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Sex Ratio in Small Mammal Populations as Affected by the Pattern of Fluctuations

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Hansson L., 1978: Sex ratio in small mammal populations as affected by the pattern of fluctuations. Acta theriol., 23, 10: 203—212 [With 4 Tables & 3 Figs.].

Earlier studies have shown that there is a predominance of females in the adult component of peak *Microtus agrestis* populations. The present studies included three areas in which the *Microtus agrestis* populations respectively reached a two year peak, a one year peak and showed no cyclic behavior at all. Each peak was associated with a surplus of females around midsummer which was apparently due to more rapid maturation or higher survival rate in female than male spring-born animals. In the sparse semi-stable population male numbers obviously did not rise to the level where an inter-male interference started. These findings were consistent with the hypothesis that the semi-stable population is regulated by predation. Another cyclic rodent species, *Clethrionomys glareolus* did not show any female surplus at peaks, from which it is concluded that the adult female surplus is not a cause of rodent cycles.

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1. INTRODUCTION

Myllymäki (1975, 1977) reported an increase in the ratio of adult (reproductive) females during years of population increase or peaks in the field vole *Microtus agrestis* (L.). At the start of the breeding season the sex ratio of the adult animals was close to 1 : 1. From the first litter of the year considerably more females than males were recruited to the breeding component. The male litter mates became mature and dispersed or remained immature (subadult). The different maturing rates were associated with different behaviour in the resident adult females and males, with the latter showing a high level of aggression. As a result the sex ratio was heavily biased towards a surplus of adult females already in July. This suprlus continued to increase during the autumn. Few observations of these conditions were made in years with low populations.

During a five-year study of small mammals throughout Sweden (Myllymäki *et al.*, 1977, Hansson unpubl.) various patterns of population fluctuations were detected. They were also associated with varying sex ratios in *M. agrestis*. An attempt will be made here to explain the latter variations and to determine the importance of biased sex ratios in the population cycles.

2. METHODS

Small mammals were censused by Small Quadrat (*SQ*, Myllymäki et al. (1971) removal trapping on some ten localities distributed over one southern, one central and one northern Swedish region in 1971—75. Trap arrangements, trapping localities and total number of animals obtained are described in detail by Myllymäki *et al.* (1977). Trapping was performed in spring (May-beginning a June) and autumn (end of September—October) and in several localities also in summer (July-beginning of August) and in midwinter. Population densities are evaluated from the mean number of animals obtained per *SQ* during two days. The animals were separated into juveniles (with remains of juvenile pelage), subadults (adult fur but not reproductively active), adults (reproductively active) and postreproductive (with regressed gonads). Overwintered and spring-born animals were distinguished in summer by examination of the pelage and fur composition.

3. RESULTS

Fig. 1 shows the seasonal variations in the indices of *M. agrestis* abundance on abandoned fields in the three regions. This type of habitat is most typical for this species. In South Sweden there was an even rhythm with low spring and high summer-autumn populations. Some years showed higher peaks than others but there was no evidence of »population cycles« as described by Krebs & Myers (1974). In Central Sweden such a cycle was observed with a peak in 1973 and very few animals in 1971—72 and in 1975 and a decline in 1974. In North Sweden the peak extended over 1973—74 with few animals trapped in 1971—72 and 1975.

The sex ratios of adult animals trapped in all habitats examined are shown in Fig. 2. In the two northern regions there was an increase in the proportion of females from spring until autumn in the peak years. A significant female surplus was found in the summer of 1973 in Central Sweden and in 1973 and 1974 in North Sweden. Significant surpluses of females also appeared in the autumn of 1973 in both Central and North Sweden while the number of adult animals obtained in autumn 1974 in North Sweden was too small for statistical evaluation. In the »semi-stable« population in South Sweden the sex ratio was balanced in summer or, in 1974 and 1975, there was a predominance of males. There was often a significant surplus of adult females in the autumn but not in 1974 or 1975. In all cases examined except one the sex ratio of adult animals was not significantly different from the 1 : 1 ratio at the start of breeding in spring. The exception was a significant surplus of males in South Sweden in spring 1975.

The summer conditions during the peak years are further examined in Table 1. It is obvious that all peaks were associated with females surplus and that such a surplus did not appear in regions with low densities during the same years. There were significant differences in

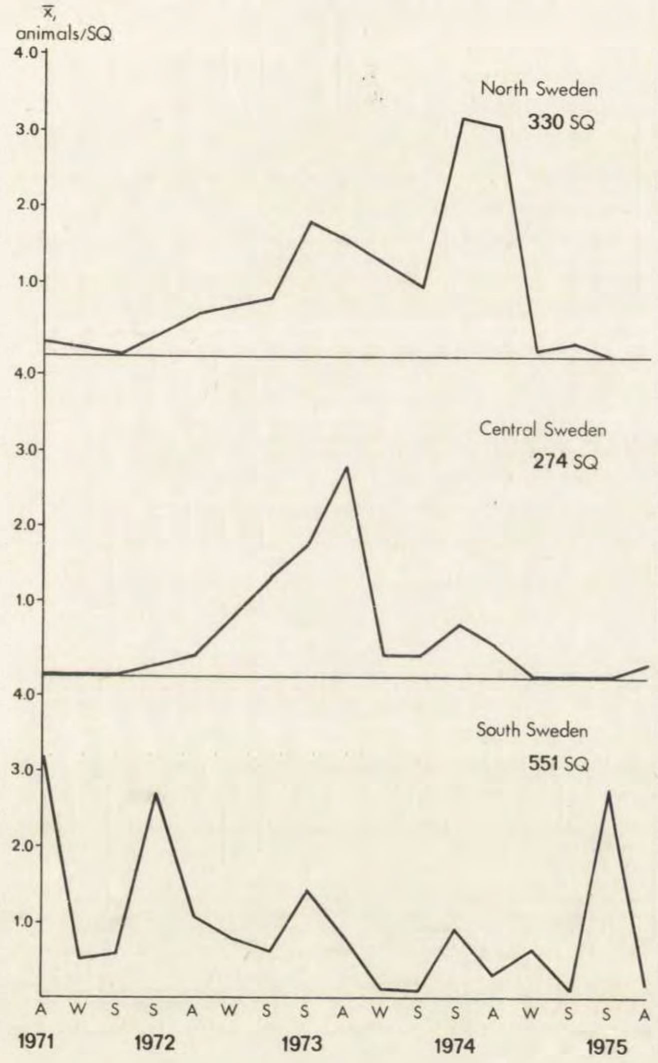

Fig. 1. Indices of density variations of *Microtus agrestis* on abandoned fields in three regions of Sweden. The studies were made with the Small Quadrat method and the total number of quadrats (*SQ*) is denoted.

sex ratios between the tree regions in 1974 ($\chi^2=9.75$, $P<0.01$) but not in 1973.

The age structure, *i.e.* proportions of overwintered and spring-born adults, were examined during summer of the peak years (1973 and 1973—74) for the two northern regions and for 1972—75, covering

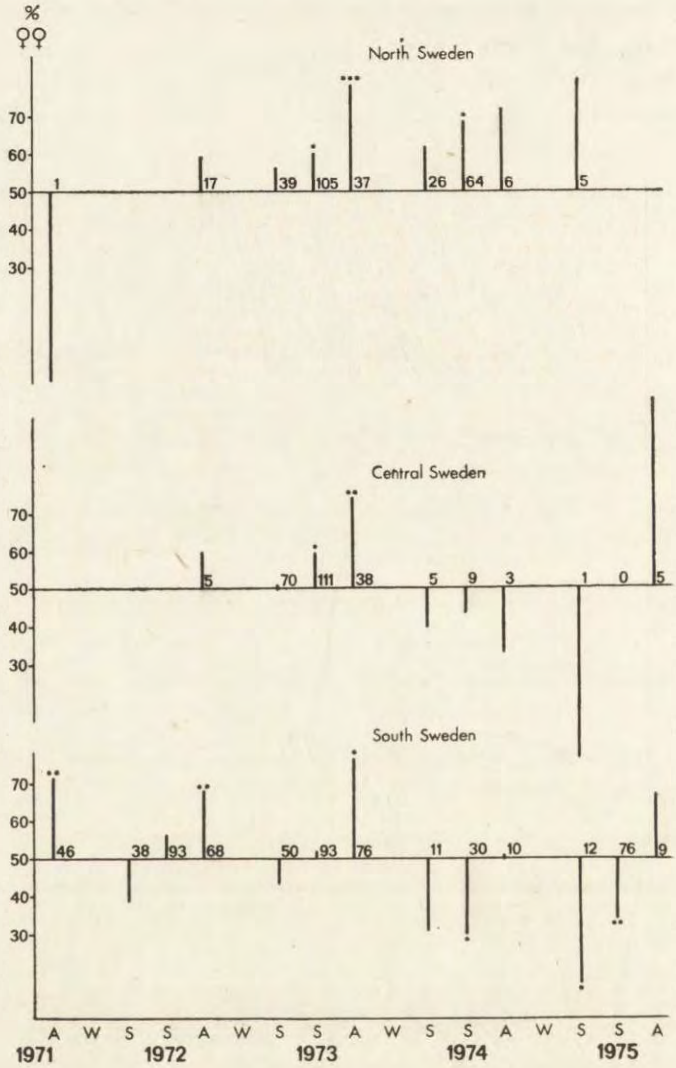

Fig. 2. Sex ratios in the adult component of *Microtus agrestis* in the three Swedish regions during spring (S), summer (S) and autumn (A). In winter (W) no adult animals were caught. The number of adult animals examined is denoted on the horizontal line. $*=P<0.05$, $**=P<0.01$ and $***=P<0.001$ in deviation from an 1:1 ratio.

Table 1

Sex ratios (males/females) of adult *Microtus agrestis* caught during summer. In 1973 there was a population peak in Central Sweden and in 1973—74 in North Sweden. * = $P < 0.05$ in deviation from an 1:1 ratio.

Region	1973	1974
South Sweden	45/48	21/9*
Central Sweden	45/66*	5/4
North Sweden	42/63*	23/41*

a potential population cycle, for the southern population (Table 2). Among males overwintered animals dominated in the peak population while in the semi-stable region spring-born animals were somewhat more frequent. The differences were statistically highly significant in the three regions ($\chi^2 = 25.16$, $P < 0.001$). Among females overwintered and spring-born animals were approximately equally common and there were no significant regional differences.

Because of a more rapid maturation of spring-born females, a male-biased sex ratio should be expected in the subadult component of peak populations at least during the summer. Examination (Table 3) disclosed mae surplus in subadult animals on most occasions in both summer and autumn. Such male surpluses appeared, however, in the juvenile component in all regions and differential maturing rates might have caused an only slight amplification of the previously biased sex ratio.

The total sex ratios of adult animals caught during all the years are examined for three small mammal species in Table 4. For *M. agrestis* from South Sweden there were balanced ratios and a predominance of males in two years. Both Central and North Sweden showed female surpluses during the peak years but not in low populations, not even when all material from such phases were pooled. There were significant differences between the regions in 1974 ($\chi^2 = 11.62$, $P < 0.01$), 1975 ($\chi^2 = 9.02$, $P < 0.01$) and for all years ($\chi^2 = 16.90$, $P < 0.001$). The small

Table 2

Age structures in breeding *Microtus agrestis* during summer.

Region	Years	Males		Females	
		Overwintered	Spring-born	Overwintered	Spring-born
South Sweden	1972—75	44	53	44	26
Central Sweden	1973	34	11	33	32
North Sweden	1973—74	52	12	56	47

Table 3

Sex ratio (males/females) in *Microtus agrestis* which did not reach sexual maturity in the year of birth. $* = P < 0.05$, $** = P < 0.01$ and $*** = P < 0.001$ in deviation from an 1:1 ratio.

Region	Year	Juveniles		Subadults	
		Before first moult	Totally	Summer	Autumn
South Sweden	1972—75	43/26*	56/34*	16/5*	145/70***
Central Sweden	1973	6/6	16/11	19/3***	37/14**
North Sweden	1973—74	36/25	47/29*	79/26***	110/99

rodent *Clethrionomys glareolus* (Schreb.) showed density variations similar to *M. agrestis* both annually and seasonally as described by Myllymäki *et al.* (1977) and as shown in Table 2. However, this species generally had a balanced sex ratio; there was only one exception with a slight surplus af adult females in an expanding but not a peak population. The shrew *Sorex araneus* L. did not show violent fluctuations as did *M. agrestis* and *C. glareolus* in Central and North Sweden, but

Table 4

Sex ratios (males/females) of all trapped adult animals of three small mammal species appearing throughout Sweden $* = P < 0.05$, $** = P < 0.01$ and $*** = P < 0.001$ in deviation from an 1:1 ratio.

	South Sweden	Central Sweden	North Sweden
Microtus agrestis			
1971	77/85	0/0	1/0
1972	80/101	2/3	7/10
1973	80/88	90/120**	67/114***
1974	33/18*	10/7	35/61**
1975	63/34*	1/5	1/4
Total	333/326	103/144**	111/189***
Clethrionomys glareolus			
1971	20/21	3/2	0/4
1972	95/89	5/16*	17/12
1973	95/81	99/106	196/195
1974	52/53	20/19	30/41
1975	28/26	29/18	0/1
Total	290/280	153/161	243/252
Sorex araneus			
1971	10/11	0/0	0/0
1972	8/11	1/1	6/1
1973	3/11	11/5	4/1
1974	4/8	3/1	2/1
1975	4/4	4/2	1/0
Total	30/45	19/9	13/3*

is was trapped in unusually low numbers at the same time as the rodents »crashed«. This species showed a general surplus of adult females in South Sweden and of adult males in Central and North Sweden, although, due to the limited material, only one significant deviation could be established. However, the differences in sex ratio between the regions were clearly significant ($\chi^2 = 12.63$, $P < 0.01$) for the total material.

4. DISCUSSION

The biased sex ratio in *M. agrestis*, established by Myllymäki (1975, 1977), was based on catch-mark-release studies. The present analysis is based on removal trapping, causing an over-representation of adult males in the samples due to the greater activity of this population category (Myllymäki *et al.* 1971). This explains the generally higher proportion of males in this study but not the annual, seasonal and regional differences in sex ratios. Juvenile and subadult males are not known to show higher trappability than corresponding females so the male biased sex ratio in these components may have emanated from birth. However, such a deviation can only be proven by examination of embryos about to be born. The adult male surplus during the early breeding period in some years in South Sweden may possibly be caused by such a natal surplus of males.

Hansson (1971, unpubl.) put forward the hypothesis that the semi-stable *M. agrestis* (and other small rodent) populations in South Sweden are regulated by predation while the northern populations are able to expand to food limitation. However, the northern populations may be exposed to a very heavy predation after the crash. The South Swedish rodents, with little or no snow cover during winter are exposed to many predators all the year round and the predators have ample opportunities to take alternative prey (*e.g.* numerous rabbits *Oryctolagus cuniculus* (L.)). Thus a fairly density-dependent predation would appear. However, the small rodents are generally scarce during spring and the predation impact, relatively speaking, may be greater during spring-early summer than after a longer period of rodent reproduction, *i.e.* in late summer-autumn. The supposed relation between the potential expansion of the adult population and the limits set by predation are tentatively shown in Fig. 3. If, as is suggested in this figure, predation keeps the densities below the level (possibly of 30 adult males/ha according to Myllymäki, 1977) where the male interference starts to affect their increase in numbers, a balanced sex ratio would result. If there is only an ultimate food limitation the adult females will expand towards this limit but not the males and a skewed sex ratio results.

It must be stressed that other explanations for the variable sex ratios may be possible, although these ratios are consistent with the hypothesis that predation regulates field vole numbers in South Sweden.

C. glareolus showed larger variations in density in Central and North Sweden than *M. agrestis* (Myllymäki *et al.*, 1977) but did not show any surplus or increase in adult females during peak years. Thus, population cycles in small rodents are not causally related to changing sex ratios. Also in a fairly stable small mammal species such as

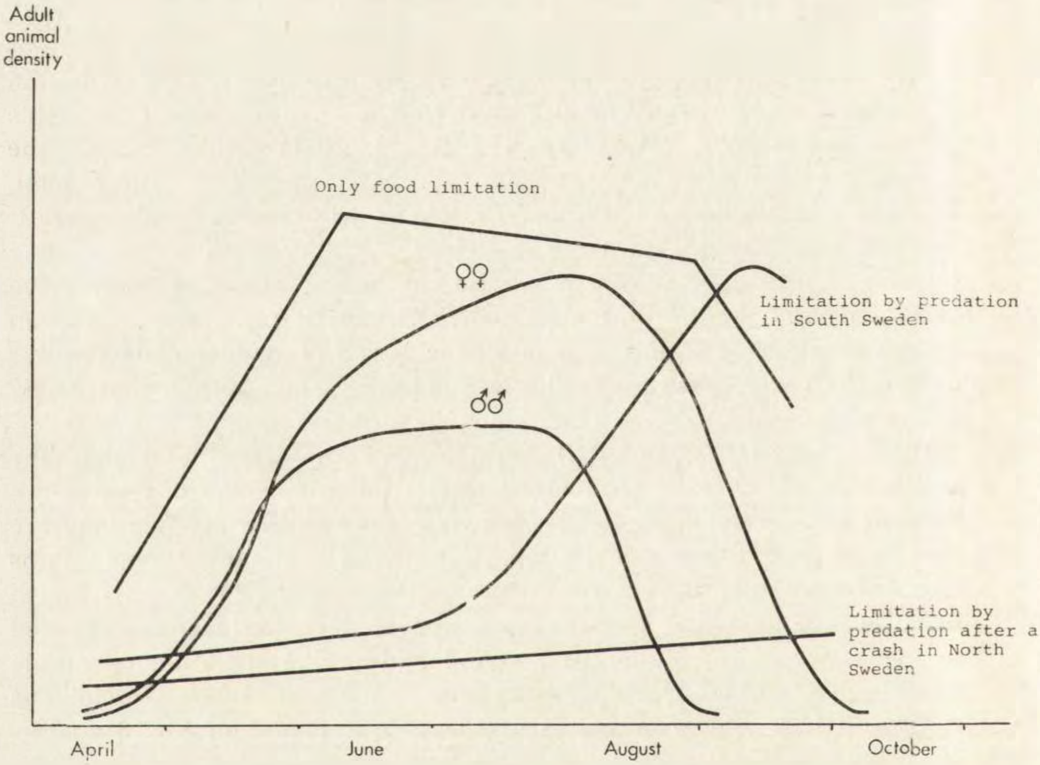

Fig. 3. Tentative model for the effects of predation and food limitation on sex ratios of adult *Microtus agrestis*.

S. araneus there were regional differences in sex ratios but in the opposite direction to *M. agrestis*. However, for species in which a surplus of reproducing females can occur in temporarily unlimited populations very rapid relative increases in numbers may be expected. Such species are *M. agrestis*, *Microtus arvalis* (Pall.) (Adamczewska-Andrzejewska, 1976) and *Clethrionomys rufocanus* Sund. (Kalela, 1971, Hansson *et al.*, unpubl.). The female surplus in *Myopus* *schisticolor* Lillj. seems to be the result of a different mechanism which includes a female surplus in the embryo stage (Kalela & Oksala, 1966). All these species are, however, extreme herbivores with high carrying capacity of food, permitting exponential growth during a long period.

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WPŁYW CHARAKTERU FLUKTUACJI NA STOSUNEK PŁCI W POPULACJACH DROBNYCH GRYZONI

Streszczenie

Wcześniej wykazano, że w fazie szczytu liczebności wśród dorosłych osobników *Microtus agrestis* przeważają samice. Obecnie zbadano stosunek płci w trzech populacjach *M. agrestis* różniących się charakterem fluktuacji. Pierwsza osiągała szczyt liczebności co 2 lata, druga rokrocznie a trzecia nie wykazywała żadnej cykliczności (Ryc. 1). Wykazano, że każdy szczyt liczebności związany jest w środku lata z nadwyżką samic (Tabela 1 i 2), która przypuszczalnie wiąże się z szybszym

ich dojrzewaniem lub wyższym stosunkiem przeżywania samic, w porównaniu z urodzonymi również na wiosnę samcami (Ryc. 2). Natomiast w słabo zagęszczonej, na poły stabilnej populacji przeważają samce, ale ich liczebność nie wzrasta do poziomu, na którym zaczynają się kolizje. Uzyskane wyniki dobrze korespondują z hipotezą o regulacji liczebności populacji częściowo stabilnych przez drapieżniki. U *Clethrionomys glareolus*, podlegającej również cyklicznym zmianom liczebności, nie wykazano przewagi samic w fazie szczytu (Tabela 4), z czego można wnosić, iż nadmiar dojrzałych samic nie jest powodem istnienia cyklów populacyjnych u gryzoni.