effects were tested using the effect \times block interaction as the error term.

* $P < 0.05$, ** $P < 0.01$.

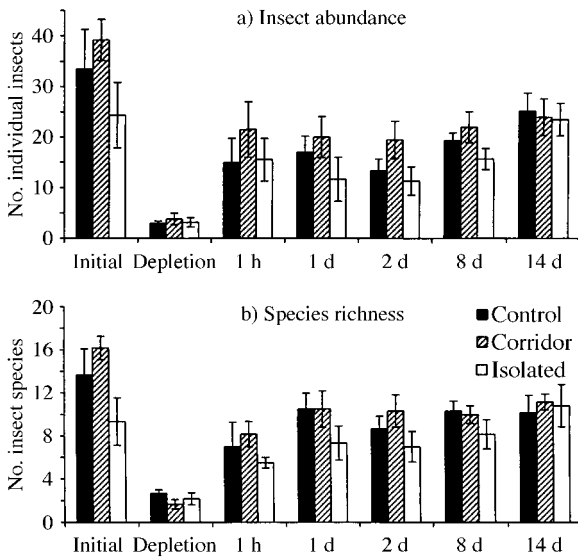


FIG. 4. (a) Number of individual insects recorded in 10-m² control, corridor, and isolated grassland plots at each stage of recolonization. Means \pm 1 SE are presented. (b) Number of insect species recorded in 10-m² control, corridor, and isolated grassland plots before and after depletion.

treatments or species (Table 4). Despite differences in relative mobility, darkling beetles, *Eleodes extricata*, moved 10–11 m; June beetles, *Phyllophaga lanceolata*, moved 4–11 m; and crickets, *Gryllus* sp. moved 8–10 m during the 30-min observation periods. The greatest discrepancy in movement distance between connectivity treatments was for *P. lanceolata*, which moved further in the presence than in the absence of corridors (Table 4), but individuals were highly variable and this difference was not statistically significant.

Comparisons between connectivity treatments of the number of observation points in the area occupied by the corridor versus points outside the corridor area revealed significant shifts in movement behavior for darkling beetles, *Eleodes extricata*, but not for June beetles or field crickets. Darkling beetles modified their movement when corridors were present ($X^2 = 80.62$, $df =$

1, $P < 0.001$). In the presence of corridors, beetles spent a much greater proportion of the observation periods in the unmowed corridor than in the adjacent mowed grassland, whereas when corridors were absent, beetles spent equal time in both areas. For June beetles and crickets, the proportion of time spent in corridors was unaffected by corridor presence (June beetles: $X^2 = 0.127$, $df = 1$, $P > 0.5$; crickets: $X^2 = 0.552$, $df = 1$, $P > 0.5$).

DISCUSSION

If habitat corridors facilitate the rescue effect as predicted from ecological theory, then fragments with corridors should have lower rates of species loss and higher rates of colonization than isolated fragments, mediated by increased animal movement via corridors. In this field experiment with grassland insects, I detected few effects of corridors consistent with these theoretical predictions. First, corridors generally failed to reduce insect species loss from otherwise isolated grassland patches, except for subtle effects in medium-sized patches. Species richness was marginally higher in medium patches with corridors than in medium isolated patches when averaged over the three years of the study (Fig. 3). Second, corridors did not significantly influence overall rate of patch colonization, and had only slight positive effects on colonization by insects with limited mobility (Table 3). And third, for one of the three species observed, corridors significantly modified movement activity.

Insect species loss

Species loss data indicated that corridors had slight positive effects in medium plots, but not small or large plots. In medium plots, species loss was marginally reduced in corridor plots compared to isolated plots when averaged over the three years of the study. This effect was only marginally statistically significant ($P = 0.069$), but may have some biological significance. If corridors infrequently but positively influence species persistence, then local extinction may be prevented under particular circumstances. These results suggest

TABLE 3. Within-subjects ANOVA results (F ratios) on species richness (by movement mode and body size) or abundance of individuals (rarity) for species groups for samples collected 1 h, 1 d, and 14 d after plot depletion.

Source	df	Movement mode			Rarity		Body size	
		Crawl/short flight	Fly	Jump	Rare	Common	Large	Small
Connectivity	2, 10	3.13	0.94	0.34	0.68	0.33	1.89	0.09
Time	2, 10	4.03	3.94	4.06	10.90**	3.30	3.56	2.36
Connectivity \times time	4, 20	1.79	0.17	2.11	1.43	0.51	1.98	1.29
Contrasts								
Corridors effective	1, 10	6.27	0.08	0.27	1.36	2.22	2.39	0.15
Corridors ineffective	1, 10	1.56	1.71	0.66	0.34	0.01	3.22	0.01
Corridors intermediate	1, 10	4.71	0.85	0.60	1.02	0.13	3.73	0.07

Notes: For these analyses, blocks were subjects ($N = 6$), and connectivity and time were within-subjects effects. Note that all effects were tested using the effect \times block interaction as the error term.

** $P < 0.01$.

TABLE 4. Movement rates (cm/min) and total distances moved (m) for 30-min observation periods of three species of grassland insects released adjacent to 10 m² fragments with corridors and without corridors.

Species	Corridor				Isolated			
	Rate (cm/min)		Distance (m)		Rate (cm/min)		Distance (m)	
	Mean	1 SE	Mean	1 SE	Mean	1 SE	Mean	1 SE
<i>Eleodes extricata</i>	35.70	17.17	10.57	5.06	38.67	13.13	11.60	3.94
<i>Phyllophaga lanceolata</i>	38.05	11.84	11.42	3.55	15.33	6.71	4.60	2.01
<i>Gryllus</i> sp.	28.28	9.38	8.49	2.82	34.00	9.60	10.20	2.88

Note: $N = 3$ for all species and treatments except for *Gryllus* sp. in the corridor treatment, where $N = 2$.

the possibility of an interaction of fragment size and connectivity; in other words, the relative effect of corridors may depend significantly on fragment size. This prospect warrants further observational and experimental investigation to identify conditions under which corridors may be beneficial.

At least two mechanisms may produce greater species loss from isolated relative to control and corridor plots: (1) greater local extinction in isolated patches or (2) differential insect movement rates from isolated patches. Higher extinction in isolated patches could be from edge effects that reduce habitat quality, or reduced habitat area and population sizes relative to patches with corridors. In this experiment, corridors added to the overall area of small plots by 1000%, of medium plots by 100%, and of large plots only by 10%. In general terms, increases in native patch area due to corridors may enhance persistence of native species if the narrow corridor is suitable habitat. Corridors are not likely to be suitable habitat for obligate interior species, however (Hill 1995, Collinge 1996, Lidicker and Koenig 1996). Random diffusion of insects from patches with different perimeter/area ratios would result in greater loss of individuals from small isolated patches than medium or large patches. Corridors may mediate loss via random diffusion by facilitating movement back into patches, thereby producing the rescue effect.

In medium plots, effects of corridors on species loss varied among years of the study. The largest difference in species richness between corridor and isolated plots eight weeks after fragmentation occurred in 1994 (Fig. 4). Because this was the third year of the study, the greater difference may have been due to cumulative effects of habitat isolation on species richness over three growing seasons. Additionally, 1994 was the warmest and driest of the three years of the study (Weather Enthusiasts of Boulder 1992, 1993, 1994). In years when resources are more limited, the effect of corridors may be more pronounced. This underscores the importance of looking further at the effects of corridors under varying resource conditions.

Ecologists have rarely measured species loss in habitat fragments with and without corridors under field conditions, so it is difficult to assess the generality of these findings. Schmiegelow et al. (1997) detected a

small but consistent increase in bird species richness in connected versus isolated forest fragments, due possibly to enhanced movement via corridors (Machtans et al. 1996) or to increased area of connected patches. In a recent study of microarthropods in moss patches, Gilbert et al. (1998) and Gonzalez et al. (1998) observed depressed rates of species extinction in connected versus isolated patches. Moreover, they found that predators declined more dramatically in isolated patches than did nonpredators. In field experiments with single species (La Polla and Barrett 1993, Andreassen et al. 1996), corridors increased population densities of voles relative to that in isolated patches. Laboratory microcosm studies suggest that corridors may increase population persistence of a single species (Forney and Gilpin 1989) and regional persistence of a protist predator-prey interaction (Holyoak and Lawler 1996).

Recolonization

Results of the recolonization experiment hinted that corridors may potentially influence the rate at which certain insect species recolonize grassland fragments. Overall, insect abundance and species richness were not significantly affected by corridors. But, corridors had a slight positive effect on recolonization by less mobile insects, which has the potential to affect species composition in recolonized fragments. As predicted, corridors did not affect recolonization probabilities of highly vagile and common species. Interestingly, corridors also did not enhance recolonization rates for rare species over the time frame of this study.

Corridors slightly decreased isolation of grassland fragments for less mobile insect species and therefore increased colonization rates, in a manner similar to the distance effect for mangrove islands (Simberloff and Wilson 1969), thistle plants (Brown and Kodric-Brown 1977), and clover patches (Kruess and Tscharrntke 1994). It is more difficult, however, to directly compare recolonization results with similar ecological investigations of corridors, because such studies are rare. In a study of chipmunks in an agricultural landscape, Henderson et al. (1985) found that chipmunks used fence-row corridors to recolonize two forest patches following local extinction. The authors concluded that these fence-rows facilitated the rescue effect and were thus

critical for species survival (Henderson et al. 1985). The rapid recolonization of grassland fragments with corridors that I observed is similar to the phenomenon observed for chipmunks (Henderson et al. 1985).

Other studies have shown that animal species vary in their use of corridors (Laurance 1990, 1991, Lindenmayer 1994) based on life history attributes. This study, however, is one of few to examine recolonization in relation to variation in species characteristics. Corridors did not facilitate recolonization by species based on body size or rarity. Of particular interest for future study is the result that, as predicted by theory, less mobile insects tended to benefit more from corridors than did more mobile insects.

During the recolonization process, most species groups were not found predictably in one connectivity treatment vs. another (Table 3), suggesting that these species did not perceive or respond to these linear grassland strips as corridors. This finding is relevant to recent suggestions that movement corridors may often be diffuse, species specific, and difficult to identify in spatially heterogeneous landscapes (Taylor et al. 1993, Gustafson and Gardner 1996). Landscape connectivity likely depends on how particular species movement patterns interact with landscape structural features (Harrison and Fahrig 1995, Schumaker 1996). Future studies should continue to assess the influence of linear habitat features on animal movement and population persistence, but should also explore individual movement patterns and population persistence in the context of a variety of spatial arrangements of native habitat (Wiens and Milne 1989, Ims 1995, Collinge and Forman 1998).

Insect movement

Differential insect movement into plots with and without corridors may have mediated insect species loss and recolonization rates in this field experiment. Observations of individual movements showed that one of the three species was strongly affected by the spatial structure of the grassland vegetation. Specifically, darkling beetles concentrated their movement activity in corridors. Movement rates and total distances moved by all three species, however, were similar in mowed and unmowed grassland vegetation. These observations are inconsistent with other studies of darkling beetle movement in similar arid grassland habitats, which have revealed that beetle movement distances are strongly influenced by vegetation structure (Wiens and Milne 1989, Crist et al. 1992). In particular, beetles moved further over bare ground than in areas scattered with cactus and shrubs (Crist et al. 1992). Members of a related group, the carabid beetles, have exhibited higher movement rates across less preferred habitats (Vermeulen 1994).

A 30-min observation period captures only a fraction of an insect's daily movement patterns. Pitfall trapping may serve as a good indicator of insect habitat use

(Loreau and Nolf 1994), because it integrates movements over a longer period of time. I obtained limited information on the three species observed here by establishing pitfall traps at this study site in July 1994 (Collinge 1995). Generally, pitfall trap data indicated that darkling beetles significantly preferred unmowed areas to mowed areas, while crickets showed no preference. June beetles were captured in low numbers, precluding a reliable interpretation of their habitat use.

Many investigations have suggested that corridors may function as both habitat and movement pathways (Bennett et al. 1994). For example, resident chipmunks in an agricultural landscape used wooded fencerows as habitat, while transient chipmunks used fencerows to travel between forest patches (Bennett et al. 1994). Here, at least one species, *Eleodes extricata*, used grassland corridors as both preferred habitat and movement pathway. Ultimately, it would be informative to directly link individual movement patterns with population dynamics (e.g., Turchin 1998). In this study, the species for which I obtained movement data were not sampled in the monthly sweep net samples, precluding such an analysis.

Several factors may interact to determine the directionality and duration of an insect's movement pattern, such as whether it is in its dispersal phase, its relative mobility (With 1994), as well as the spatial distribution of its resources (such as food plant or mates, Loreau and Nolf 1994). Furthermore, the amount and extent of movement likely depends upon habitat quality; carabid beetles moved less in high quality than in poor-quality hedgerows (Petit 1994).

Further, detailed studies and models of habitat use and animal movement in relation to habitat spatial structure are needed. Movement patterns may serve as a record of animal perception of, and response to, particular structural elements in the environment (Mader et al. 1990, Loreau and Nolf 1994, With 1994, Turchin 1998). Perception and response to spatial heterogeneity in the environment may also provide clues to the persistence capabilities of particular species (den Boer 1981). As humans continue to alter the spatial structure of native habitats, it is critical to understand and accurately predict how animals will move through and be affected by these altered environments.

Conclusions and future directions

Ecological theory predicts that corridors should increase movement among habitat patches, thereby increasing species persistence and probability of recolonization. In this study, corridors functioned as predicted for some insect species some of the time. While the magnitude of the effects was relatively small, the direction of the effects was qualitatively consistent with predictions. Corridor effects varied among species, among years of the study, and among plot sizes.

Overall, these results suggest four main conclusions. First, corridors have the potential to bolster exchange

of organisms among habitat patches. Marginal, positive effects of corridors were observed for medium plots over the three-year study period. Second, corridors did not enhance recolonization of plots by rare species, which are often the subject of conservation concern. If corridors differentially benefit common species, perhaps because of strong edge effects, then their use as a conservation tool may have limited value. Third, corridors had slight positive effects for less mobile insect species, but did not affect recolonization of grassland fragments by highly vagile insects. This underscores the importance of linking the spatial scale of a habitat corridor to the spatial scale at which animals perceive and move through the habitat. Fourth, the majority of variation in insect species richness observed in this study was attributable to plot area, not corridor presence. Assuming equal habitat quality, fragment area is likely the most critical determinant of species richness. In a recent study that distinguished habitat loss effects from fragmentation per se, loss, not fragmentation, determined species persistence (Fahrig 1997). Given that corridor effects may be weak and difficult to detect, conservation monies may be better spent increasing the size of protected areas than establishing corridors.

This study suggests future directions for research on habitat linkages and species persistence. In this experiment, grassland fragments were surrounded by mowed areas composed of the same habitat type, but reduced in quality for most insect species. In many fragmentation studies, habitat fragments are embedded in a surrounding matrix of a different habitat type, such as boreal forest fragments and nearby clear cuts (Schmiegelow et al. 1997), moss patches surrounded by bare rock (Gilbert et al. 1998), and remnant deciduous forest patches in an agricultural matrix (Wegner and Merriam 1979, Bennett et al. 1994). The weak effects of corridors that I observed here may have been due to the fact that the mowed grassland was less suitable habitat for these insect species (i.e., habitat degradation) (Doak 1995), but was not completely unsuitable habitat (i.e., habitat loss). In contrast, for specialist woodland bird and mammal species or microarthropods in moss patches, clear cuts, cultivated fields, and bare rock may represent unsuitable, not less suitable habitat. Hence, the landscape context of particular habitat fragments and corridors may importantly modify corridor function, and warrants further examination. Additionally, the results identify a potential interaction between corridor function and habitat patch size, as well as a possible link between corridor function and environmental variation. Further understanding of these relationships will help to refine our discussion of habitat corridors, from an emphasis on whether corridors affect species persistence, to predictions of the particular conditions under which corridors may modify species persistence.

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LITERATURE CITED

- Andreassen, H. P., S. Halle, and R. A. Ims. 1996. Optimal width of movement corridors for root voles: not too narrow and not too wide. *Journal of Applied Ecology* **33**:63–70.
- Andreassen, H. P., K. Hertzberg, and R. A. Ims. 1998. Space-use responses to habitat fragmentation and connectivity in the root vole *Microtus oeconomus*. *Ecology* **79**:1223–1235.
- Arnold, G. W. 1995. Incorporating landscape pattern into conservation programs. Pages 309–337 in L. Hansson, L. Fahrig, and G. Merriam, editors. *Mosaic landscapes and ecological processes*. Chapman and Hall, London, UK.
- Bach, C. E. 1984. Plant spatial pattern and herbivore population dynamics: plant factors affecting the movement patterns of a tropical cucurbit specialist (*Acalymma innubum*). *Ecology* **65**:175–190.
- Bach, C. E. 1988. Effects of host plant patch size on herbivore density: patterns. *Ecology* **69**:1090–1102.
- Beier, P. 1993. Determining minimum habitat areas and habitat corridors for cougars. *Conservation Biology* **7**:94–108.
- Bennett, A. F. 1990. Habitat corridors: their role in wildlife management and conservation. Department of Conservation and Environment, Melbourne, Australia.
- Bennett, A. F., K. Henein, and G. Merriam. 1994. Corridor use and the elements of corridor quality: chipmunks and fencerows in a farmland mosaic. *Biological Conservation* **68**:155–165.
- Binford, M. W., and M. Buchenau. 1993. Riparian greenways and water resources. Pages 69–104 in D. S. Smith and P. C. Hellmund, editors. *Ecology of greenways*. University of Minnesota Press, Minneapolis, Minnesota, USA.
- Borgella, R. 1995. Population size, survivorship, and movement rates of resident birds in Costa Rican forest fragments. Thesis. Cornell University, Ithaca, New York, USA.
- Borror, D. J., and R. E. White. 1970. *A field guide to insects of America north of Mexico*. Houghton Mifflin, Boston, Massachusetts, USA.
- Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* **58**:445–449.
- Brown, J. H., P. A. Marquet, and M. L. Taper. 1993. Evolution of body size: consequences of an energetic definition of fitness. *American Naturalist* **142**:573–584.
- Bueno, J. A., V. A. Tsihrintzis, and L. Alvarez. 1995. South Florida greenways: a conceptual framework for the eco-

- logical connectivity of the region. *Landscape and Urban Planning* **33**:247–266.
- Burkey, T. V. 1989. Extinction in nature reserves: the effect of fragmentation and the importance of migration between reserve fragments. *Oikos* **55**:75–81.
- Collinge, S. K. 1995. Spatial arrangement of patches and corridors in the landscape: consequences for biological diversity and implications for landscape architecture. Dissertation. Harvard University, Cambridge, Massachusetts, USA.
- Collinge, S. K. 1996. Ecological consequences of habitat fragmentation: implications for landscape architecture and planning. *Landscape and Urban Planning* **36**:59–77.
- Collinge, S. K., and R. T. T. Forman. 1998. A conceptual model of land conversion processes: predictions and evidence from a field experiment with grassland insects. *Oikos* **82**:66–84.
- Crist, T. O., D. S. Guertin, J. A. Wiens, and B. T. Milne. 1992. Animal movement in heterogeneous landscapes: an experiment with *Eleodes* beetles in shortgrass prairie. *Functional Ecology* **6**:536–544.
- DeFerrari, C. M., and R. J. Naiman. 1994. A multi-scale assessment of the occurrence of exotic plants on the Olympic Peninsula, Washington. *Journal of Vegetation Science* **5**:247–258.
- den Boer, P. J. 1981. On the survival of populations in a heterogeneous and variable environment. *Oecologia* **50**:39–53.
- Diamond, J. 1975. The island dilemma: lessons of modern biogeographic studies for the design of nature reserves. *Biological Conservation* **7**:129–146.
- Doak, D. F. 1995. Source–sink models and the problem of habitat degradation: general models and applications to the Yellowstone grizzly. *Conservation Biology* **9**:1370–1379.
- Doak, D. F., and L. S. Mills. 1994. A useful role for theory in conservation. *Ecology* **75**:615–626.
- Dooley, J. L., Jr., and M. A. Bowers. 1998. Demographic responses to habitat fragmentation: experimental tests at the landscape and patch scale. *Ecology* **79**:969–980.
- Dunning, J. B., Jr., D. J. Stewart, B. J. Danielson, B. R. Noon, T. L. Root, R. H. Lamberson, and E. E. Stevens. 1995. Spatially explicit population models: current forms and future uses. *Ecological Applications* **5**:3–11.
- Edwards, P. J., R. M. May, and N. R. Webb, editors. 1994. *Large-scale ecology and conservation biology*. Blackwell Scientific Publications, Oxford, UK.
- Evans, H. E. 1984. *Insect biology*. Addison-Wesley, Reading, Massachusetts, USA.
- Fahrig, L. 1997. Relative effects of habitat loss and fragmentation on population extinction. *Journal of Wildlife Management* **61**:603–610.
- Fahrig, L., L. P. Lefkovich, and G. Merriam. 1983. Population stability in a patchy environment. Pages 61–67 in W. K. Lauenroth, G. V. Skogerboe, and M. Flug, editors. *Analysis of ecological systems: state-of-the-art in ecological modeling*. Elsevier, New York, New York, USA.
- Fahrig, L., and G. Merriam. 1985. Habitat patch connectivity and population survival. *Ecology* **66**:1762–1768.
- Fahrig, L., and G. Merriam. 1994. Conservation of fragmented populations. *Conservation Biology* **8**:50–59.
- Forman, R. T. T. 1995. *Land mosaics: the ecology of landscapes and regions*. Cambridge University Press, Cambridge, UK.
- Forman, R. T. T., and M. Godron. 1981. Patches and structural components for a landscape ecology. *BioScience* **31**:733–740.
- Forney, K. A., and M. E. Gilpin. 1989. Spatial structure and population extinction: a study with *Drosophila* flies. *Conservation Biology* **3**:45–51.
- Gilbert, F., A. Gonzalez, and I. Evans-Freke. 1998. Corridors maintain species richness in the fragmented landscapes of a microecosystem. *Proceedings of the Royal Society of London B* **265**:577–592.
- Gonzalez, A., J. H. Lawton, F. Gilbert, T. M. Blackburn, and I. Evans-Freke. 1998. Metapopulation dynamics, abundance, and distribution in a microecosystem. *Science* **281**:2045–2047.
- Gustafson, E. J., and R. H. Gardner. 1996. The effect of landscape heterogeneity on the probability of patch colonization. *Ecology* **77**:94–107.
- Haas, C. A. 1995. Dispersal and use of corridors by birds in wooded patches on an agricultural landscape. *Conservation Biology* **9**:845–854.
- Hanski, I., and M. Gilpin. 1991. Metapopulation dynamics: brief history and conceptual domain. *Biological Journal of the Linnean Society* **42**:3–16.
- Hanski, I., T. Pakkala, M. Kuussaari, and G. Lei. 1995. Metapopulation persistence of an endangered butterfly in a fragmented landscape. *Oikos* **72**:21–28.
- Hansson, L. 1991. Dispersal and connectivity in metapopulations. *Biological Journal of the Linnean Society* **42**:89–103.
- Harris, L. D. 1984. *The fragmented forest: island biogeography theory and the preservation of biotic diversity*. University of Chicago Press, Chicago, Illinois, USA.
- Harris, L. D., and J. Scheck. 1991. From implications to applications: the dispersal corridor principle applied to the conservation of biological diversity. Pages 189–220 in D. A. Saunders and R. J. Hobbs, editors. *Nature conservation 2: the role of corridors*. Surrey Beatty & Sons, Chipping Norton, Australia.
- Harris, L. D., and G. Silva-Lopez. 1992. Forest fragmentation and the conservation of biological diversity. Pages 197–237 in P. L. Fiedler and S. K. Jain, editors. *Conservation biology*. Chapman and Hall, New York, New York, USA.
- Harrison, S. 1993. Metapopulations and conservation. Pages 111–128 in P. J. Edwards, R. M. May, and N. R. Webb, editors. *Large-scale ecology and conservation biology*. Blackwell Scientific, London, UK.
- Harrison, S., and L. Fahrig. 1995. Landscape pattern and population conservation. Pages 293–308 in L. Hansson, L. Fahrig, and G. Merriam, editors. *Mosaic landscapes and ecological processes*. Chapman and Hall, London, UK.
- Harrison, S., and A. D. Taylor. 1997. Empirical evidence for metapopulation dynamics. Pages 27–42 in I. A. Hanski and M. E. Gilpin, editors. *Metapopulation biology*. Academic Press, San Diego, California, USA.
- Helfer, J. R. 1987. *How to know the grasshoppers, crickets, cockroaches and their allies*. Dover Publications, New York, New York, USA.
- Henderson, M. T., G. Merriam, and J. Wegner. 1985. Patchy environments and species survival: chipmunks in an agricultural mosaic. *Biological Conservation* **31**:95–105.
- Henein, K., and G. Merriam. 1990. The elements of connectivity where corridor quality is variable. *Landscape Ecology* **4**:157–170.
- Herkert, J. R. 1994. The effects of habitat fragmentation on midwestern grassland bird communities. *Ecological Applications* **4**:461–471.
- Hess, G. 1996. Disease in metapopulation models: implications for conservation. *Ecology* **77**:1617–1632.
- Hill, C. J. 1995. Linear strips of rain forest vegetation as potential dispersal corridors for rain forest insects. *Conservation Biology* **9**:1559–1566.
- Hobbs, R. J. 1992. Corridors for conservation: solution or bandwagon? *Trends in Ecology and Evolution* **7**:389–392.
- Holyoak, M., and S. P. Lawler. 1996. Persistence of an extinction-prone predator–prey interaction through metapopulation dynamics. *Ecology* **77**:1867–1879.
- Ims, R. A. 1995. Movement patterns related to spatial struc-

- tures. Pages 85–109 in L. Hansson, L. Fahrig, and G. Merriam, editors. *Mosaic landscapes and ecological processes*. Chapman and Hall, London, UK.
- Johnson, A. R., B. T. Milne, and J. A. Wiens. 1992. Diffusion in fractal landscapes: simulations and experimental studies of Tenebrionid beetle movements. *Ecology* **73**:1968–1983.
- Jules, E. S. 1998. Habitat fragmentation and demographic change for a common plant: *Trillium* in old-growth forest. *Ecology* **79**:1645–1656.
- Kareiva, P. 1987. Habitat fragmentation and the stability of predator-prey interactions. *Nature* **326**:388–390.
- Kareiva, P., J. G. Kingsolver, and R. B. Huey, editors. 1993. *Biotic interactions and global change*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Keppel, G. 1982. *Design and analysis: a researcher's handbook*. Second edition. Prentice-Hall, Englewood Cliffs, New Jersey, USA.
- Kim, K. C. 1993. Biodiversity, conservation, and inventory: why insects matter. *Biodiversity and Conservation* **2**:191–214.
- Klein, B. C. 1989. Effects of forest fragmentation on dung and carrion beetle communities in central Amazonia. *Ecology* **70**:1715–1725.
- Kruess, A., and T. Tschardtke. 1994. Habitat fragmentation, species loss, and biological control. *Science* **264**:1581–1584.
- Lankester, K., R. van Apeldoorn, E. Meelis, and J. Verboom. 1991. Management perspectives for populations of the Eurasian badger (*Meles meles*) in a fragmented landscape. *Journal of Applied Ecology* **28**:561–573.
- La Polla, V. N., and G. W. Barrett. 1993. Effects of corridor width and presence on the population dynamics of the meadow vole (*Microtus pennsylvanicus*). *Landscape Ecology* **8**:25–37.
- Laurance, W. F. 1990. Comparative responses of five arboreal marsupials to tropical forest fragmentation. *Journal of Mammalogy* **71**:641–653.
- Laurance, W. F. 1991. Ecological correlates of extinction proneness in Australian tropical rain forest mammals. *Conservation Biology* **5**:79–89.
- Laurance, W. F., and R. O. Bierregaard, Jr. (Eds.). 1997. *Tropical forest remnants*. University of Chicago Press, Chicago, IL.
- Laurance, W. F., L. V. Ferreira, J. M. Rankin-de Merona, and S. G. Laurance. 1998. Rain forest fragmentation and the dynamics of Amazonian tree communities. *Ecology* **79**:2032–2040.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* **15**:237–240.
- Lidicker, W. Z. Jr., and W. D. Koenig. 1996. Responses of terrestrial vertebrates to habitat edges and corridors. Pages 85–109 in D. R. McCullough, editor. *Metapopulations and wildlife conservation*. Island Press, Washington, D.C., USA.
- Lindenmayer, D. B. 1994. Wildlife corridors and the mitigation of logging impacts on fauna in wood-production forests in southeastern Australia: a review. *Wildlife Research* **21**:323–340.
- Lindenmayer, D. B., R. B. Cunningham, and C. F. Connelly. 1993. The conservation of arboreal marsupials in the montane ash forests of the central highlands of Victoria, southeast Australia. IV. The presence and abundance of arboreal marsupials in retained linear habitats (wildlife corridors) within logged forests. *Biological Conservation* **66**:207–221.
- Lindenmayer, D. B., and H. A. Nix. 1993. Ecological principles for the design of wildlife corridors. *Conservation Biology* **7**:627–630.
- Loreau, M., and C. L. Nolf. 1994. Spatial structure and dynamics of a population of *Abax ater*. Pages 165–169 in K. Desender, M. Dufrene, M. Loreau, M. L. Luff, and J. P. Maelfait, editors. *Carabid beetles: ecology and evolution*. Kluwer Academic Publishers, Boston, Massachusetts, USA.
- Louda, S. M. 1984. Herbivore effect on stature, fruiting, and leaf dynamics of a native crucifer. *Ecology* **65**:1379–1386.
- Luginbill, P. Sr., and H. R. Painter. 1953. *May beetles of the United States and Canada*. USDA Technical Bulletin No. 1060, USDA, Washington, D.C., USA.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey, USA.
- Machtans, C. S., M. A. Villard, and S. J. Hannon. 1996. Use of riparian buffer strips as movement corridors by forest birds. *Conservation Biology* **10**:1366–1379.
- Mader, H. J., C. Schell, and P. Kornaker. 1990. Linear barriers to arthropod movement in the landscape. *Biological Conservation* **54**:209–222.
- Manly, B. F. J. 1992. *The design and analysis of research studies*. Cambridge University Press, Cambridge, UK.
- Mann, C. C., and M. L. Plummer. 1995. Are wildlife corridors the right path? *Science* **270**:1428–1430.
- McCullough, D. R., editor. 1996. *Metapopulations and wildlife conservation*. Island Press, Washington, D.C., USA.
- Merriam, G., and A. Lanoue. 1990. Corridor use by small mammals: field measurements of three experimental types of *Peromyscus leucopus*. *Landscape Ecology* **4**:123–131.
- Miller, J. C. 1993. Insect natural history, multi-species interactions and biodiversity in ecosystems. *Biodiversity and Conservation* **2**:233–241.
- Naiman, R. J., H. Decamps, and M. Pollock. 1993. The role of riparian corridors in maintaining regional biodiversity. *Ecological Applications* **3**:209–212.
- Newman, J. A., J. Bergelson, and A. Grafen. 1997. Blocking factors and hypothesis tests in ecology: is your statistics text wrong? *Ecology* **78**:1312–1320.
- Nicholls, A. O., and C. R. Margules. 1991. The design of studies to demonstrate the biological importance of corridors. Pages 49–61 in D. A. Saunders and R. J. Hobbs, editors. *Nature conservation 2: The role of corridors*. Surrey Beatty & Sons, Chipping Norton, Australia.
- Noss, R. F., and A. Y. Cooperrider. 1994. *Saving nature's legacy: protecting and restoring biodiversity*. Island Press, Washington, D.C., USA.
- Petit, S. 1994. Diffusion of forest carabid beetles in hedgerow network landscapes. Pages 337–341 in K. Desender, M. Dufrene, M. Loreau, M. L. Luff, and J. P. Maelfait, editors. *Carabid beetles: ecology and evolution*. Kluwer Academic Publishers, Boston, Massachusetts, USA.
- Robertson, K. R., R. C. Anderson, and M. W. Schwartz. 1997. The tallgrass prairie mosaic. Pages 55–87 in M. W. Schwartz, editor. *Conservation in highly fragmented landscapes*. Chapman and Hall, New York, New York, USA.
- Robinson, G. R., R. D. Holt, M. S. Gaines, S. P. Hamburg, M. L. Johnson, H. S. Fitch, and E. A. Martinko. 1992. Diverse and contrasting effects of habitat fragmentation. *Science* **257**:524–526.
- Robinson, G. R., and J. F. Quinn. 1988. Extinction, turnover, and species diversity in an experimentally fragmented California annual grassland. *Oecologia* **76**:71–86.
- Samson, F., and F. Knopf. 1994. *Prairie conservation in North America*. BioScience **44**:418–421.
- SAS Institute. 1990. *SAS Version 6*. SAS Institute, Cary, North Carolina, USA.
- SAS Institute. 1997. *JMP Version 3.2*. SAS Institute, Cary, North Carolina, USA.
- Saunders, D. A., and K. H. Hobbs, editors. 1991. *Nature*

- conservation 2: the role of corridors. Surrey Beatty & Sons, Chipping Norton, Australia.
- Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* **5**:18–32.
- Schmiegelow, F. K. A., C. S. Machtans, and S. J. Hannon. 1997. Are boreal birds resilient to forest fragmentation? An experimental study of short-term community responses. *Ecology* **78**:1914–1932.
- Schultz, C. B. 1998. Dispersal behavior and its implications for reserve design in a rare Oregon butterfly. *Conservation Biology* **9**:845–854.
- Schumaker, N. H. 1996. Using landscape indices to predict habitat connectivity. *Ecology* **77**:1210–1225.
- Shafer, C. L. 1997. Terrestrial nature reserve design at the urban/rural interface. Pages 345–378 in M. W. Schwartz, editor. *Conservation in highly fragmented landscapes*. Chapman and Hall, New York, New York, USA.
- Simberloff, D. S., and J. Cox. 1987. Consequences and costs of conservation corridors. *Conservation Biology* **1**:63–71.
- Simberloff, D. S., J. A. Farr, J. Cox, and D. W. Mehlman. 1992. Movement corridors: conservation bargains or poor investments? *Conservation Biology* **6**:493–504.
- Simberloff, D. S., and E. O. Wilson. 1969. Experimental zoogeography of islands: the colonization of empty islands. *Ecology* **50**:278–296.
- Sokal, R. R., and F. J. Rohlf. 1995. *Biometry*. Third edition. W. H. Freeman and Company, New York, New York, USA.
- Soulé, M. 1986. *Conservation biology*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Southwood, T. R. E. 1978. *Ecological methods*. Second edition. Chapman and Hall, London, UK.
- Strong, D. R., J. H. Lawton, and T. R. E. Southwood. 1984. *Insects on plants*. Harvard University Press, Cambridge, Massachusetts, UK.
- Taylor, P. D., L. Fahrig, K. Henein, and G. Merriam. 1993. Connectivity is a vital element of landscape structure. *Oikos* **68**:571–573.
- Tilman, D. and P. Kareiva, editors. 1997. *Spatial ecology: The role of space in population dynamics and interspecific interactions*. Princeton University Press, Princeton, New Jersey, USA.
- Tilman, D., C. L. Lehman, and P. Kareiva. 1997. Population dynamics in spatial habitats. Pages 3–20 in D. Tilman and P. Kareiva, editors. *Spatial ecology: The role of space in population dynamics and interspecific interactions*. Princeton University Press, Princeton, New Jersey, USA.
- Turchin, P. 1998. *Quantitative analysis of movement*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Vermeulen, H. 1994. The effects of different vegetation structures on the dispersal of carabid beetles from poor sandy heaths and grasslands. Pages 387–392 in K. Desender, M. Dufrene, M. Loreau, M. L. Luff, and J. P. Maelfait, editors. *Carabid beetles: ecology and evolution*. Kluwer Academic Publishers, Boston, Massachusetts, USA.
- Watt, A. S. 1947. Pattern and process in the plant community. *Journal of Ecology* **35**:1–22.
- Weather Enthusiasts of Boulder (WEB). 1992. William Callahan, editor. Volume 7. University Archives, University of Colorado at Boulder, Boulder, Colorado, USA.
- Weather Enthusiasts of Boulder (WEB). 1993. William Callahan, editor. Volume 8. University Archives, University of Colorado at Boulder, Boulder, Colorado, USA.
- Weather Enthusiasts of Boulder (WEB). 1994. William Callahan, editor. Volume 9. University Archives, University of Colorado at Boulder, Boulder, Colorado, USA.
- Wegner, J. F., and G. Merriam. 1979. Movements by birds and small mammals between a wood and adjoining farmland habitats. *Journal of Applied Ecology* **16**:349–357.
- Wiens, J. A. 1976. Population responses to patchy environments. *Annual Review of Ecology and Systematics* **7**:81–120.
- Wiens, J. A., T. O. Crist, and B. T. Milne. 1993. On quantifying insect movements. *Environmental Entomology* **22**:709–715.
- Wiens, J. A., and B. Milne. 1989. Scaling of landscapes in landscape ecology, or, landscape ecology from a beetle perspective. *Landscape Ecology* **3**:87–96.
- Wilcove, D. S., C. H. McLellan, and A. P. Dobson. 1986. Habitat fragmentation in the temperate zone. Pages 237–256 in M. Soule, editor. *Conservation biology*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Wilcox, B. A., and D. D. Murphy. 1985. Conservation strategy: the effects of fragmentation on extinction. *American Naturalist* **125**:879–887.
- Wilson, E. O., and E. O. Willis. 1975. Applied biogeography. Pages 522–534 in M. L. Cody and J. M. Diamond, editors. *Ecology and evolution of communities*. Harvard University Press, Cambridge, Massachusetts, USA.
- With, K. A. 1994. Using fractal analysis to assess how species perceive landscape structure. *Landscape Ecology* **9**:25–36.
- Zar, J. H. 1996. *Biostatistical analysis*. Third edition. Prentice-Hall, Upper Saddle River, New Jersey, USA.