Z. Säugetierkunde 59 (1994) 342–348
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ISSN 0044-3468

Fates of fossorial Water voles, *Arvicola terrestris*, as revealed by radiotelemetry

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Receipt of Ms. 28. 2. 1994
Acceptance of Ms. 18. 7. 1994

Abstract

The fates of 94 fossorial water voles were studied in Switzerland from 1984 to 1986 using radiotelemetry. Fifty-six individuals were recaptured on the study plots at the end of the radiotracking sessions. Taking into account that 34 individuals either died, dispersed or were killed by predators, the fates of 95.7 % of the voles could be assessed, as compared to only 59.6 % if losses were tallied by classical capture-recapture analysis. In most cases, death in situ (10 cases) could be distinguished from the 13 recorded cases of predation (including 4 cases of predation on dispersers). Only 4 tags (4.3 %) were lost. Moreover, the position of the tags and the marks left on the radio-collars allowed the identification of mammalian and avian predators in most cases of predation. Finally, the fates of the 15 dispersers could also be assessed.

Introduction

Dispersal and predation strongly affect population dynamics of small rodents (Lidicker 1985; Krebs 1992; Pearson 1985; Korpimäki 1993). Unfortunately, classical trapping data do not allow the distinction between losses due to mortality and to dispersal. Moreover, mainly because of technical limitations, actual rates of dispersal or of predation are difficult to estimate. Therefore, there is still little data reported from natural populations. However, the recent widespread use of radiotelemetry in small mammal studies allows one to investigate these questions in greater detail (Madison et al. 1985; McShea 1990; McShea and Madison 1992).

The water vole, *Arvicola terrestris*, is a widespread Palaearctic species that presents various ecological forms (review in Reichstein 1982). Contrasting with the lowland populations of *A. terrestris* that are semi-aquatic and live in wet habitats (Wijngaarden 1954; Pelikan and Holisova 1969; Stoddart 1970; Wieland 1973), the fossorial populations (*A. t. scherman*) occur in dry habitats in mountainous parts of Central Europe (Meylan 1981). Fossorial water voles live permanently in underground burrows in grasslands and meadows and they differ from the aquatic populations by many features, including body size, population dynamics, social and mating behaviour (reviews in Reichstein 1982; Saucy 1994a), as well as genetic variability (Saucy et al. 1994). Furthermore, the fossorial populations undergo multiannual fluctuations in density with an unusually long cycle that lasts for 6 years, on average (Saucy 1988a, 1988b, 1994b).

The aim of this study was to investigate the fates of radio-collared fossorial water voles under natural conditions during the course of a multiannual cycle. In this study, data are reported that were collected during experiments conducted in fossorial populations of the water vole in the Jura mountains, as well as the Swiss Alps. In the Jura mountains, the fates of radio-monitored voles were assessed during a decline, a period of low numbers, and the beginning of the increase phase, whereas in the Swiss Alps voles were studied during phases of high density.

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Material and methods

Population estimates

Before the beginning of a radiotracking session, population numbers were estimated during two-day live-trapping sessions using the capture-mark-release sampling technique adapted for *A. t. scherman* by Airoldi (1976, 1978). In all cases, densities (individuals/ha) were computed as the number of captured voles divided by the surface of the plots actually sampled (Tab. 1). Because of the diversity in density conditions (< 1 ind/ha–> 300 ind/ha), varying areas have been sampled during the different experiments. At Les Cluds (near Bullet, Jura Mountains, Switzerland, 1200 m, Tab. 1), where radiotelemetry was applied as a complementary technique during the course of a long-term population study (1982–1986; Saucy 1988a), population changes were monitored monthly (April–November) on a 0.16 ha quadrat (40 m × 40 m) and three times a year on a larger rectangular 0.5 ha grid (20 m × 200 m) (May, August and October; Saucy 1988a). Following the decline of the population that occurred in 1984 (the populations became extinct in the above grids), trapping was extended to the remainder of the grassland (15 ha). In the four localities from the Swiss Alps, population densities were estimated on rectangular grids ranging from 0.13 to 0.20 ha.

Table 1. **Study sites, dates, duration of the experiments, density, and phases of the population cycle**

Exp. No.	Location (coordinates)	Dates	Duration of the experiments (days)	Density (ind/ha)	Phase of the cycle
1	Les Cluds (6° 34′ E 46° 51′ N)	7. 6.–25. 10. 1984	35	50	Decline
2	Les Cluds	22. 5.– 5. 7. 1985	56	< 1	Low numbers
3	Les Cluds	17. 8.– 4. 9. 1986	19	20	Increase
4	Flendruz (7° 10′ E 46° 30′ N)	15. 8.–21. 8. 1985	7	185	Peak
5	La Comballaz (7° 04′ E 46° 23′ N)	28. 9.–23. 10. 1985	26	311	Peak
6	Le Sépey (7° 03′ E 46° 23′ N)	12. 7.–21. 7. 1986	10	171	Peak
7	Rougemont (7° 14′ E 46° 29′ N)	31. 7.– 6. 8. 1986	7	300	Peak

Radiotelemetry

Following the technique described by several authors (Brooks and Banks 1971; Banks et al. 1975; Madison 1977; Mineau and Madison 1977) 94 voles were equipped with radio-collar transmitters. Ten SM-1 (AVM Instrument Co., Ltd, Livermore, USA) and 10 SS-1 (Biotrack, Wareham, UK) transmitters were used during this study. The tags, weighing 3–4 g and transmitting in the 148–149 MHz frequency band, were powered by 85 mAh batteries that lasted for 35 days, on average. They were shaped with a dental acrylic resin to fit the throat of the voles. Spent batteries were replaced by dissolving the resin in acetone. The radio-collars were fitted around the necks of the animals under ketamine anaesthesia (5 mg/100 g of body weight). The voles were then held in cages overnight to permit recovery from the anaesthesia. Two 3-element Yagi antennae and a LA12-DS (AVM) radio-receiver were used to detect transmitting voles at a range of 50 m to several hundred meters depending on the local conditions. Implant-type transmitters, used by other authors (Mihok et al. 1988; Madison et al. 1985), were tested and soon discarded because of an approximately 10-fold reduction in detection range. In order to minimise disturbance, the two Yagi antennae were mounted on tripods and were placed within a range of 20 to 30 m of the voles in such a position that the bearings formed an approximately 90° angle. Localisations of voles were mapped using a reference grid of stakes placed at 2.5 m intervals. Variation in the signal intensity and in the rhythm of transmission enabled determination of whether an animal was active or resting. Voles found to be inactive for more than 5 successive localisations were considered to be dead animals. The radio-collars were then searched out and the causes of deaths were determined. Individuals that left their home-ranges to settle at a distance in new burrows and that were never relocated in their former home-range were classified as dispersers.

Radiotracking sessions

Voles were radiotracked during long-term (up to 8 weeks), as well as short-term (1–4 weeks) sessions (Tab. 1). Long-term sessions involved the few and isolated individuals that could be trapped during the population decline (1984) and the period of low numbers (1985) at Les Cluds (Exp. 1–2; Tab. 1). The animals were monitored once a day or every second day and the sessions were terminated by the death or the disappearance of the animals. During short-term sessions, a selection of 10 to 20 voles, including all those individuals living in a restricted area, were studied simultaneously. These short-term sessions were carried out in the four Alpine localities in 1985 and 1986 and in the Jura mountains in 1986 (Exp. 3–7; Tab. 1). During these experiments, the voles were monitored 3–4 times each day during the 1-week sessions or every second day during the 3- or 4-week experiments.

Finite survival and mortality rates have been estimated for each session. According to Krebs (1989), all rates have been converted into standard time intervals (7 days). The following rates have been considered: 1) Gross survival rates = number alive at the end of a radiotracking session/number of radiocollared individuals released at the beginning of the experiment, 2) Disappearance rate = 1 – gross survival rate. The latter has subsequently been partitioned into death, dispersal and predation rates according to the primary causes of disappearance from the study plots.

Results

At Les Cluds, the population peaked in 1983 (150 ind./ha), declined in 1984 and was nearly extinct in 1985 (Saucy 1988a). No voles could be caught on the 0.5 ha grid in 1985 and extensive additional trapping carried out in the 15 ha neighbouring the grid did not yield more than 7 individuals (0.5 ind/ha; Saucy 1988a). In the Alps, the high densities (> 150 ind/ha) recorded in the four localities suggest that these populations were in a peak phase (Tab. 1).

The fates of the 94 voles that were monitored in all five localities during seven distinct experiments are shown in table 2. Globally, 56 voles (59.6 %) were recaptured alive within the limits of their trapping grid at the end of the experiments, while 10 animals (10.6 %) died in their burrows, 9 individuals (9.6 %) were killed on the study site by a predator and 15 animals (16.0 %) dispersed. The fates of only 4 voles (4.3 %) remained unexplained. These animals disappeared from their burrows and the transmitters could not be located over several square kilometres of surrounding terrain.

Including 4 animals that were killed after having dispersed, 13 cases of predation were recorded during the study (Tab. 2). The level of predation was possibly highest at Les Cluds in 1985 (Exp. 2). Two of the 3 monitored voles were killed by stoats and the fate of the third animal, although unknown, might also be explained by predation (a foraging stoat was observed in the close vicinity of the study plot a few hours before the vole

Table 2. **Fates of the 94 radiotracked voles**

The primary causes of disappearance from the study plots are indicated in columns 4–6, while the fates of the dispersers are given in column 8

Experiment No.	Number of voles radio-tracked	Alive on site	Dead in situ	Killed by a predator	Dispersed	Unknown fate	Killed or disappeared after dispersal
1	14	3	6	1	3	1	2
2	3	0	0	1	2	0	2
3	16	10	0	1	5	0	1
4	11	9	0	0	2	0	0
5	20	12	3	4	0	1	0
6	16	13	0	1	2	0	0
7	14	9	1	1	1	2	0
Totals	94	56	10	9	15	4	5

Table 3. **Finite weekly rates of gross survival and of apparent mortality**

Disappearance rates have been partitioned into 3 components (death, dispersal and predation) according to the primarily identified causes of disappearance (i.e. columns 4–6 of Tab. 2). All rates have been converted into standard 7-day time intervals

Exp. No.	Gross survival rate	Disappearance rate	Death rate	Dispersal rate	Predation rate
1	0.73	0.27	0.15	0.07	0.02
2	0.87	0.13	0.00	0.09	0.04
3	0.84	0.16	0.00	0.13	0.03
4	0.82	0.18	0.00	0.18	0.00
5	0.87	0.13	0.05	0.00	0.06
6	0.86	0.14	0.00	0.09	0.05
7	0.64	0.36	0.07	0.07	0.07
Mean (± sd)	0.81 (0.09)	0.19 (0.09)	0.04 (0.06)	0.08 (0.04)	0.04 (0.02)

disappeared). Several cases of predation were also observed at Les Cluds in 1984 and at La Comballaz (sessions 1 and 5) where 3 and 4 of the monitored voles were killed by predators. In the former case, two individuals were caught by predators after having dispersed. Overall, 4 of the 15 dispersers (26.7 %) were killed or disappeared soon after dispersal.

Voles disappeared from the study plots at an average rate of 0.19 per week (Tab. 3; extremes ranging between 0.13 and 0.36). On average, deaths, as well as predation on site contributed to approximately 20 % of weekly losses, while dispersal accounted for approximately twice this amount.

In most cases the predators could be identified owing to the localisation of transmitters and to marks left on the tags. In seven cases, predation was attributed to domestic cats *Felis silvestris* f. *catus*, which, when predating on voles, left many clearly visible biting or chewing marks (little holes) on the collar. The tags were often relocated in barns or houses. Predation by the stoat, *Mustela erminea*, was suspected on several occasions, but could be established beyond doubt in only two cases (at Les Cluds in 1985). In both occurrences, biting marks, similar to those left by cats, were found on the collars. The prey was either devoured in the nest or conveyed over a distance and hidden under a mound of stones. Finally, four cases of predation by avian predators were recorded on the basis of the distinctive marks left by the birds' beaks on the collars. In one case, the transmitter was relocated on a tree. The actual avian predator could be visually identified in three cases. Predation was then attributed to the common buzzard, *Buteo buteo*, in two cases, to the black kite, *Milvus migrans*, in one case, and once to an unknown nocturnal avian predator.

Discussion

It has been frequently reported from vole studies, that a high proportion of animals disappears between successive trapping sessions (reviews in Krebs and Myers 1974; Taitt and Krebs 1985). Few studies, however, have attempted to quantify the relative impact of predation and of dispersal on the vole population dynamics under natural conditions.

Among others, Hilborn and Krebs (1976), using radioactive tags, were mostly unsuccessful in explaining the fates of disappearing meadow voles (*M. pennsylvanicus*) during a population decline, while Mihok et al. (1988) were unable to determine the death causes of radio-tracked individuals. In contrast, McShea (1990), in a pooled analysis of three different studies on *M. pennsylvanicus*, reported estimates of losses to predation varying between 14 and 41 % of the radiotracked voles. Correspondingly, unexplained losses, however, ranged between 22 % and 36 % (McShea 1990).

Apart from this study, radiotelemetry has been used in previous studies on *Arvicola terrestris* by Leuze (1976) and by Jeppsson (1986, 1990). Both authors, however, studied aquatic populations (in Scotland and Sweden, respectively) and only the former used this method in a demographic perspective. Therefore, the results reported here provide the first estimates of predation and of dispersal in *A. t. scherman* using radiotelemetry.

In this study, I was able to explain the fates of 90 out of the 94 (95.7 %) individuals that were monitored. Moreover, the predator could be identified in 12 of the 13 (92.3 %) instances of ascertained predation. Besides the 19 individuals that died or were killed by a predator in situ, 15 voles dispersed and had left the study plot by the end of the experiment. If these populations had been monitored by trapping, only 56 individuals (59.6 %) would have been recaptured within the study area. Therefore, the fates of 40.4 % of the voles would have remained unexplained instead of only 4.3 % in this study.

Moreover, and in spite of the few numbers involved, these results indicate that dispersal is a risky event in *Arvicola terrestris*, since 4 of the 15 dispersers (26.7 %) were eventually killed by predators. This finding confirms observations made by Leuze (1976) who recorded even higher losses due to predation (mainly from herons) during the dispersal phase of young water voles (up to 50 % of dispersing females).

Several interpretations can be invoked to explain the fates of the voles that disappeared. Transmitter failures can be dismissed, as the voles would have been recaptured in their burrows. It is possible, although unlikely, that the tags suddenly stopped functioning following the death or the dispersal of an animal. Long distance dispersal movements are similarly unlikely. Fossorial water voles usually disperse within 30 to 100 m (Saucy 1988a) and transmitters were searched over large areas, encompassing several hundreds of metres around the study plots. A likely explanation is that the voles were killed by predators that either damaged the transmitters or conveyed them over large distances. Foxes, *Vulpes vulpes*, which were common on the study sites could be, among others, responsible for damaging tags when preying on *A. t. scherman*. The transports of tags over long distances (200–800 m) by various predators (including domestic cats, stoats and avian predators) were recorded on several occasions.

There is a strong trophic relationship between the stoat and the fossorial form of the water vole (Debrot 1981). Stoat populations undergo cyclic fluctuations lagging 1 year behind those of *A. terrestris*. The impact of the stoat on populations of *A. terrestris* is likely to be especially high during declines and periods of low numbers. Although the data are few, this study supports the hypothesis that stoats, which reach their highest densities at the end of the population peaks of *A. t. scherman* (Debrot 1981), might drive already declining populations to extinction. During the course of this study, the few voles that were found to survive the decline at Les Cluds were suspected to have been killed by stoats (Saucy 1988a).

In conclusion, the present study provides preliminary estimates of survival, dispersal and predation rates in *A. t. scherman* using radiotelemetry. It also confirms the potentially strong impact of predators on the population dynamics of this vole. This suggests a role for predation in the unusually long population cycle reported in this species.

Acknowledgements

This study was carried out during the course of a PhD thesis supported by the Station Fédérale de Recherches Agronomiques de Changins, Nyon, Switzerland. I am very grateful to Dr. A. Meylan who supervised the study and to G. Mayor and J.-L. Bertholet for their technical and field assistance. I also would like to thank Drs. J.-P. Airoldi, R. K. Rose and A. Buchala who read and greatly improved earlier drafts of the manuscript. Anonymous referees made helpful comments. The summary was translated into German by M. Krieg.

Zusammenfassung

Erfassung von Einzelschicksalen bei Ostschermäusen (Arvicola terrestris) mit Hilfe der Radiotelemetrie

Mittels Radiotelemetrie wurde in der Schweiz von 1984 bis 1986 das Leben von 94 Ostschermäusen (*Arvicola terrestris scherman*) verfolgt. Am Ende der Radiotelemetrie-Versuche konnten in den Untersuchungsparzellen 56 Individuen wieder gefangen werden. In Anbetracht der Tatsache, daß 34 Individuen entweder starben, auswanderten oder durch Prädation getötet wurden, konnte das Schicksal von 95.7 % der Schermäuse beurteilt werden, im Gegensatz zu 59.6 %, wenn die Verluste mittels der klassischen Fang-Wiederfang-Methode erfaßt worden wären. In den meisten Fällen konnte der Tod in situ (10 Fälle) vom Tod durch Prädation (13 Fälle) unterschieden werden. Nur vier Radiosender (4.3 %) gingen verloren. Darüber hinaus konnten in zwölf von 13 Fällen die Art der Säuger- und Vogelprädatoren bestimmt werden. Zur Identifizierung der Prädatoren wurden die Position der Radiosender und die auf den Halsbändern hinterlassenen Spuren verwendet. Schließlich wurde auch das Schicksal der 15 Auswanderer beurteilt.

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