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From individuals to population cycles: the role of extrinsic and intrinsic factors in rodent populations

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Abstract. Rodent population cycles have fascinated scientists for a long time. Among various hypotheses, an interaction of an extrinsic factor (predation) with intrinsic factors (e.g., sociality and dispersal) was suggested to lead to the generation of population cycles. Here, we tested this hypothesis with an individual-based model fully parameterized with an exceptionally rich empirical database on vole life histories. We employed a full factorial design that included models with the following factors: predation only, predation and sociality, predation and dispersal, and predation and both sociality and dispersal. A comprehensive set of metrics was used to compare results of these four models with the long-term population dynamics of natural vole populations. Only the full model, which included both intrinsic factors and predation, yielded cycle periods, amplitudes, and autumn population sizes closest to those observed in nature. Our approach allows to model, as emergent properties of individual life histories, the sort of nonlinear density- and phase-dependence that is expected to destabilize population dynamics. We suggest that the individual-based approach is useful for addressing the effects of other mechanisms on rodent populations that operate at finer temporal and spatial scales than have been explored with models so far.

Key words: density dependence; dispersal; individual-based model; phase dependence; population cycle amplitude; predator–prey interactions; social behavior; vole.

INTRODUCTION

Multiannual population cycles of rodents have fascinated population ecologists for a century (Krebs 1996, 2013, Boonstra et al. 1998, Korpimäki et al. 2004). Both extrinsic, e.g., predation and disease, and intrinsic factors, e.g., dispersal and sociality, have been used to explain these cycles. Predation has probably received the most support (Hanski and Korpimäki 1995, Hanski et al. (2001), Krebs 1996, Gilg et al. 2003), both from field experiments (Korpimäki and Norrdahl 1998, Korpimäki et al. 2002) and modelling studies (Hanski et al. 1991, Hanski and Korpimäki 1995, Turchin and Hanski 1997, Gilg et al. 2003). However, predation appears not to be a sufficient factor, as cycles were not affected by the removal of a key specialist predator in a manipulative large-scale experiment (Graham 2001, Graham and Lambin 2002, Oli 2003). Such empirical results have also been supported by models invoking delayed density-dependent mechanisms other than predation that readily generate

multi-annual population cycles (Turchin and Batzli 2001, Smith et al. 2006).

Most empirical research (e.g., Korpimäki and Norrdahl 1998, Korpimäki et al. 2002, Rémy et al. 2013) has focused on testing a single-factor hypothesis. However, a single factor, such as predation, may not be sufficient to produce the characteristic features of population cycles in small mammals (Lidicker 1988). Indeed, Krebs et al. (1995) demonstrated that food availability and predation interact to generate snowshoe hare cycles. Similarly, Pedersen and Greives (2008) showed that only an interaction of increased food availability with suppressed parasite pressure prevents population crashes in mice (*Peromyscus* spp.). For voles, analyses of long-term time series suggest that the extrinsic factor (predation) is likely to be enhanced by intrinsic factors, resulting in cyclic population dynamics (Stenseth et al. 1996).

Recently, Andreassen et al. (2013) synthesized a large body of empirical data on experimental vole populations and proposed how two intrinsic and one extrinsic factor could interact to shape population cycles. The essential intrinsic mechanisms were (1) *sociality*, which is modified by resource distribution in combination with phase-dependent turnover of dominant males impacting female reproductive success, and (2) negative density-dependent *dispersal*, which generates different population growth in the increase and decline phase

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of the cycle. The extrinsic factor necessary for the generation of cycles was assumed to be resident *specialist predators* acting in a delayed density-dependent manner (Andreassen et al. 2013).

Here we developed an individual-based mechanistic model (IBM) that describes the demographic processes implied by Andreassen et al. (2013). The model allows a quantitative assessment of intrinsic and extrinsic factors leading to the population cycles with the characteristics (i.e., topology sensu Ims et al. 2011) observed in natural populations. The IBM approach was deemed to be appropriate as it allowed us to (1) exploit high temporal resolution of individual life-histories contained in studies of experimental vole populations and (2) compare alternative models depicting different combinations of the factors supposedly leading to population cycles (Grimm and Railsback 2005). Compartments of the IBM describing the intrinsic mechanisms (sociality and dispersal) were based on results of a series of short-term field experiments conducted in controlled settings (i.e., the setting of an experimental model system; Ims et al. 1993) over more than two decades at Evenstad Research Station (Ims and Andreassen 2000, Andreassen and Ims 2001, Aars and Ims 2002, Andreassen et al. 2013). The information about the extrinsic factor was derived from the literature on vole–predator interactions in natural Fennoscandian populations. Thus the IBM allowed us to derive the expected long-term population dynamics of the experimental model system resulting from its intrinsic properties and addition of predation (by weasel *Mustela nivalis nivalis*) as an external factor. Specifically, we investigate the relative roles of the intrinsic and extrinsic factors by means of a factorial design yielding four models: predation only, predation and dispersal, predation and sociality, and predation and both dispersal and sociality. The results of these four models were expressed in a comprehensive set of metrics, which allowed comparison with time series data from natural populations of similar species living in the habitats with boreal seasonality. We demonstrated that only a combination of the extrinsic (predation) and both intrinsic (dispersal and sociality) factors yields the cyclic pattern that is the closest to the one observed for vole populations in the field.

METHODS

Model description

We used two alternative models with different implementations of predator population dynamics. In a simpler model, predator population dynamics was modeled phenomenologically, using the Type 2 functional response of the weasel; whereas in a more complex model it was modeled mechanistically (i.e., individual based). Qualitatively, the results obtained with both models were similar. The simpler model generated vole

cycles with a topology closest to the empirical population cycles, therefore we present it in the main text. The description and analysis of the more complex model are provided in Appendix S1. A full description of a simpler model following the ODD protocol (Overview, Design concepts, Details; Grimm et al. 2006, 2010) can be found in Appendix S2. The models were implemented in NetLogo (Wilensky 1999) and the codes are available in Supplementary Material.

The purpose of the model is to assess which factors (or factor combinations) lead to the population cycles characteristic of natural vole populations. Here we define a population cycle as a multi-annual fluctuation in population density with a statistically significant periodicity of peaks and lows. The goal of the model is achieved by contrasting alternative model versions by “switching off” some of the submodels in order to reflect how the four combinations of the intrinsic and extrinsic factors drive vole cycles. The modeled system closely imitates the experimental model system at Evenstad Research Station from which most of the parameters on root voles (*Microtus oeconomus*, northern strain) were derived. A system represents a 0.5-ha enclosure containing six habitat patches (225 m² each) submerged into the hostile matrix (Andreassen et al. 1998, Andreassen and Ims 1998, 2001, Ims and Andreassen 1999, Ims and Andreassen 2000, Huitu et al. 2003). The model advances in weekly time steps, with year consisting of 52 weeks. The duration of each simulation is 35 yr.

The voles in the model are unique individuals characterized by *age* (weeks), *stage* (weanling, <3 weeks old; subadult, 3–4 weeks old; and adult, >4 weeks), *sex* (female or male), *family* (identity of the family an individual belongs to), a Boolean variable indicating adult maturity (*mature*), and a Boolean variable *reproductive*, indicating whether the mature individual is reproducing or not. Seasonality is important in the life cycle of the voles: some demographic processes occur only in summer (Gliwicz 1990, Ergon et al. 2001, Korpimäki et al. 2004, Smith et al. 2006). Therefore we distinguish two seasons: summer (S, weeks 17–43; approximately 1 May–1 November) and winter (W, weeks 1–16 and 44–52). The majority of model processes for voles were parameterized with data on root voles collected at Evenstad Research Station. The only process for which no data for root voles were available is the effect of sociality on reproduction (Eq. 1), which was parameterized with data collected for *Myodes glareolus* in a similar model system setting at Evenstad Research Station.

The following vole demographic processes are modeled (Fig. 1).

Reproduction.—Occurs only in summer. The maximum number of reproductive adult females in the patch is limited to two because the reproduction of other females is suppressed (Gliwicz 1990). For each

reproductive female, the number of litters to be produced is drawn from the empirical Poisson distribution (H. Andreassen, *unpublished data*), and then one litter is produced every three weeks (Ims 1997). The number of weanlings in each litter is a function of the number of reproductive females in the patch, reflecting the kinship effect (Lambin and Yoccoz 1998) on reproductive output (as demonstrated for *M. glareolus* by Rémy 2011, Chapter III)

$$\text{Num}_{\text{wean}} = \exp(\alpha_{\text{rep}} + \beta_{\text{rep}} * \text{overlap} + U[0, b_{\text{rep}}]); \quad (1)$$

where α_{rep} and β_{rep} are an intercept and slope, $U[0, b_{\text{rep}}]$, is a uniform distribution with parameters 0 and b_{rep} , which is used to incorporate the among-female and within-season variation (Table 1), and overlap is the percentage of home range overlap for reproductive females, which is set to 50% if two reproductive females are present in the patch and 0% if only one female is present or no sociality in reproduction is included (for testing the hypothesis of no sociality effect on cycle generation). The value Num_{wean} obtained with Eq. 1 is rounded to the integer.

Survival.—In winter, the survival is negatively density dependent so as to yield the population rate of change during winter estimated by Aars and Ims (2002). Aars and Ims (2002) ascribed the negatively density-dependent winter population growth rate to winter recruitment. However, since we do not model reproduction during the winter period (due to the lack of data and knowledge to parameterize it; Krebs 2013), we implement winter survival as being negatively density dependent. In summer, the baseline survival probability is fixed, irrespective of the stage, age, and sex of individuals (s_{sum} , Table 1). In case of the death of the reproductive female, all of her weanlings die (Andreassen and Gundersen 2006). If the sociality submodel is activated, then in case of a male turnover (the death of the dominant male or its replacement by another adult male), the survival probability of a female and her weanlings decreases (s_f and s_w respectively; Andreassen and Gundersen 2006).

Dispersal.—Only adults and subadults disperse, and this occurs only in summer. The emigration probability is sex, stage, and density dependent (Andreassen and Ims 2001). An emigrant is first confronted with dispersal mortality, and then checks five other patches in the enclosure until it finds the one that does not contain an adult of the same sex as its own. It then settles in this patch and becomes dominant (if it is a male) or reproductive (if it is a female). If such patch does not exist, the individual returns to its patch of departure.

Maturation.—Maturation probability is decreasing as a function of the week number (Gundersen and Andre-

assen 1998): voles have probability of one to become mature at week 17, and this probability decreases by week 39.

The predation is modeled using the predator–prey model commonly used for voles. It represents a specialist predator (i.e., *M. nivalis nivalis*) exhibiting a Type 2 functional response (see Hanski et al. [1991], Hanski and Korpimäki [1995], Turchin and Hanski [1997] for parameter estimates used). For the sake of computational efficiency, predation is modeled once a year (cf. Stenseth 1999) in week 44 starting from the fifth year of the simulation (to let the prey population establish). The predation submodel is implemented in two steps. In the first step, predator population density is updated using the predator growth rate (R_{pred}). It is calculated in one of two ways, depending on the vole population density relative to the critical prey density below which the predator cannot reproduce (N_{crit})

$$R_{\text{pred}} = \exp\left(S_{\text{max}} \cdot \left(1 - \frac{Q \cdot P}{N}\right)\right) \text{ if } N > N_{\text{crit}}; \quad (2)$$

$$R_{\text{pred}} = \exp(d_{\text{low}}) \text{ if } N \leq N_{\text{crit}}; \quad (3)$$

where S_{max} is predator intrinsic rate of increase, P and N are the predator and vole population densities, respectively, and Q is the equilibrium prey–predator ratio (Table 1). If vole population density is below N_{crit} , there is no reproduction and the predator population density declines exponentially with the predator growth rate d_{low} (Hanski and Korpimäki 1995; Table 1). We included the possibility for predators to prey on alternative prey by setting the fixed lower limit for predator population density, $P_{\text{min}} = 0.005$ individuals/ha, i.e., modeling the predator refuge sensu Hanski and Korpimäki (1995).

In the second step, the number of prey to be killed by predator is determined only if the vole population density is higher than N_{crit} , as following:

$$n\text{kill} = \exp\left(\frac{c \cdot P}{(N + D)}\right) \quad (4)$$

where $n\text{kill}$ is the number of voles to be preyed on, c is the maximum per capita predation rate, P and N are the predator and vole population densities, respectively, and D is the predation half-saturation constant (Table 1). If the estimated number of voles to be preyed on ($n\text{kill}$) is lower than the vole population density (N), then $n\text{kill}$ number of voles are killed, otherwise the prey population can only be reduced as far as N_{crit} , such that N_{crit} acts as a refuge population that is invulnerable to predation. The voles to be killed are chosen randomly.

TABLE 1. Model parameters, their description, values, and sources from which they were obtained.

Parameter	Description (units)	Value	Range		Source
			Min	Max	
Survival					
s_w	survival rate of weanlings due to male turnover (week ⁻¹)	0.38	0.22	0.58	Andreassen and Gundersen (2006)
s_f	survival rate of reproductive females due to male turnover (week ⁻¹)	0.87	0.82	0.92	Andreassen and Gundersen (2006)
s_{sum}	baseline survival rate in summer (week ⁻¹)	0.98	0.96	1	H. P. Andreassen, unpublished data
R_{max}	winter maximum population growth rate (week ⁻¹)	0.4	0.3	0.6	Aars and Ims (2002)
K_{win}	carrying capacity in winter (individuals/patch)	6.5	4.5	8.5	Aars and Ims (2002)
Dispersal					
α_{em}	intercept in the emigration equation	-1.247	-1.965	-0.529	Andreassen and Ims (2001)
β_{sex}	effect of sex in the emigration equation	-0.554	-1.004	-0.104	Andreassen and Ims (2001)
β_{stage}	effect of stage in the emigration equation	0.221	-0.256	0.698	Andreassen and Ims (2001)
β_{dens}	effect of density in the emigration equation	-0.846	-1.092	-0.601	Andreassen and Ims (2001)
β_1	coefficient for sex × stage interaction in the emigration equation	-1.502	-1.889	-1.114	Andreassen and Ims (2001)
β_2	coefficient for density × stage interaction in the emigration equation	0.493	0.234	0.753	Andreassen and Ims (2001)
β_3	coefficient for density × sex interaction in the emigration equation	0.287	0.039	0.536	Andreassen and Ims (2001)
b_{em}	maximum in the uniform distribution for the random effect in the emigration equation	0.814	–	–	Andreassen and Ims (2001)
s_{disp}	dispersal survival rate (week ⁻¹)	0.94	0.9	0.96	H. P. Andreassen, unpublished data
Reproduction					
$numlit_{Pois}$	lambda for Poisson distribution to define the number of litters produced per female	3.12	2	5	H. P. Andreassen, unpublished data
Min_{numlit}	minimum number of litters	1	–	–	H. P. Andreassen, unpublished data
Max_{numlit}	maximum number of litters	5	–	–	H. P. Andreassen, unpublished data
Weeks	number of weeks between two reproduction events	3	–	–	Ims (1997)
α_{rep}^\dagger	intercept in the reproduction equation	0.775	0.492	1.058	Rémy (2011)
β_{rep}^\dagger	effect of sociality in the reproduction equation	0.011	0.004	0.018	Rémy (2011)
b_{rep}^\dagger	maximum in the uniform distribution for the random effect in the reproduction equation	0.45	–	–	Rémy (2011)
Max_{wean}	maximum number of weanlings	6	–	–	Ims (1997)
Predation					
S_{max}	predator intrinsic rate of increase (yr ⁻¹)	2.8	2.4	3.2	Hanski and Korpimaki (1995)
Q	predator–prey ratio constant (voles/predator)	42	40	100	Turchin and Hanski (1997)
c	maximum consumption per predator (voles·yr ⁻¹ ·predator ⁻¹)	200	150	300	Hanski and Korpimaki (1995)‡
d_{low}	predator mortality rate when prey is scarce (yr ⁻¹)	-4	-5	-2	Hanski and Korpimaki (1995)§
N_{crit}	critical prey density for predator reproduction (voles/ha)	30	20	80	Turchin and Hanski (1997)¶
D	predation half-saturation constant (voles/ha)	6	4	12	Turchin and Hanski (1997)
P_{min}	lower limit for a predator population density (predator/ha)	0.005	–	–	Hanski and Korpimaki (1995)

Notes: Model parameters are grouped under the demographic processes that they act upon. For each model parameter, we also report lower extreme (Min) and upper extreme (Max) values that were used for the sensitivity analysis.

†Demographic parameters parameterized with the data on *Myodes glareolus* (unlike the rest of the parameters, which are derived for *M. oeconomus*).

‡Maximum consumption per predator was adjusted because predation occurs only once a year.

§Similar to the d_{high} estimated by Hanski and Korpimaki (1995) of -5.

¶Critical prey density is slightly higher than estimated by Turchin and Hanski (1997): 14 voles/ha.

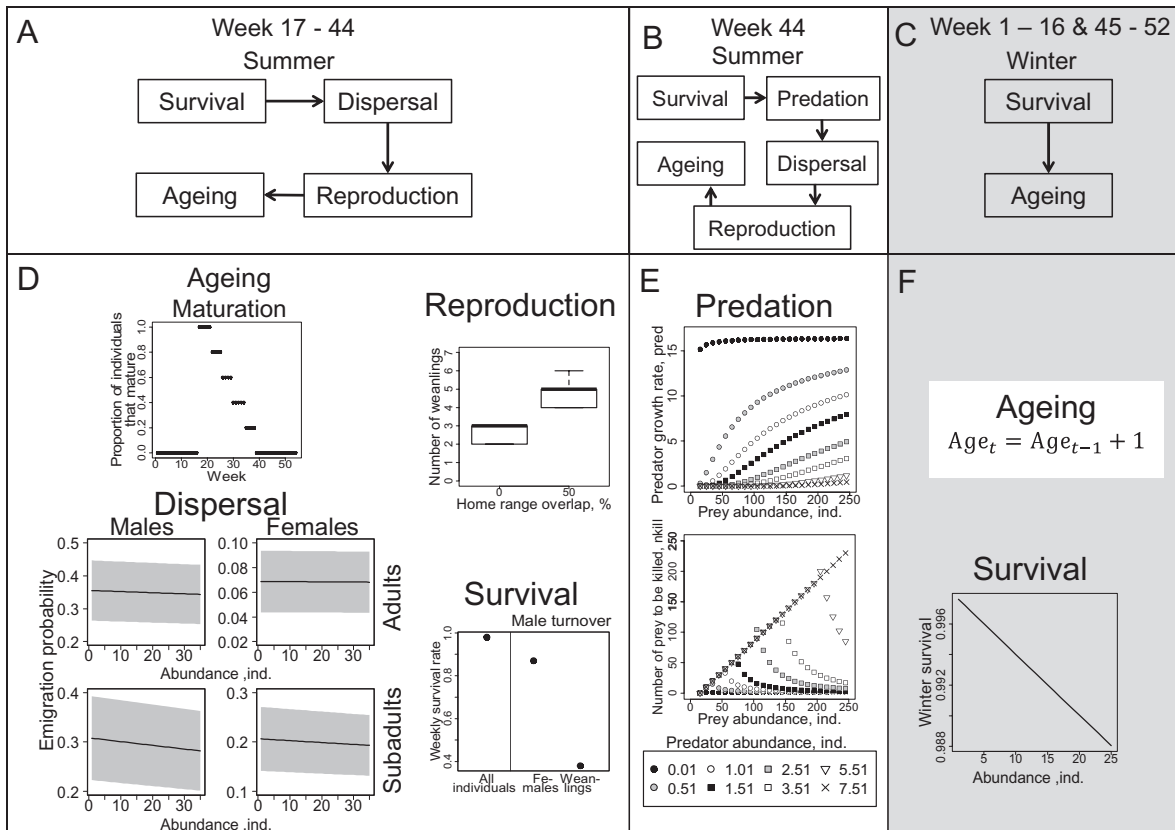


FIG. 1. Schematic representation of the model structure. Scheduling and timing of the major processes is shown in a top row separately for each season: (A) summer; (B) week 44; (C) winter. Processes occurring during the summer season are shown on a white background, and those occurring in winter are shown on a gray background. The bottom row presents more details on the processes specified in the upper row: (D) shows how dispersal, reproduction, survival, and maturation (a submodel within “ageing”) of voles are implemented in the summer; (E) demonstrates how predation affects vole populations in week 44; and (F) shows details on winter survival and ageing. Ageing is the same in summer and winter seasons and is therefore shown on the white background in (E), but maturation occurs only in summer.

Assessing relative roles of extrinsic and intrinsic factors

We tested models representing the following combinations of extrinsic and intrinsic factors: (1) predation only (extrinsic factor); (2) predation and dispersal (intrinsic factor); (3) predation and sociality (intrinsic factor); (4) full (including predation and both intrinsic factors). As suggested by Andreassen et al. (2013), the sociality effect comprises (1) negative effects of male turnover on the survival of weanlings and reproductive females and (2) increased reproductive output due to females’ sociality. Therefore, these two processes must be activated to reflect sociality in the model.

To compare the population dynamics generated by the different models with that of natural vole populations, each model was run 1000 times for 35 yr (or until the population went extinct) and the first 5 yr were discarded (to omit the vole population prior to weasel presence). We monitored the vole population size in week 44 (1 November), which corresponds to the period in autumn when most natural populations

are monitored (Stenseth 1999, Krebs 2013) and simulated (Turchin and Hanski 1997). We used the following metrics to describe the multiannual vole population cycles:

1. *Autumn population density.* The mean autumn population densities of *Microtus* voles in habitats from which the life-history data for model parameters were derived range between 70–200 individuals/ha (Aars and Ims 2002, Huitu et al. 2003). So, the models that reproduce these values would resemble realistic behavior.
2. *Periodicity.* Models are expected to produce the cycles with the typical periods of the natural populations: 3–5 yr (Stenseth 1999, Korpimäki et al. 2004, Cornulier et al. 2013). Periods were obtained from the autocorrelation functions (acf) of the autumn population sizes. We define the period as either (1) a time lag at which the largest positive autocorrelation is >2 SE of acf or (2) twice the time lag at which the largest

negative autocorrelation is < 2 SE of acf (cf. Turchin and Hanski 1997, Turchin 2003). If no significant correlations are found, the population is considered to be non-cyclic. Due to model stochasticity, the period lengths vary among the simulations; therefore, we focus on the distribution of periods.

3. *Amplitude.* We calculated amplitude as the ratio of maximum to minimum autumn population size observed in each simulation (Hanski et al. 1991, Hanski and Korpimaki 1995). According to Hanski et al. (1991), the median amplitude observed for vole populations in Norway is 13.5 (5th and 95th percentile, 7 and 41, respectively, mean = 20.1, SD = 14.2). We aim at reproducing a set of summary statistics on amplitude, reflecting both its mean and variability.
4. *Population growth rate.* We extracted yearly population growth rates (ln-transformed) from all simulations that exhibited cycles and calculated summary statistics on these growth rates. These statistics from the model-generated cycles were compared with the equivalently computed statistics (median = 0, 5th and 95th percentiles, -2.543 and 2.265, respectively, SD = 1.389) from Fennoscandian vole population time series (>20 yr) exhibiting cycles. The time series were obtained from Cornulier et al. (2013), using autumn population counts, corrected for the sampling effort, and to which a constant (1) was added to avoid zero observations (Stenseth 1999). Visually, half of the empirical growth rate time series showed

unimodal distributions, whereas the other half was characterized by nonnormal, rather tri-modal distributions (Fig. 2). Our interest was twofold: (1) detect which model can reproduce the summary statistics on population growth rates resembling the empirical ones and (2) which model reproduces growth rate distributions different from unimodal.

To compare model-estimated summary metrics with empirical ones we used simulation runs that resulted in a stationary population dynamics (defined as simulations with a mean of the ln-transformed population growth rates ≤ 0.1 and ≥ -0.1). The proportion of simulations with stationary dynamics was 71.4% for the model with predation only, 96.2% for the model with predation and dispersal, 82% for the model with predation and sociality, and 93.4% for the full model.

Sensitivity analysis

We used an improved version of the elementary effects method (Morris method; Morris 1991, Campolongo et al. 2007) to identify the most sensitive parameters. 22 model parameters were varied across five levels using central values from model simulations, as well as four additional levels: lower extreme, lower median, upper extreme, and upper median (Table 1, Appendix S3). The experimental design consisted of 50 trajectories, yielding 50 elementary effects per parameter obtained for a total of 1150 model runs

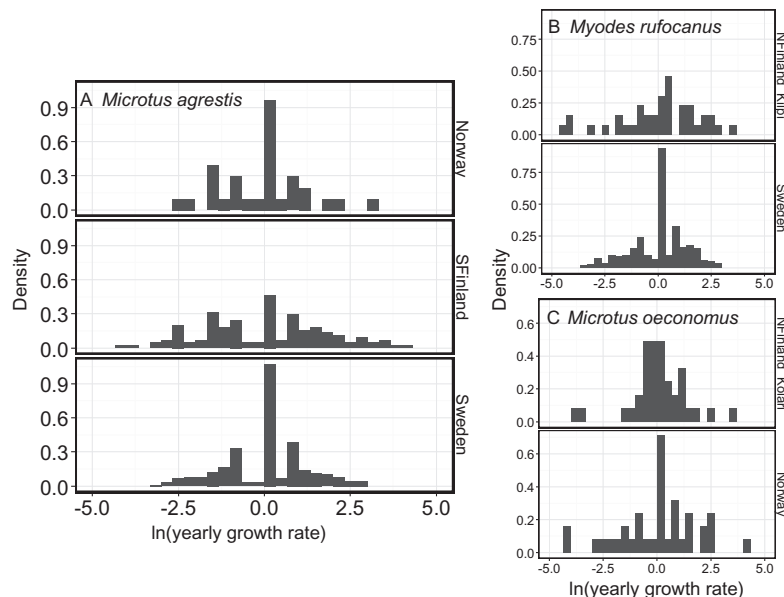


FIG. 2. Density histograms of the yearly population growth rates (natural-log-transformed) calculated using autumn population densities (derived from the trapping indices) for (A) *Microtus agrestis*, (B) *Myodes rufocanus*, and (C) *M. oeconomus*. Data from Cornulier et al. (2013). Each panel shows data for a population (sensu Cornulier et al. 2013), with locations as following: Sweden, Sweden, Umeå; SFinland, South Finland, Heinola; NFinland_Kolari, North Finland, Kolari; NFinland_Kilpi, North Finland, Kilpisjärvi; Norway, Norway, Finse.

($50(22 + 1)$). The sensitivity of the model to each parameter was evaluated using the mean of the absolute values of elementary effects (μ^*), which is a measure of the overall impact of a parameter on the output; and the standard deviation of the elementary effects values σ , which measures higher order effects (nonlinear and/or interaction effects; [Campolongo et al. 2007](#)). As output, we used two groups of variables, describing different aspects of population dynamics: (1) the effect on overall vole population dynamics (mean and SD of autumn population size) and (2) the cyclicity of time series (amplitude and period of the cycles). Sensitivity analysis was performed with the package sensitivity in R (R Core team 2013; [Thiele et al. 2014](#)).

RESULTS

Performance of alternative models vs. empirical patterns

Two models yielded autumn population densities that most closely approximated those of the vole populations in the field (Table 2, Fig. 3): the full model (mean \pm SD of 158 ± 108.4 individuals/ha), somewhat closer than the model with predation and dispersal (87.5 ± 56 individuals/ha). The full model version incorporating predation and both intrinsic factors

yielded period cycles that were closer to those found in natural vole populations compared with other models: 45.6% of the simulations produced cycles of 3–5 yr (Table 2, Fig. 3). Exclusion of one of the intrinsic factors (either dispersal or sociality) resulted in shorter periods, the majority of which were 2-yr cycles (Table 2, Fig. 4). The amplitude was the highest in the full model version with a median value closer to the empirically observed one (11.5 vs. 13.5, Table 2), as opposed to much lower medians obtained with other models (Figs. 3 and 4). However, none of the models reproduced the high variation of amplitudes observed in the field (empirical SD = 14.2), or extreme values: the 95th percentile was 23 for the model with predation only, 17.7 for the model with predation and sociality, 17.5 for the model with predation and dispersal, and 16.9 for the full model (40.8 in the field data). All model versions except for the one including predation only yielded multimodal distributions of the population growth rates, resembling the nonnormal distributions observed in half of the empirical time series (Figs. 2 and 3). Interestingly, the model with predation and sociality yielded a bimodal distribution of the population growth rates, as opposed to the trimodal distribution obtained with both full model and the model with predation and dispersal. However, only the full model was able to reproduce the variation

TABLE 2. Performance of models against four empirical patterns summarizing the multiannual vole population cycles.

Pattern	Model version				Empirical values
	Full	Predation	Predation + Dispersal	Predation + Sociality	
Autumn population density (individuals/ha)					
Mean	158	30.5	87.5	46.1	70–200
SD	108.4	10.2	55.8	27.3	
25th percentile	30	26	30	30	
75th percentile	248	32	136	56	
Maximum	446	102	250	294	
Periodicity					
Runs with no cycles (%)	10.5	46	5.7	15.9	
Runs with 2-yr cycles (%)	40.8	18.5	70.5	53	
Runs with 3-yr cycles (%)	28.1	2.5	19.9	21.1	
Runs with 4-yr cycles (%)	17	5.5	1	1.9	
Runs with 5-yr cycles (%)	0.5	6	2.4	4	
Runs with >5-yr cycles (%)	3.1	21.5	0.5	4.1	
Amplitude					
Mean	12.4	6.6	8.4	7.5	20.1
SD	4.9	6.1	6.1	7.2	14.2
Median	11.5	4.3	6.5	5.6	13.5
5th percentile	9.9	2.4	5.5	2.9	7
95th percentile	16.9	23.0	17.5	17.7	40.8
ln(yearly population growth rate)					
Median	0.2064	0.0000	0.1391	0.0000	0.000
SD	1.6868	0.4316	1.3203	0.6978	1.389
5th percentile	-2.3354	-0.6931	-1.7693	-1.2234	-2.543
95th percentile	2.1823	0.6242	1.6740	1.0296	2.265

Notes: The last column shows the statistics from empirical data (when available).

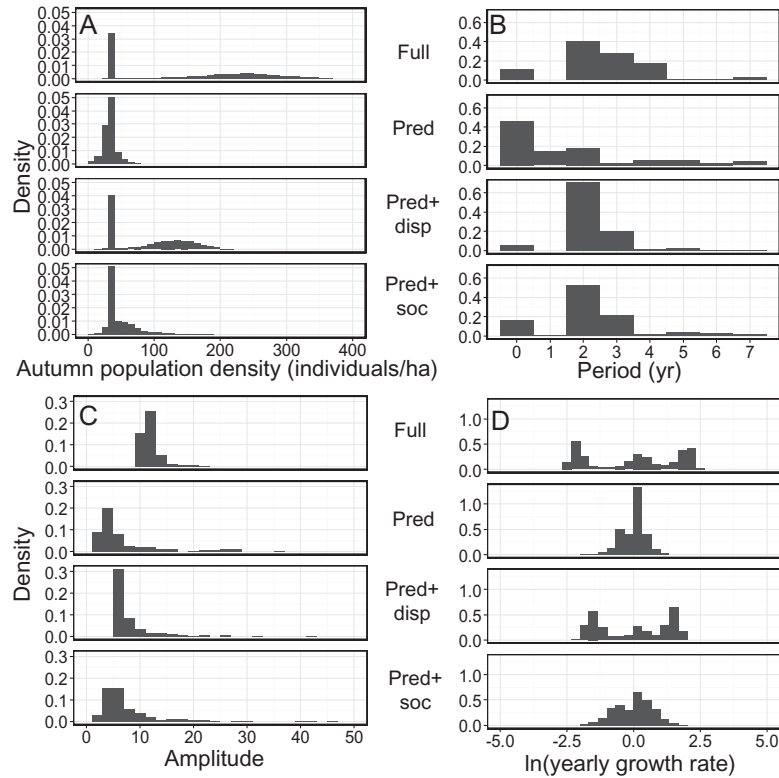


FIG. 3. Performance of the four models against the four patterns summarizing the empirical multiannual vole population cycles: (A) autumn population density, (B) cycle period, (C) amplitude, and (D) annual population growth rates (ln-transformed). Models reflecting the prevailing hypotheses about the drivers of vole cycles are: full (predation and both intrinsic factors), Pred (predation only), Pred + disp (predation and dispersal), and Pred + soc (predation and sociality). Only the full model version yields the amplitude and period of the cycles closest to those characterizing natural populations.

and extreme values most similar to those observed in the field, whereas other model versions underestimated the variation of population growth rates (Table 2).

Sensitivity analysis

When using as output the variables that relate to vole population dynamics (mean and SD of autumn population size), the model was most sensitive to summer survival parameter (s_{sum}), predator-prey ratio constant (Q), and two parameters related to reproduction (β_{rep} and $numlit_{Pois}$, Fig. 5). However, when the model output was quantified by variables describing cyclicity (cycle amplitude and period), the model was sensitive to parameters that are acting on both intrinsic, i.e., sociality (α_{rep} , β_{rep}) and dispersal (s_{disp} , α_{em} , β_{sex}); and extrinsic, i.e., predation (Q) processes. Such higher sensitivity of cyclicity to parameters reflecting both intrinsic and extrinsic processes highlights their importance in regulating vole population cycles. Importantly, most of the parameters that largely affected either of the output variables were involved in higher order effects, such as interactions and nonlinear effects (Appendix S3).

DISCUSSION

In summary, our results highlight that, in addition to predation, other aspects of vole ecology, sociality and dispersal, can play a key role in regulating vole population dynamics. Our study goes further than most of the modeling exercises on vole cycles to date in that it explicitly distinguishes the role and importance of each demographic factor. The majority of vole population models are either differential equation models in continuous time, depicting the vole population dynamics by means of aggregated parameters such as carrying capacity and intrinsic rate of increase, or stage-based models, which discriminate each stage of the population life cycle (Hanski and Korpimaki 1995, Turchin and Hanski 1997, Oli and Dobson 1999). While tractable, these models do not easily allow assessing the effect of each separate factor (either intrinsic or extrinsic) on the vole population dynamics. On the contrary, this is inherent to our modelling approach, which permits one to assess the effect of sociality, dispersal, and predation either separately or in combination on the resulting vole population sizes and, respectively, growth rates. The description of population dynamics in differential equation models

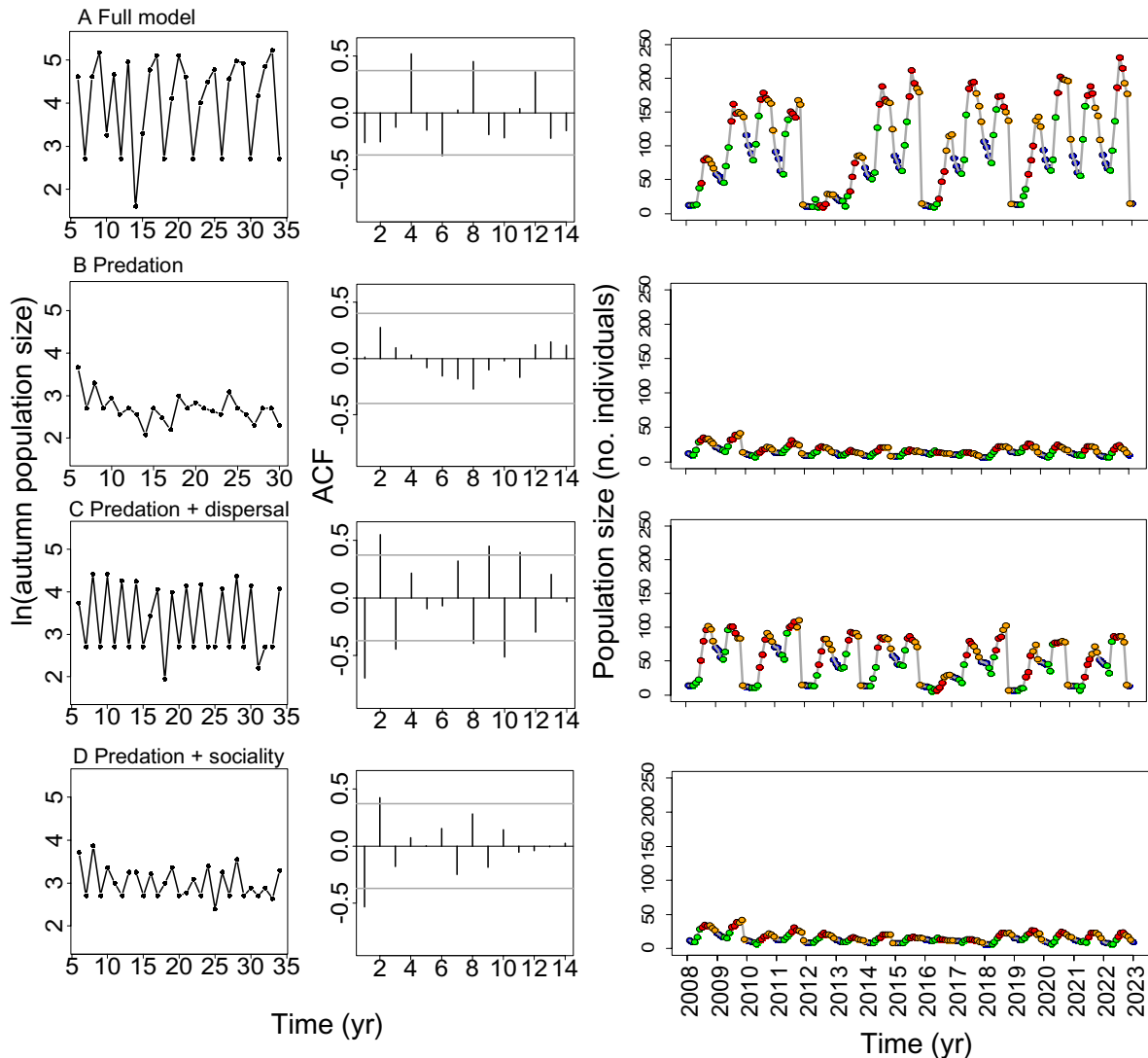


FIG. 4. Examples of the representative simulation runs for each of the tested models, indicated in rows: (A) full model, (B) predation only, (C) predation and dispersal, and (D) predation and sociality. The left column shows the time series for the observed autumn population size (natural-log transformed); the middle column shows the autocorrelation function for the corresponding time series; and the right column shows the monthly population size, with each point corresponding to the vole population size at the first day of the month (for years 8–23). In the right column, the point colors represent different seasons: blue, winter (Dec, Jan, and Feb); green, spring (Mar, Apr, and May); red, summer (Jun, Jul, and Aug); and orange, autumn (Sep, Oct, and Nov); and the date labels are set against 1 January each year.

is highly aggregated, thus making it difficult to explicitly tease apart the role of intrinsic and extrinsic drivers of the cycles. And, although different extrinsic factors may be modeled with differential equations (e.g., effect of plant quality, Reynolds et al. 2012), one cannot disentangle the effects of intrinsic factors, such as sociality and dispersal on the growth rate of the vole population.

By using constituents (“building blocks”) of the vole demography derived from an empirical model system subjected to boreal seasonality, we found that predation without inversely density-dependent dispersal and social mechanisms leads to 2-yr cycles in the majority of

the simulation runs, and to amplitudes that are much lower than those reported from the field. Similarly, Dalkvist et al. (2011), using an individual-based model to explore the effect of habitat fragmentation and predation on vole cycles, failed to produce amplitudes in the range of those observed in the field (the maximum amplitude obtained by Dalkvist et al. [2011] was 4). Our findings, therefore, provide a support for the suggestion by Stenseth et al. (1996) that previous aggregated models reproduced the period and amplitude of the empirical vole cycles correctly because they already implicitly incorporated the intrinsic vole mechanisms in form of aggregated parameters, such as vole

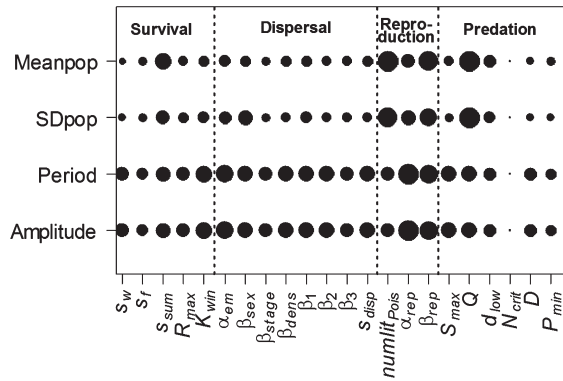


FIG. 5. Results of sensitivity analysis using Morris (elementary effects) method. All 22 parameters were grouped into categories representing the processes they are acting on in the model: survival, dispersal, reproduction, and predation. For each parameter, we computed the mean of the distribution of the absolute values of elementary effects (μ^*) using the following output variables: mean autumn population size (44th week; Meanpop), SD of the autumn population size (SDpop), cycle period (Period), and amplitude. The circles' radius is proportional to μ^* values. Parameters are defined in Table 1.

intrinsic rate of increase and carrying capacity. We further underline the importance of interactions between intrinsic and extrinsic factors for generating vole cycles by running simulations that only included intrinsic

factors. These simulations failed to reproduce the empirical patterns on vole cycles (results not shown), highlighting the need to focus on the interaction of the two types of factors to represent vole populations. Moreover, the interaction among social factors themselves seems to be important for the formation of the population cycles characteristic of the vole populations in the field. Indeed, compared to the full model, the models that excluded one of the social factors (either infanticide or increased reproductive output due to female sociality) resulted in much lower proportions of simulations with the empirically observed periods of the cycles (Fig. 6).

Our conclusion about the importance of both intrinsic and one extrinsic factor for the formation of the characteristic vole population pattern is further supported by the results of the sensitivity analysis, which demonstrate that the inspected model output is sensitive to the parameters involved in all of these processes. Such importance of certain parameters to the model output, however, indicates that the conclusions may change if the values used for those parameters were to change. In this light, the values for predator-prey ratio (Q) and the effect of female sociality on reproductive output (β_{rep}) deserve more attention, as these parameters affected all four output variables we measured. We therefore underline the need for

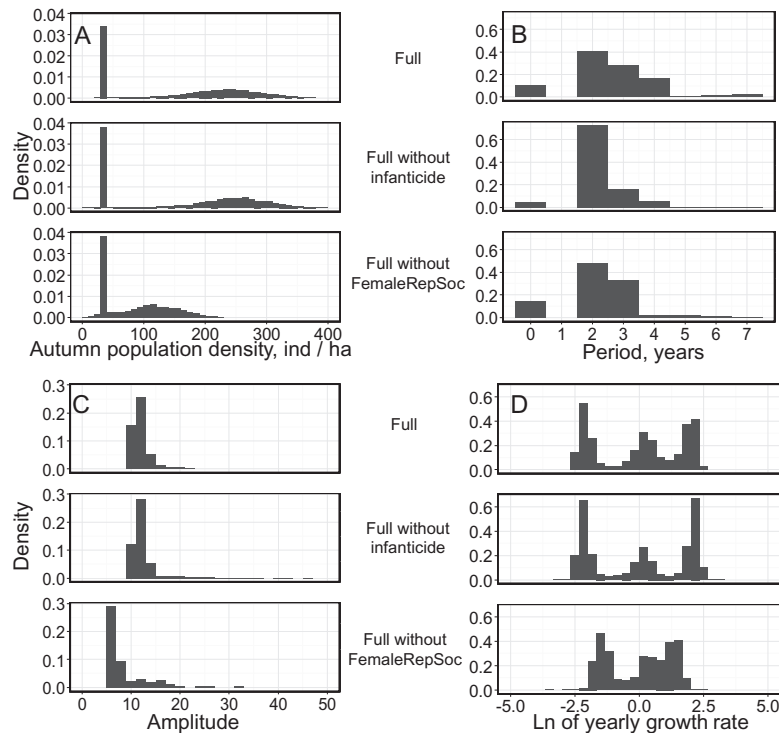


FIG. 6. Contrasting full model version with the versions excluding one of the social factors: the model without infanticide (Full without infanticide) and the model without the social component in female reproduction (Full without FemaleRepSoc). The models are compared using the four patterns summarizing the empirical multiannual vole population cycles: (A) autumn population density; (B) cycle period; (C) amplitude; and (D) annual population growth rates (ln-transformed).

further research on the effects of female sociality on vole population dynamics, as this was the only submodule parameterized with the data on a different species, *M. glareolus*. Moreover, unlike the majority of the parameters used in the model, predator–prey ratio (Q) is notoriously difficult to estimate from the field data, the main reason being that this parameter stems from theoretical demographic models, and no conceivable manipulative experiments or field measurements exist that would enable estimation of Q . On the other hand, the model was not exceptionally sensitive to winter survival parameters, justifying our modeling decision to represent the density-dependent winter population growth in survival and not in reproduction because of the data scarcity.

The use of a mechanistic model with a fine temporal resolution allowed us to describe the within-season population dynamics. This, in turn, permits one to explore the within-year timing of all population cycle phases. The low phase according to simulations usually lasts one winter (Fig. 4A, right column), which corresponds to all models developed to date, where the low phase does not last longer than a year (Hanski and Korpimäki 1995, Turchin and Hanski 1997, Boonstra et al. 1998, Gilg et al. 2003, Smith et al. 2006, Dalkvist et al. 2011). However, as suggested by Boonstra et al. (1998) and Boonstra and Krebs (2012), natural vole populations exhibit longer low phases, lasting 1–3 yr (on average 1.5 yr). On the one hand, it is possible that the model predictions correctly reflect the natural processes, but the field observational studies fail to correctly measure the very small increases in population size in some years following the low phase (e.g., Fig. 4A, right column, 2012–2013), leading to the apparent extended low phases. If this is the case, measurement of such low densities is indeed difficult in the field and likely leads to an underestimation of the real population densities and growth rates (Steen and Haydon 2000). On the other hand, and more likely, the fact that our model produces much shorter low phases than found in nature signals the omission of some crucial factor(s).

Many simulations produced by our model that included a mechanistic description of the predator (Appendix S1) successfully reproduced the low phases longer than 1 yr. This suggests the importance of using a detailed description of predator population dynamics to better understand temporal processes in predator–prey systems. However, this model with mechanistic predator description performed less well than the phenomenological model in reproducing the periods of the cycles and growth rate distributions. In contrast, it reproduced amplitude variability closer to that observed in natural vole populations, which was not possible with the phenomenological model presented in the main text (Appendix S1). We suggest that a wider spectrum of periods generated by the mechanistic model may be a result of a higher parameter uncertainty

inherent in parameters on weasel population dynamics, which were obtained from very different literature sources and collected under widely varying environmental conditions (Jedrzejewska 1987, Sheffield and King 1994, Sundell et al. 2000, McDonald and Harris 2002). The poor availability and quality of the weasel demographic data underscores the importance of the future empirical research directed at addressing these gaps. Overall, the model with the mechanistic predator description deserves further attention as it may shed light on the mechanisms acting on both prey and predator at much finer temporal resolution than studied to date.

Here, we used pattern-oriented modeling, a model selection technique that is well established in individual-based modeling (Wiegand et al. 2003, Grimm et al. 2005, Railsback and Grimm 2012). It is based on contrasting alternative model versions against a set of multiple patterns summarizing different aspects of the natural system that is modeled. Such use of multiple patterns is advantageous in a sense that despite many models could reproduce one single pattern correctly, it is more unlikely that the model with wrong structural assumptions will reproduce several different patterns (Grimm and Railsback 2005). Nowadays, more sophisticated approaches to model selection in individual-based modeling are available, which are based on the likelihood of different model versions (POMIC [Piou et al. 2009], synthetic likelihood approach [Wood 2010]). In our case, the use of synthetic likelihood approach was prevented by the lack of a single data set from which all four summary statistics could be extracted. Indeed, the most extensive compilation of time series of cyclic rodent populations to date provided by Cornulier et al. (2013) reports raw trapping indices, from which only a limited set of relevant statistics can be derived. On the other hand, to apply POMIC, one has to be explicit about the weights of each pattern, and there is no data available to judge this. Moreover, this approach requires exact replication of the sampling procedure as it is conducted in the field, and this is not possible due to the lack of data on the catching probability during the trapping sessions. Therefore, it would be desirable to collect empirical long-term population size estimates (not based on trapping indices) for voles in the field to facilitate an application of such more comprehensive techniques in the future.

It is important to stress that the patterns we used are as specific as possible to the experimental study system to which a model was parameterized (i.e., a system with boreal seasonality). This is a precondition for contrasting the output of the model parameterized with the life history data collected in these settings. This implies, however, that the conclusions we derive are applicable within these settings, i.e., the scope of *Microtus* populations living in productive habitats with boreal seasonality. Therefore our findings

may serve as only one possible interpretation of the multi-factor hypothesis, when looking more broadly at the phenomenon of vole cycles observed elsewhere. And, it is possible that any other process resulting in the 2nd order dynamics (Stenseth 1999) can act as an extrinsic factor in reality, e.g., pathogen or availability of food resources.

Lidicker (1988) suggested that if a phenomenon cannot be explained by a single-factor hypothesis, this phenomenon likely requires a multi-factor explanation. Previous studies have found experimental support for multi-factor hypotheses involving two extrinsic factors; food and predation in case of snow-shoe hare cycles (Krebs et al. 1995) and parasites and food in case of population crashes of mice (Pedersen and Greives 2008). In this study, we have shown by means of empirically based modeling that three factors, one extrinsic and two intrinsic, were needed to provide a realistic description of vole cycles observed in nature.

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