

# Rodent Dynamics as Community Processes

Lennart Hansson and Heikki Henttonen

*Small rodent fluctuations are mentioned in many textbooks as examples of regular population cycles with constant interval and amplitude. However, recent evidence and analyses have indicated much more complex patterns, with geographic trends in frequency and amplitude of fluctuations and covariation with many interacting community components. These new findings indicate that extrinsic factors are much more important for the generation of regular rodent cycles than was earlier believed, and that regular cycles represent only a minority of the dynamic patterns found in rodents.*

Ideas about general and regular density variations in rodents go back to reviews from the 1960s and 1970s<sup>1</sup>. The popular view at that time was that this supposed regularity was due to intrinsic, social and/or genetic factors. However, at the same time a few authors still thought in terms of extrinsic factors, such as disease, food and predators, as driving processes of population cycles.

The conceptual basis for understanding rodent dynamics has changed considerably during the 1980s, and evidence has accumulated showing that the key parameters of population fluctuations (amplitude, frequency and interspecific synchrony) vary geographically. Here we review the new data and examine the extent to which geographical trends in rodent dynamics are correlated with physical and biological variables. Such correlations may be due to rodents affecting other species in a unidirectional way (e.g. prey to predator). Alternatively, species in other trophic levels may decide the growth rates of the rodent populations. Thus, predators or parasites may either affect a 'doomed rodent surplus', which in any case would disappear, or drive the dynamics of the rodents.

## Theoretical explanations and predictions

### *Intrinsic factors*

Although great fluctuations in rodent populations were detected many years ago, it was not until the

1950s that general explanations for these fluctuations were proposed. The first to emerge involved physiological stress, thought to develop at high density due to both physical and social stimuli<sup>2</sup>. Later, intraspecific aggression was emphasized; rodents were thought to experience benign and malign conditions alternatively, the latter affecting both reproduction and survival for the benefit of the population.

Such views were at odds with the notion of individual selection, but it was also difficult to imagine populations of the same quality either increasing or decreasing from the same density. Thus, a new theory – that individuals are of different genetic quality in low- and high-density populations (the Chitty Hypothesis<sup>3</sup>) – was developed. Timid, well-reproducing animals should be selected against in increasing populations, and large poorly reproducing and aggressive individuals should dominate at high densities. The increasing proportion of aggressive and poorly reproducing individuals should lead to a population decline. This polymorphic system was – like the stress-regulated system – thought to produce very regular cycles under most environmental conditions.

Populations regulated by these two intrinsic mechanisms should change in size according to a stereotypic pattern without any geographic variation. Species with distinct adaptations to food or climatic factors should show independent cycles, and no common pattern should emerge for different rodent species occupying the same habitat. Populations of predators might fluctuate in synchrony with rodents but they were not assumed to affect rodent dynamics, and no community-wide patterns were predicted.

### *Extrinsic factors*

Of the possible extrinsic factors affecting population dynamics, food has received the most attention. Suggestions for the role of the

quantity and quality of food range from simple hypotheses of overgrazing<sup>4</sup> to ideas about variation in plant production<sup>5</sup>, nutrient cycling<sup>6</sup>, hormonal precursors<sup>7</sup> and, more recently, plant defence<sup>8</sup>. Some ideas about the significance of habitat heterogeneity and patchiness may also be related to food resources.

Most rodent species have specialized diets and feeding strategies, e.g. granivory, folivory and bryovory, and have different amounts of food available to them. For multispecies rodent communities in which there are several feeding habits, aspects of the biology of a particular food-plant group do not explain synchronous population patterns in the rodent species, but may be sufficient to explain non-synchronous ones. For example, hormonal precursors found in graminids obviously cannot explain a synchronous decline in shrub and moss eaters, though they may account for the seasonal breeding pattern of grass eaters. If rodents are limited only by food, then experiments with supplemental food should have clear effects on population dynamics.

Plant production cycles ('flowering cycles') have been thought to result from an interaction of plant growth rhythms and temperatures in harsh climates<sup>5</sup>. The plant cycle should be independent of grazing effects. As the response to temperature differs between plant species, the dynamics of the consumer species should also differ, even if warm summers tend to synchronize the plant production. Nutrient cycling due to small rodents themselves could affect other species in the same habitat. Nevertheless, folivores and granivores, eating plant parts with different nutrient contents, should react differently from each other.

Habitat heterogeneity can affect the amount of food available. If the amount of suitable habitat for a species is small in winter (or at other seasons) in relation to its total area, or if there are large seasonal differences in habitat

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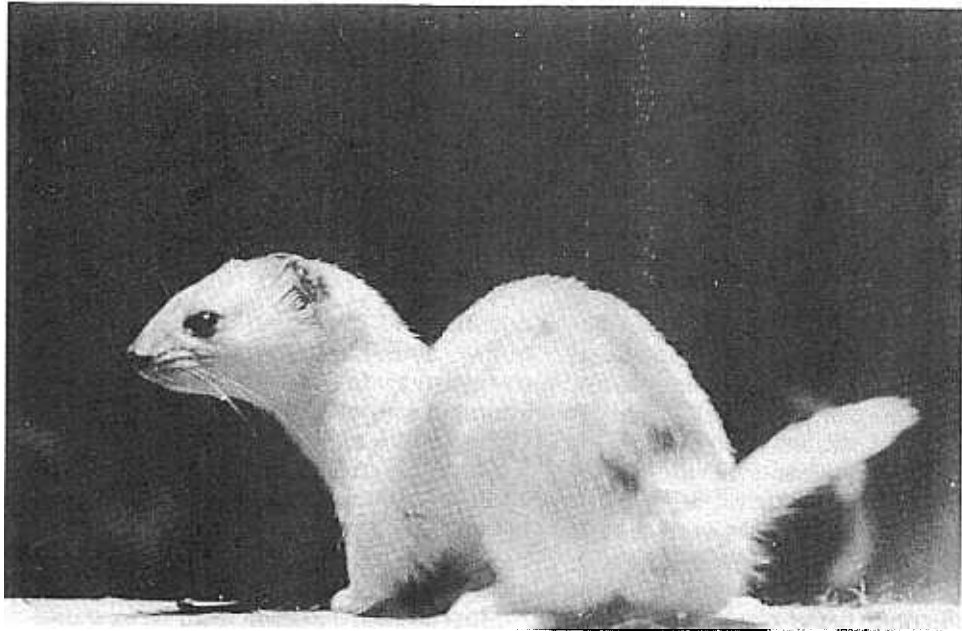


Fig. 1. Weasels, here the least weasel (*Mustela nivalis*), may play an important role in regular vole cycles. Photograph by Asko Kaikusalo.

quality between summer and winter, then large overwintering populations leading to cyclic peaks would not develop. However, the seasonal dynamics predicted for such conditions may change (for instance to very low summer densities) if other community processes (e.g. predation) are more important than food supply.

Predation has attracted less attention than food as a factor influencing rodent fluctuations. Simple predator-prey models predict regular cycles due to a time lag in the numerical response of specialist predators (Fig. 1), but the

main idea in small rodent research has been that predation will deepen and prolong low-density phases caused by other factors<sup>9</sup>. It has also been suggested that more generalized predators switch to alternative prey in rodent declines and thus keep the main and alternative prey populations covarying with some delay<sup>4</sup>. This should occur especially in relatively simple communities with few alternative prey species. At the other end of the scale, very generalized predators can stabilize prey populations by switching between prey species according to density

or biomass<sup>10</sup>. The variability predicted in predator effects is consistent with non-cyclic populations being regulated by generalist predators and cyclicity occurring only in communities with few generalists.

Different types of parasites show different capacities in regulating their host populations<sup>11</sup>. Microparasites (viruses, bacteria, etc.) often cause epidemics and high mortality in high-density host populations, and therefore will be potential causes of host population crashes. Macroparasites (helminths, arthropods) have long generation times and often less virulence, which makes them less probable agents of rapid host population decline. Many microparasites are rather host-specific and might well account for declines of single populations; high density, and impaired nutrition and immunity, may be necessary prerequisites. However, if pathogens are to cause synchronous cycles at the community level, generalist microparasites have to be responsible. In such a case, high density of one host could be sufficient to cause pronounced declines in several species.

#### General trends in density variations

##### Rodents

Recent analyses (Box 1) have shown that only a minority of microtine populations is cyclic<sup>13,14,16</sup>. Northern European *Clethrionomys* and *Microtus* species show a declining amplitude in their fluctuations from the north towards the south and west (Table 1). Northern populations have a three to four (in very northern areas sometimes five) year cycle, while southern Scandinavian and British populations are usually non-cyclic (Fig. 3). Central Eurasian populations, at least of *Clethrionomys*, are mostly non-cyclic. Japanese populations of *C. rufocanus* conform, by and large, to this non-cyclic pattern<sup>17</sup>.

In contrast to Europe, North American *Clethrionomys* and *Microtus* species do not show any geographical trends in cyclicity<sup>14,16</sup>, though some American *Microtus* populations are distinctly cyclic. Temperate American *Microtus* populations often seem to change between 'annual and multi-annual' dynamics<sup>18,19</sup>, resembling in this respect populations in a transition

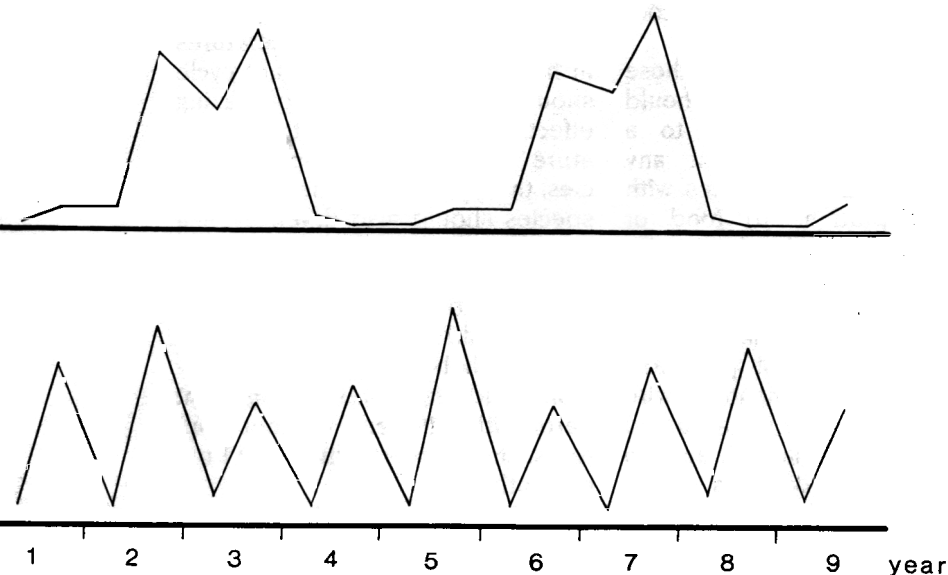


Fig. 2. Generalized picture of cyclic (above) and non-cyclic (below) microtine population fluctuations. Examples of cyclic populations can be found in Refs 32 and 33 and of non-cyclic ones in Refs 7, 16, 19 and 37.

zone from cyclic to non-cyclic populations in central Scandinavia. Certain northern North American *Clethrionomys* populations may have a 10–11 year cycle. *Clethrionomys rutilus*, for example, which shows a four to five year cycle in northern Scandinavia and has short-term non-cyclic dynamics in central Alaska and in the Canadian North-West Territories, has shown an 11 year cycle in Yukon (S. Gilbert 1987, PhD thesis, University of Lund, Sweden). Lemmings – the classical example of cyclicity – in fact sometimes show more irregular fluctuations than many vole populations<sup>20,21</sup>.

The highest indices of cyclicity for voles (Fig. 4) are reported from northern Scandinavian populations<sup>16</sup>, where the dynamics of different rodent species are strongly synchronized; this synchrony is gradually lost with decreasing cyclicity southwards<sup>15</sup>. In regions where populations are generally non-cyclic, certain populations may nevertheless show regular and high-amplitude cycles. Such populations seem to be associated with extensive areas of uniform habitats, e.g. afforestations in Britain and agricultural land in central Europe<sup>14</sup>.

The muskrat (*Ondatra zibethica*), which is an unusually large microtine, demonstrates 10–11 year cyclicity in North America<sup>22</sup>, while introduced populations in northern Scandinavia instead show a three to four year cycle<sup>23</sup>.

The snowshoe hare (*Lepus americanus*) has a 10–11 year cycle in the major parts of its North American range<sup>22</sup>. However, this cycle disappears at the southern distribution border in Wisconsin, Colorado and Utah<sup>24</sup>. Mountain hares (*L. timidus*) in central parts of the USSR are also claimed to have approximately a 10 year cycle, as do jackrabbits (*L. californicus*) in central parts of the USA<sup>25</sup>. Northern Scandinavian mountain hares show three to four year cycles<sup>26</sup> on a very low density level (except on islands) and cannot be considered as primary cyclic populations (see below).

**Predators**

The cycle lengths of predators are generally three to four years in

northwestern Europe<sup>12</sup> and 10–11 years in North America<sup>22</sup>. However, recent studies demonstrate a change in predator patterns with latitude in Scandinavia<sup>26</sup>, with the cycles disappearing towards the south. This applies to the red fox (*Vulpes vulpes*) and to its alternative prey, hares and grouse; the recruitment of alternative prey is diminished during vole crash years<sup>26</sup>. In southern Finland and Sweden neither voles, predators nor alternative prey show regular cycles (Fig. 5).

**Parasites**

Most of the few studies on micro-parasites in microtine rodents come from zoonotic diseases, rodents being the main host. Several disease outbreaks have been associated with vole peaks in Scandinavia. Tularemia cases in humans show a peak at and just after small rodent peaks<sup>27</sup>, and the zoonotic disease *Nephropathia epidemica*, a kind of hemorrhagic fever, closely tracks *Clethrionomys glareolus* cycles<sup>28,29</sup>. Furthermore, the incidence of *Nephropathia* disappears southwards, at around 60°N, where the cycles in this rodent species also become weak or non-existent<sup>14</sup>. The prevalence of viral antigens or antibodies has been examined in some microtine populations<sup>28–31</sup> and there is some evidence of a coincidence of viral epidemics and rodent declines. Certain viruses have been found in several sympatric rodent species<sup>30,31</sup>. Very little is known about the joint or synergistic effects of different pathogens in wild populations, but such synergism is known to occur in laboratory rodents.

**Box 1. Methods and definitions**

A fundamental reason for a re-evaluation of the regularity of rodent cycles is the more numerous and longer population studies now available. Most long-term studies are still from Europe and the USSR while the North American series cover mainly the few years needed for a doctoral thesis. Another reason for better understanding is the easier access to statistical tools like time series analysis (auto-correlation and spectral analysis<sup>12,13</sup>), facilitating comparisons of geographic variation in fluctuations with quantitative indices such as the index of cyclicity<sup>14</sup> and analyses of interspecific synchrony<sup>15</sup>. The cyclicity index (the standard deviation of logarithmically transformed yearly density estimates), although strictly measuring only the amplitude of fluctuations, clearly distinguishes the populations with regular cycles and deep crashes from populations with more irregular fluctuations and higher minimum densities<sup>14</sup>.

Rodent fluctuations have been dichotomized as 'cyclic' or 'non-cyclic'<sup>14</sup> and as 'multi-annual' or 'annual'<sup>16</sup>, respectively. These two independent analyses seem to have produced equivalent definitions but different terms. We prefer the term cyclic to multi-annual as multi-annual fluctuations as such do not need to be cyclic unless they are defined to have that meaning. Cyclic fluctuations are distinguished by the magnitude of fluctuations, high spring densities before peak numbers, and deep declines extending over summer. Non-cyclic fluctuations are characterized by regular declines in winter and increases in summer (Fig. 2). However, there have also been more general discussions of 'non-cyclic populations with irregular outbreaks'<sup>14</sup> and 'annual fluctuations with cyclic peaks'<sup>17</sup>. These two types of dynamics may not be equivalent and further analyses of various non-cyclic fluctuations may be needed.

**Observed patterns in relation to various predictions**

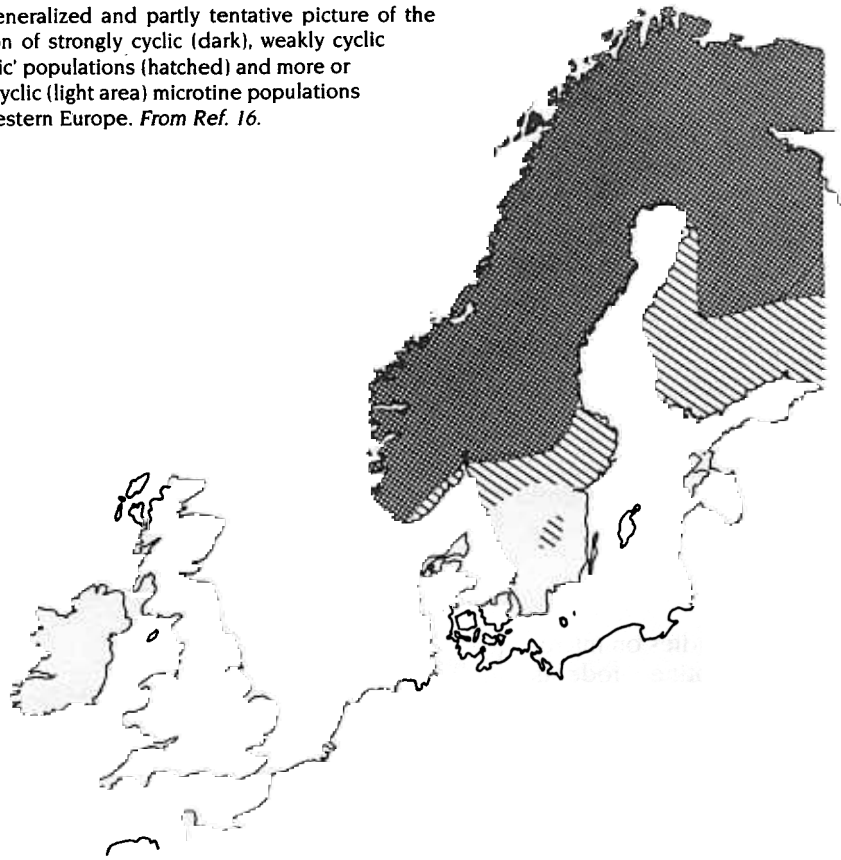
Regular small rodent cycles are restricted to certain regions or, elsewhere, just to a limited series of years; the global pattern predicted by theories of intrinsic mechanisms simply does not occur. This does not exclude the existence of some inherent social or genetic regulating mechanism that is overridden by extrinsic factors<sup>32</sup>, but such a scenario is not en-

Table 1. Cyclicity indices (Box 1) and distribution of population declines over summer (probably caused by specialist predators) in various Scandinavian regions.

Species	Region	n	Mean cyclicity index	% studies with summer declines
<i>Clethrionomys glareolus</i>	<59° N	7	0.22	14
	59–61° N	11	0.47	57
	>61° N	27	0.52	76
<i>Microtus agrestis</i>	<59° N	8	0.30	0
	59–61° N	12	0.53	25
	>61° N	19	0.62	90

Data recalculated from Ref. 14.

**Fig. 3.** Generalized and partly tentative picture of the distribution of strongly cyclic (dark), weakly cyclic 'semi-cyclic' populations (hatched) and more or less non-cyclic (light area) microtine populations in northwestern Europe. From Ref. 16.



feeding strategy, food supply and social behaviour (territoriality or non-territoriality in breeding females – see Fig. 4) may explain why folivores, for instance, have higher breeding densities and greater tendencies to cycles or outbreaks than granivores. On the other hand, distinct synchrony in processes such as the timing of the decline is difficult to understand from nutritional factors, especially if the decline is not related to density, feeding strategy or social behaviour of each species<sup>32</sup>. Temporal variation in the production of different plant material is obviously not so synchronized that it could cause the type of rodent synchrony and crash found, for example, in northern Scandinavia<sup>33</sup>. Flowering cycles seem to be mainly caused by rodent grazing<sup>33</sup>. A strict synchrony in a rodent community is also hard to reconcile with plant defence hypotheses unless defence communication between very different food plants or plant products is assumed (but see criticism<sup>34</sup> against 'talking trees'). Recent studies do not support the role of defensive chemicals in rodent cycles<sup>35,36</sup>. Neither do nutrient dynamics in the region of pronounced cycles in northern Scandinavia explain microtine dynamics<sup>35</sup>. However, conditions in permafrost areas, for which nutrient dynamics have been proposed as an explanation of rodent dynamics, might be

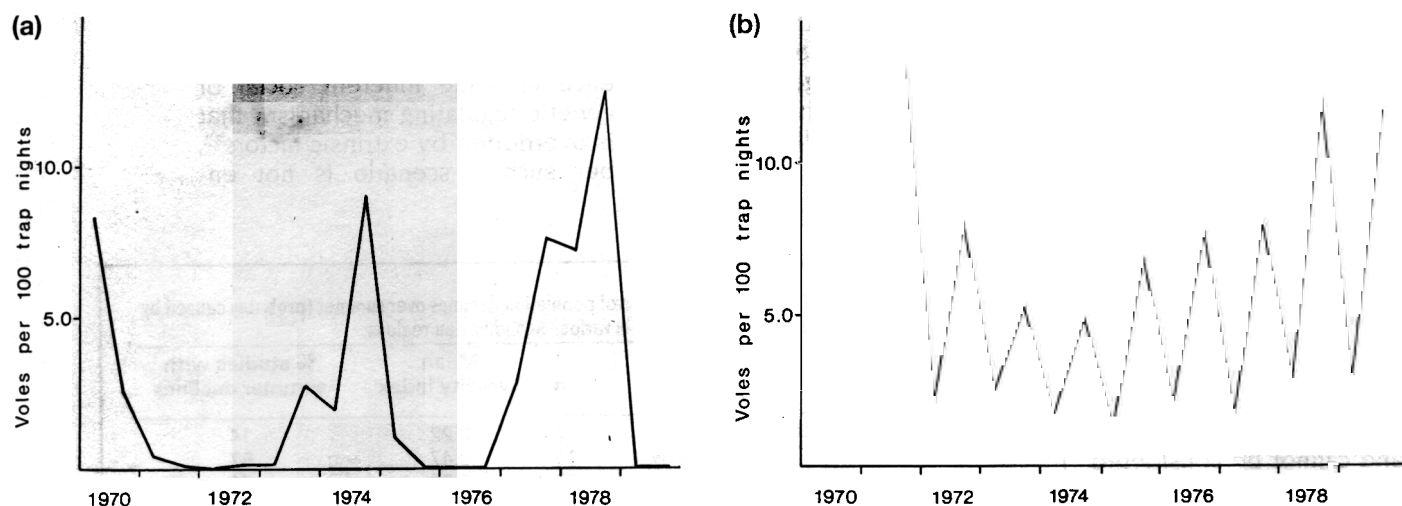
visioned in the main theories on intrinsic density regulation. Social behaviour may be involved in determining peak numbers (Fig. 4), but much confusion has resulted from the widespread belief that such factors are also causing the cyclic performance.

*Interactions with resources*

The non-synchronous and non-cyclic dynamics of rodents with different feeding habits can partly be understood as their indepen-

dent reactions to specific resources. Non-cyclic patterns in many regions could be responses to nutritional factors, possibly in interaction with social ones, and to climatic hazards. The rarer occurrence of cyclic populations of one species in one habitat and non-cyclic ones of another species in other habitats in the same region may be related to feeding habits and the abundance of suitable habitats.

A common relationship between



**Fig. 4.** Density indices of the field vole, *Microtus agrestis*, obtained with the same trapping method in (a) northern Finland (Pallasjärvi<sup>32</sup>) and (b) southern Sweden (Revinge<sup>37</sup>). This species shows differences in peak numbers between cyclic and non-cyclic populations while, e.g. *Clethrionomys* spp. do not increase to very high numbers at cyclic peaks, and thus comply still better with the generalized picture in Fig. 2. Female territoriality in the partly granivorous *Clethrionomys* spp. may limit reproduction and peak numbers while male *M. agrestis*, as many other pronounced folivores, are polygynous and females non-territorial.

different<sup>20</sup>. Experimental additions of food generally cause temporary increases in density but they do not determine the long-term dynamics<sup>16</sup>.

#### Interactions with predators

Observations and experiments on non-cyclic rodent populations in southern Scandinavia indicated that most (80%) rodent individuals were taken by generalist predators (foxes, buzzards, cats, etc.) with abundant alternative prey<sup>37</sup>. Specialist predators (mustelids, certain owls, etc.) may be more important in limiting northern cyclic rodent populations, and field data from northern Finland indicate indirectly that they have a depressive function during rodent declines<sup>32</sup>.

Also, the decline in the degree of interspecific synchrony among microtine rodents from northern to southern Scandinavia<sup>15</sup> suggests a change in the main limiting factors, possibly from specialist predation in the north to generalist predation on folivores and food limitation of granivores in the south. For generalist predators, snow diminishes both rodent availability and number of alternative prey; specialist weasels are well suited for hunting under snow, where they are also protected from their own predators. Rodent cyclicity shows a significant positive correlation with snow cover in Scandinavia.

At the southern distribution limit of the snowshoe hare, 'facultative' (generalist) predators have been implicated as the limiting factor<sup>38</sup>, causing non-cyclic dynamics. When a north Scandinavian fox population (being rather specialized on small rodents in this region) was severely reduced by a sarcoptic mange outbreak, mountain hares increased to much higher density levels than before and became non-cyclic<sup>39</sup>.

#### Interactions with pathogens and parasites

Outbreaks of opportunistic pathogens, commonly found in the environment, can cause episodic declines in microtine populations<sup>31</sup>, and this may contribute to the unpredictability of microtine dynamics in many regions. Latent infections may also be common, and may become acute when im-

munological function is impaired due to nutritional or stress factors<sup>18,21,30</sup>. The occurrence of certain murine viruses in several microtine species suggests that the disease may be important also at a community level. Generalist micro-parasites could be an alternative to specialist predators in causing synchronous dynamics.

#### Conclusions

When populations of the same species show clearly distinct dynamics in different regions<sup>14</sup>, differences in extrinsic factors are implied. Geographical (or habitat) trends may indicate clinal variation in the effects of different factors. Instead of considering vague multifactorial hypotheses, alternative causal mechanisms for further study can be suggested, as indicated above.

New data and re-analysis of old data demonstrate three changes in our understanding of rodent dynamics: (1) Most rodent populations are not cyclic; regular cycles are restricted to certain areas, while irregular outbreaks may occur worldwide; (2) Many other components of the surrounding community which interact directly or indirectly with rodents show synchronous population changes; (3) The earlier weak emphasis on food or nutrition as a driving factor of cycles is changing to predators and probably also disease.

The widespread idea that all rodent fluctuations follow the same pattern and are generated by the same intrinsic mechanism has to be abandoned. However, no single extrinsic factor may emerge to replace the old theory; instead, various factors may play important roles in different geographic locations, and possibly in the same locations at different times. The composition of the local biotic community, and its interaction with physical factors, such as snow cover and habitat heterogeneity, may be decisive. The data indicate that many rodent populations have only seasonal fluctuations but that habitat and/or community changes, either temporary or permanent, may influence such a regulation and lead to outbreaks or cycles with their own type of regulatory processes.

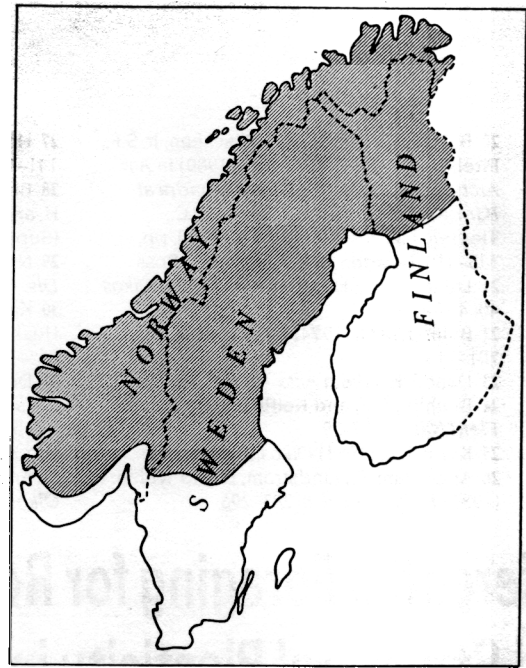


Fig. 5. Regions with (shaded) and without (light) game cycles in Scandinavia. Reproduced, with permission, from Ref. 28.

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# Differential Foraging for Resources and Structural Plasticity in Plants

Michael J. Hutchings

Although ecologists have spent much effort in analysing the foraging behaviour of animals, the study of plants as foraging organisms is a relatively unexplored subject. There is often, however, much greater potential for analysis of foraging behaviour in plants than in animals. Unlike most animals, many plant species leave permanent or semi-permanent records of their foraging activities because their resource-acquiring structures (primarily leaves and roots), persist for a considerable time, as also do the structures (trunks, branches, stolons, runners or rhizomes) which enable leaves or roots to be projected into particular positions in the habitat. In addition, plant ecologists are not burdened with the difficulties associated with determining how changes in foraging behaviour affect fitness in animals<sup>1</sup>, because plant mass (or, in the case of clonal species, number of ramets produced), is usually closely correlated with fitness.

The term 'foraging' can be defined as the process whereby an organism searches or ramifies within its habitat in the activity of acquiring essential resources<sup>2</sup>. Unless the pattern of search changes when the organism encounters patches of habitat containing different concentrations of resources, however, acquisition of resources will not be achieved efficiently. In plants, changing search patterns are usual-

ly achieved through morphological plasticity<sup>2–6</sup>.

Interpretations of experimental data on plant form in terms of differential foraging were almost entirely lacking from the ecological literature until recently. For such interpretations to be possible experiments on plants in controlled environments, rather than observations of plant behaviour under field conditions, are essential. This is because the natural environment is highly heterogeneous even at a very small scale; the genetical origin (and therefore the morphological properties) of plants in the field may be uncertain even within a species, and the effects on morphology of the interactions between the plants under study and neighbouring plants are very complex<sup>7</sup>. Altogether these considerations confound attempts to interpret morphological differences within a species from place to place in the field in terms of differential foraging.

## Greenhouse experiments on foraging

Most references to plants as foraging organisms concern herbaceous clonal species that grow primarily in the horizontal plane, branching and spreading laterally rather than acquiring height<sup>8–10</sup>. Most of the available data about plant foraging are from such species. The behaviour of these species is clearly easier to analyse than

that of species with markedly three-dimensional growth forms.

In the clonal herb *Glechoma hederacea* (ground ivy), resource acquisition is primarily carried out by two-leaved structures termed ramets, which are produced at every node along stolons which creep over the soil surface (Fig. 1). The plant also produces roots at its nodes. Two further stolons can grow from lateral buds at each node, so that the clone develops as a branched, connected population of ramets. For descriptive purposes, the principal stolons and the ramets they bear are described as primaries, whereas lateral buds give rise to secondary (and tertiary) stolons and ramets. Although the ramets are strictly determinate in form, the whole clone is markedly plastic in structure.

Plants of *G. hederacea* for experimentation can be proliferated from a single clone, so that all observed variation in morphology can be ascribed to differences in the growing conditions applied to replicate clones. Each ramet is large enough, and far enough from its neighbours on the same stolon, to be subjected in experiments to its own personalized set of growing conditions. Thus it could be provided, if wished, with a supply of light, nutrients and water which is different from that given to every other ramet. Experiments have been performed to compare the morphology of whole clones given either ample or very limited supplies of either nutrients or light<sup>2,5,7</sup>.

In addition to the expected reduction in biomass of clones when resource supply was low, there were marked differences in the morphologies of clones receiv-

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