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Dispersal and Use of Corridors by Birds in Wooded Patches on an Agricultural Landscape

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Abstract: *Dispersal behavior has important effects on the persistence and recolonization of populations, but is one of the least understood traits of most organisms. Knowledge of patterns of fledgling, natal, and breeding dispersal of birds in a patchy environment will assist in decisions regarding reserve design and protection or construction of corridors. I present data on movement patterns of three migratory bird species, American Robin (*Turdus migratorius*), Brown Thrasher (*Toxostoma rufum*), and Loggerhead Shrike (*Lanius ludovicianus*). These birds are relatively common breeders in south-central North Dakota (U.S.) in riparian woodlands and in shelterbelts (woodlots planted as windbreaks in the open agricultural environment). Field assistants and I individually marked and monitored the movements of more than 500 adults breeding in a network of shelterbelts across an 8 × 11 km study area. Most movement occurred at relatively short distances within a shelterbelt. Movements by adults between shelterbelt sites, although rare, occurred significantly more frequently between sites connected by a wooded corridor than between unconnected sites. For robins, there were on average 2.5 dispersal events between each pair of connected sites, but only 0.17 dispersal events between each pair of unconnected sites (Mann-Whitney test, significant at $p < 0.009$). Because unconnected and connected sites were similar in average area (1.7 to 1.9 ha), distance to next wooded habitat, and tree-species composition, this result provides a test of the hypothesis that organisms disperse preferentially along connecting corridors.*

La dispersión y el uso de corredores por aves en parches boscosos de un paisaje agrícola

Resumen: *El comportamiento de dispersión tiene efectos importantes sobre la persistencia y recolonización de las poblaciones, pero es una de las características que menos se comprende en la mayoría de los organismos. El conocimiento de los patrones de dispersión de los volantes así como también de la dispersión natal y reproductiva de los pájaros en un ambiente fragmentado asistirá en la toma de decisiones con respecto al diseño de las reservas y a la protección o construcción de corredores. Presento datos de patrones de movimiento en tres especies de pájaros migratorios, *Turdus migratorius*, *Toxostoma rufum* y *Lanius ludovicianus*. Estos pájaros son reproductores relativamente comunes en el centro-sur de Dakota del Norte en bosques ribereños y en cinturones de resguardo (parcelas de bosque plantadas para cortar el viento en ambientes agrícolas abiertos). Asistentes de campo y yo marcamos y monitoreamos individualmente los movimientos de más de 500 adultos que se estaban reproduciendo en una red de cinturones de resguardo a lo largo de un área de estudio de 8 × 11 km. La mayoría de los movimientos involucraron distancias relativamente cortas dentro de un mismo cinturón de resguardo. Los movimientos de los adultos entre cinturones de resguardo distintos, aunque raros, ocurrieron con una frecuencia significativamente mayor entre sitios conectados con un corredor boscoso que entre sitios conectados. Para *Turdus migratorius* hubo, en promedio, 2.5 eventos de dispersión entre cada par de sitios no conectados, pero solamente 1.17 eventos de dispersión entre cada par de sitios no conectados (Mann-Whitney test, significativo con $p < 0.009$). Dado que los sitios conectados y los no conectados fueron similares en cuanto al área promedio (1.7 a 1.9 ha), la distancia al hábitat boscoso más próximo y en la composición específica de los árboles, este resultado provee una prueba para la hipótesis de que los organismos se dispersan preferentemente a lo largo de corredores conectados.*

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Introduction

Birds are highly vagile organisms, and consequently their movements cannot be easily followed. What we know of avian movement is limited primarily to data from recapture of birds banded along migratory routes, recovery of banded birds (either found dead or killed by hunters), and movements of birds on discrete study areas. Telemetry studies are more practical on larger species because they can carry packs that transmit longer and stronger signals (e.g., Thompson & Fritzell 1989). Hunted waterfowl are relatively well-studied (see references in Brownie et al. 1978; Hestbeck & Malecki 1989), owing in part to the high probability that marked birds will be recovered. Because recoveries of banded passerines are less common, many estimates of movements by passerines come from intensive studies of single populations. But areas in which breeding passerines are studied are often too small to allow observation of long-distance dispersal. Examples of such intensive studies are those of Harvey et al. (1985) on Pied Flycatchers (*Ficedula hypoleuca*) in a 25-ha area, Jakobsson (1988) on Willow Warblers (*Phylloscopus trochilus*) in a 35-ha area, Bijlens (1988) on Blue Tits (*Parus caeruleus*) in a 153-ha woodland, and Lombardo (1989) on Tree Swallows (*Tachycineta bicolor*) in a 160-ha refuge. Much of our knowledge of the population biology of passerines comes from studies such as those of tits conducted in a 231-ha site in Wytham Wood (Greenwood et al. 1979; Harvey et al. 1979) or of Splendid Fairy-Wrens (*Malurus splendens*) in a 125-ha woodland-heath (Rowley et al. 1991), and studies of island populations (Kikkawa & Wilson 1983; Smith et al. 1991). A long-term study on Florida Scrub Jays (*Aphelocoma c. coerulescens*) at Archbold Biological Station is unusual in that it has occurred on an increasing area over time (Woolfenden 1973). Exceptions include studies of some *Parus* species (Winkel & Frantzen 1989) and Pied Flycatchers (*Ficedula hypoleuca*) (Berndt & Sternberg 1969) in areas of 120,000 and 250,000 ha, respectively.

Between the data that can be collected on dispersal from intensive studies on a single study area and the information on large-scale movements that can be detected by band recoveries, there is a gap in our knowledge of the frequency and importance of different lengths of dispersal (Moore & Dolbeer 1989). Saunders and de Rebeira (1991) conducted a mist-netting study in native remnant patches in a 625-km² agricultural area of western Australia, and they presented data on the movement of 328 birds recaptured during the four-year period. This work has yielded valuable information on the movement of birds in an agricultural landscape, but, because of the effort involved in netting, the reproductive status of the dispersing birds is unknown. In some intensive single-area studies, there have been attempts to estimate dispersal off the study area by censusing the sur-

roundings at one or more times. Jakobsson (1988), for example, censused 230 ha of woodland surrounding his 35-ha study area and found no banded male Willow Warblers. Because censuses of a large expanse of suitable habitat are extremely time-consuming, however, censuses around small, main study areas also tend to be limited in size. Assuming a circular 35-ha study site (Jakobsson's actual study site was not circular) and a circular 230-ha census area, the diameter of the larger census area would still be only 1.8 km.

Information on long-distance dispersal from band-recovery studies has biases and limitations. Recoveries may be biased in two ways by the banders themselves. A higher proportion of banded birds may be reported closer to banding stations than away from them because banders at banding stations are more likely to examine birds found dead than are members of the general public. The data may be biased in the opposite direction as well, at least for studies in the U.S., because recaptures and recoveries made within the same 10-min block as the banding station are not reported to the U.S. Fish and Wildlife Service. Band-recovery studies contain little information about the reproductive status of birds involved and therefore the biological importance of detected movements are unclear. Better knowledge of the patterns of movement of birds is important to our understanding of avian population genetics, range expansion and colonization ability, mortality, social behavior, and the conservation and management of bird populations.

I describe the movements of marked individual American Robins (*Turdus migratorius*), Brown Thrashers (*Toxostoma rufum*), and Loggerhead Shrikes (*Lanius ludovicianus*) breeding on a study area of over 8000 ha. These three species are abundant breeders in woodlands on the study area, adults are readily caught in mist nets, and their nests are accessible for study. All three species are short-distance migrants. Individuals from the study population winter in the southern Great Plains states and northern Mexico. The nesting season for Brown Thrashers extends from late May to late July, for Loggerhead Shrikes from late April to late July, and for American Robins from late April to late August (Stewart 1978; Haas 1985). I chose the study area as a system in which intermediate-distance dispersal (1 to 5 km) could be observed. By censusing certain patches of habitat spread across a larger landscape, it is possible to observe dispersal between patches. This method has been used successfully to differentiate mortality and dispersal in small-mammal populations (Zeng & Brown 1987). Winkel and Frantzen (1989) used this method to observe dispersal among tit populations in 20 nestbox areas established over a large area. Tree-nesting birds that breed on the prairie occur naturally in a series of habitat patches on the landscape. This patchy distribution of suitable nesting habitat allowed me to monitor the dispersal of marked birds throughout the study area, rather than

only observing the proportion of dispersal events that occurred between selected trapping sites (as in the studies cited above). The relatively large study area allowed me to determine the frequency of intermediate-distance movements (1 to 5 km) and to examine whether these occurred preferentially along dispersal corridors. I also determined levels of natal-site fidelity in the three species.

Methods

The study area encompassed patches of wooded habitat distributed over an area 8 by 11 km of agricultural land in Sioux County in south-central North Dakota. Most of the land in south-central North Dakota is used for range, hay, or small grains. Trees occur only along river or creek beds where they grow naturally (riparian woodlands and woody draws), or where they are planted as shelterbelts around farmsteads, pastures, or field. Shelterbelts are rows of trees planted as protection from the wind (Titus & Haas 1990). Woody draws are native woodlands occurring where topographic features concentrate moisture (Faanes 1987). My study area contained 16

sites (Fig. 1), each composed of one to seven shelterbelts. Individual sites ranged in size from 0.3 to 2.7 ha. The average shortest distance between shelterbelts within a site was 60 meters. The average shortest distance between sites was 1.5 km. Sections of woody draws also occurred on the study area. Two of these draws virtually connected two pairs of sites. The 16 sites included only trees planted as shelterbelts and did not include adjacent woody draws.

Less than 2% of the state of North Dakota is wooded (Cassel & Wiehe 1980). This is probably similar to, or somewhat larger than, the amount of wooded area found in the state historically. Although tree planting by European settlers has increased the amount of wooded habitat, damming of the Missouri River flooded some native riparian woodlands. Extensive natural forests did not occur in this Great Plains state. The 16 shelterbelt sites on the study area totaled 26 ha. I did not calculate the area of woody draws, but an estimated total did not exceed the area of land covered by shelterbelts. Total wooded habitat on my study area was therefore less than 1%. (Substantial riparian woodlands do occur along some rivers in this region, but none of these were in-

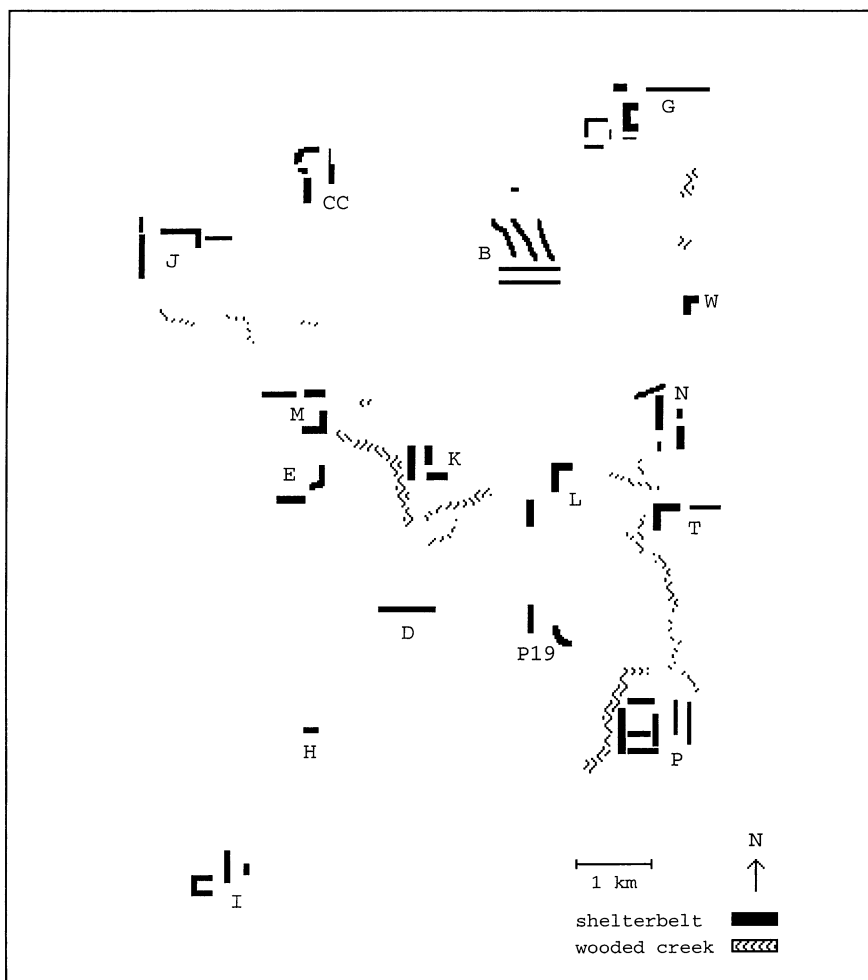


Figure 1. Schematic diagram of wooded habitat on the study area, Sioux County, North Dakota. The 16 shelterbelt sites are identified by the letters adjacent to them.

cluded in the study area.) Common species of woody plants included Siberian elm (*Ulmus pumila*), green ash (*Fraxinus pennsylvanicus*), and Russian olive (*Eleagnus angustifolia*) in the shelterbelts, and American elm (*Ulmus americana*), green ash, and buffaloberry (*Shepherdia argentea*) in the draws. (*U. pumila* and *E. angustifolia* are exotics that resemble the native species *U. americana* and *S. argentea*, respectively, in growth form.)

During the breeding seasons (April–August) of 1985 to 1988, my field assistants and I mist-netted adult robins, thrashers, and shrikes and marked them with individual combinations of three colored plastic leg bands and one U.S. Fish and Wildlife Service aluminum band. We located nests during weekly censuses and banded nestlings and fledglings with one color band and one aluminum band. These birds had to be recaptured to be identified individually. All wooded habitat within the study area was censused for marked birds approximately weekly from 1985 through 1989. This design allowed observation of movements of distances up to 13.8 km. The average distance from the center of the study area to the four corner sites was 5.4 km. (For a further description of the study area, see Haas [1990].)

I measured dispersal distance both within and among breeding seasons. I used Greenwood and Harvey's (1982) definitions of breeding and natal dispersal; all discussions of adult dispersal refer to breeding dispersal, unless specifically stated otherwise. Dispersal distances of individual birds that moved between sites were estimated by plotting the locations in which they had been sighted on a U.S. Geological Survey topographic map and calculating the minimum straight-line distances between the locations. Distances moved within one site, up to approximately 500 meters, were measured directly with a 50-meter tape or paced by observers whose stride length was known. I report actual distances rather than the number of territories over which birds dispersed, because birds in this system did not regularly defend territories (Titus & Haas 1990). Between-nest distances among years were measured as the distance between the location of the last nest of year n and the first nest of year $n + 1$. Because shrikes re-nested infrequently on the study area in a given breeding season, and because very few adult shrikes returned in subsequent years (Haas & Sloane 1989), I examined movements of shrikes from fledging to their second year only.

I measured the distances moved by fledglings on the study area by mist-netting fledglings in July and early August. By recapturing fledglings that had been banded previously, I could measure the minimum linear distances moved between the two capture locations. All of the birds used in this analysis were originally banded when they were incapable of sustained flight (that is, while the young were either in or near their nests), but within a few days of fledging (usually at the age of 7 days

for robins and thrashers and 10 days for shrikes). Young of these species are fed and accompanied by their parents for approximately 2–3 weeks after leaving the nest (personal observation). I included only birds that were recaptured 21 or more days after they were originally banded. When we recaptured birds banded as young of the year in subsequent years we could measure their natal dispersal distances. I measured the distance from the original banding location to the location where the return nestling bred by identifying the two points on a U.S. Geological Survey topographic map. For this analysis I used birds banded both as nestlings and as fledglings.

Results and Discussion

We marked a total of 238 adult American Robins, 279 Brown Thrashers, and 47 Loggerhead shrikes between 1985 and 1988. Despite the opportunity to observe movements, we observed few instances of intermediate-distance dispersal by breeding adult robins or thrashers either within a breeding season or among years (Figure 2a–d, Table 1). In Fig. 2, dispersal distances are reported as the shortest distance between subsequent nests of individual robins and thrashers that re-nested on the study area, either within a single breeding season or in the following year. Data from 1985 through 1989 are combined. These distributions of dispersal distances were all strongly skewed toward short dispersal distances, and yet in three out of four cases they include some dispersal distances greater than 1 km. The occurrence of these isolated points might not have been expected from the shape of the distribution had sampling stopped at 0.5 km, for instance. The scarcity of dispersal distances recorded in the range of 201–500 meters could lead to the erroneous conclusion that all dispersal events

Table 1. Movements of adult Brown Thrashers and American Robins on the study area.

Species	Same Shelterbelt		Same Site		Moved to Draw		Moved to New Site	
	N	%	N	%	N	%	N	%
Thrasher								
within year								
male	19	83	22	96	1	4	0	0
female	21	81	26	100	0	0	0	0
among years								
male	25	74	33	97	1	3	0	0
female	12	54	21	95	1	5	0	0
Robin								
within year								
male	19	66	22	76	6	21	1	7
female	27	71	30	79	7	18	1	5
among years								
male	15	50	21	70	5	17	4	13
female	23	60	30	79	7	18	1	3

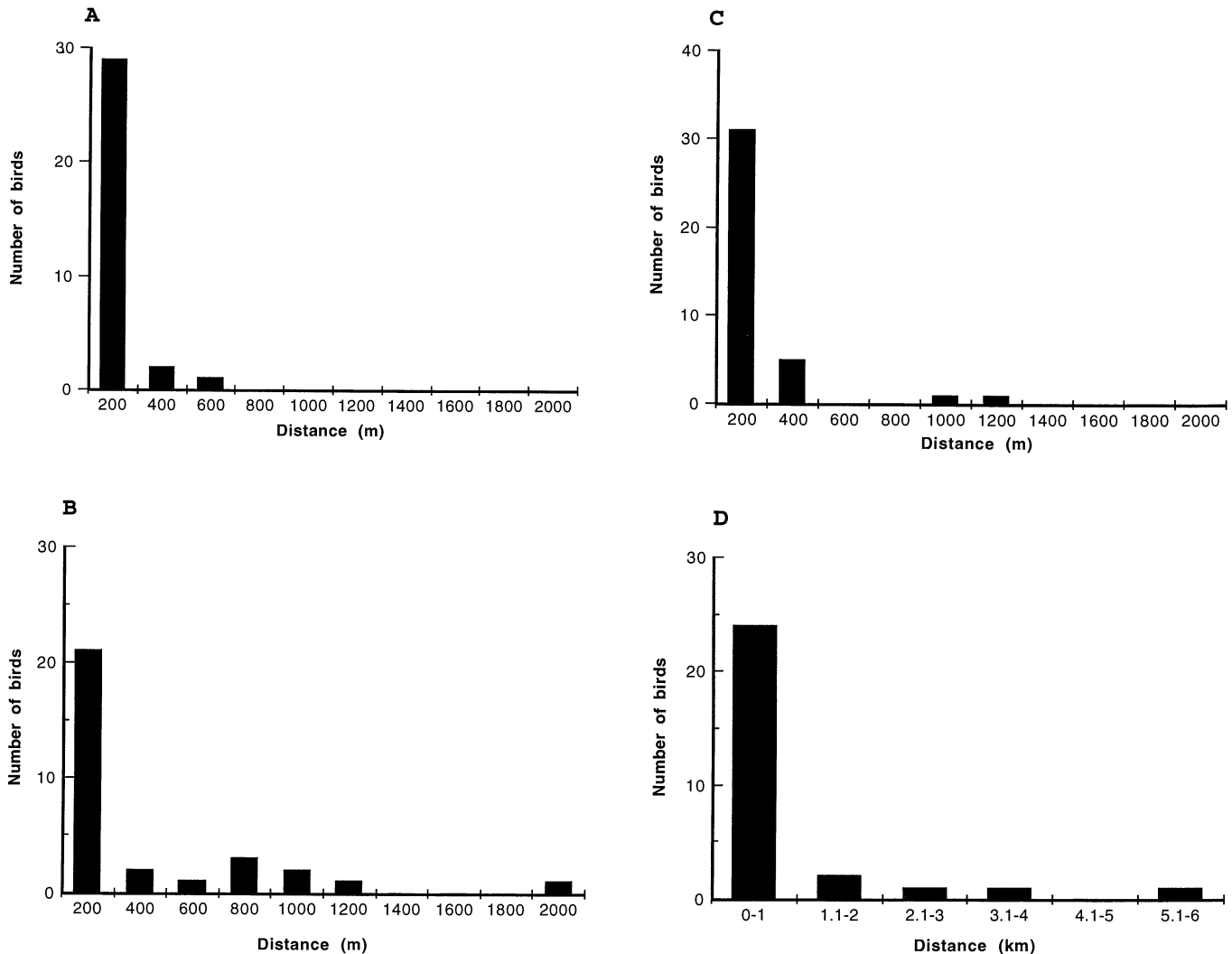


Figure 2. Distances moved between subsequent nests (A) by Brown Thrashers within a breeding season; (B) by Brown Thrashers among years, including movement by one individual whose exact nest location was unknown; (C) by American Robins within a breeding season; (D) and by American Robins among years, including movements by four individuals whose exact nest location was unknown.

occurred over short distances (less than 1 km). Robins moved a mean distance between nests of 142 meters ($n = 37$, range = 4–1200 m) within a breeding season and 170 meters among years ($n = 24$, range = 27–1300 m). Thrashers moved a mean distance between nests of 86 meters ($n = 32$, range = 7–464 m) within a breeding season and 259 meters ($n = 30$, range = 0–1200 m) among years.

For a variety of reasons, some movements by both robins and thrashers were not included in the calculations of between-nest dispersal distance. In most cases, between-nest dispersal distance could not be calculated because either the first or a subsequent nest was not found. To calculate between-nest dispersal distances, it was necessary to locate two successive nests of individual birds. In a number of instances I observed move-

ments of marked birds but was unable to locate a nest at either the first or a subsequent site where the bird was seen. Some of these movements obviously were not instances of breeding dispersal and were not included in my analyses. For instance, in late summer a male robin that had bred at one site was observed in a small woody draw a few kilometers away. There were no active robin nests in the draw at the time, and the male was not seen associating with any female or fledgling robins. This was presumably just a feeding area the male used before migration. In other cases, however, there was evidence that the birds did nest or could have nested in those sites where they were observed. For example, in 1986 YWXG male robin was sighted in site K1. Two robin nests were active in that shelterbelt at the time, but both failed before YWXG could be assigned to a particular nest.

YWXG did not breed again in 1986, but in 1987 he nested in M3. Sometimes in these cases the adult was seen with fledglings incapable of sustained flight, so the nest was known to be reasonably close by. Because I failed to locate the nests, such data could not be included in the analysis of between-nest dispersal distances, but I considered them instances of breeding dispersal and included them in the analyses of movements within and among sites. Movements of eight individuals or pairs were excluded from the analysis of between-nest dispersal instances but included in the analysis of movements among sites.

No birds banded as adults were reported from band recoveries off the study area.

BIRDS BREEDING IN SHELTERBELTS

Most adults remained in the same shelterbelt (Table 1). Within a breeding season, 81% (40/49) of the thrashers that renested after nest failure or after successfully fledgling young did so within the same shelterbelt; 98% remained in the same site. Only one individual left its original site to breed in a woody draw. A similar pattern held for thrashers that returned to the study area in the subsequent year. Of the returning thrashers, 66% (37/56) renested in the same shelterbelt in which they had last nested in the previous breeding season, and 96% (54/56) renested in the same site. Two individuals changed nesting locations from the sites in which they had bred the previous year to move into a woody draw.

American Robins were significantly more likely than Brown Thrashers to move to a woody draw or a different site both within a year ($X^2 = 10.6$, d.f. = 1, $p < 0.005$) and among years ($X^2 = 12.2$, d.f. = 1, $p < 0.005$). Nevertheless, within a breeding season, 69% (46/67) of robins that renested did so in the same shelterbelt and 78% (52/67) remained in the same site; 19% (13/67) moved into woody draws and 3% (2/67) moved to other sites. Again, movements among years were similar to movements within years. Of the robins that returned to the study area in the subsequent year, 56% (38/68) were found in the same shelterbelt in which they had last nested and 75% (51/68) returned to the same site; 18% (12/68) moved into woody draws and 7% (5/68) switched sites.

Of the five American Robins that switched sites among years, three moved between two sites connected by a draw, one moved to the nearest site, and one skipped over two sites moving 4 km after losing his nest and mate to a predator the previous year. The two robins that switched sites within a year were a pair that moved between two sites connected by a draw. In 1984 I had few marked birds in the area, but I did observe one marked pair of robins switch sites between nesting attempts in 1984. This pair moved 2.4 km between two isolated sites. For robins, five out of nine movements to

a noncontiguous habitat patch, within and among breeding seasons, occurred along draws. All thrashers (3/3) that moved out of their original site moved into draws. Of robins that left their site within a year, 76% (13/17) moved to draws. Among years, 71% (12/15) of robins that left their original sites moved to draws.

BIRDS BREEDING IN WOODY DRAWS

Because I rarely netted along woody draws, few birds along draws were marked. The pattern of movement of the small number of banded thrashers and robins in the draws resembled that in shelterbelts (Table 2). Almost all (14/15) of the banded thrashers in the draws remained in the draws, but 24% (5/21) of the banded robins in the draws moved into one of the shelterbelt sites either within a breeding season or in a subsequent year.

Including all movements within, out of, or into draws, only 21% (3/14) of movements of banded thrashers among years occurred between isolated patches; within years, only 20% (1/5) did. These movements included both movements between draws and nonadjacent shelterbelts and movements from one draw into another nonadjacent draw. The rest of the movements occurred along a draw or between a draw and an adjacent site. For robins, only 11% (3/27) of movements among years occurred between unconnected patches; within years, 26% (5/19) did.

WOODY DRAWS AS CONNECTING CORRIDORS

The results that most movement occurred within sites and that most movement out of sites was to draws rather than to other sites suggests a stepping-stone effect. Dispersing birds tended to move to nearby patches. The result that 56% of movements by robins to other sites were between sites connected by draws suggests that these draws may also serve as travel lanes between sites. Although sample sizes were small, this result was even more striking because on the study area there were only two pairs of sites connected by draws but 118 possible paired combinations of unconnected sites. Of course, among all the 118 possible combinations of pairs, there

Table 2. Movement of adult Brown Thrashers and American Robins within woody draws.

Movement Time	<i>Brown Thrasher</i>		<i>American Robin</i>	
	<i>Stayed In</i>	<i>Moved Out</i>	<i>Stayed In</i>	<i>Moved Out</i>
Within Year				
male	1	1	1	1
female	2	0	4	0
Among Years				
male	7	0	3	1
female	5	0	8	3

were some pairs separated by dispersal distances longer than any actually observed on the study area. Limiting the discussion only to those pairs formed by each site with its closest neighboring site yielded 12 pairs (excluding four reciprocal combinations), none of which were connected by draws. These nearest-neighbor pairs were separated by distances ranging from 0.65 to 2.5 km, while the two pairs connected by draws were separated by distances of 1.1 and 2.6 km. Because both connected and unconnected sites were separated by a similar range of distances, this comparison avoided the confounding effect of isolation that Nicholls and Margules (1991) suggest often occurs in studies of the effects of corridors. Considering only these 14 pairs (two connected pairs and 12 unconnected closest pairs), movement occurred 15 times more frequently between connected pairs of sites than between unconnected pairs. From 1985 to 1989, dispersal events occurred on average 2.5 times between the pairs of sites connected by draws (five dispersal events in two pairs of connected sites) but only 0.17 times per pair of nearest-neighbor sites (two dispersal events in 12 pairs of unconnected sites). Dispersal events occurred significantly more often in the two pairs of connected sites than in the 12 pairs of unconnected sites (one-sided Mann-Whitney test, adjusted for ties, median_c = 2.5, median_u = 0, $p < 0.009$). (Actually only one of the dispersal events between unconnected sites did occur between a nearest neighbor pair, but I used the number of nearest neighbor pairs to be conservative.)

This study was originally designed to study dispersal, not necessarily to look at the effects of corridors. Because only two pairs of sites connected by wooded draws occurred on the study area, this comparison does not provide the most definitive evidence that the presence of corridors increases dispersal events between sites. Nevertheless, these results strongly support the hypothesis that wooded corridors channel the movements of birds between wooded habitat patches.

Movements by Young Birds

Return rates of birds banded as nestlings or fledglings differed among species. Sex of nestlings or fledglings could not be determined. Robins returned to the study area at a rate of 9% (33/368), thrashers at a rate of 2% (8/392), and shrikes at a rate of 1% (2/243). The difference between these return rates were statistically significant ($X^2 = 30.5$, d.f. = 2, $p < 0.001$), with most of the difference attributable to the greater return rates of robins.

Movement of fledglings on the study area occurred over a wide range of distances (Table 3). Median dispersal distances of robins were not significantly different from those of thrashers and shrikes (Mann-Whitney tests with thrashers $U = 144.0$, $p = 0.14$; with shrikes $U =$

77.5, $p = 0.81$). Dispersal distances of robin fledglings tended to be intermediate (mean = 1.9 km) between those of thrashers (mean = 0.9) and shrikes (mean = 2.4). Dispersal distances of fledglings were not strongly correlated with time elapsed between banding and recapture (correlation coefficients were 0.33 for thrashers, -0.02 for robins, and 0.28 for shrikes; the null hypothesis of no linear relationship between the variables was not rejected at $\alpha = 0.05$; $Z_{BRTH} = 1.073$, $Z_{AMRO} = -0.042$, $Z_{LOSH} = 0.508$). The mean elapsed time between banding and recapture also did not differ significantly among species (robin mean = 42.5 days, thrasher mean = 35.1 days, shrike mean = 43.3 days; in a t -test for robins versus thrashers, $T = 1.66$, d.f. = 14, $p = 0.12$; for robins versus shrikes, $T = -0.18$, d.f. = 13, $p = 0.86$).

Natal dispersal distances showed a greater range than fledgling dispersal distances, but no returning birds nested in their natal shelterbelts (Table 3). Robins and shrikes had the same median natal dispersal distance (3.5 km) within the study area. Thrashers moved farther than robins (4.9 km), but this difference was only marginally significant (Mann-Whitney $U = 235.0$, $P = 0.09$).

Only one recovery was made off the study area (480 km NW) during the breeding season. Including data from this recovery, the median natal dispersal distance for robins was 3.6 ($n = 21$, range 0.1–480 km).

Conclusions

Although most adult birds usually moved within a shelterbelt, it would be incorrect to assume that longer-distance movements were unimportant. Nine robins switched sites moving one or more kilometers either within or among years. In addition to the birds that switched sites, eight robins and four thrashers moved into (or out of) draws that were not adjacent to their former breeding location. One female robin moved 1.0 km from an isolated site into a draw. Another female robin moved out of a draw to a site 5.2 km away. A female thrasher moved 2.0 km from one draw to another that was not connected with the first. The distribution of dispersal distances of birds on the study area was not

Table 3. Median distance (range) of fledgling movement and natal dispersal on the study area (distances in km).*

Movement Time	Thrasher	Robin	Shrike
Fledgling	0.2 (0–5.4)	1.1 (0–6.3)	1.6 (0–7.7)
Movement	$n = 13$	$n = 10$	$n = 6$
Natal Dispersal	4.9 (3.8–8.9)	3.5 (0.1–9.4)	3.5 (3.2–3.8)
	$n = 5$	$n = 20$	$n = 2$

*Recaptures of fledglings occurred between 21 and 63 days from date of banding. Sample sizes given below distances.

continuous. Most movements occurred within a shelterbelt or site at distances of less than 1 km. The infrequent longer-distance movements would not have been predicted from the distribution of short-distance movements. Skewed distributions of dispersal distances are not unexpected (Murray 1967). A study that found no dispersers in an intensive search of an area within a 1-km radius around the principal study site could therefore be misleading if it claimed that all surviving birds bred on the study area. Barrowclough (1978) made a similar point in his discussion of estimating dispersal distributions from data collected in finite areas.

Occasional long-distance movements can have important effects on the genetics and colonizing ability of populations and should be considered in the development of appropriate habitat-preservation plans and management techniques. Payne (1990) demonstrated that long-distance dispersal events can have large effects on estimates of neighborhood size and effective population size. Studies of bird dispersal conducted in limited areas may seriously underestimate the dispersal distances of birds and therefore underestimate effective population size as well. This is likely to be true especially for returning nestlings, which tend to disperse greater distances than adults (review by Greenwood 1980; Greenwood & Harvey 1982; Payne 1990).

Conservation biologists have applied theories of island biogeography to problems of wildlife reserve design. The inclusion of connecting corridors between reserves has been proposed (Wilson & Willis 1975; Frankel & Soulé 1981). The purpose of these corridors is to allow movement between reserves that would otherwise be isolated. There has been little evidence that organisms actually disperse along corridors at higher rates than they do outside of corridors, and the value of corridors for conservation has been questioned (Simberloff et al. 1992). The importance of such corridors for migratory birds has seemed especially doubtful, for these species fly over large expanses of unsuitable nesting habitat on an annual basis to reach their breeding grounds. One would assume that such species would be able to move over unsuitable habitat on the migration route to reach other suitable habitat on the breeding grounds. Contrary to that expectation, the results of this study indicate that the wooded draws that connect planted sites on the study area are important stepping stones and may function as local travel lanes for robins and thrashers. This is especially interesting because these are both birds of relatively open country. Birds that breed in small woodlots on the prairie might be expected to be less dependent on wooded travel routes than species that breed only in large tracts of mature forest. It is important to note, however, that my observations of dispersal events of 1 to 5 km between unconnected patches of wooded habitat demonstrate that corridors are not essential for dispersal.

Experimental designs for studies to test the importance of corridors have been proposed by Nicholls and Margules (1991) and critiqued and elaborated upon by Inglis and Underwood (1992). Both studies acknowledge the extreme logistical and statistical difficulties involved in studying the use of dispersal corridors by looking at the rate of recolonization of patches, an indirect but important measure of dispersal. Because I collected data from marked individuals as they moved among habitat patches on a large study area, I was able to tabulate and compare actual dispersal events. Although I did not manipulate habitat to conduct a controlled experiment, the connected and unconnected sites resembled each other in all but their connectedness. Shelterbelts are not natural habitats, and because they are all planted for the same purpose, they are quite similar in plant-species composition, spacing, and tree height (Martin 1981; Haas 1990). Connected and unconnected site pairs were separated from each other by a similar range of distances. Connected and unconnected sites had the same range of total wooded area, although connected sites were on average slightly larger (1.9 ha mean area compared to 1.7 ha, respectively). My results constitute strong evidence that connecting corridors may be important in "leading" birds between isolated reserves. Behavioral data to support this result were found in a study of birds moving between woodlots and fencerows in Ontario farmland (Wegner & Merriam 1979). Although this study has demonstrated that birds do preferentially disperse between patches connected by wooded corridors, the role of differential dispersal in the persistence of populations is unknown.

The three species show different degrees of natal-site fidelity. These differences may result from differential mortality or differential dispersal. Relatively little is known about natal-site fidelity in passerines or about the movements of fledglings before their first winter. Because the return rates of passerines banded as nestlings tend to be low (summary in Farner 1945), there has been some speculation that second-year birds of many species are not faithful to their natal sites. Band-recovery studies show, however, that second-year birds do not disperse randomly throughout the species' range to their first breeding site but rather are more likely to occur within a certain distance of their natal site (Farner 1945; Werth 1947; summary in Greenwood & Harvey 1982). If young birds move off their natal territory before their first winter, it is possible that they would be faithful not to their natal site but to sites they occupied as fledglings. This has been demonstrated in a nonmigratory population of Black-capped Chickadees (*Parus atricapillus*) (Weise & Meyer 1979). Bufflehead (*Bucephala albeola*) and Common and Barrow's Goldeneye (*Bucephala clangula* and *B. islandica*) prospect for nest sites as yearlings in the late summer of the year before they reach breeding age and return to breed within 1.5

km of where they were marked as ducklings, some within 100 meters of the nest boxes they visited (Eadie & Gauthier 1985). Brewer and Harrison (1975) suggested that prospecting for breeding sites in late summer or early fall might be the typical pattern for young migratory birds. If this were the case, we would expect birds that dispersed long distances as fledglings to breed farther from their natal site and birds that remained close to the natal site as fledglings to breed close to the natal site. Such a pattern is supported by information on movements and return rates of White-crowned Sparrows (*Zonotrichia leucophrys*) (Morton 1992). Comparisons of distances moved by each of the three species in this study as fledglings and their natal dispersal distances lend no support for the hypothesis that young may be faithful to sites they occupied as fledglings rather than to the natal territory.

Because of the difficulties inherent in its study, the dispersal of migratory passerines has been a relatively neglected area of research. Further research on dispersal could yield important advances in our understanding of behavior, population dynamics, population genetics, and conservation of birds. Especially important are studies of dispersal linked to other behavioral or ecological phenomena. In the Sioux County population of thrashers, for example, although wooded draws seem beneficial as dispersal corridors, the breeding success of thrashers was higher in isolated sites than in sites adjacent to wooded draws (Haas 1990). Further research is necessary before we can accurately weigh the benefits and costs of habitat or population management practices.

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