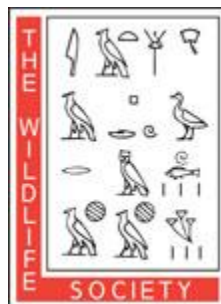WILEY

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Source: *The Journal of Wildlife Management*, Vol. 57, No. 3 (Jul., 1993), pp. 526-533
Published by: Wiley on behalf of the Wildlife Society
Stable URL: http://www.jstor.org/stable/3809277
Accessed: 27-01-2016 10:28 UTC

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DISPERSAL PATTERNS OF RED FOXES RELATIVE TO POPULATION DENSITY

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Abstract: Factors affecting red fox (*Vulpes vulpes*) dispersal patterns are poorly understood but warranted investigation because of the role of dispersal in rebuilding depleted populations and transmission of diseases. We examined dispersal patterns of red foxes in North Dakota based on recoveries of 363 of 854 foxes tagged as pups and relative to fox density. Foxes were recovered up to 8.6 years after tagging; 79% were trapped or shot. Straight-line distances between tagging and recovery locations ranged from 0 to 302 km. Mean recovery distances increased with age and were greater for males than females, but longest individual recovery distances were by females. Dispersal distances were not related to population density for males ($P = 0.36$) or females ($P = 0.96$). The proportion of males recovered that dispersed was inversely related to population density ($r = -0.94$; $n = 5$; $P = 0.02$), but not the proportion of females ($r = -0.49$; $n = 5$; $P = 0.40$). Dispersal directions were not uniform for either males ($P = 0.003$) or females ($P = 0.006$); littermates tended to disperse in similar directions ($P = 0.09$). A 4-lane interstate highway altered dispersal directions ($P = 0.001$). Dispersal is a strong innate behavior of red foxes (especially males) that results in many individuals of both sexes traveling far from natal areas. Because dispersal distance was unaffected by fox density, populations can be rebuilt and diseases transmitted long distances regardless of fox abundance.

J. WILDL. MANAGE. 57(3):526–533

Red foxes are important to wildlife managers because of their recreational and fur value (Deems and Pursley 1978, Foner 1982), predation on game (Trautman et al. 1974, Sargeant et al. 1984) and poultry, and role in disease transmission (Voigt and Tinline 1982, Trewhella et al. 1988). Considerable effort has been expended to reduce local populations (e.g., Balser et al. 1968, Trautman et al. 1974). Red fox populations contain family groups that occupy well-defined, largely non-overlapping territories (Sargeant 1972). Most families produce a litter of pups annually, and many pups disperse from the parental territory during their first year of life (Storm et al. 1976). Pils and Martin (1978)

suggested that littermates may occasionally disperse together or follow similar routes. Storm et al. (1976) and Pils and Martin (1978) found that physical barriers such as rivers can affect dispersal directions. Dispersal is important in rebuilding depleted populations and in long-distance transmission of disease. Thus, this aspect of fox biology has received attention both in North America and Europe (Errington and Berry 1937, Marcstrom 1968, Jensen 1973, Storm et al. 1976, Pils and Martin 1978). The effects of red fox population density on dispersal patterns, however, are largely undetermined.

During 1969–73 we tagged red fox pups at dens annually in a 3-county area of eastern North

Dakota where the fox population on 6 study townships increased from 0.05 fox families/km^2 in 1969 to 0.14 families/km^2 in 1973 (Allen and Sargeant 1975, Sargeant et al. 1975). Herein, we evaluate dispersal patterns of tagged foxes from this population. We examine effects of population density on dispersal distances and on the proportion of foxes recovered that had dispersed. Additionally, we evaluate dispersal direction among littermates and the effect of a 4-lane interstate highway on dispersal direction.

STUDY AREA AND METHODS

Field work was conducted in Barnes, Kidder, and Stutsman counties (3-county area): about half of the 3-county area was in the Drift Plain and half in the Missouri Coteau physiographic regions of North Dakota (Sargeant et al. 1984). This part of North Dakota is intensively farmed for small grain and cattle production. The climate is characterized by hot summers and cold winters (Stewart and Kantrud 1972). The wild canid community during our study was almost exclusively red foxes; only 1 coyote (*Canis latrans*) and no coyote dens were observed. Six 93.2-km^2 townships were selected (2 in each county) for intensive study (Sargeant et al. 1984). The 2 most eastern townships were in the Drift Plain physiographic region and the 4 most western townships were in the Missouri Coteau physiographic region. A 4-lane east-west interstate highway (I-94) bisects the 3-county area, and in each county, 1 study township was north and one was south of I-94. The 6 study townships were located nearly equal distances from I-94. The most distant study township boundary was 19.2 km from the highway. Additional description of the study area was provided by Sargeant et al. (1975).

We captured, tagged, and released red fox pups at rearing dens (nearly all during mid-May–Jun). Dens on the 6 study townships were located by systematic aerial searches (Sargeant et al. 1975) and by interviewing landowners. We located dens opportunistically off the study townships in the 3-county area during irregular aerial searches and by contacting landowners. We captured pups with nets after chasing them from dens with a wire ferret (Storm and Dauphin 1965) or by hand during den excavation. Dens were excavated in a manner that allowed at least partial restoration. One numbered tag similar to that described by Storm et al. (1976) was placed in each ear of every pup. Pups were handled so as to minimize stress and injury. Nearly all pups were released back into their rearing den. At landowner request, a few pups were transplanted to rearing dens occupied by other red foxes. We considered transplanted pups to have originated from the den into which they were released. Andrews et al. (1973) found that recovery rates for transplanted pups were not significantly different and recovery distances were not markedly different from those of pups released in their natal ranges.

We alerted fur harvesters and fur buyers throughout North Dakota to the presence of tagged foxes and asked them to notify the Game and Fish Department of recoveries. Because dispersal of young red foxes begins about 1 October annually (Storm et al. 1976, Pils and Martin 1978, Tullar and Berchielli 1980), we classified foxes recovered before 30 September of their first year of life as pups, and those recovered after that date as adults (Trewhella et al. 1988). Straight-line distances between release and recovery locations were determined for foxes whose recovery locations were known. Foxes recovered ≥8 km from their release site were considered to have dispersed following the criteria of Storm et al. (1976). Dispersal directions (direction of recovery from release site) were: north (316–45°), east (46–135°), south (136–225°), and west (226–315°). Numbers of fox families on each intensive study township were determined each spring by systematic aerial searches (Sargeant et al. 1975) and averaged annually to reflect overall populations in the 3-county area (Allen et al. 1974, Allen and Sargeant 1975). The average number of fox families/km^2 for the 6 study townships was our measurement of fox density. We defined a study year as the period April through March (e.g., 1969 refers to 1 Apr 1969–31 Mar 1970).

We used a 2-way ANOVA to compare recovery distances among age-classes and between sexes. A natural log transformation, $\ln(y + 1)$, was used to normalize recovery distances. Orthogonal polynomials (Snedecor and Cochran 1980) were used to test recovery distances for linear and quadratic trends across age-classes. We compared the pairwise distribution of angular differences in dispersal directions of littermates recovered as adults with the pairwise distribution of angular differences in dispersal directions of nonlittermates recovered as adults. This analysis reduced effects of potential biases associated with uneven harvest and tag reporting rates and with the tendency for all foxes to disperse in the same general direction.

We used Chi-square analysis to examine differences in recovery directions of all foxes tagged and released as pups and recovered as adults, and to examine effects of I-94 on dispersal directions of pups tagged and released within 19.2 km of I-94 and recovered as adults. We restricted this analysis to foxes tagged within 19.2 km of I-94 because most foxes were tagged in the study townships. We tested for differences in dispersal directions associated with the 2 physiographic regions among foxes tagged north and south of I-94. We used Pearson correlation coefficients to assess the strength of the relationships between the annual fox population density and the annual percentage of foxes that dispersed and were recovered their first year.

RESULTS

We tagged 854 fox pups in the 3-county area; 26 were transplanted to different rearing dens. We obtained partial or complete recovery data for 363 (43%) of the tagged foxes, 45% for males and 40% for females (Table 1). First-year recovery rates were 31% for males and 23% for females.

Fifty-one percent of the recovered foxes were trapped, 28% were shot, and 21% died from other causes (e.g., collision with vehicles). Foxes were recovered up to 8.6 years after being tagged. Twenty-two foxes were recovered as pups and three of those (1 F, 2 M) had dispersed. Those pups were recovered 12, 14, and 24 km from their release sites on 6 June, 15 August, and 24 September, respectively. Two of 4 foxes (3 F, 1 M) recovered ≥7 years after being tagged had not dispersed; both were females.

Recovery Distances

Straight-line recovery distances were determined for 322 adult foxes tagged as pups (Table 2). Recovery distances ranged from 0 to 302 km. Thirty foxes were recovered >80 km from release sites; there was no difference ($\chi^2 = 0.189$, 1 df, $P = 0.66$) in proportion of males (9.9%) and females (8.5%) recovered >80 km from release sites. Three foxes recovered >200 km (246, 274, and 302 km) from release sites were females. There was no interaction ($F = 0.27$; 2, 316 df; $P = 0.76$) between age-class and sex for recovery distances. Recovery distances increased as age-class increased and was greater for males (Table 2). Recovery distances increased linearly with age-class ($F = 21.6$; 1, 316 df; $P < 0.001$). No quadratic trends were detected ($F < 0.01$; 1, 316 df; $P = 0.99$).

Proportion of Foxes Recovered That Dispersed

One hundred eighty-four (57%) foxes, for which recovery distances were available and which were recovered as adults, dispersed. However, the proportion of recovered foxes that dispersed varied by sex and age-class (Table 2). Sixty-four percent of males and 29% of females recovered as adults during their first year after tagging had dispersed ($\chi^2 = 22.5$, 1 df, $P < 0.001$). Of foxes that were recovered as adults, 77% of males and 36% of females had dispersed the second year after tagging ($\chi^2 = 10.3$, 1 df, $P = 0.001$), and 97% of males and 52% of females had dispersed during years 3–8 after tagging ($\chi^2 = 15.7$, 1 df, $P < 0.001$). For males, proportionally more recovered from older age-classes had dispersed ($\chi^2 = 12.9$, 2 df, $P = 0.002$); a similar but weaker relationship was found for females ($\chi^2 = 4.9$, 2 df, $P = 0.09$).

Dispersal Direction

Recovery directions of the 137 males that were recovered as adults and were known to have dispersed were: east (34%), south (18%), west (16%), or north (32%) of the release sites. This distribution was not uniform ($\chi^2 = 13.7$, 3 df, $P = 0.003$). Recovery directions of the 47 females that were recovered as adults and were known to have dispersed were: north (43%), east (26%), south (6%), or west (26%) of the release sites. This distribution also was not uniform ($\chi^2 = 12.3$, 3 df, $P = 0.006$).

Table 1.   Number of red foxes tagged as pups in eastern North Dakota and recovered, 1969–73.

Year	Sex	No. tagged	No. recovered	Recoveries by age-class[a] (yr) as a percentage of number tagged			
				<0.5	0.5–<1.0	1.0–<2.0	>2.0[b]
1969	M	62	32	1.6	38.7	4.8	6.5
	F	68	28	1.5	25.0	2.9	11.8
1970	M	79	26	1.3	13.9	8.9	8.9
	F	76	29	1.3	11.8	6.6	18.4
1971	M	120	71	3.3	35.8	10.8	9.2
	F	90	39	4.4	18.9	8.9	11.1
1972	M	160	60	3.8	23.8	5.6	4.4
	F	125	45	1.6	24.0	7.2	3.2
1973	M	51	23	2.0	31.4	5.9	5.9
	F	23	10	4.4	26.1	4.3	8.7
Total	M	472	212	2.8	28.0	7.4	6.8
	F	382	151	2.4	20.7	6.5	9.9

[a] Years after tagging; year starts annually on 1 April and ends on 31 March.
[b] Includes 1 male and 1 female that were 7.7 years old and 2 females that were 8.6 years old.

We evaluated the hypothesis that littermates dispersed in similar directions. Eighty-two pairwise combinations of recovered littermates involving 102 foxes from 43 litters were used in the analysis of within-litter similarities in direction of dispersal. Pairwise dispersal angles of 39% of recovered littermates were ≤45° of each other and 65% were ≤90° of each other compared with expected values of 27% and 53% for nonlittermate tagged foxes recovered as adults, respectively ($\chi^2 = 6.43$, 3 df, $P = 0.09$).

We hypothesized that I-94 affected fox dispersal directions. Seventy-five pups tagged and released north of I-94 and 64 pups tagged and released south of I-94 in the 2 physiographic regions and recovered as adults were used in the analysis. We found no differences in the dispersal direction between physiographic regions among foxes tagged north ($\chi^2 = 1.33$, 3 df, $P = 0.72$) or south of I-94 ($\chi^2 = 3.04$, 3 df, $P = 0.39$). Therefore, we combined data from the 2 physiographic regions on each side of I-94 to compare dispersal directions between foxes released north and south of I-94. Analysis of combined data revealed a difference ($\chi^2 = 16.8$, 3 df, $P = 0.001$) in dispersal directions of foxes tagged north compared with those tagged south of I-94. Inspection of data revealed the most logical explanation for the difference was in the percentage of recoveries in the direction toward I-94. Sixteen percent of recoveries of dispersing foxes tagged south of I-94 were north of respective tagging sites compared with 22–39% in each of the other quadrants. For foxes tagged north of I-94, 7% of recoveries of dispersing foxes were south of respective tagging sites compared with 24–43% in each of the other quadrants.

Effects of Population Size

We could not evaluate the actual proportion of all foxes tagged that had dispersed because

Table 2.   Dispersal and straight-line recovery distances of 322 adult red foxes tagged as pups in eastern North Dakota and recovered as adults, 1969–73.

Sex	Age-class[a]	No. recovered[b]	Recovery distance (km)			Dispersed %
			Mean[c]	Median	Range	
Males	0.5–<1.0	128	24	12	1–153	64
	1.0–<2.0	35	35	21	0–147	77
	2.0–<8.0	29	46	26	8–131	97
Females	0.5–<1.0	72	19	3	0–302	29
	1.0–<2.0	25	24	5	1–246	36
	2.0–<8.0	33	33	9	0–274	52

[a] Years (Apr–Mar) after tagging.
[b] An additional 7 males and 12 females were recovered but recovery location information was insufficient to calculate recovery distance.
[c] Recovery distance increased with age-class ($F = 11.5$; 2, 316 df; $P < 0.001$) and was greater for males ($F = 26.6$; 1, 316 df; $P < 0.001$).

Table 3. Relationship between fox population density in spring and corresponding percentages of foxes that dispersed and were recovered as adults during November–January of their first year, eastern North Dakota, 1969–73.

Variable	Year					Correlation coefficient[a]
	1969	1970	1971	1972	1973	
Families/km² for 6 townships[b]	0.05	0.07	0.10	0.12	0.14	
Recovered males						
n	17	11	40	29	14	
% dispersed	76	64	65	55	50	−0.94
Recovered females						
n	12	8	15	26	4	
% dispersed	33	88	7	27	0	−0.49

[a] Pearson correlation coefficient weighted by n to account for unequal sample sizes. For males $P = 0.02$ (3 df); for females $P = 0.40$ (3 df).
[b] Density during spring when foxes were tagged (Allen and Sargeant 1975).

tag recovery rates were undetermined, and duration of the harvest season and harvest intensity varied annually. However, the annual fur harvest season always included November through January. We found only small monthly differences in annual distributions of first-year recoveries for November–January for males ($\chi^2 = 6.67$, 8 df, $P = 0.57$) and females ($\chi^2 = 9.24$, 8 df, $P = 0.32$), and large differences in annual distributions for males ($\chi^2 = 35.0$, 20 df, $P = 0.02$) but no differences for females ($\chi^2 = 22.0$, 20 df, $P = 0.34$) when first-year recoveries from portions of other months were included. To avoid the problem of unequal harvest periods, we limited our evaluation of effects of population density on dispersal to the percentage of foxes recovered during November–January of their first year that had dispersed, and to distances dispersed during November–January. There were 69 male and 19 female foxes in these recovery class cohorts. We found a strong inverse relationship between fox density and the proportion of recovered males that had dispersed but no indication of a similar relationship for females (Table 3). Proportions of foxes that had dispersed and were recovered during November–January of their first year ranged from 76% (1969) to 50% (1973) for males, and from 88% (1970) to 0% (1973) for females (Table 3).

We evaluated average straight-line dispersal distances of male and female foxes recovered during November–January of their first year relative to fox population density during spring of tagging. Correlation coefficients (weighted by the no. of foxes to account for unequal sample sizes) for males ($r = 0.53$, 3 df, $P = 0.36$) and females ($r = -0.03$, 3 df, $P = 0.96$) indicated no relationship between population density and dispersal distances.

DISCUSSION

Our recovery of 43% of all foxes tagged as pups is within the range of 40–54% reported from other areas of North America (Storm et al. 1976, Pils and Martin 1978, Tullar and Berchielli 1980, Voigt 1987). Those workers also found recovery rates were greater for males than for females, and greater during the first year of life than later.

Interest in fox trapping and hunting was high throughout our study period because fur prices were relatively high (Sargeant 1982); most of our recoveries came from trappers and hunters. Nevertheless, we found higher survival of foxes tagged as pups than reported by others. Storm et al. (1976), Pils and Martin (1978), and Tullar and Berchielli (1980) tagged a total of 2,692 red fox pups, but in each study only 3–4% were recovered >2 years after tagging; 1 fox was recovered >7 years after tagging (an 8.5-yr-old female reported by Tullar [1983]). Seven percent of males and 10% of females we tagged were not recovered until >2 years after tagging, including 1 male and 3 females that survived >7 years. Female foxes surviving >2 years are especially important to populations because of age-related increases in reproductive performance (Allen 1984).

We found both the mean recovery distance and the percentage of foxes recovered that dispersed increased with age-class, and were greater for males than females, similar to findings of others (Storm et al. 1976, Jensen 1973, Pils and Martin 1978, Tullar and Berchielli 1980, Voigt

1987). Storm et al. (1976) found monthly increases in mean dispersal distances generally occurred in both sexes. The increases we observed likely reflected many first-year foxes being captured before or during dispersal, as well as additional dispersal by some adults after their first year (Storm et al. 1976). However, harvesting may select a different part of the population than nonreportable mortality such as disease and old age.

Our findings differ from those of Storm et al. (1976) for red foxes in Iowa-Illinois and Pils and Martin (1978) for red foxes in Wisconsin, the only 2 data sets from midcontinent North America suitable for comparison with our findings. The percentage of North Dakota foxes recovered that dispersed was 15–47% lower by sex and age-class than in the Iowa-Illinois and Wisconsin studies. Mean straight-line dispersal distances for males by age-class were similar in all 3 studies, but the dispersal distances for females by age-class were about one-half as great in Iowa-Illinois as in North Dakota and Wisconsin.

Storm et al. (1976) noted that onset of dispersal may be related to litter age. North Dakota red foxes breed about 2–3 weeks later (Sargeant et al. 1981) than red foxes in Iowa-Illinois (Storm et al. 1976) and Wisconsin (Pils and Martin 1978). Thus, we hypothesize dispersal by some North Dakota red foxes may be delayed, thereby affecting the proportion of recovered foxes that dispersed by age-class. Statistical analysis was not possible because of differences in data presentation among studies. However, in our study, as in the Iowa-Illinois and Wisconsin studies, >95% of males recovered in the oldest age-class examined had dispersed. In the Iowa-Illinois and Wisconsin studies, ≥95% of males recovered during the second recovery year had dispersed (assumed for the Wisconsin study because 88% of first-year recoveries had dispersed), whereas in our study 77% of males recovered during the second recovery year had dispersed. In the Wisconsin study 58% of females recovered as adults during their first recovery year had dispersed and in the Iowa-Illinois study 37% of those recovered the first year and 58% of those recovered the second year had dispersed. We found 29% of females recovered as adults their first recovery year had dispersed; this increased to 36% for the second year and to 52% for the third recovery year age-classes. Thus, comparable dispersal percentages appear to occur 1 year later

in North Dakota red foxes than in those from Iowa-Illinois and Wisconsin.

We found greater mean straight-line recovery distances for males than females, as did other studies (e.g., Storm et al. 1976, Pils and Martin 1978, Lloyd 1980, Tullar and Berchielli 1980, Trewhella et al. 1988). Much of the disparity in recovery distances between males and females probably occurred because a greater percentage of males than females had dispersed when recovered (Storm et al. 1976). However, Harris and Trewhella (1988) and Storm et al. (1976) showed that males disperse farther than females.

Frequently, the longest dispersal distances are by males (Storm et al. 1976, Tullar and Berchielli 1980, Trewhella et al. 1988), but we found the longest dispersal distances in each age-class were by females. While some females apparently did not disperse (e.g., 2 females recovered ≥7 years after tagging were recovered <8 km from their release sites), other females were recovered long distances (up to 302 km) from their release sites. The retention of at least some females in or near natal areas helps explain the frequent instances of communal denning and helper foxes (Pils and Martin 1978, MacDonald 1979, Tullar and Berchielli 1980). Such foxes have social ties with mothers and siblings that would contribute to an extended family and to possible maintenance of the parental territory after parents die.

Several investigators have shown that dispersal directions of recovered foxes were not uniform. For midcontinent North America, Arnold and Schofield (1956), Storm et al. (1976), and Pils and Martin (1978) reported a tendency for more foxes to be recovered north of release sites than expected by chance. Our findings also show that dispersal directions of both sexes were not uniform. Although these findings suggest a tendency for midcontinent foxes to disperse in certain directions, they could be biased by unequal harvest rates in surrounding areas (Storm et al. 1976, Pils and Martin 1978). Major rivers (Storm et al. 1976) and interstate highways (Pils and Martin 1978) may block or alter direction of dispersing foxes. Our data indicate that an interstate highway deflected dispersal directions and provide further evidence of the importance of major physical barriers and terrain features in altering dispersal directions. Pils and Martin (1978) suggested that littermates sometimes disperse together or use the same routes. Our find-

ings support that suggestion and indicate the need for more data to determine the nature, magnitude, and biological importance of the above aspects of fox dispersal.

We found a negative relationship between fox family density in spring and the percentage of recovered male foxes that dispersed, but no such relationship for females. Thus, at least for males, the proportion of recovered foxes that dispersed was highest where there appeared to be the least reason for them to disperse (e.g., presumably largest home ranges [Andelt 1985 for coyotes, Trewhella et al. 1988 for red foxes] resulting in lowest probability of interactions with neighbors, and greatest probability of vacant or lightly occupied habitat near parental territories). Increased contact with conspecifics, which would occur as population density increases, may inhibit male dispersal. Other factors that may influence the probability of fox dispersal include family size (primarily litter size), survivorship of pups to autumn, and food supply. However, Allen (1984) found no relationship between estimates of fox family density in North Dakota in spring and embryonic litter sizes. Also, there was no evidence of any epizootics or food shortages affecting foxes during our study. Such population influences are generally noticed and reported by the populace in North Dakota.

Our data provided a unique opportunity to examine effects of fox density on dispersal distances because the population in the study area nearly tripled during the study period, a regional phenomenon (Allen and Sargeant 1975). Although our 1973 population was relatively high compared with other times and areas (Storm et al. 1976, Pils and Martin 1978, Tullar and Berchielli 1980, Sargeant et al. 1984, Voigt 1987), our population was much lower than most populations studied in Europe (e.g., Lloyd 1980, Harris 1981, MacDonald 1981, Harris and Rayner 1986, Trewhella et al. 1988). We found no effect of population density on straight-line dispersal distances of foxes of either sex. Thus, within the range of fox densities we studied, once dispersal was initiated, the abundance of foxes in surrounding areas appeared to have no effect on straight-line distances traveled before death occurred. This suggests that dispersal distance was strongly influenced by innate species traits (Howard 1960) that prompted the foxes to travel a set distance before stopping, or by habitat features (Tullar and Berchielli 1980), or both. In contrast, studies of red fox dispersal in Great Britain generally suggest an inverse relation between population density and dispersal distance (Lloyd 1980, Harris 1981, MacDonald and Bacon 1982, Trewhella et al. 1988).

MANAGEMENT IMPLICATIONS

Red fox dispersal serves to equalize fox densities over large areas, and our data show that dispersal is a strong phenomenon over a wide range of population densities. Thus, managers concerned about maintaining annual fox populations in areas subject to localized heavy harvest need not be overly anxious. Annual harvests in localized areas in 1 or more years likely will have little effect on population size in subsequent years. Because foxes are major predators of upland game and waterfowl, and they potentially are important in the spread of some epizootics, there is interest in reducing fox populations in local areas. Encouraging greater harvests during autumn and winter, when fox pelts are prime, is a more acceptable way to reduce populations than conducting fox control in spring, because of the greater use made of the autumn and winter pelts. However, because large numbers of foxes disperse during October through January, and possibly later, efforts to substantially reduce spring populations by even the most ambitious removal efforts during autumn and winter likely will fail (Knowlton 1972, Hewson 1986) unless the population is isolated from ingressing foxes by some type of physical barrier. Managers who ignore the effects of dispersal in management plans to maintain or reduce local red fox populations may needlessly restrict harvest opportunities or may at best succeed minimally in their population reduction efforts.

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