

Low survival of long distance dispersers of the root vole (*Microtus oeconomus*)

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In the summer of 1992, 18 males and 20 females were equipped with mortality transmitters. In the course of the summer 7 of the 18 males dispersed average 722 meters pr. dispersing (450–1000 m) night. None of the females showed any long distance dispersal. The dispersing animals seem to have a very high mortality rate during or immediately after dispersal, but survived as resident if they made it through the first couple of days.

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The importance of dispersal for both evolutionary and ecological processes is theoretically well documented (Johnson & Gaines, 1990, Stenseth & Lidicker 1992 for a review). In contrast to the extensive theoretical literature about the effects of dispersal, little data exists on the rate of long distance dispersal and the fates of dispersers, we lack good data. Most of the data published concerns short range movements which can almost be regarded as home range shifts on a very local scale (Krebs et. al 1975, McShea & Madison 1992) and records of long range dispersal are mostly anecdotal. In this study on the root vole, *Microtus oeconomus*, I have tried to answer the following four questions: 1) Who are the long distance dispersers, 2) what fraction disperses, 3) how far do they go? and 4) what are their chances of survival in comparison with resident animals?

Study site, methods and decision criteria:

The study site was 1040 m.a.s right above the timberline, in the Nore-Uvdal County of Norway. The area is characterized by mires covered by *Carex* spp. broken into patches by drier parts covered by *Betula nana* and *Salix* spp. and *Juniperus communis*, with grasses and *Vaccinium* spp. covering the ground. Root voles were studied on a trapping grid situated on abandoned farmland measuring approx. 100 × 150 × 150 m (triangle) with 70 Ugglund live traps permanently placed at suitable locations through the summer. The trapping started on 3 July 1992 and the area was trapped for two days every 9–16 days to the end of September 1992. At the start of the summer 46 animals were caught, this number being reduced to 34 animals at the end of the summer,

with a monotonic decrease. The area has not been trapped for a long time, but trapping on grids nearby in 1991, 1992 and 1993 gave autumn densities of 123, 45 and 106 animals, respectively. The variation is not as great as seen at Finse (Framstad, pers comm.) 100 km away, where there was a crash in the small mammal population during the 1991/92 winter, but the area would normally be characterized by cyclic small mammal populations.

All root voles larger than 30 grams were equipped with a radio transmitter weighing 2.7 g (Biotrack SS-2, collar type). The transmitters emitted a slow pulse-rate (1.8 sec. pulse period) when the animal was alive (and the transmitter warm), and a fast pulse-rate (0.3 sec. pulse period) when the animal was dead. A total of 18 males and 20 females received a transmitter. With this extra device on the transmitters I was able to check far more animals for the cause of death than if I had used the “see if it moves” technique to determine if the animal was dead or not.

The grid was searched almost daily in the period between 3 July and 23 Sept (60 of 82 days; longest continuous leave 4 days) with a receiver to detect missing or dead animals. The cause of death of the animals found was determined according to the following criteria:

— For animals whose transmitters were found in pellets, predation by a raptor or owl was assumed to be the cause of death. The following criteria suggest that they were taken by the European kestrel, *Falco tinnunculus*. A non-breeding pair of European kestrels were the only resident avian predators in the area. The size and positioning of the pellets also support this.

- If only the body, without the head or viscera/ part of the viscera, was found, and the vegetative cover was such as to exclude raptors, a mustelid predator was assumed to be the killer.
- If the transmitter was found in a stoat’s lair, a stoat was blamed for the killing.

However, as the area was searched with the receiver only once a day, the animals could lie dead for as long as 24 h before they were found. I could not from this method alone conclude that predators were the cause of death. The animals could have died of other causes and then been eaten. To check this, I placed 20 newly snap trapped animals in runways known to be used by voles. Of these 20 only one small 15 g animal disappeared, and all others remained untouched until they were eaten by blow fly larvae or *Sorex spp.* (approx. a week). Hence, from this I feel confident that my criteria are well suited to determining the cause of death.

The dispersers

Five out of the total of 18 radiotagged scrotal males dispersed between 21 July – 2 August, whereas none of the females dispersed (see Table 1). The dispersing males were lighter and perhaps younger than resident males (dispersers: mean = 34.8 SE = 1.0, residents: mean = 44.4 SE = 3.3, two tailed z-test for difference in means $P < 0.001$). All long distance dispersing males could be young of the year.

As seen from Table 1 all dispersal occurred between 20 July and 2 August. To give an idea of the magnitude of the number of dispersers I will

Table 1. Summary of data concerning the 5 dispersing males.

Male	Dispersal (m)	Weight (g)	Survival	Days before disp.	Trapped <30g	Date
15	900	39	22	4 (8)	yes (20g)	20 Jul.
140	1000	39	< 2	2	no	31 Jul.
124	850	28	1	4	no	22 Jul.
105	750	39	> 7	14 (6)	yes (14g)	2 Aug.
	550	—	—	—	—	—
	450	—	—	—	—	—
	600	—	—	—	—	—
20	900	36	13	4 (8)	yes (20g)	20 Jul.
	550	—	4	—	—	—

use the number of animals at the end of each trap session as a basis. By 14 July a total of 9 males had a transmitter and by 22 July 2 males had dispersed. Six animals had a transmitter on the 22 July and 1 male had dispersed by the 28 July. On 28 July 11 males had a transmitter and 2 had dispersed by the 2 August.

The dispersing animals were located alive at a mean distance of 722 metres ($SE = 65$, $n = 9$) from the last location (Table 1). This distance was traversed in one night. Animal no. 105 was special as he moved over several consecutive nights: moving about 600 metres on the first two nights, staying one night, moving again 500 metres and staying one night, and again moving 500 metres and staying one night. On day 7 the transmitter was removed from the animal. By that time the vole had moved 2.3 km on the ground, ending up about 1.8 km from the trapping grid. The animal weighed 39 g before this dispersal and weighed 35 when the transmitter was removed.

Of the five dispersers, two (nos 20 and 15) lived for 17 and 22 days respectively before being taken by mustelids. Animal no. 15 stayed at the same place where it was first located, the other moved once, viz. 550 metres 13 days after the initial dispersal.

Two (nos 140 and 124) of the five were taken the first day after dispersal by raptors. The transmitters were found in a pellet dropped by a European kestrel, and the last was removed by me.

There were too few dispersers tagged to permit any rugged analysis of survival *ovt.* to be performed. But by plotting the fraction alive as a function of days after receiving a tag or dispersing for residents and dispersers respectively, we can see the differences in survival rate quite clearly (Fig. 1). There were also great differences in the mean "lifetime" of a disperser, 12.6 ($SE 4.7$) days and residents, 40.5 ($SE 4.7$). The two survival functions were significantly different (SAS proc LIFETEST, $P < 0.05$ for Log-Rank, Wilcoxon and -2 Log (LR) test). From Fig. 1 we can also see that dispersers have a very high probability of being taken by a predator while dispersing or immediately after. But, if the animal survives this initial phase of dispersing, it seems to survive as a resident, which is quite natural since it has become a resident.

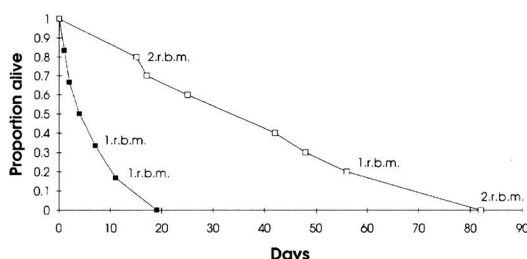


Fig. 1. Plot of fraction alive after x days. Open squares are residents and closed dispersers. "r.b.m." refers to animals removed by me. All the residents was removed at the end of the study. The R.B.M. disperser was removed after 7 days of dispersing (no. 105). The r.b.m. at day 11 is one animal that moved after staying for 11 days. For residents the proportion survival is calculated from the day they received the transmitter, for dispersers from the day they dispersed.

Discussion

Aside from having a low sample size (which is a feature of this kind of study) another shortcoming is that only animals larger than 30 g were equipped with a transmitter. This leads to a large bias if conclusions about dispersal in microtines in general were to be drawn. Since females larger than 30 g are most likely to be pregnant and already holding a territory, dispersal would not be expected for this group. Males, on the other hand, seem to mature later (Lambin 1993, Yoccoz et al. 1993), and do not have such fixed territory boundaries (Ims et al. in rev, Lambin et al. 1992).

Daly et al. (1992) stressed the importance of the adverse effects of the tags. Earlier studies on *Microtus pennsylvanicus* by Webster & Brooks (1980) showed that animals' survival was affected by the transmitters only in the winter time when food was scarce. Since this study was carried out in the summer I feel the results reflect the natural survival rate. Also, in this study I compare the fate and weights of animals all having transmitters. Thus, if it has an effect, it will have the same adverse effect on both dispersing and resident individuals.

In spite of its weaknesses, a striking finding is that all the dispersing male root voles (*Microtus oeconomus*) moved quite far when dispersing a longer distance. A mean of 722 m per night is very

far compared with the previous dispersal movements that have been reported. Mostly, dispersal distances less than 50 m are noted and rarely as much as 100 m (McShea & Madison 1992, Lambin 1994). These earlier results are probably constrained by the size of their trapping grids, and thus do not give good estimates of dispersal distances for mature males. Lambin (1993) reported that only 9% of the males matured inside the grids in his quite extensive study on Townsend's vole *Microtus townsendii*, and the rest were never seen. This study might throw some light on the fate of the large proportion of disappearing males, but before any firm conclusions can be drawn, more extensive studies are needed.

I suggest that future studies on the fate and success of dispersing animals could be carried out using the described technique and a suitable work force. Also, using the transmitters described (with the thermocouple) in all kinds of radio-tracking studies not necessarily aimed at finding the cause of death would give as a by-product data required on survival rates and the cause of death in small mammals.

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