

Population dynamics and survivorship patterns in the common shrew *Sorex araneus* in southern England

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Results of a four-year, mark-recapture study of a high-density population of *Sorex araneus* Linnaeus, 1758 inhabiting grassland are reported. The population showed regular cycles of abundance between seasons and differences between years. Captures were not related to ambient temperature or rainfall, and population numbers showed no consistent correlation with winter weather conditions. Immigration and dispersal occurred throughout the year but were lowest in winter. Fifty-five percent of males and 35% of females in the breeding population were immigrants. Shrews underwent an autumn-winter weight loss of 12–19% but there was no evidence that weather conditions affected seasonal or annual patterns of weight change. There were no significant differences in body mass between resident and transient (and dispersing) young or between resident and immigrant adults. Weather conditions affected neither monthly survival, nor annual winter mortality rate which was 21–48%. Onset of sexual maturity was not affected by time of birth, but early-born cohorts had better survival rates at all stages than did late-born cohorts. There were significant differences in survival between cohorts born in different years but these were not correlated with weather conditions or population density.

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Introduction

The seasonal population cycles of small mammals, including shrews, in northern temperate regions are well documented, along with many fundamental data on the dynamics of their populations (for example Dehnel 1949, Mezhzherin 1960, Bobek 1969, Pernetta 1977, Churchfield 1980, Flowerdew 1985). But the factors which govern population processes, particularly patterns of survival and dispersal are poorly understood. Soricine shrews, in common with many small rodents, are typically short-lived mammals which complete their life cycles within 12–18 months (Dehnel 1949, 1950, Pernetta 1977, Churchfield 1980, 1984). Although soricine shrews are capable of maturing and breeding within the calendar year of their birth (Shwarz 1959 cited in Pucek 1970, Pucek 1960, Sheftel

1989), the frequency of this is correlated with population density and, probably, food supply (Stein 1961). Most shrews pass the autumn and winter period following birth in an immature state before achieving breeding condition the following spring. Breeding is limited to the summer months and, unlike many rodents, wild soricine shrews seem unable to prolong the breeding season, even under favourable conditions. Therefore, individuals have only one brief season in which to breed, and survival until this time is critical. Winter, with its attendant problems of food supply and inclement weather conditions, is likely to be the most difficult period for small mammals. Although population studies have shown that winter survival of shrews can be high (Croin Michielsen 1966, Pernetta 1977, Churchfield 1980, 1984), little is known about the influence of weather, population density, time of birth, or body weight on their overwintering success.

These small insectivores generally maintain low population densities compared with those of many small rodents (Churchfield 1990, Corbet and Harris 1991). Hence, interpretation of survival patterns based on mark-recapture data have been hampered by low trapping success and small sample sizes. Moreover, live-trapping studies are usually short-term exercises, commonly over a two-year period. This is insufficient time to reveal differences between years in population numbers and survivorship patterns, and the influence of weather conditions.

The seasonal and annual patterns of survival among different ages, sexes and cohorts of *S. araneus* were studied over four years which included two relatively cold winters followed by two mild ones.

Methods

The study area

The study was conducted in grassland plots of different, known successional ages at Imperial College at Silwood Park, near Ascot, Berkshire. Six plots were used which had been established between 1977 and 1983 on bare ground which was allowed to colonise naturally. All were adjacent to each other and together they provided a grassland study area of approximately 0.3 ha ranging in habitat-type from a perennial grass and herb community to a scrub-grassland with saplings of *Quercus robur*, *Betula pendula* and *Sarothamnus scoparius* in the later successional stages. The grass-dominated community covering most of the study area comprised mainly *Holcus lanatus* and *Agrostis stolonifera* with smaller amounts of *Dactylis glomerata*, *H. mollis* and *Agrostis stolonifera*. Common forbs were *Veronica chamaedrys*, *Plantago major*, *Cirsium arvense*, *Senecio jacobaea* and *Rubus fruticosus*. The study area was fenced to exclude rabbits and was surrounded by ploughed land on one side and unmanaged grassland heavily grazed by rabbits on the remaining three sides.

Trapping methods

Trapping was carried out under Nature Conservancy Council licence using Longworth live-traps provided with cotton wool bedding and food in the form of *Calliphora* sp. pupae and oats. Trapping was carried out for a continuous period of three days and nights at 4–6 weekly intervals from May 1985 to September 1989. Trap points were established at approximately 9 m intervals with two traps per point, giving a total of 58 trap points and 348 trap nights per trapping period. In addition, a

boundary strip was established in rough grass approximately 5 m outside the main study area. Here traps were placed singly at approximately 10 m intervals.

Traps were inspected 4–5 times daily, depending on weather conditions. All shrews captured were weighed and individually marked by toe-clipping. Their sex and reproductive condition were noted, and they were assigned to an age class (juvenile, sub-adult, mature adult) depending upon their body weight, month of capture, condition of pelage and stage of moult (see Churchfield 1990). Sub-adults were distinguished as young shrews having undergone the autumn moult and which were overwintering in an immature state. All shrews were released at the place of capture and the trap point recorded. Results were expressed as the number of individuals captured per 348 trap nights and as the minimum number known to be alive (calendar of captures method, after Petruszewicz and Andrzejewski 1962).

Winter mortality rate (%) was calculated (after Henttonen *et al.* 1989) as follows:

$$1 - \frac{N_s(n+1)}{N_a(n)} \times 100$$

where $N_a(n)$ and $N_s(n)$ are the numbers of residents in autumn and spring in year n , respectively.

An index of breeding success was calculated (after Pankakoski 1985), as follows:

$$\text{Breeding success} = \frac{N_{\text{juv}}(n)}{N_{\text{ad}}(n)}$$

where N_{juv} is number of recently-weaned juveniles captured between June and September in year n , and N_{ad} is number of adults known to be alive between April and September in year n .

Results

Seasonal and annual population cycles

The shrew population showed typical seasonal cycles with greatest numbers in summer when young were produced, followed by a decline into winter as old adults and many young shrews disappeared (Fig. 1). By September and October most old adults had gone, presumed dead, but one adult survived until December. Shrews overwintered as immature individuals when numbers remained relatively stable. Population density ranged from $27 \text{ ind} \times \text{ha}^{-1}$ in winter/spring to $120 \text{ ind} \times \text{ha}^{-1}$ in summer.

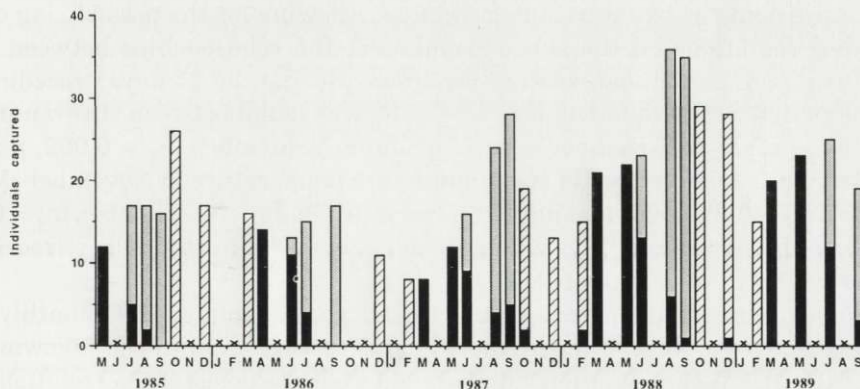


Fig. 1. The numbers of *S. araneus* captured during each trapping period: adults (shaded), juveniles (dotted) and sub-adults (hatched). Crosses denote months not sampled.

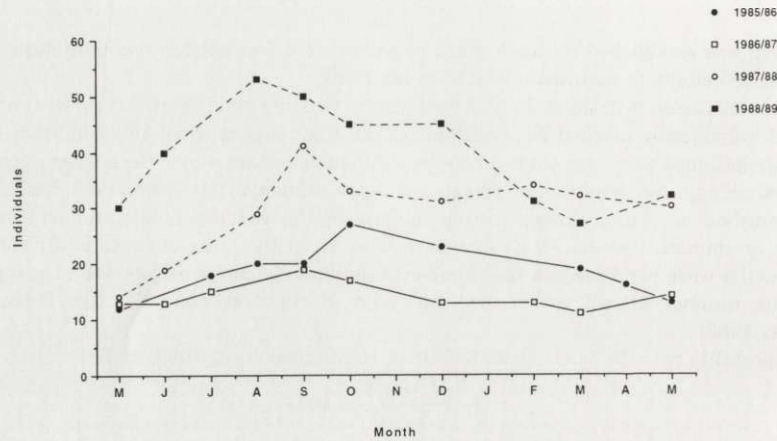


Fig. 2. Minimum numbers of *S. araneus* known to be alive (MNA) in each of the four years sampled.

Differences in yearly population numbers are compared in Fig. 2 where the minimum numbers known to be alive (MNA) are shown, commencing with breeding adults of one cohort in May through to the adults of the next (overwintered) cohort in the following May. Mean numbers of shrews differed significantly between each year ($t = 2.46$, $p < 0.05$ to $t = 10.0$, $p < 0.001$; Student's t -test) but numbers were greater during the last two years of sampling than in the previous two years (mean 34.5 and 16.7, respectively; $t = 14.13$, $p < 0.001$).

There was no evidence that numbers of captures were influenced by prevailing weather conditions during trapping periods. There was no correlation between individuals caught per trapping period and either total rainfall ($r_s = 0.042$, $p > 0.1$, Spearman correlation coefficient), mean daily minimum temperature between November–March ($r_s = 0.081$, $p > 0.1$) or mean daily maximum temperature between June–September ($r_s = 0.005$, $p > 0.1$).

Shrew numbers did show seasonal variation coincident with mean monthly temperatures but the two were not correlated. Allowing for the possible lag effects of weather conditions on the shrew population, the relationships between MNA at each trapping period and weather conditions during the 21 days preceding the trapping period were examined. No correlation was found between shrew numbers and total rainfall in November–March or June–September ($r_s = 0.002$, $p > 0.1$; $r_s = 0.039$, $p > 0.1$, respectively), mean minimum temperature in November–March ($r_s = 0.002$, $p > 0.1$), mean maximum temperature in June–September ($r_s = 0.032$, $p > 0.1$) or the number of days when ambient temperature fell below freezing in November–March ($r_s = 0.08$, $p > 0.1$).

Summer temperatures were similar in all years sampled but monthly temperatures in winter were lower in 1985/86 and 1986/87 than in the following two years (Table 1). Yet, population numbers showed no consistent correlation with the relative severity of winter weather: MNA between November and February were significantly greater during the last two winters of the study compared with

Table 1. Comparison of winter weather conditions (November–March inclusive, 151 days) during the period of sampling.

Weather conditions	Winters			
	1985/86	1986/87	1987/88	1988/89
Mean minimum temperature (°C)	0.6	1.3	3.1	2.6
Mean maximum temperature (°C)	6.6	7.6	8.7	9.8
% of days with minimum temperature < 0°C	42	39	19	23
% of days with minimum temperature < 5°C	83	81	68	67
% of days when maximum temperature fails to reach > 5°C	42	25	9	6
% of days with rain > 1 mm	48	33	36	25

those of 1986/87 (winter 1987/88: $t = 25.68$, $p < 0.001$; winter 1988/89: $t = 3.01$, $p < 0.05$), coincident with the milder conditions, but they were also relatively high during the cold winter of 1985/86 (Figs 1 and 2). Moreover, the population declined markedly in January/February 1989, despite the relatively mild conditions. Overwintering numbers of shrews were linked to summer recruitment levels, which were greater in 1987 and 1988 than in 1985 and 1986 (Fig. 2). An index of activity of shrews, based on the ratio of the numbers of individuals trapped to the total number of recaptures, showed that shrews were significantly less active on the ground surface during the two cold winters than in the subsequent two mild ones ($t = 3.9$, $p < 0.01$).

Seasonal input, dispersal and population turnover

Input of new (unmarked) individuals (both those born in the study area and immigrants) was greatest during the summer (Fig. 3). Young first appeared in June and successive cohorts of juveniles (distinguished by their smaller size, lower

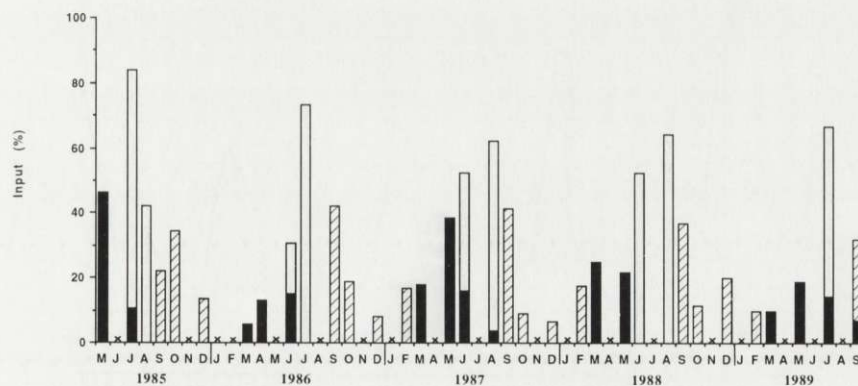


Fig. 3. The percentage of unmarked shrews captured during each trapping period: adults (shaded), juveniles (dotted) and sub-adults (hatched). Crosses denote months not sampled.

body weight and condition of the pelage) were identified in July, August and September. The October input was caused by dispersing sub-adults entering the study area.

Immigration occurred all year but was low in winter. Numbers of immigrants increased in spring when mature shrews, especially males, showed greater mobility and many entered the study area. Mark-recapture data revealed that only 45% of all mature males and 65% of mature females found in the study area during summer were likely to have been born there. The remaining 55% of breeding males and 35.4% of females were unmarked immigrants which took up residence there in May–June.

The role of dispersal in the population dynamics of small mammals is difficult to assess since it cannot readily be distinguished from mortality. In an attempt to gain an insight into patterns of dispersal, individuals captured in at least two consecutive trapping sessions were designated 'residents' while individuals captured during only one trapping session and never subsequently were designated 'transients' (which may have dispersed or died). Transients ranged from 0–66.7% of the population per trapping period (mean 14.2%). They showed a seasonal cycle with highest numbers in summer (comprising mostly juveniles), a decline in autumn and lowest numbers in winter. December and February trapping sessions often revealed zero transients. Numbers increased in March–June when mature adults showed greater mobility and several, particularly males, moved out of the study area.

The proportions of new individuals which became transients or residents varied greatly between trapping periods. A mean of 38% ($\pm 27\%$) were transients which failed to be recaptured in successive trapping periods, while the rest (62%) stayed as residents. No statistically significant seasonal differences were found.

The proportions of immigrants and transients were similar each year, and were not correlated with population numbers in autumn and winter.

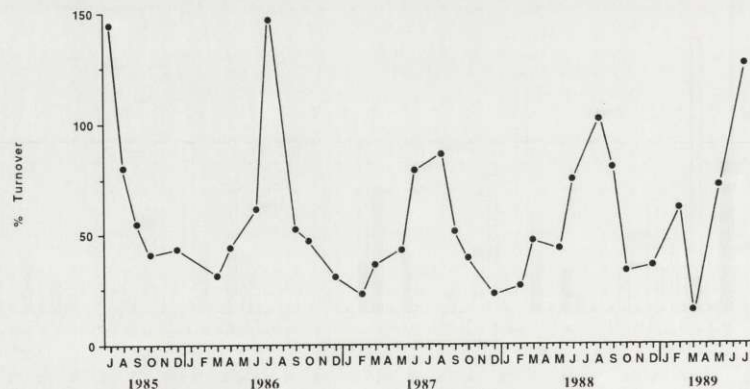


Fig. 4. Index of population turnover (%) of *S. araneus* (see text for details).

An index of population turnover (%) was calculated for each trapping period as follows: the number of marked individuals lost since the previous trapping period plus the number of new individuals, divided by MNA. Population turnover showed a marked seasonal cycle, being highest in summer and lowest in mid-winter (Fig. 4).

Variations in body mass

Summer-born young generally underwent a small increase in body weight until October but from then until February a decline in weight of 12.3–19.2% occurred (Fig. 5). While mean percentage weight loss differed yearly, absolute weight loss by individuals was very consistent (1.0–1.5 g), with no inter-sex differences. Shrews entered winter at 7–8 g, occasionally up to 9 g. Most of the larger individuals (representing early-born young) maintained higher body weights than others through the winter.

The earliest signs of sexual maturity were in mid-February but the majority did not mature until the middle or end of March. This was well-synchronised in both sexes, and from year to year: all trapped individuals achieved sexual maturity within a three-week period and this was accompanied by a rapid rise in body weight (Fig. 5). There was no evidence that early-born cohorts reached sexual maturity earlier than late-born cohorts. Many old adults underwent a decline in body weight at the end of the breeding season (Fig. 5).

Weight losses in autumn and winter were not correlated with temperatures prevailing at the time, and colder winters did not result in lower body weights of

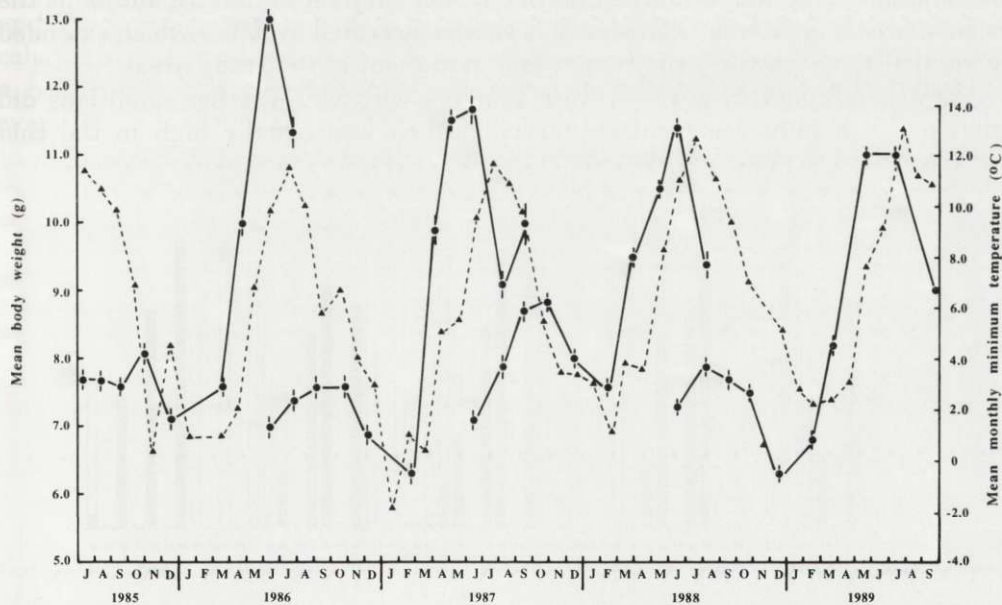


Fig. 5. Mean body mass (\pm SE) of shrews belonging to each summer-born cohort captured during successive months (solid line), together with mean monthly minimum temperature (dotted line).

shrews: comparing mean body weight during the trapping periods in October, December and February each year with mean minimum temperature for the 21 days including and preceding the trapping periods, $r = 0.312$, $p > 0.1$. Despite relatively mild conditions throughout autumn and winter 1988, a decline in body weight commenced in August/September and totalled 19.2% by December, the maximum weight loss recorded. Similarly, there was no evidence that the rate of growth to sexual maturity was affected by annual differences in ambient temperature in spring.

There were no significant differences in body mass between resident young and transient young in summer (mean 7.5 g and 7.6 g, respectively). Neither were there any significant differences in body mass between resident adults and immigrant adults in spring/summer. For example, mean body mass of resident males was 10.9 g and of immigrant males was 10.5 g.

Survival and longevity

Seasonal and annual patterns of monthly survival

Here survival is synonymous with residency in the study area since animals disappearing may have died or emigrated. Survival showed a seasonal cycle each year (Fig. 6). It was lowest in summer months due to the death of old adults, coupled with high mortality or dispersal of juveniles. By late summer–autumn the population stabilised and monthly survival rose to 62–86% between November and March. There was a marked decline in the survival of mature adults at the onset of breeding (March–May) but this was exaggerated by males which extended or vacated their winter home ranges and moved out of the study area.

Patterns of monthly survival were similar each year. Weather conditions did not appear to influence monthly survival which was equally high in the cold



Fig. 6. The percentage of shrews captured during each trapping period which had survived from the previous sampling session: adults (shaded), juveniles and sub-adults (dotted). Crosses denote months not sampled.

winters and in the two subsequent, mild winters. Survival of young shrews was unaffected by the particularly high rainfall in October 1987. Neither was overall winter mortality rate (based upon the numbers of residents in October and their survival until the following March/April, see Methods) affected by weather conditions. Both highest and lowest mortality rates occurred in the milder winters (48% in 1988/89, 21% in 1987/88), with the colder winters having intermediate values (33%).

There was no correlation between monthly population numbers and survival or input in the ensuing months ($p > 0.1$). Although winter mortality rate was greatest following a particularly high population density in October 1988, annual winter mortality rate was not related to the density of sub-adults in the previous autumn.

Survival of cohorts born in different months

Is there any evidence that time of birth and weaning affects survival or residency in subsequent months? Figure 7 shows mean survival rates of recently-weaned young captured for the first time in different summer months. All cohorts showed a similar pattern of survival but life-time survival curves, based on log₁₀ plots, revealed that August- and September-born cohorts had a greater rate of loss from the time of first capture until August of the following calendar year ($b = -7.044$ and $b = -7.350$, respectively) than the June and July cohorts ($b = -5.861$ and $b = -5.015$, respectively). The June and July cohorts also had a better survival rate over winter and into the breeding season, between November and April ($b = -3.200$ and $b = -2.800$, respectively) than the August and September cohorts ($b = -5.400$ and $b = -7.057$, respectively). The July cohort generally had a better survival rate than the other cohorts (Fig. 7), with greater juvenile, overwintering and breeding season survival, and individuals lived longer.

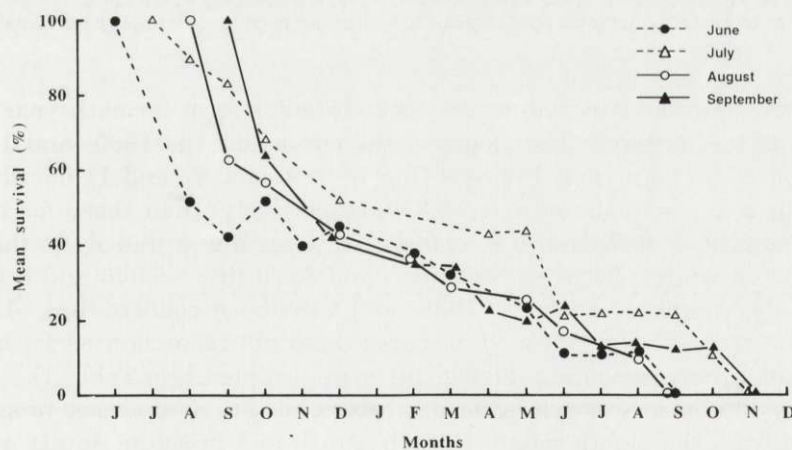


Fig. 7. The mean percentage survival (from time of first capture) of cohorts of *S. araneus* born in different months.

Survival of cohorts born in different years

The survivorship curves for each year's cohort followed a similar pattern (Fig. 8), but there were some differences between years which reflected two important phases: juvenile survival and overwintering survival. The 1988-born cohort, for example, suffered particularly high juvenile loss (at 1–3 months of age) and the survival curve falls well below that of the other years. Mean survival at age one month in the 1988 cohort was significantly different from that of the 1987 cohort ($t = 3.32$, $p < 0.002$). This may be associated with particularly high population numbers in 1988 which encouraged dispersal from the study area. In contrast, the 1987-born cohort had considerably greater survival of juveniles and overwintering subadults (37–45% compared with 16–18% in the 1988 cohort; see Fig. 8).

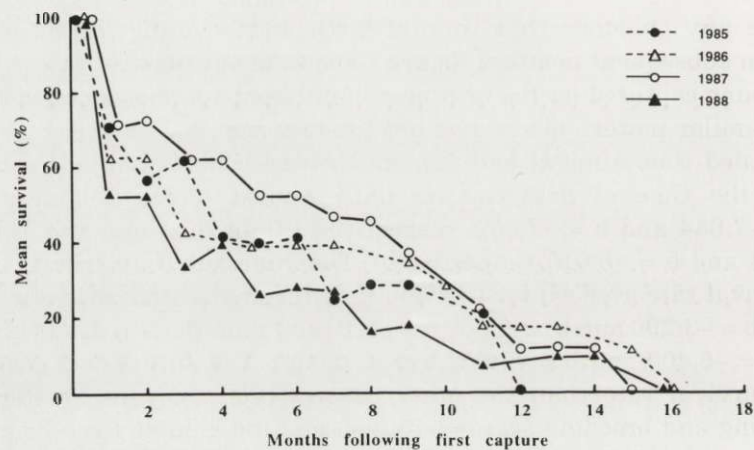


Fig. 8. The mean percentage survival of cohorts of *S. araneus* born in different years. Time zero is the date of first capture.

Although life-time survival curves took a similar form for each year's cohort, the rates of loss differed. The slopes of the curves for the 1985- and 1988-born cohorts, based on \log_{10} plots between time of first capture and 11 months of age, were steeper ($b = -5.842$ and $b = -8.379$, respectively) than those for the intervening years ($b = -4.878$ and $b = -4.981$). This was due primarily to the greater rate of loss in winter, between November and April ($b = -6.543$ and $b = -6.143$, respectively) compared with the 1986- and 1987-born cohorts ($b = -1.311$ and $b = -3.114$, respectively). These differences could not be accounted for by winter weather conditions prevailing during the years sampled (see Table 1).

Despite differences in overwintering success, the survival curves progressively converged from the eighth month (March–April) and breeding adults suffered a high rate of loss before the breeding season was well-advanced. By the eleventh month (June–July) only about 18% of the resident 1986 and 1987 cohorts and 8%

of the 1988 cohort remained. Maximum life expectancy was similar in all years except the 1985-born cohort where it was considerably shorter.

High juvenile and overwintering survival did not lead subsequently to a large reproductive output. Numerous young were produced in 1989, despite relatively low survival of the resident 1988-born cohort, indicating the importance of large litter size and/or the role of immigrant adults in reproduction. Breeding success (based on MNA in April/May onwards and the total number of recently-weaned juveniles appearing between June and September) was not related to the number of mature adults present.

Longevity and survival of males and females

The maximum life-span recorded for males was 17 months and for females was 14 months, but the mean maximum life-span for both sexes was 10 months. Mark-recapture results showed that 85% of young males and 73% of young females which became resident in the study area successfully overwintered and entered the breeding season, compared with a mean of 31% for the whole population of young shrews (residents and transients). The remainder (15% and 27%, respectively) survived well into the winter but were not captured beyond February–March. However, the differences between the sexes may be biased by the greater activity of mature males in spring, and their greater trappability compared with pregnant or nursing females.

The survival of immature males and females could not be compared directly because of the high rate of loss of juveniles from the study area as a result of mortality or dispersal, coupled with the inability to confirm the sex of all the very young shrews. Between 26% and 46% (mean 37%) of juvenile shrews trapped in the study area during each summer failed to be recaptured within two subsequent trapping periods, and either died or dispersed. The proportion of lost juveniles differed between months and years but conformed to no discernible pattern. Those born early or late in the summer were equally likely to disappear from the study area.

Discussion

Population numbers and turnover

Population densities of *S. araneus* in this study were high compared with those recorded by other investigations (Churchfield 1990) but the seasonal cycles in numbers were similar to those found elsewhere in Britain and Europe (Borowski and Dehnel 1952, Mezhzherin 1960, Pernetta 1977, Churchfield 1980). There was no evidence of the erratic annual population fluctuations found in longer-term studies by Skarén (1972) or by Henttonen *et al.* (1989) in Finland, nor of the regular four-yearly cycle of population peaks and crashes found by Sheftel (1989) in central Siberia.

Mortality and dispersal helped to reduce population density in summer and autumn but this was partly offset by immigration of new individuals. The low numbers of transients and immigrants, and low turnover, in winter suggests that the population was stable at this time. The numbers of transients (which includes dispersers) and immigrants were not correlated with population density in autumn and winter, suggesting that their impact on the population dynamics at this time was minimal.

More significant was the large proportion of the breeding population which comprised immigrants which had not overwintered in the study area. Although established residents had a high overwintering success compared with the population as a whole, only 45% of males and 65% of females in the breeding population were life-time residents, the remainder being spring immigrants.

Despite high overwintering mortality and low numbers of adults in spring, breeding success can be high (Kaikusalo and Hanski 1985, Sheftel 1989) and, as found in this study, breeding success may not be correlated with the number of mature adults present. Henttonen *et al.* (1989) even found that summer growth rate was negatively correlated with spring population density.

Activity of shrews, and hence trapping success, may be related to weather conditions, showing a negative correlation with seasonal or daily temperature and a positive correlation with humidity and rainfall (Borowski and Dehnel 1952, Jánský and Hanák 1960, Mystkowska and Sidorowicz 1961, Pankakoski 1979, Churchfield 1980, 1984). Although individual shrews were generally less active under winter than summer conditions in this study, there was no evidence that daily or seasonal temperatures and rainfall directly affected trapping success and population trends.

Variations in body mass

The seasonal weight changes of soricine shrews in northern temperate regions are well-documented (Borowski and Dehnel 1952, Niethammer 1956, Shillito 1963, Pucek, 1965, 1970, Croin Michielsen 1966, Hyvarinen 1969, Churchfield 1981). The winter weight loss tends to be greater in northern and eastern Europe with its more severe, continental, winter climate than in the milder, maritime conditions of Britain: in Poland and Finland it can reach 37% and 45%, respectively (Pucek 1965, Hyvarinen 1969) compared with less than 20% in the present study.

There was no evidence that colder winters resulted in greater weight loss in this study but the winter climate in England is seldom, if ever, as severe as in north-eastern Europe. Although shrews can mature in their first calendar year (Pucek 1960, Stein 1961) there was no evidence of this in the present study, all shrews overwintering as immatures. The reason for this may be high population density (Stein 1961).

The onset of sexual maturity in spring was similarly unaffected by weather conditions, and seems to be triggered more by increasing daylength than temperature (Crowcroft 1964, Churchfield 1990). Pankakoski (1985) found that high

precipitation promoted breeding success in *S. araneus*, and Getz (1989) also found some correlation between high summer rainfall and population density in *Blarina brevicauda*.

There was no difference in size between transients or immigrants and residents but body mass may be too crude an indicator of social status since Hanski *et al.* (1991) found evidence only of small morphological (skeletal) differences amongst young *S. araneus*, with residents being larger than so-called dispersers and more socially dominant. However, such morphological differences were found only in years of low population density. At high population density, many young shrews will have to disperse, regardless of age, size and social status.

Survival patterns and longevity

The seasonal patterns of survival of *S. araneus* in the present study were similar to those reported in other studies of this species (Croin Michielsen 1966, Pernetta 1977, Churchfield 1980, 1984). The most vulnerable time for shrews is the post-weaning period when they are locating and establishing home ranges. There is evidence that social factors, particularly dominance relationships, may affect the ability of both young shrews and old adults to establish and maintain home ranges (Croin Michielsen 1966, Platt 1976, Moraleva 1989). Young shrews which establish home ranges promptly may have social and competitive advantages as residents over non-residents or dispersers (Platt 1976, Moraleva 1989), and early-born cohorts might be expected to survive better than late-born ones. This is supported by the results of the present study. The increased mortality of adults in spring and summer is consistent with their mobility (especially of males) providing greater opportunities for predation coupled with dispossession of home ranges by more aggressive and competitively superior juveniles (Moraleva 1989).

Differences in survival between years, including juvenile survival and overwintering success, were not correlated with weather conditions or population density and the impact of weather on population dynamics of shrews is equivocal. Even in the harsher climate of Scandinavia, Henttonen *et al.* (1989) found little correlation between weather (temperature and snow depth) and winter mortality, although Pankakoski (1985) found that survival in normal or cold winters was better when the insulating snow cover was thick, and was particularly good in a mild winter with little frost and snow.

Although shrews' lives can be prolonged in captivity (Pucek 1964), wild ones seldom enter a second winter (Borowski and Dehnel 1952) and the maximum life-span of 17 months was a record for wild *S. araneus* (Churchfield 1990). Tooth wear, general senescence, poor competitive ability and other sociological factors lead to their demise in the wild (Moraleva 1989, Churchfield 1990). The greater life-span and overwintering success of males compared with females was probably merely a result of differential trappability of the two sexes during the breeding season.

Population limitation in shrews

The causal factors of population limitation in shrews remain obscure. Weather conditions play an equivocal role in their population limitation. There is little correlation between winter temperature and mortality in northern temperate areas (Henttonen *et al.* 1989), although snow cover aids survival (Pankakoski 1985). During long-term studies of population cycles of shrews in central Siberia, Sheftel (1989) found that multi-annual changes in population density were not related to general weather parameters; population crashes were not correlated with severe or snowless winters, and winters preceding peak densities were not particularly mild. However, he did find evidence of exceptional weather conditions (such as very cold springs) affecting populations. Weather conditions seem unlikely, therefore, to have an impact on survival of shrews in Britain which rarely experience the extremes of the more northerly and easterly parts of the range of *S. araneus*. However, it is noteworthy that residents in the study area had the greatest overwintering success. Weather conditions may affect survival and exert a selective role in regulating certain groups within the population.

Food supply has often been implicated as a regulator of shrew numbers, particularly in winter. This may be the case in the more severe northern and continental winters, although many invertebrate prey of shrews remain active here in winter (Aitchison 1984). Food limitation may also affect breeding success and juvenile survival in summer, and Kaikusalo and Hanski (1985) found evidence that it acted in a density-dependent way during summer in Lapland. Despite seasonal variation in prey availability, no evidence of food shortage has been found in the milder conditions of southern Britain (Churchfield 1982, 1993).

There is evidence that population dynamics of shrews are influenced by predation (Henttonen 1985, Kaikusalo and Hanski 1985, Korpimäki 1986), in a similar way to those of microtine rodents, and dispersers may be at greatest risk of predation.

Social factors may also play an important role in the population dynamics of shrews, including social dominance, patterns of home range use and territoriality. The demise of ageing adults, particularly males, may well be hastened by the social dominance of juveniles as they take over home ranges (Moraleva 1989). Territory-holding residents are socially dominant over strangers (Platt 1976). So, social status (resident, disperser, immigrant, young, old) probably influences survival and population density. While seasonal changes in captures of shrews during years of low abundance may depend mostly on weather conditions, sociological factors (including intra- and inter-specific interactions) may become more important in times of high population density (Ivanter 1976, Moraleva 1989, Sheftel 1989).

All these factors can operate in a density-dependent way, either directly or indirectly. There is some evidence of density-dependence in shrew populations: Henttonen *et al.* (1989) found that winter mortality rate was positively correlated

with autumn density. However, no evidence of density-dependence was forthcoming in the present study, despite high and variable population densities.

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