LONG-DISTANCE HOMING IN MEADOW VOLES, *MICROTUS PENNSYLVANICUS*

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During a field experiment on density-dependent processes in meadow voles (*Microtus pennsylvanicus*), we removed 848 voles from field enclosures and released them 1,200 m away. Eleven animals (1.3%) returned to the enclosure from which they had been removed, which entailed traversing inhospitable habitat (forest, wetland), obstacles (permanent stream, roads), and climbing a 0.9-m hardware-cloth fence surrounding the enclosures. For six of the 11 voles, returning home was accomplished in >2 but <4 weeks; the others returned in ≤2 weeks. Voles returning home, which averaged ca. 30 g, lost on average 5.3% of their body mass during homing, unlike their resident counterparts, which gained mass. The voles that homed could not have used familiar objects as cues for navigation, but whether they used distant points of reference or wandered randomly is unknown. Our findings suggest that meadow voles are capable of travelling >1 km toward home, and thus, it is likely that they could travel similar distances while dispersing.

Key words: *Microtus pennsylvanicus,* meadow vole, dispersal, long-distance homing, movement distances

Animals displaced from their home ranges may return, a process known as homing. Most research on homing in small mammals has been concerned with elucidating the proximate mechanisms involved. Some support exists for both orientation using familiar cues in the environment and navigation using remote cues, such as landscape features, sun, stars, or magnetic fields (August et al., 1989; Drickamer and Stuart, 1984; Etienne et al., 1986; Fisler, 1962; Fluharty et al., 1976; Joslin, 1977; Karlsson, 1984; Robinson and Falls, 1965). Alternatively, displaced mammals may wander in random directions and succeed in finding their original home ranges by chance alone.

The evolutionary and ecological significance of homing in small mammals is poorly understood, in part because little information exists to indicate the likelihood or frequency that animals are displaced from home. However, studies of homing are useful in evaluating the capacities of animals to travel long distances over unfamiliar terrain. If animals can return home from great distances once displaced, it is likely that they have the capacity to disperse long distances away from home. The ability to travel long distances is believed to be particularly important in species such as the meadow vole (*Microtus pennsylvanicus*), which probably occupied patchy and ephemeral habitats throughout much of its evolutionary history (Christian, 1970; Getz, 1985). In such landscapes, the ability to disperse long distances through unfamiliar terrain to locate and colonize suitable habitat should have been favored by selection (Christian, 1970). The chances of finding new, suitable habitats during explorations generally may have been low, thus favoring the ability to return to known suitable habitat.

In this paper, we report data collected during an experiment in which we removed large numbers of meadow voles to control population density within field enclosures (Ostfeld and Canham, 1993, 1995). We did not expect the removed voles to return, but took advantage of their having done so to examine their capabilities of long-distance movements.

Materials and Methods

Our study was conducted in a mesic, fertile, old field at the Institute of Ecosystem Studies in Millbrook, Dutchess Co., New York (41°50′N, 73°45′W). The field had been abandoned from agricultural use in the early 1970s and mown about once per year until 1990, when we began our study. Vegetation consisted of grasses (*Bromus inermis, Poa pratensis, Arrhenatherum elatius, Phleum pratense*) and forbs (*Galium mollugo, Solanum carolinense, Glecoma hederacea, Oxallis repens, Potentilla, Hieracium pratense, Solidago*). Further details of habitat and vegetation are in Ostfeld and Canham (1993).

In May and June 1990, we built nine 40- by 40-m enclosures using 1.4-m wide galvanized hardware cloth (1.3-cm mesh) with 0.5 m extending belowground and 0.9 m aboveground. Trapping grids, consisting of 5 by 5 arrays of Longworth livetraps placed 7.5 m apart, were established inside enclosures. To detect escapees from the enclosures, we occasionally set a ring of Longworth traps surrounding the enclosures. Four percent of the 3,094 voles we marked inside enclosures were captured outside fences or moved between enclosures (Ostfeld, 1994); thus, the fences were not completely impermeable. Because holes beneath the fences were rare and filled upon discovery, we suspect that most voles that crossed fences did so by climbing.

Our study was designed to examine density-dependent processes (Ostfeld and Canham, 1993, 1995; Ostfeld et al., 1993) and consisted of experimentally reducing the density of meadow voles inside six of the nine enclosures. From early June 1990 to April 1992, we trapped for 2 consecutive days every other week. We estimated density of voles on the 1st day of each trapping session, and removed voles on day 2 to manage populations at either low or medium density, with three replicates of each. During periods of rapid population growth, we also trapped selected low- and medium-density enclosures in the intervening weeks. We marked voles with numbered metal ear tags. For each vole, we recorded tag number, gender, body mass, reproductive condition, and trap station. Most animals were released at the site of capture, but some were removed to achieve desired densities.

Voles selected to be removed were returned to their live traps until all traps had been checked, usually by late morning or early afternoon. We then placed traps in the trunk of a car and drove them in a direct path to one of two release points. Release points were in grassy fields managed by mowing once or twice per year. The straight-line distance between both release points and the field enclosures was 1,200 m. Between one release point (weather station) and the enclosures lay ca. 300 m of deciduous forest, 600 m of wetland dominated by purple loosestrife (*Lythrum salicaria*) and willows, and 300 m of grassy, lowland fields. From the other release point (Conover House) to the enclosures, ca. 50 m is forested, 800 m is wetland, and 350 m is grassy fields. A dirt road, two narrow, low-traffic, paved roads, and a permanent stream separated the release points from the enclosures. The stream is third order, has a mean annual flow volume of 1 m^3/s, and is spanned by a few fallen trees as well as a road bridge. Voles were released by opening traps and allowing animals to walk or run out; those that did not leave immediately were gently shaken out. Voles that exhibited homing were detected during the regular live-trapping schedule inside enclosures. Up to 30 voles were removed from enclosures in any given week.

Results

We removed 848 voles from six of the nine experimental enclosures and released 712 at the weather station release point and 136 at the Conover House release point. Voles were removed during all seasons in both years, with a slight peak in late summer to mid-autumn. We preferentially chose subadults (20–30 g) to remove from the enclosures (Ostfeld and Canham, 1993), although some voles were >30 g.

Eleven voles returned to the enclosures of their origin; nine from the weather station and two from Conover House. One of three voles that was removed a second time returned again. Of the 11 animals that homed, five were females and six were males; the one that returned twice was a male. Three voles returned in spring (April or May), six in summer (late June–mid September), and two in autumn (October).

None of the voles removed was captured in the ring of traps placed outside the enclosures. Thus, all voles that returned home climbed a 0.9-m-high hardware-cloth fence to enter their enclosure of origin. None of the 11 voles had climbed a fence to disperse between enclosures before being removed, and none of the voles returned to an enclosure other than that from which it had been removed.

The average (±1 *SD*) mass of voles that returned home was 30.73 ± 4.1 g, which was not significantly different from the average of all voles removed ($t_{10} = 1.82$, $P = 0.10$). Of the 11 voles, five had returned by the trapping session following that of their removal (2 weeks later), and six returned 2–4 weeks after removal. The male that homed twice returned 4 weeks after his first and 8 weeks after his second removal. On average, voles that returned home lost 1.64 ± 3.47 g, or 5.3%, of body mass between the day of removal and the 1st day captured following their return home. This loss of mass, averaging 0.28%/day, was in marked contrast to resident voles of ca. 30 g, which tended to gain ca. 1–2% of their mass each day (Ostfeld and Canham, 1995).

DISCUSSION

We do not know the mechanism by which the 11 voles might have oriented themselves and then navigated home. However, because all of the voles we removed had been born and raised within an enclosure, they could not have been familiar with habitat features at the release sites 1,200 m away (cf. Joslin, 1977; Robinson and Falls, 1965). Navigation by distant landscape or celestial features seems unlikely, because voles tend to travel beneath dense vegetation or litter, which would seriously hinder their view of distant objects. At best, their horizon is a few meters away. Orientation by auditory cues (the enclosures are near a busy road) seems unlikely because the large distance of displacement placed them out of range of road noises. If voles had begun by orienting toward the site of origin using a directional sense, a sun-compass (Fluharty et al., 1976) or magnetic orientation (August et al., 1989), they may have been able to draw close enough to orient toward local cues, such as road noise. Because only 1.3% of the 848 voles returned home, we cannot rule out the possibility that voles departed the release points in random directions, and the few that successfully homed did so by fortuitously choosing the right direction (Fisler, 1962).

Homing behavior by voles has been reported in a few studies. The maximum distance from which displaced California voles (*Microtus californicus*) homed was 183 m (Fisler, 1962). In an extensive study of meadow voles, Robinson and Falls (1965) found that none of >700 animals returned home from >427 m. Rodents such as deer mice (*Peromyscus maniculatus*), which typically occupy home ranges much larger than those of voles, show good homing ability from distances >1,500 m (Teferi and Millar, 1993). Cooke and Terman (1977) found that white-footed mice (*Peromyscus leucopus*) homed well from 335 m, but not from 671 m. Kirkland (1988:83) trapped three meadow voles in a forest clearcut that was "... at least 2.6 km from the nearest appreciable suitable habitat for this species." However, he had no direct evidence regarding distance traveled by the voles. To our knowledge, the 1,200-m homing events we observed represent the longest homing distance described for voles.

Although homing is not synonymous with dispersal, we believe our results indicate the capacity of meadow voles to travel long distances, whether that travelling is toward or away from the home range. More than one-half of the voles required >2 weeks to return home, and, on average, homing voles lost >5% of their body mass. We believe that homing was costly in terms of time and energy. Much of the distance covered by homing voles was through inhospitable habitat (forest, wetland), through suitable habitat (grassy fields) in which they could have settled, and past obstacles (stream, roads, and fences). Thus, we believe that the voles that homed were highly motivated to return. The motivation to return may have been enhanced by high-habitat quality in the home enclosures, which was due in part to our management of the populations of voles at levels considerably below carrying capacity (Ostfeld and Canham, 1995). High motivation to return home may have been advantageous for meadow voles in their historical landscapes, in which explorations may rarely have been successful in locating new, suitable patches. Whether dispersing voles experience levels of motivation similar to homing voles is not known. Nevertheless, the physical ability of meadow voles to travel >1 km through unsuitable habitat, and potentially to locate new and suitable patches is evident.

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