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Population estimates of the wood mouse (*Apodemus sylvaticus*) as an apparent function of grid size

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Abstract

Density estimates, survival rates and trappability in *Apodemus sylvaticus* (LINNAEUS, 1758) as a function of grid size were studied. The four grid sizes ranged from 1.2 to 8.2 ha. Density estimates obtained with the minimum number alive method were similar for all grid sizes but those obtained with the Jolly-method were highly biased for the two smallest grids. Survival rates and trappability improved considerably as grid size increased. Differences between small and large grids were most pronounced in summer when the animals averaged longer movements than in winter. The size of the grid as well as rapid seasonal changes in the movement patterns of the animals does have a definite influence on the magnitude of the edge effect.

Key-words: *Apodemus*, Rodentia, density, survival rate, seasonal variation.

Introduction

Most small mammal population studies are conducted with live traps set at regular intervals to form a grid. Depending on the information desired and the kind of animals involved one has to choose for a trapping scheme in which the bias produced by the operation of all kind of variables is minimal. Among variables like the type, size and location of the traps, the type of bait and prebaiting procedures, the duration of the trapping, etc. grid size is also an important variable.

The size and shape of the grid will influence the magnitude of the edge effect (i.e. not all animals subject to capture have their entire home ranges within the trapping grid) (RYSZKOWSKI, ANDRZEJEWSKI & PETRUSEWICZ, 1966; ADAMCZYK & RYSZKOWSKI, 1968; HANSSON, 1969; SWIFT & STEINHORST, 1976), density estimates (TROJAN & WOJCIECHOWSKA, 1967; SOUTHERN, 1973, VAN HORNE, 1982; ANDERSON *et al.*, 1983), mortality estimates and estimates of the distances moved by the animals (TAYLOR, SHORTEN, LLOYD & COURTIER, 1971; FAUST, SMITH & WRAY, 1971). Even though these problems have been known for decades (DICE, 1941; STICKEL, 1954), existing methods still do not handle the estimation of the edge effect and the consequences it has on population estimates.

The objective of this study was to investigate the influence of grid size on certain population estimates in the wood mouse, *Apodemus sylvaticus* (LIN., 1758).

Materials and Methods

The data were collected in a reserve South of the municipal Turnhout (Belgium, 51°61'22" N. Lat. and 4°55'45" E. Long.). Details of the study area can be found in VERHAGEN (1980).

The basic field technique was regular live trapping with collapsible aluminium Sherman traps (76x89x229mm). Trapping sessions of mostly three nights were undertaken at regular intervals from May 1976 to November 1982. In the first

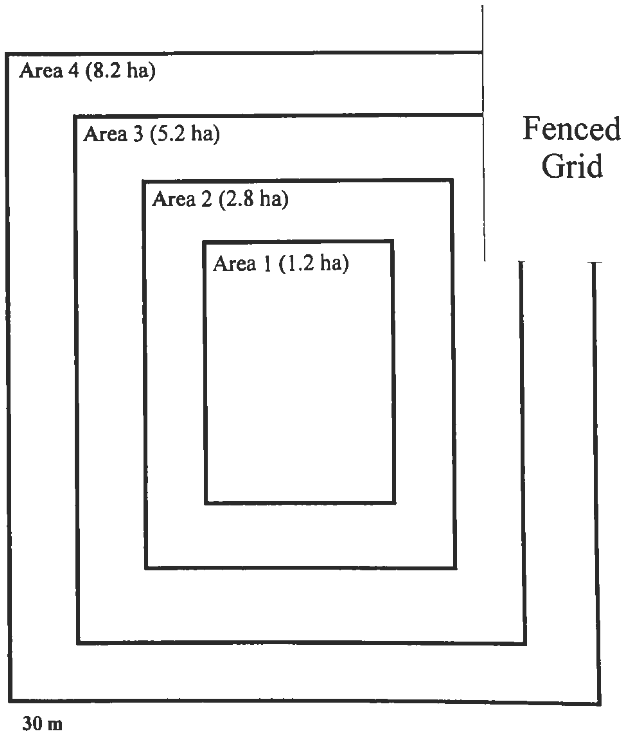

Fig.1. – Schematic map of the live-trap study area showing the position of the four grids used.

two years of this study the interval between trapping sessions was two weeks, from March 1978 on trapping sessions were every three or four weeks.

Trapping stations were spaced 15 m apart and at each station two traps were placed and baited with peanut butter. The catch was examined three times a day (sunrise, afternoon and around midnight). From May 1976 to March 1980 the area of the grid measured 4.1 ha but was enlarged to 8.2 ha in April 1980. Only the trapping data collected after April 1980 will be used here.

Newly captured wood mice were individually marked by toe clipping and all animals were released at their original point of capture after the necessary data were recorded. Each animal was weighed to the nearest gram and sex and reproductive condition were noted. Females were considered as sexually active if they had a perforate vagina, were lactating or pregnant and males if the testes were scrotal.

Calculations were made for four different grid sizes. The core area measured 1.2 ha and was positioned central in the 8.2 ha grid. The other areas measured 2.8, 5.2 and 8.2 ha and were formed by adding each time two trap rows around the central core area (Fig. 1). The data for the four grids were treated independently from each other.

Results

DENSITY ESTIMATES

Density estimates for the four grids were calculated using the total enumeration method (MNA-method) of KREBS (1966) and the JOLLY-SEBER method (JOLLY, 1965; SEBER, 1965). With the JOLLY-SEBER method it was not always possible to obtain a density estimate since at some trapping sessions as one or more of the necessary statistics were equal to zero. From the data presented in Table 1 we can conclude that:

Table 1:
Density estimates of wood mice for four different grid sizes calculated according to the total enumeration method (MNA) and JOLLY–SEBER method. Densities expressed as numbers/ha.

Trapping Period	area 1 (1.2ha)		area 2 (2.8ha)		area 3 (5.2ha)		area 4 (8.2ha)	
	MNA	Jolly	MNA	Jolly	MNA	Jolly	MNA	Jolly
5/1980	12.5		9.3		10.6		11.2	–
6	10.8	–	9.6	–	10.8	–	12.3	12.7
7	13.3	25.9	11.8	12.6	12.3	14.6	11.1	12.0
8	10.8	10.4	9.3	10.3	9.6	10.7	10.7	11.6
9	11.7	11.3	10.4	12.6	10.0	10.7	12.1	12.6
11	10.0	–	8.2	8.8	11.3	14.2	12.9	13.4
12	8.3	10.4	6.8	8.0	8.4	9.9	9.0	9.4
1/1981	5.8	–	5.4	6.4	7.5	7.3	7.1	7.3
3	8.3	12.0	6.4	9.5	6.7	7.6	6.3	6.7
4	4.2	10.0	3.6	4.4	4.0	4.4	5.1	5.6
5	5.0	11.7	3.6	–	3.6	–	4.5	5.3
6	5.8	–	3.9		3.3		5.1	8.4
7	6.7	–	6.1	–	5.6	–	6.3	9.1
8	3.3	–	3.9	12.5	3.8	9.4	5.6	7.2
9	3.3	–	3.6	8.0	3.5	5.8	4.7	7.5
10	8.3	–	7.9	10.5	8.5	14.7	9.0	14.5
11	14.2	–	10.7	13.6	11.7	13.4	14.2	17.7
12	8.3	–	13.2	23.2	11.0	18.4	14.2	24.3
1/1982	9.2	12.6	12.9	20.5	10.6	16.3	14.0	18.1
2	9.2	13.0	10.7	13.3	9.2	10.6	12.1	14.2
3	7.4	8.6	8.6	10.9	7.1	8.2	10.5	11.8
4	11.7	26.0	10.4	10.6	910	12.4	12.1	14.3
5	13.3	21.9	10.7	12.8	10.0	13.4	12.7	16.2
7	24.2	–	16.1	19.6	14.6	15.8	17.9	19.1
8	16.7	19.3	15.7	21.1	13.8	16.3	15.7	17.9
9	24.2	37.0	25.0	40.7	1919	22.1	20.0	22.3

- Densities calculated with the MNA-method were very similar for the four areas considered here. This might suggest that the animals were more or less uniformly distributed.
- JOLLY-SEBER estimates were much more variable. Only for the 5.2 and 8.2 ha grids they were in close agreement with the MNA-estimates (area 5.2 ha: n=21, r=0.88, p<0.01, Y=2.41+1.01X; area 8.2 ha: n=25, r=0.91, p<0.001, Y=1.03 + 1.11 X). For the two smallest areas the JOLLY-SEBER estimates were much higher than the MNA values as can be seen from the slope of the regression equation (area 1.2 ha: n=14, r=0.85, p<0.05, Y=1.11 + 1.40 X; area 2.8 ha: n=21, r=0.92, p<0.05, Y=-0.94 + 1.46 X).

The mean relative deviations of the JOLLY-SEBER estimates in comparison with the MNA estimates are presented in Table 2. For this purpose we recognised a summer (5/80-9/80; 4/81-10/81 and 4/82-9/82) and a winter period (11/80-3/81 and 11/81-3/82).

Table 2:
Mean relative deviation in summer and winter of the JOLLY-SEBER density estimates in comparison with the MNA estimates.

	Area 1 (1.2ha)	Area 2 (2.8ha)	Area 3 (5.2ha)	Area 4 (8.2ha)
Winter	32.8%	34.7%	24.4%	19.0%
Summer	68.4%	48.2%	36*8%	24.3%
Total	55.7%	42.4%	31.5 %	22.4%

For both periods the deviation between the two density estimates became smaller as grid size increased. Beside this size effect a very pronounced difference between summer and winter can be observed with a much smaller deviation in winter than in summer.

SURVIVAL

We measured mortality in the trappable population as minimum survival rates per 28 days. Minimum survival rates of the trappable population summed over two months are presented in Fig. 2. It must be noted that an individual mouse was tallied each time it was trapped.

Fluctuations in survival rate were more or less similar for the four areas considered but there were rather large quantitative differences. These differences were more obvious in males than in females and more pronounced during the breeding season.

For both sexes and periods minimum survival rates increased progressive with increasing grid size and again this difference is more pronounced in summer than in winter (Table 3). Indeed, summer survival rates for area 4 (8.2 ha) were 28 % higher in comparison with those of area 1 (1.2 ha) while in winter this difference was only 11 %.

MOVEMENTS

Movements of mice are not easily studied by live trapping procedures because the relation between trap – revealed movements and actual movements is difficult to evaluate. However when comparing mean movements over a year it can give a rough idea of how the movement pattern is changing seasonally. We analysed only movements recorded on individuals between successive trapping periods. For each trapping period the geometric centre of capture points was calculated for each individual. The distance between the geometric centres of two adjacent trapping periods was taken as a measure of mobility of an individual. Despite the fact that the distribution of movements is highly skewed we calculated for each two-month period the mean length of movements between trapping periods for males and females. In this way most of the samples are large so that normal statistical procedures may be used with only a small error.

Changes in mean length of movement between two-month periods are given in Fig. 3 (every point is based on data of 15 individuals or more). Movements showed a strong seasonal variation with minima in autumn-winter and maxima in spring-summer. Males always averaged longer distances between trapping periods than females and the differences were most pronounced during the breeding season.

Table 3:
Pooled 28-days minimum survival rates of male and female wood mice for the summer and winter period.
Number of mice for which the survival estimate was calculated is given between brackets.

	Area 1 (1.2ha)	Area 2 (2.8ha)	Area 3 (5.2ha)	Area 4 (8.2ha)
Winter				
Males	0.680(66)	0.673(140)	0.700(245)	0.733(515)
Females	0.612(49)	0.653(131)	0.697(250)	0.706(433)
Total	0.651(115)	0.663(271)	0.698(495)	0.721(948)
Summer				
Males	0.506(91)	0.565(205)	0.600(369)	0.665(678)
Females	0.530(107)	0.577(192)	0.606(336)	0.666(547)
Total	0.519(198)	0.571(397)	0.603(705)	0.665(1225)

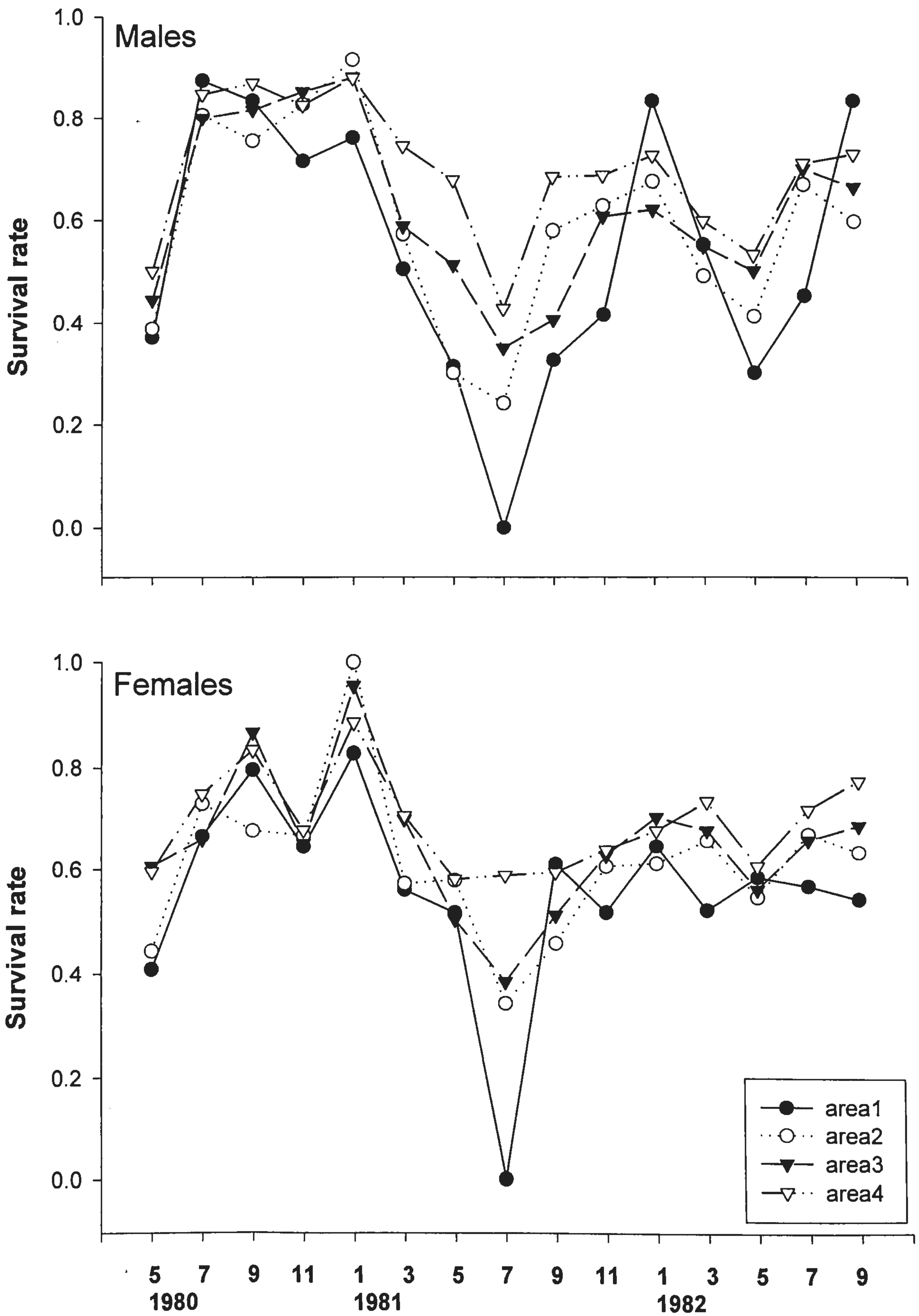

Fig. 2. – Seasonal variation in minimum survival rates per 28 days of male and female wood mice on the four grids: area 1 (1.2ha); 2 (2.8ha); 3 (5.2ha); 4 (8.2ha).

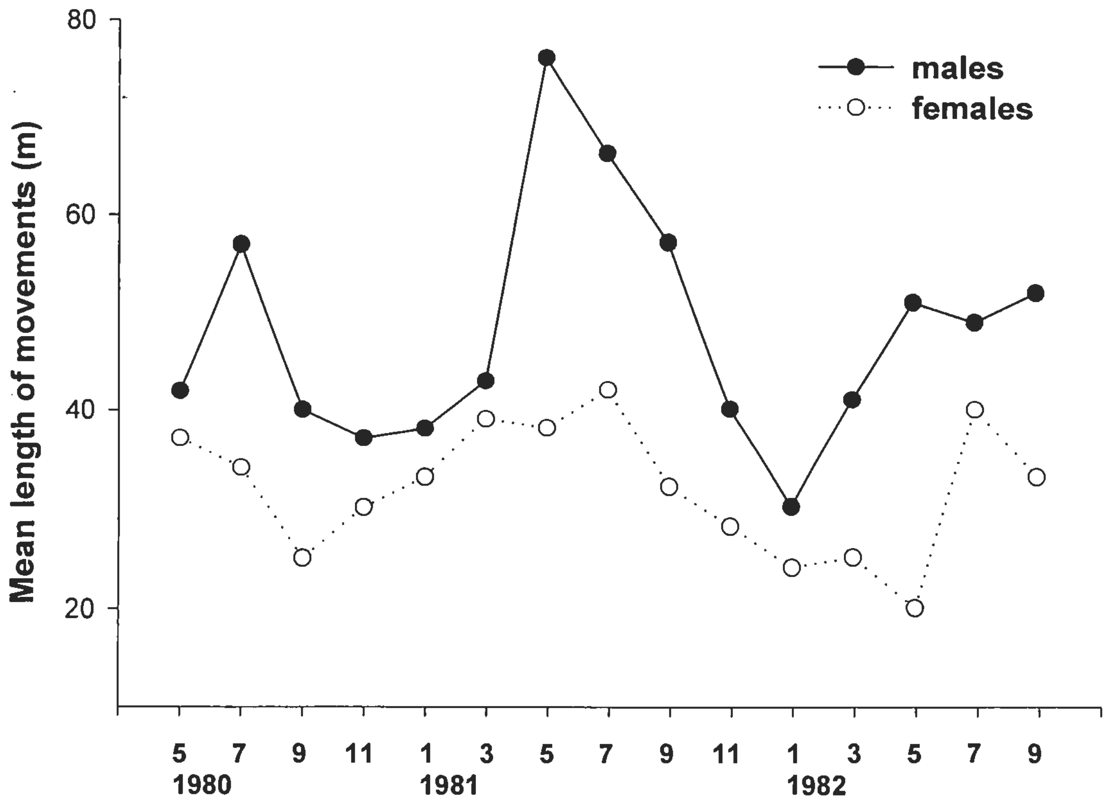

Fig. 3. – Seasonal variation in mean movements between trapping sessions of male and female wood mice.

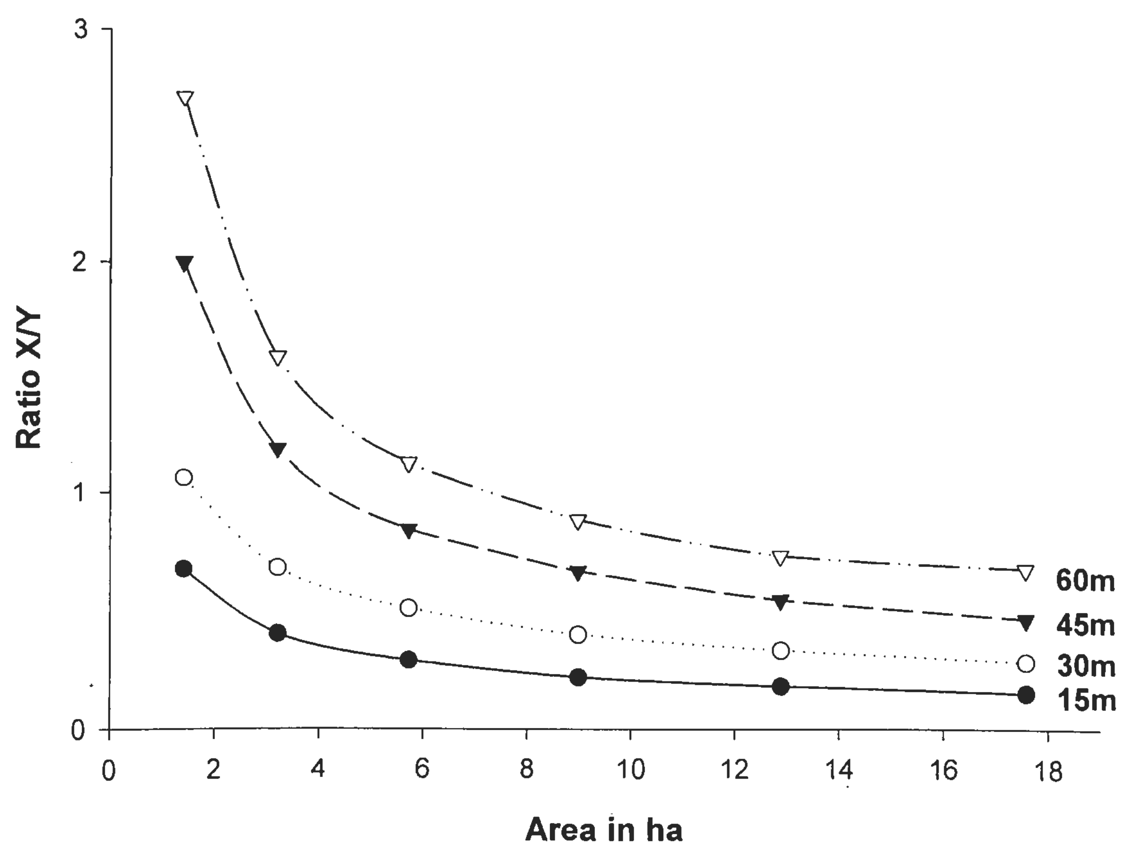

Fig. 4. – The ratio (X/Y) of the number of animals whose activity centre is without the grid to those whose activity centre is located entirely within the grid in function of grid size and for four different movement patterns.

INFLUENCE OF GRID SIZE AND MOVEMENTS ON POPULATION PARAMETERS

The probability of capturing animals, except from those whose activity ranges entirely within the grid, will change when the mean distance moved by the animals increases or decreases. This can be illustrated by using a simplified model where we suppose that the animals are uniformly distributed within the trapping grids. In the model we adopt a spacing distance of 30 m between the activity centres (HAYNE, 1949) of the individuals which corresponds with a density of approximately 11 ind./ha. Considering that the individuals move four different distances between trapping sessions (15, 30, 45 and 60 m), we can calculate for each distance and for each grid size the number of animals whose activity centre is located entirely within the grid (Y). Beside those there are animals whose activity centre is outside the grid but due to their movements run the risk to be caught within the grid (X).

The ratio X/Y in relation to grid size was calculated for the four mean distances (Fig. 4). If we regard the X/Y ratio as a measure of the edge effect than it is obvious that when the animals range over long distances the edge effect is extremely great in small grids. As grid size increases the edge effect diminishes quickly and remains rather constant for grids larger than 5.7 ha.

Table 4:
Trapping data of male and female wood mice for the four different grid sizes.
(NC: nr. of newly captured mice; RC: recaptures; NRC: individuals known to be alive but not recaptured in a given trapping session; R1: NC/(RC+NRC); R2: trappability (RC/(RC+NRC); R3: NC/(nr. animals recaptured one or more times)). Both NC, RC and NRC are expressed as numbers per ha.

	NC	RC	NRC	R1	R2	R3
Winter period						
Area 1 males	14.2	15.8	14.2	0.47	0.53	1.43
females	15.0	15.8	5.8	0.69	0.73	1.25
Area 2 males	12.1	20.0	9.3	0.41	0.68	0.79
females	16.8	20.0	4.6	0.68	0.81	0.96
Area 3 males	13.1	23.3	5.0	0.46	0.82	0.84
females	15.0	21.5	5.8	0.55	0.79	0.77
Area 4 males	14.3	32.7	7.8	0.35	0.81	0.63
females	15.2	25.2	5.0	0.50	0.83	0.62
Summer period						
Area 1 males	51.7	22.5	10.0	1.56	0.69	2.44
females	50.0	34.2	5.0	1.28	0.87	2.33
Area 2 males	46.1	24.2	9.6	1.36	0.72	1.61
females	36.8	30.7	3.9	1.06	0.89	1.44
Area 3 males	40.0	30.2	5.4	1.12	0.85	1.07
females	31.9	29.0	5.8	0.92	0.83	1.15
Area 4 males	44.5	41.0	6.8	0.93	0.86	0.80
females	30.6	36.9	5.2	0.73	0.88	0.91

Table 5:
Model in which the influence of changes in the movement pattern on survival rates is demonstrated.

	Nr. of animals	Change in mean distance moved		
Area		60m – 45m	60m – 30m	60m – 15m
Area 1 (1.4ha)	55	0.82	0.56	0.45
Area 2 (3.2ha)	91	0.85	0.65	0.54
Area 3 (5.7ha)	135	0.87	0.70	0.60
Area 4 (9.0ha)	187	0.88	0.74	0.65
Area 5 (12.9ha)	247	0.88	0.77	0.68
Area 6 (17.6ha)	325	0.88	0.77	0.69

The rapid change of the X/Y ratio with grid size will have an influence on several population estimates. In Table 4 the number of newly captured animals, recaptures and animals not recaptured in a trapping period were pooled for the winter and summer periods and expressed per hectare.

For both the winter and the summer period a decrease in the ratio of newly captured mice to recaptures can be observed. Since the number of recaptures increases with increasing grid size it is reasonable to expect that trappability improves in a similar way which is the case in winter for both sexes and for males in summer. Trappability of females in summer, however, remained constant whatever grid size was.

If we assume that animals which are captured only once, were at least partly animals whose activity centre was situated outside the grid, than we might expect that the ratio of animals caught only once to those who were caught more times would follow a similar distribution as the theoretical X/Y distribution. In summer, the proportion of males and females caught only once was much higher than in winter. This difference might be due to differences in the distances moved and/or differences in mortality. However, the decrease of the ratio with increasing grid size was very pronounced for both periods. It is rather surprising that although males range over much wider distances than females, the ratio for both sexes was almost similar.

From Table 3 an improvement of survival rates with increasing grid size could be observed. Using the simple model described above it is easy to demonstrate that both grid size and rapid alterations in the mean distances moved by the animals can have a considerable effect on the calculated survival rates. In the hypothetical case that no animals died during a 28 day period, and that within the same period the mean distance moved by the animals was reduced from 60 to respectively 45, 30 and 15 meter than we can calculate the survival rates for the different grid sizes used in the model (Table 5).

When we compare the 28 days minimum survival rates of the smallest and largest sized grids, for the three particular cases than we find that the survival rates are respectively 7.3 % , 37.5 % and 53.3 % higher on the largest grid. Survival rates are improving fast with increasing grid size up to an area of 5.7 ha after that the influence of area size is becomes smaller.

Discussion

Spacing behaviour in the wood mouse was found to be very variable throughout the year and between sexes (KIKKAWA 1964; BERGSTEDT 1966; RANDOPLH, 1977; GREEN, 1979; MONTGOMERY 1980; VERHAGEN, 1980; ATTUQUAYEFIO *et al.*, 1986). The alteration of spatial organisation in a population is probably the result of significant changes in behavioural interactions between individuals during the year (KORN, 1986; TEW & MACDONALD, 1994). It is suggested that these relationships play an important part in the regulation of wood mouse numbers (WATTS, 1969; FLOWERDEW, 1974; RANDOLPH, 1977; GURNELL, 1978; VERHAGEN & VERHEYEN, 1982). The finding that distances moved by the animals showed considerable variation poses serious problems in defining the edge effect. Indeed, if the probability of capturing animals, except of those whose activity ranges entirely within the grid, will change with the mean distance moved by the animals, than as a consequence the edge effect will be a variable in time. Males during the breeding season always averaged longer movements than females. In the non-breeding season this was not the case. This implies that beside a seasonal variation in the magnitude of the edge effect there will also be a sex-related difference. Both factors have to be taken into account when trying to assess the magnitude of the edge effect or in calculating the effective trapped area for live-trap grids.

Beside changes in movement patterns, grid size has a definite influence on the magnitude of the edge effect. The larger the grid the smaller the ratio of animals whose activity ranges partly within and partly outside the grid to those with an activity centre entirely within the grid, will be. With increasing grid size we found that density estimates with the Jolly method became more reliable, trappability improved and survival rates were higher. Changes in the magnitude of the edge effect, trappability and survival rates as a function of grid size were relative small once the size of the grid exceeded 5 ha.

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