EFFECTS OF THE LANDSCAPE ON SHOREBIRD MOVEMENTS AT SPRING MIGRATION STOPOVERS[1]

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Abstract. We monitored the inter-wetland movements of 115 radio-tagged Pectoral Sandpipers (*Calidris melanotos*) at three migration stopovers in the Great Plains of North America during April and May from 1992 to 1995. While resident at a stopover, individuals were very localized in their movements. Over 40% of the birds made no inter-wetland movements, and over 90% of individuals moved less than 10 km from their original release site. Characteristics of wetlands where birds were released did not affect bird movements. However, the structure of the surrounding landscape explained up to 46% of variation in individual bird movements. As the distance between wetlands decreased, and the proportion of the landscape composed of wetlands increased, individual birds moved between wetlands more frequently and moved longer distances from their release site. These movement patterns indicate that a more connected landscape allows shorebirds to exploit more feeding sites with reduced searching costs; a result consistent with foraging theory. We estimate a degree of landscape connectivity at which a wetland complex functions as a single large wetland as measured by sandpiper feeding patterns. Our data provide support for the idea that complexes of small, closely spaced wetlands can be important migration stopovers and may have significant conservation value.

Key words: *migration, stopover, shorebird, landscape, foraging behavior, conservation*, Calidris melanotos.

INTRODUCTION

Migration "stopovers" provide a crucial link between wintering and breeding areas for migratory birds. Food obtained at stopovers provides energy for continued migratory flight and nutritional reserves that may be essential for successful reproduction upon arrival at the breeding grounds (Ricklefs 1974, Davidson and Evans 1988). Shorebirds and other migratory species that depend on wetland stopovers in North America are being challenged by a rapidly changing landscape. In the Great Plains of North America, for example, 90% of the wetlands in some areas have been lost to agricultural development since the early 1900's (U.S. Department of the Interior 1994, Ducks Unlimited 1994). Furthermore, wetlands may be altered in the future by global warming (Houghton et al. 1990, Poiani and Johnson 1991). Such large-scale habitat changes raise concerns about maintaining an adequate network of stopover habitats in the future.

Ensuring adequate migration stopovers in the future is complicated because there are several concepts associated with the term stopover. For Sandhill Cranes (*Grus canadensis*), Melvin and Temple (1982) define two types of stopovers based on site fidelity and temporal factors. "Traditional " stopovers are medially aligned in the migration route, used in successive years, and occupied for extended periods each year. "Nontraditional" stopovers are selected opportunistically at the end of each day's flight, may not be used every year, and are used only for short periods. On the other hand, the Western Hemisphere Shorebird Reserve Network defines several types of stopovers based on the

numbers of shorebirds that annually use an area (Myers et al. 1987). A "hemispheric" site harbors more than 250,000 birds or at least 30% of a population, whereas a "regional" site has more than 20,000 birds or 5% of a population. Stopovers also have been defined for shorebirds based on an individual's length of stay. Hands (1988) defines shorebird "staging" areas as those where birds spend extended periods of time and during which considerable fat gains occur. "Resting" areas are used for shorter periods and birds accumulate less fat. However, Hands acknowledges that these definitions were somewhat arbitrary because they merely represent points along a continuum of possible stopover durations.

The stopover concept also has been applied at different spatial scales and different levels of biological organization. The term has been used to describe relatively large geographic areas that are important to shorebird populations on a hemispheric scale (Senner and Howe 1984, Myers et al. 1987). Examples include Delaware Bay for Red Knots (*Calidris canutus*) (Myers 1986), Iceland for Nearctic waders and geese (Alerstam and Jonnson 1986), and the Copper River Delta for Western Sandpipers (*Calidris mauri*) (Senner 1979). These large wetland areas provide abundant food for thousands of shorebirds, although the spatial location of food patches within the areas may vary annually. At a small spatial scale, stopovers have been defined as the area used by an individual bird during a refueling stop (LaGrange and Dinsmore 1989, Gruenhagen and Fredrickson 1990). At this scale, the spatial distribution of food patches affects the energy expenditure required in searching for food and the rate at which individuals replenish their energy reserves.

In this paper, we focus on the small spatial scale and analyze local movements of individual Pectoral Sandpipers (*Calidris melanotos*) at three spring migration stopovers in the Great Plains of North America. Our goals are to characterize individual shorebird movements while they refuel at a stopover, and to investigate the association between bird movements and the landscape.

STUDY AREAS

Pectoral Sandpipers were radio-tagged during April and May in Texas (1992-1993), Missouri (1993-1995), and Nebraska (1994). The Texas site is one of the first stopovers used by Pectoral Sandpipers when they arrive in North America in early spring. The Missouri and Nebraska sites are situated just south of a major physiographic transition in wetland density, at the southern edge of the prairie pothole region.

The Texas site is in Chambers County south of the town of Anahuac, about 80 km east of Galveston ($29^0 40'$ N, $94^0 30'$ W). The site encompasses the Anuahac National Wildlife Refuge and surrounding private lands. Historically, this area was part of a tall-grass prairie ecosystem (Hobaugh et al. 1989); however, it has been extensively converted to rice farming, and rice fields are now the dominant landscape feature. Thousands of shorebirds use these rice fields during the spring migration, which coincides with the flooding of fields for the planting of rice. During the spring, a given field may provide shorebird habitat for a period of 1-3 weeks while it is being irrigated and seeded. A rice field is planted to rice during one year and then lies fallow for up to three years. Thus, the abundance and specific location of suitable shorebird habitat changes from year to year.

The Missouri site is located in northwestern Missouri along the Missouri River about 50 km north of St. Joseph and west of Mound City ($40^0 10'$ N, $95^0 15'$ W). The site encompasses the Squaw Creek National Wildlife Refuge and surrounding State and private lands. Although many of the historical wetlands have been converted to farmland, the area contains a number of man-made wetlands managed

specifically for waterfowl and shorebirds. These managed wetlands, especially on the Squaw Creek National Wildlife Refuge, provide some shorebird habitat in all years. Additionally, the area contains "sheetwater" wetlands (LaGrange and Dinsmore 1989) that are abundant during periods of above-average precipitation, as was the case during the springs of 1993 and 1995.

The Nebraska study site lies in southeastern Nebraska in York and Clay Counties ($40^0 30'$ N, $97^0 45'$ W). The area is the eastern portion of the Rainwater Basin, an extensive area of natural wetlands that historically occurred across the southern half of the State (Erickson and Leslie 1987). The Rainwater Basin once contained about 4,000 individual wetlands, but agricultural drainage has reduced the number to less than 400 (Nebraska Game and Parks Commission 1984). Nevertheless, the area remains an important spring stopover for waterfowl, cranes, and shorebirds. Many of the larger wetlands in the study area are owned and managed by the U.S. Fish and Wildlife Service or the Nebraska Game and Parks Commission. Many of the smaller wetland basins are on private land and, depending on previous management history, provide excellent spring shorebird habitat.

METHODS
BIRD MOVEMENTS
We used mist nets to capture Pectoral Sandpipers in wetland-edge areas where they were feeding (Table 1). We attached 1.5-g radio transmitters to selected birds with Titan quick-drying epoxy cement, using a modification of Raim's (1978) procedure. We aimed to attach transmitters to 20 females per year at each site, and to select these birds across the observed range of body fat. When the transmitters were firmly attached, birds were released at the capture point and visually monitored to insure they returned to normal feeding behavior. Transmitters had a battery life of 40 days, and a range of about 2 km from ground level and about 15 km from an aircraft altitude of 1,500 m.

Radio-tagged birds were relocated by searching the study areas from vehicles. Each bird's radio signal was located twice daily until it left the study area. The first daily observation was generally between 08:00 and 10:00, and the second generally between 16:00 and 18:00. Radio locations were made from a distance so that radio-tagged birds were not disturbed. However, we obtained a visual sighting if a radio signal remained constant for several observation periods to verify that the bird was in satisfactory condition with the transmitter in place.

When a bird's signal was lost from the ground, we searched from aircraft (Gilmer et al. 1981). Aerial searching was conducted from about 1,500 m altitude along parallel transects to insure complete coverage within a 50-km radius of the bird's last known location. If a bird was located from the air, the location was recorded and further ground tracking resumed from that point. If the bird was not located within a 50-km radius, it was assumed to have left the study area.

Bird locations were recorded in the field as being within a particular wetland. At a later date, the observed bird locations were plotted on USGS topographical maps (1:24,000) for Texas and Nebraska, and on State Department of Transportation maps (1:126,720) for Missouri.   We plotted bird locations at standard reference points defined within each wetland. For large wetlands (greater than 0.5 km in length or width [25 ha]) bird locations were plotted at the nearest of four standard points, systematically chosen at the wetland edge in each of the principal compass directions (i.e., north, south, east, and west sides). In smaller wetlands, birds were assumed to be at the centroid of the wetland.

We computed several inter-wetland movement statistics for each individual bird based on plotted locations. Distance moved (DM) was the inter-wetland distance moved between observations.

Frequency of movement (FM) was calculated as the number of times a bird moved to a new wetland between observations divided by the number of observation periods (OBS) for that bird. When a bird changed wetlands between consecutive observations, the distance moved was measured as the Euclidean distance between consecutive locations to the nearest 0.4 km. Longest movement (LM) was the longest inter-wetland distance moved by an individual between any two observations. Farthest distance (FD) was the farthest a bird was ever observed from its original release site before leaving the study area.

LANDSCAPE MEASUREMENT AND ANALYSIS

Habitat maps for the three study areas were digitized to produce a digital map, or "coverage" of the landscape using ARC/INFO (Environmental Systems Research Institute 1995). A coverage was created for each site-year; thus, there were a total of six coverages (Texas 1992-1993; Missouri 1993-1995; Nebraska 1994). The aerial extent of each coverage included the ground area considered to be our study site for purposes of capturing birds, plus additional areas visited by radio-tagged birds.

We created coverages that represented actual habitat conditions each spring, but the procedures for developing coverages varied. In Texas, we conducted extensive, weekly ground surveys to identify newly flooded rice fields. U.S. Geological Survey (USGS) color infrared aerial photographs (1:40,000) were used to identify the boundaries of flooded rice fields which were then delineated on USGS base maps (1:24,000). In Nebraska, we started with National Wetlands Inventory (NWI) maps (1:24,000), visited each mapped wetland, and modified the NWI maps to show only those wetlands which provided some suitable habitat during the spring of 1994. In Missouri, we used Landsat photographic images (1:250,000) taken during the spring, and combined them with seasonal habitat maps to produce the coverages. Wetland conditions changed throughout the spring study period, but individual wetlands usually maintained some suitable microhabitats.

The coverages consisted of only one cover type, wetland, interspersed in an upland matrix. The upland matrix, an aggregate of all unsuitable Pectoral Sandpiper habitat, was treated as background and not used for analysis. The wetland type consisted of all wet areas including palustrine wetlands, moist soil management areas, rice fields, and sheetwater wetlands that contained some suitable feeding habitat. Feeding occurs in wetland-edge microhabitats, including moist and saturated soils with water depths # 2.5 cm. Pectoral Sandpipers will use, and sometimes seem to prefer, vegetated areas so long as the vegetation does not exceed about 0.1 m in height.

Delineating the boundary of individual wetlands was a straightforward process. However, in a few cases a wetland was bisected by earthen dikes (e.g., rice fields, man-made moist soil impoundments), splitting it into discrete parts. We delineated separate wetlands only when the physical separations were at least as wide as a one-lane gravel road.

The Fragstats (McGarigal and Marks 1993) statistical package was used to characterize landscape patterns (Turner 1989), treating each wetland as a single patch. For each of the coverages, we computed several metrics pertaining to the individual wetlands where birds were released (patch area, shape index, fractal dimension) and to the surrounding landscape (mean patch size, patch density, mean nearest-neighbor distance, landscape similarity index, mean shape index, mean fractal dimension, and mean proximity index). These landscape metrics were paired with the bird-movement statistics (FM, LM, FD) data for each of the site-years. The paired data were analyzed using multiple linear regression to model variation in bird-movements as a function of landscape metrics.

RESULTS

BIRD MOVEMENTS

We collected location data distributed over 6 site-years on 115 radio-tagged Pectoral Sandpipers. Location data were collected on each bird while it was within a 50-km radius around its release site. However, there was some uncertainty in determining when a bird actually departed because there was a time lag between when a bird was lost from the ground and when a follow up telemetry flight occurred. This time lag ranged from 0 to 8 days ($\bar{x}$ = 1.7 days). However, for the 90 birds that had follow up telemetry flights, only 9 were found again within a 50-km radius. Thus, ground searching was effective in maintaining contact with radio-marked birds, and when a bird was lost from the ground it was generally because it had moved more than 50 km.

While in the study area, individual Pectoral Sandpipers were very localized in their movements at spring migration stopovers. In over 80% of all observations, birds made no inter-wetland movements (Fig. 1a). Forty percent of the individuals made no inter-wetland movements during their residence, 30% moved < 30%, and the remaining 30% moved between 30% and 60% (Fig. 1b).

Although some individuals moved frequently, the distances tended to be relatively short. About 90% of the birds never traveled more than 10 km between observations (Fig. 1c). Moreover, over 90% of the radio-tagged birds never were observed more than 10 km from their original release site (Fig. 1d).

Bird-movement statistics varied with the length of time a bird remained in the study area, as measured by the number of observations. We found that the number of observations was correlated with longest movement ($r = 0.43$; $P = 0.03$) and farthest distance moved ($r = 0.53$, $P < 0.01$). However, the number of observations was not correlated with frequency of movement ($r = -0.07$, $P = 0.72$).

LANDSCAPE CHARACTERISTICS

The six site-years represented a spectrum of landscape conditions (Fig. 2). The differences between site-years are characterized (Fig. 3) by four landscape metrics: (1) mean nearest-neighbor distance (MNN) is the Euclidian distance (km) from the perimeter of each wetland to its closest neighbor's perimeter, (2) mean patch size (MPS) is the average area (ha) of individual wetlands, (3) patch density is the number of individual wetlands (wetlands/km^2), and (4) landscape similarity (LSIM) is wetland abundance measured as a percentage of the total area. The 1993 and 1995 Missouri coverages reflect abnormally high precipitation during those years which created a landscape with a large wetland component (LSIM), composed of small wetlands (MPS) spaced relatively close together (MNN). Missouri and Nebraska in 1994 had approximately median values for LSIM, PD, and MNN. The Texas coverages represent the other extreme, with a relatively large MPS and a high MNN, with wetlands covering a relatively smaller percentage (LSIM) of the landscape.

For purposes of modeling bird movements, however, we computed landscape statistics within circular areas of 10-km radius centered on the centroid of wetlands ($n = 27$) where radio-tagged birds were released. These circular areas represented only a portion of the corresponding study areas. However, Wiens et al. (1986) proposed that a proper scale for landscape analysis is defined by the cruising range of an individual or group of individuals in the performance of a particular function. Thus,

10-km sampling units were chosen for landscape analysis because over 90% of the birds were located less than 10 km from their release sites while resident at the stopover.

RELATIONSHIPS BETWEEN THE LANDSCAPE AND BIRD MOVEMENTS
We modeled bird movements as a function of landscape metrics; however, bird movements were not directly comparable because the number of observations per bird differed among release sites. To minimize the confounding effect of the number of observations on bird movement statistics, we included the number of observations as a covariate in analyses for longest movement (LM) and farthest distance (FD). Individual bird statistics were pooled by release site, and we used calculated mean values for number of observations, frequency of movement, longest movement, and farthest distance.

Bird movements were not correlated with characteristics of the wetlands where radio-tagged birds were released. Wetlands where birds were released ranged in size from 1.7 to 547 ha ($\bar{x}$ = 66 ha), but size was not related to FM ($P = 0.89$), LM ($P = 0.83$), or FD ($P = 0.72$). The wetland shape index varied from 1.08 to 2.7 ($\bar{x}$ = 1.47), but was not related to FM ($P = 0.75$), LM ($P = 0.89$), or FD ($P = 0.80$). Release wetlands had fractal dimensions from 1.01 to 1.13 ($\bar{x}$ = 1.06), but this metric had no effect on FM ($P = 0.46$), LM ($P = 0.77$), or FD ($P = 0.67$).

Much of the variability in inter-wetland movements among radio-tagged birds was explained by variation in landscape patterns within 10 km of the release sites. Each of seven landscape metrics that we initially computed were correlated with bird movements, but these metrics were not independent of one another. Two shape metrics (mean shape index and mean fractal dimension) were inter-correlated with MNN and PD metrics because Missouri landscapes had higher densities of closely spaced wetlands which also tended to be irregular in shape (Fig. 2). We dropped these shape metrics from further analyses because we believed that MNN and PD provided a better biological explanation of inter-wetland bird movements. Mean proximity index also was eliminated from further analyses because it was a mathematical function of first-order metrics, patch area and inter-patch distance, and we wished to perform the analyses on the more basic measurements. The four remaining landscape metrics (Fig. 3) analyzed with the bird movement data also were not independent of one another. Correlations were evident between PD and LSIM ($r = 0.87$, $P < 0.001$) and also between MPS and MNN ($r = 0.71$, $P < 0.001$) (Fig. 3). Thus, we used a forward selection approach to build regression models.

The best single predictor of frequency of movement was LSIM ($R^2 = 0.27$, $P < 0.006$) (Fig. 4a) When additional variables were considered, a two-variable model incorporating MNN explained a small amount of additional variance ($R^2 = 0.28$, $P = 0.02$). Adding PD or MPS to the model explained relatively little additional variation in frequency of movement. Although not immediately obvious, this result has a straightforward interpretation. In this study, landscapes with a relatively high LSIM also had a high PD and a low MNN. Thus, birds made more frequent inter-wetland movements where there were more wetlands, spaced more closely together, and that collectively occupied a larger proportion of the landscape (FM = 7.847 + 3.136LSIM - 0.006MNN).

The best single predictor of farthest distance was PD ($R^2 = 0.41$, $P = 0.002$) (Fig. 4b). When additional variables were considered, a two-variable model including MPS explained a small amount of additional variance ($R^2 = 0.42$, $P = 0.005$). Adding either of the other variables explained little of the remaining variation. The coefficient for PD was positive. Thus, birds did not respond to lower patch

densities by traveling farther. Instead, they traveled shorter distances as the number of wetlands declined and wetlands became more dispersed in the landscape (FD = 1.893 + 0.114OBS + 14.142PD - 0.04MPS).

The relationships for longest movement were similar to those of farthest distance. The best single predictor of longest movement was PD (R^2 = 0.46, P = 0.001) and a two variable model including MPS explained a small amount of additional variance (R^2 = 0.47, P = 0.002; LM = 0.588 + 0.167OBS + 14.003PD - 0.020MPS).

LIMITS OF BEHAVIORAL RESPONSE TO LANDSCAPE

The preceding results show that as the landscape becomes more connected, in terms of having more wetlands spaced more closely together, birds moved more frequently between wetlands. What are the limits to this response? We hypothesize that as the distance between wetlands decreases, there is a point at which the birds begin to perceive the complex as though it were a single large wetland. Conversely, as distance between wetlands increases, there is a point at which inter-wetland movements virtually cease, and the wetlands no longer form an interacting complex from the perspective of individual Pectoral Sandpipers. We analyzed our most connected and least connected sites in an attempt to estimate these conditions.

First, we analyzed our movement data for several radio-tagged birds (n = 12) that were released in relatively large wetlands and made no inter-wetland movements while in residence. Their frequency of intra-wetland movement between reference points in their home wetland was relatively high (27.6%). This estimate is similar to the frequency of inter-wetland movements (32.9%) in Missouri 1995, the most connected landscape in our study. Therefore, the Missouri 1995 landscape (LSIM = 7%; PD= 0.33 km^{-2} ; and MNN = 200 m) may approximate conditions at which Pectoral Sandpipers perceive a wetland complex as functionally connected.

Second, we used data from the most disconnected landscape in our study, Texas in 1992. The 20 birds that were radio-tagged at five release sites had an average frequency of movement of 8%. Thus, even our most disconnected landscape still had some inter-wetland movement, although the frequency of movement was low. Therefore, wetlands would not be functionally isolated, from the perspective of Pectoral Sandpipers, until the landscape is more disconnected than Texas in 1992; or LSIM < 3%; PD < 0.056 km^{-2}; and MNN > 1100 m.

DISCUSSION

Our data illustrate the influence of landscape structure on the movement behaviors of shorebirds. However, birds also may be responding to other factors not taken into account, for example wetland quality (e.g., food availability). Wetland quality most certainly affects bird-movement patterns, and variation in wetland quality is a likely source of error in our analysis. Because wetland quality was not included, our analysis is potentially confounded by inherent differences in wetland quality that may have occurred between site-years. However, relationships between wetland distribution and bird movements also were evident within study sites, further suggesting that landscape pattern does have a significant influence on bird movements independent of wetland quality.

Our results show that landscape structure accounts for up to 46% of the variance in bird movements, but this may be an overestimate of the importance of landscape structure. The 10-km radius sampling units were not mutually exclusive; the wetlands on which they were centered were close enough such that the sampling units overlapped to varying degrees. Thus, the sampling units were not

independent, but we could not model the degree of dependence due to the heterogeneity of the landscape on a larger scale. A possible consequence of the lack of independence is to have artifactually reduced the sample variance and P-values.

The landscape metrics that we computed were correlated with one another; some were related mathematically, and others changed simultaneously due to site characteristics. If one looks at the differences between Texas in 1992 and Missouri in 1995 (Fig. 2), it becomes clear that Missouri had a higher wetland density, but also had wetlands that were smaller with higher edge/area ratios. We could not draw inferences about whether any particular landscape metric was most responsible for influencing bird movements, although it is possible that sandpipers were not responding to any single landscape attribute, but to a suite of characteristics.

Why do shorebird movement patterns at a stopover change in response to the landscape? Pectoral Sandpipers typically feed and roost in the same wetland. Therefore, the inter-wetland movements that we observed represented a shift of their daily center of activity, presumably associated with the continual search for food. In this sense, movements between wetlands within a landscape have the same ecological function as movements between food patches. Invertebrate densities are highly variable in space and time (Buchmann 1967, Resh 1979, Rosillon 1989), and foraging by conspecifics can rapidly deplete local invertebrate densities (Helmers 1991). Foraging theory (Charnov 1976, Pyke 1983) suggests that it is adaptive for individual shorebirds to move in search of higher prey densities as local prey is depleted. As the distance between wetlands decreases, the number of food patches that can be exploited by an individual bird increases. Moreover, movements are energetically costly, and a highly connected landscape allows shorebirds to exploit higher quality food patches while minimizing the energetic costs of searching.

However, as wetlands spacing increases, Pectoral Sandpipers do not respond by making longer foraging flights. Just the opposite occurs. Spacing wetlands farther apart not only reduces movement frequency, but also reduces the distances moved. Thus, as the landscape becomes more disconnected, it begins to constrain feeding opportunities by altering movement behavior in favor of a more sedentary nature.

The behavioral response of Pectoral Sandpipers to the landscape underscores the importance of landscape connectivity in determining the quality of a migration stopover. Individual wetlands (and invertebrates within them) must be distributed so that individuals can achieve relatively high ingestion rates for low energetic costs of searching. Thus, an area must meet at least two criteria to become an important stopover: (1) it must provide sufficient food for the population as a whole and (2) the food must be distributed to meet the needs of individual birds on a small scale. Each of our study areas met the second criterion to varying degrees. At one extreme, the low frequency of inter-wetland movements in Texas during 1992 indicated a landscape that was approaching the point of being disconnected, as measured by the behavior of Pectoral Sandpipers that had stopped there to refuel. We suspect these conditions may partially explain the relatively short period of time birds stayed at the Texas stopover. As a rice field begins to decline in food quality, it may be better to continue migration to the next stopover rather than expending time and energy searching for food in a dispersed landscape. At the other extreme, the Missouri flood plain was a highly connected wetland landscape and potentially a very important stopover area, especially during wet springs such as 1993 and 1995.

Traditionally, however, shorebird stopover sites receiving the most recognition, and consequently the most conservation support, have been those that provide habitat for large numbers of shorebirds at

one viewing location (Myers 1983, Myers et al. 1987, Castro et al. 1990). Conservation of these highly visible areas is necessary, but may not be sufficient to meet population needs. Complexes of small, closely spaced wetlands and sheetwater areas such as the Missouri River floodplain may be just as important to some shorebird species on an annual basis as more contiguous wetland areas (Skagen and Knopf 1994). If shorebirds can recognize and utilize a group of disjunct wetlands in the same way they would a single, large wetland, it seems appropriate for us to approach wetland conservation in the same manner.

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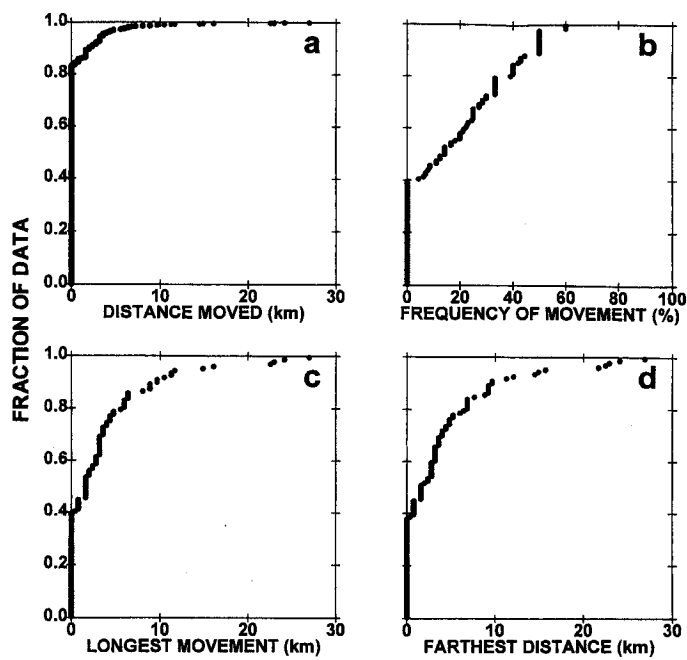
FIGURE 1. Cumulative frequency distributions of bird movement: (a) distance moved between observation periods for all birds combined, (b) frequency of movement by individual birds, (c) longest movement between any two observations by individual birds, and (d) farthest distance moved from initial release site by individual birds.
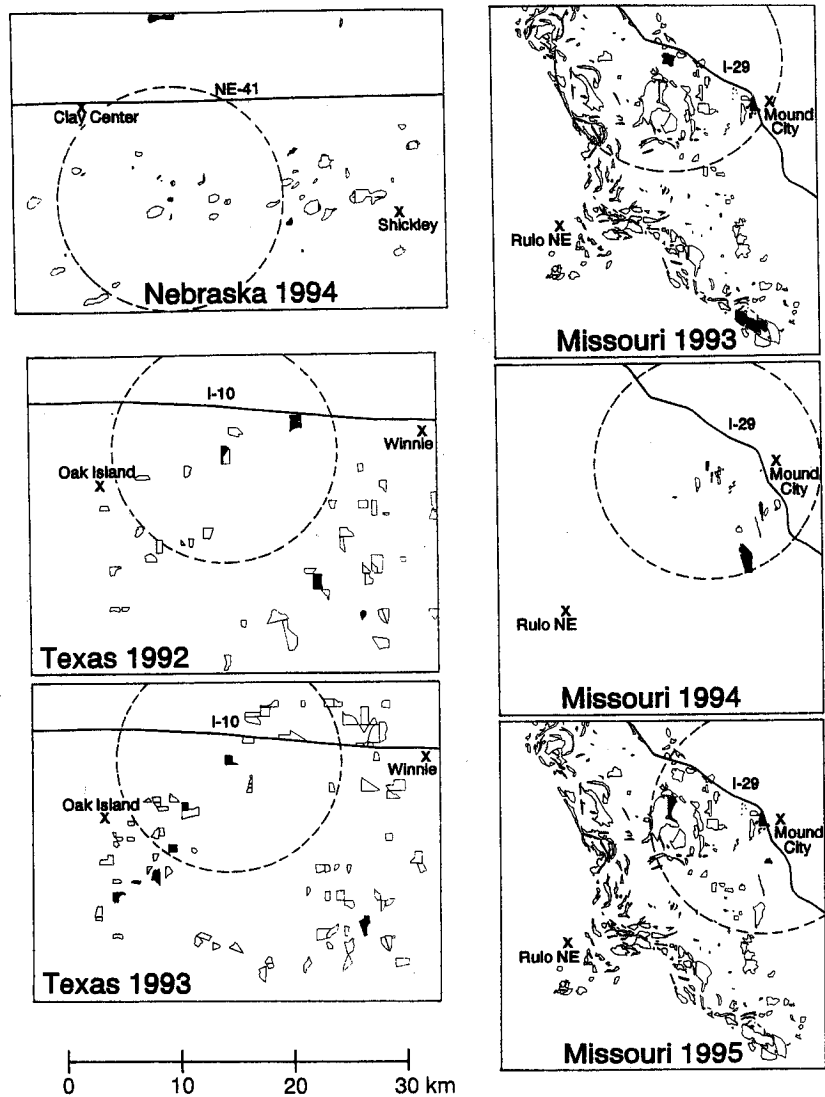
FIGURE 2. Habitat maps for the central portion of each of the six site-years. Wetlands boundaries are outlined and wetlands where radio-tagged birds were released are shaded. An example 10-km landscape sampling unit is shown for each site-year.
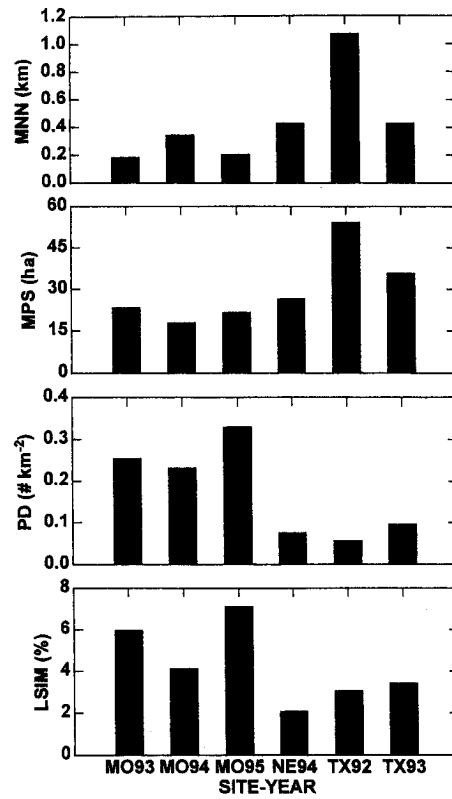
FIGURE 3. Landscape metrics for six site-years. Maximum values were: LSIM = 7.11% (Missouri 1995); PD = 0.33 km^{-2} (Missouri 1995); MPS = 54.18 ha (Texas 1992); MNN = 1.07 km (Texas 1992).
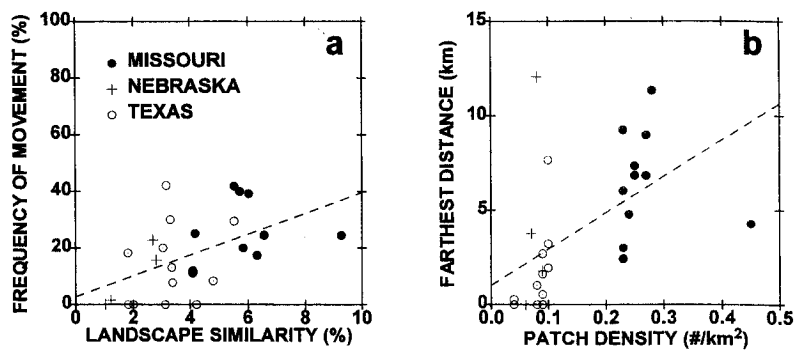
FIGURE 4. Bird movements versus landscape metrics for 27 release sites: (a) frequency of movement versus landscape similarity, and (b) farthest distance moved from release site versus patch density.

TABLE 1. Summary of radio-tagged bird data.

State	Year	Number of release sites	Number of individuals	Number of observations
Missouri	1993	4	22	187
Missouri	1994	4	21	248
Missouri	1995	3	16	176
Nebraska	1994	4	20	354
Texas	1992	5	20	72
Texas	1993	7	16	85
Total		27	115	1,122