

Population dynamics of territorial species in seasonal and patchy environments

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We present a seasonal model of a population in which there are differences between individuals. Dominant individuals defend breeding/feeding territories and are always assumed to obtain sufficient resources during the summer; in the winter there is no breeding, no territorial defence, and no individual differences. During the summer there is contest competition, and during the winter there is scramble competition. We study the effect of varying the length of the winter and summer seasons relative to each other, and varying the degree of patchiness in the distribution of food resources. Both longer winters and more patchily distributed resources decrease the stability of the population from year to year, causing it to exhibit cyclic behavior of increasing period and ultimately chaotic dynamics and population crashes. The kind of resource patchiness implemented in this model has a different effect on the population dynamics than in most patch models, where increased patchiness is generally considered to have a stabilizing effect. We discuss our results in light of observed mammal cycles in the the arctic and north temperate zone, and particularly with respect to the tendency for northern populations to be more cyclic than southern populations.

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There appears to be a consensus in the ecological literature that habitat heterogeneity and patchiness has a stabilizing effect on the dynamics of populations and on species interactions (e.g. Huffaker 1958, Levins 1970, Levin 1974, Atkinson and Shorrocks 1983, Nisbet and Gurney 1982, Hastings 1990; see Kareiva 1990). This stabilizing effect has been suggested in single species systems as well as in predator-prey and competitive interactions. To our knowledge, only the studies by Rosenzweig and Abramsky (1980), Forney and Gilpin (1989) and Burkey (1989) provide examples to the contrary: Rosenzweig and Abramsky (1980) argue that habitat heterogeneity may prevent precise coadaptation between voles and their food. Burkey (1989) shows that, in a single species model with demographic stochasticity, dividing the available habitat area into patches increases the probability of extinction. This is consistent with Forney and Gilpin's

(1989) laboratory experiment. It is, however, premature to state that increased patchiness generally increases the probability of population extinction, since this depends on the curvature of the probability of extinction as a function of patch area (Burkey, unpubl.).

Published studies typically consider patchiness at a relatively large spatial scale, with individual patches larger than several home ranges for the focal species. Here we present a model where resource patchiness is considered at a smaller spatial scale, and where the value of the resource to each individual may be reduced due to its patchy distribution. The model is developed with small rodents in mind, but may be relevant for many taxa in a patchy and/or seasonal environment. Small rodents (living in a highly patchy environment; cf. Stenseth 1983) are known for their multiannual density cycles. Snow cover and seasonality seems to be associated with these

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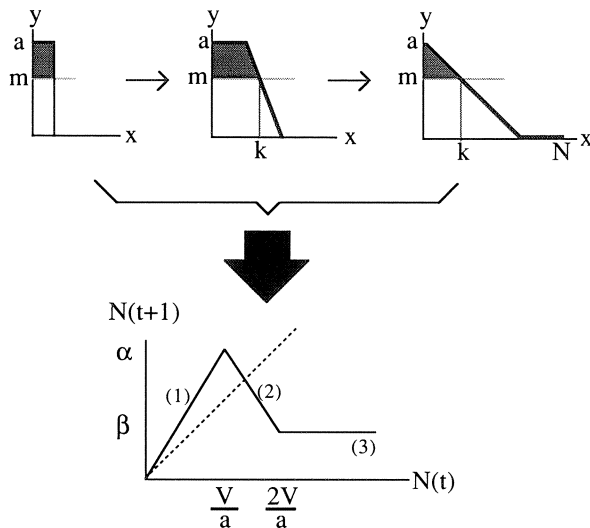


Fig. 1. The summer model. Top: the amount of resources, $y(x)$, available to an individual of rank x , as population size increases. The amount of resources the population as a whole has to put into reproduction is equal to the shaded area above the dotted line $y(x) = m$. The amount of total resources, V , is equal to the total area under the curve in the two graphs on the top right. The way in which resources are allocated (top) determines the shape of the model in phase space (bottom). The dotted line $N(t+1) = N(t)$, may be used for cobwebbing. (Modified from Łomnicki 1988).

density cycles (cf. Hansson and Henttonen 1985). Such density cycles typically have a three to five year period in the case of rodent populations (e.g. Stenseth and Ims 1993), and a ten year period in the case of snowshoe hares and their predators (e.g. Akçakaya 1992).

Our simple model unifies the effects of quality and quantity of food resources, climate and seasonality, temporal and spatial heterogeneity, and individual behavior (with individual differences and territoriality, with a potential link to predation) – all of which have been key candidates for explaining the cycles (Stenseth and Ims 1993) – in a single body of theory. We have built on Łomnicki's (1988) ideas on the population dynamics of individuals, by combining two of Łomnicki's models to make one. We use this model to study the effects of resource patchiness and the effects of a seasonally variable environment on the population dynamics of a herbivore species. Our model incorporates habitat patchiness in a spatially non-explicit manner (cf. Wiens et al. 1993). Preliminary results of this model were briefly discussed by Stenseth (1992).

The model

Assume reproduction and survival to be related to the amount of resources available to each individual. During the summer, individuals defend reproductive territories.

Differences between individuals lead to a dominance hierarchy and different abilities to defend territories. The total amount of resources, V , is proportional to the total area of appropriate habitat patches. Let a be the maximum number of resource units one individual can obtain, and let m represent the maintenance cost, i.e. the number of resource units one individual needs to survive (see Łomnicki 1988). Let $y(x)$ denote an individual's resource intake as a function of its rank, x , in the dominance hierarchy. Let k be the number of individuals that receive more than m units of resources. At low densities ($N(t) \leq V/a$) each individual takes as much resources as it can, a , and the population size in the next time step is given by (1), where h is the efficiency with which individuals convert consumed resources into new offspring. When $(V/a) < N(t) < (2V/a)$, $(2V/a) - N(t)$ individuals take a units of resources each, while the rest get a smaller share that decreases linearly with their rank, and the population size in the next time step is given by (2) (see Łomnicki 1988). For even higher values of $N(t)$, high ranked (territorial) individuals still get nearly the maximum possible amount of resources, while the low ranking individuals, competing for what is left, do not obtain enough resources to reproduce nor survive. The population size in the next time step is given by (3).

During the summer, the model is given as

$$N(t+1) = \begin{cases} (a-m)hN(t), & \text{for } N(t) \leq V/a \\ h[V(1 - (m^2/a^2) - mN(t)(1 - (m/a))], & \text{for } V/a < N(t) < 2V/a \\ hV(1 - m/a)^2, & \text{for } N(t) \geq 2V/a. \end{cases} \quad (1)$$

During winter food is scarce and individuals burn more energy to stay warm and search for food. Let V_w and m_w be the resource value and maintenance cost, respectively,

Table 1. Parameters in the model.

V	= Value of the resource (total) in the summer season
a	= maximum number of resource units one individual can obtain
m	= maintenance cost, i.e. resource units one individual needs to survive in the summer
k	= the number of individuals that receive more than m units of resources
x	= an individual's rank in the dominance hierarchy
$y(x)$	= an individual's resource intake as a function of its rank, x
h	= the efficiency of converting resources into offspring
V_w and m_w	= resource value and maintenance cost in the wintertime: $V > V_w$ and $m < m_w$
c	= patchiness coefficient; decreases V and V_w , increases m and m_w

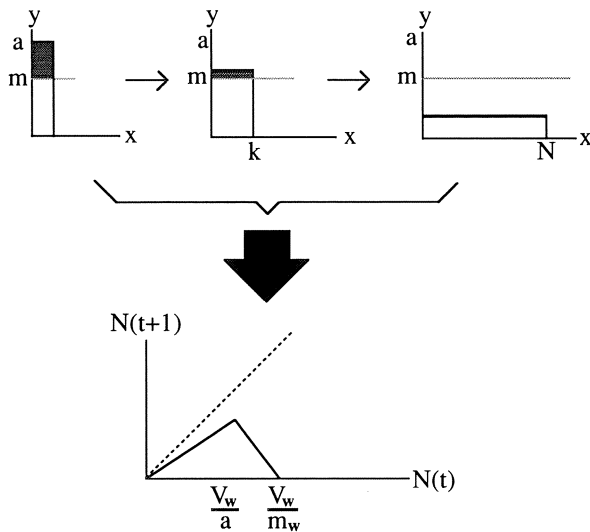


Fig. 2. The winter model. Top: the amount of resources, $y(x)$, available to an individual of rank x , as population size increases. The amount of resources the population as a whole has available for winter survival is equal to the shaded area above the dotted line $y(x) = m$. The way in which resources are allocated (top) determines the shape of the model in phase space (bottom). The dotted line $N(t+1) = N(t)$, may be used for cobwebbing. (Modified from Łomnicki 1988).

in the winter time, such that $V_w < V$ and $m_w > m$. In the winter, there is no breeding and individuals are assumed to be non-territorial, i.e. all individuals are "equal" in the winter. At low densities ($N(t) \leq V_w/a$), all individuals obtain the maximum amount of resources, and the population size in the next time step is given by (4). Scramble competition for available resources, when the population size exceeds that where individuals obtain less than a resources, yields (5). When $N(t)$ exceeds V_w/m_w , all individuals obtain less than m resources and die (6).

During the winter the model is given by

$$N(t+1) = \begin{cases} (a-m_w)h_w N(t), & \text{for } N(t) \leq V_w/a \\ (V_w N(t) - m_w)h_w, & \text{for } V_w/a < N(t) < V_w/m_w \\ 0 & \text{for } N(t) \geq V_w/m_w \end{cases} \quad (4)$$

Since there is no winter reproduction, the parameters for the winter model are constrained so that $N(t+1) < N(t)$ (i.e. $(a-m_w)h_w < 1$). The coefficient h_w converts resources in excess of m into increased winter survival.

A year is divided into ten time steps. Starting with N_0 individuals, a computer program calculates the population time series by running s time steps through the summer model and w time steps through the winter model ($s+w=10$) – before returning to the summer model for s new time steps, and so on.

Increasing patchiness means that less of the total area is considered appropriate habitat, so resource values are reduced, and individuals use more energy moving between patches in search of food, territories, and/or mates. Hence, both winter and patchiness are incorporated by reducing the resource value and increasing the maintenance cost. Let c be a coefficient which modifies the resource value and the maintenance costs with increasing patchiness, such that $V' = Vc$, $V'_w = V_w c$, $m' = m/c$, and $m'_w = m_w/c$.

Our analysis focuses on the non-trivial equilibrium point and its stability. If the population persists for 1200 years (1200×10 time steps), yet no pattern of repetition is found, we call its dynamics "chaotic" (although many of these populations might better be described as "quasi-periodic", we will not make this distinction here). Populations that crash rapidly and go extinct probably also deserve to be called chaotic, but we simply dub them "crashed", and distinguish them from populations that approach extinction asymptotically. A population is "stable" if it approaches an equilibrium population size, and

Table 2. The stability traits of the summer model depends on the population trajectory on the 3 segments of the graph in Fig. 1 (corresponding to equations (1)–(3)). The slopes and level of the three segments are dependent upon the relative magnitudes of four points $\alpha < \beta < V/a$, and $2V/a$ (see Fig. 1), where $\alpha = hV(a-m)/a$, and $\beta = hV(a-m)^2/a^2$. The slope of (2), which intersects the $N(t+1) = N(t)$ line, is given by its first derivative, $|f'((2))| = hm(a-m)/a$. Note that all four points are proportional to V . Thus, V does not affect the summer model's dynamic properties, and is merely a scaling parameter.

Case	Constraints on α and β	Constraints on $ f'((2)) $	Dynamic property
1	$\alpha \leq 2V/a, \beta \geq V/a$		Stable equilibrium point
2	$\alpha \leq 2V/a, \beta < V/a$	$ f'((2)) < 1$	Stable equilibrium point
		$ f'((2)) > 1$	Chaos
3	$\alpha > 2V/a, \beta \geq V/a$	$ f'((2)) < 1$	Stable equilibrium point
		$ f'((2)) > 1$	Stable 2-cycle
4	$\alpha > 2V/a, \beta < V/a$		Stable cycle of arbitrary length (n-cycle)

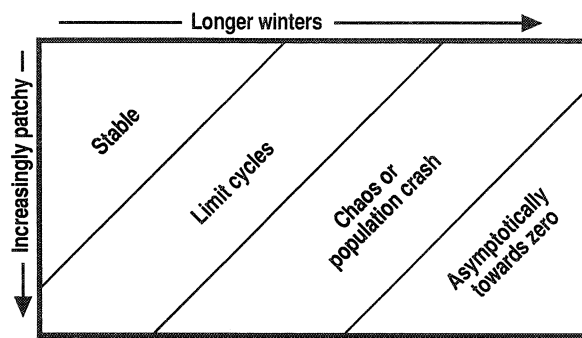


Fig. 3. Schematic illustration of the stability traits of the two-season model with increasing degree of patchiness (downward) and increasing the relative length of the winter season (towards the right).

“cyclic” if the population size repeats itself *exactly* with a period of $n=2,3,4 \dots$ years (each year being ten time steps in the numerical iteration). We recognize a transition of decreasing stability from “stable” through “2-cycle”, “4-cycle”, ... , “n-cycle”, “chaos”, “crash”, to “asymptotically to zero”.

Results

Summer model only

The dynamics of the summer model alone can be studied analytically, but numerical calculations were also run for different degrees of patchiness. The winter model alone is always unstable (has no non-trivial equilibrium), since there is no reproduction in the winter.

The stability of the summer model depends on the population trajectory on the 3 segments of the graph in Fig. 1 (corresponding to equations (1)–(3)), and is summarized in Table 2. If the population increases up to segment (3), it will always return to the same point, β (cf. legend to Table 2). Thus, populations whose dynamics

are determined solely by the summer model are always persistent, because the dominance hierarchy ensures that dominant individuals always get adequate resources. For the non-trivial cases where $\alpha > \beta$, $\alpha > (V/a)$, and $2V/a > \beta$ (as in Fig. 1), the stability traits of the summer model can be shown to be as in Table 2; the quantities α and β are defined in the legend to Table 2.

Two-seasonal model

The effects of increased patchiness and seasonality are schematically summarized in Fig. 3.

Both longer winters and greater degree of resource patchiness lead to greater instability. Table 3 shows the results of a model where we have coupled a summer model of case 3a (stable equilibrium) with the winter model. Columns to the left in the table represent environments with long summers and short winters (large s , small w); columns to the right represent environments with shorter summers and longer winters. Different rows represent environments with different degrees of patchiness. Patchiness increases with a decrease in the values of c (downwards in the table). We see that stable populations are found in environments with relatively long summers and short winters, and low degrees of patchiness. As winters get longer or resources are distributed more patchily, the dynamics of the populations become increasingly unstable, going progressively through bi-annual and multi-annual cycles, to chaotic/quasi-periodic behavior, crashes, and finally asymptotically towards zero.

Table 4 shows results of the same numerical analysis for a different set of parameter values. By changing the degree of patchiness (c), we can alter the summer model through several cases for the same set of parameters (e.g. two-cycles to n-cycles to chaos to stasis). As in the simulations in Table 3, both longer winters and increased patchiness increase the complexity of the dynamics and decrease stability. Many more simulations have been carried out with other parameter values, the results of

Table 3. Results from numerical analysis of the model, with parameter values $V=250$, $a=2.7$, $m=0.5$, $h=1.0$, $V_w=200$, $m_w=1.0$, $h_w=0.55$. Summer model corresponds to a case 3a throughout (see Table 2). Smaller values of c indicate greater degrees of resource patchiness.

c	Long summer/short winter → Short summer/long winter								
	s=9 w=1	s=8 w=2	s=7 w=3	s=6 w=4	s=5 w=5	s=4 w=6	s=3 w=7	s=2 w=8	s=1 w=9
1.0	Stable	Stable	Stable	Stable	Stable	3 year	6 year	Crash	Crash
0.95	Stable	Stable	Stable	Stable	2 year	Crash	Crash	Crash	Crash
0.90	Stable	Stable	Stable	2 year	Crash	Crash	Crash	Crash	Crash
0.88	Stable	Stable	3 year	2 year	2 year	Crash	Crash	Crash	Crash
0.86	Stable	Stable	6 year	Crash	Crash	Crash	Crash	Crash	Crash
0.84	2 year	8 year	Crash	Crash	Crash	Crash	Crash	Crash	Crash
0.83	2 year	Crash	Crash	Crash	Crash	Crash	Crash	Crash	Crash
0.82	Crash	Crash	Crash	Crash	Crash	Crash	Crash	Crash	Crash
0.80	Crash	Crash	Crash	Crash	Crash	Crash	Crash	Crash	Crash
0.75	Crash	Crash	Crash	Crash	Crash	Crash	Crash	Crash	Crash

Table 4. Results from numerical analysis of the model, with parameter values $V=250$, $a=2.9$, $m=1.5$, $h=1.429$, $V_w=240$, $m_w=1.5$, $h_w=0.6$. Left column indicates the kind of dynamics exhibited by the summer model alone (see Table 2). Smaller values of c indicate greater degrees of resource patchiness.

Case, summer model	c	Long summer/short winter → Short summer/long winter									
		s=9 w=1	s=8 w=2	s=7 w=3	s=6 w=4	s=5 w=5	s=4 w=6	s=3 w=7	s=2 w=8	s=1 w=9	
3b	1.20	Stable	4 year	Stable	4 year	Stable	4 year	2 year	14 year	Crash	
3b	1.15	2 year	4 year	2 year	Stable	2 year	Crash	Stable	Crash	Crash	
3b	1.10	6 year	2 year	Crash	12 year	Stable	Crash	Stable	Crash	Crash	
4	1.00	Stable	Crash	Crash	Crash	Crash	Crash	Crash	<i>Asym → 0</i>	<i>Asym → 0</i>	
2b	0.95	Stable	Crash	Crash	Crash	Crash	Crash	Chaos	<i>Asym → 0</i>	<i>Asym → 0</i>	
2b	0.90	Crash	Crash	Crash	Crash	Crash	Crash	Chaos	<i>Asym → 0</i>	<i>Asym → 0</i>	
2a	0.85	Crash	Crash	Crash	Crash	Chaos	<i>Asym → 0</i>	<i>Asym → 0</i>	<i>Asym → 0</i>	<i>Asym → 0</i>	

which are not reproduced here. However, all display the same general pattern.

The dynamics of the model is significantly richer than can be seen from as crude a representation as Tables 3 and 4. Take for instance, the seventh column of Table 3 ($s=4$ $w=6$) for c between 0.95 and 1.0. The population rapidly crashes to extinction for c less than 0.993984. For $c=0.993984$ the population exhibits stable 13 year cycles; for $c=0.993985$, nine year cycles; for $c=0.99399$, 21 year cycles; $c=0.994$, 7 year cycles; $c=0.995$, 3 year cycles; $c=0.999$, 6 year cycles, and so on.

Winter is not inherently destabilizing as one might expect on the basis of the winter model lacking a non-trivial equilibrium point: an inherently cyclic summer model may be stabilized by a short winter.

Some cases were identified in which there were two alternative dynamic behaviors, depending upon the initial population size. Even then, the general pattern of increasingly complex dynamics with increased patchiness and longer winters is maintained. For instance, in the second column of Table 3 ($s=9$ $w=1$) with $c=0.84$ and $c=0.83$ the population can exhibit either chaotic dynamics (as listed) or stable 2 year cycles, given another initial population size. Similarly, the population in the sixth column ($s=5$ $w=5$) for $c=0.88$, crashes rapidly to extinction for some other initial population sizes. The magnitude of V does affect the magnitude of the peak in the winter model (Fig. 2), and thus affects the dynamics of the complete model.

Inspection of Table 3, and especially Table 4, shows occasional winks back and forth in the complexity (instability) of the dynamics with increasing patchiness or longer winters, that run counter to the general pattern of increasing complexity. These "windows", are related to arbitrary minutiae of how the population is passed among the different segments of the two models, and back and forth between the two. In the top row of Table 4 ($c=1.20$), for instance, the shift back and forth between "stable" and "4 year cycles" occurs because the summer model brings the population up to the flat section beyond $N=(2V/a)$ (Fig. 1). Thus, the population is mapped back to the same population size in the next time interval and the same value of N is always passed to the winter model.

An even number of iterations in the summer model ($s=8$, 6, 4) passes one value to the winter model, and an odd number of iterations ($s=7,5$) passes another. This is somewhat arbitrary. Considering the complexity involved in cobwebbing s times around the summer model, passing the result on to the winter model, cobwebbing w times in the winter model, sending the result back to the summer model, and so on, it is perhaps most surprising that there is such a clear trend as there is. (Recall that a stable population is one that returns to exactly the same size each year (i.e. after ten iterations of the model); a two year cycle returns the same population size after twenty iterations, and so on).

The existence of "windows" as described above, presents a case for caution in the interpretation of field observations, since this type of model can lead to such complicated patterns. Even in the summer model alone, it is possible (for example), by increasing the degree of patchiness, to change from a set of parameter values that yield 2 year cycles (case 3b; see Table 2), to n -cycles (case 4), to chaos (case 2b), and from there to stasis (case 2a). Finally, the non-trivial equilibrium point is lost when $h(a-m)<1$ and the population declines asymptotically to zero (summer growth rates are insufficient to counter-balance the decline during winter).

Discussion

Patchiness may be destabilizing

The reduced stability with increased patchiness seen in this model runs contrary to the conventional wisdom based on patch dynamics models (e.g. Levins 1970, Atkinson and Shorrocks 1983, Nisbet and Gurney 1982, Hastings 1990; see Kareiva 1990) and laboratory experiments (e.g. Huffaker 1958, Pimentel et al. 1963). The discrepancy is due to the distinction between coarse-grained and fine-grained patchiness. The present model is perhaps most applicable to a situation where individual animals move frequently between local patches of resources. In contrast, patch dynamics models pertain to patches on a larger spatial scale, where patches are typ-

ically larger than several home ranges and most individuals spend large periods of their lives within a single patch. In most metapopulation models and patch dynamic models, patchiness does not reduce resource availability (e.g. Hastings 1990). It is conceivable, however, that the present model applies generally to the effects of habitat loss and subdivision suffered by many animals at the hand of human beings. If this is so, we might expect the dynamics of such populations to become increasingly complex and erratic, and extinctions more frequent, as natural habitat is lost and the remnants are increasingly subdivided. In this connection, see the model by Burkey (1989), which although it is different from ours and incorporates a type of patchiness that is more akin to the patch models above, shows increasing probabilities of stochastic extinction as habitats are divided into more and smaller patches (even without any net loss of habitat area).

The duration of snow cover increases with latitude, but also from coast to inland. Snow tends to melt faster on exposed sites, producing a patchwork of freshly exposed sites with nutritious forage which may persist for long periods where the snow is deep. This correlates with the tendency of microtines to cycle more in the north and inland than in the south and coastal regions (Hansson and Henttonen 1985).

Longer winters may be destabilizing

Changing the model parameters in the way corresponding to moving further north, increases the model population's tendency to cycle. A similar result was obtained, without incorporating patchiness, by Stenseth and Fagerström (1986). This result coincides with the cyclical nature of northern small mammal population in Fennoscandia (e.g. Henttonen et al. 1985, Stenseth et al. 1985). Thus, longer winters, by affecting the amount of resources available to individuals (mediated by individual differences and territoriality), is a possible explanation for why more northern populations of microtine species are cyclical while southern populations are non-cyclical. Our result is reassuringly similar to that obtained by Kot and Schaffer (1984) with a logistic map of a bivoltine population. They found that strong seasonality was destabilizing, but that mild seasonality could have a pronounced stabilizing effect. The argument that increased cyclicity in the north is due to the relatively depauperate and specialized predator community (Hansson 1987, Henttonen 1985, Henttonen et al. 1987, Akçakaya 1992) is very compelling. Our argument and theirs are not mutually exclusive: For instance, longer winters may have a destabilizing effect on the prey species, that in interaction with the dynamics of a specialized predator may produce the characteristic 3–5 year cycles found in many northern microtine populations.

The frequently occurring deterministic population crashes seen in Tables 3 and 4 would probably be re-

placed by cycles or persistent chaos if the model's assumptions were relaxed. These crashes are partly due to our modeling the population as a closed system without dispersal and recolonization, and partly due to the strict assumption that absolutely no individuals survive the winter if N at the end of summer exceeds V_w/m_w (see Fig. 2). With such high population sizes at the end of the summer, the winter model maps the population trajectory directly to zero. Allowing some small differences between individuals in the ability to obtain food and survive during winter, or recolonization from outside, would instead lead to persistent cycles or quasi-periodicity. This would accentuate the dichotomy between stable populations in areas with relatively short winters and low degree of patchiness and cyclic populations in areas with relatively long winters and high degree of patchiness.

Although we have cast the seasonality in terms of winter and summer, the model may also apply to other types of seasonality, such as dry and wet seasons in the tropics.

Conclusion

The model demonstrates one way in which the longer winters in the north may be responsible for the propensity of many mammal populations to cycle at northern latitudes. Furthermore, deeper snow cover may increase the patchiness of resources throughout the spring and summer, as bare patches of vegetation are gradually exposed following snow melt on exposed sites (cf. Hansson and Henttonen 1985). A complete explanation of the Fennoscandian rodent cycles will undoubtedly be multifaceted and incorporate several different mechanisms (Stenseth and Ims 1993), but we think that this model may contribute to an increased understanding of the phenomenon and be profitably incorporated into a more comprehensive theory of small mammal dynamics.

A frequently mentioned and influential damper on the appeal of chaos theory in population dynamics, has been the claim that the population growth rate necessary to get chaos is so high that chaos seldom, if ever, will be observed in natural populations (e.g. Hassell et al. 1976; but see Turchin and Taylor 1992). In the present model, chaotic dynamics are encountered frequently, at quite "reasonable" parameter values. By coupling two simple models for a territorial species we have substantially lowered the threshold for chaotic dynamics. Both Table 3 and Table 4 seem to indicate, however, that the regions of parameter space wherein the population exhibits *persistent* chaotic dynamics (i.e. without going extinct) are relatively narrow. Populations in the chaotic domain typically crash to extinction quickly. Such populations would of course be difficult to observe in the field unless there were frequent recolonizations.

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References

- Akçakaya, H. R. 1992. Population cycles of mammals: evidence for a ratio-dependent predation hypothesis. – *Ecol. Monogr.* 62: 119–142.
- Atkinson, W. D. and Shorrocks, B. 1981. Competition on a divided and ephemeral resource: a simulation model. – *J. Anim. Ecol.* 50: 461–471.
- Burkey, T. V. 1989. Extinction in nature reserves: The effect of fragmentation and the importance of migration between reserve fragments. – *Oikos* 55: 75–81.
- Forney, K. A. and Gilpin, M. E. 1989. Spatial structure and population extinction: a study with *Drosophila* flies. – *Conserv. Biol.* 3: 45–51.
- Hansson, L. 1987. An interpretation of rodent dynamics as due to trophic interactions. – *Oikos* 50: 308–318.
- and Henttonen, H. 1985. Gradients in density variations of small rodents: the importance of latitude and snow cover. – *Oecologia* 67: 394–402.
- Hassell, M. P., Lawton, J. H. and May, R. M. 1976. Patterns of dynamical behavior in single-species populations. – *J. Anim. Ecol.* 45: 471–486.
- Hastings, A. 1990. Spatial heterogeneity and ecological models. – *Ecology* 71: 426–428.
- Henttonen, H. 1985. Predation causing extended low densities in microtine cycles: further evidence from shrew dynamics. – *Oikos* 45: 156–157.
- , Macquire, A. D. and Hansson, L. 1985. Comparisons of amplitudes and frequencies (spectral analysis) of density variations in long-term data sets of *Clethrionomys* species. – *Ann. Zool. Fennici* 22: 221–227.
- , Oksanen, T., Jortikka, A. and Haukialmi, V. 1987. How much do weasels shape microtine cycles in northern Fennoscandian taiga? – *Oikos* 50: 353–365.
- Huffaker, C. B. 1958. Experimental studies on predation: dispersion factors and predator-prey oscillations. – *Hilgardia* 27: 343–383.
- Kareiva, P. 1990. Population dynamics in spatially complex environments: theory and data. – *Phil. Trans. R. Soc. Lond. B* 330: 175–190.
- Kot, M. and Schaffer, W. M. 1984. The effects of seasonality on discrete models of population growth. – *Theor. Popul. Biol.* 26: 340–360.
- Levin, S. A. 1974. Dispersion and population interactions. – *Am. Nat.* 108: 207–228.
- Levins, R. 1970. Extinction. – *Lect. Math. Life Sci.* 2: 75–107.
- Łomnicki, A. 1988. Population ecology of individuals. – Princeton Univ. Press, Princeton, NJ.
- Nisbet, R. M. and Gurney, W. S. C. 1982. Modelling fluctuating populations. – Wiley, NY.
- Pimentel, D., Nigel, W. and Madden, J. 1963. Space-time structure of the environment and the survival of host-parasite systems. – *Am. Nat.* 97: 141–166.
- Rosenzweig, M. L. and Abramsky, Z. 1980. Microtine cycles: the role of habitat heterogeneity. – *Oikos* 34: 141–146.
- Stenseth, N. C. 1983. Causes and consequences of dispersal in small mammals. – In: Swingland, I. and Greenwood, P. J. (eds), *The ecology of animal movement*. Oxford Univ. Press, pp. 63–101.
- and Fagerström, T. 1986. Population density regulation in *Clethrionomys*: the effect of changing litter size and length of reproductive season. – *Acta Theriol.* 31: 365–382.
- and Ims, R. A. 1993. The biology of lemmings. Chapter 4. Academic Press.
- , Gustafsson, T. O., Hansson, L. and Ugland, K. I. 1985. On the evolution of reproductive rates in microtine rodents. – *Ecology* 66: 1795–1808.
- 1992. Models for predicting ecological change. – In: Sandlund, O. T., Hinder, K. and Brown, H. D. (eds), *Conservation of biodiversity for sustainable development*. Scandinavian University Press, Oslo, 137–154.
- Turchin, P. and Taylor, A. D. 1992. Complex dynamics in ecological time series. – *Ecology* 73: 289–305.
- Wiens, J. A., Stenseth, N. C., Van Horne, B. and Ims, R. A. 1993. Ecological mechanisms and landscape ecology. – *Oikos* 66: 369–380.
- 1992. Models for predicting ecological change. – In: Sandlund, O. T., Hinder, K. and Brown, H. D. (eds), *Conservation of biodiversity for sustainable development*. Scandinavian University Press, Oslo, pp. 137–154.

