A multiple phenotype predator-prey model with mutation

Gavin M. Abernethy, Rory Mullan, David H. Glass and Mark McCartney

School of Computing and Mathematics, University of Ulster,
Shore Road, Newtownabbey, Co. Antrim, BT37 0QB

abernethy-g1@email.ulster.ac.uk, mullan-r8@email.ulster.ac.uk, dh.glass@ulster.ac.uk,
m.mccartney@ulster.ac.uk

Abstract

An existing multiple phenotype predator-prey model is expanded to include mutation amongst the predator phenotypes. Two unimodal maps are used for the underlying dynamics of the prey. A predation strategy is also defined which differs for each of the predators in the model. Results show that the introduction of predator mutation enhances predator survival both in terms of the number of phenotypes and total population for a range of values of the predation rate. In general, the dominant predator phenotype is the one which is most focused on the prey phenotype with the largest population.

1. Introduction

The mathematical modelling of predator-prey population dynamics goes back to the work of Lotka [1] and Volterra [2] and their independent discovery of the pair of coupled non-linear differential equations which now bears their names [3]. Since this work predator-prey systems have been modelled via a wide range of mathematical and computational techniques, including the use of discrete time population models, spatial models, and individual agent based models, with the sophistication of the modelling increasing with the rise in computer power.

In the field of ecological modelling significant research has focused on two species predator-prey models, which have been used to investigate chaotic population dynamics [4-8], the effect of the prey growth rate [9] and spatial dispersal [10-12]. Two species models have been generalized to multiple predator-prey systems, including the study of resulting chaotic behaviour, and the effect of implementing various functional responses (the effect of predation, per predator, upon the prey species) upon the dynamics [13-16]. However, in

general less work has been undertaken looking at multiple species predator-prey models where the system has been expanded to allow for multiple competing predators and prey.

The modelling of the functional response is one of the most studied aspects of mathematical ecology, with Holling's Type II disc equation [17] proving particularly popular. Several sophisticated forms have been proposed, and their relative ecological merits have been debated [18]. Other studies have suggested that models featuring nonlinear functional responses and adaptive foraging may be essential for the maintenance of stable, complex ecosystems [19]. The relationship between complexity and stability [20] has remained a significant issue within theoretical ecology since May's 1973 [21] work on random graphs challenged the intuitive belief that greater complexity increases the stability of an ecosystem. The issue has been explored in some detail using both models and empirical data. Various definitions of stability [22] have been investigated in the context of ecological networks in which predator-prey ratios, the proportion of possible feeding links in the network [23], the effects of competition between species, and the proportion of weak feeding links [24] are varied.

A key area of the study presented in this paper is the inclusion of mutation in a predator-prey ecosystem. Mutation has previously been introduced into both single species predator-prey ecosystems [25,26] where it was used to simulate adaption towards the environment, and in multiple species predator-prey models [27] where the various traits of the predator and prey are allowed to evolve, introducing new phenotypes into the ecosystem. Several eco-evolutionary models have been developed that combine random mutation and resulting natural selection within population dynamics models [28-33]. A key feature of these models is that the species themselves are not pre-selected, and the trophic relationships that are present in the resulting food web are an emergent result of the selection process operating on population dynamics. An overview of the development of one such model in the light of historical food web research can be found in [34].

A further approach is to allow populations to occupy a spatially extended region, thus producing a predator-prey system that models the dynamics of the species in both space and time. Such models have been developed in continuous space and time, via reaction-diffusion based predator-prey models [35,36], and in discrete space and time via coupled map lattice (CML) based models [37-39], with the latter being the approach taken in the current paper.

Studies in the physics literature have considered the dynamics on such models [40-41], and they have been applied to modelling population dynamics on spatial systems of plants [42] and insects [43]. Multiple-species predator-prey relationships on a lattice are studied using the discrete generalised Lotka-Volterra equations in [44]. Using a lattice has the advantage of being relatively simple to compute, whilst providing an approach to the modelling of neighbouring ecological environments. How these ideas are implemented in the present study will be discussed in more detail later.

This paper uses a generalised multiple phenotype form of a discrete time predator-prey model proposed by Neubert and Kot [4] that has been previously studied by Mullan et al [45]. Here it is further expanded to allow mutation amongst the various predator and prey phenotypes that occupy the ecosystem, forming a mutating predator-prey model with much heterogeneity. A variation of the model studied here where a single predator predates upon a set of mutating prey has been studied by Mullan et al [46].

The work presented here expands on [46] to consider mutation for both the predators and the prey. Results from a 10 predator – 10 prey ecosystem, both with and without mutating predators are discussed, first showing a broad overview of where survival occurs in the model based on the assigned control parameters, and then with a focus being placed on the underlying dynamic behaviour of the phenotypes within the model as its configuration changes. Both the Ricker model and logistic map are used to model the prey dynamics with comparisons being drawn between the two unimodal maps.

2. Multiple phenotype predator-prey model

In [46] a multiple phenotype model based on work by Neubert and Kot [4] was defined as

$$N_{t+1}^{(j)} = \exp\left(-\left(\sum_{i=1}^{m}(f^{(ij)}c_{ij})\,P_t^{(i)}\right)\right) N_t^{(j)}\exp(r_j\left(1 - N_t^{(j)}\right)) \qquad (1a)$$

$$P_{t+1}^{(i)} = \sum_{j=1}^{n}(f^{(ij)}c_{ij})N_t^{(j)}P_t^{(i)} \qquad (1b)$$

where $N_t^{(j)}$ represents the population density of the jth prey phenotype at time step t and $P_t^{(i)}$ represents the ith predator phenotype at time step t, with c_{ij} and r_j acting as the control

parameters. The two generalised equations allow for *m* predators and *n* prey to occupy the ecosystem, with each prey having an individual *r* value corresponding to its growth rate, and a c_{ij} term, which measures the predatorial effectiveness of the ith predator at predating upon the jth prey. The term $f^{(ij)}$ models how predator *i* divides its effort hunting the jth prey phenotype.

Here the model is further expanded with the introduction of mutation amongst the predators and prey. This has been achieved by introducing CML based mutation. A variation of (1) which utilizes the Ricker model to govern the dynamics of the prey is as follows:

$$N_{t+1}^{(j)} = \sum_{k=1}^{n} p_{kj}^{prey} \exp\left(-\left(\sum_{i=1}^{m} (f^{(ik)} c_{ik}) P_t^{(i)}\right)\right) N_t^{(k)} \exp(r_k \left(1 - N_t^{(k)}\right)) \qquad (2a)$$

$$P_{t+1}^{(i)} = \sum_{k=1}^{m} p_{kj}^{pred} P_t^{(k)} \sum_{j=1}^{n} f^{(kj)} \max(0, c_j N_t^{(j)} - P_t^{(k)}) \qquad (2b)$$

with the variables understood to be as for (1a) and (1b) but with the inclusion of two mutation matrices, one for the predator, and one for the prey. Here the probability of prey *k* mutating into prey *j* is defined as p_{kj}^{prey} and the probability of predator *k* mutating into predator *j* is defined as p_{kj}^{pred}.

Note that equation (2b) is a variant of (1b) which effectively introduces a carrying capacity on the prey. This change is introduced to prevent a pathological scenario discussed in [46], whereby a predator can focus on one prey, resulting in an increase of its own population and corresponding depletion of the prey population, then at the next time step move on to another prey, again increasing its population and so on. At each time step prey which are not being hunted have a chance to recover their population levels, and then can be predated on at a later time. In some cases this allows the predator population to increase without bound. The use of the carrying capacity term in (2b) prevents this.

Further a logistic map based model where the logistic map governs the underlying dynamics of the prey phenotypes is defined as

$$N_{t+1}^{(j)} = \sum_{k=1}^{n} p_{kj}^{prey} \left(N_t^{(k)} + \left(r_k N_t^{(k)} \left(1 - N_t^{(k)}\right)\right) - \sum_{i=1}^{n} \left(N_t^{(k)} (f^{(ik)} c_k) P_t^{(i)}\right) \right) \qquad (3a)$$

$$P_{t+1}^{(i)} = \sum_{k=1}^{m} p_{kj}^{pred} P_t^{(k)} \sum_{j=1}^{n} f^{(kj)} \max(0, c_j N_t^{(j)} - P_t^{(k)}) \qquad (3b)$$

where the terms are understood to be as for (2a).

2.1 Mutation

It is necessary that that the sum of the probabilities for each possible mutation of prey or predator phenotype k to any of the other phenotypes, plus the probability that it does not mutate must sum to one. In what follows we discuss mutation in terms of prey phenotype, noting that the statements apply equally to predator mutation via the simple substitution of p_{kj}^{pred} for p_{kj}^{prey}. Thus for prey mutation,

$$\sum_{j=1}^{n} p_{kj}^{prey} = 1 \quad \forall k \qquad (4)$$

subject to

$$p_{kj}^{prey} \in [0,1] \ \forall j,k . \qquad (5)$$

Using nearest neighbour (N-N) mutation to the probability matrix takes the form:

$$p_{kj}^{prey} = \begin{cases} p & |j-k| = 1 \\ 1-2p & j = k \neq 1 \text{ or n} \\ 1-p & j = k = 1 \text{ or n} \\ 0 & otherwise \end{cases} \qquad (6)$$

where p is the probability of a prey mutating into a neighbouring phenotype, n being the total number of prey phenotypes and the term 1-p accounting for the prey phenotypes at the edges of the system. The fact that $p_{kj}^{prey} \geq 0$ means the maximum probability of a prey mutating into a neighbouring prey is 0.5. Here each phenotype will contribute half of its population to each of its neighbouring phenotype in the next iteration of the model. This means that those populations that are not along the edges make no contributions to their own population at the next time step.

In the case of no mutation, equation (6) reduces to,

$$p_{kj}^{prey} = \delta_{kj} \qquad (7)$$

where δ_{kj} is the Kronecker delta, which is defined as

$$\delta_{ij} = \begin{cases} 1 & if \quad i = j \\ 0 & f \quad i \neq j \end{cases} \tag{8}$$

Although high mutation rates ($p_{kj}^{prey} > 0.1$) would not be considered biologically relevant, if we were considering the model spatially, with increased reproductive or predator fitness being determined by the ecological environment, these higher probabilities would correspond to the probability of a geographical move, and hence may be relevant. Hence the whole range of possible probabilities is considered here.

2.2 Assignment of control parameters

The r_j control parameter dictates the growth rate of the jth prey phenotype in the model. We consider a class of models for r_j which give monotonic growth of r_j with respect to j via

$$r_j = r_{max} \left(\frac{j}{n} \right)^{\beta} \tag{9}$$

where $j \epsilon \{1, \dots, n\}$ and r_j is the control parameter corresponding to the jth prey. We consider three values of $\beta = 0.5, 1, 2$ corresponding to concave, linear, and convex increase respectively.

The c values have all been set equal, meaning that the predators all have an equal efficiency of predating upon all the prey phenotypes,

$$c_{ij} = c. \tag{10}$$

We choose a predation strategy $f^{(ij)}$ for how predator i divides its effort hunting the jth prey phenotype to be based on the relative sizes of prey populations via

$$f^{(ij)} = \frac{(N_t^{(j)})^{\alpha(i)}}{\sum_{k=1} (N_t^{(k)})^{\alpha(i)}} \tag{11}$$

where the exponent α specifies the degree of focus of the ith predator. We set

$$\alpha(i) = i - 1. \tag{12}$$

Thus, with increasing i the ith predator focuses an increasing proportion of its effort on the prey phenotype with the largest population. For the first predator phenotype ($i=1$), $\alpha = 0$ corresponding to the predator spending an equal amount of effort hunting each of the

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surviving prey phenotypes, regardless of their current population density. For the second predator phenotype, $\alpha = 1$ corresponding to the predator distributing its effort in linear proportion to the relative sizes of prey populations, then as α increases further the predator focuses more sharply towards the prey phenotype with the highest current population density.

3. Numerical Results

The Ricker based model (2a), (2b) and logistic based model (3a), (3b) have been run for a 10 prey – 10 predator ecosystem. In the logistic model the maximum value for which the prey will survive is $r = 3$, and so r_{max} has therefore been fixed to $r_{max} = 3$ for all runs in both the logistic and Ricker based models. This allows for a direct comparison to be made between the two unimodal discrete time maps.

For all runs $N_0^{(1)}$ is populated with an initial population density of $N_0^{(1)} = 0.5$. The system is then run for 1000 time steps to allow all prey phenotypes to be populated, after which the predators are introduced as discussed below. This means that at the time of introduction of the predators, all prey phenotypes are populated, and behaving as they would in their CML form with no predation. After the introduction of the predators, the predator-prey ecosystem is then run for 9000 time steps before results are collected over the next 1000 time steps. 10000 time steps were deemed to be sufficient for the system to converge upon its post transient state. It was found that running for a greater number of iterations did not show significant differences in the output of the model.

To enable analysis of the large amounts of data generated by the models we introduce the following measures:

(a) Average phenotype survival. The average number of predator or prey phenotypes which are in existence (defined as having a population greater that 10^{-6}), with the average taken over the last 1000 iterations.

(b) Average total population size. The average of the sum of the populations of all 10 phenotypes of predators or prey averaged over the last 1000 iterations.

(c) Average expected value of predator or prey. At a given iteration t the expected value of the predator phenotype is defined to be

$$E_t = \frac{\sum_{i=1}^{10} i P_t^{(i)}}{\sum_{i=1}^{10} P_t^{(i)}} \quad , \tag{13}$$

and similarly for prey. We define the average expected value for the predators as the average of (13) taken over the last 1000 iterations. A corresponding value is defined for the prey.

(d) Average standard deviation of the expected value. At a given iteration t the standard deviation of the expected value of the predators is defined as

$$\theta_t = \sqrt{\frac{\sum_{i=1}^{10} (i - E_t)^2 P_t^{(i)}}{\sum_{i=1}^{10} P_t^{(i)}}} \quad . \tag{14}$$

We define the average standard deviation of the expected value for the predators as the average of (14) taken over the last 1000 iterations. A corresponding value is defined for the prey.

(e) Most frequent largest phenotype, l. This is the predator or prey phenotype which most frequently had the largest population over the last 1000 iterations.

(f) Frequency of the largest population, f. This returns the number (out of 1000) of time steps out of the last 1000 which the phenotype recorded in (e) was largest.

(g) Average largest population lead. This is defined as

$$L = \frac{1}{f} \sum_{t \in A(l)} \frac{P_t^{(l)} - P_t^{(s)}}{\mu_t} \tag{15}$$

where l is defined in (e), s denotes the second largest predator at iteration t, $A(l)$ is the set of iterations in the final 1000 where phenotype l dominates, f is defined in (f) and is equal to $|A(l)|$, and finally μ_t is given by

$$\mu_t = \frac{1}{10} \sum_{i=1}^{10} P_t^{(i)} \quad . \tag{16}$$

A corresponding value is defined for prey.

(h) Average largest population deviation. This is defined as

$$L = \frac{1}{f} \sum_{t \in A(l)} \frac{P_t^{(l)} - \mu_t}{\mu_t}. \tag{17}$$

where all the terms are defined as specified in (g). A corresponding value is defined for the prey.

Both maps were run for three scenarios, involving the introduction of 10 non-mutating predators, 10 mutating predators and 1 mutating predator. In these last two cases the results were found to be virtually identical, and hence we do not present results for the case where just 1 mutating predator is introduced. Runs were performed for a range of initial predator values [0.1,0.2,0.3,0.4,0.5]. These differing initial conditions did introduce some differences in the results, but only in terms of changing the placing of the edges of regions of total population collapse, with such differences being more significant for the logistic based model, see Figure 1.

In what follows we will restrict ourselves to presenting results where the initial predator populations are 0.1, and discuss a selection of scenarios using the metrics (a) to (f) above to illustrate the behaviour of the models in (c,p) space. However in supplementary material accompanying this paper full graphical results are shown for metrics (a) and (b) for all initial predator values specified above and for all of the metrics (a) to (h) for an initial predator value of 0.1. In all these cases the results are presented for logistic and Ricker based models with and without predator mutation, for $\beta = 0.5, 1, 2$.

In terms of the broad behaviour of the results, we make the following observations. Firstly for both the logistic and Ricker based models the results for prey populations for both mutating and non-mutating predators have broad similarities over the range $0 < c < 2$. This is illustrated in Figure 2 for the logistic based model. Thus all prey phenotypes survive in this region, with the onset of a gradual decrease in total prey population numbers as c increases beyond values which allow predator survival. In this region of c total prey populations and prey phenotype survival show limited dependence on p, though what dependence exists is more pronounced in the Ricker based model.

Predator survival shows greater variation (see Figures 3 and 4). For values of c below 1 for the logistic based model, and below 0.8-0.9, for the Ricker based model, predator populations collapse. For a range of c values above this, mutating predators can maintain the survival of the full phenotype range, while some non-mutating predators go extinct. For relatively low values of c (about 1.5 for the Ricker model and 2 for the logistic model), mutation only affects the number of predator phenotypes surviving, allowing all to survive unless the

mutation rate is very low, but has little or no effect on the total populations of predators or prey. For higher values of c, mutation clearly allows greater predator survival in terms of both the number of phenotypes and total population over a wider range of c values, and increases the smoothness of variation of overall prey populations in (c,p) space. For mutating predators, the total population of predators typically increases with c in the regions where predator survival occurs, but the behaviour is more variable for non-mutating predators. Note comparing Figures 3 and 4, the logistic based model generally sustains predator populations over a wider range of (c,p) space, and at higher levels.

Further, looking again at Figures 3(c,d) and 4(c,d), in the case of mutating predator phenotypes, for both the logistic and Ricker models, the maximum value of c which permits the survival of all (10), or nearly all (9), predator phenotypes decreases as the mutation rate p increases. However, there is a region for higher values of p (around 0.35-0.45 in the logistic model, see Figure 3(d)) that allows predator survival at higher c values than this general trend would suggest.For both logistic and Ricker models, there is a region for relatively small values of p (around 0.1) where the total predator population is high and this extends to high values of c as can be seen in Figures 3(d) and 4(d). Interestingly, the corresponding total prey population is rather low in this region (see Figures 2(d) and 5(b)), indicating the efficiency of the predators. Both models also have a region where the total predator population is relatively high at higher values of p, although this region is larger for the logistic model (see Figure 3(d)).

In the case of the logistic model, non-mutating predators increase the region of (c,p) space which allows all prey phenotypes to survive as compared to corresponding results for mutating predators (compare Figures 2(a) and 2(c)). As can be seen in Figures 2(a) and 2(c) for the logistic based model for both mutating and non-mutating predators, total prey population collapse can occur for large p and c values. Predator mutation increases the collapse region, with over-predation leading to collapse of the prey population and hence, the predators. In contrast to this, in the case of the Ricker model, for both mutation and non-mutation of predators, survival of all prey phenotypes occur for virtually all of the (c,p) space considered. Where here 'virtually' means that for a few small regions of (c,p) space prey phenotype survival lies between 9 and 10 when $\beta = 2$ (see Figure 53(a) in supplementary material, Appendix A).

In the results discussed so far the figures presented have all been based upon an assignment of prey phenotypes via (9) with $\beta = 1$. The variation of β does not have a dramatic effect on the results at the level of the total numbers of different phenotypes of predator or prey that exist. Results for the overall total population are also similar, but as β increases the overall total population size tends to decrease for all models. Thus, for example as illustrated in figure 5 for the mutating predator Ricker based model, for most of the (c,p) space (noting particular the region $1 < c < 3$), as we move from $\beta=1/2$ to $\beta=2$ total prey populations tend to decline (Figure 5 (a-c)), with high values of prey population becoming increasingly restricted to lower values of c. Total predator populations also decline (Figure 5 (d-f)), though note the much stronger dependence of total predator populations on the variation of p than for corresponding prey populations.

Turning to the expectation value of the prey and predators (Figure 6) we see that increasing from $\beta=1/2$ to $\beta=2$ also tends to increase the predator expectation value for lower values of c (with this occurring over a wider range of (c,p) space for the logistic model). Prey expectation value increases for larger values of c in regions where the predator populations are diminished.

As c approaches from above the limit at which predator collapse occurs (which is around c=1 for the logistic based model, and c=0.8 for the Ricker based model) the predator expectation value increases, corresponding to dominance of more focused predators. This is most obvious in the case of non-mutating predators, and the Ricker based mutation predator model. The dominance of the most focused predator is made clear by examining the most frequent largest phenotype. For example, for the mutating Ricker based model (Figure 7), over a wide range of (c,p) space the most frequent largest population is the most focused predator, and for values of c close to the region of predator collapse this predator forms the largest population for all of the last 1000 iterations of the model. Similar behaviour occurs for the logistic based model, though over a wider range of c values. The strategy of such a highly focused predator, targeting almost all its effort on the largest prey population in a given cycle, leads to diversity across the corresponding region of c values for the most frequent largest prey population. This is not surprising since if a particular prey phenotype has the largest population at time step t, it will be heavily depleted if the most focused predator is dominant, and thus might be expected to have a low population at time step $t+1$.

In fact, it turns out that the most frequent largest prey population is almost always at most 50%. This wide range of largest prey population is illustrated in Figure 8. In particular, note in Figure 8(a) the region where a single prey dominates along with a single predator (figure 7b) for values of c around 2 and for high values of p around 0.45. A similar region occurs at similar values of c and p in the Ricker model results for both the $\beta=1/2$ and $\beta=2$ variants (see Figures 56(c) and 60(c) in supplementary material, Appendix A) and in the logistic model results for a smaller region of (c,p) space for values of c slightly greater than 1 and values of p just below 0.5, again for all values of β (see Figures 38(c), 40(c) and 42(c) in supplementary material, Appendix A). In these regions, the predator in question is the most focused phenotype, while the prey is the phenotype with the second highest growth rate as defined in (9). While this prey phenotype is heavily predated upon, its population is increased by mutation from neighbouring prey phenotypes (with the highest and third highest growth rates), which are effectively ignored by the focused predator. For appropriate values of c and mutation rate, p, which needs to be high, the prey phenotype in question can be sustained with the highest population. Finally, the variation in most frequent largest prey population serves to highlight the wide ranging and complex dynamics which are summarised by the figures giving phenotype survival and total population size over the (c,p) space, a single example of which is shown in Figure 9.

4. Conclusions

This paper has built on earlier work [45,46] to present a multiple phenotype predator-prey ecosystem with CML based mutation amongst the phenotypes that occupy its ecosystem. Heterogeneity was established by each predator phenotype having its own value of α specifying its individual rate of focus and each prey phenotype having its own individual growth rate. Logistic and Ricker models have been used for the prey dynamics with three values of $\beta = 0.5, 1, 2$ corresponding to concave, linear, and convex increases in the growth rate across the prey phenotypes. A single predation rate (or predatorial effectiveness, as specified by the parameter c) was used dictating the relationship between all the predators and each of the prey phenotypes, with the differential between the predator phenotypes being how they focus their predatorial effort on the prey phenotypes. The model was run both with and without mutation amongst the set of predators.

The results for both logistic and Ricker models are broadly similar and, in particular, they generally exhibit similar changes as other aspects of the model are varied. The results are also similar for different values of β. There is very little difference in terms of the number of phenotypes surviving, but the total populations of both predators and prey decrease as β increases. Comparing results with and without mutation amongst the predators, it is found that in both cases no predators survive for sufficiently low values of the predation rate. For values of the predation rate slightly above the threshold where predators could survive, mutation increases the number of predator phenotypes surviving, but has little effect on their total population. For higher values of the predation rate, mutation has a much more dramatic effect, increasing both the number of predator phenotypes surviving and their total population. Finally, at still higher levels of the predation rate, no predators survive due to over-predation.

Mutation amongst the predators allows large predator populations to survive in the presence of correspondingly low prey populations for high values of the predation rate provided the mutation rate is relatively low. In general, the maximum value of the predation rate that permits almost all predator phenotypes to survive decreases as the mutation rate increases, whereas this region is largely independent of mutation rate when there is only mutation amongst prey, which is consistent with earlier findings [46]. It was also found that the most focused predator is generally the dominant predator phenotype, with this dominance being particularly pronounced for lower values of the predation rate, whereas there is more diversity in the prey phenotypes.

Having extended the model to include mutating predators, future work will develop it further to consider the effect of introducing competition, particularly insofar as it could enhance diversity (see for example [28,31]).

Appendix A. Supplementary material

Supplementary material related to this article can be found online at http://dx.doi.org/10.1016/j.physa.2016.08.037.

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Figure Captions

Figure 1 (a) Predator survival (number of differing phenotypes) for initial predator population $P_{9001}^{j} = 0.1, \forall j = 1,...10$ $\beta = 0.5$ for the Ricker based model with mutating predators. (b) As for (a) with $P_{9001}^{j} = 0.5, \forall j = 1,...10$. (c) Predator survival (number of differing phenotypes) for initial predator population $P_{9001}^{j} = 0.1, \forall j = 1,...10$ $\beta = 0.5$ for the logistic based model with mutating predators. (d) As for (c) with $P_{9001}^{j} = 0.5, \forall j = 1,...10$. [Figure 23(a), 23(m), 11(a), 11(m) of supporting materials]

Figure 2 Variation of prey survival, and overall prey populations, in (*c,p*) space for the logistic based model (3), with β=1, for both non-mutating and mutating predators. For non-mutating predators: (a) number of distinct prey phenotypes which survive, (b) total population of prey. For mutating predators: (c) number of distinct prey phenotypes which survive, (d) total population of prey. [Figure 33(a), 33(c), 39(a), 39(c) of supporting material]

Figure 3 Variation of predator survival and overall predator populations in (*c,p*) space for the logistic based model (3) with β=1, for both non-mutating and mutating predators. For non-mutating predators: a) number of distinct predator phenotypes which survive, (b) total population of predators. For mutating predators: (c) number of distinct predator phenotypes which survive, (d) total population of predators. [Figure 33(b), 33(d), 39(b), 39(d) of supporting material]

Figure 4 Variation of predator survival and overall predator populations in (*c,p*) space for the Ricker based model (2) with β=1, for both non-mutating and mutating predators. For non-mutating predators: a) number of distinct predator phenotypes which survive, (b) total population of predators. For mutating predators: (c) number of distinct predator phenotypes which survive, (d) total population of predators. [Figure 51(b), 51(d), 57(b), 57(d) of supporting materials]

Figure 5 Variation of total population size for both prey and predator for the mutating predator Ricker based model in (*c,p*) space. Total prey population (a) β=1/2, (b) β=1, (c) β=2. Total predator population (d) β=1/2, (e) β=1, (f) β=2. [Figure 55(c), 57(c), 59(c), 55(d), 57(d), 59(d) of supporting material]

Figure 6 Variation of expectation value (13) for predator and prey populations for the mutating predator Ricker based model in (*c,p*) space. Prey expectation (a) β=1/2, (b) β=1, (c) β=2. Predator expectation (d) β=1/2, (e) β=1, (f) β=2. [Figure 55(e), 57(e), 59(e), 55(f), 57(f), 59(f) of supporting material]

Figure 7 Variation of (a) the most frequent largest predator population, and (b) the frequency of the largest predator population over the last 1000 iteration of the model for the Ricker based mutating predator model with β=1. [Figure 58(b), 58(d) of supporting material]

Figure 8 Variation of (a) the most frequent largest prey population, and (b) the frequency of the largest prey population over the last 1000 iteration of the model for the Ricker based mutating predator model with β=1. [Figure 58(a), 58(c) of supporting material]

Figure 9. Bifurcation diagrams showing the behaviour of predators for two different values of *c* for the non-mutating logistic based model with β=1 (a) *c* = 1, a value at which 6 predators survive, and (b) *c* = 1.3, a value at which all ten predators survive with *p* > 0.125. Compare with Figure 3(a).