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Effects of Landscape Corridors on Seed Dispersal by Birds

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Habitat fragmentation threatens biodiversity by disrupting dispersal. The mechanisms and consequences of this disruption are controversial, primarily because most organisms are difficult to track. We examined the effect of habitat corridors on long-distance dispersal of seeds by birds, and tested whether small-scale (<20 meters) movements of birds could be scaled up to predict dispersal of seeds across hundreds of meters in eight experimentally fragmented landscapes. A simulation model accurately predicted the observed pattern of seed rain and revealed that corridors functioned through edge-following behavior of birds. Our study shows how models based on easily observed behaviors can be scaled up to predict landscape-level processes.

Habitat fragmentation poses a widespread threat to biodiversity by disrupting the dispersal of organisms (1, 2). Corridors—narrow strips of habitat that join patches of similar habitat—are thought to provide a general solution by restoring dispersal among patches, thereby increasing gene flow and reducing the probability of local extinctions (3, 4). Yet corridors are controversial (5, 6). Their efficacy can vary greatly among systems, depending on the complex interaction between disperser behavior and landscape structure (3, 7). Controversy about corridors has been difficult to resolve because corridors operate at a landscape scale, where both experimental and observational (tracking) studies are difficult (8).

Here we test and validate an alternative approach to examine corridor function: individual-based behavioral models (9). Our goal was to predict corridor effects on long-distance (>250 m) dispersal of seeds by birds. We collected data on small-scale (<20 m) movements of seed-dispersing birds in experimental landscapes and used these movements to parameterize a model that predicted the effects of corridors on seed dispersal at the landscape scale. We then tested our model using data on actual seed rain from the same large-scale experimental landscapes. Importantly, our model links observations of local bird behavior to population-level impacts on the recruitment of plants, showing how corridor effects on one taxon can affect the other. More generally, the control and replication provided by our experimental landscapes allow a rigorous validation of individual-based models, which are widely applicable to other systems.

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Our experimental landscapes were designed to test two alternative hypotheses about how corridors function. The traditional corridor hypothesis posits that corridors act as dispersal conduits, channeling organisms between connected patches (3, 4). The drift-fence hypothesis posits that corridors intercept organisms dispersing through matrix habitat and direct them into associated patches, thereby increasing colonization of patches with corridors, regardless of whether the corridors connect patches (10, 11). These hypotheses are not mutually exclusive.

Each of our experimental landscapes contained five patches of regenerating vegetation in a matrix of mature pine forest (Fig. 1) (12). A central “source” patch (100 m by 100 m) was separated by 150 m from four peripheral “receiver” patches. One receiver patch in each landscape was connected to the source patch by a 25-m-wide corridor. Another receiver patch had two 25 m by 75 m corridors (“wings”) extending from opposite sides of the patch, perpendicular to the direction of organisms dispersing from the source patch, but not con-

nected to any other patch. A third type of receiver patch was rectangular (100 m by 137.5 m).

Because the areas of winged and rectangular patches were equal to the summed area of the connected patch and its corridor, we could test for corridor effects while controlling for area. The traditional corridor hypothesis predicts that seed dispersal from the source patch into the connected receiver patch will be greater than dispersal into unconnected receiver patches. The drift-fence hypothesis predicts that dispersal into winged patches will be higher than dispersal into rectangular patches, because the cross-sectional area of winged patches from the perspective of an organism in the source patch is greater than that of rectangular patches.

Our results are most directly applicable to savannah (historically, the habitat at our site), prairie, or other open habitats. However, our system also provides a general model for testing corridor theory, applicable to any fragmented landscape in which patches and corridors of suitable habitat are surrounded by a matrix of unsuitable habitat (e.g., patches of mature habitat in matrices of disturbed habitat).

Our study species were wax myrtle (*Myrica cerifera*) and one of its major seed dispersers in South Carolina, Eastern Bluebirds (*Sialia sialis*). Both species generally prefer open habitat. We placed fruiting wax myrtle bushes in the central patch of each landscape. Each time bluebirds were observed eating fruit from these bushes, we tracked their movements with a team of three people, using voice-activated radios to coordinate observations. Trackers stayed as far away as possible (>25 m), taking care not to influence the bird’s direction of travel. Bluebirds did not seem to be affected by human presence (13). To increase independence of observations, we generally restricted ourselves to tracking one bird per experimental landscape per day. Bluebirds are not territorial in the winter, when wax myrtle bears fruit.

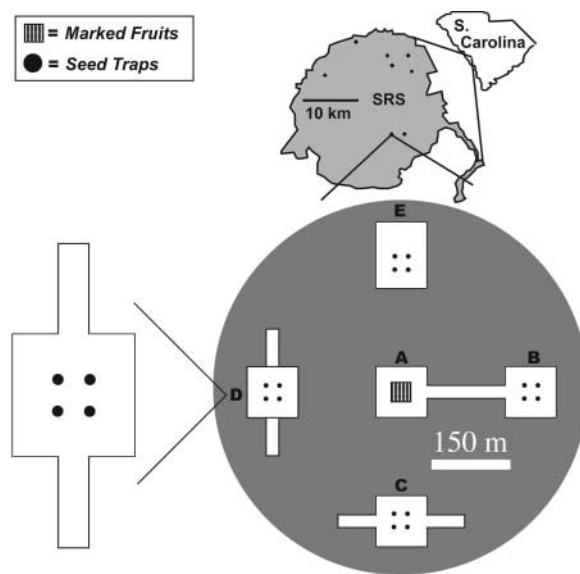


Fig. 1. One of eight experimental landscapes (black dots on map of SRS, the Savannah River Site National Environmental Research Park), showing the four patch types. Each experimental landscape had a source patch (A), where marked fruits were placed in the patch’s center, and three types of receiver patches, where seed traps were placed. One receiver patch in each landscape was attached to the source patch by a corridor (B). In four landscapes two of the remaining three receiver patches were winged (C and D) and one was rectangular (E; as pictured here), and in the other four landscapes, two receiver patches were rectangular and one was winged.

Edges strongly influenced movement directions ($\chi^2 = 48.9$, $df = 15$, $P < 0.001$; moves combined into 16 groups of 22.5°) (Fig. 2) (13). When a bird encountered an edge, it was most likely to fly parallel to it (0° or 180°) or less often, directly perpendicular, across or away from it (90° or 270°). We used these and other tracking data to estimate distributions of move direction, move length, and perch time (time between moves) as a function of habitat, distance to edge, and the orientation of the nearest edge and previous move (13). The median number of perch locations was 10 (1st and 3rd quartiles = 6 and 14), and median flight distance between perches was 17 m (1st and 3rd quartiles = 11 and 29 m).

To predict where seeds ingested by bluebirds in the source patch would be defecated, we simulated bluebird movement based on the fitted models, starting with the bird at the center of the source patch and ending after 45 min of movement (an estimate of seed retention time in bluebirds) (13). We calculated the proportion of simulated individuals located within the center 25 m by 25 m of receiver patches at the end of one simulation in each experimental landscape ($n = 8$ total), where one simulation consisted of 20,000 dispersal events. We used the center 25 m by 25 m of patches for simulation results because we had collected empirical data on dispersed seeds in this area (see below), thereby allowing a perfect match between the scales at which we modeled and measured seed dispersal. From the perspective of most plants, this constitutes movement at the landscape scale, because most vertebrate-dispersed seeds travel <50 m (14).

The distribution of birds at the end of 45 min was highly nonrandom ($F_{1,29} = 79.2$, $P < 0.001$). Birds were 31% more likely to be found in the center of connected patches than the center of unconnected winged and rectangular patches (Fig. 3). The percentage of birds in the two types of unconnected patch types did not differ ($F_{1,29} = 1.97$, $P = 0.17$). These results support the traditional corridor hypothesis and not the drift-fence hypothesis.

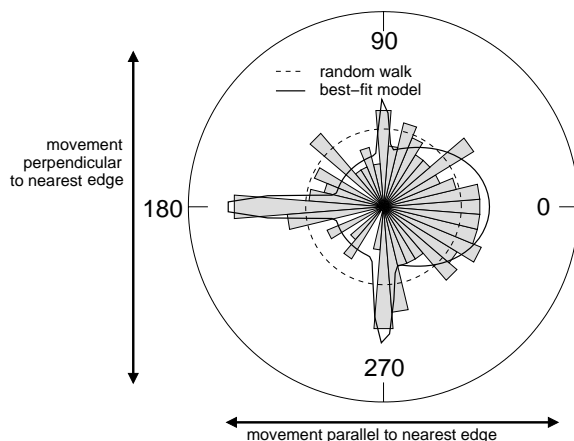
To independently test model predictions, we tracked the movement of individual seeds

from wax myrtle plants in the source patches to seed traps suspended from the tops of poles in the center of all receiver patches (Fig. 1). Bluebirds were responsible for depositing most seeds found in the traps, because they accounted for 79% of observations of fruit-eating birds perched above traps ($n = 90$). We tracked seeds from wax myrtle planted in the central patches to our traps in receiver patches by spraying their fruits with a dilute solution of fluorescent powder and examining defecations for fluorescence (15). Defecated seeds without fluorescent powder were eliminated from analyses. We report data from two field seasons.

The model accurately predicted the observed distribution of wax myrtle seeds collected from $>11,000$ defecations in seed traps (Fig. 3). On average, seeds in traps were 37% more likely to be found in the center of connected patches than in the center of unconnected winged and rectangular patches, thereby supporting the traditional corridor hypothesis ($F_{1,60} = 20.64$, $P < 0.0005$). Winged and rectangular patches received similar proportions of seed rain ($F_{1,60} = 0.13$, $P = 0.724$), leading us to reject the drift-fence hypothesis. These patterns did not differ between years ($F_{1,60} = 0.62$, $P = 0.804$).

These results have conservation relevance. Land managers must frequently decide whether to allocate limited resources to improving connectivity versus alternatives such as acquiring unconnected land. Our results provide a landscape-level demonstration that habitat corridors substantially increase the movement of birds and seeds between connected patches of habitat. Given that all receiver patches were equal in area, we conclude that the benefits of corridors extend beyond the increased amount of habitat they provide. Also, the benefits of corridors clearly apply more broadly than typically presumed. In this case, plant populations prosper through their interactions with animal mutualists. Although we studied dispersal of a common species, bluebirds disperse seeds of many species, including some of management concern. Our results extend to these species because of their shared dispersal agent.

Fig. 2. Distribution of movement directions of bluebirds located in the forest and close to a single edge. Gray wedges show observed data; solid line shows the best-fit movement model. All directions are relative to the consistent direction of travel—a vector parallel to the nearest edge, oriented in the same 180° arc as the previous move direction (supporting online text).



Models are most useful when they yield unexpected insights that become obvious in hindsight. Because bluebirds tended to follow edges, the corridor effect we observed was not due to the corridor per se, but rather to its edge. Indeed, we never witnessed a bluebird traveling between patches through a corridor; they always did so through the matrix, traveling alongside the corridor. Because all corridors have edges, this mechanism has broad implications. First, it shows that the functional connectivity of corridors extends beyond the structural connectivity they provide (7, 16). This complicates the evaluation of corridors—contrary to common sense, lack of travel in a corridor and frequent dispersal through the matrix do not necessarily contradict the value of corridors in maintaining habitat connectivity. Second, corridor width and other attributes of corridor quality may be irrelevant to organisms that behave like bluebirds—for such organisms, the defining attribute of a corridor is its edge. It follows that different types of edges may influence landscape connectivity in much the same way that different types of matrices do (17–20). The emerging lesson is that corridor effects and edge effects are intertwined; understanding how organisms respond to edges is central to understanding how corridors function (21, 22).

More generally, our results show how local behaviors can be scaled up to reveal larger-scale patterns of dispersal. In our system, flights that were typically <20 m were used to successfully predict long-distance seed dispersal that occurred over hundreds of meters. The importance of understanding how landscape structure affects the behavior of dispersing organisms is a common theme in landscape ecology (1, 20, 23–27), yet following animals across large landscapes for time periods long enough to characterize dispersal and colonization is nearly impossible. This problem is exacerbated by co-occurrence of corridors with waterways, roads, and other uncontrolled features of natural landscapes, preventing causal inference about corridor effects. The most common solution is to model how individuals react to habitat features, then extrapolate

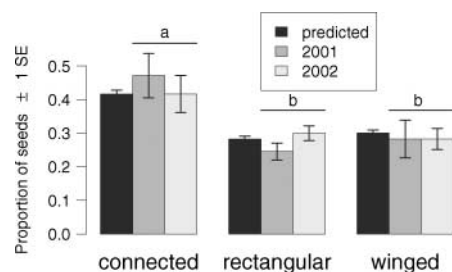


Fig. 3. Predicted distribution of seeds among receiver patches, based on simulated movements of bluebirds within experimental landscapes (“predicted”), and observed distributions of wax myrtle seeds captured in seed traps for two field seasons (“2001” and “2002”). Error bars denote SE and matching letters indicate nonsignificant differences between their corresponding patch types.

olate dispersal behavior to the landscape level (17, 21, 27, 28). Explicit tests of such models are needed (18). The tight fit between observed and predicted patterns of seed rain in our habitat patches provides strong support for the key assumption that small-scale behavioral responses can drive landscape-scale distributional patterns. From a conservation perspective, impacts of corridors can be predicted on the basis of behaviors that are relatively simple to measure (29).

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Supporting Online Material

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Materials and Methods

Fig. S1

Tables S1 to S4

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Identification of a Universal Group B *Streptococcus* Vaccine by Multiple Genome Screen

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Group B *Streptococcus* (GBS) is a multiserotype bacterial pathogen representing a major cause of life-threatening infections in newborns. To develop a broadly protective vaccine, we analyzed the genome sequences of eight GBS isolates and cloned and tested 312 surface proteins as vaccines. Four proteins elicited protection in mice, and their combination proved highly protective against a large panel of strains, including all circulating serotypes. Protection also correlated with antigen accessibility on the bacterial surface and with the induction of opsonophagocytic antibodies. Multigenome analysis and screening described here represent a powerful strategy for identifying potential vaccine candidates against highly variable pathogens.

Group B *Streptococcus* (GBS) is the foremost cause of life-threatening bacterial infections in newborns (1). In about 80% of cases, neonatal GBS infection is acquired during delivery by direct mother-to-baby transmission of the pathogen, which colonizes the anogenital mucosa of 25 to 40% of healthy women (2). Despite the introduction of intrapartum antibiotic prophylaxis, in the United States GBS still causes ~2500 cases of infection and 100 deaths annually among newborns in the first 3 months of life (3). About half of these cases occur in the first week after birth. Thus, it is

commonly believed that effective vaccination will be the only way to reduce the incidence of GBS disease over the long term. The rationale for GBS vaccine development is supported by the observation that the risk of neonatal infection is inversely proportional to the maternal amounts of specific antibodies to the capsular polysaccharide (CPS) antigen that surrounds GBS (4, 5), the implication being that protective immunoglobulin G (IgG) antibodies are transferred from the mother to the baby through the placenta.

As a first approach to vaccine development, CPS-tetanus toxoid conjugates against

all nine GBS serotypes were shown to induce CPS-specific IgG that is functionally active against GBS of the homologous serotype (6). Clinical phase 1 and phase 2 trials of conjugate vaccines prepared with CPS from GBS types Ia, Ib, II, III, and V revealed that these preparations are safe and highly immunogenic in healthy adults (7). Although these vaccines are likely to provide coverage against the majority of GBS serotypes that currently cause disease in the United States, they do not offer protection against pathogenic serotypes that are more prevalent in other parts of the world (e.g., serotypes VI and VIII, which predominate among GBS isolates from Japanese women) (8). Hence, a universal protein-based vaccine against GBS is highly desirable. To date, a few potential protective antigens have been described. These include the tandem repeat-containing α and β antigens of the C protein complex (9) and Rib (10); surface immunogenic protein, Sip (11); and C5a-ase, a serine protease that inactivates complement factor C5a (12). However, of these proteins, only Sip and C5a-ase are conserved at the gene level in the majority of GBS isolates (11, 13), and no systematic analysis on the extent of cross-protection is available.

To identify possible antigens suitable for use in a universal GBS vaccine, we compared the genome sequences of eight GBS strains belonging to serotypes Ia (515 and A909), Ib

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