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ANALYSIS OF PREDATOR MOVEMENT IN PRAIRIE LANDSCAPES WITH CONTRASTING GRASSLAND COMPOSITION

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Mammalian predation influences waterfowl breeding success in the U.S. northern Great Plains, yet little is known about the influence of the landscape on the ability of predators to find waterfowl nests. We used radiotelemetry to record nightly movements of red foxes (*Vulpes vulpes*) and striped skunks (*Mephitis mephitis*) in two 41.4-km^2 study areas in North Dakota. Study areas contained either 15–20% grassland (low grassland composition) or 45–55% grassland (high grassland composition). Grasslands included planted cover, pastureland, and hayland. We predicted that the type and composition of cover types in the landscape would influence both predator movement across the landscape (as measured by the fractal dimension and displacement ratio) as well as localized movement (as measured by the rate of movement and turning angle between locations) within patches of different cover types. Red fox movements were straighter (lower fractal dimensions and higher displacements) across landscapes with a low grassland composition, indicating directed movement between the more isolated patches of planted cover. Striped skunk movements did not differ between landscape types, illustrating their movement along wetland edges, which had similar compositions in both landscape types. The high variability in turning angles by red fox in planted cover and pastureland in both landscape types is consistent with restricted-area foraging. The high rate of movement by red foxes in planted cover and by striped skunks in wetland edges suggests that spatial memory may influence movement patterns. Understanding the behavior of predators in fragmented prairie landscape is essential for managing breeding habitat for grassland birds and for predicting the spatial and temporal dynamics of predators and their prey.

Key words: fractal dimension, landscape composition, *Mephitis mephitis*, movement, North Dakota, predation, red fox, striped skunk, *Vulpes vulpes*, waterfowl

Understanding animal movement is fundamental to interpreting spatial–temporal patterns of habitat selection, foraging behavior, and the interactions between predator and prey (Bell 1991; Stenseth and Lidicker 1992; Swingland and Greenwood 1983). Animal movements are influenced by intrinsic physiological factors (e.g., hunger and reproduction) and the sensory capabilities of organisms (Bell 1991; Zollner and Lima 1997). They are also influenced by extrinsic factors, such as spatial structure of the landscape (Burrough 1981; Kotliar and Wiens 1990; Palmer 1988). Movement patterns are influenced by heterogeneity and composition of cover types in the landscape for both invertebrates (Crist et al. 1992; Crist and Wiens 1994; Wiens et al. 1995; Wiens and Milne 1989; With 1994) and vertebrates (Bascompte and Vila 1997; Edwards et al. 2001; Etzenhouser et al. 1998; Ferguson et al. 1996, 1998). Spatial structure will influence movement as long as there is a perceived difference in quality of the varying cover types as individuals search for resources such as food, mates, or den sites or use different cover types to avoid intraspecific and interspecific agonistic encounters (Kotliar and Wiens 1990; Zollner and Lima 1997).

Grasslands in the prairie pothole region are productive waterfowl breeding habitat (Batt et al. 1989; Bellrose 1980), and mammalian predation is a major factor influencing waterfowl nest success in the region (Johnson et al. 1989; Klett et al. 1988; Sargeant and Raveling 1992; Sargeant et al. 1993). Dramatic loss and fragmentation of grasslands as a result of agricultural practices in the prairie pothole region (Batt et al. 1989; Sugden and Beyersbergen 1984) have very likely altered predator movement both between and within patches of

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grassland and therefore influenced the rate of waterfowl predation.

Foraging theory provides a framework to make predictions about the effect of landscape composition on the interactions between nesting waterfowl and predators in the prairie pothole region of central North Dakota. The theory assumes that behaviors are governed by decision rules whereby a predator maximizes its rate of intake of some currency, such as the encounter rate with prey (Charnov 1976; Emlen 1966; MacArthur and Pianka 1966; Schoener 1971). Foraging theory recognizes the importance of the rate of return of resources within patches and the distribution of discrete patches of required resources on predator movement. The greater the rate of return of resources within a cover type, the more time a predator will spend foraging in that cover type. The greater the distance between patches in the landscape, the more energy a predator must invest in traveling between patches and, therefore, the more time a predator will spend in a patch. Assuming a predator perceives a greater reward of resources in patches of grassland than in agricultural fields, predator movement will be faster and straighter as it moves through agricultural fields toward a patch of grassland. Once within a grassland patch, a predator will increase its foraging efficiency by moving in a more tortuous manner and will move more slowly as it spends more time foraging than traveling.

We examined the movement patterns of red foxes (*Vulpes vulpes*) and striped skunks (*Mephitis mephitis*) in North Dakota landscapes with contrasting grassland composition. Grasslands and wetland edges contain food resources that are attractive to both red foxes and striped skunks (Larivière and Messier 2000; Pasitschniak-Arts and Messier 1998). Previous analyses of movement data indicate that the composition of grassland in the landscape influences selection of planted cover by red foxes (Phillips et al. 2003). Red foxes exhibit a low selection for the interior areas of planted cover in landscapes with a high grassland composition. Striped skunks are attracted to wetland edges that are surrounded by agricultural fields and do not exhibit a strong selection for grassland (Phillips et al. 2003).

Our objective was to examine how movement patterns are influenced by the composition of grassland in the landscape. We examined both movement across the landscape (as measured by the fractal dimension and displacement ratio) as well as localized movement (as measured by the rate of movement and turning angle between successive radiotelemetry locations) within patches of different cover types. A fractal dimension is a useful index to compare species from different taxa as well as to compare the effect of landscape heterogeneity on movement pathways (Wiens et al. 1995; With 1994).

We predicted that movement pathways of red foxes would be straighter and displacements greater across landscapes with a low composition of grassland as they moved longer distances between isolated patches of grassland. In landscapes with a high composition of grassland, red foxes need not travel long distances to find resources, and therefore their overall movement pathways should be more tortuous and displacements smaller. The movement pathways of striped skunks will depend more on the distribution of wetland edges in the landscape and therefore will not be a function of grassland composition in the landscape.

We predicted that localized movement patterns of red foxes and striped skunks would reflect the behavioral response by predators to different resources in patches of grassland or wetland edges compared to surrounding agricultural fields. We expected predators to move more slowly with large turning angles between successive radiotelemetry locations in patches of grassland or wetland edges (characteristic of foraging behavior) in contrast to faster movement with smaller turning angles (more directed movement characteristic of traveling) across agricultural fields.

Materials and Methods

Study Areas

In each of the 2 years, 1996 and 1997, we selected two 41.4-km^2 study areas with contrasting amounts of grassland (defined as planted cover, pastureland, and hayland) in the prairie pothole region of central North Dakota. We selected study areas with a low grassland composition in Litchville, North Dakota (Svea Township in Barnes County), in 1996 and in Bowdon, North Dakota (Berlin Township in Wells County), in 1997. Landscapes with low grassland composition contained isolated patches of grassland surrounded by cropland. There were 26 patches of planted cover on study areas with a low grassland composition that ranged 2–192 ha (45 $\pm$ 10.6 ha; $\bar{X} \pm SE$) in size. Cropland on all study areas was planted in either row crops (corn, beans, and sunflowers) or grain crops (wheat and barley). The Litchville site (hereafter referred to as Litchville) contained 66.9% cropland, 12.5% planted cover, 2.3% pastureland, and 0.3% hayland. The Bowdon site (hereafter referred to as Bowdon) contained 56.4% cropland, 13.8% planted cover, 2.7% pastureland, and 3.2% hayland.

In contrast, we selected study areas with a high grassland composition in Medina, North Dakota (Iosco Township in Stutsman County), in 1996 and Hurdsfield, North Dakota (Silver Lake Township in Wells County), in 1997. Landscapes with a high grassland composition contained large patches of grassland adjacent to cropland. These study areas contained 22 patches of planted cover that ranged 4–606 ha (153 $\pm$ 36.6 ha) in size. The Medina site (hereafter referred to as Medina) contained 34.3% cropland, 22.1% planted cover, 19.0% pastureland, and 4.1% hayland. The Hurdsfield site (hereafter referred to as Hurdsfield) contained 23.0% cropland, 22.5% planted cover, 27.8% pastureland, and 1.5% hayland.

We used data from the National Wetland Inventory (NWI; U. S. Fish and Wildlife Service, St. Petersburg, Florida) to identify the wetland basins on the study areas. We used Stewart and Kantrud (1971) classifications that had been converted from NWI classifications by the Habitat and Population Evaluation Team (U.S. Fish and Wildlife Service, Bismarck, North Dakota). Each study area contained a similar composition of wetlands (Litchville = 11.6%, Bowdon = 18.5%, Medina = 13.4%, and Hurdsfield = 21.2%). Wetlands were predominantly temporary and seasonal.

All study areas also included a road system constructed on a grid with roads at 1 mile (2.2 km) intervals (<2% of each study area) and other cover types, including farmsteads, trees, and miscellaneous cover types (each <1.0% of the study area). The Medina study area included a predator exclosure (2.4%) that contained planted cover enrolled in the Conservation Reserve Program and hayland. Since the exclosure restricted predator movement, it was classified as a miscellaneous cover type instead of a grassland cover type in the analysis of predator movement.

Capture and Handling

We captured red foxes and striped skunks in April and May (1996 and 1997) and in June (1997) using live traps for striped skunks and either snares with stops or leg hold traps for red foxes. A professional trapper from Wildlife Services (U.S. Department of Agriculture, Bismarck) assisted us in capturing red foxes. We trapped intensively and systematically across all study areas with the goal of capturing all resident animals of both predator species. Sex was determined for all captured animals, and they were weighed, examined for tooth wear and reproductive status of females, and ear tagged (National Band and Tag Company, Newport, Kentucky). Each animal was fitted with a collar containing a telemetry transmitter (Advanced Telemetry Systems, Isanti, Minnesota) with a 1-h mortality switch. The transmitters weighed approximately 60 g for striped skunks and 110 g for red foxes. All trapping and handling procedures for this project were developed following recommendations by the American Society of Mammalogists Animal Care and Use Committee (1998) and the Northern Prairie Wildlife Research Center's Animal Care and Use Guidelines and were approved by the Iowa State University Committee on Animal Care.

Radiotelemetry

Radiotelemetry locations were estimated from 2 or more bearings using vehicle-mounted null-peak directional antennas (Advanced Telemetry Systems). Locations based on 2 bearings were estimated using a fixed standard deviation determined for each crew member based on 2 field tests given before and midway through the field season. Standard deviations ranged from 1.7–3.0°. Bearings were taken from permanent telemetry stations positioned along roads or at other accessible positions with known Universal Transverse Mercator (UTM) coordinates. Locations and their 95% error ellipses were estimated using LOCATE II software (Nams 1990).

We recorded predator movements intensively at night (2000–0800 h) 3 times each week from the first week in June to the last week in August. We recorded locations for a sampled animal every 15–20 min. We defined a trajectory as a series of locations for 1 animal for 1 night of tracking. We recorded how often and how long each animal was tracked in order to ensure complete coverage of the study area and minimize sampling bias.

We used several methods to minimize error and improve the resolution of movement within a trajectory. First, we examined the statistical distribution of the error ellipses and deleted any location with an error ellipse that was greater than 3.0 times the interquartile range above the 75th percentile, which defined as an extreme outlier by Devore and Peck (1986:94). This resulted in an upper limit of 11.7 ha for locations used in the analysis. The resulting median area for error ellipses was 1.1 ha. Second, trajectories with fewer than 10 locations ($n = 155$) did not give us enough information on movement patterns and were not included in the analysis. Trajectories averaged 17.7 locations ($SE = 0.30$) and ranged from 10–40 locations. Third, occasionally more than 60 min elapsed between locations. To eliminate these gaps, we either deleted locations from the data set if they were at the beginning or end of a trajectory ($n = 185$ trajectories) or split the trajectories into shorter trajectories ($n = 164$ trajectories). Fourth, we recorded locations more frequently in 1997 than in 1996. The average time between locations was 19.5 min ($SE = 0.11$) in 1996 and 9.9 min ($SE = 0.07$) in 1997. The time between locations can affect turning angle between successive locations and the fractal dimension (Ferguson et al. 1996). Therefore, to standardize the telemetry between the 2 years, we systematically deleted every 2nd location from the 1997 data. After editing the data, the average time between locations for 1997 was 19.4 min ($SE = 0.15$) and did not differ from time intervals for 1996 ($t = 1.10$, $d.f. = 9, 281$, $P = 0.27$).

For our analyses, we used 9,977 locations grouped within 608 trajectories for 105 individuals. There were 5 red foxes and 21 striped skunks in Litchville, 5 red foxes and 16 striped skunks in Medina, 7 red foxes and 20 striped skunks in Bowdon, and 9 red foxes and 22 striped skunks in Hurdsfield. For comparisons between landscape types, we pooled study areas with similar grassland compositions, resulting in 12 red foxes and 41 striped skunks in landscapes with low grassland composition and 14 red foxes and 38 striped skunks in landscapes with high grassland composition.

Delineation of Cover Types

Land cover data were recorded from low-altitude aerial photography and videography for each study area plus a 1.6-km surrounding border (Cowardin et al. 1988). Cover types were digitized and classified using the Map and Image Processing System (MicroImages, Lincoln, Nebraska). Classification of cover types was verified by ground observations. We used ARC/INFO software (ESRI, 1994, Redlands, California) for management and analysis of the land cover and movement data.

We divided grassland into 3 cover types: planted cover, pastureland, and hayland. Planted cover was dense nesting cover seeded to perennial grasses and forbs by landowners and enrolled in the Conservation Reserve Program, the Water Bank Program, or set aside as federal Waterfowl Production Areas. Our definition of a patch of planted cover is similar to that of Sovada et al. (2000, figure 2) except that we allowed gravel and paved roads to divide adjacent areas of planted cover into separate patches. We defined hayland as an agricultural cover type since it is disturbed by mowing at least once during the field season.

We focused our analyses of localized movement patterns (the rate of movement and turning angle between successive radiotelemetry locations) on the response of predators to planted cover, pastureland and wetland edges in contrast to the surrounding agricultural landscape (the agricultural matrix). Wetland edges were defined as areas ≤ 50 m from the boundary of a wetland. Cover types in the surrounding agricultural matrix included cropland, hayland, and miscellaneous cover types.

Movement Analyses

Rate of movement and turning angle.—Movement between 2 successive locations within a trajectory was defined as a step (Turchin 1998). We examined steps that had both locations in planted cover, pastureland, wetland edges, or the surrounding agricultural matrix. We examined the rate of movement and turning angle of steps within each cover type (Fig. 1). The rate of movement for a step was computed in meters per minute. The turning angle (θ) was computed as the change in the direction of movement made by an individual from 1 location to the next. The turning angle is a right-hand turn that ranged from 0–360°.

Fractals.—The fractal dimension and displacement ratio are measures of the overall shape of trajectories. The fractal dimension (D) of a trajectory is a scale-independent measure that ranges from the Euclidean limits of 1.0 (a straight line) to 2.0 (a trajectory so tortuous that it eventually fills a 2-dimensional plane). A larger value for D indicates a more tortuous trajectory and a greater likelihood that a trajectory will intersect itself (Dicke and Burrough 1988; Mandelbrot 1983).

We used the Fractal Mean estimator in the Fractal software constructed by Nams (1996) to compute a fractal dimension for each of the trajectories. The estimator uses the divider method (Mandelbrot

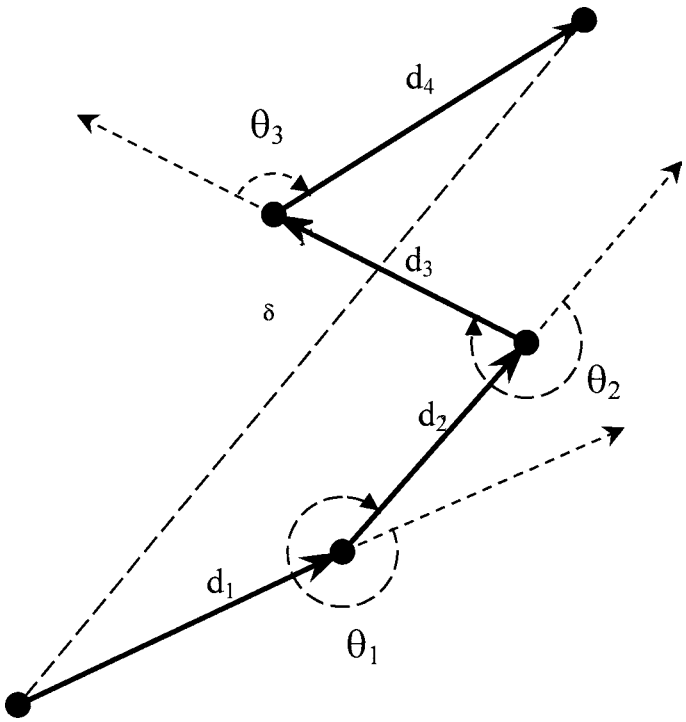

FIG. 1.—Components of a trajectory. Solid lines indicate the distance (d_i) traveled for each step in a trajectory. The total distance traveled (τ) is the sum of the individual steps. The dashed lines indicate the turning angle (θ) computed as right-hand turns and the displacement (δ) defined as the distance from the first to the last location in a trajectory.

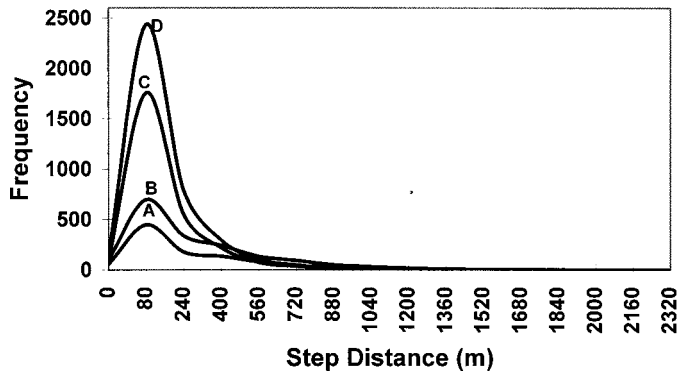

FIG. 2.—Distribution of step distances. A) Red foxes in landscapes with a low grassland composition ($\bar{X}$= 271.8, SE = 9.67, and median = 162.8 m). B) Red foxes in landscapes with a high grassland composition ($\bar{X}$= 290.8, SE = 7.99, and median = 184.6 m). C) Striped skunks in landscapes with a low grassland composition ($\bar{X}$= 150.8, SE = 3.18, and median = 95.0 m). D) Striped skunks in landscapes with a high grassland composition ($\bar{X}$= 150.8, SE = 2.67, and median = 96.4 m).

1967) to estimate the fractal dimension by estimating the length of the pathway (L) over a range of divider sizes (λ) such that

$$L(\lambda) = k\lambda^{1-D}$$

where k is a constant and D is the fractal dimension of the pathway. The fractal dimension of a trajectory is computed from a regression of $\log(\bar{L})$ as a function of $\log(\lambda)$.

Since the path length is poorly estimated at large divider sizes, the Fractal Mean estimator computes a mean path length ($\bar{L}$) for each divider size beginning at a random point along the trajectory (Nams 1996). We used 15 replications to estimate $\bar{L}$ for each divider size. We used 30 divider sizes (λ) that ranged from 5–1,500 m for red foxes and striped skunks. We examined the distribution of distances for steps (Fig. 2) and set the minimum nonzero divider size at 5 m (which was approximately the 5th percentile for the distribution). We examined the distribution of the total distance traveled (Fig. 3) and set the maximum divider size to 1,500 m (which was approximately the 25th percentile of the distribution for both red fox and striped skunks on both landscape types).

Displacement ratio.—The trajectories were also analyzed by computing a displacement ratio:

$$\Delta_{ijk} = \frac{\delta_{ijk}}{\tau_{ijk}}$$

where δ_{ijk} = the displacement (the distance from the first to the last location in a trajectory; Fig. 1) and $\tau_{ijk} = \sum d_s$, for $s = 1 \ldots n$ steps in a trajectory (the total distance traveled) for each animal (i) of each species (j) on landscape type (k). The ratio will range from 0 (trajectory started and ended at the same location) to 1 (the trajectory is a straight line).

The displacement ratio is a scale-dependent measure of a trajectory that is related to the fractal dimension. In general, the greater the fractal dimension, the smaller the displacement ratio. However, it is possible for trajectories to have the same displacement ratio but have the different fractal dimensions. For example, given 2 species that are both central place foragers, both will tend to have small displacement ratios, but the fractal dimension will depend on whether they travel in a directed manner or in a tortuous, back-and-forth manner. The fractal dimension is an index of the overall shape of a trajectory, whereas the displacement ratio is an index of the extent of net movement by an individual.

Statistical models.—Data collected on movement patterns were structured in a hierarchical, nested model with each step (m) nested within each trajectory (l) for each animal (k) of a particular species (s) in each study area (j) of a different landscape type (i). The rate of movement of steps as well as the fractal dimension and displacement ratio of trajectories were treated as mixed-effect models with landscape type, study area, species, and step modeled as fixed effects while animal and trajectory were random effects. Locations were treated as repeated measures within trajectories. We used an autoregressive order 1 covariance structure for locations assuming a decreasing correlation over time between locations within a trajectory (Littell et al. 1996).

The rate of movement for steps was modeled as

$$y_{ijklm} = \alpha_i + \beta_{ij} + a_{ijk} + t_{ijkl} + \sigma_{ijklm} + (\alpha\sigma)_{ijklm} + \varepsilon_{ijklm}$$

The term ($\alpha\sigma$) is the interaction between landscape type and cover type. Species were modeled separately.

The fractal dimension and displacement ratio of trajectories were modeled as

$$y_{ijklm} = \alpha_i + \beta_{ij} + a_{ijk} + t_{ijkl} + \gamma_{ijkls} + (\alpha\gamma)_{ijkls} + \varepsilon_{ijkls}$$

Species were included in the model. The term ($\alpha\gamma$) is the interaction between landscape type and species.

The turning angles were analyzed using circular statistics (Batschelet 1981). We computed the mean turning angle (a), mean vector length (m), and angular deviation (s) for the distribution of

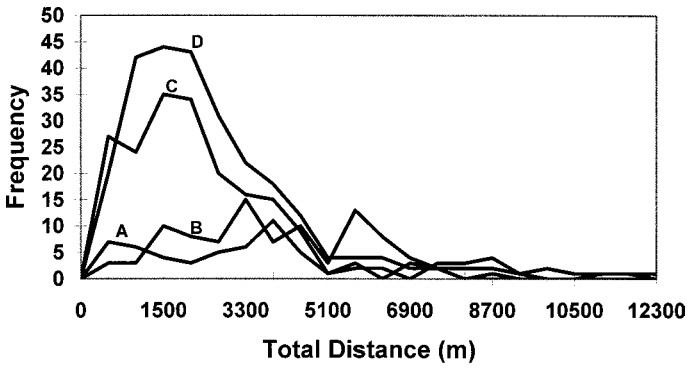

Fig. 3.—Distribution of total distances traveled. A) Red foxes in landscapes with a low grassland composition ($\bar{X}$ = 4,164.1, SE = 380.31, and median = 3,692.9 m). B) Red foxes in landscapes with a high grassland composition ($\bar{X}$ = 4,755.0, SE = 307.57, and median = 4,193.7 m). C) Striped skunks in landscapes with a low grassland composition ($\bar{X}$ = 2,196.7, SE = 110.67, and median = 1,928.8 m). D) Striped skunks in landscapes with a high grassland composition ($\bar{X}$ = 2,357.1, SE = 98.66, and median = 1,985.70 m).

turning angles for each cover type in each landscape. The mean vector (m) is a measure of the strength of directionality for circular data that ranges from 0 (when the distribution of turning angles is completely uniform) to 1 (when all turning angles are in the same direction). For circular data, m may be underestimated if the distribution of the angular data is not unimodal. The distribution of turning angles within cover types were not unimodal; therefore, we transformed the data by doubling all turning angles and subtracting 360° if the turning angle was ≥360° (Batschelet 1981). We tested for directionality of movement within each cover type using Rayleigh's z-statistic (Batschelet 1981). We used the Watson–Williams F-statistic (Batschelet 1981) to compare movement for each species among cover types within each landscape type and between landscape types for each cover type.

Results

Rate of movement.—The rate of movement should be interpreted cautiously because of large sample sizes for steps (Steidl et al. 1997). Large sample sizes may increase the probability of Type I error. We argue that the statistics for the rate of movement are biological meaningful and not an artifact of large sample size.

There was no overall difference in the rate of movement for red foxes (Table 1) between the 2 landscape types (F = 0.09, $d.f.$ = 1, 28, P = 0.77). There was a difference among cover types (F = 3.53, $d.f.$ = 3, 1,690, P = 0.01) but no interaction between landscape type and cover type (F = 0.34, $d.f.$ = 3, 1,690, P = 0.80). The differences among cover types is the result of higher rates of movement in planted cover (t = 2.88, $d.f.$ = 1, 1,690, P = 0.004) and the agricultural matrix (t = 2.40, $d.f.$ = 1, 1,690, P = 0.02) than wetland edges.

There was no overall difference in the rate of movement for striped skunks (Table 1) between the 2 landscape types (F = 0.52, $d.f.$ = 1, 91, P = 0.47). There were differences among cover types (F = 7.90, $d.f.$ = 3, 4,673, P < 0.0001) and an interaction between landscape type and cover type (F = 6.54, $d.f.$ = 3, 4,673, P < 0.001). Differences among cover types were due to higher rates of movement in wetland edges (t = 3.58, $d.f.$ = 1, 4,673, P = 0.0003) and the agricultural matrix (t = 4.57, $d.f.$ = 1, 4,673, P < 0.0001) than in planted cover as well as a higher rate of movement in the agricultural matrix than in pastureland (t = 2.16, $d.f.$ = 1, 4,673, P = 0.03). The interaction between landscape types and cover type is the result of different rates of movement in the agricultural matrix in 2 landscape types. There was a higher rate of movement in the agricultural matrix relative to the other cover types in landscapes with a low grassland composition (t = 1.93–5.56, $d.f.$ = 1, 4,673, P < 0.05), while the rate of movement in the agricultural matrix is not different from other cover types in landscapes with a high grassland composition (t = 0.73–1.46, $d.f.$ = 1, 4,673, P > 0.14).

Table 1.—Rate of movement (m/min) by red foxes and striped skunks for each cover type in landscapes with low grassland composition and high grassland composition (1996 and 1997).

	Grassland composition			
	Low		High	
	$\bar{X}$	SE	$\bar{X}$	SE
Red fox				
All cover types combined	11.3	1.73	11.8	0.85
Cover type				
Planted cover	14.0	1.65	13.1	1.37
Pastureland	9.2	4.21	11.0	1.64
Wetland edges	10.1	1.18	10.1	0.99
Agricultural matrix	11.7	1.28	13.1	1.19
Striped skunk				
All cover types combined	6.5	0.49	6.1	0.29
Cover types				
Planted cover	5.2	0.53	5.7	0.41
Pastureland	5.4	1.64	5.5	0.50
Wetland edges	6.6	0.36	6.8	0.31
Agricultural matrix	8.6	0.41	6.1	0.49

Turning angle.—There was a wide distribution of turning angles in all cover types for red foxes and striped skunks as demonstrated in the mean vector lengths (m) that ranged from 0.053–0.352 and the wide angular dispersions (s) that ranged from 32.6–39.4° (Table 2). The relatively small values for mean vector and the wide angular dispersion indicate a lack of strong directionality in each of the cover types. In these cases, the statistical analyses were not powerful and should be interpreted cautiously. Nevertheless, the analyses indicated important movement patterns.

Red foxes exhibited directional movement along wetland edges in both types of landscape (Table 2). Red fox movement was directional in the agricultural matrix in landscapes of high grassland composition but not of low grassland composition. There was no significant directional movement for red foxes in planted cover or in pastureland. In contrast, striped skunks exhibited directional movement in all cover types except pastureland in landscapes with a low grassland composition (Table 2). The lack of directionality in pastureland in

Table 2.—Summary statistics and Rayleigh's *Z*-statistic for distributions of turning angles within each cover type for red foxes and striped skunks in landscapes with a low grassland composition and high grassland composition (1996 and 1997).

	n	$\bar{X}$ turn angle (a)	$\bar{X}$ vector length (m)	Angular dispersion (s)	Z	P
Red fox						
Low grassland composition						
Planted cover	121	340.9	0.129	37.8	2.00	0.14
Pastureland	9	10.2	0.352	32.6	1.12	0.34
Wetland edges	285	6.0	0.156	37.2	6.90	<0.001
Agricultural matrix	191	33.8	0.105	38.3	2.10	0.12
High grassland composition						
Planted cover	209	14.8	0.053	39.4	0.59	0.56
Pastureland	108	0.8	0.127	37.8	1.75	0.17
Wetland edges	394	351.0	0.094	38.6	3.51	0.03
Agricultural matrix	231	2.7	0.137	37.6	4.35	0.01
Striped skunk						
Low grassland composition						
Planted cover	382	357.4	0.117	38.1	5.21	0.01
Pastureland	19	20.9	0.241	35.3	1.10	0.34
Wetland edges	925	10.2	0.066	39.2	4.00	0.02
Agricultural matrix	544	358.0	0.132	37.8	9.43	<0.001
High grassland composition						
Planted cover	585	5.4	0.123	37.9	8.87	<0.001
Pastureland	325	3.1	0.127	37.9	5.23	0.01
Wetland edges	1,381	2.4	0.100	38.4	13.69	<0.001
Agricultural matrix	326	9.2	0.107	38.3	3.75	0.02

landscapes with a low grassland composition may be due to a low number of steps in pasture for red foxes and striped skunks.

We observed a difference in the distribution of turning angles among cover types for red foxes in landscapes of low grassland composition ($F = 12.83$, $d.f. = 3, 602$, $P < 0.0001$) and in high grassland composition ($F = 3.56$, $d.f. = 3, 938$, $P = 0.014$). In landscapes with a low grassland composition, the difference is likely the result of the larger mean vector ($m = 0.352$) for steps in pasture (Table 2). Differences among cover types in landscapes with a high grassland composition are likely the result of the low mean vector ($m = 0.053$) in planted cover (Table 2).

We observed a difference in the distribution of turning angles among cover types for striped skunks in landscapes with a low grassland composition ($F = 5.05$, $d.f. = 3, 1{,}866$, $P = 0.002$) but not in landscapes with a high grassland composition ($F = 0.91$, $d.f. = 3, 2{,}613$, $P = 0.43$). In landscapes with a low grassland composition, the difference is likely due to the larger mean vector ($m = 0.241$) for movement in pastureland and the low mean vector ($m = 0.066$) for movement in wetland edges (Table 2).

We observed differences in the distribution of turning angles between landscape types for red foxes in planted cover ($F = 15.71$, $d.f. = 1, 328$, $P < 0.0001$), wetland edges ($F = 7.96$, $d.f. = 1, 677$, $P = 0.005$), and the agricultural matrix ($F = 20.10$, $d.f. = 1, 420$, $P < 0.0001$) but not in pastureland ($F = 0.36$, $d.f. = 1, 115$, $P = 0.55$). For striped skunks, we observed differences in the distribution of turning angles between landscapes in wetland edges ($F = 5.50$, $d.f. = 1, 2{,}304$, $P = 0.019$) and the agricultural matrix ($F = 5.09$, $d.f. = 1, 868$, $P = 0.02$) but not in planted cover ($F = 3.10$, $d.f. = 1, 965$, $P = 0.08$) or in pastureland ($F = 2.13$, $d.f. = 1, 342$, $P = 0.15$).

Fractals.—The fractal dimension ranged from 1.000–1.318 for red foxes and ranged from 1.000–1.505 for striped skunks (Table 3). The 3 examples of observed striped skunk trajectories in Fig. 4 illustrate differences in the shape of trajectories for fractal dimensions that range from 1.1–1.5. The overall mean for red foxes and striped skunks on both landscapes was 1.128; therefore, most trajectories resembled the trajectory in Fig. 4A.

The mean fractal dimension of trajectories was higher in landscapes with a high grassland composition than with a low grassland composition ($F = 3.63$, $d.f. = 1, 101$, $P = 0.059$) (Table 3). There was no difference in the mean fractal dimension between the 2 species ($F = 0.30$, $d.f. = 1, 101$, $P = 0.59$). Although we did not observe a strong interaction ($F = 1.48$, $d.f. = 1, 101$, $P = 0.23$), the results suggest that the difference between landscapes is due to red foxes. The fractal dimension of red fox trajectories was higher in landscapes with a high grassland composition than in landscapes with a low grassland composition ($t = 1.81$, $d.f. = 1, 101$, $P = 0.07$), whereas there was no difference in the fractal dimension of striped skunk trajectories between low grassland composition and high grassland composition landscapes ($t = 0.69$, $d.f. = 1, 101$, $P = 0.49$).

Displacement ratios.—The displacement ratios were greater in striped skunks than in red foxes ($F = 4.68$, $d.f. = 1, 101$, $P = 0.03$) (Table 3). Displacement ratios were marginally greater in landscapes with a low grassland composition than high grassland composition ($F = 2.86$, $d.f. = 1, 101$, $P = 0.09$). Although we did not observe a strong interaction ($F = 1.89$, $d.f. = 1, 101$, $P = 0.17$), the difference in species was the result of a lower displacement ratio for red foxes in high grassland composition than in low grassland composition landscapes ($t = 1.79$, $d.f. = 1, 101$, $P = 0.07$), whereas there is no difference for striped skunks between low grassland composition and high grassland composition landscapes ($t = 0.30$, $d.f. = 1, 101$, $P = 0.76$).

Discussion

Predator movement was influenced by landscape features and was consistent with the selection of cover types by red foxes and striped skunks (Phillips et al. 2003). Movement pathways of red foxes depended on the distribution of planted cover in the landscape. In landscapes with a low grassland composition, red fox trajectories were slightly straighter (lower fractal dimensions and higher displacement ratio), suggesting that red foxes traveled in a directed manner between the more isolated patches of planted cover. Pathways with straighter movements are a more efficient search pattern in landscapes where patches of quality habitat are widely dispersed

TABLE 3.—Summary of fractal dimensions (D) and displacement ratios (Δ) of trajectories for red foxes and striped skunks in landscapes with a low grassland composition and high grassland composition (1996 and 1997).

	Fractal dimension					Displacement ratio				
	n	$\bar{X}$	SE	Minimum	Maximum	n	$\bar{X}$	SE	Minimum	Maximum
Landscape composition										
Low grassland	255	1.107	0.0102	1.000	1.505	255	0.298	0.0170	0.000	0.767
High grassland	353	1.134	0.0095	1.001	1.434	353	0.260	0.0146	0.003	0.998
Species										
Red fox	172	1.117	0.0120	1.000	1.318	172	0.255	0.0191	0.003	0.998
Striped skunk	436	1.125	0.0070	1.000	1.505	436	0.304	0.0116	0.000	0.838
Species × landscape composition										
Red fox										
Low grassland	66	1.095	0.0177	1.000	1.318	66	0.289	0.0292	0.003	0.741
High grassland	106	1.139	0.0162	1.000	1.245	106	0.221	0.0247	0.007	0.998
Striped skunk										
Low grassland	189	1.120	0.0099	1.000	1.505	189	0.307	0.0174	0.000	0.767
High grassland	247	1.129	0.0098	1.001	1.434	247	0.300	0.0155	0.003	0.838

(Dusenberry 1989; Zollner and Lima 1999). In landscapes with a high grassland composition, red fox trajectories tended to be more tortuous (higher fractal dimension and lower displacement ratio). Red fox movements in landscapes with a high grassland composition were likely influenced by the presence of pastureland and planted cover. Red foxes exhibit selection for pastureland but not hayland or for the interior areas of planted cover in landscapes with a high grassland composition (Phillips et al. 2003). Therefore, red foxes did not have to travel as far before encountering resources in the large, interconnected blocks of grassland.

Striped skunk trajectories had a consistent shape and displacement on both types of landscape. Striped skunks strongly selected wetland edges regardless of grassland composition in the landscape (Phillips et al. 2003). Our study areas contained similar compositions and classifications of wetland edges. Therefore, it is not surprising that striped skunks displayed similar movement patterns across landscapes as they focused their movement among wetland edges.

Localized movement also reflected cover type selection by predators but showed greater variability than expected. The lack of directed movement by red foxes in planted cover and pastureland in both landscape types is consistent with increased foraging behavior and suggests that the composition of grassland in the landscape does not affect the behavior of red foxes once they are within a patch of grassland. Foraging efficiency would increase by concentrating movement within a restricted area (Tinbergen et al. 1967). Red fox movements within the agricultural matrix were not as directed as predicted (especially in landscapes with a low grassland composition). Conflicting behavioral motivations such as foraging, exploring territories, and risk avoidance that potentially influence movement may have resulted in increased vagility of movement.

The rate of movement by red foxes in planted cover and striped skunks in wetland edges was greater than predicted. These localized movement patterns suggest the use of spatial memory. If a predator has no information about the spatial distribution of patches or prey within patches, then movement patterns will be slower (and more tortuous) as the animal spends time searching in a random fashion in an effort to maximize its searching efficiency (Sugihara and May 1990). If a predator uses spatial memory to revisit patches or profitable areas within patches, then faster more directed movement, both between and within patches, would be more efficient than

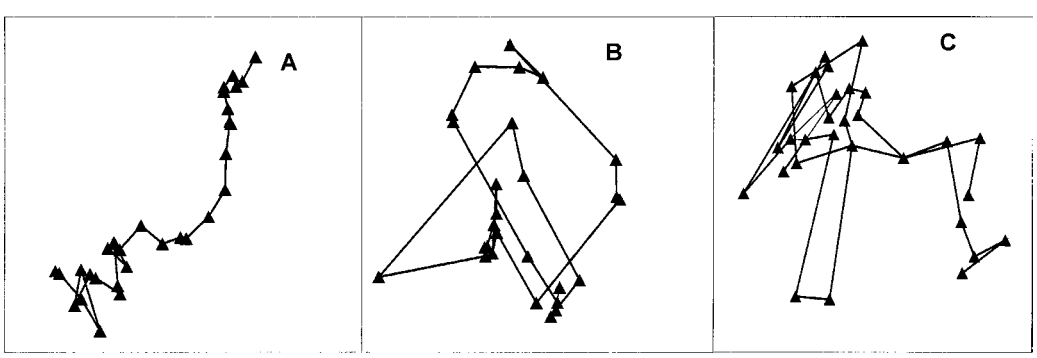

FIG. 4.—Examples of observed striped skunk trajectories with fractal dimensions (D) of A) 1.148 (n = 30 locations), B) 1.308 (n = 30 locations), and C) 1.505 (n = 32 locations). The average trajectory for red foxes and striped skunks resembled the trajectory in A.

a random search pattern (Mellgren and Roper 1986; Tinbergen et al. 1967). Red foxes may use spatial memory to improve searching efficiency by revisiting profitable patches or moving quickly through patches recently searched. Striped skunks may form long-term search images that associated with wetland edges (Nams 1997).

We observed a difference between landscape types for localized movement by striped skunks within the agricultural matrix. Striped skunks moved quickly and in a directed manner through the agricultural matrix in landscapes with a low grassland composition (as predicted by foraging theory). However, in landscapes with a high grassland composition, striped skunks moved relatively slowly with a wide distribution of turning angles. These localized movement patterns may result from an attraction to a variety of food resources used by striped skunks that are potentially found in the agricultural matrix (Greenwood et al. 1999), or they may simply be due to less agricultural matrix for the striped skunks to travel through in landscapes with a high grassland composition before reaching another profitable patch.

Our observations of foxes and striped skunks demonstrated that heterogeneity of cover types at both the patch and the landscape scale can influence basic ecological processes of predator movement. Differences in movement patterns suggest that the 2 predator species perceive the landscape differently (Zollner and Lima 1997). Changes in the structure of the landscape can alter the behavioral response of predators to contrasting cover types, depending on the perceived costs or rewards associated with differing cover types. An understanding of the behavioral responses of predators to landscape features is an essential component of predicting the consequences of an increasingly fragmented prairie landscape on the spatial and temporal interactions between predators and prey.

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