

The predictive power of R^* in a two-predator-one-prey Lotka-Volterra model

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Abstract The R^* rule predicts that when two consumers are competing for one limiting resource, the consumer with a lower requirement for the resource (i.e. lower R^*) would competitively exclude the other consumer. Experimental studies that assess the predictive power of R^* focus on primary producers due to the difficulty of conducting experiments for organisms at higher trophic levels. A two-predator-one-prey Lotka-Volterra would therefore provide some theoretical insight into the link between R^* and competition outcome. The model was simulated stochastically using the Gillespie algorithm. The predictive power of R^* diminished as the predators became more similar in their resource requirements. This reduction in predictive power was more prominent when attack rate and assimilation efficiency were altered than when predator mortality rate was altered, which suggested that predators with low mortality rates were less likely to be affected by demographic stochasticity than predators with more efficient predatory and assimilation mechanisms. The variant of the model that incorporated constant immigration rates showed that a critical immigration threshold existed above which the inferior competitor would dominate over the superior competitor. However competitive exclusion did not occur in the immigration model as the constant influx of new individuals rescued the inferior competitor from extinction. The results of the stochastic simulations thus demonstrated that R^* was a good predictor of competitive outcome when the population sizes were large, the R^* values of the two predators were markedly different, the predators differed in their mortality rate, or the immigration rate of the superior predator was higher than that of the inferior predator.

1 Introduction

The consumer-resource interaction is a basic unit of population dynamics and one of the fundamental paradigms concerning resource competition is that of the competitive exclusion principle, which states that no two species that occupy sufficiently similar niches can coexist. The better competitor persists whilst the inferior competitor head to extinction. This principle has been demonstrated in simple organisms such as *Paramecium* species (Gause, 1936). When separately grown in media, *P. aurelia* and *P. caudatum* each reached a different equilibrium level. In a mixed population, however, *P. aurelia* persisted at a lower equilibrium than when cultivated in isolation whilst *P. caudatum* became extinct. Levin (1970) extended the competitive exclusion principle further by proposing that a system with n number of resources cannot stably support more than n number of consumers.

Tilman (1982) outlined a method for predicting competition outcome based only on each consumer's resource requirement and usage, namely the R^* (R star) rule. Each consumer species has a inherent mortality rate and the minimum level of resource level required to sustain a sufficiently high growth rate and keep the consumer population at equilibrium is the R^* for that consumer. If consumer 1 can achieve equilibrium at a lower R^* than consumer 2, then consumer

1 can competitively exclude consumer 2, because when the resource level drops below the R^* of consumer 2 it is still above the R^* of consumer 1, therefore consumer 1 continues to grow while consumer 2 declines in population size. Consumer 1 depletes the resource down to its own R^* , at which point its growth rate exactly balances its mortality rate; consumer 2 continues to decline until it reaches 0 population size and becomes extinct.

Field and laboratory experiments have demonstrated the validity of the R^* rule for certain plankton and plant species (Tilman, 1981; Sommer, 1986; van Donk and Kilham, 1990; Grover, 1991; Tilman and Wedin, 1991). However these experiments have all focused on the interaction between primary producer and inorganic resources. Experimental studies at higher trophic levels, in particular the predator-prey relationship, are lacking for obvious reasons (slower generation time, behavioural changes in an artificial environment, spatial constraints to name but a few). Thus mathematical models of the predator-prey relationship could provide valuable insight that could not be obtained from experiments.

The simplest resource competition model is the classic Lotka-Volterra competition model that captures the relationship between two consumer species competing for a limiting resource (Lotka, 1932). This model shows that coexistence of two competing species can only occur if intraspecific competition is greater than interspecific competition. One drawback with using the Lotka-Volterra competition model is its assumption of a constant competition coefficient, which may not always be the case (Abrams, 2001). Moreover, the model does not provide predictions of the outcome of competition because the competition coefficient can only be determined once competition between the two species has been observed.

A modified version of the Lotka-Volterra predator-prey model that includes two predators would provide more insight into the predictive power of R^* as the parameters that contribute to the R^* value could be directly controlled. According to the competitive exclusion principle and the R^* rule, the predator with a lower resource requirement would displace the other predator. However the predictive power of R^* in systems with stochasticity was not guaranteed. Demographic stochasticity, which refers to random fluctuations in fecundity and mortality, is a prominent contributor to small population dynamics (Lande, 1998). Because species at higher trophic levels generally have smaller population sizes (Fowler, 2009), the predator-prey population dynamics would be expected to be affected by the introduction of demographic stochasticity. In a stochastic system, even the better competitor may not be safe from extinction. Thus, a more relevant marker for competitiveness in stochastic systems would be consumer extinction risk.

In the present thesis, the extent to which demographic stochasticity could alter the predictive ability of R^* was tested through stochastic simulations of a two-predator-one-prey Lotka-Volterra model. Furthermore, the contribution of underlying parameters to the R^* value was assessed. If an investigator were to evaluate R^* empirically, the underlying properties of the consumer that contributed to the R^* value would remain unknown. Utilisation of mathematical models therefore enables specification of parameter that contribute to R^* . Competitive exclusion only predicts the coexistence or extinction of two competing consumers but it does not provide any insight into how coexistence is achieved. If the pre-equilibria dynamics of two predator populations with the same R^* value were different, the predictive power of R^* might depend on the composition of the underlying parameter values.

Besides being affected by stochasticity, the power of R^* in predicting the outcome of competition could also be influenced by dispersal. The original definition of R^* was based on a closed system, however movement in and out of the system could alter the competitive interaction. Abrams and Wilson (2004) showed through metapopulation models that an inferior competitor with a higher R^* could achieve dominance in the global system by having a sufficiently high migration rate. Moreover the effect of immigration on inferior competitor persistence has also been demonstrated experimentally, for example the immigration of the *Tetrathermophila thermophila* enabled its

persistence in the presence of the better competitor *Colpidium striatum* whereas *T. thermophila* always headed to extinction in the absence of immigration (Long et al., 2007). Hence, a variant of the two-predator-one-prey Lotka-Volterra model that included constant immigration of prey and predators into the system was used to determine if immigration could change the predictive power of R^* .

2 Methods

The two-predator-one-prey Lotka-Volterra model used in this thesis was implemented both deterministically and stochastically to investigate the ability of R^* to predict the outcome of exploitative competition. The 3 state variables in the model represented the prey population, R , and the 2 predator populations, P_j where $j = 1$ or 2 .

2.1 Deterministic model

The deterministic version of the model used in this thesis was based on the Lotka-Volterra predator-prey equations. The original formulation of the Lotka-Volterra equations captured the simplest interaction between a prey population and a predator population in a closed biological system (Lotka, 1925; Volterra, 1926). The model reported here differ from the original Lotka-Volterra equations in that the prey grows logistically instead of exponentially due to the presence of density-dependence and that 2 predators instead of 1 feed on the prey. Such a model could be described by the following ordinary differential equations (ODEs; **Eqs.1-3**)

$$\frac{dR}{dt} = R(r(1 - \frac{R}{K}) - a_1P_1 - a_2P_2) + i_R \quad (1)$$

$$\frac{dP_1}{dt} = P_1(c_1a_1R - d_1) + i_1 \quad (2)$$

$$\frac{dP_2}{dt} = P_2(c_2a_2R - d_2) + i_2 \quad (3)$$

in which r is the intrinsic growth rate of the prey and K is the prey carrying capacity; $r(1 - \frac{R}{K})$ denotes the per-capita prey fecundity. a_j is the attack/predation rate for predator j , c_j ($0 \leq c_j \leq 1$) is the assimilation efficiency with which energy from the prey is transferred to predator j , d_j is the predator j mortality rate, and i_R/i_j are the immigration rates of prey and predator j , respectively. The parameters in orange only apply to the immigration variant of the model.

The R_j^* value is calculated from the equilibrium prey level when only one predator is present **Eq.4**.

$$\begin{aligned} \text{At equilibrium, } \frac{dP_j}{dt} &= P_j(c_ja_jR - d_j) = 0 \\ &\text{Either } P_j = 0 \text{ (predator extinction)} \\ &\text{Or } (c_ja_jR - d_j) = 0 \\ &\quad c_ja_jR = d_j \\ &\quad R^* = \frac{d_j}{c_ja_j} \end{aligned} \quad (4)$$

Table 1: A list of 10 events that alter population size of prey and predator j ($j = 1$ or 2) in the two-predator-one-prey Lotka-Volterra model. The **immigration events** are only relevant to the immigration variant of the two-predator-one-prey Lotka-Volterra model. The total rate of all the events described in the table add up to h .

Event	Population Change	Rate
Prey birth	$R \rightarrow R + R$	$rR(1 - \frac{R}{K})$
Prey death due to predator 1	$R + P_1 \rightarrow R$	a_1RP_1
Prey death due to predator 2	$R + P_2 \rightarrow R$	a_2RP_2
Predator 1 birth	$P_1 \rightarrow P_1 + P_1$	$c_1a_1RP_1$
Predator 2 birth	$P_2 \rightarrow P_2 + P_2$	$c_2a_2RP_2$
Predator 1 death	$P_1 + P_1 \rightarrow P$	d_1P_1
Predator 2 death	$P_2 + P_2 \rightarrow P$	d_2P_2
Prey immigration	$R \rightarrow R + R$	i_R
Predator 1 immigration	$P_1 \rightarrow P_1 + P_1$	i_1
Predator 2 immigration	$P_2 \rightarrow P_2 + P_2$	i_2

2.2 Stochastic model

A fundamental difference between deterministic and stochastic models is that inputting the same set of parameter values and initial conditions into the former always leads to the same results. The latter, however, incorporates randomness by describing the probability of something happening. For example if the per capita prey fecundity is 1, it is highly unlikely for each prey to have exactly 1 offspring each year. Instead, each prey will have a range of offspring numbers, but the average number of offspring per parent is 1. Variability in growth or mortality rate is known as demographic stochasticity. Unless the population is sufficiently large, the actual number of offspring on a given year may significantly differ from the average growth value. Thus, demographic stochasticity may cause a small population to become extinct purely by chance. Furthermore, the continuous nature of deterministic processes is incompatible with the description of small populations, because a population of 0.5 may still be viable according to the deterministic equations but is clearly impossible in reality. Although discrete population sizes may not make a difference when population size is large, e.g. 1000 vs. 1000.5, but they are a necessity when describing smaller populations.

Stochastic simulations in this thesis were carried out using the simple algorithm set out by Gillespie (1977). Although originally written with chemical kinetics in mind, the Gillespie algorithm could be applied to *event*-based modelling in a number of fields including population ecology. The basis of the algorithm are as follows: (1) Events occur that alter the size of one or more state variables. (2) In an infinitesimally small time interval, δt , a maximum of one event can occur. The events that occur in the two-predator-one-prey Lotka-Volterra model are listed in **Table.1**. Prey fecundity is dependent on the current prey population size as well as the size of the carrying capacity. Prey death only occurs from predation, but this event is not directly coupled to predator birth. As the predator can only assimilate a proportion of each prey they eat, prey birth event can only occur once the predator has consumed enough prey. Predator death naturally occurs irrespective of any other processes and its rate is proportional to the current predator population density.

In a given time interval δt either one event occurs or no event occurs (**Fig.1**). The waiting times follow an exponential distribution, i.e. the probability of a length of time being the waiting time decays exponentially as the length of time increases. This distribution can be derived mathematically (**Eq.5**) by considering waiting time T as the sum of X number of infinitesimally small time intervals δt . Suppose that the total rate of events is h , then the probability of any

event occurring in δt is defined as $P(\text{event in } \delta t) = h\delta t$ and the probability of no event occurring is $P(\text{no event in } \delta t) = 1 - h\delta t$. The distribution of *waiting time* T is described by the probability that an event occurs after waiting time T is the multiple of the probability that no event occurs in any of the X number of δt time intervals before T and of the probability that an event occurs in the δt right after T .

$$\begin{aligned}
P(\text{event occurring in the interval}[T + \delta t]) &= (1 - h\delta t)^X \cdot h\delta t \\
\text{Given that } \delta t &= \frac{T}{X} \\
(1 - h\delta t)^X \cdot h\delta t &= (1 - h\frac{T}{X})^X \cdot h\delta t \\
\text{Using l'Hopital's rule, } \lim_{X \rightarrow \infty} (1 - h\frac{T}{X})^X &= e^{-hT} \\
(1 - h\frac{T}{X})^X \cdot h\delta t &= e^{-hT} h\delta t
\end{aligned} \tag{5}$$

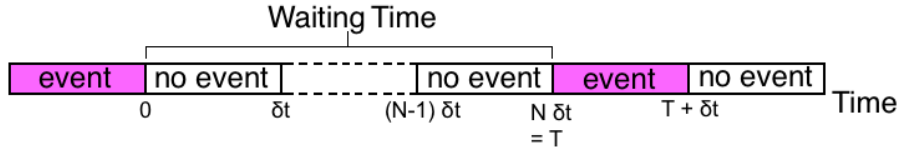


Figure 1: The waiting time T between two consecutive events can be subdivided into X smaller time units δt that are infinitesimally small, such that only one event can occur in δt .

In step 3 of the Gillespie algorithm (**Fig.2**), a random number between 0 and 1 is generated from a uniform distribution. Each event is attributed an interval between 0 and 1, and the interval size is proportional to the rate of that event. For example, if a random number falls in the interval $[0, 0.09]$, a prey birth event occurs, if the number falls in the interval $[0.09, 0.15]$, prey death event occurs etc. As the simulation proceeds the interval sizes may change if the rate of an event is dependent on population density.

2.3 Assumptions of the model

The main assumptions of the two-predator-one-prey Lotka-Volterra model are as follows:

1. Prey grows to carrying capacity logistically in the absence of predators.
2. Prey can only die as a result of predation.
3. Predators die in the absence of prey
4. The rate of predation depends on the abundance of prey and the population density of predator.
5. The two predator populations are in exploitative competition with each other; however there is no interference competition between members of the same predator population.
6. Predators do not become saturated even at high rates of predation.
7. The conversion of prey biomass into predator biomass occurs with a constant efficiency.
8. The per capita rate of predator death is constant.

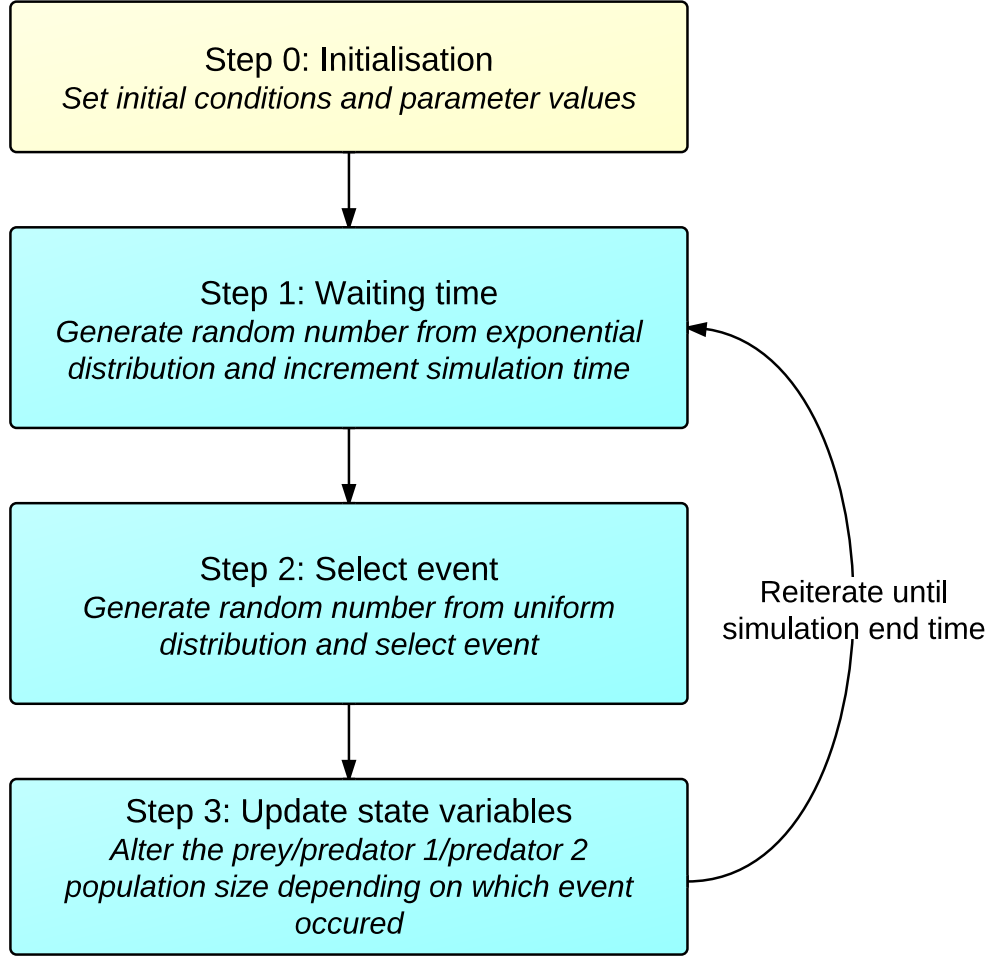


Figure 2: The Gillespie stochastic simulation algorithm. The simulation comes to an end once the simulation end time has been reached.

9. The immigration of prey and predator is density-independent and occurs at a constant rate (only applies to the immigration variant of the model).

2.4 Simulations

The simulation of the two-predator-one-prey Lotka-Volterra model was carried deterministically and stochastically using the *deSolve* package (Soetaert et al., 2010) and the *GillespieSSA* package (Pineda-Krch, 2010) in *R* (R Development Core Team, 2012), respectively.

The initial prey density was set to be equal to the carrying capacity K and the predator densities are equal to $\frac{1}{2}K$. Unless otherwise stated, the default values for parameters listed in **Table.2** were used for the deterministic and stochastic model simulations.

The stochastic model simulation end time was chosen such that at least 90% of simulations

resulted in one or both predators heading to extinction. If too many of the runs resulted in both predators persisting, the comparison of extinction risk between the two predator populations would be less accurate due to the smaller sample size.

Table 2: The default parameter values used in the deterministic and stochastic simulations of the two-predator-one-prey model. Parameters in orange are only applicable to the immigration variant of the model.

Intrinsic prey growth rate r	1
Carrying capacity K	10
Attack rate a_j	0.2
Assimilation efficiency c_j	0.1
Predator mortality rate d_j	0.1
Prey immigration rate i_R	0.1
Predator j immigration rate i_j	0.2

The ability of R^* to predict competition outcome in the stochastic model was measured by the extinction risk. Thus if the R^* of predator 1 was lower than that of predator 2, the R^* rule would predict the extinction risk of predator 1 to be 0% and that of predator 2 to be 100%. If the extinction risks differed from these percentages, the predictive power of R^* would be lower than expected.

In simulations that required varying of the R^* ratio, i.e. $R_1^*:R_2^*$, the R^* parameters for predator 2 remained unchanged whilst the R^* parameters for predator 1 were altered. The ratio was then increased from 0 to 4 in increments of 0.1. Similarly, the immigration ratio was varied by keeping the predator 2 immigration rate i_2 constant whilst changing i_1 . In all cases, the extinction risk of predator 1 in the stochastic model corresponded to the proportion of simulations that resulted in predator 1 becoming extinct before predator 2; and *vice versa* for predator 2.

To determine the effect demographic stochasticity might have on the predictive power of R^* , the outcome of competition in the stochastic model was measured by the relative extinction risk of the two predator species. The competitiveness of each predator was predicted by the R^* ratio, so the superior competitor was expected to have a lower extinction risk than the inferior competitor. The d_1 value was varied to obtain the different R^* values. The same was repeated twice, with variations in a_1 and c_1 .

Using the immigration variant of the two-predator-one-prey Lotka-Volterra model, the i_1 value was altered to increase the immigration ratio from 0 to 10 in increments of 0.1. For each set of immigration ratios, the extinction risk for the predators were calculated for a specific R^* ratio, and this R^* ratio was increased by altering the d_1 value. The critical immigration ratio for each R^* ratio was then calculated as the lowest immigration ratio required for predator 1 to have a lower extinction risk than predator 2.

3 Results

3.1 Demographic stochasticity

In the deterministic model, predator 1 always headed to extinction first when its R_1^* was lower than R_2^* whereas predator 2 always heads to extinction first when the reverse was true (**Fig.3a**). Only when the two R^* values were the same did coexistence occur. Thus R^* could predict deterministic competitive outcome with 100% certainty.

In contrast to the deterministic model, a lower R^* in the stochastic model did not guarantee later extinction. For example, when the R^* ratio was 1.1, the probability that predator 1 (the inferior competitor) went extinct before predator 2 was just over 50% (**Fig.3b**) whereas in the deterministic model, the probability of earlier extinction for predator 1 was 100%. The distribution of extinction risk was sigmoidal in shape and as the R^* ratio increased above 1, the rate of extinction risk increase for predator 1 slowed down.

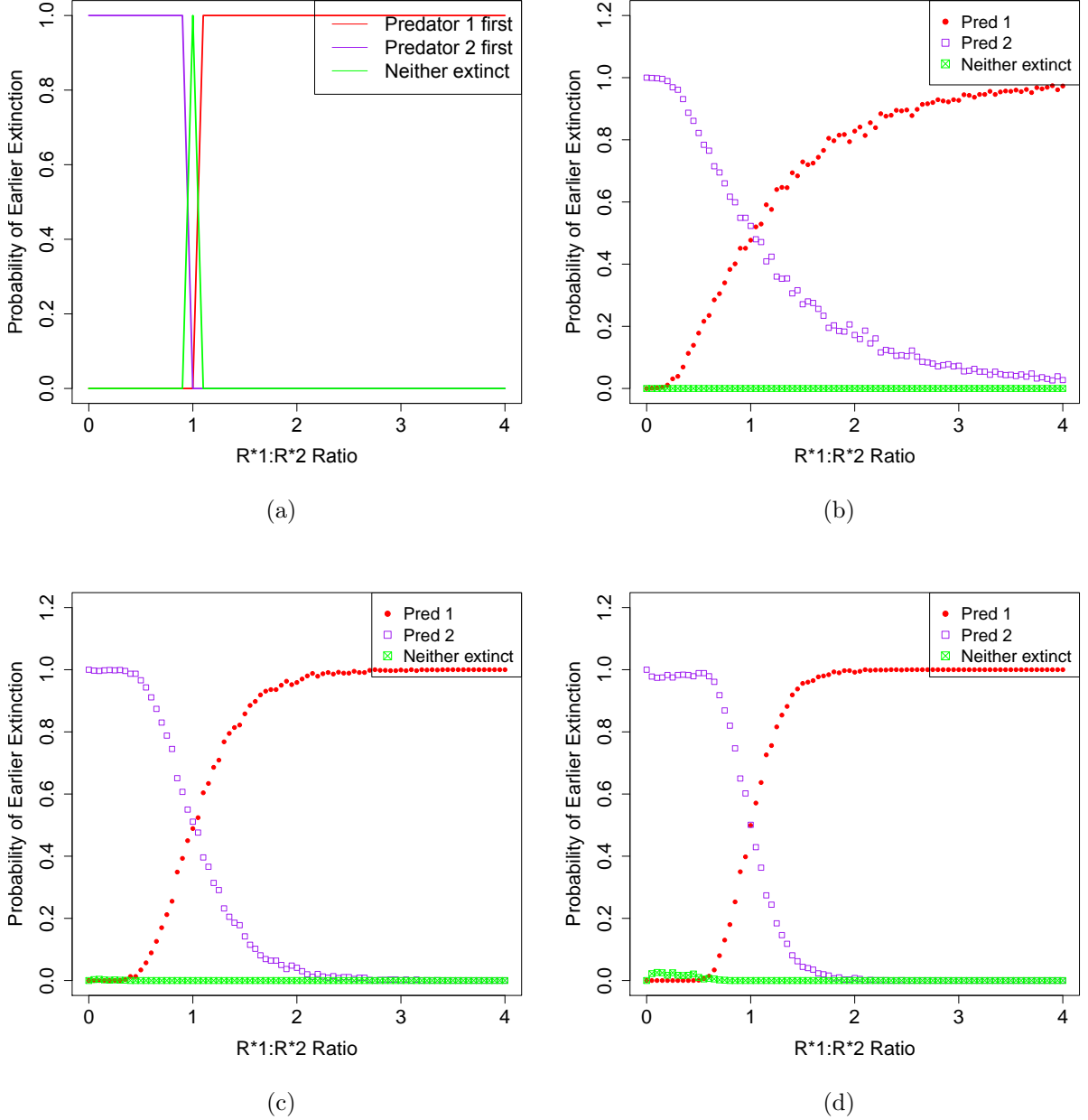


Figure 3: (a) shows the probability that one predator reaches extinction before the other as a function of the $R^*_1:R^*_2$ ratio in the deterministic model. The distribution of extinction risk as a function of $R^*_1:R^*_2$ ratios (only d_1 is changed) in the stochastic model is shown for three different initial conditions: (b) $K = 10, R = 10, P_1 = 5$ and $P_2 = 5$; (c) $K = 100, R = 100, P_1 = 50$ and $P_2 = 50$; and (d) $K = 1000, R = 1000, P_1 = 500$ and $P_2 = 500$.

The minimum R^* ratio required for an increase in predator 1 extinction risk was positively correlated with population size (**Fig.3b-d**), which indicated that the distribution of extinction

risk tended towards the deterministic version as the population size increased and that in small populations the influence of stochasticity on outcome was greater than in larger populations. However, even when the carrying capacity was increased to 1000, a reduction in extinction risk was still possible for R^* ratios close to 1.

3.2 Underlying parameters of the R^* value

In **Fig.3** the R^* ratio was adjusted by altering the mortality rate of predator 1. However, the R^* value comprised 3 separate parameter values: $\frac{d_j}{a_j c_j}$. In the deterministic model, altering the underlying parameter values whilst keeping R_1^* and R_2^* equal still lead to coexistence of the two predator populations, but some combinations resulted in different equilibrium levels (results not shown).

In the stochastic model, the change in predator extinction risk was very small when either a_1 or c_1 was varied (**Fig.4**) compared to when d_1 was varied (**Fig.3b-d**).

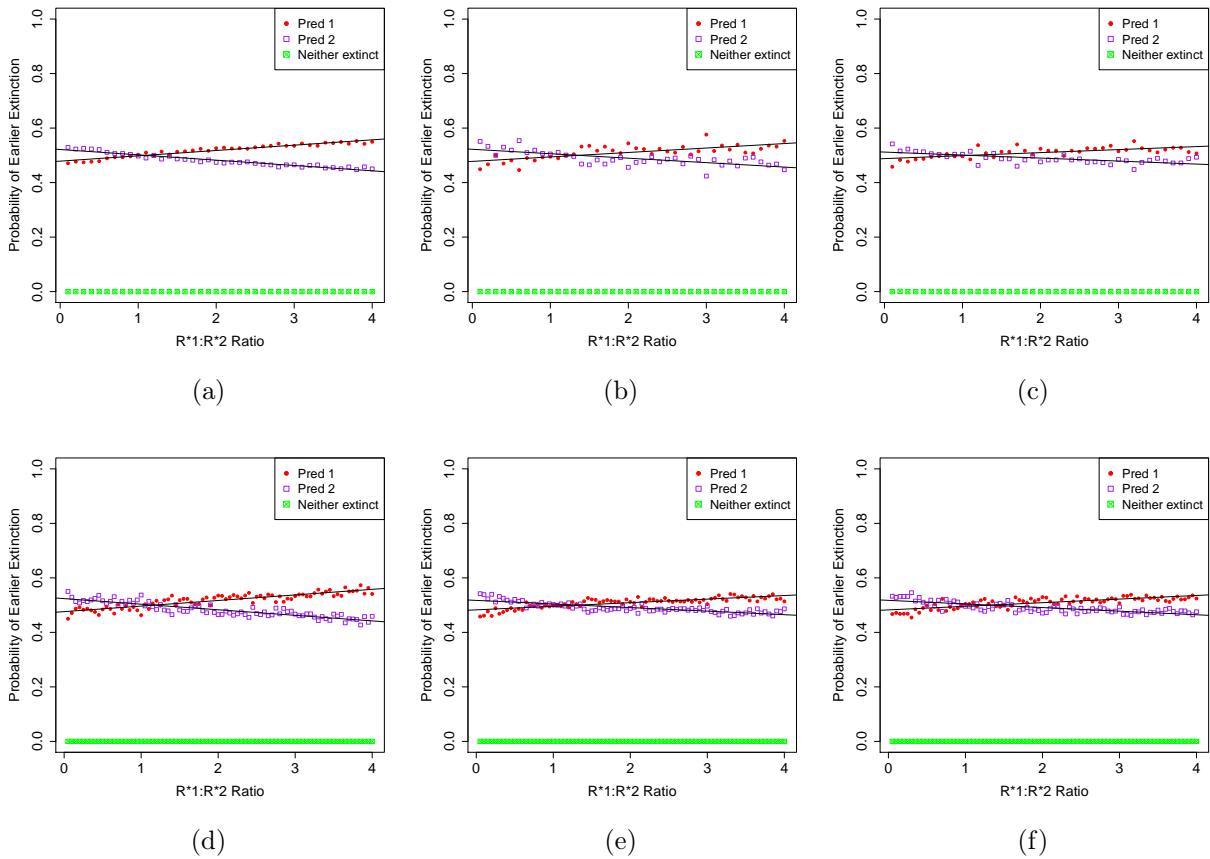


Figure 4: The distribution of predator extinction risk as a function of the R^* ratio when only a_1 was adjusted (top three figures) and when only c_1 was adjusted (bottom three figures). The initial conditions were altered as in (**Fig.3b-d**): (**a&d**) $K = 10$, $R = 10$, $P_1 = 5$ and $P_2 = 5$; (**b&e**) $K = 100$, $R = 100$, $P_1 = 50$ and $P_2 = 50$; and (**c&f**) $K = 1000$, $R = 1000$, $P_1 = 500$ and $P_2 = 500$.

To find a possible explanation for the apparently little effect that attack rate and assimilation efficiency have on extinction risk, the stochastic simulation results were compared with deterministic simulation results. When the R^* ratio was below 1, the extinction risk of predator 1 was expected to decrease. In all deterministic simulations, the prey and predator populations

dipped either immediately or soon afterward initiation. This was usually followed by further, dampened oscillations, eventually leading to equilibria. This initial dip decreased in magnitude as d_1 was reduced (**Fig.5a,d&g**), but a similar decrease was not observed when either a_1 or c_1 was altered. The magnitude of the initial dip increased as a_1 increased (**Fig.5b,e&h**). In fact, when R^* was set to 0.1, despite the fact that predator 1 was the superior competitor in terms of its R^* value, the initial drop was so large that the predator 1 population appeared to have gone extinct (**Fig.5h**) although the population later underwent further fluctuations before settling to the equilibrium value (not shown). Similarly, the magnitude of the initial dip also increased as c_1 increased (**Fig.5c,f&i**); when the R^* ratio was set to 0.1, the predator 1 population increased immediately after the simulation began but quickly dropped to below 1 (**Fig.5i**).

To determine if attack rate and assimilation efficiency could have a greater impact on risk if the magnitude of the initial dip in population density was smaller, the initial prey density:predator density ratio was increased. When the initial conditions were set to $K = 100$, $R = 100$ and $P_j = 5$, the extinction risk distributions obtained for variations in d_1 , a_1 and c_1 similar to those observed in **Fig.3**, although the impact on extinction risk when either attack rate (**Fig.6b**) or assimilation efficiency (**Fig.6c**) was changed was still smaller compared to when mortality rate was changed (**Fig.6a**).

3.3 Immigration

When R^* ratio < 1 , predator 1 was predicted to be the superior competitor and was expected to have a lower extinction risk. When R^* ratio < 0.6 , the extinction risk of predator 1 was always smaller than that of predator 2, irrespective of the immigration ratio (**Fig.a-c**). Note that only i_1 was altered in the simulations. When i_2 was sufficiently high, predator 2 had a lower extinction risk than predator 1 (not shown). When R^* ratio > 0.6 , for each R^* ratio, there existed a *critical immigration threshold* above which predator 1 had a lower extinction risk than predator 2 (**Fig.7d-k**). The relationship between critical immigration threshold and R^* was linear (**Fig.7l**).

Furthermore the probability that neither predator species went extinct within the specified simulation time of 120 time units increased with the immigration ratio and the increase was observed over a broader range when the R^* ratio was lower (**Fig.7**). This observation corresponded with the decreasing number of simulations in which predator 1 went extinct as i_1 increased.

In the deterministic simulations, constant predator immigration allowed predators to coexist in equilibrium (**Fig.8**). The critical immigration ratio in the deterministic model corresponded to the minimum immigration ratio necessary for the predator 1 equilibrium to exceed that of the predator 2 equilibrium. For example at $R^* = 2$, an immigration ratio greater than the critical immigration threshold of 3 allowed predator 1 to maintain itself at a higher equilibrium level than predator 2.

4 Discussion

The R^* value was a definitive indicator of competition outcome in the deterministic simulations of the two-predator-one-prey Lotka-Volterra model; R^* ratios less than or greater than 1 led to extinction of predator 2 or predator 1, respectively, and the persistence of the other predator population. In stochastic simulations of the model, the predictive power of R^* decreased as the R^* ratios tended towards 1. Moreover the predictive power of R^* was reduced over a broader range when population was small, which concurred with findings of other models that highlight demographic stochasticity as a significant extinction risk factor of smaller populations than in

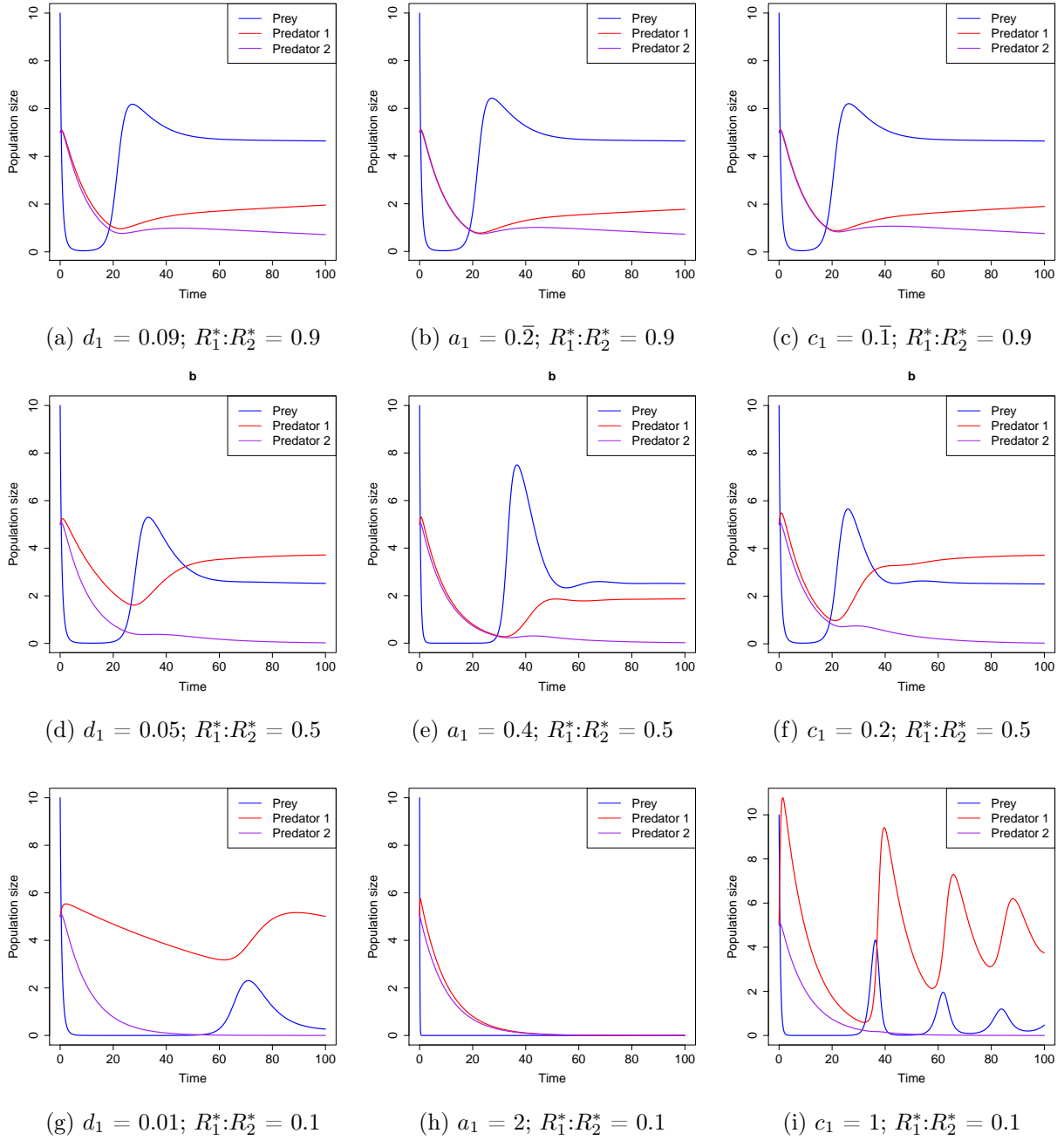


Figure 5: The dynamics of prey, predator 1 and predator 2 during the first 100 time units of the deterministic model. In (a)-(c), the $R_1^*:R_2^*$ ratio is set to 0.9 by separately changing the mortality rate d_1 , the attack rate a_1 and the assimilation efficiency c_1 . The $R_1^*:R_2^*$ ratio was then changed to 0.5 for (d)-(f), and to 0.1 (g)-(i).

larger populations (Lande, 1993). These results suggested that demographic stochasticity eroded the predictive power of R^* if stochastic extinction was much more likely than extinction due to competitive exclusion.

Small changes in predator mortality rate caused greater disparity in extinction risks of the two predators than a similar change in attack rate or assimilation efficiency. R^* was therefore more likely to predict the outcome of competition if predators had differential mortality rates. Early experiments that assessed the validity of the R^* rule made no predictions regarding the com-

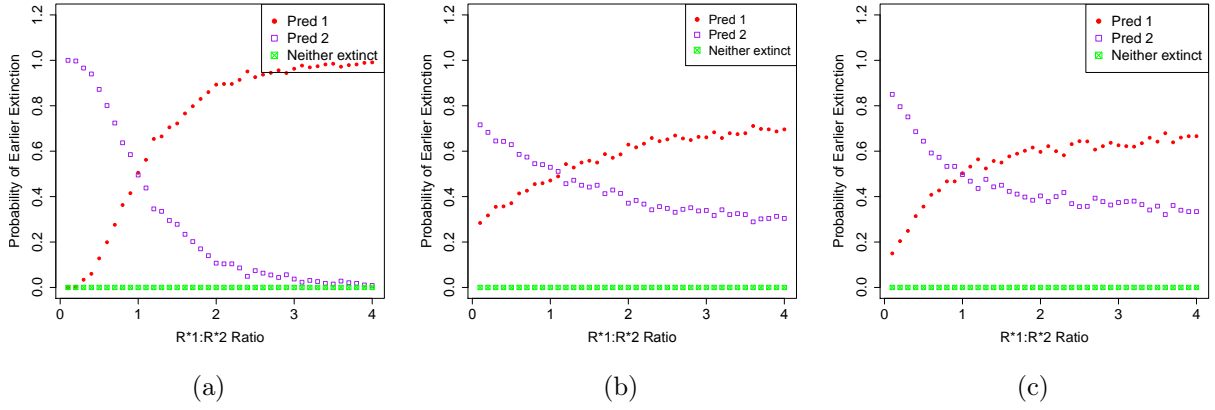


Figure 6: The extinction risk distribution with respect to changes in R^* , when d_1 was altered (a), when a_1 was altered (b) and when c_1 was altered (c). The initial conditions were changed from the default values to $K = 100$, $R = 100$ and $P_j = 5$.

petitive outcome of consumers with differential mortality rate, instead focusing on consumption characteristics (Tilman, 1981; Sommer, 1986; van Donk and Kilham, 1990; Grover, 1991). These experiments were carried out using plankton in continuous media and the mortality rate of the consumers was kept constant for all competing species by controlling the flow rate of medium. When van Donk and Kilham (1990) accidentally allowed *Fragilaria crotonensis* to grow on the wall of the container in which experiments took place, this algal species dominated over other algal species despite R^* predicting *Asterionella formosa* to dominate. It therefore seems that despite having no direct effect on consumption, predator mortality rate was less influenced by demographic stochasticity than attack rate of assimilation efficiency. In natural systems a predator with lower mortality rate than other predators would require fewer kills to sustain its population. During years in which prey are scarce, predators with high attack rates or assimilation efficiencies might not be able to persist due to the lack of prey to kill whereas predators with lower mortality rates would survive for longer without food. Given that starvation due to demographic stochasticity or environmental factors such as drought are common causes of die-offs in large mammals (Young, 1994), predator mortality rate could be an important factor in determining competition outcome and shaping community structure.

Another noteworthy observation from the simulations in which the underlying parameters were separately varied was that the predictive power of R^* improved when the initial predator population densities were reduced from 50% to 5% of K (**Fig.3&Fig.4 vs. Fig.6**). This was likely due to large initial predator population size driving the prey population to extinction before the system manages to recover and equilibrate (**Fig.5**). Even with different initial conditions, nonetheless, the superior competitor as predicted by R^* was less likely to become extinct than the inferior competitor. The deterministic result lends support to the argument that competition outcome is independent of initial conditions (Sommer, 1986; Wedin and Tilman, 1993) however the stochastic results demonstrated that demographic stochasticity could alter how well R^* could predict competition outcome and this may contribute to the opposite argument that initial conditions affect competition outcome (Hu and Zhang, 1993). Roques and Chekroun (2011) probed a Lotka-Volterra competition model with 4 competitors and uncovered certain initial conditions that led to chaos in the system, thereby increasing extinction risk.

The stochastic simulations of the immigration variant of two-predator-one-prey Lotka-Volterra model revealed that the inferior competitor as predicted by R^* could reduce its extinction risk below 50% and even to 0% if its immigration rate was sufficiently higher than that of the other competitor. Not only did the predictive power of R^* decrease as the immigration ratio increased,

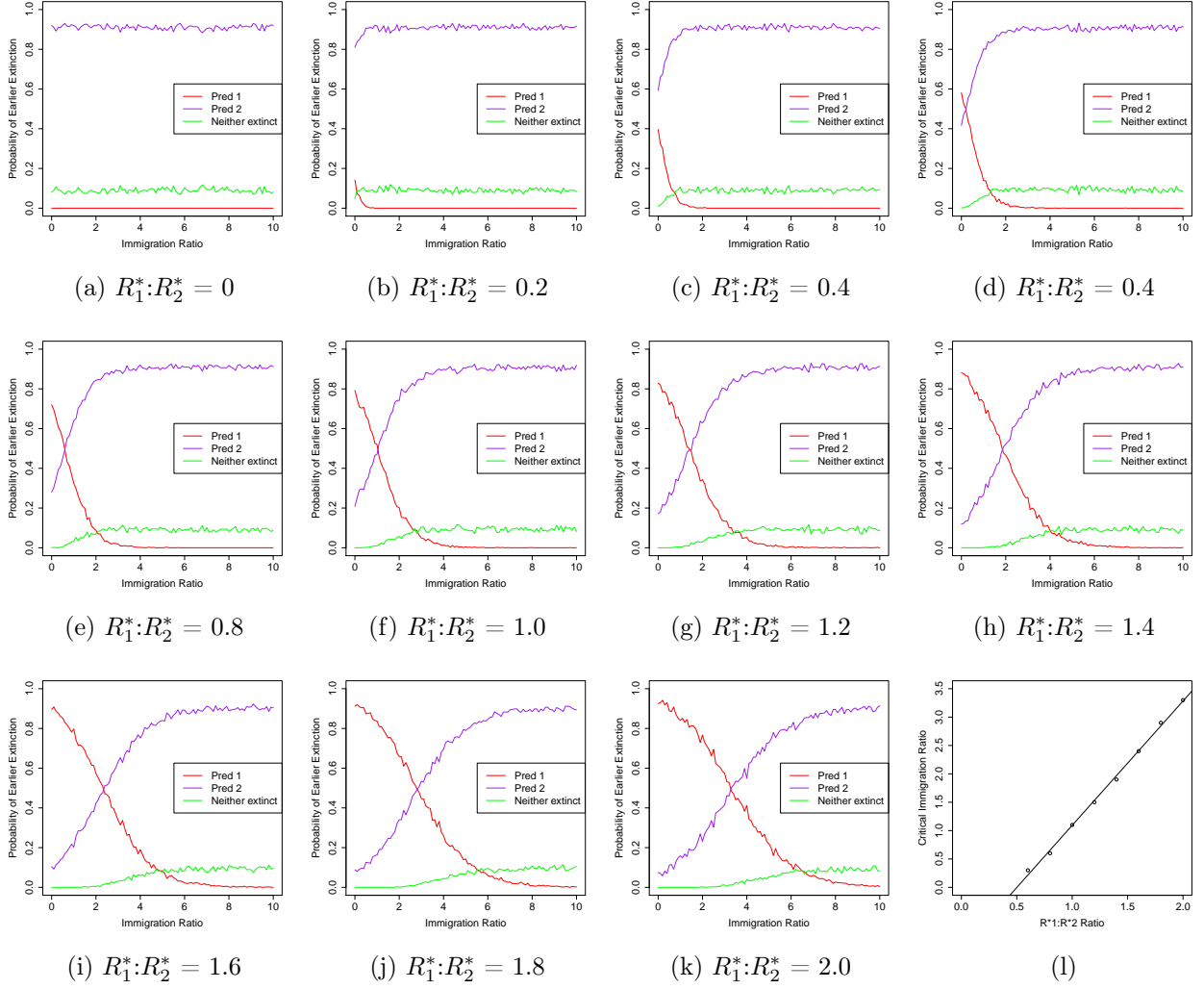


Figure 7: The extinction risk as a function of immigration ratio $i_1:i_2$ is illustrated for a range of $R_1^*:R_2^*$ values (a)-(k). The critical immigration threshold is the lowest value of $i_1:i_2$ that the extinction risk of predator 1 is lower than that of predator 2. The critical immigration ratio is positively correlated with the $R_1^*:R_2^*$ ratio (l).

R^* made the wrong predictions when the immigration ratio was above the critical immigration threshold. Moreover, according to the competitive exclusion principle only competitors with the same R^* values could coexist; nevertheless constant immigration facilitated the persistence of both the superior and inferior competitors (**Fig.8**). Immigration thus seemed to be an important factor in supporting survival. Anthropogenic habitat fragmentation often cause isolated patches to form, thereby preventing immigration to certain patches to occur (Harrison and Bruna, 1999). This isolation would increase crowding and the intensity of competition. Thus systems with few limiting prey species and at risk of being cut off from other patches could be potential targets of conservation efforts.

In this thesis, the two-predator-one-prey Lotka-Volterra model was used to generate predictions regarding competition outcome. Systems described by other models have different methods of calculating R^* , for example the Monod equation used in resource competition experiments involving algae requires knowledge of growth kinetics to provide an estimate of R^* (Monod, 1950). However the Monod equation would not be suitable for estimating R^* of predators, because in the Monod equation the resource is not self-renewing and the uptake of resource is

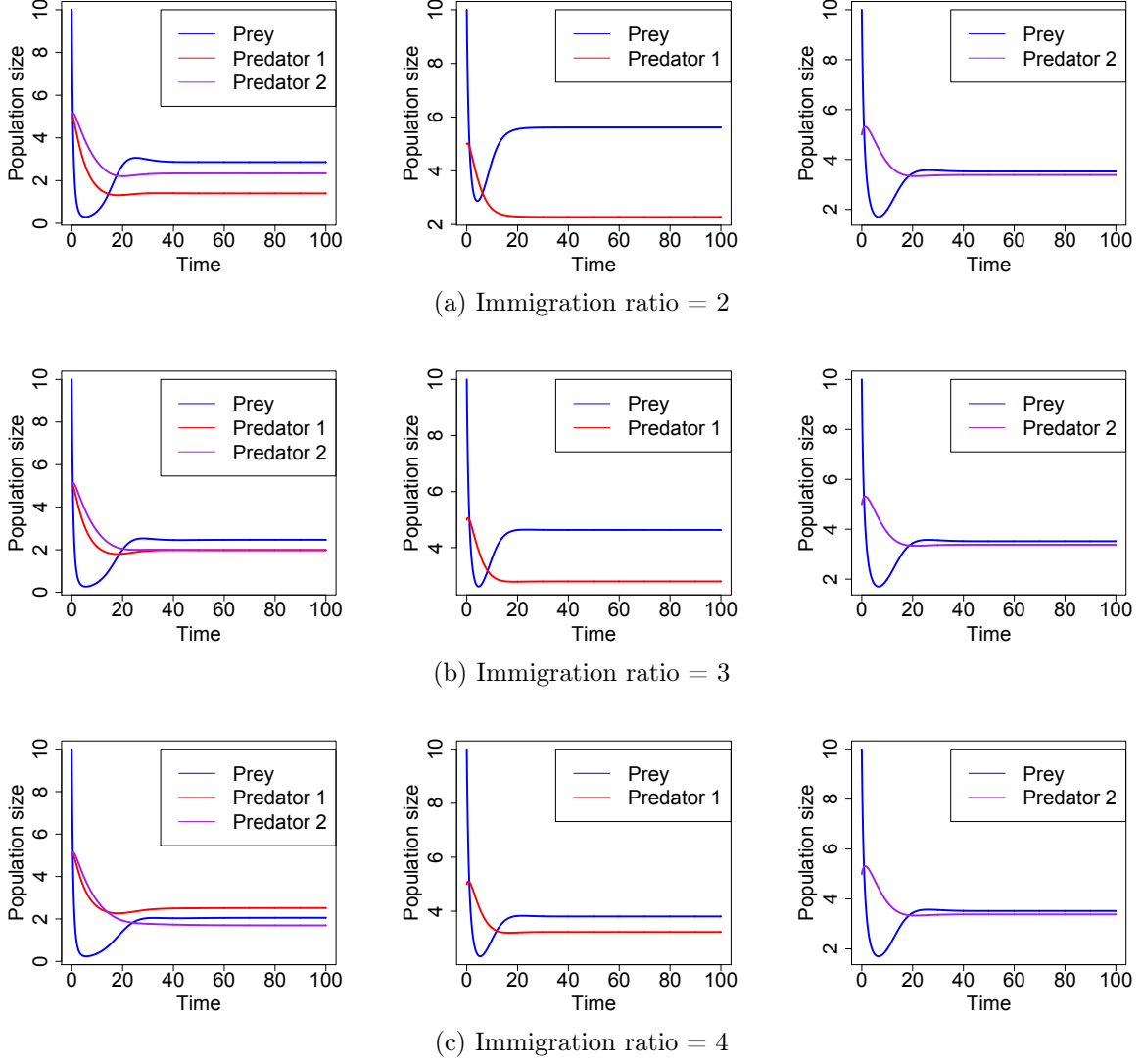


Figure 8: At R^* ratio = 2 ($d_1 = 0.2$), predator 2 equilibrium level was higher than predator 1 equilibrium level when immigration ratio < 3 a; predator 2 equilibrium level was lower than predator 1 equilibrium level when immigration ratio > 3 a; and the predator equilibria levels were equal when immigration ratio = 3.

directly coupled to growth.

Extensions of the model could be made by the changing the predator functional response from type I (linear) to type 2 (saturating) as described by Holling (1959). If prey densities are small, then type 2 functional response would not make a big difference to the attack rate because the handling time is trivial compared to the time used to search for prey (O'Neil, 1989). If prey densities are large, then attack rate would gradually plateau because the predator needs to spend very little time finding prey so the limiting factor is the handling time (Dale et al., 1994). Because R^* is dependent on predator attack rate, changing to a type 2 function response could affect the predictive power of R^* .

Despite providing statistically accurate results, the Gillespie stochastic simulation algorithm is computationally intensive because a very large number of simulations is required to obtain a representative result, which necessitates a great deal of computational power (Gillespie, 1977). Methods of speeding up this algorithm were offered by the *GillespieSSA* package (Pineda-Krch,

2010) in R. The general principle behind these methods was to trade computational efficiency with accuracy by making tau-leaps in time and to estimate the number of occurrences of an event within that tau-leap. No approximation methods were used in the present report because the time saved could not justify the accuracy trade-off.

5 Conclusions

The results of the simulations demonstrated that R^* was a good predictor of competitive outcome when the population sizes were large, the R^* values of the two predators were markedly different, the predators differed in their mortality rate, or the immigration rate of the superior predator was higher than that of the inferior predator.

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