DISPERSAL AND SOCIAL CONTACT AMONG RED FOXES: RESULTS FROM TELEMETRY AND COMPUTER SIMULATION

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The occurrence of dispersal in the red fox (Vulpes vulpes) is well documented (Errington and Berry, 1937; Sheldon, 1950; Arnold and Schofield, 1956). However, published reports provide few details of dispersal such as seasonal timing, rates and routes of travel, proportions of the sex and age segments of the population which disperse, and amounts of social contact between transient and resident foxes. These details are essential for understanding gene flow among foxes.

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populations, range extensions, epidemiology of fox-borne diseases, and social control of dispersal. This paper reports on details of dispersal of red fox through use of radiotelemetry and other field techniques, and of social contact through computer simulation of red fox movements.

FIELD RESEARCH

Field work was conducted in the northcentral United States (Illinois, Iowa, Wisconsin, and Minnesota) during the period of 1965 through 1971 using two general methods. In the first method, foxes (mainly young of the year) were captured from underground dens (Storm and Dauphin, 1965) ear-tagged, and released at the dens. When the tags were recovered, mainly from hunters and trappers during the October–March period of each year, the location and date of recovery were recorded. The recovery information from 786 foxes, all tagged as juveniles, provided most of the data to estimate timing of dispersal, proportions of the sex and age classes which dispersed, dispersal direction, and distances traveled during dispersal. The second method involved capturing foxes in steel traps or from dens in late summer, fitting each with a radio-transmitter, and releasing the foxes where captured. Signals from the transmitters were monitored daily prior to dispersal, and dispersing animals were followed with a combination of aircraft-mounted and truck-mounted receiving equipment (Storm, 1972).

The red fox in North America tends to be restricted to discrete spatial areas (home ranges), at least during spring, summer, and early fall. Each home range is typically occupied by a family group consisting of an adult male, 1 or 2 adult females, and seasonally by young born to the females. Home ranges are about 259 to 777 hectares in size (Scott, 1943; Storm, 1965; Ables, 1969a). Sargeant (1972) indicated that neighboring family groups occupy well-defined, nonoverlapping home ranges; mutual avoidance between members of neighboring groups is apparent.

DISPERAL PATTERNS

Beginning in late September and early October, and continuing through fall and winter, some foxes, primarily young born during the preceding spring (see below), leave the home ranges which they occupied during spring and summer, and disperse through unfamiliar terrain. By mid-October, some juveniles have moved more than 32 km from their natal home range (Phillips, et al., 1972).
The onset of dispersal coincides with a marked increase in the size of nests during September and October. Venge (1959) reported that the female fox reached sexual maturity by late November and December of their first year. Since the cyclic pattern of gonadal activity is similar for adults and juveniles, the onset of dispersal corresponds not only to puberty, but also to increased gonadal activity in adult males (Stone 1972).

Most juvenile males and a substantial proportion of juvenile females dispersed from their natal home ranges. Of males which were tagged as juveniles and were recovered during their first year, 80% had moved more than 8 km from their natal home range. The corresponding figure for juvenile females was 37%. Foxes tagged as juveniles whose tags were recovered before they were 2 years old showed that 46% of males and 58% of the females went more than 8 km from their natal home range. Thus, less than 5 and 45% of the males and females, respectively, remained near the locality where they were born.

Dispersal occurred, although less commonly, among adult red foxes as well. For those ear-tagged as adults, 30% of 22 adult males and 21% of 7 adult females whose ear-tags were recovered had moved more than 8 km from where they were tagged, within the year following tagging. Only 2 of the 26 adults which dispersed were recovered more than 8 km from where they were tagged, indicating that adults tended to disperse shorter distances than juveniles. Some of the movements made by adults outside their home ranges in fall and winter may have been related to mating behavior rather than to dispersal per se.

The onset of dispersal by radio-marked animals was sudden; a disperser left its home range by traveling in a nearby straight-line course, which appeared to be in a random direction. During dispersal, some individuals moved along this course for 3 to 6 consecutive nights. Others dispersed during 1 to 7 nights, remained in an area for 1 day, and then resumed dispersal. The longest recorded period between the onset and apparent cessation of dispersal was 18 days.

The pattern of movement preceding the cessation of dispersal varied among the radio-marked animals. Some simply stopped and began to occupy a new home range after dispersing for several nights. Others traveled in a circular manner for 1 or 2 nights, returned to an area through which they had passed previously, and then apparently settled on a home range.

Travel paths during dispersal were generally straight, although the path of travel was often temporarily changed by cities and lakes. For example, the travel path of one dispersing juvenile was influenced at least four lakes (Figure 16-1). After passing around such a barrier, the course along which they had previously traveled was taken again.
traveled. Large rivers apparently formed a barrier to dispersal, while smaller rivers and creeks did not. None of the marked foxes, including both radio-marked and ear-tagged individuals, was known to have crossed the Mississippi River where it forms the boundary between Illinois and Iowa. Dispersing foxes in Minnesota, however, crossed the Mississippi River above Minneapolis. Other smaller creeks and rivers encountered by dispersing foxes in Minnesota, Illinois, and Iowa were readily crossed; movements of the animals sometimes became more erratic, and the average rate of travel decreased before the river was crossed.
Dispersing foxes traveled 10 to 16 km during a typical night of dispersal, with males moving further than females. During 33 nights of dispersal, 5 radio-marked males traveled an average of 15 km per night; 3 females traveled an average of 9 km per night during 14 nights of dispersal. When it is considered that a very high proportion of the foxes from a local population disperse, and that an individual often travels 81 km in less than 1 week, it is apparent that red fox can readily invade formerly occupied home ranges or invade new habitats. It is also apparent that dispersing foxes have a great potential for social contact with resident foxes. For example, if one assumes a high fox population density and uniform spacing of the animals, there would be about 1 male–female pair of residents per 4 km of dispersal path. A transient moving 81 km during 5 nights could thus interact with 40 or more individual resident animals.

COMPUTER SIMULATION

A field study of social contact between dispersers and residents would be extremely difficult since a very large number of foxes would have to be observed (perhaps by radio-tracking) to insure that an observed disperser would pass through the home range of an observed resident. The field problems may well be insurmountable. Thus, computer simulation was used to give preliminary estimates of the magnitude of such contact.

A computer-simulation program was developed to allow us to control the movements of dispersing and resident foxes, and to measure the potential for social contact between the simulated animals. The program (Montgomery, 1973) was written in Fortran IV, and simulations were run on a CDC 6600 computer at the University of Minnesota. The program used the same means for controlling movements of the animals as those described by Siniff and Jessen (1969).

In each simulation, a disperser attempted to pass through the home range of a resident without being close enough to the resident so that communication between them could occur. To simplify interpretation of the results, some of the factors which could influence such social contact were standardized. These included the size and shape of the home range (Figure 16-2) and the disperser’s initial location. All home ranges corresponded to an ellipse with axes of 1.6 and 2.4 km. Dispersers began their movements 0.3 km from the right home range boundary on the line of the major axis. The initial location of the resident was fixed by random processes, and could be anywhere within the elliptical home range boundary.
Figure 16-2  The beginning of each simulation. The disperser begins his movements to the right of the home range; his movements are biased so that he tends toward a point to the left of the home range (dashed circle). The resident, beginning from any point on the home range, moves about in a manner similar to the movements of real resident foxes on their home ranges. As the simulation proceeds, both the resident and the disperser move once each 5 minutes. The method for controlling movements of the simulated animals is given in the text.

Movements of the animals during the simulation were controlled by a modified random walk procedure (Siniff and Jessen, 1969; Montgomery, 1973). Both disperser and resident moved from location to location simultaneously, once per 5 minutes. At each move, directions and distances which the animals moved were determined by random choices from appropriate frequency distributions. These distributions of direction of travel and distance moved per 5 minutes were derived by radio-tracking real red fox (Siniff and Jessen, 1969).

Direction of travel of dispersers was biased by causing them to seek a point beyond the left home range boundary (Figure 16-2), so that they tended to move in a straight line across the home range at its maximum dimension. Residents moved about the home range in a manner similar to the movements of real resident foxes. A disperser could traverse the maximum dimension of the home range with about 25 moves, thus remaining on a home range for about 2 hours while traveling at about 1.2 km per hour.

Social contact between the animals depended on them being close enough to each other so that visual, vocal, and direct olfactory communication could occur. Social contact was assumed to occur each time the animals were within some distance (contact range) of each other. Use of the contact range allowed us to measure potential for visual, vocal, and direct olfactory communication; scent trails or marks
could not affect the disperser. Different values were used for the “contact range” distance (see Figure 16-4); these distances are reasonable guesses to obtain some notion of the probability of social contact between transient and the resident. In a more complete study (Montgomery, 1973), the role of various means of communication, including scent trails and marks between a resident and a transient fox was studied by computer simulation; such scent communication was not included in this report.

![Diagram](image)

**Figure 16-3** A typical sequence of movements of resident and invader taken from one of the simulations: Note that social contact would have occurred when the animals reached their respective locations marked 15, if the contact range had been approximately ½ greater.

Social contact between the animals was measured in the following way. At the end of each simulated 5 minutes (after each move) the program measured the distance between the animals and compared this distance with the contact range programmed for the simulation. When the distance between the animals was greater than the contact range, the animals continued to move. A simulation was terminated when the distance was less than the contact range, or when the disperser had passed through the home range.

The sequence of movements of a resident and a disperser during a typical simulation is shown in Figure 16-3. Twenty-six moves were required for the disperser to traverse the home range. As the disperser moved across the home range from right to left, the resident moved about near the center of the home range. None of the distances between disperser and resident was less than the contact range, thus the simulation terminated when the disperser passed the left home range boundary. Had the animals been slightly closer together at the 15th location used by each, the distance between them would have been less than the contact range, and the simulation would have terminated.
We tested 8 different contact ranges within the limits 0.05 to 0.50 miles (81 to 805 m). For each contact range, 8 different movement patterns were programmed for both resident and disperser. Because of the biased travel directions, however, the movement patterns of all dispersers were very similar. In the results of the simulations, we present data for 8 contact ranges; for each contact range, 1 disperser attempted to pass through the home ranges of 8 different residents.

No social contact between a disperser and a resident occurred when the contact range was 0.01 miles (16 m) or less, and social contact was unlikely with contact ranges of about 35 m or less (Figure 16-4). This result suggests that transfer of disease organisms such as those causing rabies, which require direct contact between the animals, is unlikely unless one or both of the foxes alters its movements to seek out the other.

Likewise, direct confrontation and communication by short-range means (reviewed by Tembrock, 1968) is unlikely to occur. These means of communication (changes in facial expression, position of the tail or other body parts, sniffing of the anal region, etc.) require that the individuals be close enough to each other to perceive fine details by sight or smell. Red fox disperse entirely at night, and often travel through heavy ground cover. The disperser would be invisible to the resident unless movements of one or both of the animals changed so as to bring them closer together.

Some means of communication which regularly reveals the location(s) of the animal(s) is necessary before altered movement pattern(s) can bring the animals closer together. Communication between disperser and resident became increasingly more likely as the contact range increased (Figure 16-4), but only if one or both of the animals chose to emit signals or to respond to signals emitted by the other. Only vocal signals would be effective; poor visibility would prevent visual communication, time required for scent dispersal would prevent direct olfactory communication, and distance between the animals would prevent communication by mechanical auditory signals produced by movement of the animals on the substrate.

If we assume that a dispersing fox attempts to travel without being detected by resident fox, it becomes clear that the disperser could avoid detection by not vocalizing as he travels. The resident might be aware that a disperser had traversed his home range by detecting the scent of a strange animal. However, by the time detection of his scent occurred, the disperser would usually have passed out of the home range.

If behavioral changes which occur when a fox begins dispersal include a reduction in response to signals which would normally lead to
avoidance of a resident fox, we can see how a disperser may move rapidly cross-country with few deviations in course resulting from social contact with residents. If this reduction occurs, a disperser can travel a relatively straight path through areas occupied by fox by ignoring vocal signals from residents, regardless of how often residents vocalize or the distance over which their vocalizations can be heard.

The straight travel paths taken by radio-marked dispersers support the view that little social control over the dispersers was exerted by residents. Had control been exerted, we would expect many changes in the direction which a disperser took, each change corresponding to an attempt to avoid further social contact with a resident. On the contrary, radio-tracking data show that foxes dispersed along relatively true courses, until they met geographical barriers such as lakes, rivers or cities.

A better understanding of the social interactions between resident and transient foxes will require more research on the ability of foxes to detect each other and respond to one another under various environmental conditions. This kind of information will provide further input for detailed computer simulation and ultimately provide further insights into the relationships between social behavior and the ecology of resident foxes.
Acknowledgments  Financial support for this study was provided by NIH Training Grant No. 5T01GM01779, and the United States Atomic Energy Commission (C00-1332-83) directed by Dr. J. R. Tester, by the Iowa Conservation Commission, and by the Smithsonian Research Foundation Grant No. 435090, directed by Dr. J. Eisenberg. We thank Dr. D. B. Sinift for advice and suggestions on all phases of this study, Drs. V. Dirks and C. Jessen for help with computer programs. Mr. M. Sunquist reviewed the manuscript.