

INFLUENCE OF TERRITORIALITY ON THE STABILITY AND CO-EXISTENCE OF COMPETING PREDATORS — A SIMULATION STUDY

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ABSTRACT

Loman, J., 1985. Influence of territoriality on the stability and coexistence of competing predators — a simulation study. *Ecol. Modelling*, 27: 95–108.

A system of two predators and one prey population was studied by simulations of two different models. The two predators were able to coexist if they had a similar ability to withstand low prey densities and if prey carrying capacity was not too high. Coexistence was also promoted if the predators had a tendency to self-regulation (e.g. territoriality). These factors also, in general, increased the stability (= numerical constancy) of the system.

INTRODUCTION

This is a study of the regulatory effect of prey for predator populations and how this is modified by predator efficiency, capacity of population growth and territoriality. These phenomena are studied by means of a model representing a simplified system, containing two predators and one prey species. Important characteristics of predator–prey systems are diversity and stability. Here, coexistence of the two predators corresponds to high diversity. Stability is a loose term that has been defined in several ways: it is here used to represent a system in numerical constancy.

It was earlier considered that two predators could not coexist if they were feeding on the same prey populations (Volterra, 1928; Levin, 1970). Later it was shown that this is true only of the feeding rates of the predators increase linearly with prey density (Armstrong and McGehee, 1976). This is probably an unrealistic situation for most vertebrate predators. Rather, feeding rate increases at a rate that decreases with increasing prey density (Keith et al., 1977, p. 164).

A model of a two-predator–one-prey system where coexistence between predators is possible under some conditions was studied by Hsu et al. (1978). Parameters that were studied in their analysis were the efficiency of the predators (measured as minimum prey density required for population growth) and the predators intrinsic rate of increase. They used a combination of analytic and simulation techniques in their study. In the present study I extend the scope by treating the importance of predator territoriality. For comparative purposes predator efficiency and intrinsic rate of increase are also treated. The simulations are further carried out for two different models, which differ in detail but are comparable (Loman, 1984). It should thus be possible (to some extent) to separate general patterns from peculiarities of each model.

Simulation versus analysis

The properties of a model can be studied by means of a mathematical analysis where the conditions for different cases (like coexistence and stability) can be completely determined and described. The different parts of the parameter hyperspace must, for the description, be delineated by hypersurfaces that are mathematically defined. For complicated systems, such an analysis may be difficult or impossible. Simulation of a model for a sample of points in the parameter hyperspace in such cases gives an impression of the essential features of the system.

There is another aspect of the choice between analysis and simulation. An analysis does not (usually) in itself give information about the time taken for the system to reach a steady state (constant equilibrium or limit cycles) nor about the magnitude of the cycles. This is probably a very important aspect in the real world as systems are influenced by factors other than those built into the model. If simulation shows that the time taken for exclusion of a species is 100 years, this species is much more likely to persist in the system than if the simulation shows that the species is excluded in 1 year. Also, if the model system exhibits damped cycles that stabilize only after 100 years ($d(c)$ in Fig. 1), it is much more likely to be permanently cyclic in the real world than if the cycles are damped in 10 years (d in Fig. 1). One can allow for such considerations by choosing simulation periods of different lengths. A long period stresses the internal properties of the system while a short one gives more weight to external influences. A short period is unfortunately very sensitive to the choice of initial values. In the present study I have made a subjective compromise, maybe biased towards a long simulation time (approximately 30 years).

It is not my opinion that simulation is superior to analysis, only that the two methods have different qualities.

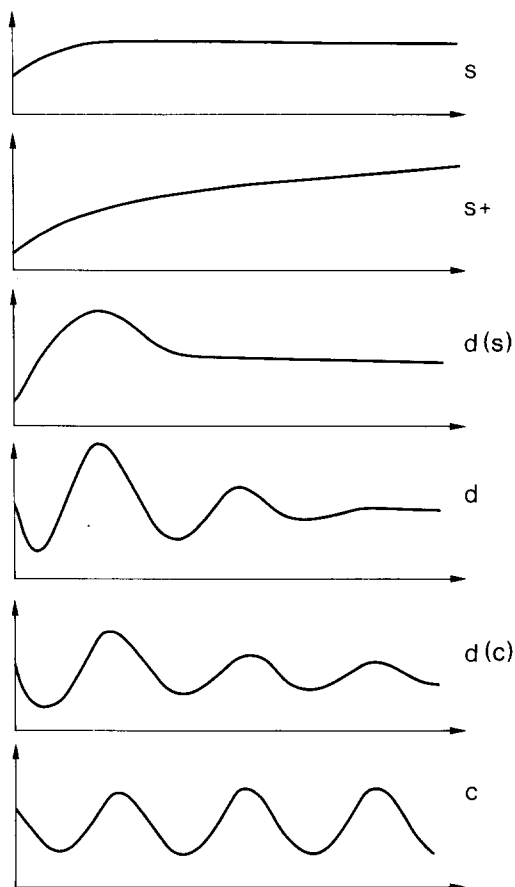


Fig. 1. Different kinds of dynamics exhibited by the populations in the simulations. The abbreviations are used in the text.

METHODS

Model I. This model is given by the equations (see Appendix):

$$\frac{dV}{dt} = Vr_{\max(v)}(1 - V/K) - F_p P - F_q Q \quad (1)$$

$$\frac{dP}{dt} = P(b - d) \quad (2)$$

$$b = \frac{F}{F_{\max}} \left(b_{\max} - r_{\max} \frac{P}{Ki} \right) \quad (3)$$

$$b_{\max} = r_{\max} + d \quad (4)$$

$$F = \frac{F_{\max} V}{Fr + V} \quad (5)$$

Equation (1) is a standard equation for resource limited prey species which are also subject to predation. Equation (3) is a modification of the equation:

$$b = \frac{F}{F_{\max}} b_{\max} \quad (6)$$

that was used by Hsu et al. (1978). This modification was made to make it possible to simulate territoriality: eq. (3) is identical to eq. (6) if $P = 0$, thus there is no selfinhibition of population growth at zero density. Equations (3) and (4) can be rewritten as:

$$dP/dt = P \left(\frac{F}{F_{\max}} (b_{\max} - r_{\max}) - d \right) \quad (7)$$

if $P = Ki$. According to this expression, dP/dt is always less than or equal to 0, with equality for predators feeding at their maximum rate ($F = F_{\max}$). The population can thus have an equilibrium for $P = Ki$ if prey is not limiting (cf. eq. (5)), otherwise equilibrium densities are less than Ki . Equation (5) was originally suggested by Holling (1965).

Model II. This model is given by the equations:

$$dV/dt = Vr_{\max(v)}(1 - V/K) - F_p P - F_q Q \quad (8)$$

$$dP/dt = P \max(r, -d) \quad (9)$$

$$r = r_{\max(p)} \left(2 - \frac{F_{\max}}{F} \frac{P + Ki}{Ki} \right) \quad (10)$$

$$F = \frac{F_{\max} V}{Fr + V} \quad (11)$$

Equation (8) is identical to eq. (1). Equations (10) and (11) are modified from an equation by Tanner (1975):

$$dP/dt = Pr_{\max(p)} \left(2 - \frac{F_{\max} - F_{\min}}{F - F_{\min}} \right) \quad (12)$$

The modification has been done by setting F_{\min} at 0, by introducing a minimum growth rate ($-d$) and by adding a factor that makes it possible to model territoriality ($((P + Ki)/Ki)$): r can never be positive if $P = Ki$ and the population cannot increase above this density (Ki). Equation (10) is identical to the corresponding part of eq. (12) if $P = 0$ and at low densities territoriality does thus not influence the population growth. The introduction of a minimum growth rate, corresponding to the rate of decrease if no food is available facilitates simulations and is probably realistic. Feeding rate (eq. (11)) is modelled in the same way as in model I.

Predator efficiency

λ is defined as the prey density at which a non-territorial predator population is in equilibrium and is called ‘predator efficiency’. A low λ value represents high efficiency. It can be shown that $\lambda = Fr$ in model I and that $\lambda = Frd/r_{\max}$ in model II. I wish to give λ the nature of a parameter that is varied in the simulations and therefore the following definitions are added to models I and II, respectively:

$$Fr = \lambda \quad (13)$$

and

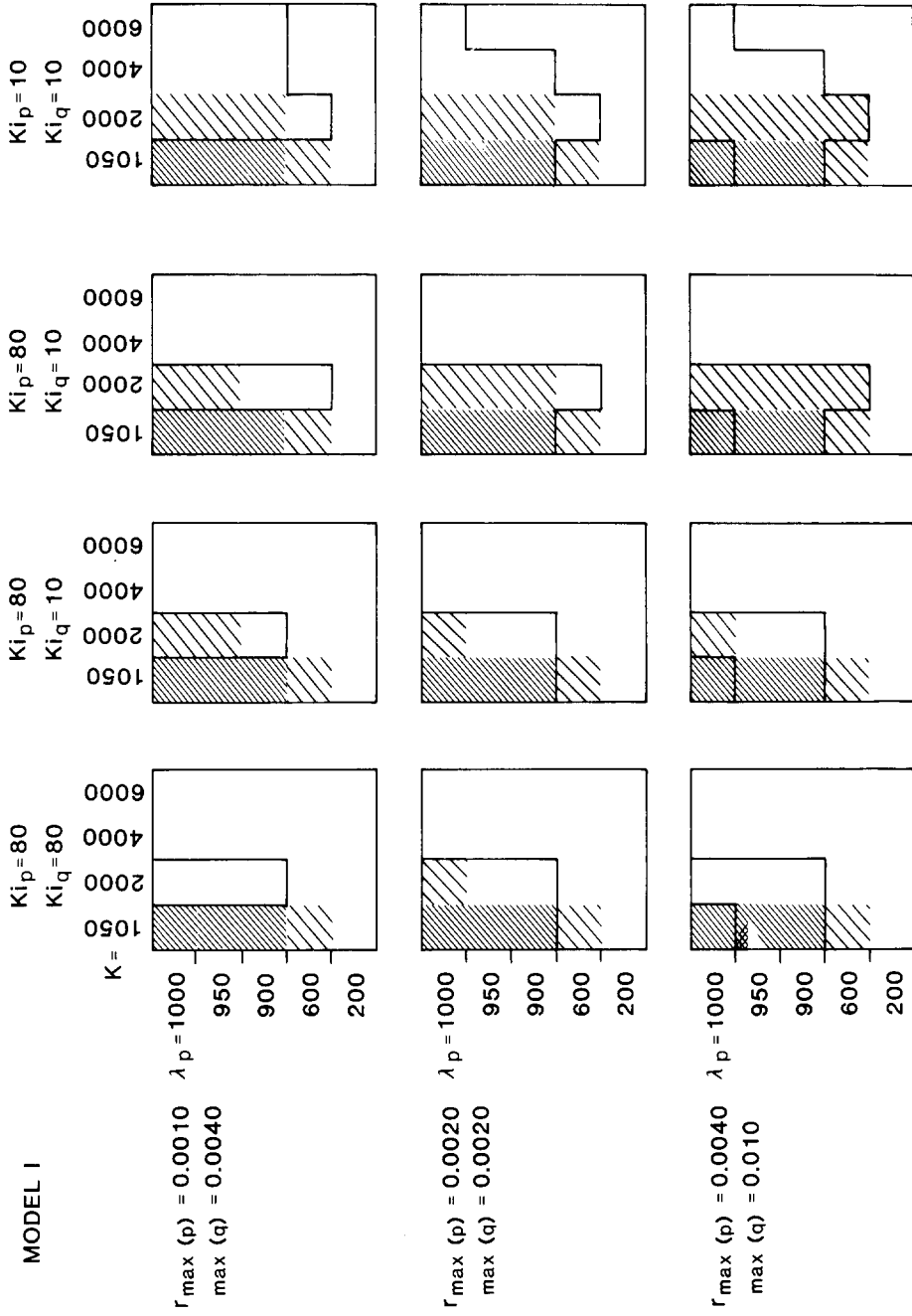
$$Fr = \lambda r_{\max}/d \quad (14)$$

Parameter space

Preliminaries. In this study I am mainly concerned with trends in stability and coexistence following changes in degree of territoriality. The exact choice of parameter values is thus not very important for the conclusions drawn. However, as the models are composed of equations that are thought to model biological processes one would expect them to produce biologically meaningful results for at least some biologically reasonable parameter values. If, for example, stable or moderately fluctuating communities were predicted by a model for quite unrealistic parameter values only, one would doubt the usefulness of this model. Here, it is shown that the parameter values used in the simulations are from biologically meaningful ranges. One test of the models as such is thus whether the patterns predicted are, at least sometimes, biologically realistic.

r_{\max} and d . Tanner (1975) gives r_{\max} as 0.0013–0.0027 (recomputed with days as time unit) for four vertebrate predators (mink, mountain lion, wolf and lynx). For *Microtus agrestis* r_{\max} has been calculated as 0.012 (Leslie and Ranson, 1940) and for another prey species, the european rabbit as 0.0052 (G. Jansson, personal communication). This suggests that the chosen values (0.001, 0.002, and 0.004 for predators and 0.008 for prey) are from a realistic range. d is the population rate of decrease when no food is available. No field estimate of this parameter is available. The chosen value (0.035) corresponds to a population which decreases by 50% every 10 days; this should at least be in the right order of magnitude.

F_{\max} and Ki . F_{\max} is essentially a scaling factor. A value of 1 (e.g. 1 kg/day) was used as an arbitrary choice. In a field situation when food was very



abundant, feral cats consumed approximately 500 g of prey per day. Their normal intake was 250 g/day (Liberg, 1981). If F_{\max} can be set to about twice the normal intake for other predators, the density of territorial predators in a study area in south Sweden can be computed in terms of 'standard predator units' (with $F_{\max} = 1.0$ kg prey per day). Combining the density of the territorial predators buzzard, fox and cat, this density was 1.9 units per km^2 (from information in Erlinge et al., 1983). The three considered predators dominate the guild of rodent predators. Supposing that the observed density can be multiplied a few times under optimal food conditions before territoriality stops further population increase, 10.0 units is a reasonable choice for K_i . On the other hand, a territorial behaviour that only stops the predator population from growing as it approaches a density of 80 is not likely to be of practical importance, food should set a much lower limit to population growth.

K , λ_p and λ_q . Determining K and λ empirically is difficult. However, the outcome of the analysis only depends on their relative value (λ/K) (first paragraph in the results section on stability). The choice made for these parameters is such that all interesting parts of the parameter space is covered. For more extreme values than those studied, the system is obviously unstable (Figs. 2 and 3) or the predators become extinct by definition (third paragraph of the discussion section on coexistence).

Summary of parameter values

The two models were simulated with the following fixed parameter values: $F_{\max(p)} = F_{\max(q)} = 1.0$, $r_{\max(v)} = 0.0080$, $d_p = d_q = 0.035$, $\lambda_q = 1000$. The time unit was days and simulation time 10 000 d (about 27 ys). Simulations were started with a prey density of 500 for both models. Initial predator densities were 2 for model I and 10 for model II. The following parameters were varied: Ki_p , Ki_q , $r_{\max(p)}$, $r_{\max(q)}$, K , and λ_p .

Ki_p and Ki_q respectively were set at 80 (virtually no territoriality) 10 (territoriality), four combinations in all. $r_{\max(p)}$ and $r_{\max(q)}$ were both set at

Fig. 2. Results from simulations of model I. The boxes represent the twelve possible combinations of degree of territoriality and predator intrinsic rate of increase. The break-even point for the Q predator's population growth is always set to 1000. The values of λ_p and prey carrying capacity (K) are varied within the boxes. Cross-hatched area represent part of the parameter space where the populations are stable (constant or asymptotically approaching a constant value) by the end of the simulation period (s , $s + d(s)$ or d). Of this, the light cross-hatched part represents parts where the populations initially oscillate ($d(s)$ and d). The area within (above) the line represents parts where the two predators are able to coexist.

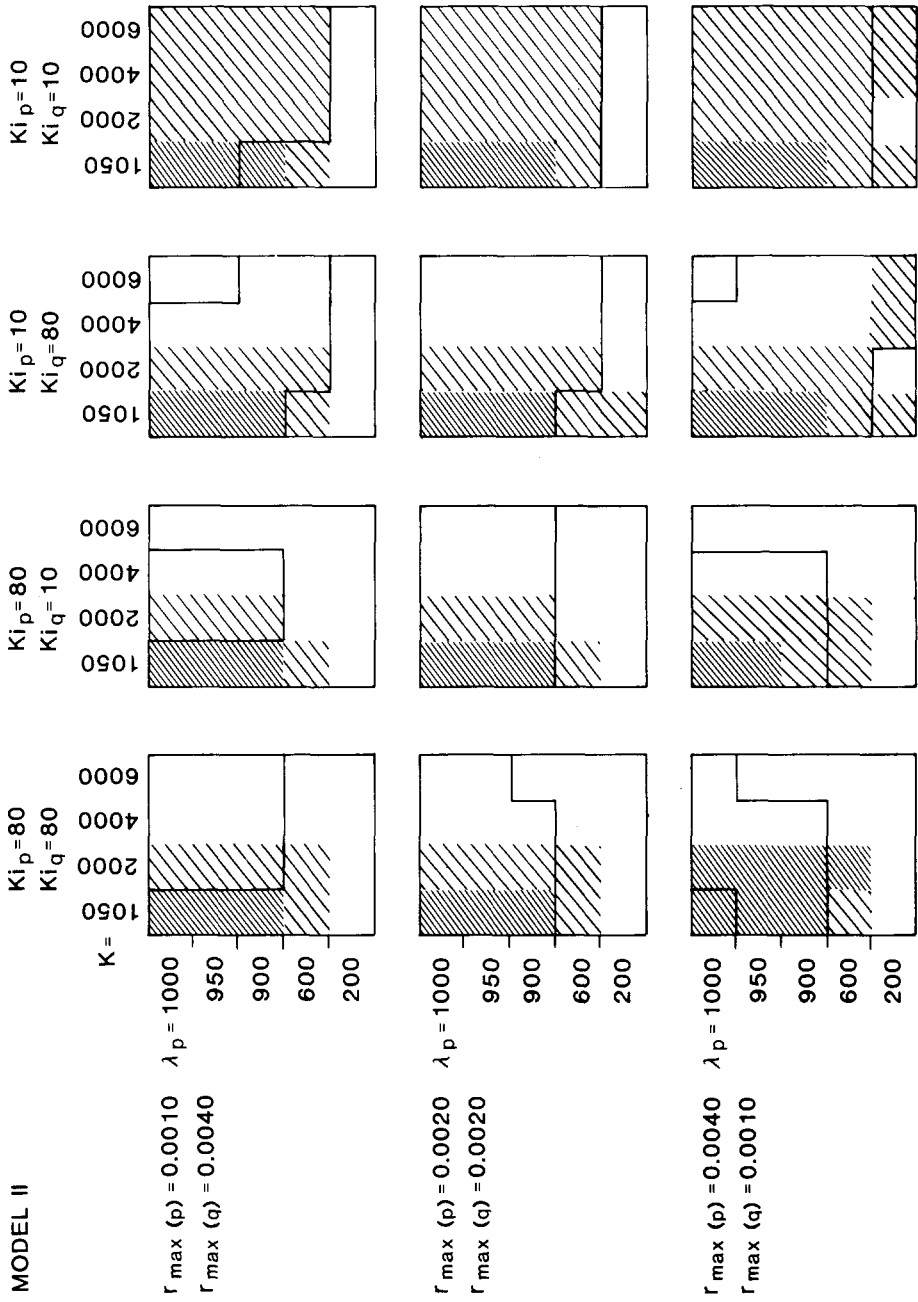


Fig. 3. Results from simulations of model II. For explanations, see Fig. 2.

0.0020 or one at 0.0010 and the other at 0.0040, three combinations in all. Varying K_i and R_{\max} thus yielded 12 combinations. For each of these K was set at 1050, 2000, 4000, or 6000 and λ_p to 1000, 950, 900, 600, or 200. A total of 12 times 16 simulations were thus made for each model. In both models, P was ($\lambda_p \leq \lambda_q = 1000$) the predator that was able to maintain an equilibrium population on the smaller prey density.

Interpretations

The dynamics of the predator populations were noted for each simulation. Populations that were stable by the end of the simulations time (Fig. 1: s , $s +$, $d(s)$, and d) were classified as stable and those that still cycled (Fig. 1: $d(c)$ and c) as cyclic. Coexistence was subjectively defined as the situation where no predator population decreased below 0.05 individuals per unit area. I analyzed another, more liberal, criterion, viz. accepting those situations where a predator periodically dropped below 0.05 but not below 0.01 as cases of coexistence. The conclusions drawn from that analysis were however not different, so for simplicity only the first analysis is presented here.

RESULTS

Coexistence

Coexistence was most common in both models if both predators had a similar efficiency (the upper part of the boxes in Figs. 1 and 2). Also, it was most common if prey carrying capacity was *not* low or very high (as to the right and left in the boxes). The effect of low carrying capacity was not a matter of scale as one could have expected when coexistence, as here, is defined in relation to a fixed level. Actually, the density of the more scarce predator increased manyfold when prey carrying capacity increased from 1050 to 2000 (Table 1).

Coexistence was possible for a wider range of λ_p and K values if both predators were territorial than if none were (31 cases vs. 14 and 45 vs. 29 for model I and II, respectively). If only the less efficient predator was territorial coexistence did not increase (14 and 26 cases of coexistence, respectively) and if the most efficient predator was territorial, coexistence was somewhat more common than if neither was (19 and 41 cases, respectively).

Coexistence was in both models more common if the predators had a similar intrinsic rate of increase (30 and 52 cases of coexistence for models I and II, respectively) or if the more efficient predator also had the higher rate (28 and 51 cases, respectively) than if the least efficient predator had the higher intrinsic rate of increase (20 and 38 cases, respectively).

TABLE 1

Equilibrium densities of the two-predator populations at two levels of prey carrying capacity

		K = 1050		K = 2000	
		P	Q	P	Q
$r_p = 0.0010$	Model I	0.51	0.09	1.17	6.04
$r_q = 0.0040$	Model II	0.52	0.03	1.18	3.16
$r_p = 0.0020$	Model I	0.30	0.43	1.07	6.12
$r_q = 0.0020$	Model II	0.32	0.21	1.10	3.14
$r_p = 0.0040$	Model I	0.07	0.88	1.06	6.11
$r_q = 0.0010$	Model II	0.10	0.50	1.11	3.06

$Ki_p = 10$, $Ki_q = 80$, $\lambda_p = 950$, $\lambda_q = 1000$ in all simulations.

Stability

Stability decreased (i.e. limit cycles were less common) if prey carrying capacity increased or the efficiency of the most efficient predator increased (Figs. 2 and 3). In fact, variation in both predators' efficiency was studied; this was a matter of scaling as simulating the models with parameter values $K = 1050$, $\lambda_p = 300$ and $\lambda_q = 500$ gave the same result as with values $K = 2100$, $\lambda_p = 600$ and $\lambda_q = 1000$.

The relative intrinsic rate of increase did not greatly influence stability. If P had the lower intrinsic rate of increase 23 and 39 simulations were stable for models I and II, respectively; if the predators had a similar rate 24 and 40, respectively; and if Q had the lower rate 23 and 46, respectively, were stable. The influence of the overall level of predator intrinsic rate of increase was not studied, however.

Model I was more stable if the more efficient predator was territorial, regardless of the properties of the other one (21 stable cases for both combinations), than if it was not territorial (16 stable cases).

DISCUSSION

Interpretation of the results

Stability. The cyclicity of the system at high prey carrying capacity and high predator efficiency is an example of "the paradox of enrichment" (Rosenzweig, 1972).

Coexistence. Elimination of the inferior competitor at high prey carrying capacity (to the right in the boxes of Figs. 2 and 3) is related to the high degree of cyclicity (large amplitude cycles) that the system has for these

parameter values. The predator that reaches the lowest densities has no time to recover during the time of high prey density: one predator increases and causes the other prey to reach a further 'low' too soon.

Elimination of the inferior competitor when the other is too efficient (low λ_p) (in the low part of the boxes, Figs. 2 and 3) takes place because the efficient predator decreases the prey density to a low level, below the density required for population increase of the outcompeted predator. This is the classical form of competitive exclusion (Volterra, 1928; MacArthur, 1972).

One of the predators (Q) is easily eliminated at low prey carrying capacity (to the left in the boxes). This is because it is, by definition, close to being eliminated also without competition ($\lambda_q = 1000$). $K = 1000$ was not even included in the analyzed parameter space as one predator by definition had a non-positive equilibrium density for this prey carrying capacity.

It should be noted that systems that were stable only after initial oscillations had damped (Fig. 1: $d(s)$ and d) are those that are most likely to hold coexisting predators (Figs. 2 and 3). This corresponds to the finding by Hsu et al. (1978) that all systems with coexisting predators were cyclic.

Fr and λ —two measures of predator efficiency

Hsu et al. (1978) found that coexistence is possible only if one of the predators is an efficient hunter (low Fr) and the other has a high intrinsic rate of increase (high r_{\max}). A corresponding pattern should in this study, have appeared as a higher tendency for coexistence if $r_{\max(p)} = 0.001$ and $r_{\max(q)} = 0.004$ than for any other combination of r_{\max} values but this was not observed. This is partly due to differences between the two models as Hsu et al. (1978) did not analyse model II. This model has the property that a high intrinsic rate of increase also leads to a high rate of decrease at low prey densities. This correlation is probably not too unrealistic and counteracts the advantage from a high intrinsic rate of increase for this predator.

As to model I, the superficial discrepancy is due to differences in the scaling of the studied parameter space. I chose for both models λ as an independent measure of efficiency. This is a measure of the predators' 'survival efficiency' at low prey densities. Hsu et al. (1978) used Fr as a measure of efficiency. This is a measure of the predators feeding efficiency at low prey densities. The analysis of model II is facilitated by the fact that these measures are interchangeable (Eq. 13). In model I the relation is affected by the values of the parameters r_{\max} and d (Eq. 14). λ was chosen as an independent measure variable which makes it easier to delineate the studied parameter space so that meaningless simulations are avoided ($\lambda > K$). However, re-analysing model I with emphasis on variation in Fr reveals the same kind of relation as found by Hsu et al. (Table 2). When $r_{\max(q)} > r_{\max(p)}$,

P is in this study always much more efficient (sensu Hsu et al., 1978) than Q ($Fr_q > Fr_p$) and P eliminates Q . When $r_{\max(p)} > r_{\max(q)}$, Q is more efficient (sensu Hsu et al., 1978). If Q is much more efficient ($Fr_q = 28$, $Fr_p = 114$) Q eliminates P but if the difference is less ($Fr_q = 28$, $Fr_p = 109$ or 103) the two predators coexist. The finding is thus corroborated but the generality of the result somewhat decreased as it only applies for one model.

Empirical testing

The main conclusion from this study is that communities of territorial predators are more likely to be stable and likely to contain more species than communities of non-territorial predators.

Empirical tests of this proposal require a numerical quantification of territoriality. Such a measure could possibly be based on population growth at different density levels, while controlling for prey density. Given such a measure, different communities could be compared with respect to diversity and stability.

TABLE 2

Equilibrium values for the two predators

			Equilibrium densities	
			P	Q
$r_{\max(p)} = 0.001$ $r_{\max(q)} = 0.004$	$Fr_q = 114$ ($\lambda_q = 1000$)	$Fr_p = 28$ ($\lambda_p = 1000$)	0.52	0.02
		$Fr_p = 27$ ($\lambda_p = 950$)	0.72	0.01
		$Fr_p = 26$ ($\lambda_p = 900$)	0.96	0.00
		$Fr_p = 17$ ($\lambda_p = 600$)	2.09	0.00
$r_{\max(p)} = 0.004$ $r_{\max(q)} = 0.001$	$Fr_q = 28$ ($\lambda_q = 1000$)	$Fr_p = 114$ ($\lambda_p = 1000$)	0.02	0.52
		$Fr_p = 109$ ($\lambda_p = 950$)	0.13	0.48
		$Fr_p = 103$ ($\lambda_p = 900$)	0.48	0.40
		$Fr_p = 69$ ($\lambda_p = 600$)	2.25	0.00

Simulations are arranged according to Fr_p values. Parameter values used in these examples are $K = 1050$, $Ki_p = Ki_q = 80$ and the r_{\max} values given in the table.

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APPENDIX

b	Predators' birth rate
d	Predators' death rate when no food is available
F	Feeding rate of the predators (prey units per predator individual and time unit)
F_{\max}	Maximum feeding rate of a predator
Fr	A parameter in the functional response equation (they prey density which gives a feeding rate that is 50% of F_{\max})
K	Carrying capacity for the prey population
Ki	An index of predator territoriality (the density that the predator population approaches when prey density is unlimited)
P, Q	Densities of the predator populations
r	Per capita rate of increase, e.g. $(dP/dt)/P$
r_{\max}	Intrinsic rate of increase
V	Density of the prey population
λ	A measure of predator efficiency (the prey density that permits a predator population to stay in equilibrium)

P , Q and V are state variables (these letters are also used when referring to the populations); d , F_{\max} , K , Ki , λ and r_{\max} are independent variables (parameters); b , F , Fr , k and r are dependent variables.

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