



Are Classical Predator–Prey Models Relevant to the Real World?

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Mathematical models of predator–prey population dynamics are widely used for predicting the effect of predators as biocontrol agents, but the assumptions of the models are more relevant to parasite–host systems. Predator–prey systems, at least in insects, substantially differ from what is assumed by these models. The main differences are: (i) Juveniles and adults have to be considered as two different entities, as the former stay within a patch and do not reproduce, while the latter move between patches of prey and reproduce there. (ii) Because of their high mobility, food availability is likely to be less restrictive for adults than juveniles, which are confined to one patch. Therefore, a functional response to prey abundance may not be important for adults. (iii) Egg and larval cannibalism are common in insect predators. Therefore, the quality of patches of prey for their larvae determines the reproductive strategy of adult predators more than the availability of food for the adults. Here we develop a new model, based on the above considerations, which is suitable for modelling these interactions. We show that selection should favour mechanisms that enable predators to avoid reproducing in patches with insufficient prey and those already occupied by predators.

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Introduction

Mathematical models of population dynamics are widely used to predict the behaviour of predator–prey systems, in particular their stability and the outcome of introducing natural enemies for the biocontrol of pests (Beddington *et al.*, 1976, 1978; Hassell, 1978; Godfray & Hassell, 1987; Murdoch, 1994). In spite of the great and long-standing interest in these models, there has been little success in, e.g. using them to account for why insect predators, compared with parasites, have generally not been very effective

in suppressing the numbers of their prey (Hafez, 1961; DeBach, 1964; Bombosch & Tokmakoglu, 1966; Galecka, 1966; Coderre, 1988; Milne, 1988; Campbell & Cone, 1994; Dixon *et al.*, 1995, 1997; Ferguson & Stiling, 1996) why predators lay so many eggs, although most of them are subsequently cannibalized (Fox, 1975; Mills, 1982; Osawa, 1989, 1991, 1992a, b, 1993; Hironori & Katsuhiko, 1997; Yasuda & Ohnuma, 1999), and for defining the important characteristics of a successful predator.

All of the many and diverse models of predator–prey dynamics have a lot in common. Voracity of each predator individual is thought to be dependent mainly on prey density (functional response), sometimes on the density of the

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predator itself (Hassell, 1978; Mills, 1982). Predator fecundity is often modelled as a function of the amount of food consumed (numerical response—e.g. Coderre, 1988). Thus no difference is made between the individual developmental stages of the predator in the hope that assuming a stable age distribution will not affect the model's predictions (Hassell, 1978). Similarly, all predators and prey are assumed to interact with each other, thus other patches with the same species, and migration between patches, are ignored in the hope that the resulting population dynamics will be similar everywhere. Once modellers take into account either age distribution or a multi-patch situation, they have to give up other assumptions or at least ignore these additional ones (e.g. Hanski, 1983), otherwise the models would very soon become intractable even if simulations are used.

McCauley *et al.* (1996) are an exception—they use individual-based models to examine how differences in mobility of age-structured predator populations affect the spatial and temporal dynamics of predator–prey populations and in this sense are substantially approaching reality. However, they—as well as most others—concentrate only on conditions for stability of these systems, not on their evolution and non-equilibrium dynamics.

What is the situation in the real world? Considering only insects, on which biological control is regularly practised, the above assumptions may be satisfied in insect host–parasitoid systems in confined and limited spaces (e.g. a greenhouse), for which these models were originally developed (Hassell, 1978). In these systems, the parasites may—in theory—complete their development within one patch of prey, reproduce there and thus coexist for several generations of both parasite and host. This may result in an asymptotical approach to a stable age distribution and no migration. When space is unlimited, which is the natural situation, and especially when insect predators, *sensu stricto*, are considered, the picture is completely different.

Few would disagree that juvenile and adult insects differ in that the latter can fly while the former cannot. Thus there is an important assumption that has to be incorporated into

models of insect population dynamics: juveniles (larvae) stay within one prey patch, while adults may not, and therefore juveniles and adults have to be considered as two different entities. Patch in this sense means the space that a larva of a predator can reach by walking, usually one or only a few adjacent plants, or even only a part of an individual plant as in the case of plants, like trees.

Adults and larvae differ in behaviour, which is not consistent with what is usually assumed in classical predator–prey models. Juvenile (larval) voracity can be considered as a function of prey density, but juveniles do not reproduce. Thus juveniles can show a functional response but not a numerical response. Adult fecundity is a function of the amount of prey eaten (Hemp-tinne *et al.*, 1992), but they can easily fly from one patch to another, and are very effective at finding host patches. Therefore, food availability seems to be much less restrictive for adults than juveniles, which are confined to one patch. Thus, although adult insect predators show a functional response, in most natural situations they are likely to find enough prey for satiation and therefore, food availability is unlikely to be the main restrictive factor for adults.

There are three different factors that determine the strategies of adult predators to a much greater extent than availability of food in a patch of prey: (1) Because of seasonal changes in vegetation, the duration of prey patches is time limited—usually only a few months. Predator developmental time tends to be much longer than that of its prey and comparable with the average duration of a patch of prey (Dixon *et al.*, 1997; Kindlmann & Dixon, 1993, 1999a, b). Thus, it is wasteful in terms of energy for predators to lay eggs in an old prey patch, as these eggs are unlikely to complete their development before the patch disappears. (2) As shown by Kindlmann & Dixon (1993), there should be a selective advantage in optimizing the number of eggs laid by one predator in a patch of prey. This is because—as stated above—predator developmental time is similar to the duration of a patch of prey. If too many eggs are laid per patch, the larvae of the predator may reduce the rate of increase of its prey, cause an earlier decline in prey abundance, and thus food

may become scarce before the larvae complete their development. (3) Cannibalism is common in insect predators (Fox, 1975; Osawa, 1989, 1991, 1992a, b, 1993), and in nature often reduces juvenile survival dramatically, as only about 1% of the eggs laid in a patch may survive (Osawa, 1989; Agarwala & Dixon, 1993). It was shown that cannibalism can be selected for and that even sibling cannibalism may have a selective advantage, if prey becomes scarce (Osawa, 1991, 1992b). To avoid cannibalism, adults should avoid patches of prey where there are older (and hence stronger) conspecifics.

Combination of (1), (2) and (3) results in a theoretical prediction that there should be strong selection for predators to lay their eggs only in patches in the early stages of development and avoid those containing conspecific larvae. This prediction is empirically supported by the discovery of an oviposition deterring pheromone that deters adults from laying eggs in patches contaminated with conspecific larval tracks. This has been found in many predatory groups (Hemptinne *et al.*, 1993; Doumbia *et al.*, 1998). Thus the reason why adults migrate between prey patches so frequently is that it enables them to optimize the distribution of their eggs (numerical response), rather than optimize foraging in the terms of maximizing food consumption per unit time (functional response). This numerical response, however, differs from that normally used as it reflects the ages of patches of a prey, rather than the amount of food they contain. It is surprising that this was completely ignored in the models of predator-prey population dynamics.

Here we investigate the following problems: (i) If cannibalism is responsible for as much as 99% mortality in natural populations, then why have predators not been selected to produce larger but fewer offsprings. (ii) In addition, predators should also evolve mechanisms that enable them to avoid reproducing in patches that contain insufficient prey and, as shown above, in patches already occupied by predators. What is the relative importance of these two life history trends and the conditions favouring their selection? This will be explored using a new metapopulation model, based on the above considerations, which—unlike the classical

models—is suitable for modelling true predator-prey interactions, as it reflects what is going on in natural systems.

The Evolutionary Model

BIOLOGICAL ASSUMPTIONS

In a natural predator-prey metapopulation, there are two thresholds: a lower threshold for the population size of prey in a patch (Kareiva, 1990) and the presence of larval tracks that deters oviposition (Doumbia *et al.*, 1998; Hemptinne *et al.*, 2001), mathematically speaking, constitutes an upper threshold for the population size of predators in a patch. Below the lower threshold of prey, the predator offspring might starve, above the upper threshold for predators there is a large risk of predator offspring being eaten by conspecifics.

If adult predators are abundant, then it is likely that adults will find lots of patches that are not suitable for reproduction, as they do not meet the threshold requirements. As eggs inside a predator are continuously developing an adult eventually runs out of time, "reluctance" to lay eggs in unsuitable patches declines.

MODEL DESCRIPTION

Kindlmann & Dixon (1993) published the within-patch component of this model. This states that at the instant when a prey patch ceases to exist the numbers of prey and predator is uniquely determined by the initial numbers. Here we shall concentrate on the model component describing the between-patch dynamics. The model construction is as follows:

Evolution of three life history traits (egg size, minimum number of prey necessary for oviposition, maximum number of predators acceptable for oviposition) in a predator population was followed for N generations. In each generation, it was assumed that the n patches are first colonized by prey, then by predators. Once colonization is over, the future of a patch is determined by the within-patch component of the model.

We assume that a total of n patches are sequentially colonized by prey individuals, the total number of which is x . Each patch is chosen

at random. In the model this was assured by sequential selection of x random numbers from a uniform distribution on the interval $\langle 0, n \rangle$. The total number of prey individuals in i -th patch was increased by 1, whenever this random number was in the interval $\langle i-1, i \rangle$.

After that, the n patches were sequentially “colonized” by predators. It was assumed that in each generation, j , there exist two predator phenotypes, A_j and B_j , which colonize patches at random. Each of the phenotypes avoids patches where prey is scarce or predators abundant for the reasons described in the previous section. This was technically done in the model as follows:

1. The phenotypes, A_j and B_j , were characterized by the following three generation-specific values, which were assumed to be subject to evolution:

1.1. s_{Aj} for phenotype A_j and s_{Bj} for phenotype B_j —size of a newborn predator (egg),

1.2. x_{Aj} , respectively x_{Bj} —the lower population threshold of prey in a patch, below which a predator will not lay eggs,

1.3. y_{Aj} , respectively y_{Bj} —the upper population threshold of predators in a patch, above which a predator will not lay eggs,

2. We assumed that each phenotype produces the same total offspring biomass M . Thus, the number of offspring in each generation was M/s_{Aj} for phenotype A_j and M/s_{Bj} for phenotype B_j . The predators “colonized” patches sequentially:

2.1. In order to keep on average the above-mentioned proportion of phenotypes in offspring numbers, a random number z was chosen from $\langle 0, 1 \rangle$. If $z < M/s_{Aj}/(M/s_{Aj} + M/s_{Bj})$, it was assumed that the predator searching for a patch in which to lay an egg was of phenotype A_j , otherwise it was assumed to be of phenotype B_j .

2.2. A patch was chosen at random in the same manner as it was colonized by prey.

2.3. If the total number of prey individuals was lower than x_{Aj} , respectively x_{Bj} , or if the total number of predator individuals is higher than y_{Aj} , respectively y_{Bj} , then the

predator was assumed not to reproduce and go to another patch—step 2.2 is repeated but the predator is assumed to become less “reluctant” to lay an egg and the tendency to reproduce to increase with each unsuccessful attempt to find a patch, the values x_{Aj} , respectively x_{Bj} , were divided and the values y_{Aj} , respectively y_{Bj} , were multiplied by the “reluctance” factor R from the interval $\langle 0, 1 \rangle$.

2.4. This was repeated for a maximum number of trials, NT , or until a suitable patch with more than x_{Aj} , respectively x_{Bj} , prey individuals and less than y_{Aj} , respectively y_{Bj} , predators was found. In the latter case, the number of predators in this patch was increased by 1.

2.5. The procedure 2.1–2.4 was repeated $M/s_{Aj} + M/s_{Bj}$ times.

3. Cannibalism is a consequence of larval competition, the strength of which is negatively correlated with food (prey) availability.

3.1. After the procedure 2.1–2.5, each of the patches was colonized by a mixture of A_j and B_j phenotypes: in each patch, k , there were x_k prey individuals, p_{Ak} phenotype A_j predator individuals and p_{Bk} phenotype B_j predator individuals. If $p_K - p_{Ak} + p_{Bk}$, then it is reasonable to assume that the proportion of predatory larvae surviving to adulthood for each of the phenotypes will be:

$$pr_{Ak} = \frac{p_{Ak} x_k PA (1 - \exp(-s_{Aj}))}{x_k PA + p_k}$$

for phenotype A_j ,

$$pr_{Bk} = \frac{p_{Bk} x_k PA (1 - \exp(-s_{Bj}))}{x_k PA + p_k}$$

for phenotype B_j ,

as larval survival is likely to be positively correlated with birth size (s_{Aj} , s_{Bj} , respectively, expressed by negative exponentials) and prey abundance, x_k . The parameter PA , the “preference for prey”, common for both phenotypes and for all generations, was the relative likelihood of eating a prey

compared to a conspecific. Thus if PA was high, then prey was preferred as food, if PA was low, conspecifics were the preferred food and cannibalism was common.

3.2. Then a random number z from the uniform $\langle 0, 1 \rangle$ distribution was chosen. If $z \leq pr_{AK}/(pr_{AK} + pr_{BK})$, then the predator phenotype A_j was assumed to win, wipe out the other phenotype and survive in patch k and vice versa.

3.3. Fitness of each of the phenotypes, FA , respectively FB , was defined as the sum of pr_{Ak} , respectively pr_{Bk} , of all patches, where the phenotype A_j , respectively B_j , “won” and their relative fitness as $FA/(FA + FB)$, respectively $FB/(FA + FB)$. If $(FA/(FA + FB)) \geq (FB/(FA + FB))$, then phenotype A_j was assumed to be more successful in this generation and tested against another B_j phenotype and vice versa. In the next generation, the parameters s_B , x_B , y_B of the new phenotype tested were chosen at random from the interval $\langle 0, MAX \rangle$. We used $MAX = 20$, so that all frequently “winning” values were well below MAX .

3.4. The program was run for 500 000 generations. The frequencies of parameter x_A , y_A combinations were plotted against their values. Those combinations, which “won” most frequently were assumed to be those that selection would favour.

Results and Discussion

SIMULATION RESULTS

Although there is a lot of randomness in the assumptions, nevertheless, there is a pattern in the predictions of our model. The parameter s_A very quickly approached zero within a few generations, which means there was a strong selection for a minimal possible egg size in the model. Thus we assumed that there must be some biological constraint for the minimum egg size (in reality, the egg cannot be infinitesimally small) and in further simulations we set a fixed value, s_A , to it and followed only the development of the parameters x_A , y_A .

The range of parameters used in our simulations is given in Table 1. There is a whole array of parameter x_A , y_A values, which “win” very frequently and thus are likely to be present in real populations. We monitored the frequencies of each possible pair x_A , y_A during the generation cycle. The highest frequencies form a hyperbola in the x_A , y_A plane (Fig. 1). This is a consequence of the “reluctance” factor, R . If initially a predator does not find a suitable patch, then in the next trial the parameter x_A is divided by R and the parameter y_A is multiplied by R . Thus when successive trials are considered the values of x_A and y_A move along an hyperbola. The hyperbola connecting the most frequently winning x_A , y_A values divides the x_A , y_A plane into two areas. The first one is the range

TABLE 1
Summary of model parameters together with the range of values used in the simulations

Parameter	Explanation	Values	Type*
s_A	Egg size	$\langle 0, MAX \rangle$	Evolution
x_A	Minimum number of prey	$\langle 0, MAX \rangle$	Evolution
y_A	Maximum number of predators	$\langle 0, MAX \rangle$	Evolution
PA	Preference for prey	0.1, 1.1, 2.1	Input
R	Reluctance	0.3, 0.5, 0.7, 0.9	Input
NT	Number of trials	1, 11, 21, 31	Input
M	Total offspring biomass for each phenotype	1000	Input
n	Number of patches	100	Input
N	Number of generations	500 000	Input
NA	Number of prey	1000	Input
MAX	Maximum value of the evolution parameters studied	20	Input

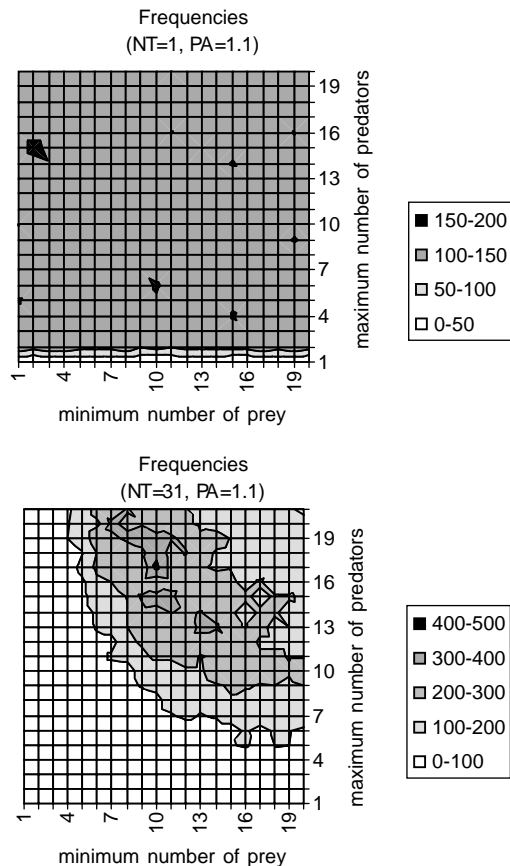


FIG. 1. Frequencies of each possible pair of x_A (minimum number of prey), y_A (maximum number of predators) values for two different values of NT . Values of NT and PA are given in the insets. For a large NT , the largest frequencies create a hyperbolic curve in the x_A, y_A plane.

when at least one of the y_A and x_A values is low. These phenotypes are not successful, as due to their low tolerance of the presence of other predators in a patch they have to devote a lot of energy to finding a suitable patch. The other area is that of the high values of both x_A and y_A . These animals require patches with a lot of food and again they have to devote a lot of energy to finding a patch with abundant prey. These results are valid for a wide range of R .

Low values of PA mean a strong tendency to cannibalism. Therefore, if PA is low, the “optimal” area of x_A, y_A is a very narrow range around the optimal hyperbola in the y_A direction. Biologically, it means a strong selection towards the optimal y_A . If PA is large and cannibalism is uncommon, the selection is weaker and the range of most frequent x_A, y_A

pairs is wider in the y_A direction. This result is robust because changing the other parameters of the model did not affect the outcome, and one example is given in Fig. 2.

In the model, the colonization of patches is a random process and the outcome of the contest between the two phenotypes, A_j and B_j , is not deterministic. Thus we cannot speak about an approach to an evolutionary stable strategy in the sense of Maynard Smith (1972). We replace it by the concept of the most often “winning” pairs of x_A, y_A . High frequencies of x_A, y_A mean that this phenotype often wins when in contest with other randomly chosen phenotypes, but is not necessarily likely to win again, if the contest with the same phenotypes were repeated. Thus our approach is a probabilistic one.

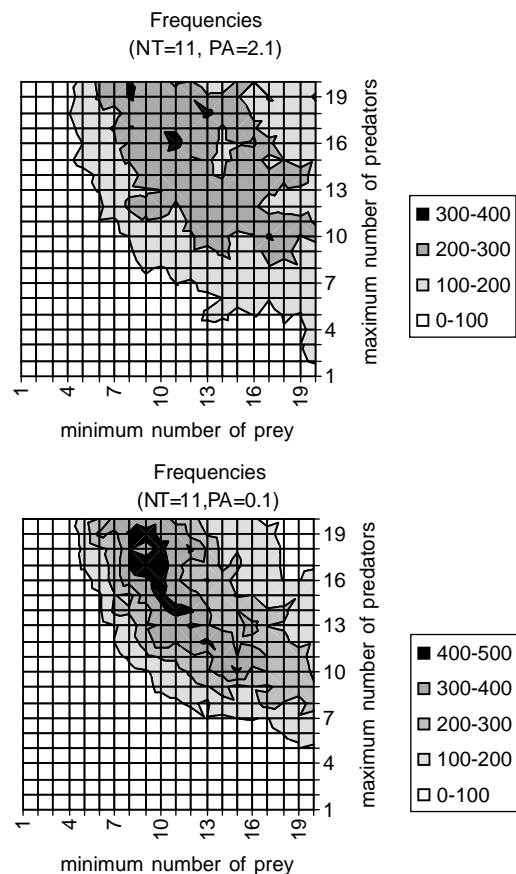


FIG. 2. Frequencies of each possible pair of x_A (minimum number of prey), y_A (maximum number of predators) values for two different values of PA . Values of NT and PA are given in the insets. The largest frequencies create a hyperbolic curve in the x_A, y_A plane.

TESTABLE PREDICTIONS

As far as offspring size is concerned, the model predicts that selection should favour adults that produce a large number of small offspring—this is supported by many empirical data, as insect predators typically produce hundreds of eggs. Interestingly, this does not hold if egg cannibalism is extremely strong: then the model predicts that a small number of large offspring is evolutionarily stable. It would be interesting to see, whether the latter prediction is supported by empirical data.

Not surprisingly, the model predicts that selection favours adults that avoid patches where predators are already present or prey is scarce. A testable prediction is, however, that there should be a range of pairs of these ESS values, in our model represented by a hyperbola, because of the “reluctance” factor. The shape of this curve strongly depends on the relative sensitivity to each of these critical values, but always there should exist some “optimal” curve in the x_A, y_A plane.

STABILITY OR REGULAR EXTINCTIONS AND COLONIZATIONS WITHIN A PATCH?

The Nicholson–Bailey model of host–parasite interactions is unstable. A lot of effort was devoted to the search for conditions that would stabilize its behaviour, as stability of the equilibrium point, especially the Liapunov one, is seen as the ultimate target of good pest control. Thus conditions that ensure stability of predator–prey interactions are seen to be the Holy Grail in modelling predator–prey population dynamics. Are they?

Again, the answer is not a unique one. Undoubtedly, there are many cases in which a stable coexistence between prey and an artificially introduced natural enemy has been achieved with the resulting equilibrium prey densities lower than those before enemy release, and below the economic threshold. Although the first great success in biological control came with the introduction of the Australian ladybird, *Rodolia cardinalis*, into California to control a coccid scale insect, nevertheless, most of the successful cases were introductions of parasites (DeBach, 1964; van den Bosch & Messenger,

1973). The life style of *Rodolia*, in addition, is very similar to a parasitic one in that the juvenile predator completes most of its development on one prey individual (Dixon *et al.*, 1997).

In true predator–prey systems, however, it is very difficult to speak about stability of the dynamics within a patch, as the patches are vacated and re-created typically every predator generation. Individuals of most prey species inhabit the suitable patches early, followed by adult predators that seek suitable patches for laying their eggs. Suitability means abundance of food and absence of older and stronger conspecifics. Thus selection should favour those predators that lay eggs only during a short “egg window”, when there is enough food, and few or no conspecifics (Dixon, 1997). Thus at the instant when the “egg window” closes, which happens early in the existence of a patch of prey, the patch dynamics is determined, as no further migration of either predator or prey occurs. Therefore, it seems more appropriate to investigate the possible outcome, given the initial predator and prey numbers at the instant when the patch was formed, the number of predator and prey that ultimately emigrate from each patch, and the numbers that survive to colonize new patches. Studying stability of an insect predator–prey system on a large, metapopulation scale makes sense. On this scale, natural selection is expected to manifest itself and the evolutionary importance of individual life history traits can be studied.

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