Ann. Zool. Fennici 22: 277-288. 1985

Regional differences in cyclicity and reproduction in *Clethrionomys* species: Are they related?

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Hansson, L. & Henttonen, H. 1985: Regional differences in cyclicity and reproduction in *Clethrionomys* species: Are they related? — Ann. Zool. Fennici 22: 277-288.

Indices of density variations (or "cyclicity") for local populations of four species of *Clethrionomys* voles were computed as the standard deviation of late summer - early autumn density-estimates transformed by logarithm of base 10. They were compared whenever possible, with litter sizes, maturation rates, frequencies of litters and lengths of breeding season as components of the total reproductive output.

A south-north increase in density fluctuations in *Clethrionomys glareolus*, accompanied by an increasing occurrence of summer declines, did not correlate with increased litter sizes as predicted earlier but with annual variations in maturation rates. *Clethrionomys rufocanus* and *C. rutilus* showed geographical variations in fluctuation patterns on approximately the same northern latitudes, with generally highest degrees of cyclicity in northern Fennoscandia. The relations between "cyclicity" and litter sizes and maturation rates were similar to those for *C. glareolus. Clethrionomys gapperi* did not show any clear gradient in cyclicity.

Laboratory breeding of *Clethrionomys glareolus* did not demonstrate any inherited difference in litter size or total reproductive output between cyclic and non-cyclic populations. Thus, the variations in maturation rates seem to be due to social or other density-related conditions.

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1. Introduction

It has been known for some time (e.g. Hansson 1979) that Scandinavian small rodents, e.g. the bank vole *Clethrionomys glareolus*, show geographically different patterns and amplitudes of density variation. In the north there are violent variations (or multi-annual "cycles") with peaks every three-five years and then pronounced declines, and extremely low densities follow for at least one year. In many southern localities densities vary annually with often very low spring densities and an autumn peak. However, this annual peak may vary considerably in magnitude (Fig. 1). We have examined this geographical variation in more detail and extended it to other regions and species (Hansson & Henttonen 1985, Henttonen & Hansson 1985).

Geographical variations in litter size, especially of birds, are well known and have been the basis for many evolutionary theories (for a review see Stearns 1976). Recently this variation has also been related to density variations or magnitudes of cyclicity (Stenseth 1978, Stenseth & Framstad 1980). Animals experiencing regular pronounced increases in population densities are predicted to evolve larger litter sizes than those always living at fairly constant densities. A positive correlation is expected to exist between litter size (or some relation between litter sizes of young and old females, the former being especially favoured at great fluctuations) and cyclicity rates in voles. Such close relations have also been reported (Stenseth & Framstad 1980, Stenseth et al. 1985). However, the ranges of density fluctuations have been limited in these examin-

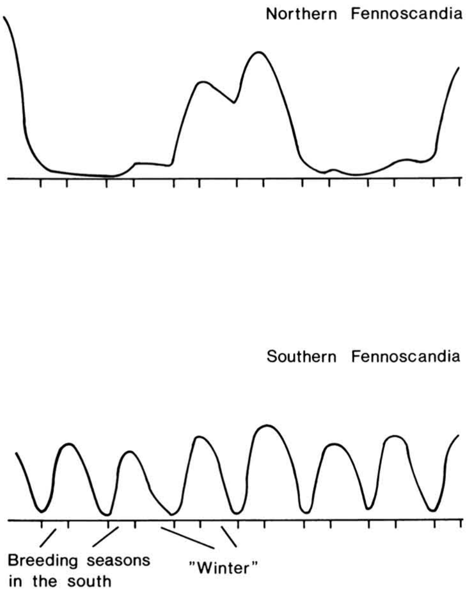

Fig. 1. Schematic picture of the difference in density variations in small rodents between southern and northern Fennoscandian localities.

ations. Here we will try to extend this examination over the whole possible scale. We will, thus, add some further observations of litter sizes under extreme conditions and compare them with local indices of cyclicity. We will also make more general comparisons with the geographical gradients in density variations.

However, we believe that variations in litter sizes are only a small part of the variation in reproductive output. Instead, maturation rates and length of breeding season may be much more important. Therefore, we will also try to compile frequencies of pregnancy or lactation from the same localities examined for litter sizes and fluctuation patterns. We hope thereby to show the futility in examining litter size separately as an index of general reproductive adaptation.

2. Methods

Data were gathered on variations in local population densities during studies extending for at least 3-4 years. We believe that we have included almost all such population studies of *Clethrionomys* species in Fennoscandia. A lot of them are still unpublished. However, studies examined from outside this area derive mainly from previous reviews (e.g. Bashenina 1981, Merritt 1981) or publications in the main international ecological journals. We computed indices of density variations, either as the coefficient of variation, or, as a way of diminishing bias due to the various trapping methods, as the standard deviation (s) of the density data transformed by logarithm of base 10 (Lewontin 1966, Stenseth & Framstad 1980). We preferred data from late summer - early autumn as the most fluctuating populations were also found to be characterized by common summer-early autumn declines in the crash phases. The term "cyclicity indices" is tentatively used as other studies (e.g. Finerty 1980, Kaikusalo & Hanski 1985, Henttonen et al. 1985, and Oksanen, pers. comm.) have demonstrated the cyclic nature of several north Scandinavian population fluctuations by time series analysis. However, we believe the most characteristic feature of really "cyclic populations" to be a continuation of the decline over the summer resulting in extremely low densities (0.1 ind./100 trap-nights or less), rather than some statistically derivable common interval between peaks. This summer decline may not appear during every interval of such a population cycle or it is difficult to observe it at very low densities.

Table 1. Variations in cyclicity of *Clethrionomys glareolus* from various Fennoscandian regions as measured by s, the standard deviation of transformed density indices by logarithms of base 10, and their correlations with geographical variables.

Region	n	Mean	SD	CV
<59°N	7	0.22	0.14	0.64
59-61°N (limes norrlandicus)	11	0.47	0.11	0.23
61-64°N (mainly central Finland)	17	0.46	0.16	0.35
65-68°N	10	0.63	0.19	0.30

Correlations. $n = 45$.	r_s	p
Latitude	0.62	<0.001
Length of snow period	0.64	<0.001
Maximum snow thickness	0.65	<0.001

Reproductive data derive also mainly from published reports. Mean litter sizes were estimated from snap-trapped young of the year and overwintered females from populations with known density variations. The same material sometimes gave also information on frequencies of maturation, i.e. pregnant and/or lactating females in relation to all non-juvenile females. The potentially fecund females consisted of subadult animals without any remnant of the juvenile fur but with undeveloped gonads and post-reproductive females with closed vulva and possibly degenerating mammary glands. They were examined for the period July-August (preferably at the turn of the month) as the maturation rate of young of the year and regression rate of earlier fecund females vary considerably at this time both between localities and population phases. However, the data in the important study by Bujalska (1970) on factors determining maturation in female *C. glareolus* could not be used as she did not distinguish between juvenile and post-juvenile females. Only animals from September could be examined from the Kilpisjärvi and Pallasjärvi areas (both in Finland) but post-reproductive animals there were considered to be part of the breeding group. Certain females are pregnant and lactating simultaneously and a further index of reproductive intensity can be obtained from the ratio pregnant plus lactating relative to all lactating, including pregnant plus lactating. Early states of pregnancy cannot be detected macroscopically and therefore this estimate is conservative but comparable between localities as first time pregnant females where not included in the calculations.

Animals from one non-cyclic (Revinge, S. Sweden) and one cyclic (Strömsund, N. Sweden) *C. glareolus* population were bred in an animal room at Uppsala. A similar number of animals were taken from increase and peak phases of the cyclic population while few were obtained at the decline. They were caught in autumn as subadults and kept as monogamous pairs in laboratory mouse cages until breeding stopped the next autumn. They were only fed laboratory-mouse pellets and water and were kept on a natural light regime at 20° C. Their first generation offspring from late summer-autumn was tested in the same way. Survival and reproductive output were examined in the resulting four types of animals.

3. Results

3.1. *Clethrionomys glareolus*

The variations in population density of local bank vole populations were clearly larger in northern than in southern Fennoscandia (Table 1). The magnitudes of these variations were also significantly related to time with snow cover and maximum snow depth (Table 1; bottom). However, latitude was significantly related to time with snow at ground ($r=0.96$) and snow depth ($r=0.82$) so it is difficult to untangle any causal relationships. There were fairly large local deviations in the Fennoscandian gradient, as is also clear from the intermediate values of the correlation coefficient. The coefficient of variation (Table 1; upper) indicated much larger local variability in southernmost Fennoscandia than in the more northern parts. Comparisons of indices of density fluctuations between South Scandinavia and Great Britain yielded no significant difference. However, fluctuations in East Europe at the same latitude as Great Britain, mainly in the U.S.S.R., were significantly greater than in South Scandinavia. Most s-values (measuring degree of cyclicity) from western Europe were very low but a few were as high as in central-north Fennoscandia. There was a clear increase in the s-values between South and central Fennoscandia. However, several low s-values appeared in a biogeographic transition zone known as *limes norrlandicus* in Sweden and also on low-lying parts of Southwest-central Finland. In these areas, time and amounts of snow cover are much more variable than in North Fennoscandia. The latter area showed generally high s-values. This was related to a larger proportion of the population studies in this region with summer declines. There were significantly fewer studies with summer declines in South Scandinavia.

Stenseth et al. (1985) found a positive correlation between litter size of *C. glareolus* females and cyclicity in Sweden. It was obtained from four localities situated between 55° and 66° N and thus covering the greatest change in density variations observed by Hansson & Henttonen (1985). However, these localities do not lie within the main distribution range of the bank vole nor close to its distribution limit. Other and probably different factors may operate in the centre and limit of the distribution and possibly affect the litter size there. Data from Zejda (1964, 1966), Döhle & Stubbe (1981) and Stubbe (1982) from the central range of *C. glareolus* and by Hansson et al. (1978), Henttonen (unpubl.) and Koshkina (1957) from the very northern distribution limit were applicable. Zejda's study area happened to contain a wildly fluctuating central European population (Holisova 1971) with $s=0.84$ or nearly exactly the same as the Finnish site, Pallasjärvi ($s=0.85$) at the northern limit. However, Zejda's litter sizes are very similar to other central and western European ones from localities with much less density variation (Zejda 1966).

With this enlarged data set from western Europe (Fig. 2) no positive relations appeared between the cyclicity indices and either the litter size of over-wintered females or the ratios in litter sizes between overwintered and young of the year females of the increase years (see Stenseth & Framstad 1980). There is a tendency towards an opposite relation in the present case but one deviating point disturbs the picture. In North Fennoscandia litter sizes were lower (see Stenseth et al. 1985) in peak than in increase years except at the northern limit (Henttonen unpubl.). The Uppsala sample from central Sweden was taken in a short combined increase/peak year and thus cannot be unequivocally compared with the other cyclic populations. The Ammarnäs animals from North Sweden showed by far the highest litter size (7.0 in overwintered females). This was no accident as Hansson (1969) independently found also very high litter sizes in the very same locality.

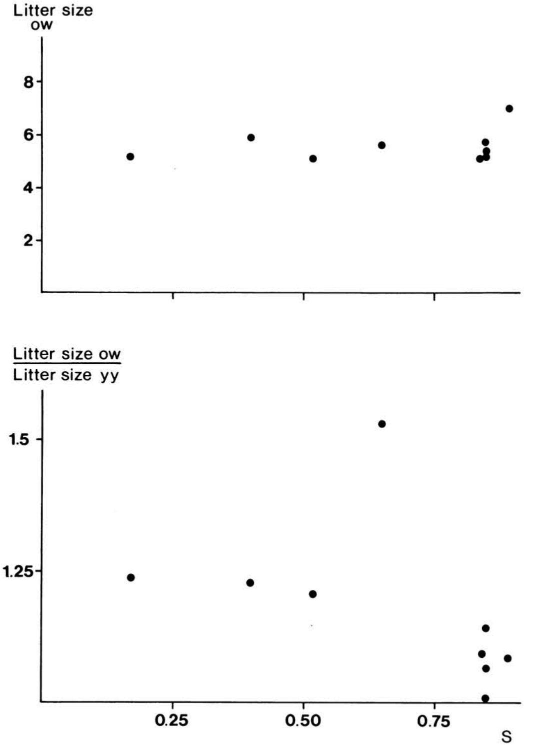

Fig. 2. Relations between the cyclicity index *s*, defined in the text, and litter sizes of overwintered (OW) and young of the year (YY) females in *Clethrionomys glareolus* from central and northern European localities. Litter sizes derive from the increase phase of cyclic populations if they were then larger than in the peak phase.

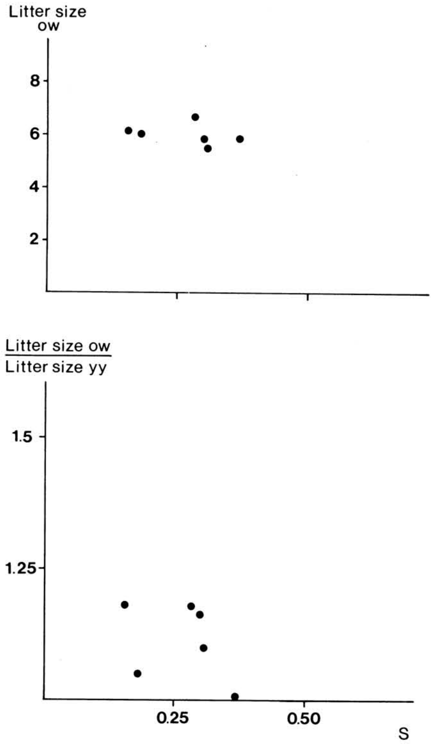

Fig. 3. Relations between cyclicity and litter sizes of *Clethrionomys glareolus* as in Fig. 2 but here from both the European and Siberian parts of the U.S.S.R.

A series of corresponding values (Fig. 3) was obtained for less fluctuating populations in Russia and Siberia from Bashenina's (1981) book. In some instances several trapping series were supplied from the same region and the mean *s*-values were accepted for an analysis of populations on generally low fluctuation levels (as in Stenseth & Framstad 1980). Neither in this case were there any clear relations between pattern of density variations and any of the two aspects of litter size. The latter was generally larger than in western Europe.

The proportion of post-juvenile females in reproductive conditions in late summer differed considerably between increase and peak years (Table 2). Their share was about 60-70% in both the stable South Swedish population and in increase years in northern populations. However, in peak years in both central Europe and northern Fennoscandia it varied between only 11 and 36%. This difference between stable and cyclic populations is thus much larger than in mean litter sizes. The variability between localities in the same population phase was also larger than the corresponding variability in litter size. Neither were all post-juvenile females breeding in the midsummer samples from increase years. However, some limited samples from the very early increase phase (Henttonen unpubl.) showed breeding in all young females (100%, $n=27$). Thus, changes in maturation rate might cause considerably higher reproductive output than the very slight variations in litter size.

The proportion of late summer females both visibly pregnant and lactating out of all lactating females was larger in the stable South Swedish Revinge population (60%, $n=70$) than in both the increase (25%, $n=118$) and the peak phase (13%, $n=53$) of the North Swedish Strömsund population. These differences are clearly significant ($\chi^2=49.69$, $p<0.001$) as is the difference between only the

Table 2. Maturation rates in *Clethrionomys glareolus* as reflected by proportions of all post-juvenile females fecund (lactating and/or pregnant) in midsummer (July - August).

Locality	*s*	Population phase	Fecundity rate *n*	%	Reference
Lednice, Czechoslovakia	0.84	Peak	98	19	Zejda 1964, Holisova 1971
Revinge, Sweden	0.17	Non-cyclic	166	70	Stenseth et al. 1985, Hansson 1979, unpubl.
Uppsala, Sweden	0.52	Increase/ Peak	74	62	"
Strömsund, Sweden	0.65	Increase	111	67	
		Peak	382	27	"
Ammarnäs, Sweden	0.89	Increase	44	77	Gustafsson 1983, pers. comm.
		Peak	76	22	"
Vittangi - Sodankylä, Sweden - Finland	(0.85)	Increase	52	56	Hansson et al. 1978
		Peak	137	36	
Pallasjärvi, Finland	0.85	Increase	133	45	Henttonen unpubl.
		Peak	89	11	

Table 3. Survival (%) and reproductive output (mean ±*SD*) in *Clethrionomys glareolus* from a non-cyclic (Revinge) and a cyclic population (Strömsund). Wild-caught animals and their laboratory-born offspring.

	Revinge		Strömsund		
	n	% or mean	*n*	% or mean	*p*
Wild-caught					
Surviving breeding period	73	84 %	48	79 %	NS
Breeding females	35	63 %	20	20 %	<0.01
Litters	22	5.1 ± 2.2	4	5.0 ± 1.4	NS
Litter size	112	4.8 ± 1.2	20	5.1 ± 1.6	NS
Total output	22	24.2 ± 10.9	4	25.5 ± 10.5	NS
Survival until weaning	522	83 %	102	93 %	<0.01
Survival weaning to 2 months	362	99 %	95	97 %	NS
Laboratory-born					
Surviving breeding period	42	90 %	36	58 %	<0.001
Breeding females	26	42 %	18	67 %	NS
Litters	10	6.0 ± 3.0	10	5.4 ± 4.0	NS
Litter size	60	4.4 ± 1.5	54	4.8 ± 1.5	NS
Total output	10	26.5 ± 18.0	20	26.1 ± 21.1	NS
Survival until weaning	261	36 %	256	24 %	<0.01
Survival weaning to 2 months	77	100 %	61	100 %	NS

stable and the cyclic increase population ($\chi^2 = 34.23$, $p < 0.001$). A further possibility to increase reproductive output without increasing litter size is to extend the breeding season. Also this option can be realized as early increase — increase populations of three *Clethrionomys* species in northern Fennoscandia have been found to breed during at least two more months in autumn than peak animals (Henttonen unpubl.).

Neither the originally wild nor the laboratory-born captive bank voles differed significantly in litter size, number of litters or total reproductive output between cyclic and non-cyclic populations (Table 3). However, there were great differences in survival rate and proportions of breeding females. Only four out of originally 24 northern wild *C. glareolus* females produced young while more than half of the non-cyclic females reproduced. Nestlings of the wild cyclic females survived a bit better than those from the non-cyclic population. However, in the laboratory-born generation difficulties arose for the cyclic animals: males became very aggressive and killed both their mates and their young, and females did not care for their litters. Marking by urination was very pronounced in these animals and even objects outside the cages were covered by urine. Such behaviour was never seen in the wild-caught animals nor in the non-cyclic bank voles. Thus, in these laboratory-born cyclic animals, survival was low for both adults and juveniles. However, significantly more second generation cyclic females bred than in the first generation. There must have been an artificial selection, which finally led to the extinction of the cyclic animals while the corresponding non-cyclic animals flourished.

3.2. *Clethrionomys rutilus*

The distribution range of *C. rutilus* is holarctic and hence much wider than that of *C. glareolus*. On the other hand, *C. rutilus* is essentially a taiga species, and therefore its patterns of density variations and reproduction cannot be compared over such a north-south gradient of biogeographic zones as for *C. glareolus* and *Microtus agrestis* (Hansson & Henttonen 1985); e.g. in Fennoscandia the distribution of *C. rutilus* is restricted only to the northernmost part (Henttonen & Peiponen 1982). In Eurasia *C. rutilus* seems also to be ecologically clearly more specialized (Henttonen & Peiponen 1982) than in North America (Whitney 1976). Henttonen & Hansson (1985), and Hansson & Henttonen (1985) analyzed the patterns of density variation and litter size of this species, and here we summarize the main trends.

On the Fennoscandian mainland the range of density variation (s) was 0.45-0.74, except in the case of a population in subarctic birch forest at the coast of the Arctic Ocean, where s was 0.31 (Table 4). Other mainland populations were both from taiga and subarctic birch forests. Interestingly, one Fennoscandian island population off the NW Norwegian coast had an s-value as low as 0.24.

Elsewhere in the distribution range (in Siberia, Kazakhstan and North America) s was usually less than 0.32. These populations were from the southern fringes of the taiga zone to the tundra. However, Fuller (1969) reported one taiga population from the southern part of the Canadian NW Territories with $s = 0.44$ and one Yakutian subarctic tundra population (Mezennyj 1975) was clearly cyclic. The latter had a spring $s = 0.68$ and fluctuated synchronously with sympatric cyclic lemmings and *Microtus* thus resembling the pattern in northern Fennoscandia. It should be emphasized that, e.g. *C. rutilus* populations from Central Alaska (West 1982, Whitney & Feist 1984), had low s (0.11-0.20) as did taiga populations from southern Yukon (Gilbert & Krebs 1981) and northern NW Territories (Martell & Fuller 1979) ($s = 0.09$-0.19), at the same latitudes and biogeographic conditions where Fennoscandian populations had pronounced density variations with s greater than 0.66 (Hansson & Henttonen 1985, Henttonen & Hansson 1985).

Table 4. Summary of density variations of *Clethrionomys rutilus* over its whole holarctic range, measured as the index s, and the occurrence of known summer declines. As for the other species, only autumn s values are included.

Region	Biogeographic zone	Range of s	Summer decline
Fennoscandia	Northern taiga	0.48-0.74	Yes
	Subarctic birch forest	0.31-0.52	Yes
	Coastal island	0.24	No
Northern Russia	Taiga	0.34-0.36	No
Siberia	Taiga	0.12-0.32	No
Kazakhstan	Taiga	0.22	No
N.W. Territories, Canada	Taiga	0.11-0.44	No
	Tundra	0.17	No
Alaska and Yukon	Taiga	0.08-0.20	No

The Fennoscandian mainland populations exhibit summer declines in the crash phase (as did the Yakutian population), thus filling our criteria for typical cyclic populations. Instead, neither other Siberian nor North American *C. rutilus* populations undergo comparable regular summer declines. Consequently, these non-cyclic populations do not show the extreme low densities which characterize Fennoscandian populations in the crash phase. Rather, data from Alaska (West 1982, Whitney & Feist 1984), from nearby Yukon and NW Territories (Martell & Fuller 1979, Gilbert & Krebs 1981) and from Siberia (Koshkina & Korotkov 1975, Okulova 1975, Okulova 1975, Cernjavskij & Korolenko 1979), lenko 1979) show quite a regular pattern of winter decline and summer increase, which is also typical for non-cyclic microtine populations in southern Scandinavia. The "non-cyclic" Siberian and North American populations of *C. rutilus* are, however, not identical in their population performance. Siberian and Alaskan *C. rutilus* generally seem to reach quite high densities, but in Yukon and NW Territories the average density is lower. Also *C. rutilus mikado* on Hokkaido, Japan, showed continuous low densities ($s = 0.26$, Nakatsu 1981, Ota 1984).

An interesting case is the situation in Archangel area (Arhangelskaja Oblast), in the northern Russian taiga east of the White Sea,

Table 5. Participation of the young of the year *Clethrionomys rutilus* females in reproduction. The data from Siberia and Canada show only common ranges for a general comparison with the Fennoscandian one. Extreme values are mentioned in the text.

Locality	Population phase	Participation of young *n*	 %	Reference
North Fennoscandia				Henttonen unpubl.
Kilpisjärvi	Increase	54	54	
	Peak	51	5	
Pallasjärvi	Increase	38	29	
	Peak	43	3	
Siberia				
Southern taiga	Non-cyclic		0-5[1] 37-72[2]	Koshkina 1967
Northern taiga	Non-cyclic		20-60	Cernjavskij & Korolenko 1979
Canada				
N.W. Territories	Non-cyclic		44-100	Fuller 1969, Martell & Fuller 1979

[1] Optimal habitat. [2] Suboptimal habitat.

not far from northern Fennoscandia. At the same latitudes and in apparently similar environmental conditions in northern Fennoscandia both *C. rutilus* and *C. glareolus* are clearly cyclic ($s>0.6$) with typical summer declines, but in the Archangel area *s* for *C. rutilus* is 0.34 and for *C. glareolus* 0.34 in Gubar's (1976) six-year data set and 0.26 and 0.36, respectively, in his four-year data set from another locality in the same region. These *s*-values have been calculated from optimum habitats for each species. Neither is there any obvious summer decline in Gubar's (1976) material. The shorter material (3 years) of Kuprijanova (1976), also from the Archangel area, supports the conclusions based on Gubar's data. Thus, the "non-cyclic" pattern in the Eurasian taiga seems to occur close to Fennoscandia.

These differences in density variations of *C. rutilus* cannot easily be correlated with the snow cover as could be done by Hansson & Henttonen (1985) with the gradient of density variations of some other microtine species in Fennoscandia. Both Siberian and North American non-cyclic populations inhabit regions with a long winter and considerable amounts of snow. However, the mean snow depth seems to be greater in the more maritime northern parts of Fennoscandia than in continental Siberia and interior Alaska (Solantie 1975, Kotljakov 1968, Whitney & Feist 1984).

The range of the mean litter size of *C. rutilus* varies from slightly less than five in eastern Finland (Kaikusalo in Henttonen & Hansson 1985) to more than nine in the northern Urals (Balakhonov 1976). Stenseth & Framstad (1980) reported a positive correlation between the ratio of litter sizes of overwintered /young of the year females of this species and cyclicity, when *s* is less than 0.32. Analyzing a larger data set with a greater range of *s*, Henttonen & Hansson (1985) found instead a significant negative correlation ($p<0.05$) between this OW/YY ratio and cyclicity (see Figs. 2-3). This was primarily due to a decreasing litter size of overwintered females with increasing cyclicity. The litter size of young of the year females did not correlate with cyclicity. On the other hand, Henttonen & Hansson (1985) found that the litter size of overwintered females correlated with the biogeographic regions: litter size seemed to be highest in the northernmost and southernmost regions but lower in the central and northern ones.

The difference in the proportion of postjuvenile females in reproductive condition between increase and peak years in cyclic populations in northern Fennoscandia (Table 5) resembles the pattern found i *C. glareolus*. The difference was significant ($p<0.01$ both in the Pallasjärvi (highest *s*-value for all *C. rutilus* populations) and the Kilpisjärvi material).

The participation of young females in reproduction in non-cyclic Siberian populations of *C. rutilus* is usually claimed to be inversely related to the spring population density (Koshkina 1967, Koshkina & Korotkov 1975, Okulova 1975, Cernjavskij & Korolenko 1979), which essentially depends on the habitat. According to Koshkina & Korotkov (1975), in optimum habitats the proportion of young breeding females is usually low (0-30%), but can incidentally increase drastically (to 63%) if the winter survival of old females has been low. In intermediate habitats the pattern resembles the previous one, and in both cases there are significant negative correlations between the density of overwintered animals and the percentage of young breeding females (calculated from Table 10 of Koshkina & Korotkov 1975). In the suboptimal habitats winter survival is low and the proportion of young breeding females is continuously high

(23-72%). Thus, southern Siberian populations in optimum habitats resemble those during cyclic peaks in Fennoscandia; instead, populations in suboptimal habitats in southern Siberia resemble cyclic Fennoscandian ones in the increase phase. In northern Siberian population studies by Cernjavskij & Korolenko (1979), the proportion of young pregnant females in relation to all young females usually varied from 20-60%, except in one year with the highest spring density when it was 5%. In the northern NW Territories 44-85% of the early cohort females matured in taiga and 50-100% in tundra (Martell & Fuller 1979). These populations were at lower density levels than Siberian taiga populations.

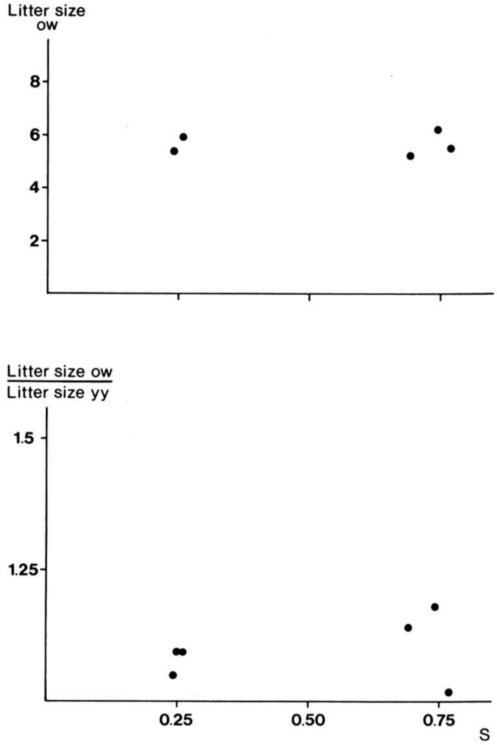

Fig. 4. Relations between cyclicity and litter size of *Clethrionomys rufocanus* as in Fig. 2, based on three Fennoscandian (see text) and three Japanese (Abe 1976 and Nakatsu 1980, 1982) studies. However, the low cyclicity indices in the latter case are each the means from several separate study areas.

3.3. *Clethrionomys rufocanus*

Again, populations in northern Fennoscandia are highly cyclic (Kalela 1957, Koshkina 1957, 1966, Semenov-Tjan Shanskij 1970, Henttonen et al. 1977, Tast 1984, Henttonen unpubl.). The range of *s* in these three long-term studies (Kilpisjärvi, Pallasjärvi and Kola peninsula) was 0.69-0.77. *C. rufocanus* in northern China is also stated to be strongly cyclic (Xia et al. 1985). Based on the Scandinavian standards, *C. rufocanus* in Japan is generally non-cyclic. In an 11-year data set compiled by Ota (1984), $s=0.22$. In fourteen study areas, ten of which were studied by Nakatsu (1981, 1982), *s* varied between 0.12 and 0.36 with a mean of 0.24. In Ota's (1984) long-term data, three seasonal density estimates are available. Even though winter survival and spring densities are variable, there is not any decline through the whole summer. Minimum autumn densities were 8-10 animals/hectare, which are of a different order to that found in declining North Fennoscandia populations. In a 4-year study by Kuwahata (1962) *s* was 0.36, and neither in this case could any typical summer decline be found: the minimum densities during the study period were 28 animals/hectare. In a six year data set from Ota (1984) autumn densities varied from 2 to 44/hectare ($s=0.52$) but this high *s* was due to severe winter mortalities and not to the "Scandinavian type" of summer decline. In Abe's (1976) 2-year material seasonal density dynamics were essentially the same in both years: however, the proportion of young breeding females varied, being much higher in the second year (79-87%, vs 43-47%). This difference could not be related to the density of overwintered females in the beginning of the breeding season. However, the higher proportion of breeding young of the year females in the second high density year is very different from the patterns found in cyclic populations, which suggests that the population studied by Abe was not cyclic. Saitoh (pers. comm.) states that "the periodicity of population change is not clear".

Cyclicity and litter sizes could only be compared in six studies (Fig. 4). The predictions by Stenseth & Framstad (1980) and Stenseth et al. (1985) could not be supported for this species either but no clear trend could be distinguished with the available data.

3.4. *Clethrionomys gapperi*

Cyclicity indices could be computed for 17 North American *C. gapperi* populations (Hansson & Henttonen 1985, Martell 1983, Mihok et al. 1985): Four populations from the U.S.A. had a mean *s*-value of 0.38 and thirteen from Canada had 0.42; this difference was not significant and neither was there any significant correlation with latitude.

There is little detailed information on litter sizes of wild *C. gapperi* (see Merritt 1981). However, Innes (1978) demonstrated a significant increase in "mean" litter size with latitude ($r = 0.65$) and with latitude and elevation together ($r = 0.76$). It is not possible to study difference in reproduction between population phases as "there seem to be no 3 to 4 year population oscillations in *C. gapperi*" (Merritt 1981). The OW/YY ratio (Fig. 2) was reported to be 1.19 (Iverson & Turner 1976) and 1.10 (Perrin 1979) in southern Manitoba (OW litter size equals 6.0 and 5.9 respectively) at a mean *s* of 0.31.

4. Discussion

The data on density variations were obtained with a plethora of methods. Certain cases of locally deviating fluctuations were probably due to this inconsistency in background information. However, this effect does not seem very important as the coefficient of variation consistently gave better correlations than *s* (Hansson & Henttonen 1985) in spite of the latter diminishing deficiencies due to methods as a result of its logarithmic nature. The variation in the cyclicity indices was generally greater in southern, usually non-cyclic *C. glareolus* populations, and one gets the impression that the non-cyclic pattern is very unstable in more productive environments. Probably vole populations occurring below the carrying capacity easily return to the cyclic pattern when subtle regulatory mechanisms are disturbed.

Some areas with, perhaps temporary, high density variations in central Europe and low density variations in, e.g., Southwest-central Finland, definitely deviated from the common gradient in *C. glareolus*. Similar exceptions applied to the other species. However, they did not show any deviating litter size in relations to the general regional mean. Thus, peculiar density variations appear to be caused by local environmental conditions independent of the mechanisms governing litter sizes.

The relations between cyclicity and litter sizes predicted by Stenseth & Framstad (1980) were supported by analyses of a limited number of populations by Stenseth & Framstad (1980) and Stenseth et al. (1985) for, respectively, *C. rutilus* and *C. glareolus*. However, a larger number of observations of these two species did not fit into the same pattern. Thus, we consider that there is presently no convincing evidence for an evolution of litter sizes in relation to fluctuation patterns (see also Slagsvold 1981). The predictions on litter sizes by Stenseth & Framstad (1980) are stated to be applicable when everything apart from fluctuation patterns is constant (Stenseth pers. comm.). However, with that limitation this hypothesis is hardly applicable to real life data. We believe, furthermore, that it is a mistake to treat litter size as a single index of reproductive output, as has obviously been done. What matters is probably the total number of young born per life-time of individual females although we realize that early maturation may confer a special advantage (Pianka & Parker 1975, Stearns 1976). Time of first maturation, and thus maturation rates in young of the year females, and total number of litters produced describe this component of fitness far better than just litter size.

At least one reproductive variable, viz. the maturation rate, is clearly related to cyclicity. Few young of the year females mature in peak populations and overwintered females show sexual regression in the middle of the summer in that phase. Such conditions do not appear regularly in non-cyclic populations even if there may be differences between habitats. Cyclic populations in regions with generally non-cyclic patterns deviate in the same way as regards the maturation rate (see Zejda 1964). Frequencies of litters and lengths of breedings season may also be related to the pattern of density fluctuations but fewer data are available in those respects.

The various *C. glareolus* bred in the laboratory under a natural light regime did not indicate any hereditary difference in total reproductive output between cyclic and non-cyclic populations as might appear from the studies by Gustafsson et al. (1983) with constant light. The difference observed in the field (Revinge vs Strömsund; both in Sweden) may thus also in this respect be due to environmental conditions. Certain laboratory observations (e.g. survival) are clearly not relevant to field conditions, e.g. due to artificial selection in breeding trials.

The fluctuation patterns vary both locally and in time and it will be difficult for evolution to make any fine-tuning to density variations easily disturbed by novel environmental conditions. Therefore, reproductive conditions are probably related to some mean regional conditions. The *C. glareolus* data on litter sizes show clear differences between central Europe and South Sweden on one hand and northern Fennoscandia on the other. The central Swedish Uppsala population cannot be judged in an appropriate way but seems closer to the North European one. We suggest that there are at least two different types of litter sizes in *C. glareolus,* one representing central-east European deciduous forests with smaller but more abundant litters (see Zejda 1966, Döhle & Stubbe 1981) and one from North European coniferous forests with larger but less frequent litters (Bashenina 1981; see also Gustafsson et al. 1983).

Litter sizes might simply be allometric consequences (and thus no adaptations) to different body sizes evolved for other reasons (see Hansson 1985). The Ammarnäs animals have remarkably large litters but they were also especially large in size. They come from a mountainous area in Scandinavia and it should be observed that also *C. glareolus* from the Ural mountains are characterized by especially large litters (Bashenina 1981). Also Innes (1978) reported large litters from North American mountain populations of *C. gapperi* at high latitudes. In Czechoslovakian mountain areas Zejda (1966) found instead smaller litters than the common central European *C. glareolus* standard. Also in the American material (Innes 1978), litters were sometimes small in southern mountains. However, biogeographic zones (or biomes) may be the units that best describe the mean environmental conditions framing the evolution of a certain litter size or other (primary) species characteristics.

Acknowledgements. Field and laboratory work reported here was supported by the Swedish Natural Science Research Council, the Finnish Academy of Science and the E. Aaltonen foundation. The Nordic Council for Ecology made it possible for us to work together. The manuscript was partly completed during HH's ASLA-Fulbright Scholarship at the Institute of Arctic Biology, University of Alaska in Fairbanks. We are grateful to Torgny Gustafsson, Steve Mihok and Nils Chr. Stenseth for data and comments. Bill Fuller and T. Saitoh kindly provided some references.

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Received 11.II.1984
Printed 11.X.1985