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Corridors and some ecological and evolutionary consequences of connectivity

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Corridors and some ecological and evolutionary consequences of connectivity

by

John Lee Orrock II

A thesis submitted to the graduate faculty
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

Major: Ecology and Evolutionary Biology

Program of Study Committee:
Brent J. Danielson, Major Professor
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For the Major Program
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This dissertation was only possible because I have been fortunate to be surrounded by truly amazing people. In the text that follows, I abandon all attempts at brevity. Their contributions to my work should be recognized without sparing any details.

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Thanks are due to the members of my committee. Tom Baker provided custom-tailored ladybeetle lures and a wealth of information about insect behavior. John Obrycki shared his knowledge of predator-prey interactions and invertebrate sampling methods. Philip Dixon offered invaluable statistical advice, and was always willing to make room in his busy schedule. Bill Clark’s suggestions and intuition were excellent contributions – if only I had heeded his advice when he mentioned that I might not have success recapturing stinkbugs...! Fred Janzen provided feedback on numerous manuscripts and helped stimulate my thinking along evolutionary lines.
Brent Danielson has been charged with overseeing my exploits over the last five years. Brent trusted me to know my own limitations, although I'm sure there were times when it looked like I might go over the edge. I know Brent well enough to know that this may be the only time I actually get the last word – so I must capitalize upon the opportunity. Although I rarely say so, I learn something from every conversation we have. I am thankful for his friendship, guidance, and candid opinions. For Brent, I reserve the greatest professional compliment: thanks to his efforts, I am a better ecologist.

My mother has always provided a rigorous proving ground for making logical arguments. Despite her occasional claim that my logic 'stinks', I suspect that it would 'stink' much more were it not for her. My father is a true naturalist whose appreciation of ecology fueled my aspirations as a youth. This work stands as a testament to them both, and as proof of a lesson they instilled in me: the only boundaries in life are those you set for yourself.

In the nearly five years after our first rebar-pounding race, Ellen Damschen has made a profound impact on my life. Since the moment we met, I have been inspired by her dedication, heartened by her patience, and strengthened by her resolve. Ellen is my dearest friend, my most trusted confidant, and my most valued colleague. Ellen, this work is as much yours as it is mine. Your influence is evident on every page that follows.
By connecting disjunct patches, corridors may offset the effects of fragmentation by promoting gene flow and population persistence. However, the ultimate effect of corridors on a focal species may hinge upon two considerations: how corridors may affect ecological interactions that impinge upon that species, and how corridors might affect the fixation of novel alleles that ultimately determine fitness and persistence. Using an experimental landscape, I show that corridor-mediated changes in patch shape change seed predation in connected and unconnected patches, and shift the behavior, abundance, and distribution of seed predators. Rodent seed predators removed more seeds in connected patches, arthropod seed predators removed more seeds in rectangular patches, and avian seed predation did not differ due to patch type. Rodent foraging was greater in the interior of connected patches because changes in patch shape influenced risk perceived by rodents while foraging. Ant communities were also affected by changes in patch shape caused by corridors, rather than corridor effects per se. The distribution and abundance of ants differed among edge-rich areas (corridors and wings), edges, and the patch interior. In rectangular patches, fire ants (Solenopsis spp.) had negative impacts on other ant species. By changing the activity of rodents, and the composition of ant communities, corridors may have important impacts on seeds. Bird-dispersed seeds may benefit from increased dispersal among connected patches, but connected patches also have greater predation risk. Using a simulation model, I demonstrate that gene flow between a stable population and a population that experiences local extinction or a reduction in size (e.g. due to natural or anthropogenic disturbance) can dramatically affect fixation of alleles in the stable population. Alone or in concert, frequent disturbance, high rates of movement, and low habitat quality make it more likely that connectivity-mediated fixation will promote fixation of harmful alleles and reduce fixation of beneficial alleles.
CHAPTER 1. GENERAL INTRODUCTION

The Importance of Space

Whether implied or explicit, it is indisputable that space mediates ecology and evolution. Andrewartha and Birch (1954) recognized long ago that local spatial dynamics might give rise to regional persistence, much akin to the metapopulation theory later named and formalized by Levins (1969) and vigorously explored in present times (see Hanski and Gilpin 1995). Huffaker (1958) demonstrated the important role of space in mediating predator-prey dynamics long before the simulations of Hasell, Comins, and May (1991, 1994, reviewed in Hassell 2000), the advent of spatial microcosms with microbes (Holyoak and Lawler 1996; Burkey 1997; Holyoak 2000), and the fragmented invertebrate communities studied by Tschamntke and colleagues (reviewed in Hunter 2002; Steffan-Dewenter and Tschamntke 2002; Tschamntke et al. 2002). Ecological invasions (Elton 1958), island biogeography theory (MacArthur and Wilson 1967), source-sink dynamics (Pulliam 1988; Pulliam and Danielson 1991), rescue effects (Brown and Kodric-Brown 1977), habitat selection theory (Fretwell and Lucas 1970; Rosenzweig 1981), and optimal foraging theory (Stephens and Krebs 1986) all contain elements of spatial ecology.

Space also plays a central role in evolution. Although the evolution of dispersal is a well-studied case (e.g. Johnson and Gaines 1990; McPeek and Holt 1992) where space and evolution interact, other examples exist. Sewall Wright's shifting balance theory (Wright 1931, 1940) invokes gene flow among, and random drift within, relatively isolated populations as a primary mechanism of adaptive evolution. Fisher (1930) formalized the rate of spread of an adaptive allele throughout a population. Whitlock, Barton, and colleagues
(see Barton 1993; Barton 1995; Hanski and Gilpin 1995; Whitlock and Barton 1997; Whitlock 2003) have integrated evolutionary genetics with metapopulation theory, building upon the spatial work of Kimura (1962), Maruyama (1970), Nagylaki (1980), and Slatkin (1977, 1981). There are no ecological and evolutionary vacuums: interactions occur within the constraints of space.

At least two compelling reasons exist for undertaking a study of spatial components of ecology and evolution. The first reason is that insight might be gained into the mechanisms underlying ecological and evolutionary change. The second reason is that spatial dynamics are likely to be affected by the rapid anthropogenic change of the biosphere. Humans are changing the spatial structure of the landscape (e.g. Saunders et al. 1991; Vitousek et al. 1997; Harrison and Bruna 1999), the flow of currents in the ocean and atmosphere (Clark et al. 2002), shifting global temperature (Walther et al. 2002), and are acting as agents of dispersal capable of homogenizing biota within and among continents (Mack et al. 2000). Suddenly, space is at a premium; we need to understand now, more than ever, how to do more with less.

Conservation biology has been called a ‘discipline with a deadline’ (Ricketts et al. 1999). In meeting this deadline, we must understand how to mitigate habitat-induced species loss, which requires maintaining the ecological and evolutionary viability of populations. By promoting population rescue and gene flow, corridors that connect disjunct populations may serve both purposes (Rosenberg et al. 1997; Mech and Hallett 2001; Tewksbury et al. 2002; Haddad et al. 2003). However, careful inspection of how corridors, and connectivity in general, influence ecological and evolutionary dynamics is required before manipulation of
connectivity can be recommended as a viable conservation tool (Simberloff et al. 1992; Beier and Noss 1996).

This dissertation focuses on two general themes. First, I use an experimental landscape to examine how corridors affect the interactions among predators and prey. Second, I use a simulation model to demonstrate how connectivity can interact with changes in population size to affect the likelihood that a new mutation will fix in a population, a critical step in the process of adaptive evolution.

**Corridors and Interactions Among Predators and Prey.**

Habitat fragmentation is presently the single greatest threat to biodiversity (Wilcove et al. 1998). Corridors are thought to be valuable conservation tools for ameliorating the effects of habitat fragmentation (e.g. Rosenberg et al. 1997). However, the acceptance of corridors as a panacea in conservation programs has been criticized because the role of patch size and shape in affecting response to corridors is not clearly understood (Simberloff et al. 1992; Beier and Noss 1996; Haddad and Baum 1999; Rosenberg et al. 1997). Corridors are long, linear elements that may affect organisms by changing patch shape (‘area effects’). Corridors may also change connectivity because organisms move between patches via the corridor (‘corridor effects’) or because organisms moving outside of the patches encounter the corridor and follow it into a patch (‘drift fence effects’). Recent work has demonstrated that patch shape can have important impacts on the behavior of individuals (Stamps et al. 1987; Dunning et al. 1993; Fagan et al. 1999), the dynamics of populations (Polis et al. 1999; Fagan et al. 1999). Similarly, connectivity can alter dispersal (Haddad 1999; Tewksbury et
al. 2002; Haddad et al. 2003), gene flow (Mech and Hallett 2001; Tewksbury et al. 2002), population dynamics (Haddad and Baum 1999; Earn et al. 2000; Hudgens and Haddad 2003), and community structure and composition (Gonzalez et al. 1998). The effects of connectivity cannot be separated from the effects of patch shape because studies that independently manipulate connectivity and patch shape are almost nonexistent. This lack of information regarding how corridors work is a severe limitation in the proper evaluation of a potentially powerful conservation tool.

Importantly, the population-level focus of most corridor studies, though often a logistical necessity, has neglected the role corridors in affecting the interactions among populations that define an ecological community (but see Gonzalez et al. 1998; Tewksbury et al. 2002). Studies of how connectivity and patch shape affect community-level interactions are sorely needed (Debinski and Holt 2000). Predator-prey interactions are a logical starting place for examining how corridors and patch shape affect interactions, because corridors may have positive impacts on predators as well as prey, i.e. corridor-mediated changed in predation could offset or outweigh corridor-mediated benefits for prey.

Much of this dissertation focuses on how corridors affect seeds and seed predators. Two chapters examine how corridors may lead to patch-specific changes in predator impact on three different plant species. Two chapters examine how corridors affect the abundance and behavior of two important seed predators: ants and rodents. By taking this comprehensive approach, my aim is to more thoroughly determine the community-level consequences of corridors and determine whether corridor effects are due to connectivity, patch shape, or both.
Connectivity and the Fixation of Alleles

Corridors could also have evolutionary impacts by changing the movement of individuals and alleles. For small populations, corridors may serve to reduce inbreeding and the accumulation of deleterious alleles, which can dramatically reduce fitness in small, isolated populations (e.g. mutational meltdown; Lynch et al. 1995). However, connectivity among populations can also have negative consequences. For example, adaptation to local conditions may be prohibited by gene flow from habitats with different selection pressures (Holt and Gomulkiewicz 1997; Gomulkiewicz et al. 1999; Kawecki 1995, 2000; Kawecki and Holt 2002). The effects of changing connectivity can be profound: gene flow among spatially subdivided populations can affect rates of fixation (Barton 1993; Whitlock 2003), heterozygosity (Nagylaki 1998), and rates of adaptation (Wright 1931, 1940; Gomulkiewicz et al. 1999; Kawecki 2000; Kawecki and Holt 2002).

Population dynamics can also have consequences for the fixation of alleles, because changes in effective population size affect the likelihood that a new mutation (or a rare new allele obtained via immigration) will fix in a population (Kimura 1962; Slatkin 1981; Barton 1993; Otto and Whitlock 1997; Nagylaki 1998; Cherry 2003; Whitlock 2003). Beneficial mutations are more likely to become fixed in growing populations because mortality and drift are less likely to remove the beneficial mutation when it is rare (Otto and Whitlock 1997). Conversely, when populations are shrinking, deleterious alleles become more likely to fix because random drift, rather than selection, is more important for determining their fate (Otto and Whitlock 1997).
Theoretically, corridors could lead to qualitatively different impacts on the fixation of alleles, ultimately either promoting continued persistence and adaptation of a population, or speeding its demise through fixation of deleterious alleles and mutational meltdown (Lynch and Gabriel 1990; Lande 1994, 1995; Frankham 1995; Lynch et al. 1995). Moreover, a wide array of practical genetics problems involve situations where organisms move among populations of changing size: the evolution of insect pests and the evolution of disease are two examples where gene flow occurs among different (often dynamic) populations and selection regimes. Given tremendous financial costs of insects that evolve resistance to pesticides (Tabachnik 1994) and microbes resistant to antibiotics (Palumbi 2001), and evidence that resistance can arise through the fixation of one or a few mutations (Daborn et al. 2002), a better understanding of how connectivity affects fixation dynamics is certainly of interest.

In this dissertation, I use a simulation model to examine how movement of individuals among spatially segregated habitats affects the likelihood that a new allele will become fixed. This work was originally conceived with the spatial design of biological reserves in mind, but is also quite applicable to conservation problems where landscape connectivity is manipulated (e.g. corridors) as well as practical problems where organisms move between dynamic populations (e.g. insect pests).

Dissertation Organization

This dissertation consists of seven chapters. The first chapter is a general introduction and overview of the work to be presented. Chapters 2-6 are written in the
format of journal manuscripts. Chapters 2 and 3 detail the impact of corridors on seed predation; chapter 2 has been submitted to *Ecology* and chapter 3 will be submitted to *Conservation Biology*. Chapters 4 and 5 examine how corridors may influence the abundance and behavior of rodent and arthropod seed predators. Chapter 4 has been submitted to the *Journal of Mammalogy* and chapter 5 has been submitted to *Ecology*. Chapter 6 describes how the movement of individuals between stable sources and ephemeral sinks can affect the likelihood that a new mutation will fix in the source, and will be submitted to *American Naturalist*. Chapter 7 contains a general discussion and synthesis of the previous chapters. All chapters were written by John Orrock, with editorial assistance by Brent Danielson. Coauthors on chapters 2, 3, and 5 were instrumental in data collection and logistical support.

**Literature Cited**


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CHAPTER 2. SPATIAL ECOLOGY OF PREDATOR-PREY INTERACTIONS: 
CORRIDORS AND PATCH SHAPE INFLUENCE SEED PREDATION

A paper submitted to Ecology
John L. Orrock, Brent J. Danielson, Molly J. Burns, and Doug J. Levey

Abstract. Corridors that connect patches of disjunct habitat may be promising tools for mediating the negative impacts of habitat fragmentation, but little is known about how corridors affect ecological interactions. In eight 12-ha experimental landscapes, we examined how corridors affect the impact of invertebrate, rodent, and avian seed predators on Pokeweed, Phytolacca americana. Over 13 months between 2000-2001, we quantified the effects of patch shape, connectivity, and predator type on the number of seeds germinating in the field (germinants), seed removal, and the viability of remaining seeds.

Corridors did not affect the number of P. americana germinants in experimental exclosures or the viability of seeds remaining in exclosures. However, corridors affected the removal of seeds in a predator-specific manner: invertebrates removed more seeds in unconnected patches, whereas rodents removed more seeds in connected patches. Seed removal by birds was similar in connected and unconnected patches. Total seed removal by all seed predators was not affected by corridors, because invertebrates removed more seeds where rodents removed fewer seeds and vice versa. Overall, seed predation significantly reduced the number and viability of remaining seeds, and reduced the number of germinants in 2000 but not in 2001. The abundance of naturally occurring P. americana plants in our experimental patches in 2000 decreased with increasing seed removal from exclosures, but
was not related with viability or germinants in 2000, suggesting that seed removal may shape
the distribution and abundance of this species.

Complementary patterns of seed removal by rodents and invertebrates suggest that
corridors alter the effects of these predator taxa by changing the relative amounts of edge and
core (non-edge) habitats in a patch. Because invertebrates and rodents do not completely
overlap in the seeds they consume, corridors may change predation pressure on seeds that are
primarily consumed by one predator type, with potential consequences for the composition of
plant and seed predator communities.

Key Words: Corridors, Patch Shape, Seed Predation, Predator-prey interactions,
Savannah River Site, Phytolacca Americana

INTRODUCTION

Habitat fragmentation and species loss are occurring on a global scale, yet few
experimental studies have examined the effects of fragmentation on ecological communities
connect habitat fragments and are thought to promote population persistence by promoting
gene flow, population rescue, and increasing abundance (Rosenberg et al. 1997). However,
corridors have been criticized because mechanisms underlying purported corridor effects are
unknown (Simberloff et al. 1992). Perhaps more worrisome, the population-level focus of
most corridor studies neglects the rest of the ecological milieu, with largely unknown
consequences. For example, imagine the impact of constructing corridors to preserve a target
species only to discover that an important predator uses corridors more effectively than the
species of concern.
By facilitating predator movement, corridors may impact prey that rely upon 'predator-free' space (e.g., Holt and Lawton 1993). Moreover, corridors could alter the spatial or temporal asynchrony that promotes the persistence of some predator-prey interactions (e.g., Earn et al. 2000). Empirical work in microcosms reveals that corridors can affect persistence of predator-prey systems (Holyoak and Lawler 1996), but also warns that connecting patches can sometimes lead to counterintuitive outcomes (Burkey 1997, Holyoak 2000). We use an experimental landscape to evaluate how corridors affect the ecology of predator-prey interactions.

**Study System: Corridors, Seeds and Seed Predators**

Seeds can be considered sedentary prey consumed by vertebrate and invertebrate predators (Janzen 1971, Hulme 1998). Seed predation can lead to dramatic reductions in the standing crop of seeds and may be the primary determinant of plant distribution in some systems (e.g. Louda 1989, Brown and Heske 1990, Hulme 1998, Howe and Brown 1999, 2000, 2001). By increasing the deposition of bird-dispersed seeds (Haddad et al. 2003; Tewksbury et al. 2002), corridors could have positive impacts on bird-dispersed plants. However, the ultimate effect of corridors on bird-dispersed plants could be negative if corridor-mediated changes in seed predation offset or outweigh corridor-mediated increases in seed deposition.

Corridors may affect seed predation by altering the movement of seed predators between connected patches of suitable habitat ('corridor effects') or by making it more likely that an individual moving through an uninhabitable matrix will encounter a suitable patch ('drift-fence effects'; Rosenberg et al. 1997). Corridors also add area to a patch, and may affect seed predation by providing more habitat for seed predators ('area effects'; Haddad
and Baum 1999). Moreover, because corridors tend to be relatively long, linear elements, they can induce area effects by changing the amount of edge habitat relative to the amount of core habitat in a patch. Mammals (Bennett 1990; La Polla and Barrett 1993, Bennett et al. 1994, Bowne et al. 1999, Coffman et al. 2001, Haddad et al. 2003), invertebrates (Haddad 1999, Haddad and Baum 1999, Haddad 2000, Collinge 2000), and frugivorous birds respond to corridors (Tewksbury et al. 2002). By affecting the movement and abundance of a particular type of seed predator, corridors could change seed predation by that predator type.

Pokeweed, *Phytolacca americana*, is a perennial plant indigenous to eastern North America that is typically found in early successional habitats (Mitich 1994). *Phytolacca americana* produces berries consumed by many bird species (Mitich 1994), which subsequently disperse *P. americana* seeds (McDonnell et al. 1984, Mitich 1994). Pokeweed seeds are 2.5-3 mm in size (Radford et al. 1968) and can remain viable in the seed bank for at least 40 years (Toole and Brown 1946). Pre-dispersal seed predation is probably minimal, as rodents reject Pokeweed fruits, but readily consume *P. americana* seeds (McDonnell et al. 1984, Hyatt 1998), and damage to *P. americana* fruits by rodents or invertebrates was never observed during field collection of several thousand fruits (personal observation). Thus, if corridors affect seed predators, there may be direct consequences for *P. americana* population dynamics.

We used an experimental landscape composed of clearcut patches separated by a pine forest matrix to evaluate the effect of corridors on seed predators and *Phytolacca* seeds. For 13 months, we measured three different metrics to determine the impact of seed predators on *P. americana*: the number of seedlings emerging (hereafter called germinants), the number of seeds removed, and the viability of remaining seeds. The duration of our study allowed us
to integrate temporal variation in seed predation (Whelan et al. 1991) not incorporated in many seed predation studies (most studies last < 4 wk, e.g. Hyatt 1998). Moreover, the duration of our experiment allowed us to evaluate the importance of corridors, patch shape, and seed predation during a critical period of establishment for *P. americana* in our study system.

Our objectives are framed as three questions: 1) Do corridors affect seed predation by invertebrates, rodents, and birds? 2) Are rates of overall seed predation affected by corridors? 3) Is the abundance of naturally occurring *P. americana* plants in our study system related to rates of seed predation, i.e. is there evidence that seed predators affect the distribution of *P. americana*?

**METHODS**

*Experimental Design*

*Experimental Landscape.*-The experiment was conducted in eight replicated experimental units created at the Savannah River Site, a National Environmental Research Park (NERP) near Aiken, South Carolina. Each experimental unit consisted of five patches created during the fall and winter of 1999 by clear-cutting mature pine forest (the matrix) followed by prescribed burning (Fig. 1). In each experimental unit, there were three different patch types: connected, rectangular, and winged (Fig. 1). Connected patches were joined by a 25 m-wide corridor that was 150 m in length. Rectangular patches consisted of a 1-ha square patch with 0.375 ha of additional area, representing the area added by the corridor (Fig. 1). Winged patches consisted of a 1-ha square patch with two extending 'drift-fence' sections, each 75 m long and 25 m wide (Fig. 1). Two connected patches were in each experimental unit. Four of the experimental units had two rectangular patches and one
winged patch, whereas the other four experimental units had two winged patches and one rectangular patch, yielding a total of 12 winged patches, 12 rectangular patches, and 16 connected patches.

*Dissecting the role of corridor, drift-fence, and area effects.*-Our design allowed us to determine the relative importance of corridor, drift-fence, and area effects on seed predation because each type of effect makes a specific prediction (Table 1). It is important to note that, although patches were of similar area, each patch type differed in the relative amounts of edge and area habitat because of changing patch shape. This is simply illustrated by the area/perimeter ratio for each patch type: 22.62 for connected patches, 19.64 for winged patches, and 28.95 for rectangular patches. If seed predation is affected by edge, edge-neutral, edge-selecting, and edge-avoiding seed predators should display different patterns (Table 1) in response to the changing perimeter (because area is relatively constant) among patch types.

Winged and rectangular patches had the same area (1.375 ha), whereas connected patches had slightly less area than unconnected patches because they shared a corridor (central patch area plus half of the corridor = 1.1875 ha). The small difference in total area between connected and unconnected patches does not change the qualitative order of our predictions (Table 1). Rather, it provides a more stringent test of the importance of movement through corridors as a means for predators to exploit seeds. If seed predation is greatest in connected patches, despite the slightly reduced overall area and drift fence in connected patches, we have a stronger case for movement-mediated changes in seed predation.
Seed Predation.—We used exclosures to determine the effect of different types of seed predators on *P. americana* seeds. All exclosures were cylindrical wire cages approximately 32 cm diameter and 16 cm height. The four treatment types were: 1) access by no seed predators (hereafter referred to as NONE); 2) access by invertebrates (I); 3) access by invertebrates and rodents (IR); 4) access by invertebrates, rodents, and birds (ALL). To exclude all seed predators, NONE treatments used exclosures with walls of 1.5 cm$^2$ hardware cloth covered with fiberglass window screen (< 1 mm$^2$ mesh); although smaller ants could enter these exclosures, they could not remove seeds. Exclosures with sides constructed of hardware cloth with 1.5 cm$^2$ openings were used to exclude birds and rodents for invertebrate-access treatments (I). IR treatments used exclosures with walls constructed of hexagonal poultry wire with 4 cm$^2$ openings. ALL treatments used exclosures with sides constructed of wire fencing with 20 cm$^2$ openings. Each exclosure had a top constructed of fiberglass window screen that excluded most seed rain, including seeds of *P. americana*.

We randomly placed one of each exclosure type along a central 8-m square within each of the 40 patches (Fig. 1), yielding 160 total exclosures (4 exclosures per patch in 40 patches). At each exclosure site, leaf litter, debris, and resident plants were removed and the top 7 cm of soil was mixed to standardize conditions among exclosures. A weighed portion of field-collected *P. americana* seeds (mean 1.98 g ± 0.01 S.E.; equivalent to 312 ± 3.7 seeds) was placed on the soil surface, and the exclosure was placed over the seeds. This amount of seeds approximates the number of seeds that collects under isolated perches at our site (D. Levey, unpublished data). A 4-cm galvanized steel ring was projected into the soil around the edge of each exclosure so that 1 cm was above the soil surface. This did not prevent access to the exclosure by seed predators (ants readily traversed the ring), but
reduced the likelihood of seeds washing or blowing into or out of the exclosures. The base of the exclosure and the retaining ring were anchored into the soil with 15-cm steel turf stakes.

Once established in June 2000, exclosures were visited twice per month during the growing season (March - September). Germinants of *P. americana* were counted and removed during each visit. Germinants of all other species were removed. During the course of the experiment, small ant hills were observed within two NONE exclosures. Ant-repellent granules (Spectrum Brands, St. Louis, Missouri) sprinkled around the outside of the exclosures eliminated this problem. At the conclusion of the seed predation trials in July 2001, all seeds were exhumed from exclosures to a depth of 7 cm by one person to minimize any bias in soil collection techniques. Pokeweed seeds were sieved from the soil and counted.

Because local habitat characteristics can affect seed predation (Reader and Beisner 1991, Hulme 1997, Manson and Stiles 1998), substrate and vegetation characteristics were measured in a 1-m radius extending from the center of all exclosures open to predators (i.e. I, IR, and ALL treatments) in late July 2000. For consistency, only two investigators quantified habitat characteristics, visually estimating the percent cover of downed woody debris, woody plant material, vegetative plant material, bare soil, and leaf litter.

*Seed Viability.*—We used germination trials to test the viability of exhumed seeds. This estimate of viability may be conservative because dormancy and sensitivity to environmental factors varies seasonally and annually in *P. americana* (Baskin and Baskin 2001). As such, seeds removed from the field in July may be less likely to germinate than seeds collected during optimal germination times earlier in the year (Baskin and Baskin 2001).
For each exclosure, we filled a 5 x 5 x 6 cm compartment of a standard plastic seedling flat with heat-sterilized sand and placed recovered *P. americana* seeds on the surface of the sand. Seedling flats were placed in a growth chamber with a 14:10 light:dark photoperiod and a 31:27° C temperature regime (Farmer and Hall 1970). Seeds were watered daily from September 1 to October 31, 2001, with the exception of one day due to logistic difficulties. Germinants were counted and removed weekly. Remaining seeds were sieved from the sand and counted.

*Surveys of Naturally Recruiting* *P. americana.*-Pokeweed plants were censused in nine 25 x 25 m plots in all patches in September of 2000. The nine plots were in a 3 x 3 array that was centered in each patch, leaving a buffer strip of 12.5 m along patch edges that was not censused. Within each plot, we walked four equally spaced transects, approximately 6 m wide, and recorded all *P. americana* plants that were visible and easily identified without squatting. In essence, this technique provided an estimate of established plants because we were rarely able to detect small seedlings. Stems that appeared joined at the base were counted as single plants. Since *P. americana* is rarely found in the understory of mature pine forest, plants counted in our census almost certainly established from seed after our plots were cleared 7 months earlier.

*Statistical Analyses*

*Corridors and Seed Predation by Invertebrates, Rodents, and Birds.*- We used multivariate analysis of covariance (MANCOVA, Scheiner 2001) to accommodate the inherent dependencies among exclosure treatments: rodents and invertebrates could forage from more than one exclosure type, interactions among predators could alter foraging among exclosures, and the recovery rate of seeds may have differed among patches. A separate
MANCOVA was used for each metric of seed predation: number of germinants, seed removal, and seed viability. Each MANCOVA had four dependent variables corresponding to the values obtained from the four different exclosure treatments (NONE, I, IR, and ALL). Because preliminary analyses indicated significant differences in field germination between 2000 and 2001 (paired t-test, $t = 3.60$, 39 d.f., $P < 0.001$), we performed two MANCOVA analyses for field germination, one for each year of germination data.

Our models specified experimental unit and the type of patch (connected, rectangular, or winged) as fixed effects (random effects cannot be modeled with MANCOVA, Scheiner 2001). Substrate and vegetation data were examined as possible covariates. Comparing the number of remaining seeds (our second metric of seed predation) assumes that the number of germinants was constant among treatments. Although the qualitative outcome of our analyses would be the same if this assumption were not met, comparison of germinants over the entire sampling period supports this assumption (paired t-tests, 39 d.f., $t < 0.77$, $P > 0.44$; see also Table 2).

If significant patch type effects were found in MANCOVAs, we used planned pairwise multivariate contrasts of patch type effects (Scheiner 2001) to test the predictions that distinguish corridor, drift-fence, and area effects (Table 1). We follow the multivariate contrasts with univariate ANCOVAs that use the difference between exclosure types as the dependent variable (Scheiner 2001) to determine if the relationship between exclosure treatments changed with patch type. For example, if rodents removed more seeds than invertebrates in one patch type, but not in another, the univariate ANCOVA would detect a significant effect of patch type on the difference between I and IR exclosures. This approach also allows us to assess the contribution of each predator type to overall seed predation in
each patch type. These analyses were all planned, i.e. we did not perform tests in an
exploratory fashion. As such, we did not adjust $\alpha$ for multiple tests (Day and Quinn 1989),
although such an adjustment would not change the significance of our comparisons at $\alpha = 0.05$.

**Corridors and Overall Seed Predation.** We use MANCOVA to examine the net
effect of all seed predators on the number of germinants in 2000 and 2001, seed removal, and
viability. For these analyses, the dependent variables were the values from NONE and ALL
treatments (analogous to Hotelling's $T^2$-test; Scheiner 2001). Our model was otherwise the
same as used for examining predator-specific effects, including covariates. If significant
effects were found due to patch type, we conducted planned pairwise contrasts to examine
the predictions that distinguish the effects of corridors (Table 1), as with our predator-
specific models. If significant differences were not found due to patch type, we used paired
t-tests for each measure of seed predation to determine if overall predator effects were
significant.

**Seed Predation and the Distribution of *P. americana.*** We used multiple regression to
examine the relationship between the abundance of naturally recruiting *P. americana* in our
study system and our experimental measures of seed predation (changes in germinants, seeds
remaining, and viability). As with the ANCOVAs, we used the difference between exclosure
treatments to partition the effects of each predator type. For example, the reduction in seed
number due to rodents was obtained by subtracting the number of seeds recovered from I
treatments from the number of seeds recovered from IR treatments. In this way, we
generated nine variables, representing the change in germinants in 2000, seed removal, and
viability due to invertebrates, rodents, and birds. Because the calculations for rodent and bird
effects include more than one predator type, the rodent and bird estimates assume that any
effect of each predator is additive (generally supported for IR and ALL treatments, see
Results). We used backward selection to identify which variables were most related to the
abundance of naturally recruiting *P. americana* plants.

Analyses were performed with SAS v. 8.1 (SAS Institute 2000). Germinant counts
were squareroot transformed and counts of *P. americana* plants were log-transformed (Zar
1999).

**RESULTS**

*Corridors and Seed Predation by Invertebrates, Rodents, and Birds.* Corridors did
not affect the number of germinants in each exclosure type in 2000 or 2001 (Table 2).
Corridors and patch type affected the number of seeds removed by each predator type, and
downed woody debris was a significant covariate (Table 2, Fig. 2). Examination of
standardized canonical coefficients suggests that more seeds were removed from treatment I
(coefficient = 1.29) and fewer seeds were removed from treatments IR and ALL as woody
debris increased (coefficients = -0.92 and -0.79, respectively). The magnitude of the
coefficients indicates that treatments I and IR were most responsible for the significance of
woody debris as a covariate (Scheiner 2001). The viability of remaining seeds in each
treatment did not differ among patch types (Table 2), although leaf litter was a significant
covariate in the analysis. The significance of leaf litter was mostly attributable to a positive
relationship between leaf litter and viability in treatments I and ALL (coefficients = 1.06 and
1.37, respectively) rather than a weaker negative relationship between viability and leaf litter
in treatment IR (coefficient = -0.83).
There were significant multivariate differences in seed removal between connected and rectangular patches, between winged and rectangular patches, but not between winged and connected patches (Table 2, Fig. 2). Univariate ANCOVA on the difference between treatments NONE and I found no significant differences due to patch type ($F_{2,15} = 1.52, P = 0.25$; Fig. 2b). The difference between NONE and I treatments was significantly different than zero in winged ($t = 3.04, 15$ d.f., $P < 0.01$) and rectangular ($t = 3.25, 15$ d.f., $P < 0.01$) patches (Fig. 2a). In winged and rectangular patches, invertebrates removed 29% and 45% more seeds relative to NONE treatments, but invertebrates did not remove a significant number of seeds in connected patches ($t = 1.38, 15$ d.f., $P = 0.19$). Univariate ANCOVA on the difference between treatments I and IR found significant effects due to patch type ($F_{2,15} = 8.59, P <0.01$; Fig. 2b). In rectangular patches, 36% more seeds were removed from treatment I relative to treatment IR ($t = -2.38, 15$ d.f., $P = 0.01$), suggesting that seed predation by invertebrates increases with area, specifically as the amount of area relative to perimeter increases (Table 1). In connected patches, rodents and invertebrates removed 33% more seeds than invertebrates alone ($t = 3.72, 15$ d.f., $P < 0.01$), suggesting that rodents are responding to corridor effects (Table 1). Rodents and invertebrates did not remove more seeds than invertebrates alone in winged patches ($t = 1.50, 15$ d.f., $P = 0.15$). Regardless of patch type, allowing birds access to seeds did not result in a significant increase in seed removal, i.e. the difference between treatments IR and ALL did not differ due to patch type ($F_{2,15} = 0.09, P = 0.91$; Fig. 2b) and was not different from zero ($t < 0.25, 15$ d.f., $P > 0.81$ for all patch types). However, rodents, birds, and invertebrates (ALL) combined to remove significantly more seeds than invertebrates alone in winged patches (paired t-test, $t = 2.52, 11$ d.f., $P = 0.03$; Fig. 2a).
Corridors and Overall Seed Predation. - Although corridors affected predator-specific seed removal, corridors did not change the overall impact of seed predators on *P. americana*: there was no effect of patch type on overall seed predation (Table 3; Fig. 2). Regardless of patch type, seed predation significantly reduced the number and viability of remaining seeds, and reduced the number of field germinants in 2000 ($t = 2.33, 39 \text{ d.f.}, P = 0.03$; Fig. 3a), but not the number of field germinants in 2001 ($t = 0.13, 39 \text{ d.f.}, P = 0.89$; Fig. 3a). Averaged across all patch types, seed predators removed 49% of the available *P. americana* seeds ($t = 8.00, 39 \text{ d.f.}, P < 0.001$; Fig. 3b), and remaining seeds were only 36% as viable as seeds from NONE treatments not available to predators ($t = 5.46, 39 \text{ d.f.}, P < 0.001$; Fig. 3c).

Seed Predation and the Distribution of *P. americana*. - The number of *P. americana* plants was negatively related to seed removal by invertebrates, rodents, and birds (Table 4). Changes in viability and the number of germinants in 2000 were not retained in the final model. Standardized partial regression coefficients suggest that seed removal by rodents was most related with reduced abundance of naturally recruiting *Phytolacca americana*, followed by seed removal by invertebrates and seed removal by birds (Table 4). Collinearity did not affect the selection or interpretation of the final model, as the largest condition index value was 4.31, below the value of 30 indicative of collinearity (Hair et al. 1998).

DISCUSSION

Corridors altered large-scale predator-prey interactions in a manner most consistent with area effects, and perhaps corridor effects (for rodents), rather than drift-fence effects. However, there was no net effect over the entire landscape because the effects of corridors on predator taxa were antagonistic: when corridors led to increased rodent seed predation, this was accompanied by reduced invertebrate seed predation and vice versa (Table 3; Fig. 2).
We suspect that there was no net corridor effect on prey (seeds) because *P. americana* seeds are readily consumed by both insects (Hyatt 1998) and mammals (McDonnell et al. 1984, Hyatt 1998). Overall seed removal from exclosures and the abundance of naturally occurring *P. americana* plants in the same patch were negatively correlated, suggesting that seed predators may affect the distribution of *P. americana* in the landscape by reducing the number of available seeds (Table 4).

**Corridors and Seed Predation by Invertebrates, Rodents, and Birds.**- Corridors did not influence the number of *P. americana* germinants or the viability of remaining seeds, but corridors did affect patterns of seed removal (Tables 2-3, Fig. 2). Moreover, seed removal and viability were significantly related to the amount of woody debris and leaf litter within a 1-m radius, emphasizing the importance of local microhabitat characteristics in affecting seed risk (Reader and Beisner 1991, Hulme 1997, Manson and Stiles 1998).

Patterns of seed removal by invertebrates were consistent with the hypothesis that invertebrate seed predators avoid edges and are affected by corridors primarily by area effects (Tables 1-2, Fig. 2). The shape of rectangular patches yields the most amount of core habitat relative to the amount of edge habitat, even though overall area is nearly equal among rectangular, connected, and winged patches (see Methods, Fig. 1). The increased core habitat in rectangular patches may represent increased high-quality habitat for early successional invertebrate seed predators. For example, fire ants (*Solenopsis* spp.) only establish in habitats where direct sunlight reaches the soil (Stiles and Jones 1998). Moreover, colony growth, abundance, and foraging are positively related to soil temperature and insolation (Porter and Tschinkel 1987, Porter 1988). The occurrence and abundance of carabid beetles and harvester ants (*Pogonomyrmex* spp.) also respond to changes in temperature, edge and core
area (Didham et al. 1998, Crist and Ahern 1999; MacMahon et al. 2000; Davies et al. 2001). Gonzalez et al. (1998) found that corridors promote population rescue for moss-dwelling arthropods. Our data suggest that the distribution of invertebrate seed predators may be limited more by habitat quality and availability than by the ability of invertebrates to colonize a patch, and support the conclusion of Collinge (2000) that corridor effects per se may be weak or nonexistent for ground-dwelling invertebrates.

Greater seed removal by rodents in connected and winged patches may arise because corridors affect rodent movement and behavior. Oldfield mice (Peromyscus polionotus) and cotton mice (P. gossypinus) were the primary rodent species in our experimental patches (Brinkerhoff et al., in review), and both consume a variety of seeds (Gentry and Smith 1968, Cothran et al. 1991). Corridors may increase patch residency time of female P. polionotus (Danielson and Hubbard 2000), and may also serve as movement conduits for P. polionotus (Haddad et al. 2003, Brinkerhoff et al. in review); both effects could increase seed removal by P. polionotus in connected patches.

We found no evidence that corridors affect avian seed predation. The most common avian granivores in our system were Mourning Doves (Zenaida macroura), Dark-eyed Juncos (Junco hynenalys), Chipping Sparrows (Spizella passerina), White-throated Sparrows (Zonotrichia albicolis), Northern Cardinals (Cardinalis cardinalis) and Eastern Towhees (Pipilo erythrophthalmus) (P. Champlin, personal communication). We suspect that seed predation by avian granivores did not exhibit a corridor effect in our study due to the scale of our experimental patches. Avian granivores forage over relatively large areas, concentrating on high-density patches of seeds (Thompson et al. 1991). As such, although birds contributed to the removal of seeds (Fig. 2), the small scale of our experimental patches
relative to the scale of foraging by avian granivores probably precluded any corridor effects on avian seed removal. Moreover, the nested design of our exclosure treatments may have made corridor effects more difficult to detect for avian granivores because rodents and ants also had access to ALL treatments that allowed bird access. If rodents and invertebrates compensate for corridor-mediated changes in avian seed predation, such changes may not be readily detected by measuring the number of remaining seeds. However, the significant partial correlation between bird seed removal from our experimental exclosures and the abundance of naturally recruiting *P. americana* plants (Table 4) suggests that there was a detectable 'signal' of avian foraging after accounting for seed losses to invertebrates and rodents. Thus, although corridors may be important short-term foraging conduits for frugivorous birds (Tewksbury et al. 2002), corridors do not appear to affect the impact of avian granivores on *P. americana* seeds in the long term.

**Corridors and Overall Seed Predation.**- Corridors led to changes in the efficacy of invertebrate and rodent seed predators (Fig. 2), but corridors did not affect total seed predation when all predators had access to seeds (Table 3, Fig. 2). Overall, seed predators significantly reduced the number of *P. americana* germinants in 2000, reduced the number and viability of remaining seeds, but did not affect the number of germinants in 2001 (Fig. 3).

The similar levels of overall seed removal among patches contrast with predator-specific patterns caused by patch shape (Fig. 2), and suggest that compensation occurs between seed predators, primarily rodents and invertebrates, as has been noted in other studies (Brown and Davidson 1977, Reichman 1979). Moreover, the difference between connected and rectangular patches provides evidence that patch shape may affect interactions
between seed predators. In rectangular patches, invertebrates removed a significant amount of seeds when they had exclusive access to seeds. When rodents were also allowed access, seed removal was no longer significantly different from NONE treatments (Fig. 2a). This suggests that some reciprocal interaction was occurring, at least in rectangular patches. If invertebrates negatively affected rodents, but not vice versa, seed removal should have been equal in I and IR exclosures in rectangular patches, which it was not (Fig. 2a). Although we cannot be certain of the mechanism, the potential for corridor-mediated interactions exists: invertebrates can alter rodent foraging (Holtcamp et al. 1997) and intra-guild predation can occur between rodents and invertebrates (Gentry and Smith 1968, Danielson and Hubbard 2000). Although additional studies are required to determine if corridors affect competition in time and space, our data provide evidence that there may be little truly 'predator-free' space from the perspective of *Phytolacca americana*.

Why were significant reductions in viability and the number of seeds reflected in the number of germinants in 2000 but not 2001? Several mechanisms may be at work. First, we may have failed to detect germinants that were lost to desiccation or herbivory between our sampling sessions. However, the lack of evidence of herbivory in the field (e.g. clipped seedlings) and the consistency of germination among all treatment types (Table 2, Fig. 3) do not support this explanation. Second, *P. americana* germination may have been affected by precipitation differences between 2000 and 2001. However, this explanation is not supported by field data, as there was no significant difference in precipitation during the study in 2000 and 2001 (t-test, t = 0.72, 233 d.f., P = 0.48). Third, *P. americana* seedlings may exhibit density-dependent germination inhibition via allelopathy, as extracts from mature *P. americana* are known to inhibit germination (Edwards et al. 1988), and seedlings may
become microsite-limited when many emerge during pulses of germination (Maron and Simms 1997). Although we removed germinants as soon as we found them, our rate of removal may not have been sufficient to avoid germination inhibition of remaining seeds. Because *P. americana* germination is expected to be greatest during the spring (Baskin and Baskin 2001), density-dependent allelopathic effects would be most likely to occur during the spring phase of our study (i.e. in 2001), in agreement with the greater number of germinants we observed from March-July 2001 compared to June-September 2000 (see Methods; Fig. 3a).

**Seed Predation and the Distribution of *P. americana***—We observed a significant negative relationship between the abundance of naturally recruiting *P. americana* and seed removal from our experimental exclosures. It is possible that the relationship between the number of seeds remaining and the number of naturally recruiting *P. americana* is spurious, because we surveyed plants in 2000, but collected seed-removal and viability data in 2001. However, the strength of the relationship between seed removal and naturally recruiting plants was strong, as seed removal explained 41% of the variance in *P. americana* abundance (Table 4).

Although seed removal by rodents was most related to the overall abundance of *P. americana* plants, removal by invertebrates and birds was also important (Table 4). Rodent seed predators may have more influence on *P. americana* than invertebrate seed predators because rodents detect and exhume buried seeds (Reichman 1979, Abramsky 1983). Because avian seed predators forage across large scales and target high-density seed patches, their impact may be to reduce spatial variation in seed density rather than dramatically reduce total seed density (Thompson et al. 1991). Moreover, each experimental unit may receive a
fraction of foraging by avian granivores compared to invertebrate and rodent granivores because the latter forage almost exclusively within each experimental unit. This is generally supported by the non-significant change in seed predation when birds are allowed access to seeds (Fig. 2), but the significant relationship between seed removal by birds and naturally occurring *P. americana* (Table 4).

**Corridors, Predators, and Prey.** Corridors may have several beneficial effects that make them amenable to conservation (Rosenberg et al. 1997; Haddad 1999; Tewksbury et al. 2002). However, our results demonstrate that corridors also affect multiple species in different ways within a given trophic level. Generally, our results suggest that corridors are most likely to alter predator-prey interactions when predators differ greatly in their response to corridors and in their impacts on prey. For example, seeds that are consumed only by a particular predator type would be more likely to exhibit a net effect due to corridors. Hence, large-seeded, early successional species, such as *Prunus* spp., that are primarily consumed by rodents (Whelan et al. 1991), may benefit from lower predation in rectangular patches, whereas the converse may be true for seeds primarily consumed by invertebrates. Moreover, by mediating interactions among seed predators, corridors could differentially affect seed banks in fragmented landscapes and thus shape the resulting plant community.

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Damschen and members of the poke posse: D. Kuefler, E. Koenig, and J. Mayer, for tireless help with collecting, sifting, and counting seeds. P. Townsend, J. Tewksbury, C. Brooks, J. Brinkerhoff and D. Corbett also provided field assistance. T. Ciravolo and K. McLeod at the Savannah River Ecology Lab kindly provided the growth chamber and logistical support. D. Catlett provided critical materials and advice on exclosure construction. The manuscript was improved by comments from T. J. Benson, R. J. Brinkerhoff, D. Coyle, E. Damschen, N. Haddad, C. Kwit, J. Tewksbury, and A. Weldon. Funding and support were provided by the Department of Energy-Savannah River Operations office through the U. S. Forest Service Savannah River under Interagency Agreement DE-IA09-00SR22188. Funding was also provided by an NSF Research Experience for Undergraduates Grant to BJD and MJB, an NSF Grant to BJD (DEB-9907365) and DJL (DEB-9815834), and a Grant-in-Aid of Research to JLO from the American Society of Mammalogists.

LITERATURE CITED


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TABLE 1. Three effects may lead to the increased predation of seeds in corridors, because corridors change patch shape as well as patch connectivity. Each effect leads to testable predictions for the intensity of seed predation in connected patches (Conn), rectangular patches (Rect), or winged patches (Wing).

<table>
<thead>
<tr>
<th>Effect</th>
<th>Description</th>
<th>Predation Intensity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Area Effects</td>
<td>Corridors increase total amount of habitat and also increase edge relative to core habitat in patch. Effects differ depending upon predator’s response to edge.</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Edge-selecting Predators:</td>
<td>Conn &gt; Rect; Conn = Wing</td>
</tr>
<tr>
<td></td>
<td>Edge-neutral Predators:</td>
<td>Conn = Rect = Wing</td>
</tr>
<tr>
<td></td>
<td>Edge-avoiding Predators:</td>
<td>Rect &gt; Conn; Conn = Wing</td>
</tr>
<tr>
<td>Corridor Effects</td>
<td>Predator abundance is increased because movement between connected patches dampens effects of stochastic events on predator populations. Predators may also harvest more seeds by moving between connected patches.</td>
<td>Conn &gt; Wing; Wing = Rect</td>
</tr>
<tr>
<td>Drift-Fence Effects</td>
<td>Predators moving through the matrix encounter the corridor and follow it into the patch.</td>
<td>Wing = Conn; Wing &gt; Rect</td>
</tr>
</tbody>
</table>
TABLE 2. Effect of patch type (connected, rectangular, winged) and experimental unit (EU) on three different metrics of seed predation. Each metric of predation is composed of four dependent variables representing data from NONE, I, IR, and ALL exclosures in connected (Conn), rectangular (Rect) and winged (Wing) patches. If significant, covariates describing microhabitat in a 1-m radius around exclosures were included (e.g. woody debris). If significant patch type effects were found, we conducted multivariate contrasts to compare patch types.

<table>
<thead>
<tr>
<th>Metric of Predation</th>
<th>Factor</th>
<th>Pillai's Trace</th>
<th>F</th>
<th>d.f.</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Field Germination 2000</td>
<td>Patch type</td>
<td>0.49</td>
<td>1.14</td>
<td>8, 28</td>
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<td></td>
<td>EU</td>
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<td>1.10</td>
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<td>Patch type * EU</td>
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<td>1.04</td>
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<td>EU</td>
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<td>1.53</td>
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<td>df</td>
<td>p Value</td>
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<td>Woody Debris</td>
<td>Conn vs. Wing</td>
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<td></td>
<td>Rect vs. Wing</td>
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<td>Viability of Remaining Seeds Patch type</td>
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<td>Leaf Litter</td>
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<td>4, 12</td>
<td>&lt;0.01</td>
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</table>
TABLE 3. Effect of patch type (connected, rectangular, winged) and experimental unit (EU) on three different metrics of seed predation. Each metric of predation is composed of two dependent variables representing data from NONE and ALL exclosures collected in connected (Conn), rectangular (Rect) and winged (Wing) patches. If significant in the previous MANCOVA model, covariates describing microhabitat in a 1-m radius around exclosures were included (e.g. woody debris).

<table>
<thead>
<tr>
<th>Metric of Predation</th>
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<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Field Germination 2000</td>
<td>Patch type</td>
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<td>0.23</td>
<td>4, 32</td>
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<td>4, 30</td>
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<td>EU</td>
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<td>14, 30</td>
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<td>Patch type * EU</td>
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<td>Leaf Litter</td>
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<td>5.44</td>
<td>2, 14</td>
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TABLE 4. Relationship between the total number of *P. americana* plants (after log transformation) found in each patch and seed predation in each of 40 patches. Independent variables for each predator type were derived by subtracting treatments with the predator from treatments without the predator. Values of F and $R^2$ for individual predator effects are partial values that describe the effects of each predator while accounting for all others in the model. Adjusted $R^2$ for the entire model was 0.36.

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<td>-0.79</td>
<td>22.53</td>
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<td>10.02</td>
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<td>Error</td>
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<td>1.57</td>
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</table>
FIG. 1. Layout of the experimental landscape at the Savannah River Site, South Carolina. Eight experimental units were created by clearing mature pine forest. Each experimental unit consisted of connected (C) and unconnected patches that were either rectangular (R) or winged (W). All patches were clear-cut habitats separated by 150 m of mature pine forest. Within each patch, one of each exclosure type was installed around the center of the patch (final inset).

FIG. 2. Seed removal from exclosure treatments located in connected (Conn), rectangular (Rect) and winged (Wing) patches. (a) Mean number of seeds remaining (± 95% Confidence Intervals) in treatments exposed to no seed predators (NONE), invertebrates only (I), invertebrates and rodents (IR), and invertebrates, rodents, and birds (ALL). (b) The effect of adding a particular predator type, as reflected by the mean difference (± 95% Confidence Intervals) between exclosure treatments that differ by only one predator type.

FIG. 3. Mean effects (± 95% Confidence Intervals) of seed predators across all patch types as measured by exclosure treatments allowing access by no seed predators (NONE) or access by invertebrate, rodent, and bird seed predators (ALL). Effects of seed predators are measured using (a) the number of *P. americana* seeds germinating in the field in 2000 and 2001, (b) the number of *P. americana* seeds remaining in experimental exclosures, and (c) the proportion of remaining *P. americana* seeds that were viable.
Figure 1.
Figure 2.
Abstract: Although corridors may offset the detrimental impacts of habitat fragmentation, corridors may also have negative impacts by affecting predator-prey interactions. We used exclosures within an experimental landscape to determine if corridors and patch shape lead to differential predation on seeds of two bird-dispersed plants: black cherry (*Prunus serotina*) and blackberry (*Rubus allegheniensis*). *Prunus serotina* was almost exclusively consumed by rodent seed predators rather than arthropod seed predators, whereas *R. allegheniensis* was consumed by both arthropods and rodents. Consumption of *P. serotina* and *R. allegheniensis* was significantly greater in connected patches compared to unconnected patches. These results suggest that, although bird-dispersed seeds may benefit from increased dispersal when corridors are present, increased dispersal may be offset or outweighed by corridor-mediated changes in seed predation. Moreover, because the magnitude of corridor-mediated changes in seed predation differed among *R. allegheniensis* and *P. serotina*, corridors may differentially affect seed survival, potentially altering the seed bank and resulting plant community.
Introduction

Habitat fragmentation is a primary cause of biodiversity loss (Wilcove et al. 1998). Among the strategies for reducing the impact of fragmentation are corridors: linear elements that connect disjunct patches of habitat (see reviews in Rosenberg et al. 1997; Beier & Noss 1998; Tewksbury et al. 2002, Haddad et al. 2003). Corridors are thought to increase population persistence by promoting population rescue after local extinction, promoting gene flow, and by increasing abundance (Rosenberg 1997). However, corridors have been criticized because mechanisms underlying purported corridor effects are unknown (Simberloff et al. 1992) and because of a lack of large-scale evidence that corridors promote population viability (but see Mech & Hallett 2001; Tewksbury et al. 2002; Haddad et al. 2003). Importantly, the population-level focus of most corridor studies also neglects interactions among populations, with largely unknown consequences (but see Gonzalez et al. 1998; Tewksbury et al. 2002; Orrock et al. 2003).

Corridors may have positive effects on plant communities by increasing pollination and seed dispersal (Tewksbury et al. 2002; Haddad et al. 2003). However, corridors may also affect the impact of arthropod and rodent seed predators: rodents may consume more seeds in connected patches whereas arthropods may consume more seeds in unconnected patches (Orrock et al. 2003). Because rodents may consume larger seeds compared to arthropods (Whelan et al. 1991), such corridor-mediated differences in the impact of rodent and arthropod seed predators could lead to changes in the plant community (e.g. Brown & Heske 1990; Howe & Brown 2001).
We coupled an experimental landscape (Fig. 1) with exclosures that controlled predator access to determine if corridor-mediated changes in seed predation lead to differential impacts on two bird-dispersed plant species. Black cherry (*Prunus serotina*) seeds are large (6.29 – 6.71 mm; 0.068 – 0.084 g; 95% CI, N = 10) and consumed primarily by rodents (Whelan et al. 1991). Blackberry (*Rubus allegheniensis*) seeds are smaller (2.31 – 2.47 mm; 0.002 – 0.003 g; 95% CI, N = 10), and probably consumed by both arthropods and rodents (Smith 1975). Our objectives were to determine if: 1) seed predation by rodents and arthropods differed with patch shape and connectivity, and 2) whether differences in seed predation affected one species more than the other, potentially altering competitive interactions and population dynamics of *P. serotina* and *R. allegheniensis*.

**Methods**

The experiment was conducted in eight replicated blocks created at the Savannah River Site, a National Environmental Research Park (NERP) near Aiken, South Carolina (Fig. 1). Each block consisted of five patches created during the fall and winter of 1999 by clear-cutting mature pine forest (the matrix) followed by prescribed burning (Fig. 1). In each block, there were three different patch types: connected, rectangular, and winged (Fig. 1). Use of three different patch types allowed us to determine if corridors influenced seed predators by changing patch connectivity ('corridor effects') or patch shape ('area effects' and 'drift-fence effects'; see Tewksbury et al. 2002 and Orrock et al. 2003). Connected patches were joined by a 25 m-wide corridor that was 150 m long. Rectangular patches consisted of a 1-ha square patch with 0.375 ha of additional area, representing the area added by the corridor
Winged patches consisted of a 1-ha square patch with two extending 'drift-fence' sections, each 75 m long and 25 m wide (Fig. 1). Two connected patches were in each block. Four of the blocks had two rectangular patches and one winged patch, whereas the other four blocks had two winged patches and one rectangular patch, yielding a total of 12 winged patches, 12 rectangular patches, and 16 connected patches.

To quantify seed predation, paired 27 x 27 x 11 cm trays were randomly placed next to one another along a central 8-m square in each patch (80 total trays; Fig. 1). Trays were covered to exclude avian granivores and had two 2.5 cm diameter openings. Each tray was filled with 1.5 liters of sand to provide a realistic foraging substrate. One tray (A) was open only to arthropods (tray openings were barred with hardware cloth with 1.5 cm² mesh), whereas the other tray (AR) was open to arthropods and rodents (tray openings unbarred). In each tray, 20 seeds of each species were scattered on the surface of the sand. Seeds were obtained from a commercial supplier (Sheffield’s Seed Supply, Locke, New York, USA). Although several Rubus spp. are present in the study area, seed sizes and characteristics are very similar (Radford et al. 1968), and seeds of Rubus spp. have been pooled for analysis in other studies of seed fate (Smith 1975).

Seed predation trials were conducted twice at all locations, from July 30 - September 10, 2002 and from September 10 to October 7, 2002. There was no difference between data collected during the two sessions within each patch type, so data were pooled for analysis (Paired t-tests, all P > 0.15). Substrate and vegetation characteristics were measured in a 1-m radius around each pair of trays in late July 2002 by visually estimating the percent cover of downed woody debris, woody plants, herbaceous plants, bare soil, and leaf litter.
We used a mixed-model analysis of covariance (ANCOVA; Quinn & Keough 2002) to analyze *P. serotina* and *R. allegheniensis* seed removal. Our split-plot design included block and patch type (connected, rectangular, or winged) as the main plot, with exclosure treatment (A or AR) as the small plot. Patch type and exclosure were fixed effects. Block was treated as a random effect because we wanted to accommodate variance due to blocks into the statistical model (Quinn and Keough 2002).

Several comparisons were of a priori interest in our analyses. First, we were interested in whether the relative roles of arthropods and rodents differed, and whether this difference changed with patch type. As such, we dissected the patch type by exclosure interaction term into three linear contrasts to determine if the effect of exclosure was significant in some patch types, but not in others. Second, we were interested in whether overall seed removal (i.e. seeds removed from AR exclosures) differed among patch types; this was also tested using a linear contrast. Third, we used the difference between the number of *R. allegheniensis* and *P. serotina* remaining in AR trays to compare removal of one species relative to the other and determine whether this differed by patch type. We tested whether the mean difference in seed removal differed among patch types and also whether it differed from zero using a mixed-model analysis of variance with patch type as a fixed effect and block as a random effect.

Vegetation data were examined as possible covariates in all three analyses: a split-plot ANOVA for each plant species, and an ANOVA for the difference between *P. serotina* and *R. allgheniensis* in rodent and arthropod trays. All analyses were performed with SAS v. 8.1 (SAS Institute 2000). The number of *R. allegheniensis* seeds remaining was squareroot transformed to improve normality (Quinn & Keough 2002).
Results

There was a significant effect of patch type on *R. allegheniensis* seed removal and a similar trend for *P. serotina* (Table 1; Fig. 2). There were significant differences in seed removal due to exclosure treatment: allowing rodents access to seeds significantly reduced the amount of *P. serotina* and *R. allegheniensis* (Table 1; Fig. 2). The effects of patch type were dependent upon seed species and exclosure treatment (Table 1). Allowing rodents access to *R. allegheniensis* seeds significantly increased seed removal in connected and winged patches, but not in rectangular patches (Table 1; Fig. 2). Allowing rodents access to *P. serotina* seeds always led to significantly greater seed removal: arthropods rarely removed *P. serotina* seeds. Overall removal (AR exclosures) of *P. serotina* seeds (Fig. 2; linear contrast, $F_{2,36} = 5.64, P < 0.01$) and *R. allegheniensis* seeds ($F_{2,36} = 3.44, P = 0.04$) was greater in connected patches. Removal of *R. allegheniensis* seeds was positively related with the amount of bare soil around exclosures (Table 1). Removal of *P. serotina* from exclosures open to arthropods and rodents decreased as woody plant cover increased (Table 1; $t = 2.49, 36$ d.f., $P < 0.02$); woody plant cover did not affect *P. serotina* removal from exclosures open only to arthropods ($t = -0.57, 36$ d.f., $P = 0.57$).

There was no significant main effect of patch type on the difference between the number of *R. allegheniensis* and *P. serotina* removed by both arthropods and rodents ($F_{2,30} = 1.90, P = 0.17$). However, there was a trend towards a smaller difference in connected patches compared to winged and rectangular patches (linear contrast, $F_{1,30} = 3.80, P = 0.06$). In winged and rectangular patches, the difference between *P. serotina* and *R. allegheniensis*
was significantly greater than zero (Fig. 2, \( t > 3.77, 30 \) d.f., \( P < 0.01 \)). In connected patches, the difference was marginally significant (Fig. 2, \( t = 1.08, 30 \) d.f., \( P = 0.06 \)).

**Discussion**

Our findings suggest that corridors can have negative impacts on bird-dispersed seeds via seed predation, potentially offsetting the positive effects corridors have on bird-dispersed seeds through increased dispersal and pollination (Tewksbury et al. 2002; Haddad et al. 2003). These effects were primarily mediated by rodent seed predators, leading to greater overall removal of both large-seeded *P. serotina* and small-seeded *R. allegheniensis* in connected patches (Table 1; Fig. 2). From a conservation perspective, this work demonstrates that corridors can have indirect effects that may alter their efficacy. Moreover, the effect of corridors may be species-specific: seeds that are primarily consumed by rodents will suffer less seed predation in unconnected patches, both in an absolute sense and relative to predation experienced by arthropod-consumed seeds. Shifts in the plant community may occur following the manipulation of dominant rodent granivores (Brown & Heske 1990; Howe & Brown 2001); this work suggests that corridors can affect the impact of rodent seed predators, and thus could have such community-level impacts on plants.

It remains unclear why rodent seed predation is greater within connected patches, since total rodent abundance in a similar corridor system was rarely greater in connected patches (Danielson & Hubbard 2000; Mabry et al. 2003). Rather, greater seed removal by rodents in connected patches may arise because corridors affect rodent movement and behavior. Recent work in our study system with oldfield mice, *Peromyscus polionotus*
suggests that edge-averse behavior may be greater in connected and winged patches, increasing foraging within the center of the patch (unpublished data). Because we measured seed removal at the patch center, this could produce the patterns of seed removal we observed and those documented in other work (Orrock et al. 2003). This mechanism predicts similar rodent seed removal in connected and winged patches, as observed for R. allegheniensis (Fig. 2) and Phytolacca americana (Orrock et al. 2003). However, patterns of P. serotina seed removal were most similar in winged and rectangular patches (Fig. 2); more work is required to fully determine how connectivity and patch shape affect rodent seed predation.

Corridors may have several beneficial effects that make them amenable to conservation (Rosenberg et al. 1997; Gonzalez et al. 1998; Mech & Hallett 2001; Tewksbury et al. 2002; Haddad et al. 2003). However, these results demonstrate that corridors may also affect predators in a fashion that impacts prey. Because of reduced rodent seed consumption, fewer P. serotina seeds were removed compared to R. allegheniensis seeds in unconnected patches (Fig. 2). Although the statistical significance of this difference was marginal (i.e. P = 0.06), the biological significance may be substantial: on average, the difference between P. serotina and R. allegheniensis was over twice as great in unconnected compared to connected patches (Fig. 2). As such, corridor-mediated shifts in predation could affect the structure of the seed bank and resulting plant community. Future work that explicitly tracks corridor-mediated changes in pollination, seed dispersal, and seed predation for the same suite of plant species is ultimately needed to determine whether the ultimate impact of corridors on plants is positive or negative.
Acknowledgements

We are indebted to J. Blake, G. Curler and J. Cooper, B. Danielson, N. Haddad, D. Levey, and J. Tewksbury for assistance during this project. We appreciate the statistical assistance of P. Dixon. Funding and support were provided by the Department of Energy-Savannah River Operations office through the U. S. Forest Service Savannah River under Interagency Agreement DE-AI09-00SR22188, an A. Brazier Howell award from the American Society of Mammalogists to JLO, a Science To Achieve Results (STAR) Fellowship from the U.S. EPA to JLO, and NSF DEB-9815872.

Literature Cited


Table 1. Seed removal by arthropods and rodents in three different patch types: connected, rectangular, and winged. The interaction between patch type and exclosure treatment (arthropod access or arthropod and rodent access) is dissected into three linear contrasts that examine the difference between exclosures in each patch type. Habitat characteristics (e.g. percent cover of woody plants and bare soil) within 1 m² of exclosures were included in the models if significant.

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<th>Species</th>
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<td>1, 36</td>
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Figure 1. The experiment was conducted in eight replicated blocks at the Savannah River Site, South Carolina, USA. Each block consisted of five patches created during the fall and winter of 1999 by clear-cutting mature pine forest (the matrix) followed by prescribed burning. In each block, there were three different patch types: connected, rectangular, and winged. All patches were of similar area: connected patches were 1.875 ha, whereas winged and rectangular patches were 1.375 ha.

Figure 2. Mean number (±95% Confidence Intervals) of (A) Prunus serotina seeds and (B) Rubus allegheniensis seeds left by arthropods or arthropods and rodents in connected (CONN), rectangular (RECT) and winged (WING) patches. (C) The difference between P. serotina and R. allegheniensis seeds left in exclosures open to both rodents and arthropods. Forty seeds of each species were available for removal over the course of the experiment.
Figure 1.
Figure 2.
CHAPTER 4. PATCH SHAPE, CONNECTIVITY, AND FORAGING BY OLDFIELD MICE (PEROMYSCUS POLIONOTUS)

A paper submitted to the Journal of Mammalogy
John L. Orrock and Brent J. Danielson

Abstract. We used foraging trays to determine how corridors, strips of habitat that connect disjunct patches, affect foraging by the oldfield mouse, Peromyscus polionotus. To separate the roles of connectivity and corridor-mediated changes in patch shape, we used foraging trays and experimental landscapes with three different patch types: patches connected with a corridor, unconnected patches with projecting corridor-like portions ('winged' patches), and unconnected rectangular patches. Corridors did not lead to different levels of P. polionotus activity among the three patch types. Rather, corridors influenced activity by changing patch shape: foraging near the patch center was greater than at the patch edge, but only in connected and winged patches where corridors or 'wings' increased the amount of patch edge relative to the amount of core habitat in the patch. Peromyscus polionotus avoided open microhabitats near the patch edge in winged and connected patches, but not open microhabitats near the patch interior, suggesting that predation risk was responsible for shifts in foraging near edges in connected and winged patches. Foraging in corridors and wings was generally low, suggesting that both are high-risk habitats where predation risk is not ameliorated by proximity to vegetative cover. By changing patch shape, corridors caused changes in within-patch P. polionotus activity, changing foraging patterns and potentially altering the dynamics of P. polionotus and the seeds they consume.
Key Words: corridor, edge, foraging, giving-up density, *Peromyscus polionotus*, Savannah River Site

**INTRODUCTION**

Corridors are narrow strips of habitat that connect disjunct patches of habitat (e.g. Beier and Noss 1998; Haddad et al. 2003; Mabry and Barrett 2003; Rosenberg et al. 1997). By promoting among-patch processes such as movement, gene flow, and recolonization, corridors may have beneficial conservation value (Andreassen et al. 1996; Coffman et al. 2001; Haddad et al. 2003; LaPolla and Barrett 1993; Mech and Hallett 2001; Tewksbury et al. 2002). However, understanding the full impact of corridors as conservation tools requires an understanding of how corridors may affect within-patch processes, if only because patch geometry can affect habitat quality and individual behavior (Dunning et al. 1993; Fagan et al. 1999; Stamps et al. 1987a; 1987b). For example, corridors influence patch shape because corridors are generally long, linear elements with a large amount of edge relative to the patches they connect (Haddad and Baum 1998; Rosenberg et al. 1997). For edge-avoiding organisms, a patch with a corridor may have less usable habitat compared to a patch of the same size that is more rounded in profile. In this case, a better conservation strategy might be to simply increase the size of one of the habitat patches, rather than invest limited resources in connecting the patches with a corridor.

If corridors affect within-patch foraging behavior, community-level consequences could arise. For example, because rodent foraging may be reduced near edges (Bowers and Dooley
1993; Lidicker 1999; Manson et al. 1999; Nickel et al. 2003; Ostfeld et al. 1997; Wolf and Batzli in press), seeds located near a habitat edge may be more likely to escape predation (Bowers and Dooley 1993; Burkey 1993; Díaz et al. 1999; Ostfeld et al. 1997). In long, linear patches, such edge avoidance by rodent seed predators could result in large areas that are relatively free of predation risk from the perspective of a seed. Because rodents are selective seed predators, changes in rodent foraging due to patch shape and connectivity could lead to shifts in plant community composition (Brown and Heske 1990).

We examined the effect of patch connectivity and shape on activity of the oldfield mouse, *Peromyscus polionotus*. Oldfield mice are common habitat specialists in early successional habitats in the southeastern United States (Cothran et al. 1991). Previous work on *P. polionotus* has focused primarily on how corridors affect movement and dispersal (Danielson and Hubbard 2000; Haddad et al. 2003; Mabry and Barrett 2003), abundance (Mabry et al. 2003), and home range (Mabry et al. 2003). Mabry et al. (2003) found that *P. polionotus* were captured more frequently in the interior of patches, suggesting that *P. polionotus* does respond to patch edges and corridors. However, corridor length varied among connected patches, and patch shape was not manipulated independently of connectivity (Mabry et al. 2003). In this paper, we focus on how both corridors and patch shape affect *P. polionotus* activity, and we specifically address a potential mechanism that could produce shifts in foraging behavior: spatial shifts in predation risk.

Examining the effect of corridors on within-patch activity requires manipulation of connectivity and patch shape. If foragers respond to patch edges, three patch types are required: a connected patch that is connected to another patch via a corridor, a patch that is unconnected but still has edgy, corridor-like extensions, and a patch with the same area as the
other patches, but without linear extensions (Fig. 1). Using these three patch types allows discrimination among responses due to connectivity, responses due to edge, and responses due to both. For logistical reasons, large-scale studies that meet these criteria are virtually nonexistent (see reviews in Beier and Noss 1998; Rosenberg et al. 1997).

Using an experimental landscape that manipulates patch connectivity and shape among patches of similar size, we examined whether corridors influence foraging by *P. polionotus* by affecting: 1) patch connectivity, 2) patch shape, or 3) both patch connectivity and patch shape. Specifically, we examined how patch shape and connectivity may lead to differences in foraging within patches, and whether foraging patterns suggest that predation risk is the mechanism responsible for shifting foraging patterns.

**MATERIALS AND METHODS**

*Experimental Landscape.*—The experiment was conducted in two replicated blocks (the 'experimental units' in Orrock et al. 2003) created at the Savannah River Site, a National Environmental Research Park (NERP) near Aiken, South Carolina (Fig. 1). Each block consisted of five patches created during the fall and winter of 1999 by clear-cutting mature pine forest (the matrix) followed by prescribed burning (Fig. 1). In each block, there were three different patch types: connected, rectangular, and winged (Fig. 1). Connected patches were joined by a 25 m-wide corridor that was 150 m in length; each connected patch consisted of half of the corridor (Fig. 1). Rectangular patches consisted of a 1-ha square patch with 0.375 ha of additional area, representing the area added by the corridor (Fig. 1). Winged patches consisted of a 1-ha square patch with two extending 'drift-fence' sections, each 75 m long and 25 m wide (Fig. 1). Two connected patches and two rectangular patches were in each experimental unit, yielding a total of 4 connected patches, 4 rectangular patches, and 2 winged patches.
Predictions that differentiate the effects of patch shape and connectivity. —Our design allowed us to determine the relative importance of connectivity and shape because each makes a unique prediction regarding among- and within-patch effects. Although patches were of similar area (connected patches were 1.19 ha, winged and rectangular patches were 1.38 ha), patch types differed in their connectivity and in the relative amounts of edge and area habitat. This is illustrated by the area/perimeter ratio for each patch type: 22.62 for connected patches, 19.64 for winged patches, and 28.95 for rectangular patches. The small difference in total area between connected and unconnected patches does not change the qualitative order of our predictions. Rather, if foraging is greatest in connected patches, despite the slightly reduced overall area and drift fence in connected patches, we have a more conservative test for corridor effects.

We examined foraging at different spatial locations within a patch (Fig. 1), to determine the role of patch shape and connectivity in affecting within-patch foraging. For example, although patch area is relatively constant, the greater amount of edge relative to core habitat in connected and winged patches may cause P. polionotus to disproportionately allocate foraging activity near the center of these patch types. Using the terminology from Fig. 1, this predicts that core locations in connected and winged patches will be equal, and both will exhibit greater foraging than the core of rectangular patches. Conversely, the reduced amount of edge relative to core habitat in rectangular patches may lead to more equitable foraging over the entire patch by P. polionotus (i.e. rectangle core = rectangle edge). As such, if the within-patch behavior of P. polionotus is influenced by edge, we expect that the difference between foraging at the edge and at the core would be greatest in connected and winged patches, and least in rectangular patches. Where predation risk is the mechanism producing differences in foraging among locations, we expect differences in foraging between paired foraging trays where one tray is protected from predators (sheltered) and one tray is exposed to predators (see below).
Corridors and patch shape may also change among-patch foraging of *P. polionotus*. If corridors affect rodent foraging by affecting connectivity alone, foraging should differ between connected and unconnected patches (connected patches ≠ winged and rectangular patches). If corridors affect rodent foraging by changing patch shape, foraging should be similar between connected and unconnected patches of the same shape (winged patches = connected patches; winged and connected patches ≠ rectangular patches). If patch shape and connectivity are important, foraging should differ between connected and unconnected patches, as well as between unconnected patches of different shape (all three patch types differ).

**Rodent foraging.** — We used paired foraging trays placed at different locations within each patch type (Fig. 1). Within each pair of trays, one tray was placed below vegetative cover (the ‘sheltered’ tray), and the corresponding tray, the ‘exposed’ tray, was placed outside of cover, <1 m away. Pairs of trays were placed in the center of each patch (the ‘core’ location) and 15 m from the edge of each patch (the ‘edge’ location). Within each connected patch, a pair of trays was also placed within the corridor (the ‘corridor’ location). Similarly, a pair of trays was also placed within one randomly selected wing of each winged patch (the ‘wing’ location; Fig. 1).

Each tray was a 27 x 27 x 11 cm plastic storage container filled with 1 liter of sand. A 2.5-cm diameter hole was drilled in each of two sides. Each tray contained a constant volume of millet seeds (3.7 ml) thoroughly mixed into the sand, and was covered with a plastic lid to exclude rain and avian granivores. As a foraging rodent depletes the seeds within a tray, diminishing returns are realized (Brown 1988; Morris and Davidson 2000). At some point the benefits of continued foraging are outweighed by the costs (Brown 1988). This threshold, called the giving-up density (GUD; Brown 1988) represents a quantitative measure of the costs of foraging (i.e. metabolic costs, missed-opportunity costs, and predation risk), because a rodent should stop foraging, or ‘give up’ when the cost of foraging equals the (diminishing) rate of gain from foraging. By pairing the trays, it is assumed that missed opportunities and metabolic costs are the same within a pair. As such, the
difference between sheltered and exposed trays can be used to quantify predation risk experienced by rodents, including *P. polionotus* (e.g. Abramsky et al. 2002; Kotler et al. 1991; Morris and Davidson 2000; Orrock et al. in press).

Trays were established on May 6, 2003 and were run for three days at each location before data collection to allow rodents to become accustomed to the tray (Morris and Davidson 2000). From May 9 to May 13, 2003, trays were visited daily. If signs of foraging were noted (hulls, rodent tracks, fecal pellets), we sieved the seeds from the sand, refilled the tray with a constant volume of millet seeds, and thoroughly mixed the seeds into the sand. On the final day of sampling, all trays were sieved and seeds collected.

*Rodent abundance and activity.* — We sampled rodents to ensure that *P. polionotus* was the predominant forager in our patches, to obtain a relative estimate of the number of rodents at a location, and to provide a separate metric of rodent activity (i.e. total captures of *P. polionotus*) for comparison with our findings from foraging trays. Four Sherman live traps (Sherman Traps, Inc., Tallahassee, FL) were placed at each location from May 13 to 17, 2003. Traps were baited with rolled oats and locked open for the first two days. Subsequently, traps were activated and checked daily for the next three days. Captured rodents were identified to species, marked with a uniquely numbered ear tag (National Band and Tag Company, Lexington, KY), and released at the site of capture.

*Data analysis.* — To examine the effect of patch shape and location on overall seed removal, we compared seed removal at each location using a mixed-model analysis of variance (Littell et al. 1996). The structure of our design represents a blocked, nested split plot, with groups of five patches representing blocks (Fig. 1), patch type (connected, rectangular, winged) representing the largest (main) plot, and location nested within patch type representing the small (split) plot. Our analysis accommodates repeated measures taken over time (i.e. we visited the same sites on consecutive days) by using a type 1 autoregressive covariance structure (Littell et al. 1996). Since we were not
interested in testing hypotheses regarding time or experimental unit, our statistical model specified
day and experimental unit as random effects. Patch type was a fixed main-plot effect, location was a
fixed effect nested within patch type. Our comparisons of patch-type effects were not compromised
by the nested nature of our design (e.g. corridor locations were only found in connected patches)
because analogous results were obtained if patch type effects were compared using only observations
from core and edge locations (i.e. locations shared by all patch types). Tray microhabitat (sheltered
or exposed) was a fixed effect fully crossed with location and patch type. Because we were
specifically interested in determining whether \textit{P. polionotus} perceived some locations as safe and
some as risky, we dissected the interaction between location and microhabitat into 8 linear contrasts.
If rodent activity was never observed at a pair of trays during the foraging experiment, those data
were not included in the analysis. Although this resulted in an unbalanced design, it makes our
conclusions more robust because we can assume that foraging is not confounded with the presence of
mice (i.e. mice must be present for a foraging choice to occur). We also did not include data from
one location where a cotton mouse, \textit{Peromyscus gossypinus}, was the only rodent captured.

We used a mixed-model ANOVA to examine trapping data, treating experimental unit as a
random effect and patch type and location as fixed effects. Capture data were pooled across the
sampling session. Dependent variables examined were the total number of captures at a site (as a
metric of total rodent activity), and the total number of unique individuals captured at a location
\((M_{t+i})\), \cite{Slade2000}. We used \(M_{t+i}\) because it performs as well or better than closed
population estimation techniques (e.g. the Lincoln-Peterson estimator) when sample sizes are low or
animals are not captured at all locations \cite{Slade2000}.

Prior to analysis, weights of seeds remaining in each tray were cube-root transformed to improve
normality and stabilize variance, as evaluated using residual plots \cite{Zar1996}. The mean weight of
seeds from unforaged trays on the last day of the foraging experiment \((2.82 \pm 0.09 \ SE, N = 9)\) was
used as the weight of seeds from 11 observations where no foraging had been observed at one tray of
a pair, although the results of the analysis were the same if only values from foraged trays were used. Because of the complex structure of our statistical model and the unbalanced nature of the foraging data, we use the Satterthwaite approximation to determine the denominator degrees of freedom for our tests (Littell et al. 1996). Analyses were conducted using SAS v. 8.1 (SAS Institute 2000); all P-values are two-tailed.

**RESULTS**

*Rodent foraging.* —Examination of 193 foraging observations revealed that there was no difference in overall seed removal in connected, rectangular, and winged patches (Table 1). There was a significant effect of location within each patch type (Table 1; Fig. 2). In connected patches, *P. polionotus* removed more seeds from the core of each patch compared to the edge ($t = -1.95, d.f. = 22.1, P = 0.06$; Fig. 2) and the corridor ($t = -2.18, d.f. = 22.6, P = 0.04$), with equivalent amounts removed from edge and corridor locations ($t = 0.7, d.f. = 22.5, P = 0.49$). In rectangular patches, seed removal did not differ between core and edge habitats ($t = -1.29, d.f. = 24.5, P = 0.21$; Fig. 2). Seed removal in winged patches was greatest in the core compared to the edge ($t = -2.18, d.f. = 21.9, P = 0.04$; Fig. 2) and the wings ($t = -5.13, d.f. = 21.8, P < 0.01$). Seed removal was also greater at the edge compared to the wings ($t = -3.80, d.f. = 22.3, P < 0.01$). Overall, seed removal was greatest in covered microhabitats (Table 1). There was no interaction between patch type and tray microhabitat (Table 1), and no overall interaction between location and tray microhabitat ($F = 1.73, d.f. = 5, 15.8, P = 0.18$). However, planned contrasts revealed that seed removal was greater in covered trays at the edge of connected and winged patches (Table 1; Fig. 2). In all other
locations, there was no difference in foraging between covered and uncovered microhabitats (Table 1).

Rodent abundance and activity. — In 312 trapnights, we captured 45 individuals representing 80 total captures. Forty-two *P. polionotus*, 18 females and 24 males ($X^2 = 0.86$, 1 d.f., $P = 0.35$), were captured 73 times. One harvest mouse, *Reithrodontomys humulis*, and 2 cotton mice, *Peromyscus gossypinus*, were also captured. There were no movements of mice among locations or patches. There was no significant difference in the number of *P. polionotus* ($M_{t+i}$) among patch types ($F = 0.45$, d.f. = 2, 6.41, $P = 0.66$; Fig. 2) and no significant differences among locations within patch types ($F = 1.96$, d.f. = 5, 10.7, $P = 0.17$). Although there was no significant main effect due to patch type, the number of *P. polionotus* was significantly greater in the core compared to the corridor ($t = 3.04$, d.f. = 10.7, $P = 0.01$; Fig. 2).

There was no difference in the activity of *P. polionotus* (as measured by total captures) among patch types ($F = 0.36$, d.f. = 2, 6.20, $P = 0.71$; Fig. 2), but activity did differ among locations within patch types ($F = 3.88$, d.f. = 5, 10.4, $P = 0.03$; Fig. 2). Within connected patches, total captures were greater in the patch core compared to the edge ($t = 2.20$, d.f. = 10.4, $P = 0.05$; Fig. 2), and greater in the core compared to the corridor ($t = 3.85$, d.f. = 10.4, $P < 0.01$). Activity in connected patches was not greater at the edge than in the corridor ($t = -1.65$, d.f. = 10.4, $P = 0.13$). There was no difference in activity between the core and edge in rectangular patches ($t = 0.82$, d.f. = 10.4, $P = 0.43$). Although marginally significant, there was a trend of less activity at the edge of winged patches compared to the core ($t = 1.94$, d.f. = 10.4, $P = 0.08$). There was no difference in activity between edge and wing locations in
winged patches ($t = -1.17, d.f. = 10.4, P = 0.27$) or between core and wing locations ($t = -0.78, d.f. = 10.4, P = 0.45$).

**DISCUSSION**

Our results suggest that corridor-mediated changes in patch shape, not connectivity, affected within-patch foraging by *P. polionotus*. In connected and winged patches, seed removal patterns suggest that the edge habitat was riskier than core habitat (Fig. 2). In these patches, there was no difference between sheltered and exposed trays in the core of the patch, but fewer seeds were removed from exposed trays than sheltered trays at the edge. In rectangular patches, seed removal was similar from trays at the patch core and patch edge, and there was no difference between exposed and sheltered trays. Trends in total captures also suggest that *P. polionotus* responded to changes in patch shape: in rectangular patches, activity did not differ at the patch edge or core, whereas there were more total captures of *P. polionotus* in the center of connected patches and a similar trend in winged patches (Fig. 2).

*Patch shape, connectivity, and rodent foraging.*—Our data suggest that proximity to edge was important in mediating risk-sensitive foraging behavior: in connected and winged patches where edges comprise a greater amount of the patch, foraging near the edge was reduced. In rectangular patches where the patch interior comprises a greater relative amount of patch area, foraging near edges resembled foraging in the patch interior (Fig. 2).

*Peromyscus polionotus* is an old-field specialist, and the aversion to edge we detected is consistent with other studies: *P. polionotus* was more frequent in the center of patches (Mabry et al. 2003), and predation risk and foraging behavior are edge-specific for other *Peromyscus* species (Wolf and Batzli in press, Morris and Davidson 2000). Our results suggest that, by changing the relative amount of edge in a patch, patch shape may also have
changed the strength of the edge effect on *P. polionotus*. That is, the response of *P. polionotus* to edge was not solely a function of the distance to nearest edge, but was a function of several edges (Malcolm 1994; Fagan et al. 1999), as supported by the decreasing difference between seed removal in core and edge locations as patch shape changed from winged, to connected, to rectangular (Fig. 2).

Seed removal patterns in wings and corridors also suggest edge-averse behavior by *P. polionotus*. In wings, where rodents were near three forest edges (Fig. 1), overall seed removal was significantly lower than at the edge or core of the winged patch (Fig. 2). Corridors, in contrast, were only near two forest edges, and overall seed removal was similar to the edges of connected patches (Fig. 2). There was no difference between covered and uncovered trays in wings and corridors, suggesting that predation risk in these locations was similar among sheltered and exposed habitats. Combined with the low abundance and activity of *P. polionotus* found in wings and corridors (Fig. 2), these patterns of suggest that corridors and wings were simply risky places that are avoided regardless of microhabitat (i.e. risk within corridors and wings may override any protection afforded by microhabitat; Abramsky et al. 2002).

*Patch shape, connectivity, and rodent abundance and activity.* —Live-trapping data suggest that patch shape and connectivity had weak effects on the abundance of *P. polionotus* (Fig. 2), with the exception of significantly greater number of mice captured in the core of connected patches compared to the corridor (Fig. 2). In a similar experimental system, Danielson and Hubbard (2000) found that *P. polionotus* abundance was also unaffected by corridors, and Mabry et al. (2003) found that abundance of *P. polionotus* was not different for 2 years of the study, but was lower in connected patches during the third year of the
study. Ongoing research in this study system may be necessary to fully evaluate whether corridors change *P. polionotus* population dynamics over time.

Differences in seed removal seem to be due to shifts in activity, rather than substantial changes in *P. polionotus* abundance (Fig. 2). Patch size, patch shape, and edge have been shown to change home range size and orientation of *Microtus pennsylvanicus* (Bowers et al. 1996; Harper et al. 1993). We observed greater activity and seed removal (Fig. 2) near the center of connected patches (Fig. 2), consistent with changing patterns of habitat use. Working in a similar experimental system, Mabry (2001) observed a trend of smaller home range for *P. polionotus* (0.5 ± 0.1 ha) compared to *P. polionotus* in unconnected patches (1.5 ± 1.0 ha). Female *P. polionotus* exhibited greater patch residency times in connected patches in the same system (Danielson and Hubbard 2000). In accordance with our results, *Peromyscus polionotus* was also more likely to be captured in core habitats than at the patch edge or in the corridor (Mabry et al. 2003). Thus, our findings provide additional evidence that *P. polionotus* home range and within-patch distribution differs in connected patches (Mabry 2001, Mabry and Barrett 2003, Mabry et al. 2003), and suggest that this pattern is not a function of connectivity, but is rather a function of patch shape. Moreover, our work suggests that predation risk is the mechanism that drives this shift.

Why would edges in rectangular patches be viewed as less risky from the perspective of *P. polionotus*? Distance to the fourth edge is 87.5 m in connected and winged patches, and 125 m in rectangular patches (Fig. 1). *Peromyscus polionotus* foraging near the edge of rectangular patches may not be able to perceive the fourth edge, whereas mice at the edge of connected and winged patches are more likely to be aware of the proximity of the fourth edge and change their foraging accordingly. White-footed mice (*P. leucopus*) are able to perceive
forest edges 90 m away at twilight and 60 m away on moonlit nights (Zollner and Lima 1999). Reduced foraging by mice in exposed microhabitats near the edge of connected and winged patches may be because these patches provide more suitable habitat for edge-selecting predators, making edges in rectangular patches inherently less risky in comparison. Mammalian predators, such as skunks, red foxes, and raccoons are also much more likely to enter and exit patches at patch corners compared to straight patch edges (Kuehl and Clark 2003). As such, connected and winged patches provide additional points of predator entry and exit not found in rectangular patches. These mechanisms are not mutually exclusive, and await examination in future work.

The design and duration of our study limited our ability to examine other potential factors that may affect *P. polionotus* activity. For example, although moon illumination and precipitation are known to affect foraging of *P. polionotus* (Orrock et al. in press), we did not examine these effects because it did not rain during our study, and our design had very low power to examine daily effects, making their examination tenuous. Bowers and Dooley (1993) found that seed removal, most likely by *P. leucopus*, at the edges of grassland plots was lower on moonlit nights. Based upon our findings, the reduced foraging of *P. polionotus* during moonlit, rainless nights observed in other studies (Orrock et al. in press) could interact with patch shape. In patches with relatively large amounts of edge (i.e. connected and winged patches), the difference in foraging between core and edge areas should be least on rainless nights or nights with little moonlight, although this has yet to be examined.

By focusing our study on within-patch effects, our study necessarily had low replication for testing among-patch effects (i.e. only 10 patches were used). As such, although we found that activity and abundance did not differ among patch types, this finding may be due in part
to the low patch-level power of our study design. However, studies in a similar system also found no difference in overall *P. polionotus* abundance among connected and unconnected patches (Danielson and Hubbard 2000; Mabry et al. 2003; Mabry and Barrett 2003), suggesting that the lack of among-patch differences we observed may reflect the true lack of difference rather than our power to detect one. However, Danielson and Hubbard (2000) observed greater numbers of males relative to females in unconnected patches, suggesting that demographic shifts may occur with connectivity. Clearly, future studies that examine among-patch foraging and demography with greater large-scale replication are necessary.

**Conclusions.** —By shifting patterns of seed removal by *P. polionotus*, changes in patch shape and connectivity could lead to changes in the distribution of seeds (Brown and Heske 1990). Orrock et al. (2003) detected greater rates of seed predation by rodents in connected patches compared to winged and rectangular patches. Because Orrock et al. (2003) measured seed predation near the center of each patch, the increased seed predation they detected may have been due, at least in part, to greater levels of foraging in the interior of connected patches by *P. polionotus*. In old fields and restored prairies, edges may affect rodent activity, granivory and herbivory (Manson et al. 1999; Nickel et al. 2003; Ostfeld et al. 1997), potentially affecting the tempo and direction of succession. Similarly, seed predation may also be greater near the edges of forested systems (Burkey 1993; Díaz et al. 1999). Our results also suggest that edges affect rodent foraging, but further suggest that the impact of edges is a function of patch shape.

Corridors affect movement, abundance, and behavior of many species (Beier and Noss 1998; Haddad et al. 2003; Rosenberg et al. 1997; Tewksbury et al. 2002). However, the impact of corridors on within-patch processes may be of equal or greater importance than the
impact of corridors on between-patch processes. For species where adults rarely disperse, such as *P. polionotus*, corridor-mediated changes in patch colonization (Haddad et al. 2003), adult residency (Danielson and Hubbard 2000), and foraging behavior (Fig. 2) may have important consequences for long-term landscape-level persistence and gene flow. Because *Peromyscus polionotus* may reside within the same patch for over two years (Orrock, unpublished data), foraging patterns shaped by patch geometry may shape the seed bank, with potential consequences for plant recruitment (Orrock et al. 2003) and community structure (Brown and Heske 1990).

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**LITERATURE CITED**


WOLF, M., AND G. BATZLI. In press. Forest edge – high or low-quality habitat for white-footed mice (*Peromyscus leucopus*)? *Ecology*.


TABLE 1.—Mixed-model analysis of variance (ANOVA) examining the effect of patch type (connected, rectangular, or winged), location within each patch (core, edge, corridor, or wing), and tray microhabitat (sheltered or exposed) on the giving-up density (GUD) of *Peromyscus polionotus*. GUD was measured as the weight of seeds remaining in a foraging tray. Denominator degrees of freedom (DDF) determined using the Satterthwaite approximation (Littell *et al.* 1996). Interactions among location and tray microhabitat are dissected into linear contrasts to determine if the relationship between sheltered and exposed trays changes with location.

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<th>Effect</th>
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FIG 1.— Depiction of the experimental landscape created at the Savannah River Site near Aiken, South Carolina. Patches were clearcuts within a matrix of mature pine forest. Within each patch, foraging stations were located in the center of the patch (Center; indicated by a circle) and 15 m from the edge of the patch (Edge; indicated by a square). Within connected patches, a foraging station was also located in the corridor (Corridor; indicated by a triangle). Within winged patches, a foraging station was located in one of the wings (Wing; indicated by a triangle).

FIG 2.— Mean (± 95% Confidence Intervals) seed removal (A), abundance (B), and number of total captures (C) of Peromyscus polionotus in an experimental landscape at the Savannah River Site, Aiken, SC, in three different patch types: connected (CONN), rectangular (RECT), and winged (WINGED). Within each patch, foraging stations were located in the center of the patch (Center) and 15 m from the edge of the patch (Edge). Within connected patches, a foraging station was also located in the corridor (Corridor). Within winged patches, a foraging station was located in one of the wings (Wing). Values for giving-up density (remaining seeds) were cube-root transformed, values for abundance and activity were not transformed.
Figure 1.
Figure 2.
CHAPTER 5. CORRIDORS AFFECT ANT COMMUNITIES BY CHANGING PATCH SHAPE.

A paper submitted to *Ecology*

John L. Orrock, Gregory R. Curler, Brent J. Danielson, and David R. Coyle

Abstract. We used a large-scale experimental system to examine how corridors, strips of habitat that connect isolated habitat patches, affect the distribution and abundance of ants. In July and August 2002, we quantified ant communities throughout eight 12-ha experimental landscapes consisting of clear-cut patches surrounded by a matrix of mature pine forest. We used three patch types to dissect the different ways that corridors can impact populations: connected patches ('corridor effects'), rectangular patches ('area effects'), and winged patches ('drift-fence effects', whereby corridors direct moving organisms into a focal patch).

The abundance of ants, ant biomass, the number of genera (richness), and evenness did not differ among patch types. Rather, ant abundance, biomass, richness, and evenness varied within each patch type in a manner consistent with area effects: corridors influenced ant communities by changing the amount of habitat available for core-inhabiting genera (*Dorymyrmex* and *Pogonomyrmex*) and for edge-inhabiting genera (*Crematogaster* and *Pheidole*). Ant biomass was consistently greater in the core of all patches compared to patch edges and areas within corridors or wings. In rectangular patches, where the amount of core habitat was greatest relative to the amount of edge habitat, richness and evenness were greater at the patch edge. This patch-specific shift appeared to be due to an increased
negative impact of fire ants, *Solenopsis* spp., on other ant genera in rectangular patches, suggesting that corridor-mediated changes in patch shape may affect interactions among ants. Because corridors are linear elements inhabited by particular ant genera, greater abundance of these genera in corridors may influence the likelihood that corridors are beneficial for other organisms, such as ant-dispersed plants.

Key Words: Conservation, *Formicidae*, fragmentation, Savannah River Site, space

**INTRODUCTION**

Corridors are landscape elements that may promote gene flow and recolonization by connecting otherwise isolated fragments of habitat (Rosenberg et al. 1997), potentially ameliorating the detrimental effects of habitat fragmentation (see reviews in Saunders et al. 1991, Harrison and Bruna 1999, Hunter 2002). Evidence suggests that corridors may increase movement and abundance of a wide variety of taxa (e.g. Beier and Noss 1998, Gilbert et al. 1998, Gonzales et al. 1998, Tewksbury et al. 2002, Haddad et al. 2003). However, the population-level focus of many corridor studies ignores the potential effects of biotic interactions, i.e. the ultimate effect of corridors depends upon how corridors affect populations and how these populations interact. Recent studies reinforce this point, revealing that corridors may promote beneficial interactions (e.g. pollination and seed dispersal, Tewksbury et al. 2002) as well as detrimental interactions (e.g. predation, Simberloff et al. 1992, Burkey 1997, Orrock et al. 2003), and that connectivity may change species richness (Gilbert et al. 1998, Gonzalez et al. 1998) and persistence (Holyoak and Lawler 1996, Gilbert et al. 1998, Gonzalez et al. 1998).

Assessing the effects of corridors on populations and communities may be difficult because, in addition to serving as conduits that promote movement and recolonization
(‘corridor effects’; Rosenberg et al. 1997), corridors may also intercept organisms moving through the matrix and direct them into a patch (‘drift fence effects’; Haddad 1999). Corridors also change patch size and shape (‘area effects’), resulting in greater patch area and increased influence of the patch edge (Rosenberg et al. 1997, Haddad and Baum 1999). By changing patch shape, corridors can also affect the amount of usable patch area and within-patch movement of edge-sensitive organisms, if only by changing the quantity and quality of edge habitat (Fagan et al. 1999, Collinge and Palmer 2002, Braschler and Baur 2003). To better understand the potentially complex effects of corridors, we examined how the presence of a corridor affects one of the most ubiquitous terrestrial organisms: ants (Hölldobler and Wilson 1990).

Ants are integral, influential components of ecosystems (Kelly 1986, Hölldobler and Wilson 1990, Holway et al. 2002a). Past studies have shown that fragmentation affects the diversity and abundance of insects (see Hunter 2002, Tscharntke et al. 2002, Steffan-Dewenter and Tscharntke 2002), including beetles (Davies and Margules 1998, Didham et al. 1998, Davies et al. 2001) and ants (Suarez et al. 1998, Carvalho and Vasconcelos 1999, Braschler and Baur 2003). Similarly, the distribution of ants on islands may be affected by the amount of habitat on the island and its relative isolation (see Morrison 1998 and citations therein). However, little is known about whether corridors (and concomitant changes in patch shape and connectivity) offset the effects of fragmentation on ants, or whether corridors affect the structure of ant communities (see Collinge 2000 for other ground-dwelling invertebrates). Ant distribution is limited by thermal habitat characteristics (Porter and Tschinkel 1987, Kaspari et al. 2000, Kaspari et al. 2003), and evidence suggests that edges and patch shape affect some invertebrates (Davies and Margules 1998, Didham et al. 1998, Davies et al. 2001).
1998, Davies et al. 2001, Collinge and Palmer 2002) including ants (Stiles and Jones 1998, Suarez et al. 1998, Carvalho and Vasconcelos 1999, Golden and Crist 2000, Braschler and Baur 2003). As such, ants may be affected by corridors if only because corridors change patch geometry. By affecting ants, corridors could affect ant-plant mutualisms (Kelly 1986, Ness 2004), nutrient cycling (Hölldobler and Wilson 1990), granivory dynamics (Brown and Heske 1990) or shift the structure of communities by changing colonization of dominant species that affect other invertebrates and vertebrates (Holway et al. 2002a), such the invasive fire ant (*Solenopsis invicta*; Porter and Savignano 1990, Gotelli and Arnett 2000), and Argentine ant (*Linepithema humile*; Suarez et al. 1998).

**Differentiating among corridor, drift-fence, and area effects.**-- Using three patches of similar size that varied in shape and connectivity (Fig. 1) allowed us to experimentally deduce how corridors affect ant populations because corridor effects, drift-fence effects, and area effects all make different predictions (Table 1). For example, if corridors affected ants via 'corridor effects', we would predict greater ant abundance in connected patches compared to unconnected patches of similar size and shape (Fig. 1). Our sampling design used pitfall samples (Hölldobler and Wilson 1990) at different locations within each patch type (Fig. 1), allowing us to examine how patch shape and connectivity affects ants among patch types and the distribution of ants within each patch type. Being able to distinguish between among- and within-patch effects may be particularly important if the main effect of corridors is to affect distribution by changing patch shape, leading to shifts in ants that are sensitive to edge habitats. For example, if ants prefer interior (core) habitats, we would predict that, among patches, more ants would be found in patches with little edge habitat relative to interior habitat (e.g. the rectangular patches in Fig. 1). We would expect within-patch patterns to
provide supporting evidence. Continuing the example above, ants that prefer core habitats would be less abundant near the edge of all patch types. If edge effects are a function of the amount of core area relative to all edges in a patch (Fagan et al. 1999), ants that prefer core habitats may be particularly abundant in the core of rectangular patches because rectangular patches have the least amount of overall edge relative to core area (Table 1).

By potentially changing immigration, emigration, and abiotic conditions within patches, corridors could also impact the interactions among ants, which are often structured by competition (Hölldobler and Wilson 1990, Bestelmeyer 2000). For example, corridors could facilitate the spread of invasive ants that are found in edge-rich habitats, such as the Argentine ant (Suarez et al. 1998). In our study area in the southeastern U.S., the red imported fire ant, *Solenopsis invicta*, is an exotic species that reduces the richness of ant communities at local (e.g. Porter and Savignano 1990, Holway et al. 2002a) and biogeographic scales (Gotelli and Arnett 2000). *Solenopsis* is associated with narrow, linear landscape elements (e.g. roads and powerlines), if direct sunlight reaches the soil surface (Stiles and Jones 1998). However, it is unknown whether edge-rich corridors change patch shape in a way that facilitates the success of *Solenopsis*.

Using experimental landscapes that allow us to tease apart corridor, drift fence, and area effects (Fig. 1), we examined how corridors impact ant distribution and abundance. Specifically, we examined: 1) how corridors might lead to differences in ant genera and communities between patches (e.g. if connected patches contain more genera); 2) how corridors might lead to differences in ant communities within patches (e.g. if the ant community in the center of rectangular patches is similar to the edge community); 3) how corridors might lead to differences in the impacts of a dominant ant genus, *Solenopsis*. 
METHODS

Experimental Design

Experimental Landscape.- The study took place in eight replicated experimental landscapes ('blocks') within the Savannah River Site, a National Environmental Research Park (NERP) near Aiken, South Carolina. Each block consisted of five patches within a mature matrix of loblolly (Pinus taeda) and longleaf (P. palustris) pine forest. Patches were clear-cut and burned in winter 1999. All patches consisted of a central 1-ha portion. 'Connected' patches were joined by a corridor 150m long and 25m wide (Fig. 1). 'Winged' patches had an area half the length and equal to the width of the corridor on opposite sides of the central 1-ha portion (Fig. 1). 'Rectangular' patches consisted of the central 1-ha portion with the area of the corridor added to the back of the core patch (Fig. 1). Winged and rectangular patches had the same area (1.375 ha), whereas connected patches had slightly less area than unconnected patches because they shared a corridor (central patch area plus half of the corridor = 1.1875 ha). Although all patch types were of similar size, the amount of edge and core habitat was different among patch types because corridors and wings were long, linear elements. Connected patches had an area/perimeter ratio of 22.62, winged patches were 19.64, and rectangular patches were 28.95.

Invertebrate Sampling.- We used pitfall traps to sample ants because pitfalls are an effective method of characterizing ant communities that have been used successfully in studies examining the effects of habitat fragmentation on arthropods (e.g. Davies and Margules 1998, Suarez et al. 1998, Carvalho and Vasconcelos 1999, Davies et al. 2001). Estimates of population size obtained with pitfalls are a function of both abundance and
activity (Holldobler and Wilson 1990). Pitfalls were constructed by sinking 475 ml plastic
drinking cups (10 cm wide at mouth, 5 cm at base, 15 cm deep) into the ground until the top
of the cup was flush with the surface. Inside the cup, we placed plastic sample cups partially
filled with approximately 40 ml of a 50/50 mixture of water and propylene glycol. Funnels
(10 cm wide at mouth) were set to direct organisms into the sample cup. While inactive, traps
were covered by a ceramic tile. Specimens were identified to genus; identifications were
later verified by comparing voucher specimens with the insect collection in the Department
of Entomology at Iowa State University.

Each patch contained four ‘core’ pitfalls located near the patch center 37.5 m from
the edge of the patch along an 8-meter square. Each patch also contained two ‘edge’ pitfalls,
located 12.5 m from the edge of the patch (Fig. 1). In winged patches, an additional ‘wing’
pitfall was placed near the center of each wing, 12.5 m from the edge (Fig. 1). In connected
patches, two pitfall traps were placed along the center of the corridor, 12.5 m from the edge,
and separated by 25 m (Fig. 1). This yielded a total of eight pitfalls from three locations in
each connected patch and winged patch, and six pitfalls from two locations in each
rectangular patch (Fig. 1). We conducted two sampling sessions at all 320 pitfalls from July 4
– 8 and August 2 – 6, 2002. After sampling was completed, twenty randomly chosen
Pheidole specimens (10 minor and 10 major workers), and ten randomly chosen specimens
of the other dominant ant genera (see Results) were allowed to dry for 48 hours and weighed
to estimate biomass.

Habitat Sampling. - Because the activity of ants around pitfalls may be related to
microhabitat near the pitfall (Carvalho and Vasconcelos 1999), a 1 m² quadrat was centered
on each of the 296 pitfall traps, and percent grass, forb, woody debris, and bare soil was
visually estimated by two observers (JLO and GRC). Woody debris was also classified according to size class by estimating diameter at the widest point: fine (<0.1 cm) small (0.1-2 cm), medium (2-10 cm), and large (>10 cm).

**Statistical Analyses**

*Patch shape, connectivity, and ant abundance.* To determine if patch size and shape affect the abundance and spatial distribution of ants, we used multivariate analysis of variance (MANOVA, Scheiner 2001). MANOVA is appropriate for our design because ants present in a given sample are not independent of each other, i.e. interactions among genera may affect the samples we collect. Our MANOVA model specified block (8 total replicates), patch type (connected, rectangular, or winged) and sample location (core, edge, wing, or corridor) nested within patch type as fixed effects (random effects cannot be modeled with MANOVA; Scheiner 2001). We used Pillai's Trace to evaluate the significance of our multivariate tests because it is more robust than other measures of multivariate significance (Scheiner 2001). Tests for the main effect of location were dissected into linear contrasts to determine how location effects may change with patch type. The mean abundance of each of the six dominant ant genera (see Results), pooled over the two sampling periods, was included as a dependent variable. We also evaluated vegetation and substrate characteristics as potential covariates in our MANOVA models. To determine which ant genera were most responsible for any significant multivariate effects, we examined univariate ANOVAs ('protected ANOVAs', Scheiner 2001) and standardized canonical coefficients. Standardized canonical coefficients are analogous to partial regression coefficients: they represent the contribution of a dependent variable to the separation among groups, accounting for correlation among dependent variables (Scheiner 2001). Because two locations were not
included in all patch types, we also compared the effect of patch type using only locations common to all patches (i.e. core and edge locations).

Pitfalls located in the core of patches may also have been located next to partridge pea (*Chamaecrista fasciculata*) in experimental plots that were part of another project (J. Orrock, unpublished data). Although *C. fasciculata* and a congener, *C. nictitans*, occurred naturally throughout experimental plots (personal observation), both species have extrafloral nectaries that may attract ants (Kelly 1986). We used correlation analysis between the number of mature *C. fasciculata* in each experimental plot and the number of ants captured in the core pitfalls to be sure that the abundance of ants from core plots was not influenced by the abundance of *C. fasciculata* nearby. There was no correlation between the abundance of ants in the core pitfalls and the number of *Chamaecrista fasciculata* growing in experimental exclosures (*N* = 160, all *r* < 0.10, all *P* > 0.25), suggesting that our core pitfall results were not confounded by the presence of *C. fasciculata*.

*Patch shape, connectivity, and ant communities.* - We used MANOVA followed by protected ANOVAs to compare total ant biomass (abundance of the six most common genera multiplied by the average weight of each individual; Table 2), richness (the number of genera present), and evenness among patch types and locations. MANOVA was used because community metrics were not completely independent, if only because each observation of biomass, richness, and evenness was collected at the same pitfall. Biomass was significantly related to total ant abundance (Pearson correlation, *r* = 0.86, *N* = 295, *P* < 0.01). Genus richness and species richness are closely related among ant communities when the communities are from the same region and habitat type (Andersen 1995, Major et al. 1999). We used the mean number of genera per site as our measure of richness, rather than using
rarefaction to generate an estimate of richness for each combination of patch type and location (see Gotelli and Colwell 2001). This approach allowed us to examine interrelationships between biomass, richness, and evenness with MANOVA, and is reasonable because examination of our data suggested that genus accumulation curves for each patch type and location combination reached clear asymptotes (Gotelli and Colwell 2001). Moreover, estimates of richness obtained by rarefaction were significantly correlated with means from sample estimates ($r = 0.83$, $N = 8$, $P = 0.01$), and the two methods yielded identical trends across patch types and location. Evenness was calculated using William’s measure of evenness as described in Smith and Wilson (1996), which is theoretically independent of richness and performs well compared to other commonly used measures of evenness (Smith and Wilson 1996). Evenness values range from 0 to 1, with values closer to 1 representing communities with more equitable representation among genera.

*Patch shape and the impact of Solenopsis.* - We assessed the impact of *Solenopsis* on the biomass, richness, and evenness of ant communities in different patch types and locations by using univariate analysis of variance (ANOVA) with patch type and location nested within patch type as fixed effects, and a *Solenopsis* abundance by location (nested within patch type) interaction term. Experimental block (Fig. 1) was treated as a random effect.

Our hypotheses and comparisons were planned *a priori*, i.e. we did not perform tests in an exploratory fashion, and the use of MANOVA helps guard against inflated error rates in subsequent ANOVAs (Scheiner 2001). As such, we do not adjust $\alpha$ for multiple tests (Day and Quinn 1989). Prior to analyses, dependent variables were transformed to improve normality. Abundances of *Crematogaster* and *Formica* were square-root transformed (Zar 1996). Values for *Dorymyrmex, Pogonomyrmex, Solenopsis*, and *Pheidole* abundance, and
ant biomass were log10 (x+1) transformed. All analyses were conducted using SAS v. 8.1 (SAS Institute 2000).

RESULTS

We captured 33820 ants from July 2002 to August 2002. Six genera comprised the majority of captures (Table 2): Solenopsis, Dorymyrmex, Pheidole, Pogonomyrmex, Crematogaster, and Formica. The remaining captures (2.2 %) were ants from the genera Dolichoderus, Aphaenogaster, Neivamyrmex, Trachymyrmex, Camponotus, and Hypoponera.

Patch shape, connectivity, and ant abundance.- Abundance of ants was significantly different among blocks (Pillai’s Trace = 2.45, $F_{42,96} = 1.53, P = 0.05$). There was no significant difference in the abundance of ants among patch type (Pillai’s Trace = 0.17, $F_{12,24} = 0.18, P = 0.99$; Fig. 2), even when only core and edge locations were compared (Pillai’s Trace = 0.51, $F_{12,24} = 0.68, P = 0.75$). The abundance of ants was significantly different at different locations within patch types (Pillai’s Trace = 0.33, $F_{30,1240} = 2.94, P < 0.01$; Fig. 2). There was no interaction between block and patch type (Pillai’s Trace = 2.56, $F_{84,96} = 0.85, P = 0.77$) or block and location within patch type (Pillai’s Trace = 3.27, $F_{210,96} = 0.55, P = 0.99$). Local microhabitat features did not have a multivariate effect on ant abundance (all $P > 0.15$).

Several genera exhibited distinct responses to location (Table 3, Fig. 2). In connected and winged patches, Dorymyrmex and Pogonomyrmex were significantly more abundant in core pitfalls, and became less abundant in edge, corridor, and wing pitfalls (Fig. 2). Formica exhibited a similar pattern, although results were not statistically significant (Table 3). Crematogaster exhibited the opposite pattern in all patch types, becoming most abundant near the edge and in corridor and wing pitfalls (Fig. 2). Abundance of Pheidole did not differ
due to location in rectangular patches, but was greater in edge and corridor pitfalls compared to core pitfalls in connected patches (Table 3; Fig. 2). In winged patches, abundance of *Solenopsis* was greater in core pitfalls compared to wing pitfalls (Table 3; Fig. 2).

**Patch shape, connectivity, and ant communities.** There was a significant multivariate effect of block on total ant biomass, richness, and evenness (Pillai’s Trace = 1.75, $F_{21,48} = 3.20, P < 0.01$). There was no multivariate effect of patch type with all locations included (Pillai’s Trace = 0.20, $F_{6,30} = 0.57, P = 0.75$) or when only core and edge locations were in the model (Pillai’s Trace = 0.12, $F_{6,30} = 0.31, P = 0.93$). Total abundance, richness, and evenness were significantly affected by location (Pillai’s Trace = 0.24, $F_{15,642} = 3.70, P < 0.01$). There was no significant interaction between block and patch type (Pillai’s Trace = 0.12, $F_{42,48} = 0.78, P = 0.79$) and block and location nested within patch type (Pillai’s Trace = 1.78, $F_{105,48} = 0.66, P = 0.96$).

The effect of location was due largely to changes in community metrics between core locations and edge-rich locations: edges, wings, and corridors (Table 4, Fig. 3). Standardized canonical coefficients suggested that the significant multivariate effects of location were generally due to changes in biomass, although richness contributed to significant differences in rectangular patches (Table 4). Opposite signs for canonical coefficients (Table 4) suggest that biomass and richness were generally changing in opposite directions (Fig. 3). Ant biomass was greater in core pitfalls compared to edge, wing, and corridor pitfalls, whereas biomass at edges and corridors and edges and wings was similar (Fig. 3, Table 4). Richness and evenness were similar at all locations within connected and winged patches (Table 4, Fig. 3), but were greater at the edge than at the core within rectangular patches (Table 4, Fig. 3).
Patch shape and the impact of Solenopsis.-The abundance of Solenopsis had strong effects on ant communities, and this impact varied depending upon patch type and location (Table 5). Solenopsis abundance was negatively related with the richness of other ant genera in several locations in connected, winged and rectangular patches, although this relationship was most significant in the core of rectangular patches (Table 5). Total biomass of non-Solenopsis ants was only related with Solenopsis abundance in the core of rectangular patches, and the relationship was also negative (Table 5). Evenness of the ant community was negatively related to Solenopsis abundance in the core of rectangular patches and, to a lesser degree, in the core of winged patches (Table 5). Examination of abundance data suggested that these community-level shifts were largely due to negative, location- and patch-specific impacts of Solenopsis on Pheidole, Dorymyrmex, and Crematogaster (unpublished data).

DISCUSSION

Corridors influenced ant populations in a manner consistent with area effects: by adding long, linear portions to a patch, corridors change the amount of suitable habitat for ants. Spatial patterns suggest that corridors were not movement conduits or drift fences. Rather, corridors represented high-quality habitat for edge-selecting ants (Fig. 2). Although patch shape led to changes in the within-patch distribution of ants, this did not translate into significant differences in the abundance of ants between patches (Table 2).

Patch shape, connectivity, and ant abundance.- Our results suggest that there were no corridor effects on ant abundance at the scale of our experimental patches. The lack of corridor effects may be because reproductive queens can travel considerable distances after
mating (Hölldobler and Wilson 1990). In this capacity, larger linear landscape elements (i.e. powerlines and roads) may be important corridors (Stiles and Jones 1998) because they span distances much greater than those used in this study. At the scales used in this study, edges affected ant abundance and distribution (Stiles and Jones 1998, Suarez et al. 1998), and were thus the primary means that corridors influenced ants. As often noted (Debinski and Holt 2000, Golden and Crist 2000), most studies that examine fragmentation confound area and edge effects. We stress that the effects we observed were strictly edge effects not confounded with area effects, because all of our patches were of similar size, but differing shape.

Why might edges affect the distribution of ants? Three explanations seem most likely. First, edges exhibit different moisture and temperature regimes (Saunders et al. 1991, Didham et al. 1998, Chen et al. 1999), and ant abundance and distribution are highly influenced by both temperature and humidity (Porter and Tschinkel 1987, Hölldobler and Wilson 1990, Kaspari et al. 2000, Kaspari et al. 2003). For example, *Pheidole* is generally active at lower temperatures compared to the other ant genera in our study (Hölldobler and Wilson 1990, Andersen 1997, Bestelmeyer 2000), which is supported by the greater number of *Pheidole* captured at the edge of connected and winged patches, where shading should reduce overall temperatures (Fig. 2). Conversely, *Pogonomyrmex* is generally considered a thermophilic genus (Golley and Gentry 1964, Andersen 1997), which may explain the greater abundance of *Pogonomyrmex* in the core of winged and connected patches. The trend of lower abundance in the core of rectangular patches may be because temperatures that are too high lead to periods of *Pogonomyrmex* inactivity (Golley and Gentry 1964). *Solenopsis* is also a thermophilic genus (Andersen 1997, Stiles and Jones 1998), which may explain the
reduction in *Solenopsis* in the wings of winged patches, where proximity to three edges (Fig. 1) likely reduces solar load. Under the less-shaded conditions found in corridors and along the edge of patches, the mound-building habit of *Solenopsis* may allow them to maintain sufficient nest temperature (Porter and Tschinkel 1993) compared to thermophilic ground-nesting genera (e.g. *Pogonomyrmex*). If so, we might predict changes in *Solenopsis* mound placement and morphology as a function of location within a patch, although this has yet to be examined.

Second, edges may have a different distribution of food resources. For example, seed rain near the edge is likely to be dominated by inputs from the surrounding matrix (e.g. seeds of *Pinus* spp.), whereas seed rain in core habitats is likely to be dominated by forbs and grasses. From the perspective of highly granivorous ants, such as *Pogonomyrmex*, this may also explain the greater abundance of ants found in the core of connected and winged patches.

Third, edges may be sites of immigration for ants that can inhabit both forest and clearcut habitats. For example, *Crematogaster* was more abundant near edges and in wings and corridors, most likely because ants in the genus *Crematogaster* often nest in pine trees (Hölldobler and Wilson 1990, Tschinkel and Hess 1999). The increased abundance of *Crematogaster* in wings compared to corridors (Fig. 2) may be because pitfalls in wings were close to three matrix edges (compared to two edges for corridor pitfalls, Fig. 1), increasing immigration of *Crematogaster* from the nearby matrix.

Although the mechanism driving edge effects is unclear, it remains clear that these effects lead to changes in the spatial distribution and abundance of ants. For example, a multivariate linear contrast comparing core and edge locations across all patch types was
highly significant (Pillai’s Trace = 0.11, $F_{6, 244} = 5.24$, $P < 0.01$). However, response to edge was often dependent upon the shape of the patch under consideration. For example, *Pogonomyrmex* and *Pheidole* were equally abundant among edge and core locations in rectangular patches, yet *Pogonomyrmex* was more abundant in the core of connected and winged patches and *Pheidole* only exhibited differences in connected patches (Table 3). Changes in abundance with location for *Crematogaster* and *Dorymyrmex* were generally consistent, although not always significant, among patch types. These genera-specific responses suggest that magnitude of the difference between edge and core habitats was a function of patch shape. That is, the influence of the edge was not fixed, rather it was a function of the interplay between the relative amounts of core and edge as mediated by patch shape (Malcolm 1994, Davies et al. 2001). Patch size and shape may thus interact to decide the extent and strength of edge effects on ant communities.

**Patch shape, connectivity, and ant communities.** – Our results suggest that connecting patches does not result in greater diversity, abundance, biomass, or evenness of ant genera. The non-significant effect of patch type suggests that the richness and composition of ant communities at the scale of a single block (Fig. 1) was not limited by movement. However, significant differences in ant abundance and diversity among blocks suggests that dispersal and colonization may play a role in determining community structure at this larger scale (Fig. 1). Because other factors known to affect ant communities (e.g. soil type; Hölldobler and Wilson 1990) were also likely to differ among blocks, it is not prudent to ascribe these differences solely to dispersal and colonization without further experimentation.

Edge effects were important for generating within-patch effects, and the nature of edge effects depended upon patch shape. Ant biomass was lower in edges, wings and
corridors compared to core locations in all patch types (Table 4), but only between the core and edge in rectangular patches were significant multivariate and univariate differences found in richness, evenness, and biomass (Table 4). This suggests that, in winged and connected patches, richness did not change from core to edge because the reduction of core-inhabiting genera near edge locations was offset by increases in edge-inhabiting genera, and vice versa. Such replacement along an edge-interior gradient was why Carvalho and Vasconcelos (1999) and Davies and Margules (1998) also found no edge-related changes in richness in arthropods in forest fragments. The increased richness found at the edge of rectangular patches may have been due to the increased abundance of *Crematogaster* along the patch edge. Similarly, increased biomass in the core relative to the edge of all patches may be due to increased abundance of larger core-related genera (e.g. *Pogonomyrmex* and *Formica*, Table 1; Fig. 2).

The significant difference in evenness in rectangular patches seems to arise from a trend of lower core richness in rectangular patches compared to the core of connected or winged patches (i.e. evenness changes little at the patch edge when compared among patch types; Fig. 3). Yet, there were no significant concomitant reductions in the abundance of any genera in the core of rectangular patches compared to the core of winged and connected patches. *Crematogaster* exhibited significant changes in rectangular patches, and this difference was not due to changes in the center of the patch (Fig. 2): *Crematogaster* became more abundant at the patch edge (Fig. 2). *Pogonomyrmex* abundance exhibited a trend of decreased abundance in the core of rectangular patches, but the pattern was not strong (linear contrast, $F_{1, 250} = 2.75$, $P = 0.10$). A potential explanation for this trend is that patch shape changes the interaction among ant genera. If so, shifts in evenness could occur without
changes in abundance because the same number of ants could have different impacts in
different patches. If the interactions among ants change with patch type, as the pattern of
evenness suggests, the replacement of core- and edge-dwelling genera may not be the only
mechanism responsible for changes in ant richness and biomass with location among patch
types.

*Patch shape and the impact of Solenopsis.* - Our findings are in agreement with other
studies that have found negative impacts of *Solenopsis* on ant communities (Porter and
Savignano 1990, Gotelli and Arnett 2000). Moreover, our results suggest that patch shape
may mediate this impact (Table 5). The patch- and location-specific differences in the
impact of *Solenopsis* may contribute to the shifts in the ant community we observed.
Specifically, the most consistent negative impact of *Solenopsis* on community metrics
occurred in the core of rectangular patches (Table 5).

Because we did not experimentally manipulate ants or observe competitive
interactions in the field, we cannot be certain of the mechanism responsible for the impact of
*Solenopsis* in the core of rectangular patches. Behavioral evidence suggests that *Pheidole*
and *Dorymyrmex* are both dominated by *Solenopsis* (Andersen 1997, Bestelmeyer 2000),
whereas foraging by *Crematogaster* exhibits little spatial overlap with *Solenopsis*,
presumably to reduce detrimental interactions (Andersen 1997, Bestelmeyer 2000).
Temperature and microclimate are known to affect competitive interactions (Bestelmeyer
2000, Retana and Cerdá 2000, Albrecht and Gotelli 2001) that play an important role in
structuring ant communities and territories (e.g. Hölldobler and Wilson 1990), and
microclimate may be different in the core of rectangular patches compared to other patches.
Moreover, temperature is also known to have important implications for the activity and size of *Solenopsis* colonies (e.g. Porter and Tschinkel 1987, Tschinkel 1993).

However, if the impact of *Solenopsis* was due to increased colony number or increased activity, why was no significant difference in *Solenopsis* density detected using pitfall traps (Fig. 2; Table 3)? A potential explanation is that the impact of *Solenopsis* on other genera we observed was due to events that occurred before our sampling. *Solenopsis* colonies undergo wide shifts in seasonal abundance (Tschinkel 1993). If patch shape influences temporal colony dynamics, patch-specific impacts on other genera could result. For example, if the stability of *Solenopsis* colonies was greater in rectangular patches, more consistent pressure may have been exerted on other genera. When captures of *Solenopsis* in the core of patches between 2001 and 2002 are compared using Pearson correlation, the positive association was greatest in rectangular patches (Pearson correlation, $r = 0.70$, $N = 48$, $P < 0.01$) compared to connected ($r = 0.36$, $N = 64$, $P < 0.01$) and winged ($r = 0.04$, $N = 48$, $P = 0.04$) patches, suggesting that populations in the core of rectangular patches may have been more stable. If patch shape does change *Solenopsis* dynamics in time, changes in worker size may also result: older, larger colonies tend to produce larger workers (Tschinkel 1993). Larger workers tend to be most effective at recruitment to food resources (Cassill and Tschinkel 1999), potentially increasing the competitive ability of *Solenopsis* without necessarily affecting the number of *Solenopsis* found in pitfalls. Finally, differences in the impact of *Solenopsis* may reflect different species of *Solenopsis* in different patch types. Two species of *Solenopsis* were common during our study: the native *Solenopsis geminata* and the exotic *S. invicta* (unpublished data), and these species may have different impacts on native taxa. Future studies that examine recruitment rates, nest density, temporal
population structure, and worker size in patches of different shape and connectivity are ultimately needed to determine the mechanisms responsible for the patch- and location-specific dominance of *Solenopsis*.

*Caveats.*- One limitation of our study is that we did not sample the pine forest matrix for ants. However, due to the extensive entomological work conducted in the area (Van Pelt 1956, Van Pelt and Gentry 1985), we are confident that *Crematogaster* was the only genus likely to primarily inhabit pine forest. Although *Solenopsis* is occasionally found in pine forests, fire ants are restricted to areas where sunlight reaches the soil (Stiles and Jones 1998), and thus reach several orders of magnitude greater density in open habitats (Porter and Tschinkel 1987) and generally prefer core locations (Fig. 2).

How robust are the patterns we observed in light of temporal variation? A preliminary pitfall session conducted from July 31 – August 3, 2001 using only pitfalls in the core of each patch provides some insight. Comparison of the abundance of the six most abundant ant genera in these samples with those collected August 2 – 6, 2002 (adjusted for the number of days traps were open) using MANOVA suggests there were no effects of patch type (Pillai’s Trace = 0.57, $F_{12,24} = 0.79, P = 0.65$) and no interaction between patch type and year (Pillai’s Trace = 0.06, $F_{12,504} = 1.22, P = 0.26$). However, ants were more abundant in the core samples in 2002 (Pillai’s Trace = 0.24, $F_{6,251} = 13.26, P < 0.01$), due to increased abundance of *Solenopsis, Pogonomyrmex, and Pheidole* in 2002 (paired t-tests, 159 d.f., all $t > 2.95$, all $P < 0.01$). Similarly, although richness, biomass, and evenness also increased from 2001 to 2002 (Pillai’s Trace = 0.11, $F_{3,254} = 10.45, P < 0.01$; paired t-tests, 159 d.f., all $t > 2.15$, all $P < 0.04$), there was no interaction among year and patch type (Pillai’s Trace = 0.03, $F_{6,510} = 1.11, P = 0.35$). These findings suggest that several ant genera were becoming more
abundant from 2001 to 2002. However, connecting patches via corridors did not change the rate at which ants increased (i.e. no patch type by year interaction).

It is also possible that our study was not conducted for long enough for ants to move down corridors via 'budding' of colonies (Hölldobler and Wilson 1990, Porter and Savignano 1990). If this were the case, we might expect significant differences in the ants in the two replicate connected patches in each block (Fig. 1). There were no multivariate differences in ant abundance (Pillai’s Trace = 0.93, $F_{6,2} = 4.3, P = 0.20$) or in community metrics (Pillai’s Trace = 0.36, $F_{3,5} = 0.92, P = 0.49$) between the two connected patches, suggesting that the distribution of ants among connected patches is not in disequilibrium. Even so, studies that document the impact of patch shape and connectivity on ant communities over several seasons are needed, if only because interactions among ants can change seasonally (Retana and Cerdá 2000, Albrecht and Gotelli 2001).

*Ants and the ultimate impact of corridors.* - Our results demonstrate that corridors have an effect on the distribution of ants because corridors add long, linear components of habitat to a patch. Although other studies have documented that edges influence the distribution of ground-dwelling arthropods in habitat fragments (e.g. Davies and Margules 1998, Didham et al. 1998, Carvalho and Vasconcelos 1999, Davies et al. 2001); our study demonstrates that this effect can arise solely as a function of patch shape.

Corridor effects on ants could impact the value of corridors for other taxa. For example, by influencing the distribution of ants, corridors and patch shape may alter the distribution of ant-dispersed (myrmechorous) seeds. In our study area, *Crematogaster* commonly disperses myrmechorous seeds without consuming them (Gaddy 1986), suggesting that ant-dispersed seeds may reap positive benefits of corridors via the effect of
corridors on *Crematogaster* (Fig. 2). However, *Solenopsis* may disrupt seed dispersal by other ant genera (Zettler et al. 2001), making overall impacts on seed dispersal difficult to predict, especially in corridors, where the abundance of *Solenopsis* also reduces the richness of ant communities (Table 5). Regardless of whether seeds are myrmecochorous, the reduced abundance of highly granivorous ants in corridors (e.g. *Pogonomyrmex* colonies can contain up to 300,000 seeds; Tschinkel 1999) may reduce seed mortality in corridors. Such indirect effects of corridors may be critical in affecting the fate of gravity- and animal-dispersed plants that require more than one generation to travel the length of the corridor. Similarly, the reduction in evenness and greater abundance of ants in the core of rectangular patches may contribute to patch-specific patterns of invertebrate seed predation found in this study system (Orrock et al. 2003).

The relationship between ants and seeds is only one example, as ants cycle nutrients and also affect herbivory, pollination, and the structure of the arthropod community (Hölldobler and Wilson 1990). Energy flow through *Pogonomyrmex* alone can be greater than that through rodent and avian inhabitants of our study system (Golley and Gentry 1964). Similarly, *Solenopsis* can have significant impacts on other invertebrates and vertebrates (Porter and Savignano 1990). Ants are also important dietary items for vertebrates, e.g. *Crematogaster* can compose up to 58% of the stomach contents of the federally threatened red-cockaded woodpecker (Hess and James 1997).

For ants in the southeastern U.S., corridors do not appear to result in increased movement or promote colonization of connected patches. Rather, corridors are edge-rich habitats that are inhabited by ants that prefer edge habitats. However, corridors may still be important for larger-scale movement (i.e. roadside and powerline habitats; Stiles and Jones
1998), and our results demonstrate that corridors do lead to shifts in the distribution and abundance of ants. Moreover, evidence from rectangular patches suggests that patch shape can alter the strength of competitive interactions among ants. Such shape-mediated shifts in abiotic factors may be particularly important given evidence that abiotic factors may change the ant community (Fig. 3) and alter the susceptibility of the community to invasion (Holway et al. 2002b). Due to the ubiquitous presence of ants in many terrestrial ecosystems and their impacts on other species, corridors may have unpredictable impacts on target populations via the effect of patch shape on ants. Because anthropogenic fragmentation also changes patch shape and the abundance (Fig. 2; Suarez et al. 1998) and impact (Table 5) of edge-dwelling ants, our results are likely to have implications outside of corridors constructed solely for conservation.

ACKNOWLEDGMENTS

This study was made possible by J. Blake, E. Olson, Timber and Fire Crews, and other members of the USDA Forest Service Savannah River, who were instrumental in the construction of the experimental landscapes. We thank N. Haddad for leadership in establishing the experimental landscapes. We thank D. Keufler, T. Slack, T. Cary, M. Beck, and D. Donato for field assistance. Previous drafts of the manuscript were improved by comments from W. Clark, E. Damschen, N. Haddad, E. Hart, F. Janzen, and S. D. Porter. P. Dixon provided statistical assistance. Funding and support were provided by the Department of Energy-Savannah River Operations office through the U. S. Forest Service Savannah River under Interagency Agreement DE-AI09-00SR22188. Funding was also provided by an NSF Research Experience for Undergraduates Grant to BJD and GRC, an NSF Grant to BJD
(DEB-9907365), an Ecology and Evolutionary Biology Fellowship to JLO, and a Science to Achieve Results (STAR) Fellowship from the U. S. Environmental Protection Agency to JLO.

LITERATURE CITED


Table 1. Three effects may affect the abundance and distribution of ants when corridors are used to connect patches of habitat. Each effect may lead to patch-level differences in the abundance of ants in connected patches (Conn), rectangular patches (Rect), or winged patches (Winged). By changing patch shape and connectivity, corridors influence the amount of edge habitat in a patch, potentially shifting the distribution of ants among and within patches. Each effect also leads to testable predictions for the abundance of ants at different locations within each patch: core pitfalls near the center of each patch; edge pitfalls (12.5 m from the nearest patch edge), and pitfalls located in corridors or wings (12.5 m from two patch edges).

<table>
<thead>
<tr>
<th>Effect</th>
<th>Predicted Ant Abundance</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Among Patches</td>
</tr>
<tr>
<td>Area Effects</td>
<td></td>
</tr>
<tr>
<td>Edge-selecting ants:</td>
<td>Conn &gt; Rect; Conn ≈ Winged</td>
</tr>
<tr>
<td>Edge-neutral ants:</td>
<td>Conn ≈ Rect ≈ Winged</td>
</tr>
<tr>
<td>Edge-avoiding ants:</td>
<td>Rect &gt; Conn; Conn ≈ Winged</td>
</tr>
<tr>
<td>Corridor Effects</td>
<td>Conn &gt; Rect; Conn ≈ Winged</td>
</tr>
<tr>
<td>Drift-Fence Effects</td>
<td>Winged ≈ Conn; Conn &gt; Rect</td>
</tr>
</tbody>
</table>
Table 2. Summary of ant genera captured. Mean individual biomass (with 95% confidence interval in parenthesis) was determined as described in text. The proportion of biomass does not include the biomass of seven genera not weighed.

<table>
<thead>
<tr>
<th>Genus</th>
<th>Number captured</th>
<th>Proportion of total ants</th>
<th>Individual biomass (mg)</th>
<th>Proportion biomass</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Crematogaster</em></td>
<td>969</td>
<td>0.029</td>
<td>0.145 (0.115, 0.175)</td>
<td>0.019</td>
</tr>
<tr>
<td><em>Dorymyrmex</em></td>
<td>7149</td>
<td>0.211</td>
<td>0.213 (0.198, 0.228)</td>
<td>0.202</td>
</tr>
<tr>
<td><em>Formica</em></td>
<td>546</td>
<td>0.016</td>
<td>1.241 (0.955, 1.527)</td>
<td>0.090</td>
</tr>
<tr>
<td><em>Pheidole</em></td>
<td>3543</td>
<td>0.105</td>
<td>0.114 (0.066, 0.162)</td>
<td>0.054</td>
</tr>
<tr>
<td><em>Pogonomyrmex</em></td>
<td>1312</td>
<td>0.039</td>
<td>1.440 (1.225, 1.655)</td>
<td>0.251</td>
</tr>
<tr>
<td><em>Solenopsis</em></td>
<td>19547</td>
<td>0.578</td>
<td>0.148 (0.134, 0.162)</td>
<td>0.384</td>
</tr>
<tr>
<td>Other genera (7)</td>
<td>754</td>
<td>0.022</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 3. Multivariate linear contrasts comparing ant communities at different locations within each patch type. Genus codes represent the first four letters of the genus name for *Dorymyrmex*, *Crematogaster*, *Formica*, *Pheidole*, *Pogonomyrmex*, and *Solenopsis*. For each genus, standardized canonical coefficients are presented. Standardized canonical coefficients represent the relative contribution of each genus toward separation of the groups defined by the contrast. For example, the significant multivariate difference between core and edge habitats in connected patches is mostly due to increased abundance of *Pheidole* and decreased abundance of *Dorymyrmex* and *Pogonomyrmex* in the edge habitat. Asterisks indicate significant contrasts from univariate ANOVAs.

<table>
<thead>
<tr>
<th>Patch Type</th>
<th>Contrast</th>
<th>CREM</th>
<th>DORY</th>
<th>FORM</th>
<th>PHEI</th>
<th>POGO</th>
<th>SOLE</th>
<th>$F_{NDF,DDF}$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Connected</td>
<td>Core – Edge</td>
<td>-0.52*</td>
<td>0.56***</td>
<td>0.12</td>
<td>-0.83***</td>
<td>0.49**</td>
<td>-0.10</td>
<td>4.58_{6,210}</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td></td>
<td>Core – Corr</td>
<td>-0.46***</td>
<td>0.83***</td>
<td>0.01</td>
<td>-0.49**</td>
<td>0.48***</td>
<td>-0.20</td>
<td>12.19_{6,210}</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td></td>
<td>Edge – Corr</td>
<td>-0.28</td>
<td>1.00***</td>
<td>-0.13</td>
<td>0.06</td>
<td>0.36</td>
<td>-0.28</td>
<td>2.13_{6,210}</td>
<td>0.05</td>
</tr>
<tr>
<td>Rectangular</td>
<td>Core – Edge</td>
<td>-0.88***</td>
<td>0.19</td>
<td>0.39</td>
<td>-0.07</td>
<td>0.48</td>
<td>0.08</td>
<td>2.29_{6,210}</td>
<td>0.04</td>
</tr>
<tr>
<td>Winged</td>
<td>Core – Edge</td>
<td>-0.33</td>
<td>0.41**</td>
<td>0.50*</td>
<td>-0.31</td>
<td>0.64***</td>
<td>0.49</td>
<td>2.04_{6,210}</td>
<td>0.06</td>
</tr>
<tr>
<td></td>
<td>Core – Wing</td>
<td>-0.67***</td>
<td>0.58***</td>
<td>0.16</td>
<td>0.02</td>
<td>0.29***</td>
<td>0.52**</td>
<td>6.39_{6,210}</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td></td>
<td>Edge – Wing</td>
<td>-0.74***</td>
<td>0.54</td>
<td>-0.19</td>
<td>0.30*</td>
<td>-0.11</td>
<td>0.37</td>
<td>2.01_{6,210}</td>
<td>0.07</td>
</tr>
</tbody>
</table>

*P < 0.10  **P<0.05  ***P < 0.01
Table 4. Multivariate linear contrasts comparing ant community metrics at different locations within each patch type. For each metric, standardized canonical coefficients are presented. Standardized canonical coefficients represent the relative contribution of each genus toward separation of the groups defined by the contrast. For example, the significant multivariate difference between core and wing habitats in winged patches was mostly due to changes in the total abundance of ants. Asterisks indicate significant contrasts from univariate ANOVAs.

<table>
<thead>
<tr>
<th>Patch Type</th>
<th>Contrast</th>
<th>Community Metric</th>
<th>Biomass</th>
<th>Richness</th>
<th>Evenness</th>
<th>$F_{NDF, DDF}$</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Connected</td>
<td>Core – Edge</td>
<td>1.25**</td>
<td>-0.61</td>
<td>0.14</td>
<td>3.033,212</td>
<td>0.03</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Core – Corr</td>
<td>1.29***</td>
<td>-0.20</td>
<td>0.18</td>
<td>5.143,212</td>
<td>&lt;0.01</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Edge – Corr</td>
<td>0.83</td>
<td>0.71</td>
<td>0.19</td>
<td>0.543,212</td>
<td>0.66</td>
<td></td>
</tr>
<tr>
<td>Rectangular</td>
<td>Core – Edge</td>
<td>-1.02***</td>
<td>0.76**</td>
<td>0.35**</td>
<td>6.793,212</td>
<td>&lt;0.01</td>
<td></td>
</tr>
<tr>
<td>Winged</td>
<td>Core – Edge</td>
<td>1.23***</td>
<td>-0.11</td>
<td>-0.10</td>
<td>3.113,212</td>
<td>0.03</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Core – Wing</td>
<td>1.23***</td>
<td>-0.47</td>
<td>-0.12</td>
<td>6.623,212</td>
<td>&lt;0.01</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Edge – Wing</td>
<td>-0.97</td>
<td>0.98</td>
<td>0.12</td>
<td>0.803,212</td>
<td>0.50</td>
<td></td>
</tr>
</tbody>
</table>

*P < 0.10  **P < 0.05  ***P < 0.01
Table 5. The effect of *Solenopsis* abundance on the biomass and richness of other ants and the evenness of the ant community. The effect of *Solenopsis* was determined by using ANOVA with *Solenopsis* abundance as a covariate crossed with location, which was nested within patch type (details in text). Each entry is the t-statistic testing the hypothesis that the slope of the relationship between *Solenopsis* abundance and the community metric is zero. All significant slopes were negative.

<table>
<thead>
<tr>
<th>Patch Type</th>
<th>Location</th>
<th>Community Metric</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Biomass</td>
</tr>
<tr>
<td>Connected</td>
<td>Core</td>
<td>-0.66</td>
</tr>
<tr>
<td></td>
<td>Corridor</td>
<td>-1.16</td>
</tr>
<tr>
<td></td>
<td>Edge</td>
<td>-0.78</td>
</tr>
<tr>
<td>Rectangular</td>
<td>Core</td>
<td>-3.58***</td>
</tr>
<tr>
<td></td>
<td>Edge</td>
<td>-0.52</td>
</tr>
<tr>
<td>Winged</td>
<td>Core</td>
<td>-1.64*</td>
</tr>
<tr>
<td></td>
<td>Edge</td>
<td>-0.83</td>
</tr>
<tr>
<td></td>
<td>Wing</td>
<td>-0.59</td>
</tr>
</tbody>
</table>

*P < 0.10  **P < 0.05  ***P < 0.01
**Fig 1.** Layout of the experimental design at the Savannah River Site, South Carolina. Eight experimental landscapes ('blocks') were created within mature pine forest plantings. Each block consisted of connected (C) and unconnected patches that were either winged (W) or rectangular (R). Within each patch, there were four core pitfall traps (denoted by circles), two edge pitfall traps (denoted by squares). Triangles represent pitfall traps within the corridor of connected patches and within the wings of winged patches. The block depicted is aligned for illustration, orientation of actual blocks was random.

**Fig. 2.** Mean abundance of ant genera captured in connected (CONN), rectangular (RECT) and winged (WING) patches. Within each patch, captures are presented for pitfall traps located at the center of each patch (CORE) and pitfall traps located at the edge of each patch (EDGE). In connected and winged patches, additional pitfalls were placed in the corridors and the wings, respectively. Although log (x+1) values are presented to facilitate visual comparison among genera, *Crematogaster* and *Formica* were square-root transformed for analyses. Bars indicate 95% confidence limits. Significance of multivariate and univariate contrasts among locations within a given patch type are presented in Table 3.

**Fig. 3.** Characteristics of the ant community in connected (CONN), rectangular (RECT) and winged (WING) patches. Within each patch, captures are presented for pitfall traps located at the center of each patch (CORE) and pitfall traps located at the edge of each patch (EDGE). In connected and winged patches, additional pitfalls were placed in the corridors and the wings, respectively. Bars indicate 95% confidence limits, biomass values are log(x+1) transformed. Significance of multivariate and univariate contrasts among locations within a given patch type are presented in Table 4.
Figure 1.
Figure 2.
Figure 3.

Mean Evenness

Mean Number of Genera

Mean Biomass

Corridor / Wing
Edge
Core
CHAPTER 6: FIXATION OF NOVEL ALLELES IN SOURCES COUPLED WITH EPHEMERAL SINKS

A paper to be submitted to American Naturalist

John Orrock

Abstract. – I demonstrate that an ephemeral population (the sink) that undergoes periodic extinction (e.g. due to natural or anthropogenic disturbance) can change the likelihood that a new allele will fix in a stable population (the source) when the two are connected by movement. Changes in fixation occur because the sink can either foster population growth or reduction, depending upon the rate of disturbance, leading to changes in the effective population size \(N_e\) of the source-sink complex. Alleles that are beneficial in the sink can readily fix in the source even when selection against them in the source is high, suggesting that ephemeral patches could influence local adaptation, including the evolution of resistance in insects and microbes, the mutational meltdown of small populations, and promote different rates of fixation among organisms in the same ecological community.

Key words. – disturbance, fixation, movement, persistence, spatial structure, viability
Some populations are more persistent than others. Predators, disease, anthropogenic disturbance, climate and a host of other factors can lead to local extinction (e.g. Shaffer 1981; Pickett and White 1985; Holt 1987). Although transient, ephemeral populations need not be inconsequential: in the view of metapopulation theory, ephemeral populations linked by movement promote global persistence in the face of local extinction (reviewed in Hanski and Gilpin 1997). In this paper, I present a simple model of two populations that are identical with one exception: one population is stable and produces a surplus of individuals (a source; Pulliam 1988), whereas the other is ephemeral and requires colonization from the source patch to remain viable (a sink, Pulliam 1988). Using a simulation model, I demonstrate that an ephemeral sink can affect the likelihood that a new allele will become fixed in a stable source.

Spatial population structure and changes in population size both have important effects on fixation (Haldane 1927; Fisher 1930; Wright 1931; Kimura 1962; Maruyama 1970; Slatkin 1977; Slatkin 1981; Barton 1993; Barton 1995; Otto and Whitlock 1997; Whitlock 2003; Cherry 2003). However, many studies of spatial structure incorporate simplified population dynamics; e.g. patches are immediately returned to carrying capacity following extinction or population size is not changed by migration (see Whitlock 2003 for a summary of these models). Similarly, studies examining the role of population dynamics in affecting fixation are not spatially-explicit (e.g. Otto and Whitlock 1997). Recent work by Whitlock (2003) has relaxed many of the assumptions of earlier work, providing general numerical solutions that allow fixation probability to be estimated as long as a few key parameters can be ascertained and selection is equal among populations.
Using different source-sink structures, other studies have focused on how gene flow from the source affects adaptation in the sink, especially when selection pressures differ between sources and sinks (Holt and Gomulkiewicz 1997; Gomulkiewicz et al. 1999; Kawecki 2000; Kawecki and Holt 2002). These models use sinks that are temporally stable, often ignore the interaction between population growth and fixation in the interest of mathematical tractability, and alleles from the sink can never migrate back to the source ('black-hole sinks', Gomulkiewicz et al. 1999). As such, these models do not address whether ephemeral patches can change fixation in stable ones. In this paper, I present a model of ephemeral sinks and stable sources that builds upon previous work by explicitly incorporating spatial structure, underlying population dynamics, and changing selection pressures among sources and sinks. By incorporating these realistic components, a new insight emerges: ephemeral patches can affect fixation in stable patches, especially when selection differs among them. The implications of these findings may provide insight into the fixation dynamics affecting rare populations within conservation reserves, the evolution of resistance among insect pests, and the dynamics of evolution in predator-prey systems.

**Model Overview**

This paper relies upon simulation to demonstrate that disturbance and gene flow between sources and sinks can affect the fixation of alleles. Due to the complexity of the dynamics in the model (i.e. population growth, selection, spatial structure, and movement can all affect fixation; Whitlock 2003), a mathematical derivation of fixation probabilities is beyond the scope of this paper. I model two habitats that are identical with two exceptions: the sink habitat experiences periodic extinction, e.g. due to disturbance, predators, or competition, and the selective advantage of a new allele can differ among the two
populations. The population that experiences disturbance is a sink because it is incapable of long-term persistence without periodic recolonization from the source (Pulliam 1988).

Population growth is determined by the discrete logistic model: $N_{t+1} = N_t + RN_t (1 - N_t/K)$; where $N_t$ represents number of individuals present in patch $i$ at time $t$, $K$ represents carrying capacity, and $R$ is the discrete rate of increase of the population. The sink is disturbed with frequency $D$, whereas the source never experiences disturbance. For simplicity, all models use $R = 0.1$ and $K = 200$ individuals, although the effect of using different parameters is also discussed. Use of small populations makes the results more germane to small populations where the impacts of fixation dynamics may be most important (Frankham 1995; Lynch et al. 1995).

At the start of each simulation, the source is filled to carrying capacity with normal alleles, with the exception of one mutant allele ($N_{source} = K$); the disturbance-prone patch is empty (i.e. $N_{sink} = 0$), as if a disturbance had just occurred (this assumption is later relaxed). Each generation, $N_t$ pairs of alleles are selected with replacement from the gene pool, and these alleles form the next generation in that patch. The likelihood that an allele will be selected is determined by: $p_t \times ((1+s)/W_{t,t})$, where $p_t$ is the frequency of the allele at timestep $t$, $s$ represents the additive selective advantage of the new allele in a heterozygote, and $W_{t,t}$ is the mean fitness of the previous generation (Otto and Whitlock 1997). After growth, a fixed proportion of alleles ($m$) disperses between the two patches. A simulation concluded when the mutant allele was either fixed in the source (frequency of mutant allele = 1) or lost from both patches. Values generated with the model were an excellent fit when compared with values obtained using the formula of Kimura (1962): on average, null values generated via simulation (table 1) differed by $< 0.47\%$. 
At least 625,000 simulations were conducted for each set of parameters at regular intervals from $D = 0$ to $D = 300$. Additional simulations suggested no change in model output when $D > 300$. Ultimately, units of $D$ are somewhat arbitrary because the impact of disturbance is a function of the relationship between $D$ and population growth, which is determined by $R$ and $K$, and to a lesser extent, $m$ (because migration links growth in both patches). As such, disturbance frequency is scaled for presentation based upon the number of times the sink population could rise to $K$ between disturbance events (related, but not strictly equivalent to, generation time).

Results

Ephemeral sinks change fixation in stable sources because the populations are linked by movement: alleles may find themselves in populations that are rapidly growing or shrinking, influencing the likelihood that they reproduce and they (or their offspring) return to the source. That is, sinks change the effective population size ($N_e$) of the source-sink complex (Kimura 1962; Otto and Whitlock 1997; Whitlock and Barton 1997; Wang and Caballero 1999; Whitlock 2003), thus affecting the likelihood that an allele will become fixed in the source. Because of rapid growth or loss, ephemeral populations can have important consequences for fixation in stable habitats, above simply changing total population size. For example, sink-mediated shifts in fixation are greater than in a stable, panmictic population of 400 individuals (the combined size of the source and sink, see table 1).

When selection is equal between sources and sinks

Movement determines the degree to which source and sink population dynamics covary and changes the ability of the sink to influence the source population. When
movement is high ($m = 0.9$; fig. 1), sinks can lead to demographic extinction in the source. Although this was only observed when disturbance rate was $< 1$ (fig. 1), it illustrates an important point. When disturbance is frequent, fixation probabilities tend to be similar regardless of whether an allele is deleterious or beneficial, because drift is of paramount importance in affecting fixation when frequent sink disturbance reduces $N_e$ of the source-sink complex. As disturbance becomes less frequent, drift becomes less important, and fixation probabilities begin to diverge under the influence of selection (fig. 1). When movement is limited (e.g. $m = 0.01$) fixation probabilities of beneficial and deleterious alleles never converge because frequent disturbance in the sink has less opportunity to influence the source population, although source-sink dynamics still lead to discernable changes in fixation probability (fig. 1).

When $s_{source} = s_{sink}$, the effect of source-sink dynamics is relatively greater for beneficial alleles of small effect and deleterious alleles of large effect (fig. 2). This occurs because sinks can greatly increase the importance of drift, such that even strong selection against a highly deleterious allele still may not prevent it from fixing (table 1). When disturbance is rare, sinks reduce the role of drift and allowing rare beneficial alleles to become frequent enough that selection is likely to carry them to fixation. Ephemeral patches also change the number of generations necessary for an allele to become fixed (results not presented). In agreement with Whitlock (2003) and Maruyama and Kimura (1974), time to fixation is reduced when ephemeral sinks reduce $N_e$ of the source-sink complex, and increased when sinks increase $N_e$. Conditional upon fixation, the time to fixation is greater as the absolute value of $s$ increases (deleterious and beneficial alleles of the same magnitude have the same fixation time; Maruyama and Kimura 1974).
When selection differs between sources and sinks

Differences in selection can exaggerate the effect of ephemeral sinks on fixation in sources (fig. 2). This occurs because the sink is not a stable population: because the population size in the sink is changing, it can exert greater control over fixation in the source by changing $N_e$ of the source-sink complex and providing a spatially segregated population where either drift or selection are heavily favored. Even if the selective value of the new mutation is of equal magnitude, but opposite sign, the sign of the mutation in the sink dictates whether it is more likely to fix. In essence, population change in the sink increases the effective selection (sensu Cherry 2003) operating on the allele in the sink, swamping the effective environment of the source, in clear contrast to situations where stable habitats swamp adaptation in marginal ones (Lenormand 2002).

Differences in selection can magnify or reduce the impact of sinks on fixation in the source. For example, when selection in the source is negative ($s_{source} = -0.001$), strong selection in the sink ($s_{sink} = 0.01$) can lead to a 10-fold increase in fixation probability in the source (table 1). This effect is even stronger for highly deleterious alleles that would be very unlikely to fix without source-sink dynamics (table 1). Because most new mutations are deleterious (Dobzhansky 1970), the greatest impact of source-sink dynamics may be in influencing the likelihood that deleterious alleles accumulate in populations, changing adaptation and potentially causing extinction via ‘mutational meltdown’ (Lynch et al. 1995).

Variations on model parameters

Additional simulations were conducted to examine the impact of changing model parameters. Many of these outcomes can be inferred from considering how source-sink
structure changes in $N_e$ (Otto and Whitlock 1997; Whitlock 2003). As such, I do not present detailed graphical depictions of simulation output in the interest of brevity.

Increasing rate of growth ($R$) makes it more likely that disturbance will have beneficial impacts on source-sink populations, because the population is more likely to maintain positive net growth when disturbance is frequent, increasing $N_e$. In general, anything that decreases the potential for the sink to increase or decrease $N_e$ will lead to reduced (but still evident) impacts of source-sink structure on population dynamics. Examples of realistic scenarios include: if sink disturbance is partial rather than absolute, if a new mutation enters the source population during a random timestep, if several sources are connected to a single sink, or if alleles move between habitats but individuals do not (e.g. pollen movement among plants).

When source and sink populations are larger in size (i.e. $K$ is greater) or when a source patch exchanges alleles with more than one ephemeral sink, greater changes in $N_e$ are possible. As such, effects on fixation can be magnified (note the null values for $K = 400$; table 1), with the rate of disturbance relative to population growth rate determining whether the effect on fixation is positive or negative.

**Discussion**

Populations that are ephemeral may have permanent influences on fixation in stable populations. This suggests that ephemeral populations may play an underappreciated role in affecting fixation, adaptation, and viability, especially by affecting deleterious mutations (table 1; fig. 2). Several examples help demonstrate the potential importance of these dynamics.
Conservation reserves provide refuge for rare populations. The edges of conservation reserves may house less stable populations compared to the reserve interior due to edge-related phenomena, e.g. frequent disturbance (anthropogenic or otherwise), the encroachment of predators, competitors, or some combination of these events (Janzen 1983; Fagan et al. 1999). Because populations within the interior of the reserve (the source) exchange individuals with more variable populations at the edge of the reserve (the sink), events outside of the reserve that affect the edge population may change fixation throughout the entire reserve. If rates of disturbance at the edge of the reserve are high, they could promote fixation of deleterious alleles throughout the reserve, promoting mutation load (Lande 1994), mutational meltdown (Lynch et al. 1995), and reducing viability.

Conservation corridors may promote population rescue and gene flow (e.g. Tewksbury et al. 2003) and are a hotly debated topic in conservation biology (e.g. Simberloff et al. 1992). This work demonstrates that corridors can have positive or negative effects, depending upon the nature of the patches being connected. For example, the impact of corridors on fixation depends upon the nature of the patches being connected: population viability could be reduced if corridors connect stable sources with highly disturbed sinks.

Insect pests often reside within stable habitats at the edge of field margins (sources), invading fields when new crops emerge. Because crops are an ephemeral resource and represent an inherently unstable habitat (due to crop harvest) with different selection pressures (e.g. due to pesticide application or the use of transgenic crops), the fixation of alleles conferring pesticide resistance may be affected. For example, a new mutation conferring resistance in the ephemeral habitat (the crop field), would be much more likely to fix in the source, and thus the population as a whole, even when the same allele carries a
heavy cost in the source (e.g. when $s_{\text{sink}} = 0.01$ and $s_{\text{source}} = -0.01$; table 1, fig. 2). Since insect pests can grow very rapidly, ephemeral crops may provide a place where resistance alleles increase with increasing populations, and stable non-crop habitats may provide a spatial refuge during times when crops are not available. Incorporating the role of population growth into traditional models of resistance development (Tabachnik 1994) would be a profitable next step, especially because the mobility, high rate of growth, and short generation time of insect pests makes it likely that they will benefit from source-sink dynamics, and resistance may be conferred by the fixation of a single beneficial allele (Daborn et al. 2002).

Refuges may exist in many predator-prey systems (Holt 1987) where prey may consistently experience ‘enemy free’ space. Periodic reduction or extinction of prey outside the refuge could lead to source-sink dynamics on fixation, potentially influencing evolutionary ‘arms races’ between predators and prey. Depending upon the rate of extinction outside the refuge, predators may thus indirectly either discourage prey adaptation (by increasing the likelihood that beneficial mutations will be lost and deleterious mutations will fix), or promote prey adaptation. Even if selection pressures inside the refuge differ from those outside the refuge (i.e. a mutation with anti-predator benefits may have no advantage, or a cost, when predators are not present), such alleles could still fix across the entire population, because alleles beneficial in the sink experience higher probabilities of fixation thanks to rapid changes increases in population size when disturbance is moderate or infrequent (fig. 2).

The ultimate impact of disturbance hinges upon population growth rate, and movement, to some degree, because growth rate and movement determine the severity to
which disturbance affects \( N_e \). As such, the same disturbance regime can be beneficial for some populations and detrimental for others, even if the populations occur within the same ecological community. Consider again a conservation reserve. If disturbance near the edge of the reserve creates a sink habitat, populations with low rates of intrinsic growth are more likely to experience negative impacts compared to populations that grow quickly. That is, among organisms with similar levels of gene flow, slowly growing taxa (e.g. large mammals) are more likely to be adversely affected than the quickly growing invertebrates that also share the reserve.

Ephemeral populations can affect fixation in stable populations, especially when selection pressures differ between the two. Given the rapid changes in connectivity (Goodwin and Fahrig 2002) and levels of disturbance (Pickett and White 1985; Vitousek et al. 1997; Goodwin and Fahrig 2002) in present landscapes, the source-sink dynamics could have important implications for contemporary evolution of organisms ranging from insect pests insects to endangered large mammals. Considering source-sink dynamics in light of more complex ecological and evolutionary dynamics that can affect fixation (e.g. (e.g. Barton 1995; Barton 2000; Whitlock 2003) would be a profitable next step.

Acknowledgements

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Table 1. Comparison of null fixation probabilities ($P^*$) with those observed under rare sink disturbance. Two null fixation probabilities are represented, one representing a single patch the size of the source ($K_{\text{source}} = 200$) and another representing a patch twice as large ($K_{\text{source}} = 400$), representing a panmictic source and sink. For calculation of null fixation probabilities, there was no movement ($m = 0$). Discrete intrinsic rate of growth, $R$, was 0.1 for all models, allowing direct comparison with results presented in fig. 2. Relative change in fixation probability calculated using fixation observed in simulation where sink disturbance was most rare (i.e. the points farthest to the right in fig. 2).

<table>
<thead>
<tr>
<th>$s_{\text{source}}$</th>
<th>Null Fixation Probability ($P^*$)</th>
<th>Relative Change in $P$ ($P_{\text{obs}} / P^*$); $K_{\text{source}} = 200$</th>
<th>$K_{\text{source}} = 400$</th>
<th>$s_{\text{sink}} = 0.01$</th>
<th>$s_{\text{sink}} = -0.01$</th>
</tr>
</thead>
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<td></td>
<td></td>
<td>$K_{\text{source}} = 200$</td>
<td>$K_{\text{source}} = 400$</td>
<td>$s_{\text{sink}} = 0.01$</td>
<td>$s_{\text{sink}} = -0.01$</td>
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<tr>
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<td>281.67</td>
<td>$&lt;4.65 \times 10^{-8}$**</td>
<td></td>
</tr>
</tbody>
</table>

*Due to the large number of simulations required, estimate produced using the formula of Kimura (1962)

**No fixation events observed in $3.11 \times 10^{12}$ simulations; the true value is less than this estimate
Figure 1. A-B. Schematic of two possible population structures that could be represented by the source-sink model. In each case, arrows represent a fraction of individuals, $m$, that migrate between a stable population (the source, unshaded) and a habitat of the same quality that experiences periodic local extinction (the sink, shaded). A. A core source habitat (e.g. a biological reserve) where activities at the patch edge lead to periodic local extinction and make the periphery of the patch a sink. B. The stable source and ephemeral sink are spatially separated, but still linked by movement. Changes in the sink patch (i.e. seasonal changes in weather, pesticide/herbicide application, disease or predation) lead to periodic extinction followed by favorable conditions. C. The amount of movement between sources and sinks affects fixation in the source as well as the size and viability of both populations. Disturbance rate is scaled relative to population growth rate (the number of times the sink population can grow from zero to $K$ between disturbance events). For example, when the ordinate equals one, the sink population has just arrived at $K$ when the next disturbance occurs. For all simulations, $K_{\text{sink}} = K_{\text{source}} = 200$ diploid individuals, $R_{\text{source}} = R_{\text{sink}} = 0.1$, and $s_{\text{source}} = s_{\text{sink}}$. Because migration links population dynamics, the sink population can grow (and the source population can shrink) faster when $m = 0.9$.

Figure 2. Changes in fixation probability due to source-sink population structure. Within each plot, the value of $s_{\text{source}}$ is the same, with different symbols representing different values of $s_{\text{sink}}$. For all simulations, $K_{\text{sink}} = K_{\text{source}} = 200$ diploid individuals, $R_{\text{source}} = R_{\text{sink}} = 0.1$, and $m = 0.1$. Note that the scale of the abscissa may vary among plots.
Figure 1.

A. [Diagram showing directional arrows and circles]

B. [Diagram showing a circle with shaded area and arrows]

C. [Graph showing fixation probability and sink growth]

- $s = -0.001$
- $s = 0.001$
- $N_{source}$
- $N_{sink}$

Sink Growth Between Disturbance ((Time to $K$)/$D$)
Sink Growth Between Disturbance ((Time to $K)/D$)

Figure 2.
CHAPTER 7. GENERAL CONCLUSIONS

The impact of corridors on seeds and seed predators

The effectiveness of corridors has been heavily debated in the literature (e.g. Simberloff et al. 1992; Beier and Noss 1996; Rosenberg et al. 1997). The lack of resolution to the corridor debate has been largely due to three reasons. First, few studies have been devised to evaluate large-scale corridor effects (Rosenberg et al. 1997; Debinski and Holt 2000). Second, large-scale studies generally confound the effects of area, connectivity, and changes in patch shape, and thus cannot tease apart the different ways corridors can impact populations (Tewksbury et al. 2002). Third, corridor studies rarely focus on ecological interactions, making the ultimate effect of corridors difficult to predict in ecological settings where competitors and predators exist (Simberloff et al. 1992).

Corridors have been shown to have beneficial impacts, affecting gene flow, population size, and colonization dynamics (e.g. Gonzalez et al. 1998; Haddad 1999; Haddad and Baum 1999; Mech and Hallett 2002; Tewksbury et al. 2002; Haddad et al. 2003). However, my research suggests that corridor benefits may not directly translate into increased viability of prey populations because corridors also affect predators. For seeds of bird-dispersed plants, increased deposition in connected patches may be offset by changes in seed predation within these patches. By conducting this research in an existing large-scale experimental system, I was able to separate the potentially different effects of patch shape, area, and connectivity (Tewksbury et al. 2002).

For at least one rodent seed predator, Peromyscus polionotus, corridors change spatial foraging behavior, leading to greater seed consumption in the interior of connected patches.
compared to the patch edge. Although other studies have documented edge-sensitive behavior in rodents (e.g. Bowers and Dooley 1993; Harper et al. 1993), this work does so in patches that are the same size, but varying shape. Documenting within-patch shifts in behavior demonstrates that within-patch effects of corridors on behavior may be as important as the among-patch effects of corridors on population dynamics that are often the focus of studies.

Corridors are capable of eliciting changes in ant communities, and these changes are in response to changes in patch shape rather than patch connectivity. Given the importance of abiotic conditions for mediating habitat use and competition among ants (Hölldobler and Wilson 1990; Bestelmeyer 2000; Albrecht and Gotelli 2001), changes in microclimate caused by patch shape seem the most likely mechanism by which this occurs. The increased dominance of Solenopsis spp. in rectangular patches provides the first large-scale evidence that corridors can shift communities via altering the competitive balance among different genera, further increasing our understanding of corridors outside of studies that focus solely on population-level impacts. Because the response of rodents and ants is to patch shape and edge rather than connectivity per se, these findings may are likely to have implications outside of corridor studies, because anthropogenic fragmentation is changing patch shape at a rapid rate (Harrison and Bruna 1999).

Connectivity and the fixation of alleles

Despite the tremendous insight already gained by those who have considered the spatial dynamics of evolution (e.g. Wright 1931; Slatkin 1977; Barton 1995; Cherry 2003; Whitlock 2003), the consequences of spatial structure may be even more profound when
coupled with changes in population size in time and space. This is evident from the work of Barton (1993), Whitlock (2003), Cherry (2003), and others (e.g. Gomulkiewicz et al. 1999). However, these models generally either simplify underlying population dynamics or do not allow realistic patterns of movement. The source-sink model is an attempt to model a simple, ecologically reasonable set of circumstances that draws the best elements from previous work (e.g. the stochasticity and spatial structure from Whitlock and Barton's work, the simplicity and population dynamics of Gomulkiewicz et al. (1999)). This model reveals that movement and disturbance mediate fixation, and that stable populations can be under the evolutionary control of their ephemeral neighbors. In a world where most research focuses on stable, long-term populations, this has important implications: we may not be focussing all of our attention in the right place. For example, source-sink dynamics may play a part in affecting the viability of rare populations, the evolution of resistance in pests and disease-causing microbes, and influence evolutionary 'arms races' between predators and prey.

Future Directions

*Corridors and ecological interactions.* Several questions remain fruitful areas for future study. Work already in progress is beginning to take a closer look at how seed predators affect synthetic seedbanks composed of several species (not just *Prunus serotina*, *Phytolacca americana*, and *Rubus allegheniensis*). Similarly, within-patch changes in rodent and ant seed predation could lead to a predictable 'landscape of risk', whereby large-seeded species (most often consumed by rodents) experience disproportionately greater survival at the edge of connected patches compared to the interior of connected patches. Because rodent
foraging within rectangular patches is less sensitive to edge, large-seeded species would be expected to recruit more evenly throughout rectangular patches. Comparison of seed rain data and plant establishment data exist for the study area, and could be examined for evidence to support this hypothesis.

Because of corridor-mediated changes in seed rain (Tewksbury et al. 2002; Haddad et al. 2003), density-dependent seed predation may occur in connected patches but not in unconnected ones. In this sense, increased input of bird-dispersed seeds into connected patches could increase predation on all seeds, whether bird-dispersed or otherwise. This interesting possibility, that corridors-mediated shifts in dispersal could foster apparent competition (Holt 1977) among seeds, is also currently under investigation. Ultimately, the role of seed predators in affecting the distribution of plants in corridor-linked patches deserves close inspection, but this will require tracking multiple plant species through their life cycle.

A clearer understanding of how other rodent granivores in the system are responding to patch shape and connectivity would also provide greater insight into the patterns of seed predation observed. Although habitat use and population dynamics of these species, *Sigmodon hispidus* and *Peromyscus gossypinus* have been studied in a similar corridor landscape (Bowne et al. 1999; Danielson and Hubbard 2000; Mabry et al. 2003; Mabry and Barrett 2003), the role of patch shape in mediating within-patch behavior remains unclear because these studies did not have unconnected, similarly-shaped patches for comparison. Preliminary analysis of trapping data for 2000-2003 suggests that abundance of these species did not change with patch shape and connectivity. However, these analyses did not consider the possibility of changing capture probability among patch types and locations, which is to
be suspected in light of the changes in *P. polionotus* apprehension documented in different locations and patch types. Conducting foraging tray studies at all 8 experimental blocks would help determine if the foraging patterns observed with *P. polionotus* are occurring with the other species. Although this has not been done, captured rodents could be fitted with PIT (passively induced transponder) tags and foraging trays could be outfitted with tag readers at the entrance. This would allow determination of which species were foraging in trays as well as documentation of temporal peaks in foraging activity (which may also change as a function of patch shape and connectivity).

Although there is evidence that shifting microclimate is responsible for shifts in invertebrate communities among habitat fragments (Carvahlo and Vasconcelos 1999; Didham et al. 1999), this hypothesis has not been evaluated in the context of corridors. The increased impact of *Solenopsis* spp. on other ant genera in rectangular patches suggests that patch shape may play a role in the competitive superiority of ant genera. This might arise because rectangular patches are colonized more quickly, providing a ‘priority effect’ whereby early colonists are able to dominate later arrivals. Rectangular patches might be colonized more quickly because the greater core area in rectangular patches may represent higher-quality habitat, a bigger target for airborne *Solenopsis* spp. queens during dispersal, or both. Alternatively, colonization may not be responsible: different patch shapes may alter microclimate in ways that promotes competitive superiority by a particular ant genus. Future studies that examine colonization and competitive dominance (i.e. via recruitment to baits and visual observations) would provide insight into the mechanism by which patch shape influences the dominance of *Solenopsis* spp. in rectangular patches.
Another interesting possibility is that the utility of corridors for other species can be affected by the species inhabiting the corridor. In the case of ants, communities in corridors are dominated by edge species, unlike communities in the patch interior. As such, plants with gravity- and ant-dispersed seeds that require many generations to travel the length of the corridor may find corridors more hospitable than the patch interior because highly granivorous *Pogonomyrmex* spp. are not abundant in corridors, but seed-dispersing ants (*Crematogaster* spp.) are more abundant in corridors. The role of larger-scale corridors, e.g. powerlines and roads, as dispersal conduits also deserves greater inspection (Stiles and Jones 1998).

*Local and large-scale implications of gene flow among stable and ephemeral habitats.* The utility of the source-sink concept lies in its simplicity: whenever a population is linked with an unstable one, the trajectory of fixation in both populations may be altered. For example, source-sink dynamics could have important implications for the evolution of resistance in pest insect and disease-causing microbes. Microcosm work could readily determine whether source-sink dynamics hasten microbial adaptation.

However, source-sink dynamics undoubtedly interact with a wide range of other ecological and evolutionary influences on fixation. For example, the relative importance of source-sink dynamics must be evaluated in light of how true metapopulation dynamics (Whitlock 2003), genetic hitchhiking (Barton 2000), mutation rate (Barton 1995), and epistatic and pleiotropic effects impinge on fixation. This integration is clearly beyond the scope of this dissertation, but is necessary to more effectively understand the interplay of ecological and evolutionary forces in determining the viability of populations and the change
in allele frequency over time. For example, it is possible that source-sink theory plays a role in 'peak shifts' in the context of the shifting-balance theory (Wright 1931). However, understanding whether source-sink dynamics are a major contributor to peak shifts in nature requires additional theoretical and empirical work.

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