

SPECIALIST PREDATORS, GENERALIST PREDATORS, AND THE MICROTINE RODENT CYCLE

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SUMMARY

(1) Two kinds of predation affecting the dynamics of microtine rodent populations have received increasing attention in recent years. It has been suggested that specialist mammalian predators (small mustelids) maintain or at least significantly contribute to the regular multi-annual cycles of rodent populations in northern Europe. Generalist predators (foxes, common buzzards, cats, etc.) are assumed to stabilize rodent populations in more southern localities.

(2) Combining the two kinds of predation in the same predator–prey model demonstrates that the generalist predators have a stabilizing effect on a cycle driven by specialist predators.

(3) In the model, the ratio of the maximum over the minimum prey population size and the length of the prey cycle decrease with increasing numbers of generalist predators. Sufficiently large numbers of generalist predators convert the limit cycle to a stable equilibrium point.

(4) The numbers of generalist predators greatly increase from north to south in Fennoscandia. In agreement with the model predictions, the ratio of the maximum over the minimum rodent density decreases by an order of magnitude, and the length of the cycle decreases from 5 to 3 years, from the seventieth to the sixtieth parallel. There is no clear multiannual cycle below 60°N.

INTRODUCTION

It has become evident during the past 5 years that there is an exceptionally regular population cycle of microtine rodents in northern Fennoscandia (Hansson & Henttonen 1985, 1988; Henttonen, McGuire & Hansson 1985; Kaikusalo & Hanski 1985; Hanski 1987). What have been called cyclic small rodent populations elsewhere in Europe and North America are not always cyclic, or the cycle is superimposed by much irregularity, or the cycle amplitude is very small (Alibhai & Gibbs 1985; Taitt & Krebs 1985). At Kilpisjärvi in subarctic Finnish Lapland, where small rodents have been studied systematically since the early 1950s, the record now consists of

nine high-amplitude cycles with little variation in cycle length. The ratio of the maximum over the minimum rodent density generally exceeds 100 in northern Fennoscandia (Hansson 1969, 1987; Henttonen 1987). In contrast, in southern Sweden and in most of Central Europe, small rodents show seasonal changes in population size but there is no regular, multiannual cycle (excepting *M. arvalis* on extensive agricultural areas; Ryszkowski, Goszczynski & Truszkowski 1973). The two extremes in the north and in the south are joined by a geographical gradient in the regularity, amplitude and interspecific synchrony of the cycle, all these parameters decreasing from north to south in Fennoscandia (Henttonen & Hansson 1990).

These and other recent observations about temporal and spatial variation in small rodent cyclicity (Taitt & Krebs 1985; Getz *et al.* 1987; Lidicker 1988) have been used to advocate a 'multi-factorial perspective' to the dynamics of small rodent populations (Lidicker 1988), combining the many specific hypotheses that have been put forward previously (Krebs & Myers 1974; Hansson 1987; Hansson & Henttonen 1988). While such an inference seems reasonable in the face of the ever more complex pattern of observations, it remains important to examine how much of the observed variation can be explained by simpler and more tractable hypotheses. Challenging the simple hypotheses with new data is an efficient way of making progress.

Our purpose in this paper is to predict the combined effects of specialist and generalist predators on small rodent dynamics, and to test these predictions with old and new data and analyses of geographical variation in the numbers of predators and in the parameters of the microtine rodent cycle. Although the (expected) qualitative effects of specialist and generalist predators on rodent dynamics are well understood, this is the first attempt to model their joint effects on prey dynamics (for a related study on insect predator-prey interactions see Hassell & May 1986). We use a very simple model, which is not suitable for generating quantitative predictions, but which is suitable for generating qualitative predictions about the effects of different levels of generalist predation. The focus of this paper is in the well-documented small rodent dynamics in Fennoscandia, but our results are relevant for the dynamics of cyclic populations in general.

SPECIALIST AND GENERALIST PREDATORS

Theoretical studies have demonstrated that specialist predators may drive a predator-prey limit cycle (e.g. May 1981), an example of which may be the regular multi-annual cycle of small rodents (Henttonen 1987; Henttonen *et al.* 1987) and their mustelid predators (Kaikusalo 1982) in northern Fennoscandia. In contrast, the functional response of generalist predators with relatively stable populations tends to be stabilizing (Murdoch & Oaten 1975; Andersson & Erlinge 1977; Hassell 1978), and may prevent multi-annual cyclicity of small rodents in southern Fennoscandia (Hansson 1971, 1987; Erlinge *et al.* 1983; 1988; Erlinge 1987). While examining the role of predation in small rodent dynamics, it is essential to distinguish between specialist and generalist predators (Andersson & Erlinge 1977).

Several birds of prey specializing on small mammals, e.g. the Tengmalm's owl *Aegolius funereus*, do not breed well if small rodents are scarce (Maher 1970; Andersson 1976; Korpimäki 1988). Nonetheless, their population dynamic effect on small rodents is akin to the effect of generalist predators, because individuals tend to move to regions with higher than average density of prey (for the Tengmalm's owl

see Lundberg 1979; Korpimäki, Lagerström & Saurola 1987; Löfgren, Hörnfeldt & Carlsson 1986; Andersson & Erlinge 1977 and references therein). Such nomadism, like the functional response of generalist predators, gives rise to rapid changes in predation rate with changing prey abundance, and has a stabilizing effect on prey populations. For the purposes of this study, it is sensible to pool the numbers of birds of prey specializing on small mammals with the numbers of generalist predators.

Table 1 lists the main species of predators and their approximate densities in three well-studied localities, in South Sweden (Revinge), in South-Central Sweden (Grimsö) and in northern Fennoscandia. Quantitative population estimates for the specialist mammalian predators, the weasel *Mustela nivalis* and the stoat *Mustela erminea*, are scarce. It is generally believed that the key factor affecting the numbers and the dynamics of small mustelids is the density of their main prey, microtine rodents (Lockie 1966; Erlinge 1974; Henttonen 1987; but see Korpimäki & Norrdahl 1989b). In Finnish Lapland, the numbers of weasels are well correlated with the numbers of small rodents, while the numbers of stoats, a larger species, typically lag behind by

TABLE 1. Densities of three kinds of predators (individuals km⁻²) and the corvids in three localities in Fennoscandia, Revinge (56°N; Erlinge *et al.* 1983), Grimsö (59°N; Angelstam, Lindström & Widén 1984) and the Pallasjärvi–Kilpisjärvi area ('North'; 68–69°N, north boreal taiga and subalpine birch forest; Tast & Kalela 1971; Andersson 1976; Henttonen *et al.* 1987; Hersteinsson *et al.* 1989; Oksanen 1990; Henttonen, unpubl.). ? denotes unknown density (the species is present). The Revinge and Grimsö results are breeding densities. The figures for the 'North' are from snow-tracking and live-trapping studies (mammals) and from surveys of breeding numbers (birds). The higher values for the 'North' refer to the peak years of the small rodent cycle

Species	Revinge	Grimsö	North
Specialist mammalian predators			
Least weasel <i>Mustela nivalis</i>	?	?	up to 20
Stoat <i>Mustela erminea</i>	0.8–1.4	?	0.5–2.0
Specialist bird predators			
Short-eared owl <i>Asio flammeus</i>	–	–	<0.1
Long-eared owl <i>Asio otus</i>	0.2–1.3	0.0–0.3	–
Hawk owl <i>Surnia ulula</i>	–	<0.1	0.1–0.2
Tengmalm's owl <i>Aegolius funereus</i>	–	0.0–0.6	<0.1
Kestrel <i>Falco tinnunculus</i>	0.1–1.3	<0.1	<0.1
Long-tailed skua <i>S. longicaudus</i>	–	–	0.1–0.6
Generalist predators			
Red fox <i>Vulpes vulpes</i>	0.9–2.0	0.4	<0.1
Badger <i>Meles meles</i>	0.8–0.9	0.4	–
Domestic cat <i>Felis catus</i>	1.8–2.5	0.2–0.4	–
Polecat <i>Mustela putorius</i>	0.6–1.4	–	–
Pine marten <i>Martes martes</i>	–	0.4	0.1
Common buzzard <i>Buteo buteo</i>	1.5–2.5	0.2	–
Rough-legged buzzard <i>B. lagopus</i>	–	–	0.1–0.4
Tawny owl <i>Strix aluco</i>	0.7–1.4	<0.1	–
Corvids			
Raven <i>Corvus corax</i>	–	<0.1	?
Hooded crow <i>Corvus corone</i>	14	0.2	?
Jay <i>Garrulus glandarius</i>	–	4.0	?
Siberian jay <i>Perisoreus infaustus</i>	–	–	0.1–0.5
Pooled density of specialist bird predators and generalist predators			
	6.6–13.3	1.9–3.0	0.3–1.5

1 year (Kaikusalo 1982). In southern Fennoscandia, the impact of the mustelids on rodents is small in comparison with the major influence of generalist predators (Erlinge *et al.* 1983).

The number of species of generalist predators and birds of prey decreases with increasing latitude, which is especially evident if only the more abundant species are considered, i.e. eight, five and two species in southern, central and northern Fennoscandia, respectively (Table 1, including species which may reach 0.4 individuals km^{-2} , but excluding the corvids). In these data, the pooled density of generalist predators and birds of prey is an order of magnitude higher in southern Sweden than in Lapland. In Europe in general, the densities of diurnal raptors decrease towards the north and the east, from thirty-six pairs per 100 km^2 in Spain, forty-two in Britain, twenty in southern Sweden, and ten in the northern half of Sweden (Nilsson 1981). In the Swedish data, there is a highly significant decrease in density with increasing latitude ($r_s = -0.95$, $P > 0.001$; calculated from Nilsson's Table 2), and the highest local density in the south is fifty times higher than the lowest density in the north. In Finland, the size-corrected ingestion rate of birds of prey is two to ten times higher in southern Finland than in Lapland (Fig. 1).

In summary, various sources of data clearly indicate that the species number and the pooled density of generalist predators and birds of prey significantly increase from north to south in Fennoscandia. We shall now turn to a simple predator-prey model and ask what difference the number of generalist predators makes to a limit cycle driven by specialist predators.

MODEL

Specialist predators

May (1973) has investigated a predator-prey model that suits well as a starting point for our analysis:

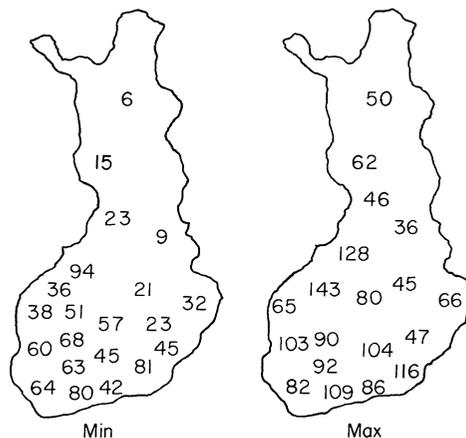


FIG. 1. Density of birds of prey in different parts of Finland using the minimum and maximum estimates given by Saurola (1985). The original densities have been multiplied by $0.032 W^{0.75}$, where W is the average weight of the species (from Järvinen & Väisänen 1980). The exponent of 0.75 corrects for changing ingestion rate with weight (Peters 1983). Multiplication by 0.032 gives the results in units of predators weighing 100 g.

$$dN/dt = rN(1-N/K) - cPN/(N+D) \quad (1a)$$

$$dP/dt = sP(1-P/qN). \quad (1b)$$

In this model, N and P are the sizes of the prey and the predator populations, r and s are their intrinsic rates of increase, and K is the prey carrying capacity. The predator carrying capacity is proportional (q) to the size of the prey population. The functional response of the predator is of type 2, with c determining the maximum rate of predation and D the rate of increase of predation with increasing prey density.

This model, as most models of specialist predator and its prey, has dynamics that converge either to a stable equilibrium point or to a stable limit cycle (Kolmogorov 1936; Rosenzweig & MacArthur 1963; May 1973; Bulmer 1976). Whether the equilibrium point is stable or not depends on three combinations of parameters: K/D , r/s and cq/r (May 1973; Tanner 1975). Cycles can be expected when the prey carrying capacity is large in relation to the searching efficiency of the predator (large K/D), and when the intrinsic rate of increase of the prey is greater than the intrinsic rate of increase of the predator (large r/s). Both conditions are probably true for small mustelids and their rodent prey in northern Fennoscandia, though quantitative parameter estimates are not available for D and s .

For our purposes it is not enough to know which parameter values give rise to cycles; we need predictions about the length and amplitude of the cycle. To obtain these predictions we first reparameterize the model into the form:

$$dX/dt = rX(1-X/Z) - aYX/(X+1) \quad (2a)$$

$$dY/dt = sY(1-Y/X) \quad (2b)$$

where $X = N/D$, $Y = P/qD$, $Z = K/D$ and $a = cq$.

We have explored numerically how the cycle length (CL) and the ratio of the maximum over the minimum prey population size (MM) depend on Z , a , r and s . The values of CL and MM were determined for 256 combinations of parameter values, as explained in Table 2. Parameter combinations that resulted in a stable equilibrium point were excluded, and the remaining points were used in a multiple regression analysis to describe the effects of the four parameters on CL and MM. The results indicate that both CL and MM increase with increasing Z , and they both decrease with increasing s (Fig. 2, Table 2). Parameter a has a highly significant

TABLE 2. Multiple regression analysis of the effect of the model parameters on prey cycle length (CL) and the logarithm of the ratio of the maximum over minimum prey population size (MM). Data points were generated by numerically solving CL and MM in eqn. (2) for the following parameter combinations: $Z = 10, 20, 40, 80$; $a = 2.9, 4.9, 8.4, 14.2$; $r = 0.9, 1.6, 2.9, 5.2$; and $s = 0.5, 0.7, 1.1, 1.7$. Parameter combinations that resulted in a stable equilibrium point were excluded from the analysis

Parameter		Z	a	r	s
CL	coeff.	0.087	0.218	-1.632	-9.003
	t -value	4.46	1.53	-3.72	-7.02
	P	0.000	0.125	0.001	0.000
$R^2 = 0.61$					
MM	coeff.	0.053	0.265	-0.011	-1.869
	t -value	15.51	10.52	-0.14	-8.21
	P	0.000	0.000	0.860	0.000
$R^2 = 0.82$					

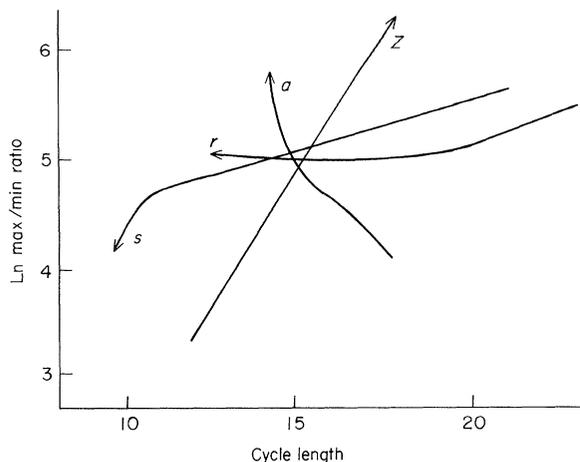


FIG. 2. Analysis of the limit cycle in May's (1973) model, eqn (1). This figure illustrates changes in cycle length and the ratio of the maximum over minimum prey population size as a function of changes in four parameters, $Z = K/D$, $a = cq$, r and s . For further explanations and the parameter values see Table 2. The four lines were drawn through the average points for the respective parameters, calculated over all possible combinations of the values of other parameters. Cycle length has arbitrary units.

positive effect on MM, while r has little effect on MM but a significant negative effect on CL (Table 2).

In summary, the simplest means to generate a correlated decrease in CL and MM in this model is to decrease Z or to increase s . Naturally, correlated changes in CL and MM may also be obtained by changing two or more parameters simultaneously.

Generalist predators

Generalist predators have, by definition, several alternative prey species between which they may 'switch', depending on which prey species are currently most abundant. Specialist but nomadic bird predators may also track high local densities of their prey (Korpimäki & Norrdahl 1989a). The essential point is that such predators add a directly density-dependent mortality to the dynamics of their prey. In the very simplest case, when the functional response of the predators does not become saturated, such predation has the same effect as lowered carrying capacity of the prey. Korpimäki's (1985; Korpimäki & Norrdahl 1989a) results on the Tengmalm's owl, the short-eared owl and the horned owl from Central Finland demonstrate an unsaturated, density-dependent response to increasing numbers of small rodents.

Assuming that mortality caused by generalist predators is given by GX^2 , where G is proportional to the numbers of predators, the previous analysis remains unchanged, with Z in eqn (2a) replaced by $rZ/(r + GZ)$ (from the sum of rX^2/Z and GX^2). Increasing the numbers of generalist predators (increasing G) increases the region of stable equilibrium point in the model (cf. May's 1973 analysis). This accords with the observations that the rodent populations are relatively stable in southern Fennoscandia, where the numbers of generalist predators are high. Furthermore, the analysis in Table 2 suggests that before the limit cycle turns to a stable point with

increasing numbers of generalist predators, both CL and MM will decrease for a large set of parameter values. MM approaches unity, and the change in its value may be large, while CL decreases less dramatically, up to 30–40% of its initial value (the value in the absence of generalist predators) in the simulations in Table 2.

We have analysed a modification of this model, in which we assumed type 3 (sigmoid) functional response for the generalist predators, by replacing the term GX^2 with $GX^2/(X^2 + E^2)$, where E gives the rate of increase of predation rate with increasing prey density. This modification did not change the previous results qualitatively, except that now r had a significant positive effect on MM. Table 3 gives one set of numerical results for fixed values of Z and $F (= E/D)$. As in the previous model, increasing G decreases CL and MM, and large enough values of G entirely stabilize the prey cycle.

CYCLE LENGTH AND AMPLITUDE: OBSERVATIONS

Cycle amplitude

Hansson & Henttonen (1985) have previously shown that the degree of cyclicity in small rodents increases northwards in northern Europe. Their cyclicity index really measures the cycle amplitude, which is well correlated with the regularity of the multi-annual cycle (Henttonen *et al.* 1985). We have used all the available long-term data from Fennoscandia to calculate the ratio of the maximum over the minimum in time-series of annual rodent densities (data in the Appendix). This ratio increases with latitude, from less than 10 below 59°N to about 100 in the most northern localities, though there is substantial variation at high latitudes (Fig. 3, Table 4). We used ANCOVA to examine the effect of habitat (forest versus field) on MM. No such effect was detected.

Cycle length

It has been observed in the past that the length of the small rodent cycle appears to increase from south to north (Hagen 1952; Myrberget 1973; Hansson, Löfqvist &

TABLE 3. Multiple regression analysis of the effect of the model parameters on prey cycle length (CL) and the logarithm of the ratio of the maximum over minimum prey population size (MM). Data points were generated by numerically solving CL and MM in a modification of eqn (2) with type 3 functional response in generalist predators for the following parameter combinations: $Z = 40$; $a = 2.9, 4.9, 8.4, 14.2$; $r = 0.9, 1.6, 2.9, 5.2$; $s = 0.5, 0.7, 1.1, 1.7$; $G = 15, 22.5, 33.8, 50.6$; and $F = 10$. Parameter combinations that resulted in a stable equilibrium point were excluded from the analysis

Parameter		a	r	s	G
CL	coeff.	-0.079	-0.431	-7.667	-0.066
	t -value	-1.88	-3.08	-19.07	-4.98
	P	0.059	0.003	0.000	0.000
$R^2 = 0.78$					
MM	coeff.	0.257	0.368	-2.16	-0.049
	t -value	8.57	3.67	-7.50	-5.14
	P	0.000	0.001	0.000	0.000
$R^2 = 0.57$					

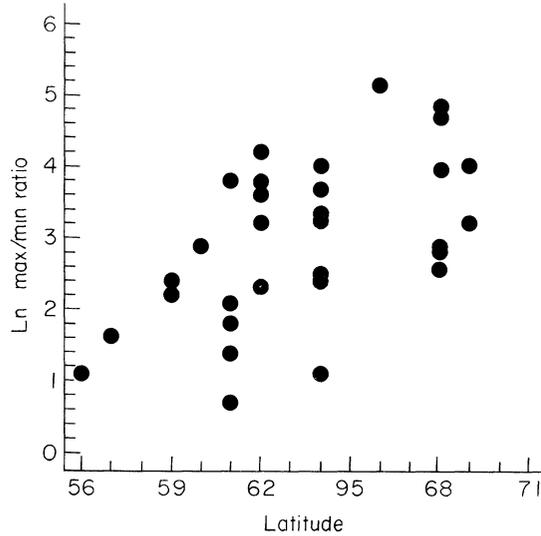


FIG. 3. The ratio of the maximum over the minimum density of small rodents (MM) against the latitude. Data in the Appendix.

TABLE 4. Regression analyses of the observed cycle length (CL) and the ratio of the maximum over the minimum annual population estimate (MM, log-transformed data) against latitude. The regressions were weighted by the length of the data series. Data from the Appendix. See Figs 3 and 4

Dependent variable	Independent variable	Coeff.	S.E.	<i>t</i> -value	<i>P</i>	<i>R</i> ²
MM	Constant	-8.91	2.64	-3.37	0.0021	0.39
	latitude	0.19	0.04	4.57	0.0001	
CL	Constant	-5.60	1.57	-3.57	0.0012	0.51
	latitude	0.14	0.02	5.81	0.0000	

Nilsson 1978), but nobody has analysed geographical variation in cycle length in any detail. We shall therefore do it here with all the data that are available.

The existing long-term records of small rodent dynamics from Fennoscandia are summarized in the Appendix. Using these records, cycle lengths were calculated as follows. Peak years were defined as years with density higher than in the preceding and in the proceeding year. The first and the last year of the series were not accepted as peak years. The intervals between the peak years were calculated, and their average was used as a measure of cycle length. Note that with this definition, any series of annual abundances has a 'cycle length'. We did not determine whether a regular cycle occurred or not, but examined any geographical trends in the value of this index. The regularity of the cycle in northern Fennoscandia has been demonstrated beyond doubt elsewhere (Henttonen *et al.* 1985; Kaikusalo & Hanski 1985).

There is a significant increase in cycle length from around 3 years below 59°N to more than 4 years in the most northern localities (Fig. 4, Table 4). The average cycle

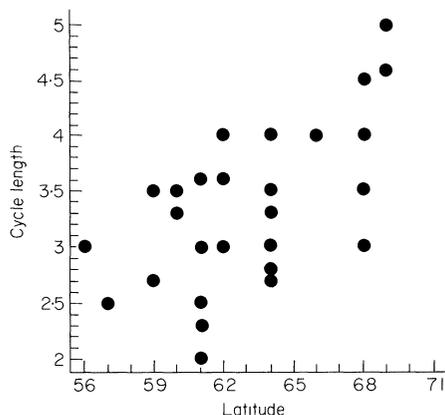


FIG. 4. Cycle length (years) against the latitude. Data in the Appendix.

length is 5 years in Kilpisjärvi, northern Finnish Lapland (Kaikusalo & Hanski 1985), from where an exceptionally long time-series is available (Appendix).

One problem with the data in the Appendix is that they have been collected by different individuals using different methods, and generally the time-series are short, i.e. 6–17 years in length. We have therefore used other data that provide indirect yet reliable information on cycle length. During the years 1973–87, nearly 20 000 nestlings of the Tengmalm's owl *Aegolius funereus* have been ringed in Finland (Saurola 1982 and pers. comm.). This species only breeds well when the availability of small rodents is high (Korpimäki 1985), hence the numbers of nestlings ringed at any one locality give a good indication of the alternation of peak and low years in small rodent populations.

We analysed the ringing records for $100 \times 100 \text{ km}^2$ squares using autocorrelation and partial autocorrelation functions. The data were log-transformed before the analysis, and we run the analyses before and after differencing the data. The results show a clear pattern (Fig. 5): (i) in the western part of southern Finland there has been a definite 3-year cycle in the owl's breeding success; (ii) in the eastern part of southern Finland some cycles have lasted 4 years while most are still 3 years long; and (iii) north of 64°N the cycle length has definitely been 4 years. Figure 5 also gives the cycle length as calculated from the best small rodent data available.

The border between the 3- and 4-year cycles coincides with the border between the southern boreal and midboreal zoogeographical zones as defined and analysed by Järvinen & Väisänen (1973; 1980, and references therein). Basically, the difference is between mostly forested areas towards the north and a mosaic, agricultural landscape towards the south. Recollect that the density of generalist predators clearly declines at this latitude (Fig. 1).

DISCUSSION

Let us summarize the above results and their interpretation. In Section 2 we demonstrated that the density of generalist predators and birds of prey increases from north to south in Fennoscandia. In Section 3 we showed that, in a simple yet reasonable

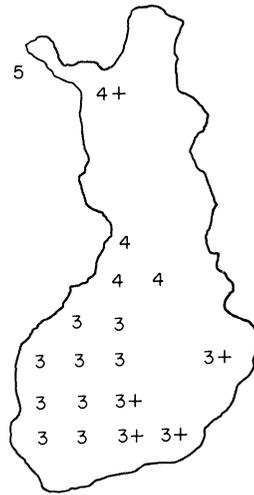


FIG. 5. Cycle length in the numbers of Tengmalm's owl fledglings with two data points based on long-term studies of small rodent populations (the two northernmost points, Pallasjärvi and Kilpisjärvi).

predator–prey model, increasing rate of predation by generalist predators decreases the length and the amplitude of the prey cycle driven by specialist predators. Ultimately, with high enough density of generalist predators, the prey cycle turns to a stable equilibrium point. In Section 4 we demonstrated that the predicted changes in cycle length and amplitude do occur in Fennoscandia. From these results we conclude that the observed patterns of small rodent cyclicity in Fennoscandia are consistent with the hypothesis that generalist predators modify a cycle driven by specialist predators.

Consistency is no guarantee of a correct explanation, however, and it may be asked which other mechanisms than predation by generalist predators could produce the observed geographical pattern in rodent cyclicity, assuming that the northern cycle is a predator–prey limit cycle. Variation in the carrying capacity of rodents (K) is not a plausible explanation, for if there is any geographical variation in it, it decreases with increasing latitude. The results in Section 3 suggest the following alternative explanations: (i) the intrinsic rate of increase of the specialist predator (s) increases from north to south, and/or (ii) the intrinsic rate of increase of the prey (r) increases but the hunting efficiency of the specialist predator (a) decreases from north to south.

Our analyses revealed a negative relationship between r and cycle length, which could be explained, in principle, by an allometric relationship between body size (negatively correlated with r) and cycle length (Calder 1983; Peterson, Page & Dodge 1984). However, the observed change in cycle length from 3 to 5 years (Fig. 4) would require an increase in body weight by nearly an order of magnitude (from 21 to 152 g, based on the relationship in Peterson *et al.* 1984). Although the body size tends to be greater in the north than in the south in, e.g. *Clethrionomys glareolus* (Hansson 1985), the difference is so small (*c.* 10%) that the allometric explanation is clearly inadequate.

Several laboratory and field studies have compared the growth rates of southern and northern populations of rodents in Fennoscandia, and all have found only small and ecologically insignificant differences (Gustafsson 1983; Gustafsson, Andersson & Westlin 1983; Stenseth *et al.* 1985; Ebenhardt 1987; L. Hansson, unpubl.; H. Henttonen unpubl.). In the weasel, the interval between successive litters is somewhat shorter in the north than in the south (Frank 1974), and there seems to be a slight increase in litter size from 5–6 in southern Fennoscandia to 7–9 in the north (H. Henttonen, unpubl.), but these differences should decrease rather than increase the cycle length from south to north (Fig. 2). We thus conclude that the observed geographical changes in cycle length and amplitude are unlikely to result from latitudinal changes in population growth rates.

Our approach in this paper has been to check whether the recent observations about geographical variation in small rodent cyclicality in northern Europe are compatible with the hypothesis that the cycle is driven by specialist predators and modified by generalist predators. We were able to demonstrate that they are. We suggest that any other hypothesis about small rodent cyclicality would also gain in credibility if it provides an uncomplicated explanation of these grand patterns in small rodent population dynamics.

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APPENDIX

Data on small rodent population dynamics in Fennoscandia. The data given are: latitude, the length of the data series (years), species concerned, habitat, cycle length (CL) and the ratio of the maximum over minimum annual population estimate (MM). For the definitions of CL and MM see the text

Locality	Lat.	Year	Species	Habitat	CL	MM	Reference
Denmark							
1 Rönde Norway	57	9	<i>Cle gla</i>	beech forest	2-5	5	Jensen 1982
2 Kviteseid	59	6	<i>Cle gla</i>	spruce forest	?	31	Wiger 1979
3 S Norway	60	7	<i>Cle gla</i>	forests	3-0	13	
4 S Norway	60	7	<i>Mic agr</i>	forests	≥4-0	45	Christiansen 1983
5 W Norway	61	7	<i>Cle gla</i>	forests	≥4-0	6	
6 W Norway	61	7	<i>Mic agr</i>	forests	≥4-0	33	
7 C Norway	65	7	<i>Cle gla</i>	forests	≥4-0	9	
8 C Norway	65	7	<i>Mic agr</i>	forests	≥4-0	14	
9 N Norway	69	7	<i>Mic agr</i>	forests	4-0	10	
Sweden							
10 Revinge	56	13	<i>Mic agr</i>	abandoned field	3-0	3	L. Hansson, unpubl.
11 Grimsö	59	11	All spp.	forest	3-5	9	Angelstam <i>et al.</i> 1984
12 Södertörn	59	9	<i>Cle gla</i>	mixed forest	3-0	15	Curry-Lindahl 1956
13 Södertörn	59	9	<i>Mic agr</i>	mixed forest	2-5	7	Curry-Lindahl 1956
14 Uppsala	60	17	<i>Mic agr</i>	abandoned field	3-3	18	L. Hansson, unpubl.
15 Uppsala	60	17	<i>Cle gla</i>	reforestation	3-5	18	
16 Strömsund	64	13	<i>Mic agr</i>	abandoned field	3-5	26	Hörnfeldt <i>et al.</i> 1986
17 Strömsund	64	17	<i>Cle gla</i>	reforestation	2-8	40	
18 Umeå	64	11	All spp.	forest	4-0	28	Gustafsson 1983
19 Ammarnäs	66	8	<i>Cle gla</i>	conifer forest	4-0	168	
20 Tsåtså	68	8	<i>Cle ruf</i>	mountain heath	4-0	52	Andersson 1976
21 Torne Träsk	68	6	<i>Cle rut</i>	birch forest	3-0	16	Hansson <i>et al.</i> 1978
22 Torne Träsk	68	6	<i>Cle ruf</i>	birch forest	≥4-0	19	
23 Vesterålen	68	6	All spp.	birch forest	3-0	13	
24 Vittangi	68	6	All spp.	birch forest	≥4-0	18	
25 Kirkenes	69	6	All spp.	birch forest	≥5-0	25	

Finland	61	12	<i>Cle gla</i>	forest	2-3	8	Lagerström & Häkkinen, unpubl.
26 Lempäälä	61	12	<i>Cle gla</i>	forest	2-3	8	Lagerström & Häkkinen, unpubl.
27 Lohja	61	6	<i>Cle gla</i>	forest	2-0	4	Pankakoski 1984
28 Lohja	61	6	<i>Mic agr</i>	field	?	14	Pankakoski 1984
29 Loppi	61	9	<i>Cle gla</i>	forest	3-0	6	A. Kaikusalo, unpubl.
30 Loppi	61	17	<i>Mic agr</i>	field	3-6	45	
31 Hausjärvi	61	6	<i>Mic agr</i>	field	2-5	2	M. Lagerström, unpubl.
32 Ylöjärvi	62	15	<i>Cle gla</i>	forest	3-0	25	
33 Ylöjärvi	62	7	<i>Mic agr</i>	field	3-0	4	A. Kaikusalo, unpubl.
34 Teisko	62	11	<i>Cle gla</i>	forest	3-0	37	
35 Teisko	62	10	<i>Mic agr</i>	reforestation	3-0	67	A. Kaikusalo, unpubl.
36 Luhanka	62	6	<i>Cle gla</i>	forest	4-0	10	
37 Luhanka	62	6	<i>Mic agr</i>	field	3-6	45	A. Kaikusalo, unpubl.
38 Lakeus W	64	12	<i>Microtus</i>	field	3-3	11	K. Norrdahl, unpubl.
39 Lakeus E	64	11	<i>Microtus</i>	field	2-7	3	K. Norrdahl, unpubl.
40 Kauhava	64	12	<i>Microtus</i>	field	3-0	55	Korpimäki 1985
41 Kauhava	64	12	<i>Cle gla</i>	forest	3-3	12	Korpimäki 1985
42 Pallasjärvi	68	19	<i>Cle gla</i>	forest	4-5	140	H. Henttonen, unpubl.
43 Pallasjärvi	68	19	<i>Cle rut</i>	forest	4-5	117	
44 Pallasjärvi	68	19	<i>Cle ruf</i>	open habitat	4-5	136	H. Henttonen, unpubl.
45 Pallasjärvi	68	19	<i>Mic agr</i>	open habitat	4-5	103	
46 Pallasjärvi	68	19	<i>Mic oec</i>	open habitat	4-5	85	H. Henttonen, unpubl.
47 Pallasjärvi	68	19	<i>Lemmus</i>	open habitat	4-5	241	
48 Kilpisjärvi	69	40	<i>Cle ruf</i>	birch forest	4-6	55	

For the analyses in Figs 3 and 4 and Table 4 these data have been treated as follows. The following data points were omitted because of missing data: (28) and (33). The data from Norway were excluded because of the short length of the time-series and uncertain determination of most cycle lengths. The cycle length of (24) was assumed to be 4 years and the length of (25) was assumed to be 5 years. The following data points for different species from the same habitat were combined to obtain independent data points: (12) and (13) (CL = 2-7, MM = 11), (21) and (22) (CL = 3-5, MM = 17), (42) and (43) (CL = 4-5, MM = 129) and (44) - (46) (CL = 4-5, MM = 108; data point (47) for *Lemmus* was excluded).