Landscape Corridors Promote Long-Distance Seed Dispersal by Birds During Winter but Not During Summer at an Experimentally Fragmented Restoration Site

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ABSTRACT

In fragmented landscapes, plant population persistence and community diversity can hinge upon plants dispersing seeds long distances between isolated patches of habitat. Landscape corridors, which connect otherwise isolated patches, have been shown to increase seed dispersal by birds moving between patch fragments. However, because bird behaviors change seasonally, the strength of this "corridor effect" may also change. We assessed the utility of corridors for promoting seed dispersal by birds during both summer and winter in a well-replicated corridor experiment conducted in early successional longleaf pine (*Pinus palustris*) savannah habitat at the Savannah River Site in South Carolina, USA. We used a single species of bird-dispersed fruiting plant, American black nightshade (*Solanum americanum*), and controlled the timing and number of fruits available to birds during summer and winter. Corridors increased long-distance seed dispersal during winter but not during summer, indicating that the effectiveness of corridors for promoting long-distance seed dispersal can depend upon plant reproductive timing and seasonal differences in bird movement. A better understanding of the seasonality of plant-animal interactions will permit better predictions about whether and how corridors provide connectivity for plants.

Keywords: habitat fragmentation, plant-animal interactions, seasonality, *Solanum americanum*, American black nightshade

Seed dispersal is a crucial aspect of life history for many plant species (Levey et al. 2002). Patterns of seed movement, for example, can determine both plant population abundance and the structure of communities (Howe and Smallwood 1982, Tilman and Kareiva 1997). In fragmented habitats, where isolation of organisms can reduce population viability and species richness (MacArthur and Wilson 1967, Hanski 1999), seed dispersal is also critical for maintaining metapopulation dynamics (e.g., immigration, emigration, colonization, and gene flow among plant populations), which guard against extinction (Hanski 1999, Cain et al.

2000, Higgins et al. 2003). Because habitat fragmentation poses one of the greatest global threats to biodiversity (Wilcove et al. 1998, Baille et al. 2004), conservation and restoration practitioners urgently need strategies that preserve the potential for vulnerable plant populations to disperse seeds between remaining patches of habitat (Trakhtenbrot et al. 2005, Montoya et al. 2008, Nathan et al. 2008).

One of the most popular strategies to mitigate the extinction threat posed by fragmentation is the creation and maintenance of landscape corridors (Groves 2003, Crooks and Sanjayan 2006, Heller and Zavaleta 2009). Corridors are useful because they promote long-distance movement of a variety of organisms, including plants via seed dispersal, between otherwise isolated habitat patches (Johansson et al. 1996, Tewksbury et al. 2002, Kirchner et al.

2003, Levey et al. 2005, Damschen et al. 2008, Brudvig et al. 2009, Gilbert-Norton et al. 2010). Yet, there are still many gaps in our understanding of seed dispersal in fragmented landscapes (Cain et al. 2000, Cousens et al. 2010). Most seed dispersal studies focus on relatively short-distance dispersal, typically <50 m, and are conducted during a single season (Willson 1993, Cain et al. 2000, Nathan and Muller-Landau 2000, Nathan 2006). While long-distance seed dispersal is increasingly recognized as important for plant gene flow and community structure, it is also rare and inherently difficult to quantify (Clark et al. 1999, Nathan and Muller-Landau 2000, Nathan 2006). Moreover, for animal-dispersed plants, long-distance seed dispersal often depends upon animal behaviors that are context-specific, varying according to disperser

Table 1. Common seed-consuming birds in the experimentally fragmented landscapes and surrounding forest matrix at the Savannah River Site, South Carolina (adapted from Mayer et al. 1997).

Species	Common During Summer	Common During Winter	Species	Common During Summer	Common During Winter
Mourning Dove *Zenaida macroura*	X	X	Summer Tanager *Piranga rubra*	X	
Red-headed Woodpecker *Melanerpes erythrocephalus*	X	X	Northern Cardinal *Cardinalis cardinalis*	X	X
Red-bellied Woodpecker *Melanerpes carolinus*	X	X	Blue Grosbeak *Guiraca caerulea*	X	
Great Crested Flycatcher *Myiarchus crinitus*	X		Indigo Bunting *Passerina cyanea*	X	
Eastern Kingbird *Tyrannus tyrannus*	X		Eastern Towhee *Pipilo erythrophthalmus*	X	X
Blue Jay *Cyanocitta cristata*	X	X	Bachman's Sparrow *Aimophila aestivalis*	X	X
Carolina Chickadee *Poecile carolinensis*	X	X	Chipping Sparrow *Spizella passerina*	X	X
Tufted Titmouse *Baeolophus bicolor*	X	X	Field Sparrow *Spizella pusilla*	X	X
Red-breasted Nuthatch *Sitta canadensis*		X	Grasshopper Sparrow *Ammodramus savannarum*		X
White-breasted Nuthatch *Sitta carolinensis*	X	X	Fox Sparrow *Passerella iliaca*		X
Brown-headed Nuthatch *Sitta pusilla*	X	X	Song Sparrow *Melospiza melodia*		X
Brown Creeper *Certhia americana*		X	Swamp Sparrow *Melospiza georgiana*		X
Golden-crowned Kinglet *Regulus satrapa*		X	White-throated Sparrow *Zonotrichia albicollis*		X
Ruby-crowned Kinglet *Regulus calendula*		X	Dark-eyed Junco *Junco hyemalis*		X
Eastern Bluebird *Sialia sialis*	X	X	Brown-headed Cowbird *Molothrus ater*	X	X
Hermit Thrush *Catharus guttatus*		X	Orchard Oriole *Icterus spurius*	X	
Gray Catbird *Dumatella carolinensis*	X		Purple Finch *Carpodacus purpureus*		X
Northern Mockingbird *Mimus polyglottos*	X	X	Pine Siskin *Carduelis pinus*		X
Brown Thrasher *Toxostoma rufum*	X	X	American Goldfinch *Carduelis tristis*		X
Pine Warbler *Dendroica pinus*	X	X	Evening Grosbeak *Hesperiphona vespertina*		X
Yellow-breasted Chat *Icteria virens*	X				

species (Wenny and Levey 1998), time of day (Russo et al. 2006), and season (Cousens et al. 2010).

Seasonality can be especially important for determining long-distance seed dispersal patterns, which may be altered by seasonal winds (Houle 1998, Nathan et al. 2000, Nathan et al. 2008), flow regimes in riparian systems (Dynesius and Nilsson 1994, Malanson 1995, Kirchner et al. 2003), and the phenology of animal migration and habitat use (Powell and Bjork 1995, Nathan et al. 2008). It is necessary to consider how seasonal variation in animal behavior may affect the utility of corridors for promoting seed dispersal in fragmented landscapes (Chetkiewicz et al. 2006).

In this study, we assessed seasonal differences in the utility of corridors for promoting seed dispersal by birds. Working in a large-scale, well-replicated corridor experiment established in early successional longleaf pine (*Pinus palustris*) savanna habitat, we

used a native species of bird-dispersed fruiting plant, American black nightshade (*Solanum americanum*), to experimentally control fruit availability and quantify long-distance seed dispersal during both summer and winter. We focused on birds because they are extremely important seed dispersers in many terrestrial ecosystems (Levey et al. 2002, Dennis et al. 2007), and they are the primary consumers of fruits produced by plants at our study site (Martin 1951, McCarty et al. 2002). In addition, previous studies in the same experimental landscapes show that corridors increase seed dispersal by birds (Tewksbury et al. 2002, Levey et al. 2005, Damschen et al. 2008), but none of these studies evaluated how corridor use by seed-dispersing birds may vary between seasons.

We tested two predictions, that corridors promote long-distance seed dispersal by birds (P1), and that this corridor effect is stronger during winter than during summer (P2). P1 is well-supported by previous studies of bird-dispersed plants at our site, and P2 arises from the recognition that most seed-consuming birds at our site are territorial during summer but not during winter (Post and Gathreaux 1989, Mayer et al. 1997). We provide a list of seed-consuming birds common during summer and winter at our study site in Table 1. Birds consuming seeds during summer may be less likely to move long distances, through corridors or otherwise, because their movement and habitat use should be driven primarily by breeding imperatives, such as establishing and defending territories, maintaining nests, and provisioning chicks. During winter, seed-consuming birds are not so constrained and presumably move longer distances and respond to larger features of the landscape, such as corridors.
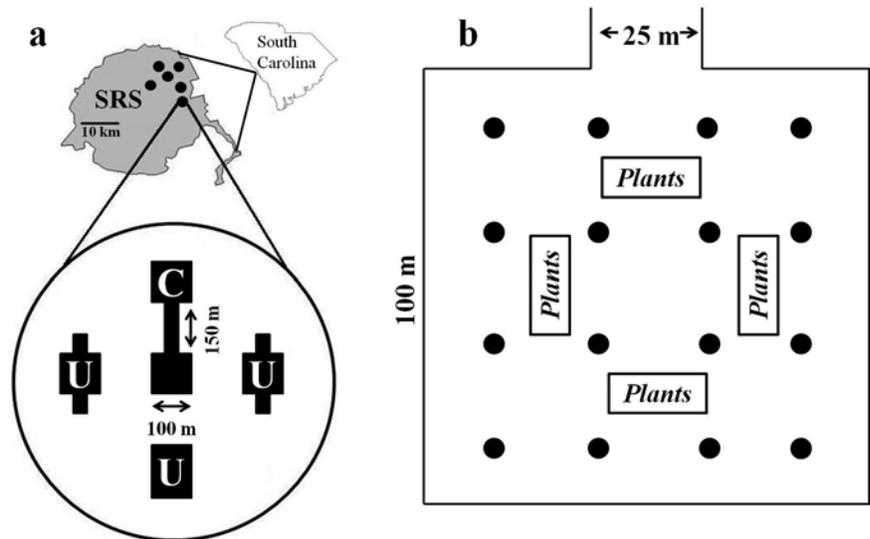

Figure 1. (a) Map of six replicated landscape blocks at the Savannah River Site (SRS), South Carolina, USA, with insert showing the patch configuration of one landscape. Each landscape has one central patch and four peripheral patches: a connected patch (C) joined to the central patch by a corridor, and three unconnected patches (U). All peripheral patches are equal in size to the area of the central patch plus the area of the corridor (1.375 ha), and all peripheral patches are equidistant (150 m) from the central patch. (The unconnected patches have different shapes to test patch-shape hypotheses that are not considered in this study.) (b) Diagram of one central patch showing locations of seed traps and study plants. Circles are seed trap locations; all patches in each landscape had 16 traps arranged in a similar grid. Each central patch also had American black nightshade plants grouped in four locations during the summer and winter experiments; equal numbers of plants were interspersed in each location in each central patch.

Material and Methods

Experimental Landscape Configuration

We conducted this study at the Savannah River Site (SRS) near New Ellenton, South Carolina. We worked in six experimental landscape replicates (blocks), created in 1999 and 2000 by clear-cutting habitat patches from mature pine plantation forest. The forest matrix of each landscape remains intact, but the patches have had hardwoods removed and have been burned four times since 1999 to promote longleaf pine savannah restoration. Each landscape is ~50 ha, including forested matrix area, and consists of five habitat patches: a central 100 × 100-m source patch surrounded by four peripheral patches equidistant (150 m) from the central patch (Figure 1a). One peripheral patch in each landscape is connected to the central patch by a corridor that is 25 m wide and 150 m long. All peripheral patches are equal in size to the area of

the central patch (1 ha) plus the area of the corridor (0.375 ha). Therefore, each experimental landscape consists of 1 central patch, 1 connected peripheral patch, and 3 unconnected peripheral patches; all patches and corridors are predominantly savannah habitat within a matrix of mature pine forest. See Tewksbury and others (2002) for a more detailed description of the landscapes.

Most native plants in the longleaf pine savannah patches in our experimental landscapes do not thrive or persist in the mature plantation pine forest matrix that surrounds the patches. Our experimental landscapes are similar to most fragmented landscapes for which corridors are proposed to conserve and restore habitat; the corridors are designed to connect patches of habitat suitable for particular ecological communities that are surrounded by an unsuitable matrix (Crooks and Sanjayan 2006).

The configuration of the landscapes permits explicit tests of the function of corridors as conduits for long-distance

seed dispersal, by comparing seed movement from the central patches to the peripheral (connected and unconnected) patches. For the purposes of this study, we define long-distance dispersal as >150 m. This threshold is similar to that used in other studies (Cain et al. 2000, Russo et al. 2006, Levey et al. 2008), and it is objectively linked to our experimental design; because a seed in our landscapes must travel at least 150 m to move from its patch of origin to a new patch, this distance represents non-local dispersal.

Focal Plant Species

American black nightshade is an early successional herbaceous plant native to the southeastern United States. It is common in South Carolina but does not naturally occur in our experimental landscapes. Any American black nightshade seeds dispersed in the landscapes as part of this study must have originated from plants that we placed in the landscapes (see Planting Design below). At SRS, American black nightshade begins producing fruits in May, and plants will flower and fruit continuously until September (Evans, personal observation). Its ripe fruits are commonly consumed by a variety of bird species (Martin 1951, Tamboia et al. 1996, Carlo 2005). In good conditions, American black nightshade can grow >1 m tall and produce >100 fruits. Plants used for this study were grown in a greenhouse until they were flowering and/or fruiting and then were transplanted into the field.

Planting Design, Seasonal Timing, and Numbers of Fruits Available to Birds

We conducted two experiments, one in summer and one in winter. The summer experiment began on 9 May 2009, when we transplanted 40 large (~1 m height) American black nightshade plants into the central patch in each landscape, with plants evenly interspersed in those patches (Figure 1b). Most plants were flowering when

planted. Plants were in 1-L plastic pots filled with Sunshine® Mix #7 (Sun Gro Horticulture, British Columbia, Canada) potting soil. We buried the pots in the ground and watered plants as needed throughout the summer, usually three times per week.

During summer, American black nightshade plants produced ripe fruits that were available to birds for approximately eight weeks. We counted ripe fruits in each landscape weekly and found that fruit production was synchronous in all landscapes. We observed the first ripe fruits in each landscape on 24 May. Plants in all landscapes produced the most ripe fruits between 7 and 14 June, when there were, on average, 2,932 ripe fruits per landscape. By 19 July, the number of ripe fruits in the landscapes had declined to <10% of their maximum numbers, except for one landscape in which the number had declined to <15% of its maximum. We did not observe birds removing American black nightshade fruits, but it is likely that birds took most of these fruits (see Discussion). Because most fruits had been removed by 19 July, and there were few remaining flowers or unripe fruits, we ended the summer experiment at that time by removing all plants from the field.

We designed the winter experiment to have approximately the same number of fruits available to birds (~3,000 per landscape) for the same amount of time as the summer experiment (8 weeks). On 30 January 2010, we transplanted ~50 large (~1 m height) fruiting plants into the central patch of each landscape. These plants quickly died due to low temperature, as is typical for American black nightshade plants during winter in South Carolina, but they remained upright and retained their fruits after dying, so the fruits were still available to birds. Like the summer experiment, all plants were in 1-L plastic pots buried in the ground, and plants were evenly interspersed in each central patch (Figure 1b). By 27 March, after the winter plants had been in the

landscapes for 8 wks, <5% of fruits remained in any landscape, and we removed all plants from the field.

Measuring Seed Dispersal

For both the summer and winter experiments, we installed 80 seed traps per landscape (16 traps per patch) on top of 3-m tall plastic poles (artificial perches, each 60 mm in diameter) arranged in a grid in each patch (following Levey and Sargent 2000; see Figure 1b). To build the traps, we used circular plastic baskets (25 cm in diameter and 10 cm deep) that were originally designed for hanging plants. We cut a 60-mm hole in the bottom of each trap, which permitted the traps to slide over the tops of the poles, so that each trap could be hung from the top of a pole and centered directly beneath it. These traps catch seeds when seed-consuming birds perch on top of the poles and defecate seeds into the traps. We glued a mesh screen in the bottom of each trap to keep seeds in the traps while permitting water to drain out, and we used wire hangers to fix the traps securely at the tops of the poles. Each trap hung ~0.25 m from the top of a pole and ~2.75 m above the ground.

During both the summer and winter experiments, all traps remained in the landscapes for the full eight weeks that fruits were available to birds. At the end of each experiment, we removed all traps from the field and counted American black nightshade seeds in each trap. We used a dissecting microscope to confirm the identity of each seed.

Because the seed traps were fixed ~2.75 m above the ground at the tops of plastic poles that were taller than almost all of the vegetation in the open habitat patches, any seeds deposited in the traps by birds were inaccessible to most ground-dwelling seed consumers. Ants conceivably could have climbed up the poles to consume seeds in the traps, and ants are abundant seed consumers in the habitat patches at SRS, but we never observed ants travelling up and down the poles
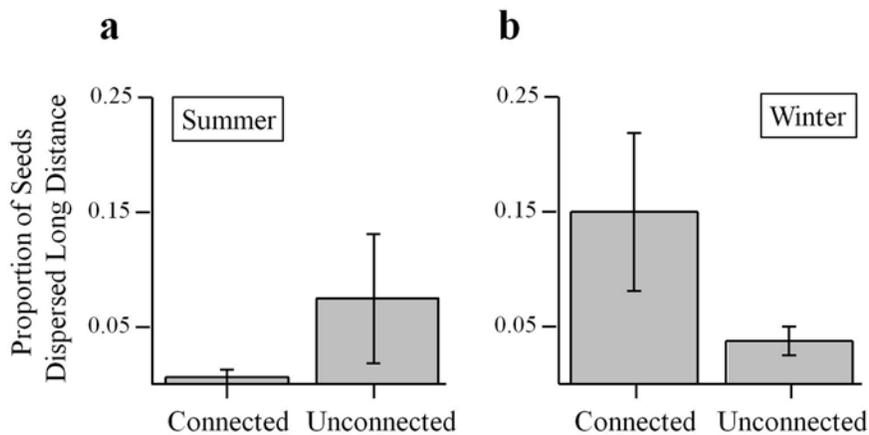
Figure 2. Average proportion (±1 SE) of seeds in connected and unconnected patches during summer (a) and winter (b), Savannah River Site (SRS), South Carolina.

during more than 1,000 person-hours in the field.

Statistical Analyses

To assess the proportion of seeds dispersed into connected and unconnected patches each season, we used a generalized linear mixed effects (GLME) model with a binomial distribution, and we analyzed data from summer and winter separately. We calculated the proportion of seeds captured in the seed traps in each peripheral patch relative to all the seeds captured in all traps in the landscape in which the patch resided. The number of seeds captured in the traps will necessarily be a subsample of the total number available to birds, and the traps cannot capture seeds dispersed by birds that do not use the artificial perches. But our purpose with these analyses is simply to compare, among seeds captured, the relative proportions dispersed into connected and unconnected patches (following Levey et al. 2005).

Within each landscape, we compared the proportion of seeds captured in the connected patch with the mean proportion of seeds captured in the three unconnected patches. For each analysis (summer and winter), we used data from all six experimental landscapes to assess the significance of the difference between the proportion of seeds dispersed into connected and unconnected patches. Peripheral patch

type (connected or unconnected) was a fixed effect, landscape (1–6) was a random effect, and we used a likelihood ratio test (LRT) to compare the full model to a null model in which the factor "peripheral patch type" was removed (Crawley 2007). This approach directly tests for a difference between connected and unconnected patches each season, since connected and unconnected are the only levels within the factor peripheral patch type.

We also used all the data from both seasons in a single model and tested for an interaction between season and peripheral patch type, again using the proportion of seeds dispersed into the peripheral patches as the response. Season (summer or winter), peripheral patch type (connected or unconnected), and their interaction were fixed effects, and experimental landscape (1–6) was a random effect. The proportion of seeds dispersed into peripheral patches was calculated as above, and we used a LRT to assess the significance of the interaction term. All analyses were fit using the statistical program R (R Development Core Team 2010) and the lme4 package (Bates and Sarkar 2010).

Results

While all landscapes had similar numbers of fruits available to birds for eight weeks during both summer and winter, birds deposited >22 times

more seeds into the seed traps during winter, with 489 and 11,091 seeds collected in the traps at the end of the summer and winter experiments, respectively.

The patterns of long-distance seed dispersal into peripheral patches were also very different between summer and winter. During the summer, the mean proportion of seeds dispersed into connected patches (0.14%) was significantly less than the mean proportion of seeds dispersed into unconnected patches (7.4%; Figure 2a) (LRT, $\chi^2 = 76.5$, df = 1, $p < 0.01$). The rest of the seeds collected in the landscapes during summer (mean proportion = 92.5%) were collected in traps in the central patches, where the source plants were located. During winter, the mean proportion of seeds dispersed into connected patches (15.2%) was significantly greater than the mean proportion dispersed into unconnected patches (3.7%; Figure 2b) (LRT, $\chi^2 = 565.6$, df = 1, $p < 0.01$). The mean proportion of seeds collected in the central patches during winter was 81.1%. The model evaluating all data from both seasons was consistent with these results and showed a significant interaction (LRT, $\chi^2 = 181.37$, df = 1, $p < 0.01$) between season and the proportion of seeds dispersed into connected and unconnected patches.

Discussion

This study shows a strong seasonal difference in the utility of landscape corridors for promoting seed dispersal by birds in this system. Corridors did promote long-distance seed dispersal during winter, but corridors did not have this effect during summer. We suggest that these results may be best explained by considering seasonal differences in bird behavior. However, we start by addressing the large disparity in the number of seeds collected in the seed traps during winter (11,091) and summer (489) since it, too, is likely tied to seasonal differences in bird behavior.

One might suppose, *prima facie*, that birds simply consumed fewer fruits during summer, resulting in fewer seeds collected in the traps. Many birds do consume relatively fewer fruits and more insects when breeding (Martin 1951, Jordano 1986, Wheelwright 1988 and references therein). However, even if birds in our landscapes consumed relatively more insects during the summer, they were still likely to be the primary consumers of American black nightshade fruits at that time. In both experiments, there were similar numbers of American black nightshade fruits in all landscapes, and the vast majority of these fruits were removed by consumers. It is well-established that American black nightshade fruits are commonly consumed by birds (Martin 1951, Tamboia et al. 1996, Carlo 2005). It is unlikely that small mammals consumed many of the summer fruits. After more than 1,000 person-hours in the field during the summer, we never observed obvious signs of mammal fruit consumption (e.g., broken or chewed plant stems). Moreover, birds are known to be the primary fruit consumers for all common plants at SRS that produce small, fleshy fruits during summer (McCarty et al. 2002).

If birds are responsible for removing most of the American black nightshade fruits during summer, then the reduced seed rain in summer must be largely attributed to seasonal differences in bird movement and habitat use (regardless of whether the same or different bird species occupied the landscapes in summer and winter). The most likely scenario is one in which summer territorial birds spend less time using the seed trap perches and more time establishing and defending territories, building and tending nests, and guarding and provisioning chicks. For example, this is likely the case for eastern bluebirds (*Sialia sialis*), who forage year-round in the savannah habitat patches of the experimental landscapes, are not territorial during winter, and use the seed trap perches more frequently during winter than

any other bird species (Levey et al. 2005). Bluebirds nest during summer in the pine forest matrix surrounding the patches (personal observation). It is likely that many seed-consuming birds, like bluebirds, use the sun-exposed patches more frequently during winter because these patches are warmer during the day than the surrounding pine forest. Conversely, birds may avoid the perches in summer because using them for more than brief periods would result in heat stress.

Putting aside the disparity in the number of seeds collected each season, a more fundamental issue is the large difference in the effect of corridors on where seeds were dispersed in winter vs. summer. The results of the winter experiment are consistent with previous studies in the same landscapes at SRS. Tewksbury and colleagues (2002) found that corridors increased long-distance seed dispersal for two winter-fruiting, bird-dispersed shrubs, yaupon holly (*Ilex vomitoria*) and wax myrtle (*Myrica cerifera*), whose fruits are consumed primarily by thrushes (Turdidae), warblers (Parulidae), and kinglets (Regulidae). Levey and others (2005) discovered that eastern bluebirds at SRS during winter prefer to travel along forest edges, including corridor edges, and disperse more seeds into connected patches. In these studies, as well as the winter experiment we describe here, corridors function, as expected, as movement conduits connecting patches of preferred habitat that are surrounded by a matrix of less-preferred habitat.

In the summer, a much smaller proportion of seeds were dispersed into connected patches than into unconnected patches. This was surprising, as we expected to find a relatively small positive corridor effect or no corridor effect, reasoning that most seed-consuming birds at SRS during summer are territorial breeders (Post and Gathreaux 1989, Mayer et al. 1997). The indigo bunting (*Passerina cyanea*), for example, is one of the most common breeding

birds in the experimental landscapes during summer and is highly territorial, with breeding pairs typically occupying 1–3 territories per patch (Weldon and Haddad 2005). Within-territory movements for this species may never require birds to travel between patches, but birds did disperse seeds between patches during summer (mean proportion = 7.5%), and almost all these seeds landed in unconnected patches. These results suggest that the forest matrix may be more permeable during summer to the movements of seed-consuming birds. Perhaps birds' movements between patches during summer were extra-territorial (Petrie et al. 1998, Arnold and Owens 2002), or perhaps some birds had territories large enough to include the forest matrix plus two or more experimental patches. This latter scenario is plausible for eastern bluebirds, which nest in pine forest and can have territories >2 ha (Twedt and Henne-Kerr 2001). Given the configuration of the landscapes at SRS, any such multi-patch territory would likely include the central patch and at least one of the three unconnected patches.

Many studies have demonstrated that birds will use corridors and other linear features to move through fragmented landscapes (Haas 1995, Machtans et al. 1996, Belisle and St. Clair 2001, Dzialak et al. 2005, Castellon and Sieving 2006, Gillies and St. Clair 2008), but no study to date has directly compared birds' movements among patches in fragmented landscapes during breeding and non-breeding seasons. Our results raise an important consideration for management of threatened and endangered bird-dispersed plants in fragmented habitats. Conservation planners and landscape managers frequently design corridors to promote movement of focal species, either because those species are threatened or endangered or because they represent ecological processes and communities that have high priority status for conservation and restoration (Beier et al. 2006,

Groves 2003 and references therein). When considering whether corridors will promote movement of plants into new patches of suitable habitat via seed dispersal, planners and managers should consider seasonal processes like changes in the landscape-scale movements of seed dispersers. Corridors in temperate regions may be most useful for promoting long-distance seed dispersal by birds during winter but may be ineffective for plants that produce fruits during summer months, when potential seed dispersers are territorial. To design corridors that effectively maintain and restore landscape connectivity, we need to understand the relationship between connectivity and mechanisms for plant and animal movement (Levey et al. 2005, Chetkiewicz et al. 2006, Gillies and St. Clair 2008, Haddad 2008, Gilbert-Norton et al. 2010). As this study indicates, seasonality can be a key driver of corridor effectiveness.

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