Juvenile dispersal in the vole Arvicola terrestris during rainy nights : a preliminary report

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Juvenile dispersal in the vole *Arvicola terrestris* during rainy nights: a preliminary report

by

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Résumé.–SAUCY F. et SCHNEITER B., 1997. Dispersion juvénile chez la forme fouisseuse du campagnol terrestre (*Arvicola terrestris*) durant les nuits de pluie: rapport préliminaire. *Bull. Soc. vaud. Sc. nat. 84.4*: 333-345.
Nous rapportons ici un mécanisme méconnu de dispersion pour la forme fouisseuse d'*Arvicola terrestris.* Dans le but d'estimer l'importance de la dispersion à la surface du sol de ce rongeur, nous avons disposé nos pièges à intervalles réguliers le long de barrières d'interception similaires à celles utilisées pour la protection des batraciens lors de leurs migrations printanières. Cette technique nous a permis de capturer plusieurs centaines d'individus durant 100 jours de piégeage ininterrompu. Nos observations indiquent que ce sont essentiellement les jeunes sujets qui se déplacent en surface. De plus, le fait qu'ils sont apparus dans nos pièges par vagues successives durant les nuits de pluie suggère que la dispersion est un phénomène discret déclenché par la pluviosité. Nos observations, de même qu'une réinterprétation des données de la littérature, indiquent qu'un tel mécanisme de dispersion pourrait être largement répandu chez les micromammifères.

Abstract.–SAUCY F. and SCHNEITER B., 1997. Juvenile dispersal in the vole *Arvicola terrestris* during rainy nights: a preliminary report. *Bull. Soc. vaud. Sc. nat. 84.4*: 333-345.
Using traps set at regular intervals along drift fences and operated continuously during 100 days, we were able to catch significant numbers of fossorial *A. terrestris* above the ground. Our observations indicate that young water voles disperse *en masse* above the ground. Furthermore, these dispersal movements occur mostly during rainy nights.

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Introduction

In mountainous regions of Central Europe (Alps, Pyrenees, Massif Central, Carpathians), the water vole, *Arvicola terrestris*, present small fossorial forms which inhabit mesic oldfields and other open habitats. This small (adult weight 65-150 g) fossorial vole lives in grasslands and meadows where it digs burrows similar to those of moles or pocket gophers. For that reason, *A. terrestris* has long been considered to be a pest by farmers who used to catch this vole with special pincel traps set inside its underground tunnels. This tradition has been applied at least since the 16th century (Körner 1993) and modern efficient sampling techniques still rely on traps being set within the vole tunnels (Pascal and Meylan 1986 for a review of the sampling techniques developed during the last 30 years).

Dispersal in this vole has been little studied. Recaptures of marked individuals and radiotracking data indicate that fossorial *A. terrestris* move over short distances, mostly within 30 to 50 m with a few occasional movements exceeding 100 m (Airoldi 1978, Saucy 1988). However, the high turnover of individuals in populations studied by Airoldi (1976, 1978), Fichet *et al.* (1989), Pascal and Boujard (1987) and Saucy (1988) suggests that our understanding of dispersal is still incomplete. Saucy (1988) suggests that populations of fossorial *A. terrestris* can be divided into two fractions: resident and transient individuals. On the one hand, there are individuals which are well established in burrows. They usually breed and have long residence times. These voles can be caught repeatedly within a few hundred square meters during several months (up to two or three years in a few cases). On the other hand, there are individuals with short residence times, which are only caught during one or two successive trapping sessions. The latter are usually young individuals, either born from local breeders or immigrants looking for suitable sites on which to settle. The fates of these young voles have been little studied and the conditions of their dispersal remain unknown.

Only a few attempts have been made to catch fossorial *A. terrestris* in traps set above the ground. Although this approach is generally considered to yield poor results (Pascal and Meylan 1986), reports indicate that these voles can occasionally be caught in such conditions (Pascal 1981), as well as along drift fences used for catching migrating amphibians (Gibbons and Semlistsch 1981, Marchesi *et al.* 1996, J.-C. Monney and J. Studer, pers. comm.). In order to determine whether fossorial *A. terrestris* disperse in significant numbers above the ground, we attempted to intercept dispersing individuals in traps set above the ground along such drift fences.

Materials and Methods

Observations were conducted in two permanent grasslands partly surrounded by woods near Magnedens, canton of Fribourg, Switzerland (46° 44' N, 7° 05' E). At the beginning of the experiments (March 1997), the density of mounds of earth (or "molehills"), of holes and of underground tunnels indicated that these plots were almost completely colonised by fossorial *A. terrestris*. In these grasslands, we fenced two 50 m x 50 m (0.25 ha) grids (FG1 and FG2, fig. 1). Fences were also established in the vicinity of the grids, along forest

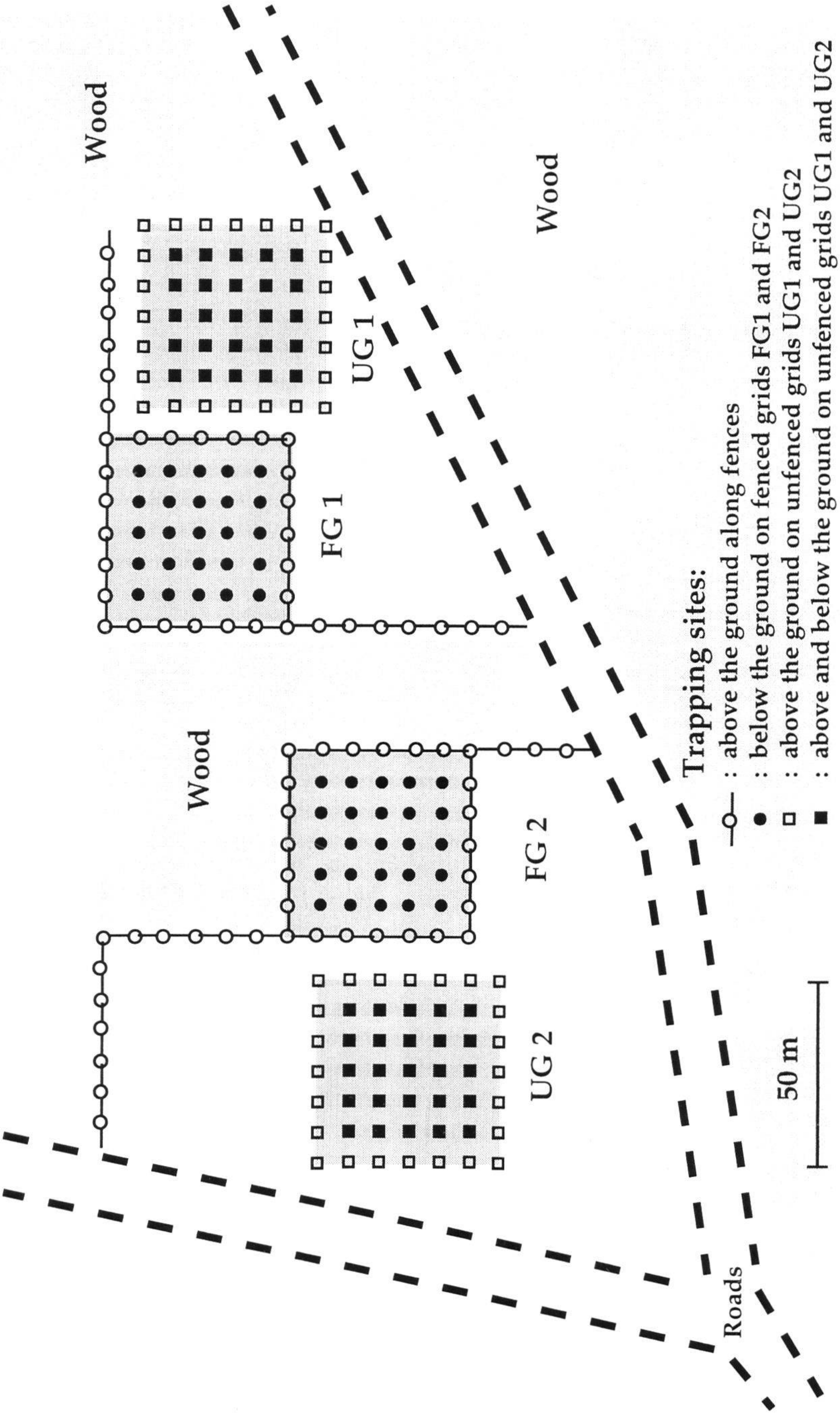

Figure 1.–Map of the study site.
FG1, FG2: fenced grids 1 and 2; UG1, UG2: unfenced grids 1 and 2.

edges and along the limits of meadows used by different farmers. The fences (40 cm high) were made of 50 cm wide plastic sheets buried 5-10 cm into the soil. Therefore, voles living on either side of the fences could possibly freely move from one side to the other side of the fences using their underground tunnels. In addition, two unfenced control grids (UG1 and UG2) were also established in the vicinity.

Below-ground capture-mark-recapture
In order to get estimates of the resident populations, the four grids were sampled at 4-6 weeks intervals using the below-ground capture-mark-recapture technique developed by AIROLDI (1976, 1978) for fossorial populations of *A. terrestris*. Using this non-destructive technique, voles were caught using Sherman traps set in communication with the underground tunnels. Because *A. terrestris* is as active during the daytime as during the night (AIROLDI 1979), the traps were operated from dawn to dusk. A typical trapping session lasted for 2-3 days with traps being checked every other hour from 9 a.m. to 5 p.m. On each grid, twenty-five below-ground trapping stations restricted to the 25 inner points of the grids were established with 8.33 m spacing intervals (fig. 1). At each trapping station, the ground was searched for tunnels in a quadrat of 5 m x 5 m using a boring tool. Two traps were set in holes dug into the ground when tunnels were found. The four grids were sampled alternatively. Animals were individually marked using ear-tags, weighed, checked for sex, age and reproductive condition and released in their underground tunnels. Three age classes are usually recognised for fossorial *A. terrestris* on the basis of body weight: juveniles (<45 g), subadults (45-64 g) and adults (>65 g; AIROLDI 1976, 1978, SAUCY 1988). Growth curves established in the laboratory by MOREL (1981) and previous observations of voles under field conditions (SAUCY 1988) indicate that voles weigh about 40 g when 3-4 weeks old and reach approximately 60 g 3-4 weeks later.

Above-ground capture-mark-recapture
Thirty-nine and thirty-seven trapping stations were established at 8.33 m intervals along the fences in grasslands 1 and 2, respectively (fig. 1). At each trapping station, four traps were set above the ground (two on each side of the fences with openings in opposite directions), corresponding to a total of 304 traps. Unbaited Sherman and Longworth traps were used. Traps were operated continuously for six months starting on March 23rd 1997. They were checked twice a day (from 7 a.m. to 9 a.m. in the morning and from 7 p.m. to 9 p.m. in the evening). Voles caught along the fences were marked as above and released on the opposite side of the fence. Using this approach in combination with fences not buried too deeply, we expected to reduce a possible fence effect (unusually high numbers in fenced enclosures; KREBS and MYERS 1974). Additionally, trapping above the ground was also conducted on the two unfenced control grids (UG1 and UG2, fig. 1). Fourty-nine trapping stations of two traps each, spaced at similar 8.33 m intervals, were established on each of them. Above-ground trapping was not as intensive on the unfenced grids as along the fences. Because of the limited number of traps, it was conducted alternatively on each of them and was also interrupted at times to allow farmers to harvest the grass.

Meteorological data
We used the temperature and rainfall data automatically recorded at the Agricultural Station of Grangeneuve, near Posieux, located approximately 5 km from our study site. From May 22nd, we also recorded rainfall using a rainfall gauge to correct for differences between the two locations.

Results

Trapping below the ground
In this preliminary note, we report results for the first 100 days of the experiment, i.e. from 23 March 1997 (when the fences were established) until the end of June 1997. During this period, two sessions of below-ground trapping were conducted on fenced and unfenced grids (one session only for UG2; Table 1). When we started the experiment, the number of below-ground voles was approximately three times greater in grassland 2 than in grassland 1 (table 1). Numbers increased between trapping sessions 1 and 2, moderately on grassland 2 and by a factor 3 on grassland 1. We estimated that with our below-ground trapping design we sampled most burrows within quadrats of approximately 40 m x 40 m, i.e. within 1600 m^2 or 0.16 ha on each grid. We then calculated rough density estimates which we consider to be conservative values. These estimates indicate that density ranged from 30 to 190 ind./ha during session 1 and reached approximately 100-300 ind./ha one month later.

Table 1.–Numbers of individuals captured below the ground on the four grids. FG1, FG2: fenced grids 1 and 2; UG1, UG2: unfenced grids 1 and 2.

	Trapping session 1			**Trapping session 2**		
Grid	**Dates**	**N ind.**	**(adults)**	**Dates**	**N ind.**	**(adults)**
FG1	25-27.3.1997	5	(5)	30.4-2.5.1997	15	(8)
UG1	1-3.4.1997	11	(8)	5-7.5.1997	33	(14)
FG2	5-8.4.1997	30	(21)	13-15.5.1997	47	(28)
UG2	8-10.4.1997	22	(19)	no trapping		

Trapping above the ground
We report here summary results of trapping above the ground using pooled data for the two grasslands. A detailed analysis of captures on the different plots will be provided elsewhere. Trapping above the ground was unexpectedly successful with 511 captures and recaptures of 328 *A. terrestris*. Most captures (453, i.e. 88%) occurred during the night and mostly along the fences. More surprisingly, highest capture numbers were registered during nights with heavy rainfall, often after periods of relative drought. The highest number, 50 voles, was recorded on June 8th after a strong and sudden storm which produced a 53 mm rainfall. On 8 occasions, we caught more than 15 voles, yielding a total of 226 captures, which means that approximately one half of the captures were recorded during 8 of our 100 trapping nights.

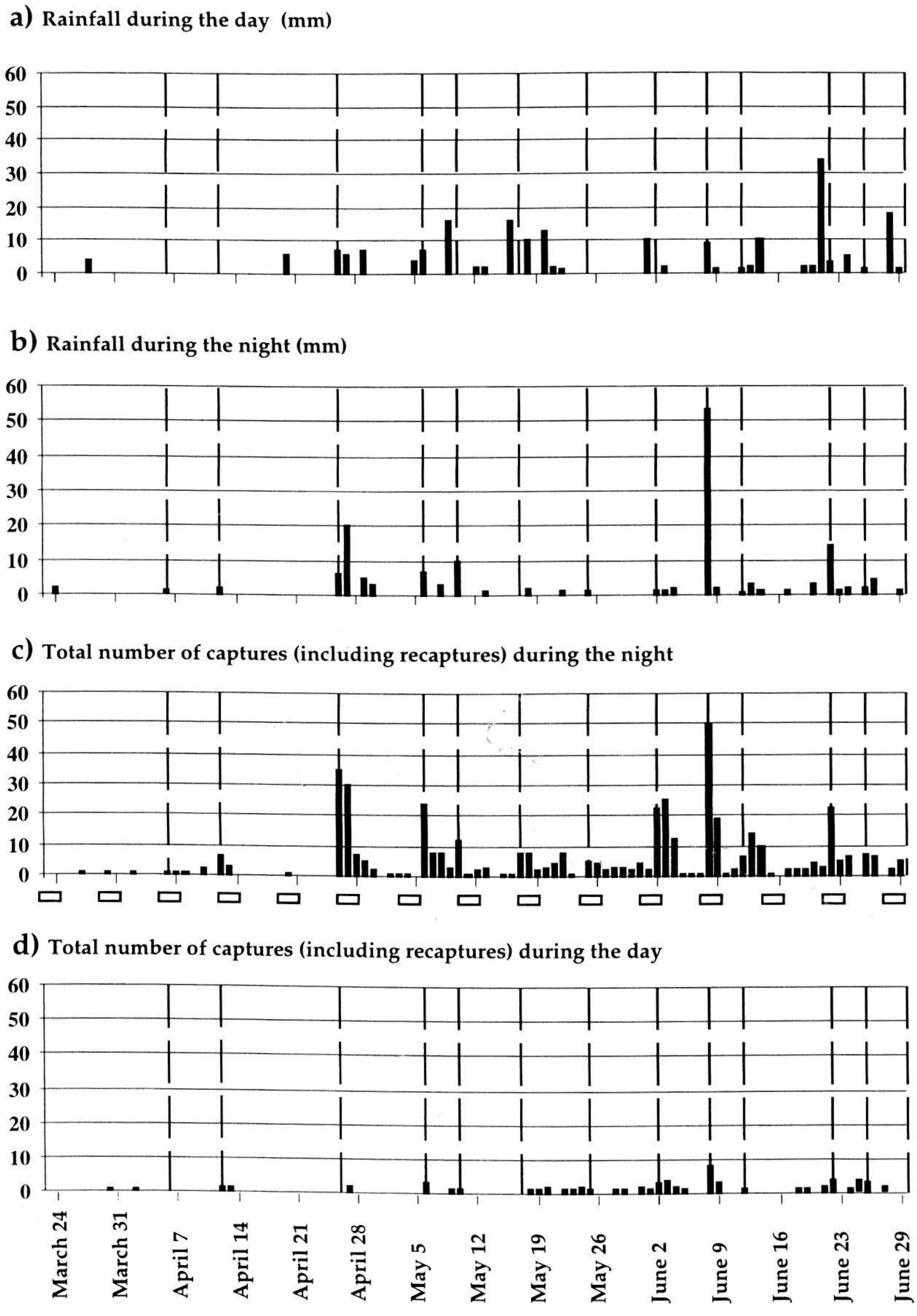

Figure 2.–Distribution of daily numbers of captures of fossorial *A. terrestris* above the ground during the first 100 days of study in relation to rainfall.

Results are given separately for the night and the day. Changes in the astronomical duration of day have been taken into account to distinguish nocturnal from diurnal rainfalls i.e. night: 7 p.m.–6 a.m. in March, 8 p.m.–5 a.m. in April, 9 p.m.–4 a.m. in May and June. Seven-day intervals are shown on the horizontal scale; ticks correspond to Mondays. White rectangles indicate weekend nights (Saturday–Monday). Dashed lines enhance major rainy nights and correspondences with number of captures.

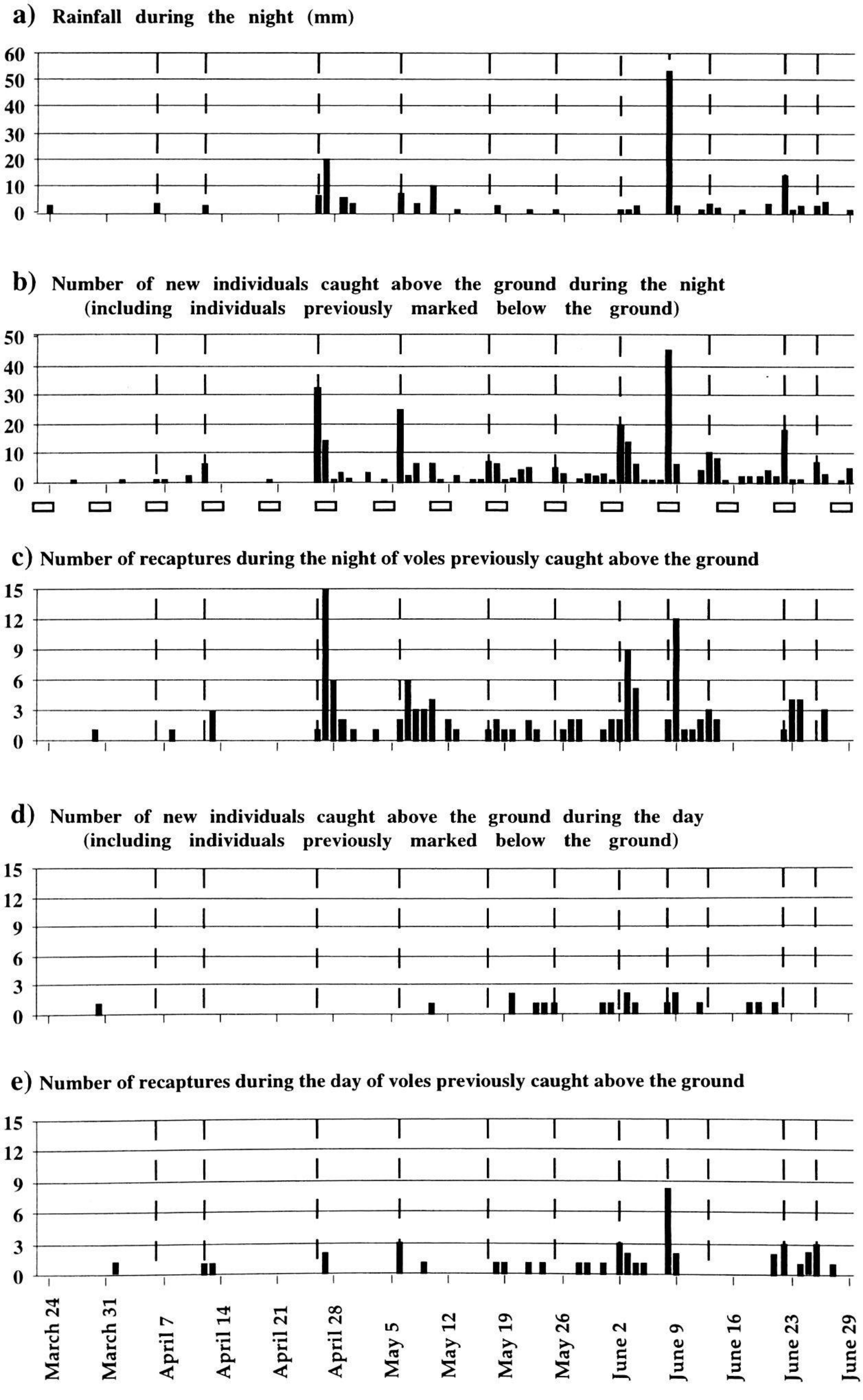

Figure 3.–Distribution of daily numbers of captures of unmarked and marked individuals above the ground during the first 100 days of study in relation to nocturnal rainfall. Same legend as Figure 2.

Interestingly, the number of captures often remained high during one or two nights following a sudden increase in captures and decreased thereafter rapidly to previous low levels. In three instances, we recorded more than 15 captures during two consecutive nights, which means that the 8 nights with high numbers of captures correspond to only 5 major events. The distribution of the captures during the day and during the night in relation to rainfall is shown on figure 2. Dashed lines enhance the correspondences between rainy nights and numbers of captures.

Figure 3 shows the distribution of the captures of unmarked individuals, as well as their subsequent recaptures above the ground during the following nights and days. Most voles caught during sudden increases in numbers were unmarked individuals (fig. 3b), whereas during the following nights we mostly caught recaptures (fig. 3c). This indicates that the new voles marked during a sudden increase in numbers were still wandering in the vicinity of our study plots during the following days. Recaptures above the ground of voles previously marked during below-ground trapping sessions were not numerous (17, i.e. 5.2%). Similarly, few voles initially caught above the ground were recaptured later in burrow systems. It is also noteworthy that very few individuals were caught for the first time between 7 a.m. and 7 p.m. (fig. 3d). Most voles caught during the daytime had already been marked during a preceding night (fig 3e).

Finally, it is worth mentioning that only a few previously marked individuals were caught during these nights of sudden increase in capture numbers (fig. 3c). They correspond, as a close examination of the data revealed, to voles that had already been caught above the ground during a previous rainy night and had probably not found a suitable burrow in which to settle in the meantime. The details of movements between grids and through the woods will be presented elsewhere.

Age and sex classes

Among the 209 individuals caught for the first time above the ground between March 23rd and June 4th, 26 were classified as adults (12.4%), 129 as subadults (61.8%) and 54 as juveniles (25.8%). This indicates that a large majority of voles caught above the ground were young individuals (not older than 6-8 weeks). No bias in sex-ratio could be found among these young individuals (88 males and 95 females). Figure 4 shows the weight distribution of the voles caught above and below the ground during the same period. It appears that adults were largely under-represented in the samples caught above the ground as compared to below-ground samples.

Other species

Although *A. terrestris* was the dominant species in our above-ground samples, other small mammals were also occasionally caught, among which the voles *Microtus arvalis* and *Clethrionomys glareolus*, the wood mice *Apodemus flavicollis* and *A. sylvaticus*, the shrews *Crocidura russula, Sorex araneus/coronatus* and *Neomys fodiens* as well as the mole, *Talpa europaea.* We also observed a tendency of these species to be caught more frequently on the mornings following rainy nights.

Four stoats, *Mustela erminea*, were caught in traps set along the fences between March 29th and April 5th. To avoid a crash of our populations, we

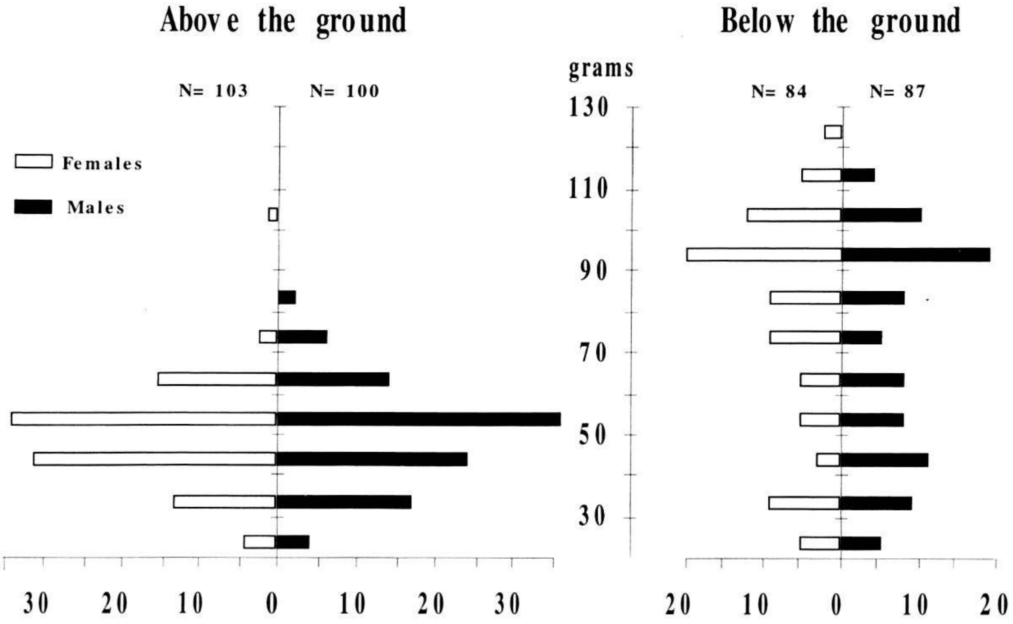

Figure 4.–Weight distribution (in 10 g-classes) of voles caught above and below the ground between March 23rd and June 4th.
Sample size are given separately for males and females. The graphs show a large excess of juveniles and subadults among the above-ground samples.

removed these mustelids from the study area and released them at distances greater than 15 km from our study area. Three additional stoats were caught during the following months indicating an unusually high density (C. Mermod, pers. comm.). Other mammalian predators were also present on our grids, among which foxes and martens caused occasional disturbances to our equipment. On mornings with large numbers of captures, up to 25% of the closed traps were moved, some were left open with blood on the doors or with remains of partly devoured voles inside.

Discussion and final remarks

The results reported here unravel unknown aspects of the dispersal behaviour of fossorial *A. terrestris*. Firstly, we show that these rodents can be caught in large numbers above the ground. Secondly, the fraction of individuals that venture above the ground is not a random sample of the populations established below the ground. On the contrary, a large majority of the voles caught along the fences were juveniles and subadults, i.e. probably not more than two months old. Thirdly, these voles dispersed mainly during rainy nights, suggesting that dispersal is a discrete phenomenon set off by nocturnal rainfalls.

Even minor peaks in numbers of captures are correlated with rainfall during the preceding nights (fig. 2). There are a few exceptions, however. On May

17th, we caught 8 individuals in the absence of rainfall at Posieux, but it might have rained on our study plots (we only started to record rainfall on the spot a few days later). On June 2nd, a major increase in captures occurred with little nocturnal precipitation (0.5 mm). This sudden increase was preceded by a long period without any major rainfalls during the night. This suggests that even little nocturnal rainfall may trigger activity above the ground after a dry period. Moreover, the grass had been mowed on grassland 2 and in the surrounding meadows during the previous week. This might have increased the motivation of voles to move and search for good vegetative cover, a phenomenon which has already been described (SAUCY 1988).

It is noteworthy that many nocturnal rainfalls occurred during weekends, i.e. between Friday evenings and Monday mornings. If we had adopted a weekly trapping schedule, opening the traps on Mondays in the morning and closing them on Fridays in the evening, we would have missed most major increases in captures and perhaps not understood the simple relationship with rainfall during the preceding nights!

To our knowlege, this is the first time that such a peculiar mechanism of dispersal is described. Although many reports mention correlations between trapping success and meteorological conditions (especially rainfall), we are not aware of any study reporting that small mammals may systematically disperse during rainy nights. For instance, it has been frequently reported that trapping efficiency is reduced during clear nights (review in PRICE *et al.* 1984), while a positive correlation between numbers of captures and rainfall has been reported in several instances both in rodents (SIDOROWICZ 1960, VICKERY and BIDER 1981) and in shrews (MYSTKOWSKA and SIDOROWICZ 1961, KIRKLAND and SHEPPARD 1994). Using pitfall traps connected to drift fences and operated continuously during two periods of 10 days and one period of 19 days, KIRKLAND and SHEPPARD (1994) report results very similar to ours for rodents and shrews in Pennsylvania with large numbers of captures correlated with precipitations.

Increased activity is the explanation which has usually been proposed for the correlation between large numbers of captures and rainfall. In none of the studies quoted above a link between dispersal and rainfall has been established. Higher capture numbers in many rodents and shrews during rainy periods suggest that the results reported here for fossorial *A. terrestris* might correspond to a widespread phenomenon among small mammals.

We have very recently realized that observations similar to ours had already been made for aquatic populations of *A. terrestris* from Siberia by Russian mammalogists in the late 1950's. PANTELEYEV (1968) reports that Folitarek developed a "plough furrow technique" in order to control water voles. Using this method, instead of drift fences, the Russians mammalogists have observed that "in the second half of June, a high, but short-lived, wave of migrations takes place; it is finished in one or two nights". Panteleyev also indicates that 88.5% of the voles were young individuals born during the current year. A link with rainfall was also made: "The first rainy night gives rise to a mass departure of young from their family sectors".

Dispersal is a complex phenomenon and conditions and motivations which prompt an animal to disperse are often obscure. It is usually difficult to identify dispersers. It is in particular not easy to discriminate between movements of an animal within its home range from excursions or from actual dispersal events. To overcome this problem, operational but often unsatisfactory definitions have been used (GAINES and MCCLENAGHAN 1980). Furthermore, the age of small mammals is usually difficult to assess.

Fossorial *A. terrestris* differ in these aspects from many small mammal species. As previous studies have shown (AIROLDI 1978, SAUCY 1988), voles which are well established and breed in underground burrows usually have long residence times and do not dwell above the ground. Therefore, in contrast with most studies of dispersal in small mammals, we probably have a simple criterion to identify dispersers in *A. terrestris* (namely, activity above the ground). Furthermore, differences in body size are large enough in *A. terrestris* to distinguish young voles from adults. This allowed us to conclude that the majority of the voles caught above the ground along our fences were young individuals. In consequence, the movements that we observed in this vole probably correspond to actual natal dispersal. In addition, residents can be sampled below the ground during the day, while above-ground dispersal occurs mostly at night.

Our study also brings a quantitative estimate of the importance of dispersal in *A. terrestris*. Our results confirm previous observations by PASCAL and BOUJARD (1987) and by FICHET and PASCAL (1989) which suggested numerous movements of young voles. Our results also shed some light on the observations of PASCAL (1981), who probably observed a phenomenon similar to what we describe here. Applying the removal method during seven consecutive days of below-ground trapping, he observed a sudden increase of captures in empty burrows on the 6th morning after a rainfall. In the same paper, PASCAL (1981) also mentions having caught significant numbers of fossorial *A. terrestris* in traps set above the ground.

Drift fences were used in several other instances in the past (e.g. VERNER and GETZ 1985, MIHOK *et al.* 1988, SINGLETON 1987). Verner and Getz used V-shaped drift fences in the neighbourhood of enclosures. Their fences were positioned in order to concentrate the dispersing voles towards traps set in a collecting zone. These investigators did not identify more than 41 dispersers during a multiannual cycle (1973-1976) of the voles *Microtus ochrogaster* and *M. pennsylvanicus* and concluded that dispersal was not a significant component in the regulation of vole populations.

If the phenomenon that we observed is common among voles and other small mammals, it remains to explain why VERNER and GETZ (1985) did not report similar results. There are several differences between the two studies. First, we did not use the same trapping design as Verner and Getz. In our case, voles had to follow the fences for a maximum of only 8.33 m before encountering a trap, in contrast to a maximum of approximately 50 m in their case (distances were read from their figure 1). Since the behaviour of the voles along the fences is not known, it cannot be excluded that in the study of Verner and Getz, a large number of voles might have missed the traps which were grouped together at one location of each fence. In our case, animals were exposed to traps regularly spaced along the fences. This probably increased the chances of capture, even if the voles avoided some of the first traps encountered. More important, our traps were operated continuously, in contrast to 23-73% of the time in the study by Verner and Getz. We have already mentioned that approximately half of our captures were recorded during 8 of 100 nights.

Our results question the foundations of traditional trapping techniques applied to populations of *A. terrestris*, and perhaps of other small mammals. Following HURLBERT's remarks (1984), the risk of sampling biases due to spatial autocorrelations has been recently emphasized in many textbooks on experimental design. Little attention has been paid, however, to the risk of sampling biases due to temporal autocorrelation when sampling occurs at regular time intervals. This is a common practice among students of small mammals who open their traps for 3 to 5 days every second or third week. During our study, we encountered a case of temporal autocorrelation in rainfalls. A beweekly sampling schedule would probably have masked or seriously altered the major pattern reported here. Moreover, the above-ground dispersal behaviour that we describe also questions the significance of population estimates obtained using classical trapping techniques. In the case of fossorial *A. terrestris*, estimates of the below-ground populations are likely to be altered by up to 50% or more, depending on whether trapping is conducted before, after or during periods with rainy nights.

Lastly, the origin and the fates of our dispersers are still poorly understood. As far as we know, very few of them are able to settle in burrows already occupied by adult breeders. Further studies are therefore needed to assess the components and determinants of successful dispersal in this vole.

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