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Trap mortality in *Microtus agrestis* (L.)

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A certain amount of trap mortality seems to be an inevitable by-product of any small mammal live-trapping programme, even when adequate food, bedding and shelter are available to the captured animals. If the cause of death is readily identifiable, steps can often be taken to reduce the mortality. For example, if wet bedding appears to be responsible (CORKE 1967), traps can be provided with waterproof and insulating covers (SHAW and MILNER 1967). In a recent study of trap mortality, PERRIN (1975) concluded that no single factor was responsible, but that environmental variables including extremes of temperature, rainfall and insolation were particularly important. In many respects, it is the remaining unexplained mortality which is of the greatest interest, because it may provide a clue to the physiological condition of the animals in the population under investigation. For example, PLATT (1968) has suggested that trap mortality tends to be high when populations are undergoing declines and that the number of trap deaths may, therefore, provide an indication of population "stress". The present study was carried out only a few

kilometres west of PERRIN's site in south-west Britain, and this analysis was made in order to determine whether environmental variables or population factors were most important in producing trap mortality.

Methods

The study area and trapping methods have been described elsewhere (FERNs 1976, and in litt.) and so only a brief outline will be given here. A grid of 196 Longworth traps were employed in a young larch plantation covering 0.64 ha of abandoned meadow, dominated by rank grasses. The plantation was situated at Darnafor, near Exeter, Devon, England ($50^{\circ} 42' N$, $3^{\circ} 36' W$), and a minimum of four days of trapping were carried out on 20 separate occasions between April 1967 and April 1969. Approximately 15–20 g of whole oats were placed in the nest-box portion of each trap, covered by a twist of hay weighing about 10 g to provide bedding (all quantities were judged by eye when setting the traps). A further quantity of whole oats was spread inside the entrance tunnel, and just outside it, to act as bait. Each trap was set in a well hidden and sheltered position with the entrance facing downhill to ensure efficient drainage.

Traps were visited once per day in the mornings and all *Microtus agrestis* (L.) were individually marked by toe-clipping. The animals were weighed at every capture in small polythene bags, using Pesola spring balances of 100 g capacity. These bags were home made, measuring only 8×5 cm, and were fitted with a small drawstring. Their small size and low weight (less than a gram) enabled reasonably accurate weighings to be made, even under difficult wet or windy conditions.

During the course of the two years of study, over 3,600 captures of small mammals were made, of which about 48% were of *Microtus agrestis*. The total number of individuals of this species which died in traps was 60, but since some of these died during subsidiary trapping outside the main four-day periods, the total sample size available for some of the analyses which follow was somewhat less than this. The sex of dead animals was determined by dissection and their age from eye lens weight (ASKANER and HANSSON 1967; MORRIS 1972). Whole eyes were fixed in 5% formalin for a month, the lenses were then removed and fixed for a further month before drying for 24 hours at $80^{\circ} C$ prior to weighing. The weight-to-age conversion was based on data from a laboratory stock of the same species kept in Edinburgh by W. N. CHARLES (pers. comm.). The calorific value of the whole body (less the eyes) was determined for each animal using a Gallenkamp ballistic bomb calorimeter.

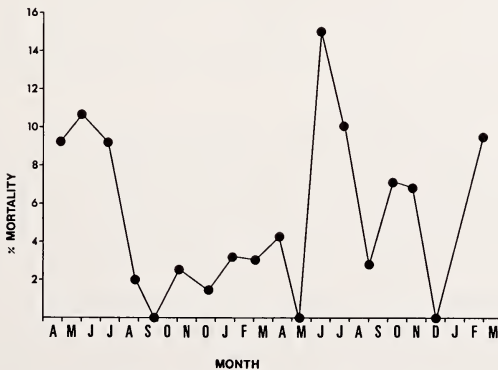


Fig. 1. Seasonal variations in trap mortality

Records of rainfall and temperature were obtained from the meteorological station at Exeter airport, which is situated about 13 km ENE of Darnafor at a slightly lower altitude. Average temperatures in vole runways amongst grass tussocks on the study area itself were determined by the sucrose inversion method of BERTHET (1960). The BERTHET temperatures were about $0.5^{\circ} C$ lower on average than the airport temperatures, but this difference was sufficiently consistent that it is not unreasonable to use the airport minimum nightly temperatures as at least an index of the coldness experienced by animals in the study area itself.

Results

During the main trapping periods, 165 female and 139 male *Microtus agrestis* were captured of which 45 died, giving an overall mortality rate of 14.8%. The sum of the number of individuals captured each month was 455 for females and 425 for males, giving an average mortality per trapping period of 5.1%. The mortality rate per capture was 2.7%. Of the grand total of 60 dead animals, 59 were dissected and of these, 43 were male and 26 female. The preponderance of males in this sample is significant ($\chi^2 = 4.2$, $p = 0.025-0.050$). Males were also more common amongst the 45 of these animals which died during the main trapping periods (30 males, 15 females, $\chi^2 = 5.0$, $p = 0.025 - 0.050$), despite the fact that fewer males than females were captured overall. Most of the extra mortality of males occurred during the spring (Table 1) at a time when the overall mortality (Fig. 1) appears to show a peak. There is, however, no significant difference between months in the number of deaths (e. g. for males in Table 1, assuming that a constant percentage of the catch should die each month, $\chi^2 = 24.3$, $p > 0.10$). Neither is there a significant difference when the months are arbitrarily grouped into four periods — spring (March–May), summer (June–August), autumn (September–November) and winter (December–February).

Within trapping periods, there is an uneven distribution of deaths, more occurring on the second and third days than on the first and fourth (Table 2), but this is mostly due to the fact that fewer animals were captured on the first and last days of trapping and the difference is thus not significant ($\chi^2 = 4.0$, $p > 0.10$). There is, however, a clear tendency for most deaths to occur to animals the first time they are captured in any trapping period (Table 3, $\chi^2 = 26.4$, $p < 0.001$). Also, a higher proportion of completely new animals tends to die each month compared with those who have some experience of capture in a previous trapping period (using the number of deaths in Table 4, corrected contingency $\chi^2 = 30.7$, $p < 0.001$).

There is no relationship between the percentage mortality in each month and the average nightly minimum temperature for the four days of trapping ($r = 0.37$, $p > 0.10$), but there is a significant negative correlation with the total rainfall for the period ($r = -0.46$, $p = 0.02 - 0.05$). Since it is unlikely that rainfall has any directly beneficial effect on survival in traps, this effect is presumably due to its association with some other variable.

The distribution of mortality within various weight classes differs significantly from that expected on the basis of a constant percentage of deaths per trapped animal in each case (Table 5, $\chi^2 = 12.7$, $p = 0.025 - 0.050$). This difference largely results from the small number of deaths which occurred in the 15–20 g class. This is the weight at which most animals overwinter and they suffer a low trap mortality at this time. A similar test cannot be conducted on the death rate in different age classes because the age distribution of neither the total population nor the captured sample is known. There is no marked indication, however, of either young or old animals suffering undue mortality (Table 6). Not surprisingly, the average age of those dying at the end of the non-breeding season in April (144 days) was somewhat greater than those dying in June and July (86 days).

There is no correlation between the numbers dying and the total number of animals captured ($r = 0.34$, $p > 0.10$) or the estimated population size ($r = 0.08$, $p > 0.10$). There is a significant negative correlation, however, between the minimal survival rates, calculated purely on the basis of the number of animals known to be alive at particular periods (CHITTY and PHIPPS 1966), and the percentage trap mortality ($r = 0.58$, $p = 0.001 - 0.010$). In other words, trap mortality is correlated with mortality (and/or emigration) in the population as a whole. Trap mor-

Number of animals dying in the first four days of each trapping period

The date given is that of the first day of each period

Date	Males	Females
25/4/67	2	2
31/5/67	1	5
12/7/67	5	1
22/8/67	1	0
23/9/67	0	0
3/11/67	2	0
17/12/67	0	1
26/1/68	1	1
1/3/68	2	0
5/4/68	1	1
10/5/68	0	0
14/6/68	4	2
19/7/68	4	0
30/8/68	1	0
4/10/68	1	2
8/11/68	3	0
13/12/68	0	0
26/2/69	2	0
3/4/69	0	0
24/4/69	0	0

Table 2

Distribution of deaths according to the day of the trapping period

Day	Number of animals captured	Number dying	Expected number dying
1	349	6	9.2
2	448	16	11.8
3	451	14	11.8
4	429	8	11.3

Table 3

Distribution of deaths according to the number of previous captures within each trapping period

Previous captures	Number of animals captured	Number dying	Expected number dying
0	323	38	19.5
1	277	10	16.7
2	136	2	8.2
3	98	3	5.9

Table 4

Number of animals dying on different capture occasions

The total number of captures in each category is given in brackets (note that the number of deaths appear to be independent of the number of captures)

	Day of initial capture	Subsequent days
Captures during the trapping period of initial capture	23 (304)	5 (297)
Captures during subsequent trapping periods (i.e. animals with some previous experience of capture)	14 (576)	8 (551)

Table 5

Distribution of deaths according to body weight

Weight class (g)	Number dying	Expected number dying
≤ 9.9	3	1.0
10.0-14.9	8	4.9
15.0-19.9	14	24.1
20.0-24.9	12	11.7
25.0-29.9	10	7.3
≥ 30.0	5	2.9

Table 6

Distribution of deaths according to age

Age range (days)	Number dying
0-24	4
25-49	4
50-74	7
75-99	5
100-124	12
125-149	2
150-174	9
175-199	7
200-224	0
225-249	1

Table 7

Average change in weight (g) between first and second captures when they occurred on consecutive days

The sample size is given in brackets

Trapping period	Weight class			All animals
	≤ 19.9g	20.0-29.9g	≥ 30.0g	
April 1967	+0.35 (10)	+0.22 (9)		+0.29 (19)
May/June "	-0.50 (8)	-0.75 (10)		-0.81 (21)
July "	-1.35 (7)	-0.95 (11)		-1.08 (20)
August "	-1.35 (9)	-1.20 (10)		-1.24 (20)
September "	-0.83 (9)	-0.13 (12)		-0.57 (22)
November "	+0.10 (31)	+0.09 (9)		+0.10 (40)
December "	+0.17 (18)	-0.23 (9)		+0.03 (27)
January 1968	+0.39 (20)	-0.11 (12)		+0.20 (32)
March "	+0.07 (16)	-1.24 (12)		-0.49 (28)
April "	-0.13 (9)	-0.74 (10)		-0.43 (20)
May "		+0.96 (7)		+0.91 (10)
June "		+0.94 (7)	-4.02 (6)	-1.35 (13)
July "	-0.98 (9)	-0.93 (6)		-1.03 (17)
Aug./Sept. "				+0.83 (8)
October "		-0.82 (5)		-0.96 (8)
November "	+0.67 (7)			+0.27 (12)
December "				-0.04 (9)
February 1969				-0.84 (7)

tality is also significantly correlated with the overall weight change of animals between first and second captures on consecutive days (Table 7, $r = -0.57$, $p = 0.01 - 0.02$). The relationship between these two variables is shown in Fig. 2,

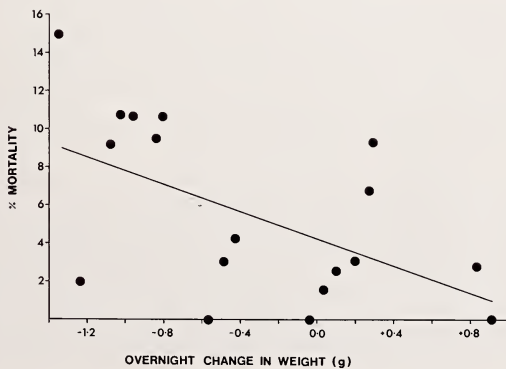


Fig. 2. Trap mortality in relation to weight change between consecutive captures. Each point represents the average for a single trapping period

together with the regression line fitted by least squares. Both males and females were included in the calculation of weight change in traps, though pregnant females showing signs of vaginal distention were excluded since they might have lost embryos or neonates. Weight losses occurred more commonly than weight gains, the largest losses being recorded in mid-summer and the biggest gains in spring or autumn. Larger animals tended to lose more weight than small ones; for example, the average weight change in the 11 months for which estimates are available in both of the smaller weight classes in Table 7, was -0.37 g for animals under 20 g, and -0.54 g for animals between 20 and 30 g. This difference is more than can be accounted for by the difference in the relative weights of the two groups of animals involved.

Discussion

The overall trap mortality per capture at 2.7% is fairly typical for microtines captured in Longworth traps. This figure is close to the 2.1% recorded by PERRIN (1975), but rather greater than that achieved by BUECH (1974) using a specially designed trap with a large nest box. The latter trap was intended for use under particularly severe conditions including snow, and during initial trials the mortality rate was only 0.3%. A variety of other methods have also been developed to cope with the problem of trapping during very cold conditions (MILLER and GETZ 1968; IVERSON and TURNER 1969). In the mild climate of south-west Britain, cold weather mortality is obviously not a significant factor. High temperatures are a different matter, and PERRIN (1975) found that temperatures above 18.3°C did result in a significant increase in the number of trap deaths. In the present study, care was taken to ensure that traps were placed in shaded locations and no such effect was observed, although individual cases of moribund or dead animals in very warm weather did occasionally occur. As temperatures in general rise, there is likely to be an increasing problem of replacing water loss for interned animals and in some circumstances, the addition of pieces of apple or potato to the trap is advisable.

It is clear from all the available studies of trap mortality that the category of animals which suffer most severely are those being captured for the first time. CHITTY (1937) noted this when using the "Tring" trap, which was the forerunner of the Longworth trap, and he suggested that slowness in learning to eat grain might be one possible explanation. PERRIN's results showed that more deaths tended to occur in the later part of each trapping period, including those which involved new captures, and this led him to suggest that the traps might have been "conditioned" by the previous occupants. Such "conditioning" might have involved dampness of the bedding caused by condensation and contamination with urine. A similar effect could also be produced by the exhaustion of the food supply within the trap, and it is thus important to see that this is replenished. The 15–20 g supplied in the present case is more than adequate to last one animal for four days of continuous occupation, but there is always the possibility of spillage when extracting animals from the traps.

The fact that the maximum trap mortality occurred at a time when mortality in the population as a whole was high, suggests that the condition of the animals themselves may be an important factor. If the year is divided into a breeding and nonbreeding season on the basis of external signs of reproductive activity (50% of males with scrotal testes, or 35% of females palpably pregnant or actively lactating), there is a significantly higher trap mortality in the breeding season (χ^2 % 4.7, $p = 0.025-0.050$). The breeding season, defined in this way, lasted

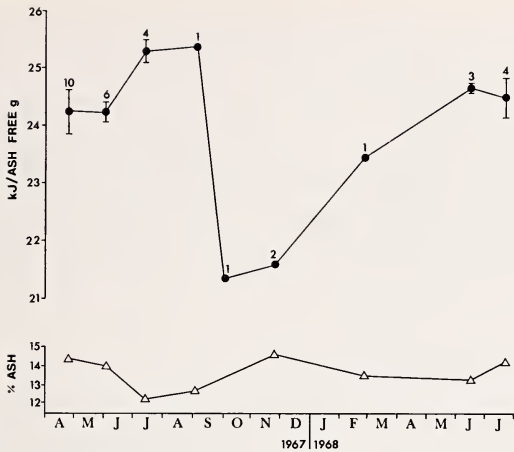


Fig. 3. Average energy and ash contents of animals dying in traps. The sample size and one standard deviation on either side of the mean are indicated in the case of the energy content

from April to November. The result of this test is particularly interesting in view of the fact that previous tests failed to reveal any significant seasonal component to the mortality.

The main period of high death rates (Fig. 1) is in the early part of the breeding season and corresponds to the time when the highest growth rates of individual animals occurs. Not only are animals growing rapidly at such times, but they are already of high body weight and should have good bodily food reserves. For example, their energy content (Fig. 3) is high, and their ash content is low, as a result of the high proportion of fat plus flesh to total body tissue at this time of year. In such a condition, animals should be more, and not less, capable of withstanding confinement in traps.

All this evidence taken together, suggests that some as yet unidentified factor causes a loss of the ability to adapt to initial capture, particularly in the case of males, during the breeding season. It is known that the males of several species of small mammal become more active during the early part of the breeding season (KIKKAWA 1964) and also that they are more aggressive then (SADLEIR 1965; TURNER and IVERSON 1973). Such animals may spend a great deal of time in attempting to escape, rather than settling down within the traps. Because of their large size and good food reserves, it seems likely that dehydration is the most important proximate cause of death, rather than starvation. This may be exacerbated by the fact that temperatures are often high at this time of year. However, the ultimate cause of death remains speculative at present.

Any factor tending to decrease viability is likely to increase the number of trap deaths, and it is not surprising to find a higher mortality in declining populations, as reported by PLATT (1968). Whether such trap mortality is at all useful as an indicator of "stress" is rather doubtful. Apart from the difficulties of defining precisely what is meant by such "stress", the number of trap deaths is anyway an extremely crude yardstick. A much more valuable and sensitive index of the reaction to trapping can be obtained from the overnight weight loss, as measured in Table 7.

CHITTY and PHIPPS (1966) describe some examples of marked changes in the survival of *Microtus agrestis* which they considered to be due to changes in behaviour within the population, in particular an increase in the aggressiveness of young animals. TURNER and IVERSON (1973) have shown that associations between aggressiveness and survival do exist in *Microtus pennsylvanicus*. One particular month in the present study does stand out as being of special interest in this regard. In June

1968, animals over 30 g in weight showed a quite remarkably high overnight weight loss in traps (Table 7), whereas those in the range 20–30 g actually gained weight. This month had the greatest trap mortality of any in the study and it was the heavier animals which suffered it. Minimum survival rates in the population as a whole were poor between June and July, and the growth rate was exceptionally low. Clearly, some kind of change had occurred within the population during June which caused a dramatic reduction in viability of the larger animals. The cause of this change remains a mystery, though competition with younger animals is clearly a strong candidate. To cause the observed increase in trap mortality, this competition would have to produce an effect in the absence of direct confrontation, since the trap effectively prevents this from occurring.

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I would like to thank G. G. VICKERS and I. J. LINN, who supervised the work, and M. R. PERRIN whose own study of trap mortality prompted me to undertake this analysis. The field work was conducted during the tenure of a Science Research Council research studentship at the University of Exeter.

Summary

71% of the trap deaths during a two-year study of *Microtus agrestis* in south-west Britain occurred amongst animals being captured for the first time. Trap mortality was highest during the breeding season, and males were affected to a greater extent than females. The number of deaths was not correlated with population size, numbers captured, or environmental temperature, but there were significant inverse correlations with minimum population survival rate and with rainfall. Trap mortality tended to be high at times when the average weight loss of live-trapped animals between consecutive captures was high. These findings are consistent with the view that the main proximate cause of death was dehydration or starvation through failure to consume the food supplied in the trap. There are, in addition, factors which make this failure more likely to occur to males in the breeding season, and these could be related to the increased levels of aggression and activity which are found at this time.

Zusammenfassung

Fallensterblichkeit bei Microtus agrestis

Bei periodischen Lebendfängen von *Microtus agrestis* im südwestlichen Großbritannien im Verlauf von 2 Jahren betrafen 71% der Todesfälle Tiere, welche zum erstenmal in die Fallen geraten waren. Die Fallensterblichkeit erreichte ihren Höhepunkt während der Fortpflanzungsperiode und war bei ♂♂ häufiger als bei ♀♀. Sie stand nicht in Beziehung zur Populationsdichte, zur Zahl der gefangenen Tiere oder zur Temperatur. Dagegen nahm sie mit sinkender Überlebensrate in der Population und mit abnehmenden Niederschlägen zu. Die Fallensterblichkeit war besonders hoch, wenn für die lebend erbeuteten Tiere aufeinanderfolgender Fangperioden besonders starke Gewichtsverluste festgestellt wurden. Überwiegend dürften deshalb die Todesfälle dadurch verursacht worden sein, daß die Tiere die in den Fallen bereitgestellte Nahrung nicht angenommen haben und verhungert oder verdurstet sind. Die Tendenz, daß vor allem ♂♂ während der Fortpflanzungszeit sterben, könnte mit der dann höheren Aktivität und Aggressionsbereitschaft zusammenhängen.

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A ciliated epithelium covering the inner surface of the glove finger in *Balaenoptera physalus* Linnaeus, 1758

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Abstract

Studied the glove finger in *B. physalus*, which is protruding from the bulla tympani into the external auditory meatus. Histological examination revealed that the inner surface of this structure is covered by an epithelium which is composed of ciliated cells alternating with secretory cells. The presence of this epithelium allowed some conclusions about the origin of the glove finger in Balaenopteridae.

Introduction

The epithelium covering the meatal surface of the glove finger in *B. physalus* is described by ICHIHARA (1959) while PURVES (1955) studied the histology of the earplug, formed on and for the main part by this epithelium. ICHIHARA also gives a short description of the glove finger.