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# Modelling prey in discrete time predator-prey systems

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*Abstract*- **A single predator, single prey ecological model, in which the behaviour of the populations is reliant upon two control parameters has been expanded to allow for multiple predators and prey to occupy the ecosystem. A focus has been placed on analysing the diversity of the ecosystem that develops as the model runs, assessing how many predator or prey species survive. This paper compares a standard Ricker model representation of prey behaviour with models based on the logistic and tent maps. It is found that the overall dynamics of the system can depend significantly on the model used.**

**Key Words – Predator-Prey, Modelling Prey, Ecosystem Diversity**

## I. Introduction

Predator-prey modelling is where a combination of mathematical modelling and computational simulations are employed to investigate real world predator-prey environments e.g. foxes preying on rabbits. These simulations calculate the effect that both the predator and prey have on each other's population. Mathematical simulations can be employed to simulate this natural ecology[1].

The Lotka-Volterra model is the earliest predator-prey model and is formed using a set of differential equations originally described by Volterra in 1926[2] to describe the interaction between predator-prey species and then independently arrived at by Lotka[3] to describe a chemical reaction.

Recent research has been undertaken looking at two species predator-prey models, where a single predator and a single prey occupy the ecosystem, these have been used to investigate the underlying chaotic population dynamics[4,5,6,7], the effect of the prey growth rate[8] and to investigate population dispersal[9,10,11]. Some work has also been carried out investigating the chaotic dynamics that occur in multispecies continuous time predator-prey models[12-14]. There has also been work carried out examining large competition models with many species[15-17], however little research has carried out investigating discrete predator-prey models in their generalised form, allowing for multiple predators and prey to occupy the ecosystem. Due to the increased computational power of modern computers, it is possible to investigate diverse ecosystems with a large number of predators and prey by employing discrete time multiple species predator-prey models.

This paper will utilise a generalised multiple species form of a discrete time predator prey model specified by Neubert et al[9] which utilises the Ricker model to simulate prey growth. We compare it to a further class of models where the Ricker model is replaced with the tent map and the logistic map. The two species Ricker based predator-prey model that has been utilised will be introduced followed by a discussion on how this model has been generalized to allow for multiple species to occupy the ecosystem, the other models that will be utilised in place of the Ricker model will then be introduced. The paper will then discuss the diversity of the ecosystems that develop in the various models and show how they are similar and how they differ.

## II. Two Species Predator-prey Model

A two species discrete time predator-prey model proposed by Neubert et al [9] is generalised to allow for a multi-species predator-prey ecosystem to be modelled. Their original model is defined as follows:

$$N_{t+1} = N_t e^{r(1-N_t-P_t)} \qquad 1.1$$

$$P_{t+1} = cN_tP_t \qquad 1.2$$

where $N_t$ represents the current prey population, and is based on the well-known Ricker model for discrete time population dynamics, and $P_t$ represents the current predator population, with predator growth being directly proportional to the number of prey present. The two control parameters here define the behaviour of the predator and prey, the control parameter $c$ defines the interaction between the predators and the prey and the control parameter $r$ defines the growth rate of the prey.

## III. Generalisation of Model

In the process of generalisation we need to allow for multiple predators and prey to occupy the ecosystem. Equation 1.2 can be easily generalised in the form of equation 2.2 below. Equation 1.1 is harder to generalise since a direct generalisation of 1.1 does not distinguish between the effectiveness of the predator in depleting the prey population as it contains no dependence on the control parameter c. It would therefore seem reasonable to include

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the matrix element $c_{ij}$. A further class of models can be written as:

$$N_{t+1}^{(j)} = \exp(-(\sum_{i=1}^{m}(c_{ij}/n)\,P_t^{(i)}))\,N_t^{(j)}\exp(r_j\left(1 - N_t^{(j)}\right)) \quad 2.1$$

$$P_{t+1}^{(i)} = \sum_{j=1}^{n}(c_{ij}/n)N_t^{(j)}P_t^{(i)} \quad 2.2$$

The set of equations now allow for $m$ predators and $n$ prey to occupy the ecosystem, with the j[th] prey having an individual $r_j$ value corresponding to its reproductive rate, and the introduction of a $[c_{ij}]$ matrix, which is a measure of the predatorial effectiveness of the i[th] predator upon the j[th] prey.

For each run of this model an initial population size of 0.5 is utilised for all predators and prey in all the runs in this paper. Further, if any population falls below a limiting value of $\varepsilon=10^{-6}$ the population is deemed to have become extinct, and is set to zero for all future iterations of the system. This ε threshold value is necessary in the case of the Ricker model to determine that any population has collapsed since without this threshold value populations will never die off . A scaling term has been introduced where the $[c_{ij}]$ matrix is scaled by the number of prey species that originally occupy the ecosystem, which corresponds to each of the predators dividing its time hunting each of the prey species equally.

## IV. Other Methods of Modelling Prey

In equation 2.1 and 2.2 in the earlier two species predator-prey model from Neubert et al, the Ricker model has been utilised to model the behaviour of prey.

However, the model is easily generalised to the form:

$$N_{t+1}^{(j)} = f(N_t^{(j)}, r_j) - N_t^{(j)}\left(\sum_{i=1}^{m}(c_{ij}/n)\,P_t^{(i)}\right) \quad 3.1$$

$$P_{t+1}^{(i)} = \sum_{j=1}^{n}(c_{ij}/n)N_t^{(j)}P_t^{(i)} \quad 3.2$$

which allows the insertion of other models in place of the Ricker model to model the behaviour of the prey species. Two obvious variants on the Ricker model are the logistic map (4) and tent map (5) below:

$$f(x, r) = x + rx(1 - x) \quad 4$$

$$f(x, r) = x + r\min(x, 1 - x) \quad 5$$

In each case the addition of the $x$ term has been included to bring the bifurcation diagrams for the models in line with the Ricker model over the control parameter range [0,2].

Figures 1.1-1.3 show the bifurcation diagram for each of the three models for a single prey in the absence of any predator. These bifurcation diagrams allow the visualisation of how changing the $r$ control parameter affects the behaviour of the prey in the models.

Figures 1.1 and visualise the bifurcation diagram for the Ricker based model in the absence of any predator populations with separate values being used for the epsilon

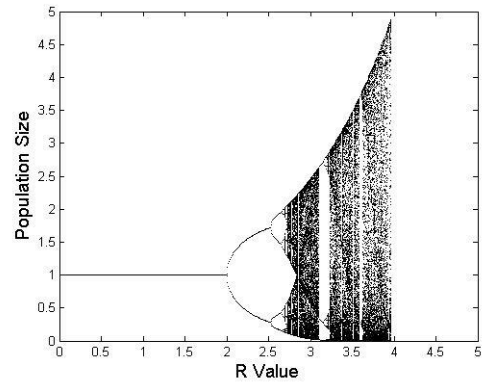



Fig 1.1 Ricker Based Model with $e = 10^{-6}$

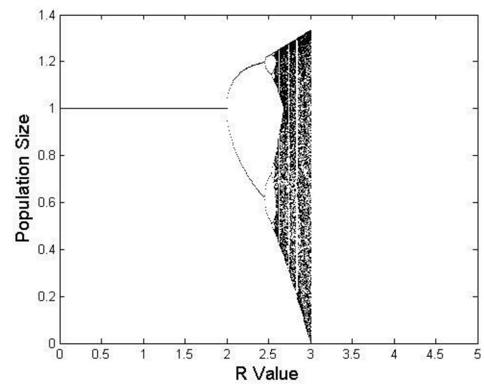



Fig 1.2 Logistic Based Model

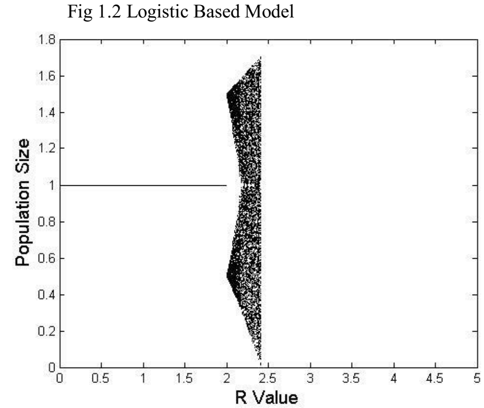



Fig 1.3 Tent Based Model

**Fig 1. Feigenbaum diagrams for the various ways of modelling prey growth**

value. Figure 1.2 visualises the bifurcation diagram for the logistic map and figure 1.3 visualises the bifurcation diagram for the tent map. These bifurcation diagrams visualise the various dynamic behaviours that take place in the models based on the $r$ control parameter that is used.

The Ricker and the logistic map show similar behaviour, with both initially converging on $N = 1$, then going through a process of bifurcation, where they converge upon multiple separate values and oscillate between them, before eventually becoming fully chaotic. The tent map's behaviour is slightly different, with it jumping straight between converging on $N = 1$ to becoming fully chaotic..

In Figure 1.1 a value of $\varepsilon = 10^{-6}$ is being utilised. This is causing a cut-off point along the $r$ axis of 3.96, above which the prey population is guaranteed to fall below $10^{-6}$, and is therefore guaranteed to collapse.

In the logistic map based model survival occurs between $r$= 0 and 3, with the tent based model seeing survival between $r$ = 0 and $r$ = 2.4. Similar behaviour is also apparent in the initial stages, with both converging on a value of 1. Both this range and this behaviour differ from a normal logistic map bifurcation diagram.

## V. Analysis Of Ricker Based Model

The $c_{ij}$ and $r_j$ control parameter values that are utilised in the model have been generated randomly, using uniform distributions over the range [0,maxC] and [0,maxR] respectively.

A focus has been placed on identifying population diversity i.e. the number of different species which survive in the model based on the maxR or maxC value that is utilised.

The model has been executed for 100 different sets for the control parameter values for each value of maxR and maxC, and executed for 5000 time steps for each set of values, with an average of the number of surviving predator and prey species being recorded for the different maxR and maxC values. The choice of 5000 time steps was found to be adequate to allow transient behaviour to die out. A step size of 0.1 has been used to scan across the maxR and maxC space.

Figure 2 below shows the population survival rates for both the predator and the prey populations for a n=m=2, n=m=100, and n=m=200, ecosystem. In what follows we will describe these are 2x2, 100x100 and 200x200 systems respectively. Each of these graphs show the average number of surviving predator and prey species in the Ricker based model for each value of maxR and maxC.

There are some areas of similarity in the maxR-maxC space across all of these graphs. For example, it can be seen that when maxC is between 0 and 1.7 there is no predator survival in the model. The $c$ matrix of control parameters is indicative of the effectiveness with which each of the predators predates on each of the prey, a maxC value of lower than 1.7 creates a $c$ matrix of values too low to support the survival of any of the predators.

In this scenario the prey populations can live on independent of the predator populations, acting as individual Ricker models controlled by their individual $r$ parameter. For this reason in this area of space similar behaviour can be expected no matter how many initial populations populate

| No. Pred | No. Prey | MaxC Position | maxR Position | Pred Diversity Rate | Prey Diversity Rate |
|---|---|---|---|---|---|
| 2 | 2 | 3.9 | 2.2 | 0.542 | 0.936 |
| 10 | 10 | 7 | 3 | 0.302 | 0.745 |
| 100 | 100 | 9.9 | 3.8 | 0.153 | 0.720 |
| 200 | 200 | 10.2 | 3.9 | 0.125 | 0.720 |
| 500 | 500 | 10.4 | 3.9 | 0.095 | 0.718 |
| 1000 | 1000 | 10.4 | 3.9 | 0.076 | 0.711 |

**Table 1. A table showing the behaviour of the Ricker based model at the position of peak predator population diversity for various initial population diversities**

the ecosystem, since the predators are dying off without extinguishing any prey populations, leaving a series of uncoupled Ricker models with no dependence on the $c$ control parameter. In this region the effect that the ε value holds upon the survival of the prey populations can be seen and related back to the earlier bifurcation diagram (Figure 1.1), it can be seen that all the prey population survive until maxR becomes greater than 3.96, at which point some of the preys' $r$ values will be greater than 3.96, which guarantees that their population size will fall below the ε threshold

Another region of similar behaviour between the various initial population diversities is with a large maxC, where maxC exceeds 12. In this situation the maxC value is too high, causing the predators to over-predate on the prey, extinguishing all the population of prey before they collapse themselves.

The area of most interest is the area of co-survival in the maxR-maxC space. In this area both the predators and prey species in the model co-exist, with some species of predators and some species of prey surviving as the model runs.

Figure 2.1 above is a visualisation of the 2x2 model. Here predator survival can be observed between maxC = 1.7 to maxC = 9.5 and maxR = 0.3 to maxR = 7.6. In this 2x2 ecosystem there is still some predator survival outside of this range. There is little correlation here in the maxR-maxC space where predator survival occurs in comparison to the runs with greater initial population sizes. It can also be visualised that the survival of predator species does not have a great impact on the survival of prey populations.

Figure 2.2 visualises the output from the algorithm for a 100x100 ecosystem. Predator survival in this case takes place in largely the same area as the 2x2 system. A very visible impact can be seen here of predator survival causing a decline in the survival rates of the prey populations. It is possible to see the shape of the surviving predator survival space in that of the surviving prey survival space. Figure 2.3 shows the surviving population rate for the maxR-maxC space in a 200x200 ecosystem. Visibly the space where survival is taking place is the same between the 100x100 and 200x200 ecosystems but it should be noted that the average number of surviving predators and prey are

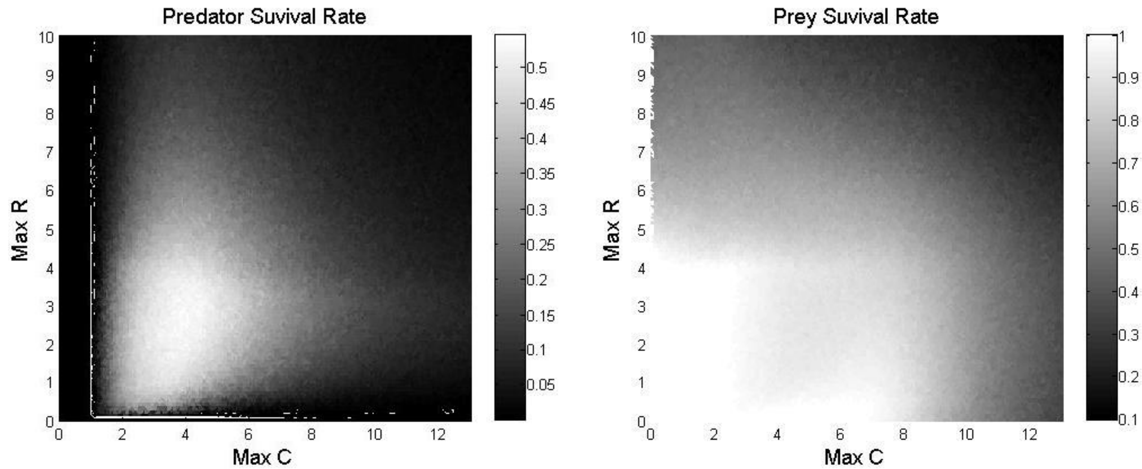



**Fig 2.1 Visualisations of population survival rates over 100 runs of a m=n=2 ecosysten**

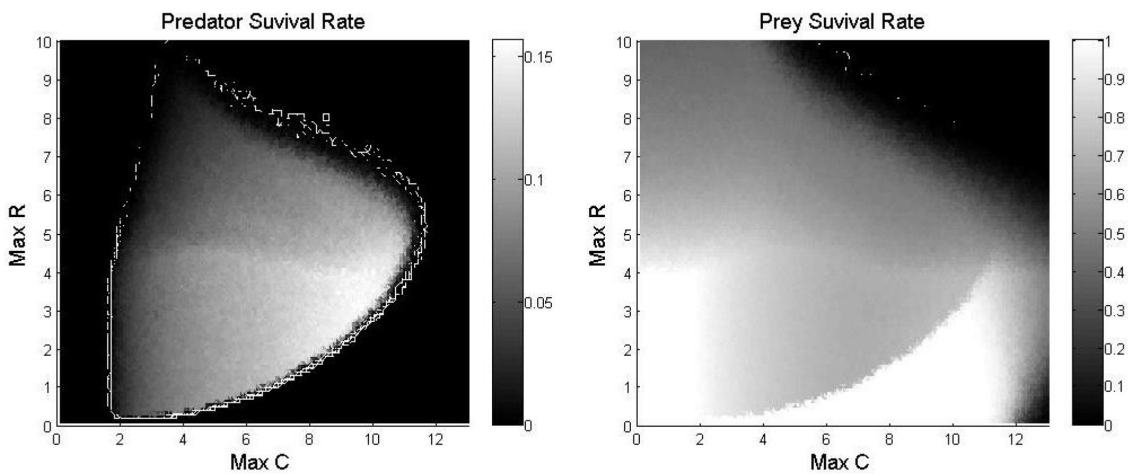



**Fig 2.2 Visualisations of population survival rates over 100 runs of am=n=100 ecosystem**

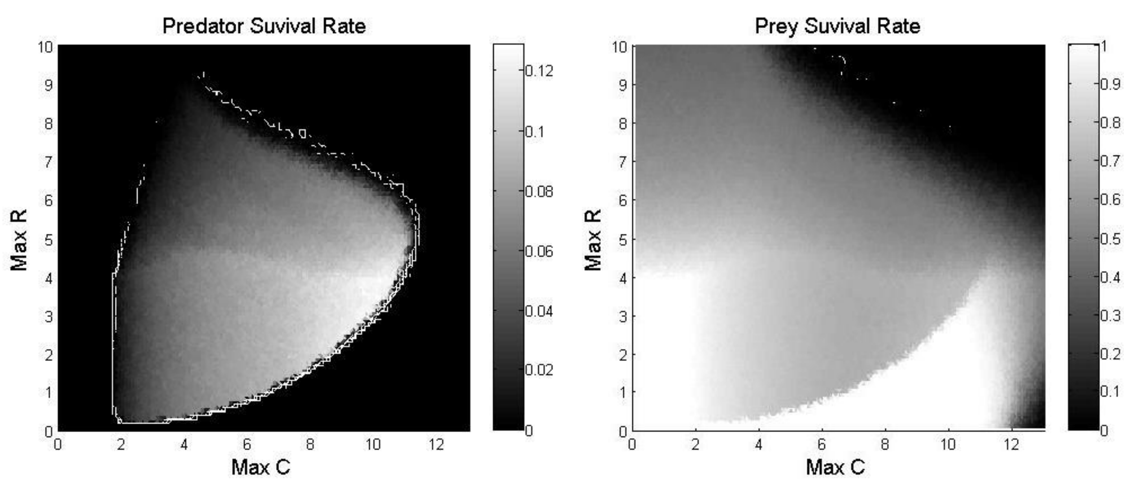



**Fig 2.3 Visualisations of population survival rates over 100 runs of a m=n=200 ecosystem**

**Fig 2. Visualisations of population survival rates for various initial numbers of populating species**

This figure visualises population survival rates after 100 runs of the model and 5000 time steps at each run for n = m = 2, n = m = 100 and n = m = 200. A greyscale colour bar is provided to identify the rate of survival at each point.

declining as the initial population diversity of the ecosystem increases. It should also be noted that as shown in Table 1, which records the maxR-maxC position of peak predator population survival in this Ricker based model, the position of this peak becomes static once the number of initial populations reaches 200x200. For this reason it is assumed that the 200x200 space is fully converged, with the same behaviours being observed for larger systems above

## VI. COMPARISON BETWEEN MODELS

As mentioned in the earlier analysis of the Ricker based model there is a small area along the maxC axis where the prey is not affected by the presence of predators, this area is present in all three models. For all three this is between maxC = 0 and maxC = 1.7. As in the case of the Ricker based model, in this area the population functions as uncoupled independent models for each of the prey; in Figure 3 these are uncoupled logistic functions and in Figure 4 uncoupled tent maps. In Figure 3 in this region total prey population is guaranteed with a maxR value of less than 3, while in Figure 4 this is guaranteed with a maxR less than 2.4. This can be related directly back to the earlier bifurcation diagrams, with survival being seen between $r$= 0 and $r$= 3 in the logistic bifurcation diagram, and $r$=0 and $r$=2.4 in the tent map bifurcation diagram. Similar to the Ricker based model when maxR exceeds the maximum $r$ value of which the uncoupled prey populations can survive in the bifurcation diagram, some prey populations begin to die off.

Similar behaviour is also observed in the convergence of the maxR-maxC space in which population survival takes place as the initial number of predator and prey species populating the ecosystem increases. As has been noted in the Ricker based model, the space for both the tent and the logistic based implementations converges and becomes visually similar between the 100x100, 200x200 and 1000x1000 systems, with the 2x2 model being visually dissimilar.

However it can be noted that the area in which predator survival occurs is visibly much smaller than the Ricker based model in the case of both the logistic and tent based models. Survival of predators takes place from 2 to 6.5 along the maxC axis and 0.3 to 6 along the maxR axis in the logistic model and from 2 to 6 along the maxC axis and 0.3 to 5 along the maxR axis in the tent based model, compared to the Ricker model that has survival from 2 to 11.8 along the maxC axis and 0.3 to 9.5 along the maxR axis. The prey species survival has also been compressed in a similar way long the maxC axis, with the predators overhunting and extinguishing all prey populations at a maximum of maxC = 6 in both cases, whereas in the earlier Ricker model predator populations were not overhunted and continued to survive until a maximum of maxC = 12. The maxR-maxC space between the tent and logistic based models are more similar to each other than to that of the Ricker based model.

The cause of this similarity of the maxR-maxC space between the tent and logistic based model and the dissimilarity found in the Ricker based model stems from the underlying behaviour of the growth function that is

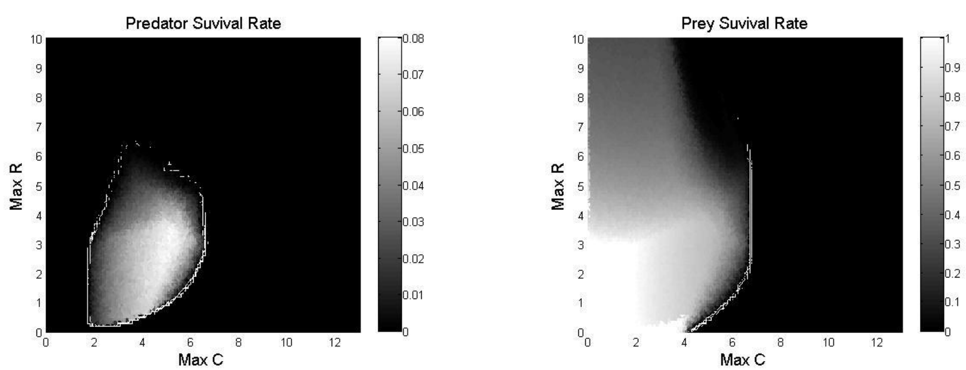



**Fig 3 Visualisations of population survival rates over 100 runs of a 200x200 with the use of the Logistic based model**

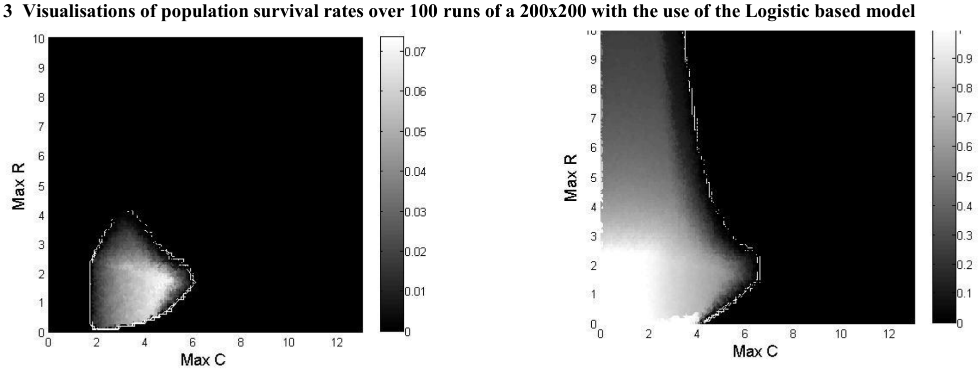


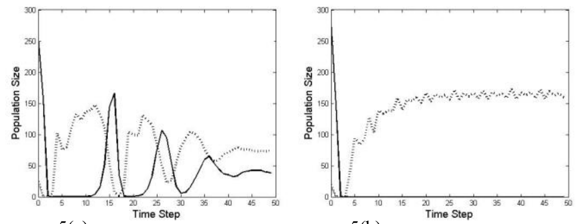

**Fig 4 Visualisations of population survival rates over 100 runs of a 200x200 with the use of the Tent based model**

being utilised. This can be seen in Figures 5(a) and 6(b), which visualise the average summation of the predator and prey population sizes as the model runs for the peak position of predator survival and 5(b) and 6(b) which visualise this at maxR corresponding to the peak position and maxC 1 greater than that of the peak position.

Each of these is averaged over 1000 separate runs of the model. It can be seen that in the case of the Ricker based model in Figure 5(a), with a high maxC value of 10.2 and a maxR value of 3.9, there is a very sudden initial drop-off in the prey population size, which causes a drop-off in the predator population sizes, however the populations do not fall below ε, which in this case is set to $10^{-6}$, and thus upon the recovery of the prey populations the predator populations can also recover. At the point where maxC = 11.2 all the predator populations fall below $\varepsilon = 10^{-6}$ and therefore all become extinct within the first 10 generations as shown in 5(b). The tent and logistic models do not behave in the same way however. The death of a predator or prey is not reliant upon the ε value as it is not used in their case. Therefore this area of suppression where predators continue to survive with very small population sizes does not occur. Figure 6 above visualises this for the logistic based function. Figure 6(a) shows the peak position of predator survival, where maxC = 5.1 and maxR = 2.9. There is a small initial drop-off in the prey and predator populations due to overhunting, but not as pronounced as the Ricker model peaks. Figure 6(b) utilises a maxC value of 6.1 with the same maxR value of that of the peak position, all predator populations overhunt the prey and completely die off, with the prey then recovering. Very similar behaviour occurs in the tent based model.

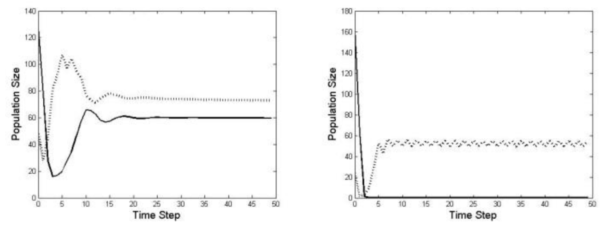
## VII. Conclusion

This paper has looked at a multispecies discrete time predator-prey model with different ways of implementing prey behaviour within the model. A focus has been placed on the final diversity of the ecosystem after 5000 generations of execution with various values utilised for the control parameters. The results show that as the size of the system increases beyond 200 predators and 200 prey survival rates converge onto a well-defined region in the maxR-maxC space in which a stable ecosystem exists. This work also shows that the choice of model for prey behaviour can strongly influence the region of survival with it being. found that the maxR-maxC space in which survival is seen is much more similar between the tent and the logistic models than that of the Ricker based model. Finally, as CPU power increases more complex systems are now within computational reach and such systems are currently under consideration




5(a) 5(b)

**Fig 5 The total surviving population sizes for the predator and the prey at the peak position and maxR corresponding to the peak position and maxC 1 greater than that of the peak position for the Ricker based model ( Predator = Solid line, Prey = Dotted)**




6(a) 6(b)

**Fig 6. The total surviving population sizes for the predator and the prey at the peak position and maxR corresponding to the peak position and maxC 1 greater than that of the peak position for the logistic based model( Predator = Solid line, Prey = Dotted)**

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