# ALTERNATIVE PREY THAT DECREASES VOLE POPULATION CYCLICITY: A SIMULATION STUDY BASED ON FIELD DATA

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#### ABSTRACT

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A model of a one predator-two prey system is presented. Different versions of the model are simulated using parameter values based on field data from a study of a vertebrate community in southern Sweden. Some versions and sets of parameter values produce a cyclic system when only one prey (based on vole-like parameter values) is included but a rather constant ('stable') system when both prey types are included. This supports the hypothesis that an alternative prey species may make the difference between cyclic and 'stable' vole populations. The hypotheses that predator territoriality and switching is important for this effect of alternative prey are supported. The results do not support the premise that the possible existence of prey refugia or of a seasonally varying prey carrying capacity and prey vulnerability are important factors for this alternative prey effect.

#### INTRODUCTION

# Hypothesis

Vole populations in northern and central Sweden cycle on a spatially large scale with population peaks every 3 or 4 years. Populations in southern Sweden fluctuate considerably less and large-scale cycles have not been detected (Myllymäki et al., 1977). Such a non-cyclic field vole *Microtus agrestis* population is found in the Revinge area in southern Sweden (55°40'N, 13°30'E). Indigenous populations of voles, vole predators and alternative prey species have been the subject of studies for several years (Erlinge et al., 1982, 1983, 1984). As a result of these studies it has been hypothesized that the absence of severe fluctuations in the vole population is due to the presence of alternative prey, mainly rabbits, for the voles' predators. Quantitatively the most important vole predators at this locality

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are foxes, cats, and buzzards. It is argued that these alternative prey support dense predator populations that, without time lag, increase their consumption of voles when these increase in numbers. The hypothesis can be extended and specified further by assuming that the dampening effect on the vole population is made possible, or at least supported, by the presence of additional characteristics of the system:

(1) Switching, i.e. disproportionate predation rate on abundant prey.

(2) Seasonal fluctuations. Of particular importance could be seasonal fluctuations in carrying capacities that allow the alternative prey to increase in spring before the vole population does so. This should contribute to a small, or absence of a, time lag in the predators' response to increasing vole population densities.

(3) Predator intraspecific population regulation. This could take the form of territoriality that could prevent the building up of very high predator populations with ensuing vole and predator crashes – cyclicity.

(4) Refugia. It could be that habitat heterogeneity, an extreme form of which is prey refugia, is critical for the levelling of population cycles. This seems to be a hypothesis that deserves to be tested as it can be argued that the south Swedish habitat, with a mixture of arable land and forest, is more heterogeneous than the north Swedish habitat which is predominately taiga. Although not obvious it could be that some habitats in south Sweden give particular good protection from predation.

# Testing the hypothesis

The hypothesis and the extensions can be tested in several ways. In a descriptive study one examines several predator-prey communities that differ in ways critical to the predictions of the hypothesis. Basic is of course the comparison of communities with and without alternative prey. There may, however, be difficulties finding communities that only differ with respect to the factors one wishes to test. In an experimental study one manipulates a community. One can eliminate an alternative prey from a community and observe the changes in dynamics. For meaningful results it may be required that such manipulations be rather extensive. The present work constitutes another kind of test of the hypothesis. I formulate a set of alternative simulation models of a predator-prey community and examine their properties when simulated with one and two prey species. This approach alone does not give a full understanding of the system, but neither do the other approaches. The importance of factors that are not included in the model is not evaluated, thus it is not possible to prove that a particular factor is necessary and without alternatives for a particular behaviour of the system. However, this approach does do two things:

(1) One can conclude that the system *can* behave in a particular way if a certain factor is operating. This is one kind of support we should request for a hypothesis — if no one is able to model a system that behaves realistically when a particular factor is included, this clearly weakens the support for the hypothesis.

(2) If a system behaves realistically without the inclusion of a factor this disproves the validity of a hypothesis that states that this factor is important. 'Behaves realistically' does not mean precise numeric correspondence, only a qualitatively correct behaviour of the model. However, a good fit increases the confidence one can have in the model and its predictions.

These two points constitute the rationale for this study.

Simulation models have been used to study hypotheses concerning vertebrate communities (e.g., Powell, 1980; Rabinowich et al., 1985). A much-abridged version of the present study is included in the paper by Erlinge et al. (1984).

# Principles used when constructing the models

The purpose of the study is to validate the following principles that have been followed when constructing the models:

(1) The models are constructed in a way that makes them predict cyclic vole populations when predators but no alternative prey are present. However, the study is *not* concerned with the origin of vole cycles. Therefore two alternative vole models are constructed. One assumes that vole cycles are generated within the vole population or by an interaction between the vole population and its food. This model predicts cyclicity in the single-species case too. The other model assumes that vole cycles are produced by an interaction between voles and their predators. In this model the vole population is constant in the absence of predators.

(2) The model is specifically made to test the hypothesis as applied to the Revinge system. Parameter values and assumed functions are usually based on and verified with data from the Revinge area.

(3) I make estimates of functions and parameter values, sometimes based on information from other studies, if no data from the Revinge area is available. A test of these estimates is available in the sense that predictions of the model in the three-species case can be compared to the real dynamics of the studied populations in the Revinge area.

(4) In some cases I do not think that verification of a parameter value or function is necessary. This is the case when a function represents a mechanism that cannot be accurately measured but is still desirable to test. For example, I represent 'seasonally fluctuating carrying capacity' with a sine function despite the fact that I have no measurements of carrying capacity that support precisely this function. However, possible qualitative effects from a naturally fluctuating carrying capacity ought to be similar to those fluctuating according to a sine function.

The rationale of the study does not require that the parameter values are numerically correct. If the model behaves as the hypothesis predicts (without taking resort to absurd parameter values) this supports the hypothesis.

## MODELS

I construct the models as combinations of four submodels: the vole model, the alternative prey model, the predator model, and the predation process model (Fig. 1). This simplifies the presentation of the models and the execution of the simulations. Each submodel takes any of several versions and may be extended with options. Some of these options apply to all versions, whilst others apply to some of them only. I use several versions to find those that are realistic in the three-species case and are thus valid for the Revinge area. The options represent factors the importance of which I want to test.

No explanations of symbols are given in the text in order to save space. The reader is throughout referred to Table 1.

#### Mathematical description of the models

#### Vole model

(1) Version I — without time-lag. I assume that vole population growth depends on the density of the vole population itself (according to the



Fig. 1. Four submodels and the relations between their inputs and outputs. A, P and V, number of alternative prey, voles, and predators, respectively; F, predator feeding rate;  $F_a$  and  $F_v$ , feeding rate on alternative prey and voles, respectively.

TABLE 1

#### List of symbols used

State variables

- A Alternative prey population (biomass per area)
- P Predator population (individuals per area)
- V Vole population (biomass per area)

# Parameters

- A given density of the alternative prey (biomass per area)
- $\overline{A}$  Mean density of the alternative prey
- a A parameter in the prey switch function
- $A_{amp}$  Measure of the magnitude of seasonal fluctuations in the density of the alternative prey
- $b_{\max}$  Birth rate of the predator when this is feeding at maximum rate (offspring per individual and year)
- $d_{\rm b}$  Basal death rate of the predator. Mortality (fraction dying per year) that is not affected by feeding rate
- $d_s$  Starvation mortality. Further mortality when no food is available
- $F_{\text{crit}}$  Feeding rate below which extra mortality (in addition to  $d_{\text{b}}$ ) takes place
- $F_{\text{max}}$  Feeding rate of a predator that is not limited by prey density (biomass per time)
- Fr A parameter in the equation for functional response
- Frr A parameter in the equation for functional response with prey refugia
- Fr Mean value of a seasonally fluctuating functional response
- $Fr_{amp}$  Measure of the magnitude of seasonal fluctuations in functional response
- Fas<sub>a</sub> Phase of the equation for the density of a given alternative prey
- Fas<sub>fr</sub> Phase of the equation for functional response
- $Fas_{K}$  Phase of the equation for a seasonally fluctuating carrying capacity
- $\operatorname{Fas}_{\operatorname{vul}}$  Phase of the equation for a seasonally fluctuating prey vulnerability
- $H_{\text{max}}$  The proportion of time that a predator spends hunting when success is low
- <u>K</u> Carrying capacity for a prey population
- $\overline{K}$  Mean value of a seasonally fluctuating prey carrying capacity
- $K_{amp}$  Measure of the magnitude of yearly fluctuations in prey carrying capacity
- Ki A measure of the strength of predator intraspecific population regulation
- P A given density of the predator population
- r<sub>max</sub> Maximum prey population growth rate
- Ref Size of prey refugia (density of unavailable prey)
- Swha A parameter in the equation for habitat switch
- Swhb Another parameter in the equation for habitat switch
- Swpa A parameter in the equation for prey switching
- Swpb Another parameter in the equation for prey switching
- T Time-lag in the voles' response to changes in carrying capacity
- t<sub>m</sub> Month of predator reproduction
- Vul Prey vulnerability. Proportion of prey biomass that is killed and consumed per time and area unit by a predator individual
- VulMean value of a seasonally fluctuating prey vulnerability
- Vul<sub>amp</sub> Measure of the magnitude of seasonal fluctuations in prey vulnerability

TABLE 1	(continue	ed)
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Variab	les
b	Current predator birth rate
d	Current predator death rate
F	Predator feeding rate (biomass per predator individual and time unit)
Fh	Netto feeding rate (biomass per predator individual and time unit)
Fr	Current value of a seasonally fluctuating functional response
Η	Current predator hunting effort (proportion of time used for hunting)
Κ	Current value of a seasonally fluctuating prey carrying capacity
Pr	Biomass of voles as a proportion of all prey present
Vul	Current value of a seasonally fluctuating prey vulnerability

relation given by the logistic model) and on the decrease caused by predation:

$$dV/dt = Vr_{\max(v)}(1 - V/K_v) - PF_v$$
(1)

(2) Version II — with time-lag. In this version I assume that the densitydependent regulation of the vole population takes place with a time-lag. This lag could be related to the time taken by food plants to recover after grazing (May, 1973) or, if voles are subject to cyclic selection with respect to density sensitivity (Krebs et al., 1973), to generation time. Whichever the background, an equation with time-lag can cause cycles that are generated within the submodel. This means in the present context a vole population that cycles even if it is not subject to predation. Such a population is modelled by the following equation:

$$dV/dt = Vr_{\max(v)} (1 - V_{(t-T)}/K_v) - PF_v$$
(2)

(3) Option — seasonal fluctuation in carrying capacity. I assume that vole carrying capacities fluctuate over the year according to a sine function:

$$K_{v} = \overline{K}_{v} + K_{\mathrm{amp}(v)}\overline{K}_{v} \sin(T2\pi - \mathrm{Fas}_{K(v)})$$
(3)

## Alternative prey model

(1) Version I – model based on the logistic equation. This submodel corresponds to the one used for the vole population:

$$dA/dt = Ar_{\max(a)}(1 - A/K_a) - PF_a$$
(4)

The vole population with a time-lag was formulated to be able to study an intrinsically regulated vole population. The hypothesis to be tested does not make any particular assumptions concerning the regulation of the alternative prey and it has not been suggested that rabbit populations cycle on their own. Therefore no model based on time-lag is studied for the alternative prey.

(2) Version II - model with constant alternative prey. The proportion of produced rabbits that were taken by predators was rather small in the years when rabbits were common in the Revinge area (Erlinge et al., 1983). This suggests that the model for the alternative prey could be simplified by making the dynamics of this prey independent of predation. Such a model is obtained by letting the size of this population take a value that is fixed and thus has the character of a parameter. This value can be varied to study the effects of different levels of alternative prey density.

(3) Option — seasonal variation in carrying capacity. As for the vole model, this condition is modelled by a sine function:

$$K_{a} = \overline{K}_{a} + K_{amp(a)}\overline{K}_{a}\sin(T2\pi - Fas_{K(a)})$$
(5)

A corresponding option for version II is obtained by letting the given population size follow a sine function:

$$A = \overline{A} + A_{amp}\overline{A}\sin(T2\pi - Fas_a)$$
(6)

### Predator model

(1) Version I — model without starvation mortality (diffuse alternative prey). This model rests on the assumption that mortality does not vary seasonally and is independent of feeding rate while reproduction takes place once per year and is proportional to the feeding rate. This model is used by Hsu et al. (1978) and discussed by Loman (1984). For average and high feeding rates it seems reasonable but hardly so when feeding rate is low. Under such circumstances it is likely that further mortality that is directly or indirectly due to starvation takes place. This condition is modelled below (version II). However, version I seems potentially realistic if it is assumed that the predators have access to prey types that are not explicitly modelled. Such prey could provide food and prevent starvation even when densities of voles and the explicitly modelled alternative prey are low. As we are not interested in the dynamics of these further prey types there is no need to model them explicitly and their effect on the system is accounted for through this predator model. The seasonal nature of predator reproduction must be modelled in order to test the second auxiliary hypothesis (seasonality). I therefore use a discrete predator model. I assume that all reproduction takes place in one specified month of the year. Yearly mortality is divided in twelve equal fractions, one for each month. The model is given by the following equations:

$$P_{(t+1/12)} = P_t (1 - d_b)^{1/12} \qquad \text{if mod}(t12, 12) \neq t_m \tag{7}$$

$$P_{(t+1/12)} = P_t (1 - d_b)^{1/12} (1 + b) \qquad \text{if mod}(t12, 12) = t_m \tag{8}$$



Fig. 2. Relation between feeding rate and death rate in the predator model with starvation mortality. d, predator death rate;  $d_b$  and  $d_s$ , basal and starvation death rate; F, predator feeding rate;  $F_{crit}$  and  $F_{max}$ , critical and maximum feeding rate.

Birth rate, number of offspring per adult animal, is proportional to feeding rate:

$$b = \frac{F}{F_{\text{max}}} b_{\text{max}} \tag{9}$$

(2) Version II — model with starvation mortality. It is assumed that further mortality (starvation mortality) is added to the basal mortality when feeding rate decreases below some critical value. This mortality increases with decreasing feeding rate (Fig. 2). The equations for this version are similar to those for the previous one with one exception: the parameter  $d_b$  is replaced by the variable d, the value of which is given by the following equations:

$$d = d_{\rm b}$$
 if  $F \ge F_{\rm crit}$  (10)

$$d = d_{\rm b} + d_{\rm s} - \frac{d_{\rm s}F}{F_{\rm crit}} \qquad \text{if } F < F_{\rm crit} \tag{11}$$

This modification of version I was suggested by Loman (1984).

(3) Version III - model with constant predator population. This model mimics the characteristics of a population of domestic cats. The density of this predator is fixed by factors external to the system. The feeding rate of this population is represented by its consumption of prey *in* the system; voles and alternative prey. The amount of food external to the system that is used (e.g. canned cat food) does not concern us and is not modelled. There is no influence from the modelled feeding rate on the density of this predator. This model is obtained by simply letting predator density take the character of a parameter.

(4) Option—intraspecific population regulation. It is reasonable to assume that the growth of a predator population is not only affected by the individuals' feeding rates but also by the population's current density. In a

dense population one expects a larger proportion of energy intake to be used for social interactions than in a more sparse one. An example of a mechanism with this effect is territoriality. This phenomenon can be modelled by modifying the equations that describe birth rate (equation 9) (Loman, 1985). With this option, birth rate is affected both by feeding rate and by population density:

$$b = \frac{F}{F_{\text{max}}} \left( b_{\text{max}} - \left( b_{\text{max}} + 1 - \frac{1}{1 - d} \right) \frac{P}{\text{Ki}} \right)$$
(12)

If P = 0, this equation is identical to equation (9) and population growth is only affected by feeding rate. If P = Ki, the equation can be written as  $b = (F/F_{max})(1/(1-d)-1)$  and thus  $P_{(t+1)} = P_t$  etc. This means that the population is constant if and only if  $F = F_{max}$ . The population decreases if feeding rate is less. The population will settle at an equilibrium if feeding rate is constant. This equilibrium can be computed from the fact that (1+b)(1-d) = 1 at equilibrium and equation (12). It is (after rearranging):

$$P = \text{Ki} \frac{F_{\text{max}}}{F} \frac{d - b_{\text{max}}(1 - d) \frac{F}{F_{\text{max}}}}{d - b_{\text{max}}(1 - d)}$$
(13)

## Predation process model

(1) Version I - hunting in one habitat. Hunting is assumed to take place in one habitat where both prey types are randomly mixed. The model is based on the idea that each prey species has a certain vulnerability with respect to the predator. This is the probability that a predator individual succeeds in capturing one prey individual during one time unit. This is equivalent to the proportion of all prey specimens (or all prey biomass) that is captured in one time unit by a given predator individual. I assume that the predator exhibits a functional response to increasing prey densities that conforms to Hollings' type II, i.e. feeding rate increases asymptotically towards a maximum value as prey density increases (Holling, 1965). In version I, I produce this mechanism by assuming that the proportion of time that is used for hunting decreases with increasing hunting success (prey captured per time actually hunting). The model is given by the following equations:

$$F = Fh H$$
(14)

$$H = \frac{F_{\text{max}}}{Fh + \frac{F_{\text{max}}}{H_{\text{max}}}}$$
(15)



Fig. 3. (A) Relation between netto feeding rate (Fh) and the proportion of all time that is used for hunting (H) (equation 15).

(B) The relation between vole density and feeding rate that is defined by the equations (14)-(16). After rearrangeing, this relation is given by (32) which is shown on the graph. H and  $H_{\text{max}}$ , hunting effort and maximum hunting effort (both measured as hunting hours per 24 h); F, Fh and  $F_{\text{max}}$ , predator feeding rate (prey per h), netto feeding rate (prey per h actually feeding) and maximum feeding rate; Vul; prey vulnerability (proportion of prey in one unit area taken by one predator individual and time unit).

The second equation states that when hunting success is low (Fh small) so is H close to  $H_{\text{max}}$ , i.e. the predator uses the maximum possible proportion of its time for hunting. Note that  $H_{\text{max}}$  is not 1 but a value less than 1 that is characteristic of the predator,  $1 - H_{\text{max}}$  represents the time that necessarily must be used for resting, body care, etc. Equation (15) also states that when hunting success (Fh) is high so is  $HF_{\text{max}}/Fh$  (as  $F_{\text{max}}/H_{\text{max}}$  in the denominator of equation (15) can be neglected compared to Fh) and thus (from equation 14)  $F \approx F_{\text{max}}$  (Fig. 3).

Hunting success is directly proportional to the density and vulnerability of the prey:

$$Fh = V \operatorname{Vul}_{v} + A \operatorname{Vul}_{a} \tag{16}$$

(2) Option 1 — seasonal fluctuation in prey vulnerability. Vulnerability is considered a variable that follows a sine function:

$$\operatorname{Vul}_{v} = \overline{\operatorname{Vul}}_{v} + \overline{\operatorname{Vul}}_{v} \operatorname{Vul}_{\operatorname{amp}(v)} \sin(T2\pi - \operatorname{Fas}_{\operatorname{vul}(v)})$$
(17)

$$\operatorname{Vul}_{a} = \overline{\operatorname{Vul}}_{a} + \overline{\operatorname{Vul}}_{a} \operatorname{Vul}_{\operatorname{amp}(a)} \sin(T2\pi - \operatorname{Fas}_{\operatorname{vul}(a)})$$
(18)

(3) Option 2 — prey switching. Switching does in this context mean that the vulnerability of the two prey species depend on their relative abundance. The model is given by the following equations:

$$\operatorname{Vul}_{v} = a_{v}(1+e) \tag{19}$$

$$\operatorname{Vul}_{a} = a_{a}(1-e) \tag{20}$$

$$e = \text{Swpb} \frac{\frac{1 - \text{Swpb}}{\text{Swpb}} V - A}{\frac{1 - \text{Swpb}}{\text{Swpb}} V + A}$$
(21)

The parameters and variables in these equations have no clear interpretations. A given combination of Swpa, Swpb, and the ratio  $a_a/a_v$  does, however, give a characteristic switching graph that, by trial and error, can be fitted to field data points in aplot of relative prey densities in nature to relative prey number in predator food. Roughly speaking, the ratio  $a_a/a_v$ represents the convexity of the switching graph, Swpa represents the degree of switching, and Swpb represents the inflection point, i.e. the prey ratio at which the predator turns from preference for one prey to the other (Fig. 4).

(4) Version II - hunting in two habitats. It is assumed that the two prey species, voles and alternative prey, live in separate habitats and that the predator spends part of its hunting time in either habitat. Total hunting time is assumed to be fixed and the functional response is modelled by assuming that the hunting success, and thus feeding rate, depends on prey abundance in each habitat:

$$H_{\rm v} = \frac{V}{V+A} \tag{22}$$

- -

$$H_{\rm a} = \frac{A}{V + A} \tag{23}$$

$$H = H_a + H_v \tag{24}$$

Feeding rate depends on hunting time and hunting success. The latter increases, as in version I, asymptotically towards a maximum as prey density increases:

$$F_{\rm v} = H_{\rm v} \frac{F_{\rm max} V}{{\rm Fr}_{\rm v} + V}$$
(25)

$$F_{\rm a} = H_{\rm a} \frac{F_{\rm max}A}{{\rm Fr}_{\rm a} + A} \tag{26}$$

It should be noted that most values of the parameters  $Fr_a$  and  $Fr_v$  lead to switching (Fig. 5), also without the special switch option described below.



Fig. 4. Examples of prey switch functions that show the influence of different parameter values. Pr = V/(V + A);  $Sw = Fh_v/(Fh_v + Fh_a)$ . (A)  $a_v = a_a$ , Swpb = 0.5: 1, Swpa = -1.0; 2, Swpa = -0.5; 3, Swpa = 0.0; 4, Swpa = 1.0; 5,

(A)  $u_v = u_a$ , Swpb = 0.5. 1, Swpa = -1.0, 2, Swpa = -0.5, 3, Swpa = 0.0, 4, Swpa = 1.0, 5, Swpa = 2.0. (B)  $u_v = u_a$ , Swpb = 0.2: 1, Swpa = -1.0; 2, Swpa = -0.5; 3, Swpa = 0.0; 4, Swpa = 0.5; 5,

(B)  $a_v = a_a$ , Swpb = 0.2: 1, Swpa = -1.0; 2, Swpa = -0.5; 3, Swpa = 0.0; 4, Swpa = 0.5; 5, Swpa = 1.0.

(C)  $a_v = 2a_a$ : 1, Swpa = 0.0, Swpb = 0.5; 2, Swpa = 1.0, Swpb = 0.5; 3, Swpa = 1.0, Swpb = 0.2.



Fig. 5. Demonstration of the predation switch effect obtained by using different parameter values in the equations for functional response. 1,  $Fr_v = 17.5$ ,  $Fr_a = 17.5$ ; 2,  $Fr_v = 17.5$ ,  $Fr_a = 35.0$ ; 3,  $Fr_v = 17.5$ ,  $Fr_a = 500.0$ .

The parameter Fr can be considered an inverse measure of predator efficiency because in feeding models where feeding rate depends on search, pursuit, and handling time, a short search time corresponds to a low Fr-value. Also a predator population with a low Fr-value can persist on a less-dense prey population than can one with a higher Fr-value (Tanner, 1975).

(5) Option 1 - prey refugia. Refugia means that all prey below a certain prey density are unavailable for predation. Prey above this density are subject to predation according to a relation that is comparable to that one described for the basic model. The model is given by the following equations:

$$F_{\rm v} = 0$$
 if  $V \leq \operatorname{Ref}_{\rm v}$  (27)

$$F_{\rm v} = H_{\rm v} \frac{F_{\rm max}(V - {\rm Ref}_{\rm v})}{{\rm Frr}_{\rm v} + V - {\rm Ref}_{\rm v}} \qquad \text{if } V > {\rm Ref}_{\rm v}$$
(28)

Comparable equations give the feeding rate on alternative prey  $(F_a)$ . This model can be considered an extreme case of habitat heterogeneity (with respect to prey vulnerability within a subhabitat).

(6) Option 2 — seasonal fluctuations in functional response. The variable Fr in the equation for functional response (equations 24 and 25) is considered a variable that follows a sine function:

$$Fr_{v} = \overline{Fr}_{v} + Fr_{amp(v)} \overline{Fr}_{v} \sin(T2\pi - Fas_{fr(v)})$$
<sup>(29)</sup>

 $Fr_a$  is given by a similar equation.

(7) Option 3 — habitat switching. The basic model of version II does not take relative prey density into account. Usually a predator should prefer

hunting in a habitat with a high prey density. This can be accounted for by extending the model with a switch function that has appropriately fitted parameters. Switching is in this section represented by the choice between the two hunting habitats. The equation is purely descriptive and contains no assumption concerning the processes leading to switching:

$$H_{v} = (\Pr^{\text{Swha}}) / (\text{Swhb}^{(\text{Swha}-1)}) \qquad \text{if } \Pr \leq \text{Swhb} \qquad (30)$$

$$H_{\rm v} = 1 - (1 - \Pr)^{\rm Swha} / (1 - \rm Swhb)^{(\rm Swha-1)}$$
 if  $\Pr > \rm Swhb$  (31)

Swha represents the degree of switching; a strong preference for the habitat with the more abundant prey type is modelled by a high value of Swha. Neutral switching, where equations (29) and (30) become identical to equations (22) and (23) of the basic model, is obtained for Swha = 1. It is also possible to model negative switching. This means that the predator spends more time in the habitat of the less-common prey than is expected from the relative abundance of this prey. A predator that spends the same time in both habitats, regardless of prey abundances, represents an extreme case of negative switching. Negative switching is modelled by values of Swha between 0 and 1. Swhb represents the relative prey density where the predator changes its preference from one prey to another (the inflection point). This parameter makes it possible to account for the predator's evaluation of the relative value of the prey types. E.g., if individual weight of the two prey types differ, the value of Swhb is affected by whether prey abundance is measured in biomass or individuals.

## DETERMINING THE PARAMETER VALUES

In this section I determine parameter values that are used in simulations of the models (Table 2). It is sometimes not entirely clear what measurable properties of natural populations that the different parameters represent. This section can thus be considered as an example, with comments, of how these measurements can be made, given a set of data from a natural community. Most values are based on data from studies in the Revinge area. Some values are based on averages from several species, others on data from one species only. Data for predators refer to the food generalists, mainly cat and fox. The use of data from cats requires special comments. Cats in the study area are either domestic but free-ranging, or feral. The former hunt wild prey, to an extent usually determined by themselves, but have also access to food offered by their 'owners'. Their number is mainly determined by humans and virtually independent of prey density. The feral cats, mainly males, live completely on food captured by themselves. Their number is affected by prey densities. Two of the predator models (versions I and II) are intended to model wild populations. Data for feral cats and in some

# TABLE 2

Section	Parameter	Value
Carrying		$150 \text{ kg km}^{-2}$
capacities	$\overline{K}_{v}$	$225 \text{ kg km}^{-2}$
•	$K_{amp(y)}$	0.85
	$Fas_{K(x)}$	2.618 ( $K_v$ peaks 1 June)
	K <sub>a</sub>	$1600 \text{ kg km}^{-2}$
	$\overline{K_{a}}$	$2500 \text{ kg km}^{-2}$
	K <sup>a</sup> mm(a)	0.80
	$Fas_{K(a)}$	$3.403 (K_{\odot} \text{ peaks 15 July})$
	A	1075 kg km <sup>-2</sup> (for other values, see Fig. 19)
	$\overline{A}$	$1075 \text{ kg km}^{-2}$
	A	0.35
	Fas	4.45 (A peaks 15 September)
Population	a r(-)	3.9
growth	$r_{max(v)}$	2.3
8	$b_{max}$	2.8
	d <sub>b</sub>	0.17
	$d_{c}$	0.83
	, Forme	$0.5 F_{max}$
Time lag	$t_m$	5
	T	0.45 (in models with constant $K_{\rm e}$ )
		0.15 (in models with fluctuating $K_{\rm u}$ )
Predator	Fmax	$1.0 \text{ kg day}^{-1}$
	Ki	$2.53 \text{ ind } \text{km}^{-2}$
One habitat	Vul.,	$0.15 \text{ day}^{-1} \text{ km}^{-2}$
	Vul	$0.0040 \text{ day}^{-1} \text{ km}^{-2}$
	Htmax	0.75
	a <sub>v</sub>	$0.15 \text{ day}^{-1} \text{ km}^{-2}$
	Swpa	1.0 (0.0)
	Swpb	0.2
Two habitats	Frv	$17.5 \text{ kg km}^{-2}$ (25 kg km <sup>-2</sup> )
	Frrv	$8.8 \text{ kg km}^{-2}$ (12.5 kg km <sup>-2</sup> )
	Refv	$10.0 \text{ kg km}^{-2} (10.0 \text{ kg km}^{-2})$
	Fr	$20.0 \text{ kg km}^{-2}$ (30.0 kg km <sup>-2</sup> )
	Fr <sub>amp(v)</sub>	0.38 (0.00)
	$Fas_{fr(x)}$	3.40 (Fr <sub>a</sub> peaks 15 July)
	Fra	$500 \text{ kg km}^{-2}$ (600 kg km <sup>-2</sup> )
	Frra	$500 \text{ kg km}^{-2} (600 \text{ kg km}^{-2})$
	Refa	$0 \text{ kg km}^{-2}$
	Fra	$600 \text{ kg km}^{-2} (1450 \text{ kg km}^{-2})$
	$Fr_{amp(a)}$	0.50 (0.76)
	$Fas_{fr(a)}$	5.76 (Fr <sub>a</sub> peaks 1 December)
	Swha	9.0 (0.1)
	Swhb	0.05 (0.05)

Parameter values used when simulating the models. Values in parenthesis are used in simulations of the submodel for a constant predator population

Spring densit Mean index	<i>ies</i> 1974–1977 (small qı	uadrat method): 0.375 (Ha	nsson, in litt., Nilsson, 198	(1, p. 90)	
Mean density 13.5 ind ha <sup>-</sup> D: o on ungr	y in removal areas o <sup>1</sup> (Erlinge et al., 198 azed mineral soil: 1	n ungrazed peat soil (1974) 33, appendix Table 3). 1.0 ind ha <sup>-1</sup> (Erlinge et al.,	–1977): 1983)	-	
	Index (I)	Density	Density	Total number	Mean biomass
	(Nilsson,	$(ind ha^{-1})$	$(ind ha^{-1})$	400 ha peat	$(kg km^{-2})$
	1981)	on peat soil	on mineral soil	and 400 ha	on 4000 ha
		$I \times 13.5 / 0.375$	$I \times 1.0 / 0.375$	mineral soil	
1972	1.4	52.5	3.9	22600	17.0
1973	1.4	52.5	3.9	22600	17.0
1974	0.3	11.3	0.8	4800	3.6
1975	0.2	7.5	0.6	3200	2.4
1976	0.5	18.8	1.4	8200	6.2
1977	0.5	18.8	1.4	8200	6.2
1978	0.8	30.0	2.2	12900	9.7
6261	0.8	30.0	2.2	12900	9.7
					$\overline{x} = 8.8$

TABLE 3

Yearly fluctuations in vole densities

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Mean index 1974–1977 (small quadrat method): 1.7 (Hansson and Larsson, 1980, p. 9; Nilsson, 1981, p. 90). Mean density in removal areas on ungrazed peat soil (1974–1977): 54 ind ha<sup>-1</sup> (Erlinge et al., 1983, appendix Table 3).

D:o on u	ngrazed mineral soil	l: 20 ind ha <sup>-1</sup> (Erlinge e	t al., 1983)			1
	Index (1)	Density	Density	Total number	Mean biomass	
	(Nilsson,	$(ind ha^{-1})$	(ind ha <sup>-1</sup> )	400 ha peat	$(\mathrm{kg}\mathrm{km}^{-2})$	
	1981)	on peat soil	on mineral soil	and 400 ha	on 4000 ha	
		$I \times 54/1.7$	$I \times 20/1.7$	mineral soil		
1972	2.8	89.0	33.0	48800	36.6	I I
1973	2.1	6.99	24.7	36600	27.5	
1974	1.1	35.0	13.0	19200	14.4	
1975	1.7	54.1	20.0	29600	22.2	
1976	1.9	60.4	22.4	33200	24.9	
1977	2.1	66.8	24.7	36600	27.5	
1978	3.3	104.9	38.9	57600	43.2	
1979	3.2	101.8	37.7	55800	41.9	
					$\bar{x} = 29.8$	

instances for domestic cats are used to determine parameter values in these versions. Data for domestic cats are used to give data on the proportion of hunting time spent in either habitat and on the proportion of voles and rabbits in wild prey. Data on total hunting time and total food intake for domestic cats is not used. However, the model for a constant predator population (version III) is specifically intended to model a population like that of domestic cats. Where relevant, I have used data from the domestic cat population for this model.

## Prey densities

Determination of parameter values require, in several instances, data on prey densities in the Revinge area at different times. These densities were determined on basis of the following data (Table 3): (a) Density indices (small quadrat method) in spring and autumn for field voles in ungrazed habitat on peat soil (Hansson and Larsson, 1980, p. 9; Nilsson, 1981, p. 90, Hansson, in litt.). These indices were available for all years of the study and gave information on yearly fluctuation in overall density. (b) Density values (removal trappings in 1-ha areas) in spring and autumn for ungrazed fields on peat soil and on mineral soil (Erlinge et al., 1983). These values were not available for all years and were made in different plots in different years.



Fig. 6. Assumed patterns of population fluctuations for voles (A) and rabbits (B). The arrows indicate when actual density estimates were made. The rest of the graph is based on interpolation.

They were used to calibrate the index values to give information on absolute densities. (c) Data on yearly pattern of reproduction and predation (Erlinge et al., 1983; Fig. 6a). These made it possible to interpolate densities between sampling occasions.

Estimates of rabbit densities were based on night counts in sample plots (Liberg, 1981, p. 33). These were corrected for the fraction of rabbits invisible in dense (G. Jansson, University of Lund, personal communication, 1976) to give absolute densities. The pattern of density fluctuations between sampling occasions was obtained from information on rabbit breeding in the Revinge area (Andersson et al., 1979; Fig. 6b).

# Carrying capacities

# Vole population

If a population is constant over time and not subject to predation I consider its density a measure of the carrying capacity in that particular habitat. These conditions are of course difficult to find. The Revinge vole population itself is ruled out as it is under heavy predation. Boonstra (1977) has described a population of the vole Microtus townsendii that exhibits some features suggesting it is at its carrying capacity. The population fluctuated seasonally but there were no substantial between-year variations. This is not very impressive for a study lasting only 2 years; however, most observed Microtus populations fluctuate even over such a short time. Furthermore, even compared to the most densely populated habitat in the Revinge area, Boonstra measured high densities. The habitat studied by him was called 'grassland'. Although further details are not available to me I'd suggest that the ungrazed fields on peat soil in the Revinge area that carry a very luxuriant herb vegetation are more productive from a vole point of view. The fact that the M. townsendii population stayed at such a high level for 2 years strongly suggests that it was not overshooting a carrying capacity but, possibly, close to it.

Spring and autumn densities of *M. townsendii* (45 g ind<sup>-1</sup>) were 5000 ind km<sup>-2</sup> (225 kg km<sup>-2</sup>) and 22000 ind km<sup>-2</sup> (990 kg km<sup>-2</sup>), respectively. Mean value for the whole year is assumed to be the mean of those two values. I assume that the carrying capacity for field voles (30 g ind<sup>-1</sup>) in fields on peat soil in the Revinge area (4 km<sup>2</sup>) was twice that density; 1200 kg km<sup>-2</sup>. The carrying capacity in ungrazed fields on mineral soil (4 km<sup>2</sup>) is assumed to be that value divided by 3.3 (Table 3); 360 kg km<sup>-2</sup>. This gives an average value for the whole Revinge area (40 km<sup>2</sup>) of 156 kg km<sup>-2</sup>.

For the basic model I estimated carrying capacity with the mean density over the year. For the optional model with seasonally fluctuating carrying capacity I performed test simulations of the model to determine which values of amplitude, mean carrying capacity, and the phase parameter that



Fig. 7. Assumed pattern of seasonal fluctuation in carrying capacity and the result of simulating densities (the graphs with smaller amplitude): (A) voles; (B) alternative prey.

produced the observed density fluctuations (Fig. 7a). For the phase parameter of this optional model it was required that it should make the population peak in the beginning of September (Fig. 6a).

#### Rabbit population

The rabbit population in the Revinge area increased until the winter of 1976/77. During that winter it decreased drastically. This was not due to long-term overgrazing but to an unusually severe winter with a thick and long-lasting snow cover. I do not consider this decline a result of overshooting the carrying capacity. However, as predation was rather light (Erlinge et al., 1983) and there was some evidence of overgrazing, I suggest that the rabbit population was coming close to its carrying capacity. I assume that this is 150% of the highest density measured before the decline. To determine the parameters in the model for a seasonally fluctuating carrying capacity I note that the seasonal fluctuations had an amplitude of 35% both when the rabbit population was very dense and later, in 1979, when it had the lowest density measured. I therefore assume that this amplitude applies to a rabbit population at its (seasonally fluctuating) carrying capacity too. The parameter values for mean, amplitude, and phase of this model was, as for the vole population, determined by means of test simulations of the model system until a fitting set of parameter values was found (Figs. 6b and 7b).

# Population growth

#### Voles

The intrinsic rate of population growth  $(r_{\text{max}})$  is computed from the equation  $e^{r_{\text{max}}} = \lambda$ , where  $\lambda$  is the number of surviving female offspring to a

female after 1 year. It is assumed that predation and intraspecific competition can be disregarded. The data used are from a cyclic population of Microtus agrestis in southern Finland (Myllymäki, 1977). As this parameter refers to an intrinsic property of a vole population there should be no objection to using data from a population outside the Revinge area. In fact, the hypothesis under test partly rests on the assumption that there are no innate differences with respect to the intrinsic rate of increase between cyclic and non-cyclic populations. Had there been, this could have been a sufficient explanation of the observed differences in population dynamics. An advantage by using a cyclic population is that the realised rate of increase during the increase phase should be close to the intrinsic (maximum) rate of increase. In this phase there is relatively little intraspecific competition and predation is light. For the parameter determination I sum all daughters born to an overwintered female during her second summer (GGR<sub>0</sub> sensu Myllymäki) and all her granddaughters born during this summer. I assume that all mortality is due either to predation or (directly or indirectly) due to intraspecific competition and thus can be disregarded when determining  $r_{\rm max}$ . I base the computation on the number of embryos per female during different months (Myllymäki, 1977, Fig. 13), a 5% prenatal mortality (Myllymäki, 1977, p. 485), and 20% density-independent nestling mortality (Myllymäki, 1977, p. 473). During two peak years these estimates yielded values of 3.1 and 3.6 and during an increase year a value of 3.9. The latter value was used for  $r_{max}$ .

# Rabbits

The computation of  $\lambda$  and  $r_{max}$  for the rabbit population is based on a total production of 10 daughters per female and year that has been measured for the Revinge area (G. Jansson, University of Lund, personal communication, 1976). All mortality is disregarded as I assume that this is light in the absence of predation and intraspecific competition. A common cause of death is myxomatosis but this is only important in dense populations.

## Predators

The predator models have a different structure than the prey species models. Population growth in the predator models is determined explicitly by birth and mortality rates which, in turn, are determined by feeding rates. Maximum birth rate is represented by the number of daughters per female and year when feeding rate is not limiting. The model thus superficially assumes that all individuals are equal in this respect. In reality it is more likely that a population is heterogeneous, and that in a year with a low mean feeding rate some individuals have a feeding rate that is close to maximum while that of others is very low. The former reproduce close to maximum



Fig. 8. Pattern of vole fluctuations obtained when simulating a system that only consists of a vole population. Different values for the lag parameter (T) are used. The x-axis is scaled in years.

(A) Constant carrying capacity: 1, T = 0.3; 2, T = 0.4; 3, T = 0.45; 4, T = 0.5; 5, T = 0.6.

(B) Seasonally fluctuating carrying capacity: 1, T = 0.1; 2, T = 0.15; 3, T = 0.2.

rate while the latter do not reproduce at all. However, the model may still give realistic predictions if mean reproductive rate is that stated by it. This heterogeneity suggests a way to determine maximum birth rate without having access to a population where one knows that all individuals are feeding at maximum rate. I compute mean litter size for all females that have *successfully* reproduced. This is done for all years when data are available (1975-1978) and the best year for each species is chosen as representative of the maximum birth rate. These values are 5.0 (fox), 7.5 (cat), and 4.0 (buzzard) (T. von Schantz, O. Liberg and M. Sylvèn, personal communication, 1980). The mean number of daughters was thus 2.8 and this value is used for  $b_{max}$ .

Basic mortality represents mortality that is independent of feeding rate. I assume that the mortality of older individuals, from their second year and on, is a good estimate of this mortality. These mortality rates are 0.15 (fox), 0.25 (cat), and 0.10 (buzzard) (T. von Schantz, O. Liberg and M. Sylvèn, personal communication, 1980). The mean value, 0.17, is used for  $d_b$ . I assume that mortality is 1.0 when feeding rate is zero. This means that starvation mortality, the maximum extra mortality caused by starvation, is 0.83. I assume that starvation begins to affect mortality when feeding rate is 50% of  $F_{max}$ . This is motivated by the fact that the daily food requirement of cats is 50% of the maximum value measured (see below).

The predators are assumed to breed once a year. As all individuals are assumed to feed at adult rate from 'birth' on I take the time of birth as half-way between the time of actual birth and the time when adult feeding rate is reached. Information from the Revinge area (Liberg, 1981, p. 73; Von Schantz, 1981a, p. 53; Sylvèn, 1982, pp. 36 and 60) suggest that 1 June is a good estimate of this.

# Time-lag in vole intraspecific regulation

This time-lag cannot be measured directly, especially as it is not known precisely what it represents. What is required from this submodel is, however, simply that it should behave in a predescribed way, i.e. to cycle. I therefore carried out test simulations of the vole population model alone with different values for the lag parameter. Only in a rather narrow interval is the population predicted to cycle without being periodically exterminated. The parameter values are chosen from this interval (Fig. 8).

# Intraspecific predator population regulation

## Maximum feeding rate

This is a scaling factor, the value of which can be chosen arbitrarily for the model predator. It does not influence the results of the simulations qualitatively. I use the value 1 kg day<sup>-1</sup>.

•	-	-	=	
	F <sub>max</sub>	Mean density 1975–1978 (ind)	$D:o (ind km^{-2})$	D: o, measured in model pre- dator units
Fox	0.9	35.3	0.88	1.0
Cat (all)	0.5	67	1.68	0.84
Polecat	0.35	25	0.63	0.22
Buzzard	0.30	40	1.0	0.30
Tawny owl	0.16	31	0.78	0.05
				2.41

Maximum feeding rate and mean densities for generalist predators in the Revinge area. The density is measured just before the breeding time. The model predator has a  $F_{max}$ -value of 1.0

In the next section I determine another parameter value (Ki). To do this I need the actual  $F_{\text{max}}$ -value for each of the predators in the Revinge area. The best direct measure of  $F_{\text{max}}$  for any of the Revinge predators is that for the cat population. In the winter of 1976/77 there was much snow and a very high abundance of rabbits in poor condition that were easy to catch. At this time the feeding rate of feral cats was measured to 496 g day<sup>-1</sup> (Liberg, 1981, p. 44). Daily food requirement was 250 g day<sup>-1</sup> (Liberg, 1981, p. 44). I thus assume that  $F_{\text{max}}$  for the other predators too is 2.0 times their daily food requirement (Table 4, Erlinge et al., 1982).

# Measure of intraspecific regulation

The optional model for intraspecific predator population regulation assumes that there is a certain density that cannot be exceeded. The proximal mechanism with this effect may be territoriality and other social processes that increase in intensity with increasing population density and that have the effect of decreasing per-caput reproduction. Different natural populations occur at very different densities despite roughly similar feeding rates. This is possible if the parameters of the assumed process vary between different populations. These parameters are possibly subject to both genetic and cultural evolution. The desired parameter Ki can be determined for the Revinge area using equation (13) if we assume that the populations under consideration are in equilibrium and if density, birth rate and death rates are known. I do this using the density of the combined predator populations in the Revinge area (Table 4) and the previously determined birth and death rates. The coefficients of variation for predator densities in 1975-1978 were relatively low (fox = 5.9, cat = 13.1, buzzard = 8.6) (Erlinge et al., 1982), supporting the equilibrium claim.

TABLE 4



Fig. 9. Relation between the prey density and the number of hours that a fox spends hunting per 24 h. The regression lines are fitted by eye. The continuous line is an approximation of actual data. Females with young (squares) are alternatively represented by two thirds of measured values (filled squares), assuming that the rest is due to their status as mothers. The broken line is fitted on basis of these values.



Fig. 10. Relation between the fraction of voles in the prey populations (Pr) and their fraction in the prey diet (Sw). Circles represent cats and squares foxes. The three switch functions shown are based on the following parameter values: 1, Swpa = 0.0, Swpb = 0.20; 2, Swpa = 1.0, Swpb = 0.20; 3, Swpa = 1.5, Swpb = 0.20. Function 1 is considered to give the best fit to the cat data and is used when modelling a constant predator while function 2 is considered to give the best fit to the fox data and is used in the other predator models.

#### Parameters in the one-habitat predation process model

## Hunting time

The model assumes that hunting time takes its maximum value when hunting success approaches zero. Assuming that this occurs when prey density is zero, this value can be determined by extrapolating a plot of hunting time vs. prey densities. Such data are available from radio trackings of foxes (Von Schantz, 1981a). These data are based on information on 11



Fig. 11. Plots of prey intake at different prey densities.  $F_{max}$  (maximum predator feeding rate) is taken from other information and with this constain functional response curves have been fitted by eye for the basic model and for the model with prey refugia. The basic model is also constrained by the requirement that the line should start in origin. Ref,  $Fr_v$  and  $Frr_v$  are parameter values determined on basis of the obtained graphs: (A) feral cat predation on voles; (B) feral cat predation on rabbits; (C) domestic cat predation on voles; (D) domestic cat predation on rabbits.



Fig. 11. continued.

different foxes, tracked during 16 different periods. The data confirms the assumption that hunting time decreases with increasing prey abundance. Extrapolating to zero prey densities gives the desired parameter value (Fig. 9).

## **Vulnerability**

Vulnerability is defined as the proportion of prey biomass living in one area unit that one individual predator captures and consumes during 24 h of hunting. Data are available for vole vulnerability with respect to fox and cat predation and for rabbit vulnerability with respect to fox predation. Foxes hunting for rabbits required 5 h to fill their food requirement while the corresponding figure when hunting for voles was 7 h (Von Schantz, 1981b, p. 64). Based on a fox feeding-rate of 450 g (Erlinge et al., 1982) and rabbit and vole densities in April (above) this gives a rabbit vulnerability of 0.0040 and a vole vulnerability of 0.144. Rescaling to the model predator with a

maximum feeding rate of 1.0 (compared to 0.9 for a fox) gives 0.0044 and 0.16, respectively. Vole vulnerability to cat predation can be determined from data on the number of minutes a cat needs to capture a vole in different months (Liberg, 1981, p. 62). After rescaling this gives the values 0.15 (Jan.-April), 0.13 (May-Aug.), and 0.13 (Sept.-Dec.). These values are remarkably close to that estimated from fox data. They do not justify the consideration of seasonal variation in vulnerability.

## Prey switching

The prey switching function gives the relation between the relative prey population density (vole/rabbit) and the relative abundance of captured



Fig. 12. Plots of prey intake at different prey densities. Functional response curves have been fitted by eye for the model with seasonal variation in functional response. Sp, = spring; Su, = summer; A, = autumn; W, = winter. The x-intercept of the dashed lines gives, as in Fig. 11, the Fr-values: (A) feral cat predation on voles; (B) feral cat predation on rabbits; (C) domestic cat predation on voles; (D) domestic cat predation on rabbits.



Fig. 12. continued.

prey. To determine the shape of this function I use the following information: (a) Fox prey during four autumns, 1974–1977. The first two were pooled because prey abundances were very similar. (b) Cat prey during seven different periods, representing different years and seasons. I compare these data points to three different switch functions (Fig. 10). Function number 1 (Fig. 10) is considered to give the best fit to the cat data and is used when modelling a constant predator, while function number 2 fits the fox data and is used for the other predator models.

Parameters in the two-habitat hunting process model

#### Functional response

Functional response refers to the relation between prey abundance and the feeding rate of an individual predator. I model this relation with a function that increases asymptotically towards a maximum value. This shape has been termed "type II functional response" (Holling, 1965). Keith et al.



Fig. 13. Seasonal variation in functional response parameters. The parameter values were estimated from the plots in Fig. 12. (A) feral cat predation on voles; (B) feral cat predation on rabbits; (C) domestic cat predation on voles; (D) domestic cat predation on rabbits.

(1977) present data that support the use of this type of function for vertebrate predators. The function has one parameter, Fr. I determine this by plotting available data points and fitting the function by eye (Figs. 11-13). The parameter value is given by the prey abundance where the function intersects the line  $F = F_{\text{max}}/2$ . This point is read off from the fitted lines. Useful quantitative information is only available for the cat population in the Revinge area. Separate determinations are made for each season, for the pooled material, for domestic and feral cats, and for a model including refugia and one without. To determine the function from the data points I must know  $F_{\text{max}}$ . I use the value 496 g for feral cats and 175 g for domestic cats (the rest of their food is supplied by 'owners') (Liberg, 1981, p. 44 (Fig. 6) and p. 43 (Fig. 5), respectively). The feeding values in the data plot represent biomass rabbit or vole consumed per day, if all hunting takes

place in one habitat. I compute this from data on total prey intake per day (Liberg, 1981, p. 43), times the fraction of the diet made up by rabbits or voles (Liberg, 1981, p. 42), divided by the proportion of total hunting time spent in rabbit or vole habitat, for which values I use 40% and 60%, respectively. This is based on 148 observations of hunting cats before the rabbit decrease and 660 after. Out of these 43% and 38% observations, respectively, were in the rabbit habitat and in the vole habitat (O. Liberg, personal communication, 1980).

The data usually support the assumption that there is a seasonal variation in the value of the functional response parameter (Fig. 13). With respect to rabbit hunting, the value is least (and thus hunting efficiency highest) during summer. This can be explained by the presence of easily caught juveniles during this season. On the contrary, vole-hunting efficiency is highest during the winter when vegetation cover is poor. The data for domestic cats do not support the recognition of seasonal variation in vole-hunting functional response. This is best explained by the decreased overall level of outdoor hunting by these cats during winter, as they prefer a warm place indoors



Fig. 14. Relation between the percentage vole of total prey biomass and the proportion of time that radiotracked foxes spent in the vole habitat. The switch function chosen to represent the data (Swha = 9, Swhb = 0.05) is also shown. The inset shows the complete graph, to 100%. Each data point represents one for that has been tracked for 1 to 2 months.



Fig. 15. As Fig. 14 but for cats. The two data points represent pooled data for all cats before and after the rabbit decrease, respectively. The switch function shown is based on the parameter values Swha = 0.1 and Swhb = 0.80.

(pers. observ.). In accordance with this interpretation, seasonal variation in rabbit-hunting functional response is even more pronounced for domestic than for feral cats.

#### Habitat switching

The habitat-switch function gives the relation between the vole density and the proportion of all hunting time that is spent in vole habitat. I have data from cat and fox populations available to describe this function. The fox observations refer to 10 different foxes that have been radiotracked during 13 different periods. Despite the wide scatter in the data points it is clear that the most simple model (neutral switching) must be refuted (Fig. 14). The function that is determined from fox data will be used in versions I and II of the predator model. The cat data are summarized as two data points, one referring to the situation before the rabbit decrease, one to the situation after (Fig. 15). The two points are superficially indistinguishable from the fox data (Fig. 14). However, as each of the cat data points is based on a large sample it is justified to conclude that the cats exhibit negative switching. This is biologically reasonable; as most cats are domestic they are not under food stress and much of their hunting may have explorative background. The cat data is used to determine parameter values for version III of the predator model.

## SIMULATIONS

#### Simulation program

The simulations were carried out at the Lund University Computer Center using the program SIMNON (Elmqvist, 1977). The subsystem de-

#### TABLE 5

One-species models	Two-species models of systems without diffuse alternative prey	Two-species models of systems with dif- fuse alternative prey	Three-species mod- els
Either of two vole population models (below)	Either of two one species models (column 1) PLUS either of three predator models with starvation mortality (below) <sup>1</sup>	Either of two one species models (column 1) PLUS either of two predator models without starvation mortality (below) <sup>1</sup>	Either of six $(2 \times 3)$ models of a two species system with starvation mortality (from column 2) PLUS either of two models of an alter- native prey popula- tion (below) <sup>2,3</sup>
A vole population without time-lag OR a vole population with time-lag	A predator popula- tion without intra- specific population regulation OR a predator popula- tion with intra- specific population regulation OR a constant predator population	A predator popula- tion without intra- specific population regulation OR a predator popula- tion with intra- specific population regulation <sup>5</sup>	A model of an alternative prey population that grows logistically OR a model of a constant alternative prey population <sup>4</sup>

Simulated combinations of submodels

<sup>1</sup> The different two-species models were simulated with each of the following three predation process models: (1) Hunting in one habitat. (2) D:o with prey refugia. (3) D:o with seasonal variation in hunting efficiency. The model for seasonal variation in prey vulnerability was not used as data did not support the relevance of this option.

<sup>2</sup> The different three species models were simulated with each of the following seven predation process models: (1) Hunting in one habitat. (2) D:o with prey switching. (3) Hunting in two habitats. (4) D:o with habitat switching. (5) D:o with prey refugia. (6) D:o with habitat switching and prey refugia. (7) D:o with seasonal variation in hunting efficiency. <sup>3</sup> The full set of simulations is carried out for the case where neither voles nor alternative prey have a seasonally varying carrying capacity. This option is used for both prey types simultaneously in a limited series of simulations.

<sup>4</sup> If a model of a predator population without intraspecific regulation is used it is obviously irrelevant to use a constant alternative prey. The predator population would grow without limit in such a model.

<sup>5</sup> The distinction between predators with and without diffuse alternative prey has no meaning if the predator population is constant.

scriptions are stored on data files. Commands issued from a terminal make it possible to combine different subsystems into a complete system, choose parameter values, carry out the simulations, and have the corresponding graph drawn on a graphic terminal. The results are permanently recorded by means of a plotter.

# Simulated systems

Logically possible and meaningful combinations of subsystems have been simulated (Table 5). Simulating the *two*-habitat hunting model with predators and only *one* prey (voles) sounds like a contradiction. This model, which was made in order to make the inclusion of an alternative switching process possible, uses other parameter values than does the one-habitat hunting model. However, both models are meaningful in the one-prey case, which is a special case of them. For this case both models use essentially the same equation, after rearranging equations (14)-(16) and (22), (23) and (25), respectively:

$$F_{\rm v} = \frac{F_{\rm max}V}{\frac{F_{\rm max}}{\rm Vul_{\,v}}H_{\rm max}} + V} \tag{32}$$

$$F_{\rm v} = \frac{F_{\rm max}V}{{\rm Fr}_{\rm v} + V} \tag{33}$$

There is an exact correspondence if one assumes that  $Fr_v = F_{max}/(Vul_v H_{max})$ . Actually, the two-parameter value determination approaches yield somewhat different values,  $Fr_v = 17.5 \text{ kg km}^{-2}$  and  $F_{max}/(Vul H_{max}) = 8.9 \text{ kg km}^{-2}$ . For comparison with the two predation process models in the three-species case I have simulated both models also

#### TABLE 6

Modified parameter values used for simulations of the models. Values in parenthesis are used in simulations of the submodel for a constant predator population

Vulv	$0.03 \text{ day}^{-1}$	
av	$0.03  day^{-1}$	
Swpb	0.6	
Fr	$52.5 \text{ kg km}^{-2}$ (75 kg km <sup>-2</sup> )	
Frrv	$26.3 \text{ kg km}^{-2} (37.5 \text{ kg km}^{-2})$	
Ref	$30.0 \text{ kg km}^{-2} (45.0 \text{ kg km}^{-2})$	
Fr	$60.0 \text{ kg km}^{-2} (90.0 \text{ kg km}^{-2})$	
Swhb	0.15	

# TERRITORIAL PREDATOR POPULATION

MODIFIED PARAMETER VALUES PREDATOR POPULATION WITH LOGISTICALLY PPEDATOR POPULATION WITH CONSTANT PREDATOR POPULATION WITH DIFFUSE PREDATOR POPULATION ALONE ALTERNATIVE PREY GROWING ALTEPNATIVE PPEY ALTERNATIVE PREY WITH VOLE POPULATION TERPLITORIAL PPEDACCO TERRITORIAL PREDATOR TERPTIORIAL PREPATOR ONF HABITAL PO OPTIONS ONE HABITAT SWITCHING . TWO HABITATS NO OPTIONS 14 12 TWO HABITATS SWITCHING .... TWO HABITATS PREY REFUGIA minnim TWO HABITATS SWITCHING AND PREY REFUGIA TWO HABIFATS SEASONALITY

Fig. 16. Plots of simulations of the described systems with territorial predators, modified parameter values and a vole population without intrinsic time lag. The arrows point at the vole population graphs.

# VOLE POPULATION WITH TIME LAG AND WITHOUT SEASONALITY

#### TERRITORIAL PREDATOR POPULATION

#### MODIFIED PARAMETER VALUES



Fig. 17. As Fig. 16 but for systems with a vole population with intrinsic time-lag.



Fig. 18. Analysing the effect of seasonal variation in vole and alternative prey carrying capacity. The left column gives simulations of systems with and the right columns systems without seasonal varying carrying capacity. A and B are systems with a vole population without time lag, a predator without intraspecific regulation and an alternative prey with logistic dynamics. C and D are corresponding systems but with a vole population with an intrinsic time lag. A and C are based on the basic two habitat models and B and D includes the option 'seasonally fluctuating functional response'.

in the one-prey case. Despite the difference in parameter values the results are essentially identical for almost all cases (Table 6, Figs. 16 and 17).

The effect of a seasonally varying carrying capacity is studied with a limited set of simulations only (Fig. 18). The different models have been simulated with two sets of parameter values. One is based directly on measured data as described above ('Revinge parameter values') (Table 2). However, for most models it turns out that the two-species systems are not feasable with these values; the vole population is quickly eliminated. The central question in this study, whether alternative prey can stabilize vole cycles, becomes meaningless. Of course it is possible that a two-species system, with voles and the Revinge predator community, is unable to persist. It does, however, seem more likely that the efficiency of the predators has been exaggerated in my parameter value determinations. This would be the case if it were based on underestimated vole-density values. Erlinge et al. (1983) present some evidence that this is so and I therefore, alternatively, assume that vole density is three or five (for the two-habitat and the one-habitat models, respectively) times higher than those presented previously (Table 2). Parameter values affected by this modification have been recalculated. This gives a second set of parameter values ('the modified parameter values') (Table 6). These values give realistic oscillations for the two-species system. Each model is simulated for a duration of 30 years. The simulations were interrupted if the dynamics of the system was obvious after a shorter time. This was done to reduce computer costs.

# **RESULTS AND DISCUSSION**

## Which models are meaningful and realistic?

My criterion for a realistic three-species model is that between-year variation is slight, thus modelling the situation in the Revinge area. Vole populations in meaningful two-species models should be cyclic.

#### Parameter values

Simulations of the three-species models give approximately the same results with both sets of parameter values. Only for one of the models (a constant predator population hunting in one habitat) is there a substantial difference (Table 7, row E vs. F, K vs. L). The model predicts the disappearance of the vole population when the 'Revinge values' are used.

The two-species models *without* intraspecific regulation of the vole population predict that the vole population is exterminated if the 'Revinge values'

**TABLE 7** 

Qualitative characteristics of vole population dynamics as predicted by the different models. In each block I give the result of simulating different predation process models; the one habitat model, ditto with switching, the two habitat model, ditto with switching, ditto with refugia, ditto with switching and refugia, and ditto with seasonal fluctuation in functional response. The upper row in a block gives the result for simulation with the 'Revinge' parameter values and the lower row for simulations with 'modified' parameter values. Cx = cyclicextinctions, C = cyclic, D = damped cycles, K = constant, -- = system not simulated

		Row	Two-species system	System with diffuse alternative prey	System with logistically growing alt. prey	System with constant alt. prey
Vole model without time lag	Predator model without territoriality	A B	$\begin{array}{c} cx - Cx - K - Cx \\ c - C - K - C \end{array}$	$\begin{array}{c} X - X - K - K - X \\ Cx - Cx - K - Cx \end{array}$	XCCCCCC	
	Predator model with territoriality	D C	$\begin{array}{c} Cx - Cx - K - Cx \\ C - C - K - C \end{array}$	$\begin{array}{c} X & -X & -K-X \\ Cx - Cx - K - Cx \end{array}$	X K K K K K K X K K K K K K	X K K K K K K X K K K K K K
	Model of a constant predator population	цц	$\begin{array}{c} X & -X & -K-X \\ X & -K & -K-K \end{array}$		XXKKKKK KKKKKK	X X K K K K K K K K K K K K K
Vole model with time lag	Predator model without territoriality	H G	$\begin{array}{c} C & -Cx & -K-C \\ C & -C & -K-C \end{array}$	$\begin{array}{c} X & -X & -K -X \\ Cx - Cx - K - X \end{array}$	XCCCCCC	
	Predator model with territoriality	J <sup>1</sup>	$\begin{array}{c} C & -Cx - K - C \\ C & -C & -K - C \end{array}$	$\begin{array}{c} X & -X & -K-X \\ Cx - Cx - K - X \end{array}$	X K D K D K D X D D C D C D	X K D K D K D X D D D D D D
	Model of a constant predator population	ГK	$\begin{array}{c} X & -X & -K - X \\ X & -K & -K - K \end{array}$		XKCKCKC DCCDCDC	XKCKCKC DCCDCDC
<sup>1</sup> Figures 16 a.	nd 17, respectively.					

are used (Table 7, rows A, C, and E) but predict a cyclic system (Table 7, rows B and D) or a constant system (only for the two habitat model) (Table 7, row F) if the 'modified values' are used. The two-species models *with* intraspecific vole population regulation predict very regular cycles (Table 7, rows G and I) or extinction of the voles (Table 7, row K) if the 'Revinge values' are used. More irregular and seemingly more realistic cycles are usually predicted if the 'modified values' are used (Table 7, rows H and J).

I consider the set of 'modified parameter values' the most realistic one.

# Predator model

The three-species models predict strong fluctuations of the system if it contains submodels of a predator population that is neither intraspecifically regulated nor constant (Table 7, rows A, B, G, and H). These models are unrealistic with respect to the Revinge system.

The model predicts a constant vole population if the predator population is intraspecifically regulated and the vole population *is not* intrinsically cyclic (Table 7, rows C and D). Weak vole cycles with a 2-year period are predicted if the vole population *is* intrinsically cyclic (Table 7, rows I and J). Both patterns may be fair approximations of the Revinge system. Thus the model can give a qualitatively correct picture of the Revinge system if the predator population is intraspecifically regulated.

The models with a constant predator population predict two-species systems that are constant or where the vole population is exterminated (Table 7, rows E, F, K, and L). This may be correct, as there is no information available on a corresponding natural system (e.g. one with domestic cats as sole predators). This shows that voles are less likely to cycle when interacting with this kind of predator than with more conventional kinds. However, as domestic cats are a minority of the predators in the Revinge area and, most likely, in southern Sweden in general, I do not consider this as an explanation to the absence of vole cycles. Voles are usually able to persist in the system with a constant predator when alternative prey is present. This makes sense as the number of predators is given and the only effect of alternative prey is to relax predation pressure on voles.

# Alternative prey model

In three-species models with a territorial or constant predator population (Table 7, rows C-F, I-L) and a logistically growing alternative prey, the latter is usually predicted to stabilize at a density close to the one measured for the rabbit population in the Revinge area in the years before the decrease, 1075 kg km<sup>-2</sup> (Figs. 16, 17). Modelling the system with an alternative prey that is constant thus gives the same predictions and this appears to be a realistic simplification.

The behaviour of this model together with a nonterritorial predator is not considered as that predator model has been shown to be unrealistic for the Revinge system.

If version I of the predator submodel (no starvation mortality) is combined with a vole submodel this gives a model that I tentatively have labelled a system with 'diffuse alternative prey'. However, unless the refugium option is included, voles are always exterminated in these systems. The reason is that the predator population in these models decreases very slowly, even at very low vole densities. Furthermore, as feeding on the alternative prey is not modelled, the predator always feeds exclusively on voles. Actually, an extreme form of negative switching is assumed (Fig. 4A: 1, 2). This version of the predator submodel is not considered realistic. This result constitutes support for my previous claim (Loman, 1984) that this model (labeled model I in Loman, 1984) is less realistic than the modification with starvation mortality (labelled model III) or the continuous version of that model (model II).

# Predation process model

The switching options affect different models in conflicting ways. The *prey-switching option* sometimes increases realism in the respect that three-species models where the basic models predict extinction of the voles turn to such models where the voles persist (Table 7, rows A–D, G–K). These cases include those two that have been considered most important from the previous results (Table 7, rows D and J, Figs. 16 and 17). In some cases the option has no qualitative effects (Table 7, rows E and F) and in one case it increases cyclicity (Table 7, row L).

The habitat-switching option usually has no qualitative effect. However, it increases cyclicity slightly in one case (Table 7, row J) and decreases it in two (Table 7, rows I and K). This is related to the fact that the basic two-habitat model (on which the habitat-switching option is applied) contains elements of switching itself (Fig. 5).

The introduction of *refugia* gives rise to drastic changes in the two-species models. Very constant systems are predicted. If introduced in the three-species models no important effects are obtained from the introduction of refugia.

The introduction of a *seasonally varying predation efficiency* does not give any changes from the predictions made by the basic models. This conclusion is reached when studying models both without a seasonally varying carrying capacity (Table 7, Figs. 16–17) and models with a seasonally varying carrying capacity (Fig. 18).

The introduction of a *seasonally varying carrying capacity* does not affect the predictions of the model with respect to between-year dynamics. The 306

within-year dynamic becomes, however, considerably more realistic (Fig. 18).

# How realistically can the Revinge system be modelled?

A qualitatively realistic behaviour was shown by a system composed of a territorial predator, a logistically growing (or constant) alternative prey and either of the two vole models. The one-habitat version requires the switching option for a realistic behaviour. In the two-habitat version, no special switching option is required. The use of refugia and seasonality options was tested for this version and found not to increase realism. A comparison of these models' quantitative density predictions and densities actually measured in the Revinge area gives a reasonable agreement (Table 8). This gives some confidence to the approximations made when determining parameter values and choosing functional relations for these models.

## TABLE 8

Predicted equilibrium densities (or mean densities of cyclic populations) for three-species models with territorial predators, logistically growing alternative prey and modified parameter values (column 3 in Figs. 16 and 17). The values that actually were measured in the Revinge area were: Predators (all generalist predators added and recalculated to model predator ( $F_{\rm max} = 1.0 \text{ kg day}^{-1}$ ) units (Table 5))—2.4 ind. km<sup>-2</sup>. Rabbits (before the decrease in the winter 1976/77 that I consider due to factors external to the system)—1075 kg km<sup>-2</sup>. Voles (yearly mean value (Table 3))—20 kg km<sup>-2</sup>. The modified parameter values were based on assumed vole densities of 60 and 100 kg km<sup>-2</sup> (for the two-habitat and one-habitat versions respectively)

		Vole mode time lag	el without		Vole mode time lag	el with	
		Predators	Rabbits	Voles	Predators	Rabbits	Voles
Vole model without time	One habitat model No options	2.5	1100	0	2.5	1100	0
lag	Ditto. Switching	2.5	950	130	2.5	1100	30
	Two habitat model. No options	2.5	1150	130	2.5	1200	120
	Ditto. Switching	2.5	1150	150	2.5	1250	85
	Ditto. Refugia	2.5	1200	120	2.5	1200	120
	Ditto. Switching and refugia	2.5	1150	145	2.5	1250	80
	Ditto. Seasonality	2.5	1200	125	2.5	1200	120





Can the presence of an alternative prey stabilize vole cycles?

Yes, if the predator is territorial it is possible to model a system that is cyclic with only voles and predators present but stable when an alternative prey is present (Figs. 16 and 17).

The version of the alternative-prey models where this is kept constant can be used to give some interesting predictions. If it is correct that vole cycles are absent from the Revinge area because of the presence of rabbits one would expect cycles to appear after the decrease in rabbit density 1976/77. This is especially true as the rabbit density stayed low for several years, even decreasing further to a minimum value in 1979 of 135 kg km<sup>-2</sup>. The top density in 1976 was 1075 kg km<sup>-2</sup>. However, no vole cycles have appeared but in light of the present model this field observation does not contradict the hypothesis. The model predicts a relatively constant vole population both at the top rabbit level (1075 kg km<sup>-2</sup>) and at the low level measured (135 kg km<sup>-2</sup>) (Fig. 19). However, the effect of alternative prey is, as one intuitively assumes, quantitative and not qualitative. A simulation with a constant alternative prey level of 25 kg km<sup>-2</sup> yielded a cyclic vole population (Fig. 19).

# CONCLUSIONS

The presence of alternative prey is a possible explanation for the relative constancy of the field vole population in the Revinge area.

A predator population that by factors external to the system is fixed at a level similar to that of the domestic cat population may stabilize vole cycles.

Switching in a broad sense may contribute to the dampening effect of alternative prey.

The presence of seasonal fluctuations in prey carrying capacity and in prey vulnerability does not affect the between-year dynamics of the vole population. This study does not support the hypothesis that such fluctuations are important for the dampening effect of alternative prey.

This study could only demonstrate a dampening effect from an alternative prey if the predators are territorial (or have other forms of intraspecific regulation). The hypothesis that territoriality increases the probability that alternative prey stabilizes vole cycles is thus supported.

Refugia have a stabilizing effect on all systems, but cyclic two-species systems can be stabilized by the addition of alternative prey even if refugia are not present. The hypothesis that their presence is important for the stabilizing effect of alternative prey is thus not supported. However, refugia and even weaker forms of habitat heterogeneity remain an alternative (to alternative prey), independent explanation for regional differences in vole population cyclicity. The present study is not a critical test in this respect.

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