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The decline and local extinction of a population of water voles, *Arvicola terrestris*, in southern England

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Abstract

A colony of water voles occupying 1.6 km of the river Windrush (England) is described before it disappeared due to mink predation. Individuals were trapped every month for a week during 19 months. In addition, some individuals were radio-tracked in order to estimate their ranges and movement patterns. The numbers of latrines were counted seasonally and compared with the numbers of captured animals. The population reached a peak in July 1996 when 20 individuals were known to be alive indicating that the population was already very small. The number of individuals caught decreased in winter and new individuals appeared during the next spring although the population crashed in July 1997 due to mink predation. The sex ratio was similar to that reported elsewhere for British populations, but densities were lower than those reported elsewhere. Body size was smaller than previously recorded in the same catchment. Home ranges were significantly smaller in summer than in spring resembling situations of high and low densities respectively. Individuals showed restricted movements and no dispersal event was recorded. Available data seem to suggest that females form linear ranges that, though overlapping other juvenile females, exclude adult females. Males, on the other hand, have linear ranges that overlap several females and males.

Key words: *Arvicola terrestris*, water voles, rodents, home range, population

Introduction

The water vole *Arvicola terrestris*, is a microtine rodent distributed widely in the Palearctic region. In most of their range, water voles are closely associated with aquatic habitats occurring along rivers, brooks, and on the shores of lakes and gravel pits. In the mountainous areas of central Europe and the Pyrenees, water voles show fossorial habits and differ widely in their population characteristics from the aquatic forms. Fossorial water vole populations undergo 5–8 year multi-annual fluctuations reaching very high densities (Saucy 1994) and are considered a pest in parts of their range. On the other hand, aquatic water voles do not show multi-annual cycles and their densities are always lower than those reached by fossorial water voles. Aquatic water voles are larger, darker and polygynous whereas fossorial forms live in monogamous pairs that defend small territories (Pelikan and Holisova 1969; Reichstein 1982; Strachan and Jefferies 1993).

In Britain, the population ecology of water voles has been previously studied by Stoddart (1970) in Scotland, Leuze (1976) in East Anglia, and Woodall (1993) in the Thames region. At the time these studies were carried out, stable populations of water voles occurred in all these study areas. Home ranges were always linear with water voles

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staying within 1–2 m from the edge of the water. These home ranges, however, differed from those of some populations of water voles in aquatic habitats of continental Europe and the former USSR that show polygonal shapes (Jeppsson 1986, 1990).

In mammals, factors affecting distribution and spatial organisation vary with the sex of individuals. In general, female distribution is dependent on the dispersion of resources whereas males depend on females distribution (Jeppsson 1990; Ostfeld 1990). In Britain, distribution of water voles varies from uniform (Stoddart 1970), to clumped (Woodall 1993), to fragmented (Lawton and Woodroffe 1991) along river banks. Woodall (1993) attributed these differences in distribution to differences in habitat between the study sites. Nevertheless, the difference might be related to the process of decline that British populations of water voles have experienced since the beginning of the century and particularly for the last 30 years (Jefferies et al. 1989). The study by Stoddart (1970) was carried out during the late 60 s, that of Woodall (1993) during the mid 70 s whereas Lawton and Woodroffe (1991)'s was conducted in late 80 s.

For a given population, it is not only dispersion that may be affected during the process of decline. The population structure is likely to change as well. As populations get smaller, the impact of stochastic factors increases and so does the probability of extinction of local populations. Metapopulation dynamics are disrupted and fragmentation increases in a way that any rescue effect is prevented. Water voles in Britain are declining (Strachan and Jefferies 1993), and whilst recent surveys indicate that the number of sites with evidence of their presence has decreased, it is possible that the population size in the remaining sites has also decreased. The gaps between colonies are becoming larger and the probability of migration between colonies lower. This phenomenon is probably due to, but also aggravated by, the presence of American mink, *Mustela vison*, and habitat disturbance (Lawton and Woodroffe 1991; Strachan et al. 1998).

The river Windrush is a tributary of the river Thames flowing from the Cotswolds in Gloucestershire and joining the Thames at Newbridge in Oxfordshire, England. During the summer of 1996, only 8 colonies of water voles were recorded along the c. 100 km of the river. On average, these colonies occupied less than 800 m of continuous riverbank showing the high degree of fragmentation of this population. The bigger of these colonies, as revealed by the length of river showing evidence of water voles, occupied 1.6 km of river and was chosen for this study. No colony was recorded downstream and the nearest neighbouring colony was located 2 km upstream. The aim of this study was to learn more about water vole populations and to compared this declining population with the stable ones previously studied in Britain.

Material and methods

Study area

The study was carried out along a 1.6 km stretch of the river Windrush (Oxfordshire, England) between grid references SP260115 and SP273117 (Fig. 1), approximately 30 km to the west of Oxford City. The river is 8–10 m wide, the flow is slow and the channel generally deep (1.5–2 m). Banks are generally steep (> 45°) and low (up to 1 m from the water surface). Adjacent land consists of semi-improved neutral grassland managed as pasture for sheep. The sward consists mainly of perennial rye-grass *Lolium perenne* and crested dog's-tail *Cynosurus cristatus*. There are some trees along the banks especially alders *Alnus* sp., (most of them dying from Phytophthora infection) and some pollarded willows *salix* sp. The channel contains considerable quantities of stream water-crowfoot *Ranunculus penicillatus*, perfoliate pondweed *Potamogeton perfoliatus*, spiked water-milfoil *Myriophyllum spicatum* and yellow water-lilly *Nuphar lutea*. Wildlife along the stretch included waterfowl (swan *Cygnus olor* mallards *Anas platyrhynchos*, coots *Fulica atra* and moorhen *Gallinula chloropus*), kingfisher *Alcedo athis*, lapwing *Vanellus vanellus*, little grebe *Tachybaptus ruficollis*, brown hare *Lepus capensis*, rabbits

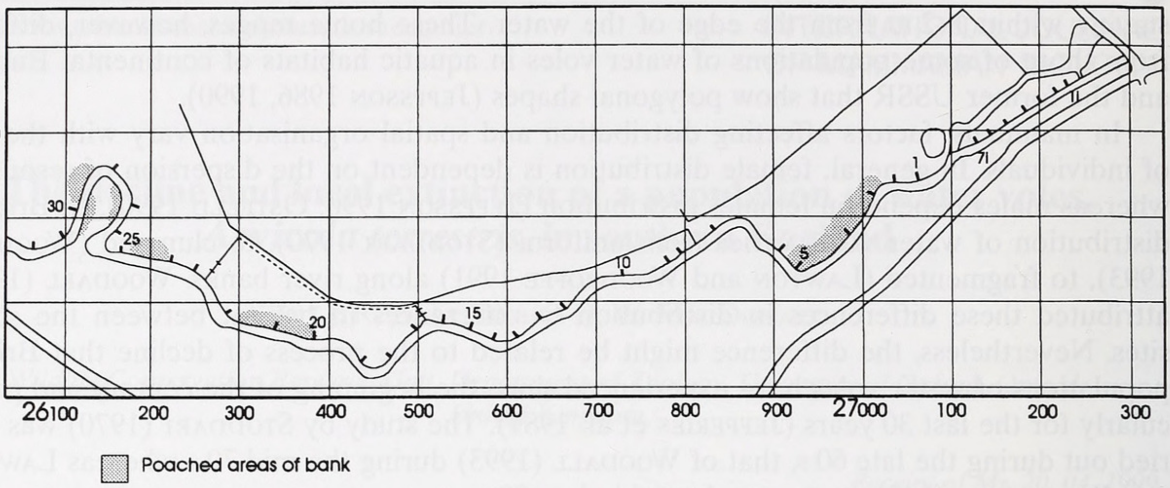

Fig. 1. Study area. The river Windrush near Widford, Oxfordshire, England. Grid references are shown. Every square represents 100 m square. Symbols along the river show trap sites. In total, 1.6 km of river was surveyed.

Oryctolagus cuniculus, bank voles *Clethrionomys glareolus*, field voles *Microtus agrestis*, woodmice *Apodemus sylvaticus* and weasel *Mustela nivalis* among other species. No sign of American mink was observed by the time the study started in May 1996.

Trapping programme

Water voles were live-caught in aluminum traps 33×10×9 cm (Elliott Ltd.; Victoria, Australia). Traps were baited with apple and placed approximately every 30 m along the river bank. Traps were set in sites where there was evidence of water vole activity (i. e. near burrows, latrines, feeding places, etc.). In some cases, artificial burrows were dug facing the river and traps set in them. Approximately 40 traps were set for a week every month from June 1996 to December 1997. The position of every trap was located on the map and maintained with slight variations for the whole study period. Prebaiting was not implemented as Woodall (1993) found it unnecessary. Traps were checked early in the morning and before sunset. During winter, the traps were covered with hay and other vegetation to protect them against rain and/or frost. Additionally, the number of latrines along the river were counted each season in order to relate this number to the number of animals caught.

Trapped animals were introduced to a gas chamber where they were briefly anaesthetised with inhalant methoxyfluorane (Metofane™) or halothene (Fluothane™) and subsequently processed. Each animal was sexed, weighed and standard body measures taken (Total, head-body, ear and hind foot length). A transponder (Trovan™) carrying an unique identification code was implanted sub-cutaneously in the back of each animal. Some of the animals were equipped with radio-collar transmitters as described below. Handling lasted for a maximum of 5 min and after a few additional minutes the animals, completely recovered, were released at the place of capture.

Radio-tracking programme

Thirteen animals were fitted with radio-collars consisting of 3–4 g TW/4 or TW/5 transmitters (Biotrack; Wareham, UK) and tracked using a Mariner receiver and a three-element Yagi antennae. Fixes were taken every 15 min from a maximum distance of 25–30 m. Batteries lasted for 6 weeks on average but problems with the signal were common throughout the study. Recaptured animals were checked and malfunctioning radios replaced. When there were any signs of abrasion to the neck of the animal, the collar was removed and the individual released. All procedures were done under Home Office project licence PPL 30/00043 and personal licence PIL 30/3873.

Results

The population

In total, 145 captures were made in 4 488 trap-nights. Forty five individuals (20 males and 25 females) were caught and tagged. Mean number of captures per individual was 1.6 (1–3) whereas the average efficiency of capture (captures/trap-nights) was 0.04 with a minimum in January 1997 (0) and a maximum in July 1996 (0.16). Captures were not evenly distributed along the stretch (Fig. 2) with some trap sites capturing more individuals with higher frequency. Figure 2 also shows three sectors along which no capture was made. These sectors coincided with areas of river bank poached by cattle or sheep.

The maximum number of latrines was observed in summer 1996. The number declined through winter when no latrines were found. Water vole activity started in spring with an increasing abundance of latrines. However, no signs of water voles were observed from July 1997 onwards. Latrine counts carried out during July 1996 simultaneously to the trapping yielded a total mean frequency of 172.6 latrines (SD = 11.8). This approximates to six latrines per vole and an index of the potential breeding population of water voles as 18 voles/km of occupied river. Interestingly, this figure coincides with that reported by Woodroffe et al. (1990) when studying water voles in Yorkshire, northern England.

Figure 3 shows the abundance of water voles along the study area from June 1996 until November 1997. The highest number of animals was observed during July 1996 but the population crashed a year later. Juveniles (6 individuals) were trapped only in June and July 1996 (Tab. 1). No water voles were trapped, or signs observed, between July and December 1997. No untagged water vole was caught in February and March 1997 but new individuals started to appear from April indicating a potential population recovery. It is important to note that signs of American mink were observed for the first time in May 1997 and a radio collared water vole was found dead inside a willow hollow on

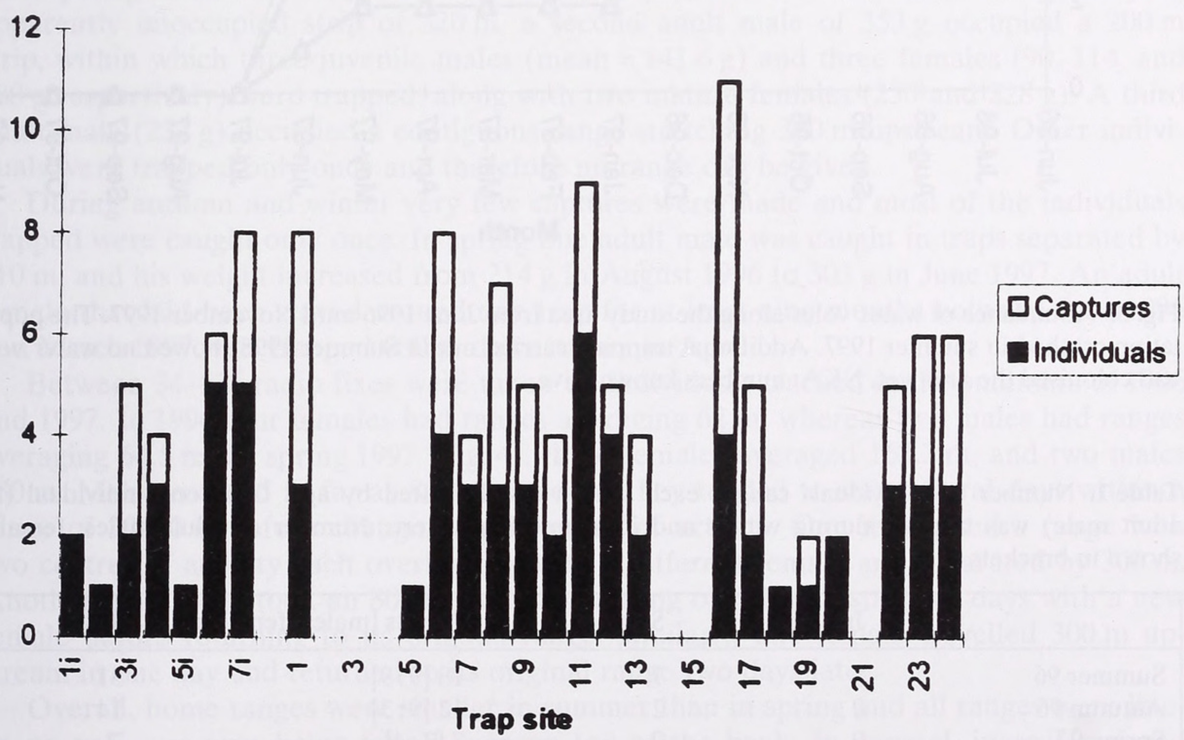

Fig. 2. Number of captures, and individuals caught, in each trap site along the study area. Trap sites with no capture coincide with trampled areas. Location of traps is shown in figure 1.

13th June. A hole was observed in the skull of this animal. In the same place there was another water vole and a coot. The presence of footprints near the site suggest that a mink had made the kills. Two juvenile mink were caught in July 1997; one female trapped around trap-site 24 and a male trapped near trap-site 1 i. A third mink, presumably an adult female, was observed in July and August but it was not trapped.

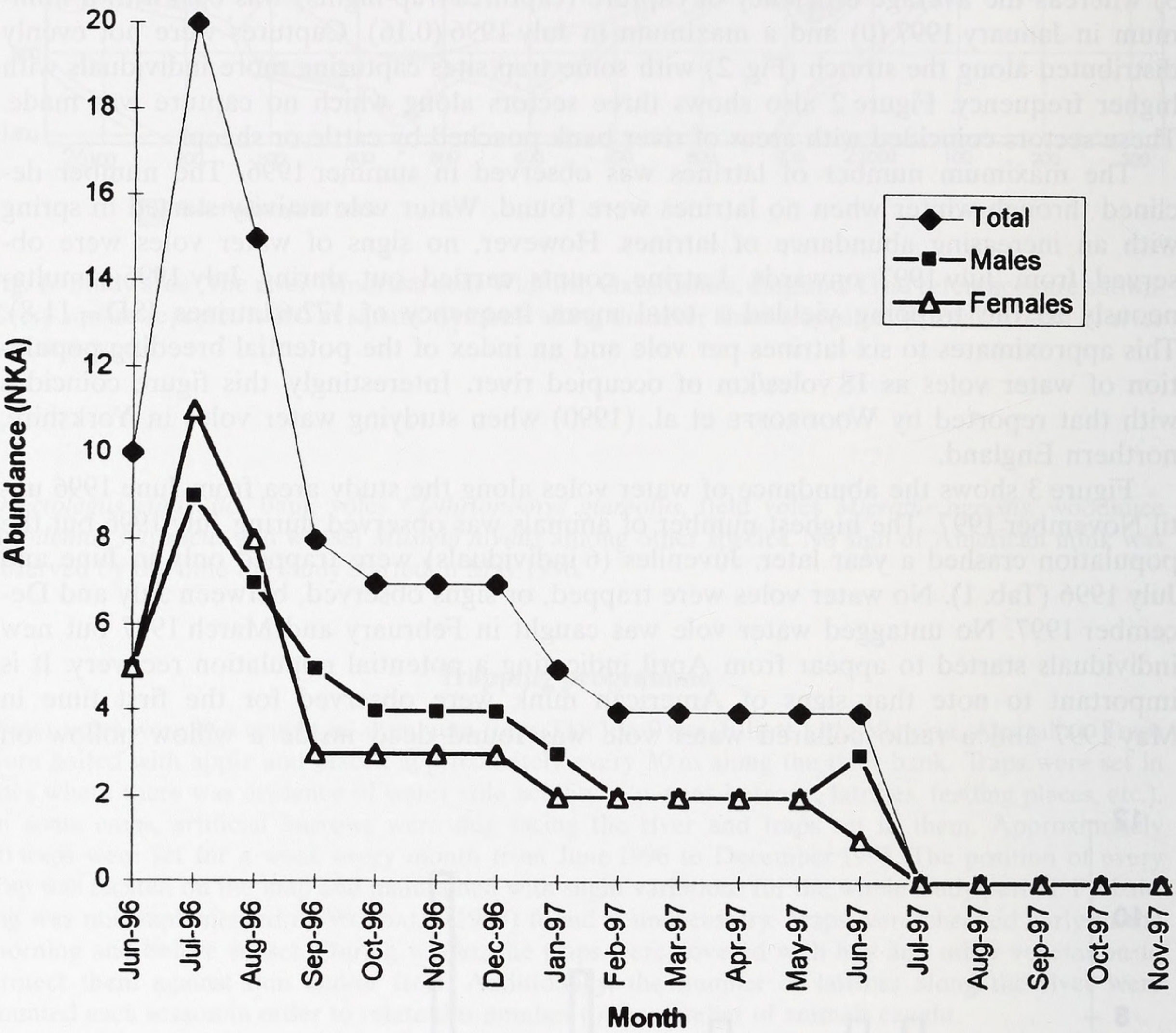

Fig. 3. Abundance of water voles along the study area from June 1996 until November 1997. The population crashed in summer 1997. Additional trapping carried out in Summer 1998 showed no water vole had colonised the area yet. NKA: numbers known alive.

Table 1. Number of individuals caught each season discriminated by age. Only one individual (an adult male) was trapped during winter and it is not shown here. Number of adult males: females shown in brackets.

	Juveniles	Sub-adults	Adults [males: females]	Total
Summer 96	6	7	18 [9:9]	31
Autumn 96	0	2	12 [9:3]	14
Spring 97	0	0	7 [3:4]	7
Summer 97	0	1	3 [2:1]	4
Autumn 97	0	0	0	0

The individuals

Comparing standard measures revealed that no significant differences were found between sexes in total length ($t = 0.82$; $df = 41$; $p > 0.05$), head-body length ($t = 0.74$; $df = 38$; $p > 0.05$), and weight ($t = 1.0$; $df = 34$; $p > 0.05$). Both ears and hind feet, however, were signiflcantly longer in males (Tab. 2) Maximum weight recorded were 350 g in a female and 360 g in a male, both caught in June. Although the average weight of adults was slightly lower during autumn, there were no significant differences among seasons ($F_{[1,5]} = 1.15$; $p > 0.05$).

Table 2. Standard measures (mean ± SE) of male (M) and female (F) water voles caught between June 1996 and July 1997 along a 1.6 km stretch of the river Windrush, Oxfordshire, England. TL: total length; HBL: head-body length; EL: ear length; HFL: hind foot length; Wt: weight. From 20 males and 21 females. P-values for t-tests are given.

	TL (mm)	HBL (mm)	EL (mm)	HFL (mm)	Wt (g)
M	302.2 ± 8.8	188.4 ± 4.8	16.9 ± 0.4	34.5 ± 0.4	196.4 ± 15.0
F	292.5 ± 4.1	180.9 ± 7.8	15.2 ± 0.4	32.9 ± 0.4	218.8 ± 17.0
p	0.421	0.491	0.0041	0.0056	0.160

Water vole ranges

Animal recaptures provided an insight into the range of water voles in this declining population. During the summer of 1996, one 257 g adult male used a range of 220 m, which embraced the 100 m range of one female, and within which seven juveniles (four males and three females) were also trapped (we were able to estimate the ranges of three of these young males and none exceeded 30 m). Separated from this cluster of voles by an apparently unoccupied strip of 320 m, a second adult male of 353 g occupied a 200 m strip, within which three juvenile males (mean = 141.6 g) and three females (90, 114, and 188 g respectively) were trapped, along with two mature females (250 and 228 g). A third adult male (232 g) occupied a contiguous range stretching 200 m upstream. Other individuals were trapped only once and therefore no range can be given.

During autumn and winter very few captures were made and most of the individuals trapped were caught only once. In spring one adult male was caught in traps separated by 110 m, and his weight increased from 214 g in August 1996 to 305 g in June 1997. An adult female that had been stayed around one trap for at least nine months between June 1996 and March 1997, was trapped 600 m downstream in April.

Between 34–525 radio fixes were taken on individuals tracked in the summers of 1996 and 1997. In 1996 four females had ranges averaging 62 m, whereas two males had ranges averaging 64.5 m. In spring 1997 (Fig. 4), three females averaged 163.3 m, and two males 550 m. Males roamed as far as 800 m although they tended to stay several days within a range of 20–30 m before changing their centre of activity. One male used a range with two centres of activity each overlapping with a different female and separated by 300 m. Another male undertook an 800 m excursion during one day, to stay two days with a new female before returning to its original range. Similarly, one female travelled 300 m upstream in one day and returned to its original range two days later.

Overall, home ranges were smaller in summer than in spring and all ranges were linear, no vole was ever being found even on top of the bank. In general, juveniles stayed within 30 m of river bank and most of the time in the same place. Male 544, for example, was tracked for three weeks and did not go further than 10 m from the nest. During this

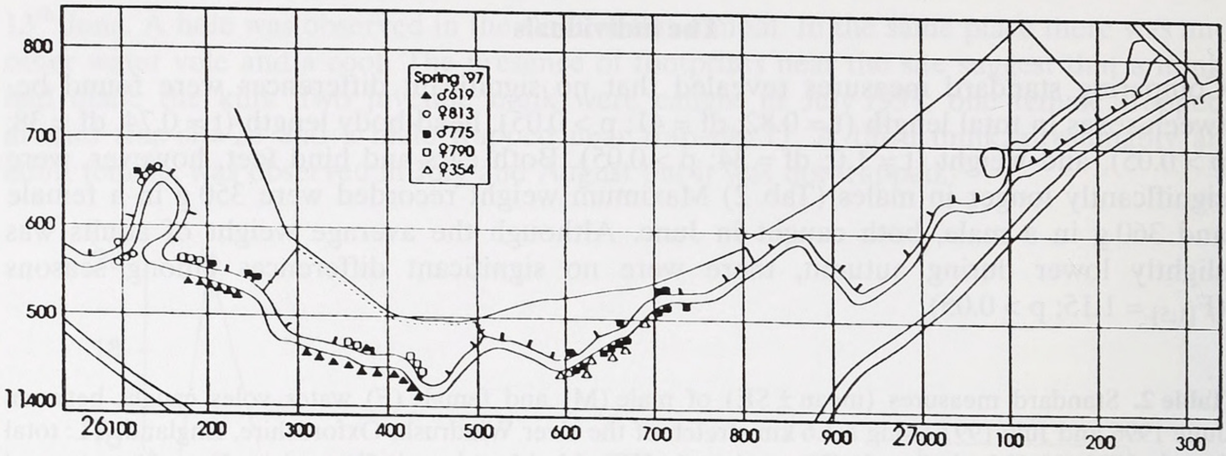

Fig. 4. Ranges of five radio-tracked individuals during spring 1997. Symbols represent locations where 80 % of fixes were recorded.

time its weight increased from 52 g to 98 g. A month later the collar was removed, it was caught 50 m away from the nest weighing 170 g.

No two adult females were ever caught in the same trap during the same trapping period. Males, on the other hand, used longer home ranges and overlapped not only other females' but other males' too. We saw one pair mating and 20 days later they were sharing the same burrow.

Discussion

The density recorded in the study area (maximum density = 1.25 ind/100 m) was lower than densities reported elsewhere. Pelikan and Holisova (1969) reported densities between 4 and 9.3 ind/100 m in a similar habitat in the Czech Republic. In Britain, Leuze (1976) found a maximum of 2.8 ind/100 m of river, and Strachan and Jefferies (1993) estimated overall densities of 4 to 16 ind/100 m for the whole country. A comparison of surveys in the Thames catchment from 1989 and 1995, showed that water voles are disappearing from many sites and it is not a surprise that the density along the sites where they still occur has diminished. Barreto et al. (1998 a) showed that the rate of decline between 1989 and 1995 was higher than during the previous 15 years. This may account for the difference found between the densities reported by Strachan and Jefferies (1993) and that reported in this study.

Despite being small, the population showed an expected maximum size in summer and a minimum size in winter. The capture of new individuals during spring 1997 suggested that the population was starting a new cycle of increase. During that spring, however, a breeding female mink established in the area. Recent studies carried out in the rivers Soar and Amber in Leicestershire and Derbyshire respectively showed that the American mink decimated a water vole population in less than a year (Strachan et al. 1998) from the time it arrived to the area. Home ranges of mink, though wider, are also linear overlapping several water vole ranges (Gerell 1970; Dunstone 1993). Strachan et al. (1998) found that a female breeding mink was likely to produce the worst effects on the water vole population as it hunts intensively around the den in order to feed its kits. The situation is aggravated because mink breeding season starts in February and kits are born in May, and by this time the water vole population is still recovering from the previous winter. The population studied by Strachan et al. (1998) occupied a longer stretch of river, so it took one year for two different breeding mink to eliminate water voles from this stretch. In the case studied here, the population was far smaller, and only one female

Table 3. Body measures of water voles from different areas. HB: head body length; HF: hind foot length. Mean ± SE. Range in brackets.

	Weight (g)	HB (mm)	Tail (mm)	HF (mm)	Source
Oxfordshire	291.5 (225–386)	222 (206–242)	134 (115–146)	34 (32–36)	Boyce (1991)
Oxfordshire	207.6 ± 16.0	184.6 ± 6.3	112.7	33.7 ± 0.4	This study
North Germany	153.6 ± 6.99	157.1 ± 3.40	118.4 ± 2.49	30.9 ± 0.21	Reichstein (1982)
South Germany	147.7 ± 6.28	159.3 ± 2.35	115.9 ± 2.38	30.1 ± 0.17	Reichstein (1982)

mink was enough to patrol the stretch where the whole colony inhabited and eliminate the population in only three months. A visit to the study area in July 1998, showed no water vole had recolonised the river. In fact, the nearest colony inhabited a stretch of river 2 km upstreams separated between each other by the town of Budford where the river banks are mostly reinforced, thus becoming a barrier for water voles. Should these colonies were a metapopulation, it is apparent that it no longer exists as such, as the degree of fragmentation is too high.

British water voles have been reported to be bigger than water voles from the continent (Reichstein 1982) and body measures taken during this study support these data (Tab. 3). However, water voles measured in this study were smaller than those studied by Efford (cit. in Boyce 1991) in Oxfordshire during the mid 80 s (Tab. 3). It is not clear why the average size obtained in this study turned out to be lower than that of water voles from the same area studied more than ten years ago. One possibility is related with a decrease in the quality of the habitats. Krebs (1978) and Boonstra and Krebs (1979) discussed a hypothesis (Chitty hypothesis) according to which extra large individuals appear during the peak phase of the multi-annual cycles observed in microtines. Regardless of the assumptions of these hypothesis, these extra-large animals would increase the average size in the population. Lidicker and Ostfeld (1991) showed later that in the case of California voles (*Microtus californicus*), extra large individuals did indeed appear in the population at high densities although they attributed this phenomenon to conditions for good growth and survival that last long enough for large size to be achieved. There is no evidence in Britain suggesting that water voles experience multi-annual cycles although it is clear that the population size is decreasing. Is it possible that current conditions for growth are not good enough and water voles are not achieving the size they used to achieve ten or more years ago? Water voles have experienced a loss of suitable habitats during the second part of this century (Barreto et al. 1998 a) and it is apparent that across the Thames catchment they have been occupying areas better characterised by the absence of mink than by any especial habitat feature (Barreto et al. 1998 b). Water voles are absent from the lower part of the river Windrush and the available data suggest that this section possesses the best habitats for water voles so it is possible that a decrease in habitat quality or the occupancy of marginal habitats is being reflected in smaller animals. This is an intriguing issue and more data on other populations will be needed to clarify these ideas.

Pooling the results from trapping and those from radio-tracked animals shows that during the summer home ranges were smaller than during spring. Spring defines the beginning of the breeding season and it is characterised by an increase in the number of latrines. An increase in the size of the home range reflects a period of major activity. Similar changes during spring have been observed in other vole species such as *Microtus californicus* (Salvioni and Lidicker 1995), *M. townsendii* (Lambin and Krebs 1991) and *M. oeconomus* (Gliwics 1997).

Regardless of the length, the range of water voles was always linear and no water vole was caught or observed out of the water edge on the bank top. They did not even run or swim along a ditch dug from the river. The situation was similar to that reported by Pelikan and Holisova (1969) in the Czech Republic and Stoddart (1970) in Scotland although different from water voles in Sweden that live in marshes and have polygonal ranges (Jeppsson 1990). During summer the home range of recaptured animals were similar to those reported by Leuze (1976) in high density areas, although radio tracked animals occupied very small ranges with females and males ranges being similar. In spring, the home ranges were longer and similar to those reported in low density areas by Leuze (1976). In the Czech Republic, home ranges were 170 m and 135 m long on average in males and females respectively (Pelikan and Holisova 1969). Over the winter, these authors reported home ranges of 500 m in males and 80 m in females. These figures came from trapping data throughout the winter. Observations from the present study revealed that although the home range of an adult water vole may reach 500 m during the spring, individuals tend to use a short sector of this range during several days and then, they move into a new burrow, stay there for another time, and so on. It is apparent, then, that during the season the individuals shift the centres of activity although staying within a short stretch for several days.

Despite their morphological conservatism, Microtine rodents are extremely variable in their social and spatial organisation (Ostfeld 1990). This variation is not only inter-specific but intra-specific. Townsend's voles (*Microtus townsendii*), for example, are territorial and monogamous during the spring but display overlapping ranges and are polygynous during the summer (Lambin and Krebs 1991). Fossorial water voles form monogamous pairs that defend small territories (Saucy 1988) but aquatic water voles seem to be polygynous with the females defending territories and the males overlapping several females (Jeppsson 1986). However, the available data are not yet clear as Jeppsson (1986) reported on females changing territories within the breeding season or living in cluster of possible relative females. Data from Stoddart (1970) and this study seem to support the idea that females form territories within which relatives are allowed to stay, and males overlap several female territories. In the middle part of the stretch, for example, there were 8 individuals within 250–300 m: six were juveniles (3 males and 3 females) and two adult females caught on the extremes of this stretch. Males, on the other hand, used longer home ranges and overlapped not only other females's but other male's too. Nevertheless, the observation of male 775 mating a female and sharing her burrow 20 days later, suggests that some kind of dominance among males is established. Female water voles are poly-oestrus with post-partum oestrus and suspension of oestrus during lactation (Perry 1943). It is therefore advantageous for a male to stay near a pregnant female just before she gives birth. In that way, the male assures a second mating.

Available data on social and spatial organisation of water voles are scarce but the evidence suggests three types of spatial organisation: 1. Small territories defended by a monogamous pair, 2. Territorial females or territorial clusters forming polygonal home ranges and males overlapping several female ranges and 3. Linear ranges with territorial females or clusters of related females and males overlapping several females and younger males to whom they compete for mates. The disappearance of the population studied here did not allow further comparisons between years, so a longer term study and a comparison of different areas will provide the necessary data to clarify this interesting problem.

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Zusammenfassung

Die Abnahme und lokale Extinktion einer Population von Schermäusen (Arvicola terrestris) im südlichen England

Eine Population von Schermäusen, welche 1,6 km des Flusses Windrush in England bewohnte, wird beschrieben, bevor sie durch Mink-Predation eliminiert wurde. Über einen Zeitraum von 19 Monaten wurden monatlich eine Woche lang Individuen eingefangen; außerdem wurden einige Individuen mit Radiosendern versehen, um Information über Wohnareal und Bewegungsmuster zu erhalten. Die Zahl der Latrinen pro Jahreszeit wurde gezählt und mit der Anzahl von gefangenen Individuen verglichen. Die Population erreichte ein Maximum im Juli 1996, als sie 20 lebende Individuen zählte, was beweist, daß sie bereits sehr klein war. Die Zahl der eingefangenen Individuen verringerte sich im Winter und neue Individuen erschienen während des darauffolgenden Frühjahrs, dennoch brach die Population im Juli 1997 infolge Predation durch eine verwilderte Farmnerzfähe zusammen. Das Geschlechterverhältnis war ähnlich jenem für andere in Großbritannien ermittelte Populationen, die Dichte war jedoch geringer. Die Körpergröße war geringer als jene, welche vorher für denselben Flußbereich angegeben war. Die „home ranges" waren deutlich kleiner im Sommer als im Frühjahr, was auf höhere und geringere Dichten schließen läßt. Die Individuen zeigten begrenzte Bewegungsmuster und kein Fall von Dispersion wurde beobachtet. Aus den vorliegenden Daten läßt sich schließen, daß die weiblichen Individuen lineare Reviere besetzen, die sich wohl mit denen junger weiblicher Individuen überschneiden können, nicht aber mit jenen ausgewachsener Weibchen. Die Männchen hingegen besetzen lineare Reviere, die sich mit jenen verschiedener Weibchen und Männchen überschneiden können.

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