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Geographic differences in bank voles *Clethrionony*s *glareolus* in relation to ecogeographical rules and possible demographic and nutritive strategies

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South and North Swedish bank voles *Clethrionomys glareolus* have been known to differ with regard to litter sizes and intervals and social behaviour on the one hand and diet and population dynamics on the other hand. Further differences in intestinal length and distribution of various intestinal parts, body sizes and proportions and activity levels and patterns are reported in the paper. The differences in intestinal morphology and function are, as also with other characteristics, hereditary but a great developmental plasticity also exists in this respect. All these differences are related to Bergmann's and Allen's rules, to possible demographic strategies evolved in relation to various patterns of density fluctuations and to various adaptations following different modes of feeding (i.e., more granivorous or more folivorous animals). However, none of these adaptive complexes explains all observed differences: many inconsistencies were indeed observed.

The geographic differences may be due to either local adaptations towards independently varying factors or dimorphies or clines in relation to one dominating factor. Many of the characteristics are common to populations in central Europe and South Scandinavia on one hand and in large parts of North Scandinavia on the other. It is suggested that the different patterns of seed-production in deciduous and conifer trees are important primary factors. However, other individual adaptations may follow as response to, for example, resulting changes in population dynamics.

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1. Introduction

Recently it has become obvious that there are considerable differences in morphology, demography, behaviour and population ecology of South and North Swedish bank voles *Clethrionomys glareolus* (Hansson 1979a,b, Gustafsson et al. 1983a,b, Stenseth et al. 1985). North Swedish animals are generally larger, have larger litters, are more active and are more sensitive to the social environment with respect to sexual development. However, they also eat food more rich in cellulose and other substances which are difficult to digest than the South Swedish animals (compare Hansson 1979b and Hansson & Larsson 1978 with Hansson 1971; see also Hansson 1985). There is also a general gradient of increasing density fluctuations from South to North Fennoscandia (Hansson & Henttonen 1985a,b).

Differences between animals from various geographical regions have hitherto mainly been related to the ecogeographical rules (e.g., Mayr 1965). Bergmann's rule states that "races from cooler climates tend to be larger in species of warm-blooded vertebrates than races of the same species living in warmer climates". Allen's rule says that protruding body parts like bill, tail and ears are shorter in cooler than in warmer climates. However, other explanations of geographic variation have recently been suggested. Stenseth & Framstad (1980) thus predicted that litter size as a measure of reproductive output should increase with increasing density variations, the reason being favourable reproductive conditions, especially for young females, in increasing populations. Physiological sexual development should, consequently, also be related to the degrees of density variation (or "cyclicity").

The food eaten by South and North Swedish bank voles differs so fundamentally that effects may be apparent in morphology and behaviour if digestive adaptations have evolved. Generally the South Swedish animals are more granivorous than northern ones. Granivorous species have a less complicated digestive system than folivores. This intestinal difference is reflected in many morphological and behavioural characteristics (Vorontsov 1962, Baker 1971; see Table 1). If there are inherited adaptations to diets being more and less rich in cellulose and other only partly digestible plant constituents, then a considerable number of other differences could be predicted for the separate populations.

Thus, I first examine possible differences in nutritional adaptations between the two types of voles (i.e., granivorous and folivorous bank voles); this comparison demonstrates inherited differences. Then I proceed to examine the inheritance of certain other predicted differences not already established by breeding experiments. Finally, I compare the potential of the two different feeding adaptations to predict several characteristics of southern and northern bank vole individuals and populations in relation to theories about demographic strategies and ecogeographical rules.

Table 1. Characteristics of granivorous and folivorous rodents of similar size (Vorontsov 1962, Baker 1971).

	Granivores	Folivores
Digestive tube	Shorter	Longer
Small intestines/ large intestines	Larger	Smaller
Tail length	Long	Short
Home range	Larger	Smaller
Locomotory activity	Larger	Smaller
Daily rhythm	Nocturnal	Daily
Shelter	Unimportant	Needed
Food storing	Common	More or less absent
Habitat	Closed	Open
Utilization of food resources	Overexploitation	Underexploitation (alternatively periodic peaks)
Interspecific competition	Uncommon	Common

2. Methods

Animals from South (Revinge area, 56°N), central (Uppsala area, 60°N) and North (Strömsund area, 64°N) Sweden have been bred in Uppsala in a laboratory with natural light conditions (like those in central Sweden). They were brought in from the field in 1980-82, and thus came from a whole density cycle. However, few animals were obtained during the crash year in the Strömsund area. The wild-caught animals and their offspring were kept in standard laboratory mouse cages on a pure diet of laboratory mouse pellets (EWOS) with a high content of seeds (cereals). Only F_1 offspring of the respective provenances were used for establishing inheritance in order to avoid unnecessary laboratory selection. The laboratory-bred animals were compared with wild-caught specimens when appropriate. All measurements were made by the author. The inheritance of differences in sexual development and litter size has been established by Gustafsson et al. (1983a,b). Their data on such characteristics will be used here, although it is not certain that their northern bank voles are completely representative (see Hansson & Henttonen 1985b).

Lengths of total intestines and their components (for definitions see, e.g., Vorontsov 1962 and Sperber et al. 1983) were measured on F_1 offspring as well as on animals caught in snap-traps in the field during the autumn. The length of ampulla coli was added to the remaining colonic parts as the total colon length; the treatment of the ampulla is, however, not clear in all other publications on this subject. In any case, its contribution is small. Two types of animals were examined from each locality: immatures without any remnants of the juvenile pelage (wild "subadults" and laboratory specimens 2-4 months of age) and post-reproductive adult animals. Pregnant and lactating females were avoided since such individuals are known to reversibly develop hypertrophied intestines, especially coeca (Myrcha 1964, Gebczynska & Gebczynski 1971). Furthermore, wild immature animals were brought to the laboratory in the autumn and kept for one year until the post-reproductive state before autopsy in order to establish a possible developmental (or ontogenetic) acclimatization to a seed diet.

Two types of laboratory-bred animals were weighed and measured regarding body and tail length: 1) Spring-born animals were autopsied at two months of age when they generally have become sexually mature, and 2) late summer or autumn-born animals at four months of age when the latter usually still remain immatures (Hansson 1983a). Weights have also been gathered from a large number of snap-trapped autumn immatures.

Locomotory activity, daily rhythm of activity, sheltering and storing behaviour were investigated in November to early March in two apparatuses consisting of a food chamber (70×35×35 cm) and a nesting chamber (same size but with a small nest) with a connecting closed runway traversed by a infrared beam of light. One apparatus had no shelter at all in the nest apartment except for the nest while in the other apparatus the whole nest chamber was covered by wilted vegetation. Water and ten laboratory mouse pellets were supplied per day in the food chamber. External light conditions were those natural for the Uppsala-region. Laboratory-bred animals were introduced for 24 hours in the apparatus without shelter and then for another day in the apparatus with shelter. A moving animal breaking the infrared light was registered, as well as the time, on an event-recorder.

Table 2. Relative lengths of intestines (in relation to body length) and lengths (in percent) of the main components.

Condition	Age	Locality	*n*	Relative length Mean	Relative length *SD*	Small intestines Mean	Small intestines *SD*	Coecum Mean	Coecum *SD*	Colon Mean	Colon *SD*
Wild-caught	Subadults	Revinge	20	8.15	0.56	61.0	2.2	14.3	1.8	24.9	1.6
		Uppsala	18	8.59	0.34	58.2	2.0	15.2	1.6	26.4	1.3
		Strömsund	4	8.38	0.19	54.3	2.2	15.5	1.0	30.3	1.3
	Postreproductives	Revinge	7	7.51	0.48	59.3	1.5	15.3	1.4	25.4	0.5
		Uppsala	9	9.16	0.68	57.4	2.7	16.1	1.2	26.6	1.7
		Strömsund	5	8.85	0.38	54.6	1.5	15.6	0.6	29.8	1.9
Laboratory-born	Subadults	Revinge	23	7.06	0.46	58.9	1.5	13.2	1.7	27.9	1.7
		Uppsala	17	7.06	0.32	57.4	1.8	15.1	1.7	27.4	2.7
		Strömsund	4	7.12	0.21	56.8	1.7	14.8	1.0	29.0	2.2
	Postreproductives	Revinge	13	6.41	0.26	59.9	1.8	13.9	1.6	26.2	1.7
		Uppsala	0	-	-	-	-	-	-	-	-
		Strömsund	8	7.36	0.50	52.4	1.4	16.1	1.0	31.1	1.6
Wild-caught but laboratory-bred	Postreproductives	Revinge	18	6.88	0.55	58.8	2.0	15.2	1.5	26.1	1.7
		Uppsala	15	6.97	0.39	55.5	2.1	15.6	2.1	28.9	1.6
		Strömsund	3	6.73	0.35	52.7	1.5	15.3	1.2	31.7	0.6

3. Results

3.1. Nutritional adaptations

There were no significant differences in relative intestinal length (total intestinal length /body length) between males and females (Table 2). Differences between subadults and adults (post-reproductives) were significant in, e.g., wild animals from Revinge ($t = 2.87$, $p < 0.001$) and from Uppsala ($t = 2.59$, $p < 0.05$). The relative lengths were shorter in adults at Revinge (as is generally the case in central Europe; see Myrcha 1964) but longer at both Uppsala and Strömsund. The same patterns were also found in laboratory-born animals.

Subadults brought up in the laboratory had significantly lower relative lengths than wild animals (Revinge: $t = 6.65$, $p < 0.001$; Uppsala: $t = 13.85$, $p < 0.001$; and Strömsund: $t = 8.48$, $p < 0.001$). The differences were equally pronounced in adults where many individuals could be compared (Revinge: $t = 5.67$, $p < 0.001$; and Strömsund: $t = 6.08$, $p < 0.001$).

There were significant differences between the three localities for both wild-caught subadults ($F = 17.95$, $p < 0.001$) and adults ($F = 4.54$, $p < 0.05$). In both cases animals from Uppsala and Strömsund had longer relative intestine lengths than those from Revinge. There were no significant differences between laboratory-born subadult animals from the three localities while the relative intestinal length of laboratory-bred adult animals from Revinge was significantly shorter than of those from Strömsund ($t = 4.92$, $p < 0.001$). Wild-caught animals brought up and kept in the laboratory for one year did not show any significant regional differences.

Wild-caught animals kept in the laboratory for one year had much shorter relative lengths than adult animals living their whole life in nature (Revinge: $t = 2.86$, $p < 0.01$; Uppsala: $t = 8.76$, $p < 0.001$; and Strömsund: $t = 8.15$, $p < 0.001$). Instead, their intestinal lengths were closer to those of laboratory-born animals.

The composition of the intestinal parts changes also geographically (Table 2); the small intestines become relatively smaller and the large intestines larger when going northwards. The coefficients of variation were generally largest for the coecum. This part takes up only some 15 % of the total intestinal length and geographical differences in relative coecum length were examined by parametric tests as the sample percentages should be normally distributed.

Coeca were, on a relative scale, consistently larger in adults than in subadults but these differences were not significant. They were only weakly significantly longer in the wild than in laboratory-bred subadults from Revinge ($t = 2.07$, $p < 0.05$). However, differences between localities were clearly significant for laboratory-bred animals (subadults: $F = 6.90$, $p < 0.01$; and adults: $t = 3.90$, $p < 0.001$). Obviously, wild animals showed individual variations in relative coecum length that were too large for a significant manifestation of the geographical trend. Wild animals kept in the laboratory for one year showed the same geographical trends in intestinal proportions as both wild and laboratory-bred animals. Relative coecum lengths were most similar to those of wild-caught animals, however, with no significant geographical difference, while the relative lengths of the colon were similar to those of laboratory-bred animals, with significant differences ($F = 22.48$, $p < 0.001$).

These relative lengths are within the ranges compiled by Vorontsov (1962) for a large series of small rodent species. Furthermore, the relative intestinal length of South Swedish (Revinge) bank voles are close to those from central Europe (Myrcha 1964, Gebczynska 1976). However, Gebczynska's (1976) relative intestinal lengths of wild bank voles from Poland (about 6.5) are rather shorter than the South Swedish ones. In the Soviet Union, Vorontsov (1961) found clear differences between northern bank vole populations mainly subsisting on green vegetables and lichens and southern ones with a diet dominated by seeds; with the northern animals having considerably longer intestines. The coecum became longer and the small intestines relatively shorter as going northwards (Myrcha 1964), as also found in Sweden. However, an inherited difference, established by controlled breeding in the laboratory, seems only to have been documented for Sweden.

The differences in relative intestinal lengths, although significant, may seem fairly small. However, the corresponding differences in volume and weight are considerably greater. Furthermore, the intestinal system of northern bank voles is often filled with bulky green vegetables or fungal tissues and causes a much greater total intestinal volume than is found in seed-eating southern animals.

3.2. Morphological variations

There were significant geographical differences in weight, body length, tail length and relative tail length (tail length as a percentage of body length) in laboratory-bred animals born both in spring (before July 1) and in late summer (to early autumn) except in females from the late summer cohort (Table 3). In these late summer females only relative tail lengths deviated significantly. Generally the Revinge animals were lighter and shorter and

Table 3. Geographic differences (significance from *F*-test given) in external morphology of laboratory-born bank voles from south, central and north Sweden. Animals born before July 1, aged 2 months, and after July 1, aged 4 months.

			Weight, g		Body length, mm		Tail length, mm		Relative tail length	
		n	Mean	*SD*	Mean	*SD*	Mean	*SD*	Mean	*SD*
2 months										
♂♂	Revinge	40	16.4	2.5	86.3	3.5	42.3	2.2	49.0	2.7
	Uppsala	17	21.1	2.6	90.2	2.8	47.1	1.5	52.3	1.5
	Strömsund	20	18.4	2.0	89.6	1.9	47.6	2.2[1]	53.2	2.6[1]
			$p<0.001$		$p<0.001$		$p<0.001$		$p<0.001$	
♀♀	Revinge	31	14.9	2.6	84.2	2.7	41.5	2.4[2]	49.2	2.7[2]
	Uppsala	13	16.6	1.4	87.4	1.9	44.8	2.8	51.2	3.4
	Strömsund	10	16.7	2.1	87.2	2.4	46.4	1.4	53.3	1.8
			$p<0.05$		$p<0.001$		$p<0.001$		$p<0.001$	
4 months										
♂♂	Revinge	40	14.7	2.4	86.4	2.7	43.2	2.6	50.1	2.4
	Uppsala	4	19.0	1.6	92.0	1.8	44.5	2.5	48.5	2.1
	Strömsund	14	22.4	3.5	93.3	2.9	47.7	1.6	51.4	1.4
			$p<0.001$		$p<0.001$		$p<0.001$		$p<0.05$	
♀♀	Revinge	22	13.7	1.5	86.1	3.1	43.4	3.1	50.4	2.3
	Uppsala	7	15.4	1.9	86.7	2.1	43.0	1.6	49.6	1.7
	Strömsund	6	14.7	1.8	85.7	3.2	45.0	2.1	52.7	1.4
			NS		NS		NS		$p<0.05$	

[1] $n = 19$. [2] $n = 29$.

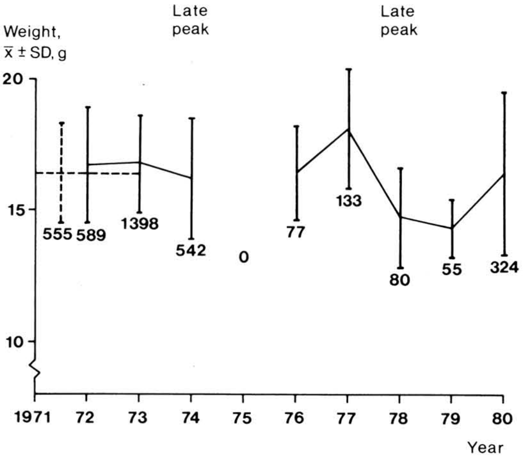

Fig. 1. Mean weight and variation in subadult bank voles caught in autumn in the Revinge (broken line) and Strömsund areas. The mean weights of Revinge animals did not show any significant annual variation in 1971-73 and there were no cycles in that area. Cycle peaks are marked for the Strömsund population. Figures denote sample sizes — no single bank vole could be trapped at Strömsund in 1975.

had a smaller tail index than animals from Uppsala and Strömsund. However, there were small differences between the animals from the two latter localities. In some respects, animals from Uppsala were larger than those from Strömsund; e.g., in male weights in spring animals ($t = 3.49$, $p < 0.01$). The relative tail length was consistently greatest in the Strömsund animals.

It is difficult to compare these values with those of field animals as it is impossible to gather a series of wild animals exactly two or four months old. Neither are age indicators for field animals particularly reliable (Hansson 1983b). Furthermore, the weight of field animals varies considerably during a vole cycle (e.g., Hansson 1969, Wiger 1979). Fig. 1 shows the significant variations in weight of autumn subadults (usually 1-3 months old, but older during peak years) from the Strömsund area in relation to the stable mean weights in this animal category from the Revinge area (Hansson 1984). This type of animal does not grow in autumn and laboratory-born animals usually lose some weight between the second and fourth month. During increase and early peak years weights were significantly larger at Strömsund than at Revinge while the reverse applied to late peak-crash years. However, male bank voles from the Strömsund area brought up in the laboratory in late summer-autumn (Table 3) showed much higher weights ($t = 3.55$, $p < 0.001$) than wild-caught males from Strömsund in autumn 1977, with the highest weight in any year (19.0 ± 1.7 g, $N = 76$). Thus, northern male bank voles may also be characterized by a high phenotypic variability in body growth (possibly related to diet). Individual variation (expressed as *SD*) was in the same order in field and laboratory animals.

Table 4. Activity counts and pellets stored per 24-hour period at two different levels of shelter for South and North Swedish bank voles (significance from *U*-test given).

	Revinge[1]			Strömsund[2]			
	Mean	*SD*	*CV*	Mean	*SD*	*CV*	
Activity counts							
Without shelter	497	271	55	2102	2977	142	$p < 0.10$
With shelter	227	132	58	1267	2408	190	$p < 0.05$
Stored pellets							
Without shelter	2.2	4.0	182	1.8	3.3	183	NS
With shelter	3.1	4.2	135	4.5	4.3	96	NS

[1] $n = 15$. [2] $n = 12$.

Animals from middle (Uppsala) and northern (Strömsund) Sweden were fairly similar as regards both sizes and intestinal lengths and distributions. This indicates a threshold somewhere in southern Sweden between central European bank voles from mainly deciduous forests and North European ones. The Uppsala animals live in a man-dominated landscape with coniferous forests fairly similar to those at Strömsund.

3.3. Some aspects of behaviour

Comparisons of locomotory and daily activity were studied by using 15 laboratory-bred male bank voles from Revinge and 12 from Strömsund. Mean activity counts where about 5 times higher for the northern animals than for the southern ones (Table 4). However, individual variations were huge in the northern but not in the southern animals, and parametric tests requiring normal distributions could not be used. Mann-Whitney non-parametric tests revealed a significant difference only for the experiment with a sheltered nest. However, there was a general decline in locomotory activity to about 50% for both types of animals when they were transferred to the chamber with the sheltered nest.

The number of hours during which each animal was active was established. The total number of hours active in comparison with the possible maximum was larger in the Revinge animals ($\chi^2 = 15.59$, $p < 0.001$) when without shelter (Fig. 2) in spite of totally much lower activity counts (Table 4). When given shelter, the two types of animals did not show any differences. Thus, the Revinge animals had the largest decline in exploratory behaviour when given shelter.

There were no significant differences in the total 24-hour distributions of activity. However, there was a clear tendency of a short-term activity cycle occurring in the Strömsund animals (Fig. 2B), appearing both without and with shelter. Such a pattern is reported to be characteristic for folivorous animals (Grodzinski 1962, Vorontsov 1962).

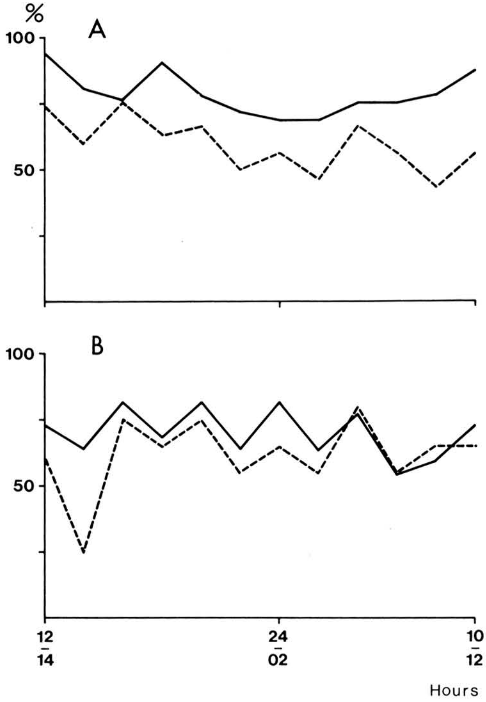

Fig. 2. Daily activity rhythms of laboratory-bred bank voles from the Revinge (A) and the Strömsund (B) area calculated as mean numbers of hours active out of all possible. These percentages are shown for animals kept with nest chambers without and with (broken line) shelter.

3.4. Reproductive performance

Gustafsson et al. (1983a) reported that North Swedish animals had larger litters but at the same time longer intervals between the litters than animals from the Revinge area. Young from the north grew faster (see Sect. 3.2) but had much lower survival rate. The latter was attributed to a higher level of activity in the northern animals (see Sect. 3.3), causing severe disturbance in the breeding cages and probably making the estimated survival rate an artifact. Furthermore, Gustafsson et al. (1983b) showed a higher sensitivity with regard to the social environment for sexual maturation in the northern animals — maturation was delayed in groups of four juvenile males per cage in northern animals but not in southern ones.

4. Discussion

According to Bergmann's rule, weight and body length should be greater in a colder climate. In Raczynski's (1983) compilation, *C. glareolus* from many northern and mountain localities were larger and had longer tails. This larger size had been related to Bergmann's rule by Saint Girons (1973). However, there are about 7 months of snow cover at Strömsund and if the animals live in a subnivean environment close to 0°C (Coulianus & Johnels 1962) they ought to be exposed to less cold than South Swedish animals with almost no snow cover and temperature often below 0°C for 2-3 months. In another small mammal species, viz. the weasel *Mustela nivalis*, there is a clear cline with smaller animals in North than in South Sweden (Stolt 1979). Thus, the main predictions according to the ecogeographical rules seem dubious for these types of animals (Table 5). It follows that neither can any unambiguous prediction be made for the growth rate or tail length.

No predictions on external morphology can be made from the hypothesis of demographic strategies. Animals with diluted food and more voluminous intestines need a slightly larger body (Schoener 1969) and differences in weight, body length and growth rates are well borne out for the more folivorous northern bank voles. However, Vorontsov (1962) proposed that folivorous species are characterized by less extruding extremities, including the

Table 5. Tests of three hypotheses possibly explaining geographical variations in bank voles. Corroborations are marked with a +, contradictions with a - and differences not related to a certain hypothesis with a = sign. However, in several cases (indicated by a ?) there are difficulties in making decisions.

Geographic differences	Ecogeographic rules	Demographic strategies	Nutritive adaptations
Weight	+?	=	+
Body length	+?	=	+
Tail length	-?	=	-?
Intestines	=	=	+
Growth rate	+?	=	+
Litter size	+?	+	+?
Litter interval	=	-	=
Juvenile survival	=	=	=
Social sensitivity at maturation	=	+?	=
Activity level	=	=	-
Exploration for shelter	=	=	-
Daily rhythm	=	=	-?
Food storing	=	=	-?
Individual variability	=	=	=
Habitat selection	=	=	+
Cyclicity	=	Presumption	+

tail. The longer tail in the north therefore seems to contradict the idea of general nutritive adaptations. Granivorous *C. glareolus* in central Europe often climb trees (e.g., Holisova 1969) and a long tail is useful for climbing. Possibly it is used in northern animals when foraging for chordate lichens up in the coniferous trees (Hansson 1985).

Litter size differences could be allometrically related to ecogeographical differences if the larger body is an adaptation to northern climate, as well as to a larger body as a nutritive adaptation. The geographic trend in litter size within Sweden clearly corroborates the idea of demographic strategies (Stenseth et al. 1985) but additional data from outside Sweden and on other *Clethrionomys* species (Hansson & Henttonen 1985b, Henttonen & Hansson 1985) do not. The greater interval between litters in northern Sweden clearly contradicts this hypothesis. The social sensitivity may support the demographic strategy hypothesis but such a prediction has not been made explicit.

According to Vorontsov (1962) and Baker (1971), granivorous rodents should show higher levels of locomotory activity and be less dependent on shelter. The significant differences between northern and southern bank voles clearly contradict these predictions (Table 5). There were no significant differences in daily rhythm or food storing but pronounced granivores are supposed to be more nocturnal and store more (Grodzinski 1962, Vorontsov 1962). However, individual variations may have been too great and numbers of animals examined therefore too low for the establishment of such differences. Neither ecogeographical rules nor demographic strategies make any predictions on these behavioural traits.

Individual variability was great in the northern bank voles; i.e., in activity counts and growth rates. This characteristic does not seem related to any of the hypotheses proposed. As they appear in the most cyclic populations they may be consistent with the Chitty Hypothesis (Krebs 1978), but this hypothesis should be equally applicable to the South Swedish animals (Krebs & Myers 1974).

Some differences between the northern and southern bank voles are not easily open to experimental tests. However, the northern voles often appear outside closed forests; e.g., on abandoned and cultivated fields and in gardens (Hansson 1979a, Hansson & Zejda 1977, Larsson & Hansson 1977), on mires (Boström & Hansson 1981) and even in alpine habitats far above the timberline (Skar et al. 1971). Folivorous animals are predicted to appear more in open and grassy habitats and such a nutritive adaptation is clearly supported by the findings in the field.

Folivorous rodents are predicted to underexploit their food basis or, alternatively, to show periodic peaks (Baker 1971). There is a certain positive correlation between folivory and density variations in bank voles in Sweden. Cyclicity is much higher in the Strömsund than in the Revinge area, but Uppsala conditions are intermediate and fairly different from the Strömsund ones (Hansson 1978, unpubl.). However, such differences may be due both to an overexploitation of food and to predation from specialist predators (Hansson 1979b, Hansson & Henttonen 1985a). In this context it should be pointed out that folivorous animals not only permit the existence of numerous predator specialists by periodic high numbers (see Erlinge et al. 1983) but also are more exposed to predation owing to their extensive intestinal tract, making the animals slow and clumsy. The latter effect may appear, to various degrees, regardless of whether there is a genetic or only a dietary change.

It is obvious that there are many differences between southern and northern bank voles which cannot be explained by any of the three hypotheses. Furthermore, the predictions from the ecogeographical rules are not clear in the present context. There is also a general question whether all or most differences can be ascribed a certain basic dimorphy (or cline) or if the differences just reflect an immense number of local adaptations in independent directions. Only some tentative suggestions can be given: From the similarities of bank vole characteristics in Uppsala, Strömsund and Ammarnäs (66°N; see Gustafsson et al. 1983a) in central-northern Sweden on one hand and in South Sweden and central Europe on the other, it seems probable that different types of bank voles have evolved in deciduous and coniferous forests. Deciduous and coniferous forests show a clear difference in seeds being available to bank voles already in summer-autumn in large quantities in the former but not until late winter-spring in smaller amounts in the latter. Conifer forests with deep snow and few alternative prey species for predators may also primarily encourage cyclicity (Hansson 1979a). The development of nutritive adaptations towards folivory will, furthermore, have made the northern population predisposed for cyclic behaviour, and secondarily, this may possibly have caused an evolution of specialized demographic strategies. Thus, the adaptations may need to be explained from two or several levels instead of as usually from only a single one (see Hilborn & Stearns 1982). However, the southern and northern Swedish bank voles do not differ very much genetically as they freely interbreed and produce healthy offspring in the laboratory (own observations).

There is at least one other case with nearby differences in both bank vole morphology and behaviour: Bank voles from Skomer island off Wales are larger, have lighter colours and somewhat smaller but fewer litters, higher population densities and more stable populations than mainland British populations (Jewell 1966). Furthermore, Skomer voles had lower levels of urinary marking, were more day-active but had a generally lower total activity than the mainland voles (Johnson 1975). It should be observed that the combinations of characteristics deviate considerably from the Swedish ones. Low predation risk has been related to some Skomer vole attributes. The lower activity level and higher exploratory behaviour when without shelter in South Swedish bank voles may also have developed as an adaptation towards a high predation rate.

Lidicker (1978) pointed out that dynamics of various local populations will differ considerably and be affected by different factors. A general dynamic pattern of microtine rodent populations as proposed by Krebs & Myers (1974) did not seem reasonable. However, Lidicker (1978) still considered the behaviour and demography of a species to be constant in large areas, at least. The present findings indicate local or at least regional adaptations, partly in the way of counteracting local factors affecting dynamics, as available type of food and predation rates. Such conditions will make modelling of population dynamics extremely difficult. Either precise models have to be developed for specified local populations or the models have to be very general and with little predictive power (see Stenseth 1977 for a discussion).

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