Predator Management in a Two-patch System

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1. EXTENDED ABSTRACT

Introduced predators have a major impact on native species, and have been identified as one of the great threats to biodiversity. As a result control of introduced predators is an important management action if we are to protect such species. Given the complexity of ecological systems and limitation to conservation budget there are many factors that managers must consider when designing control operations. Such factors include the allocation of resources between sites, changes in management efficiency with predator densities and connectivity between sites.

This study investigated how dispersal between multiple predator populations affects the success of predator control as measured by a prey species' long-term survival. The model is based on the Lotka-Volterra set of equations but modified to include two patches, predatory efficiency, spatial separation, management on a limited budget, management efficiency and predator dispersal. We also included three different dispersal functions to determine whether this was an important factor to take into account when designing control programmes. The three dispersal functions were no dispersal, proportional dispersal based on the density of predators, and proportional dispersal based on the availability of prey.

We investigated analytical solutions to the model and then performed stochastic simulations. There was limited success in finding analytical solutions to the model. The only solution that we obtained was for the case when there was no dispersal, and resources should be spent equally between the patches. The two cases where dispersal was included were too complex to find analytical solutions.

In the stochastic simulations we also considered two different methods of allocating management resources between the patches. In the first, resources were divided between patches at a fixed level. The second method divided the resources between the two patches at each time step in proportion to the density of predators. We tested the performance of these options over a range of dispersal probabilities, and to the budget allocation in the first simulation..

We found that [1] in the case of no dispersal optimal allocation is ½; [2i] simple dispersal and fixed allocation has best prey survival when the probability of dispersal is low and allocation is split equally; [2ii] with simple dispersal and proportional allocation the probability of prey extinction is the same as proportional allacation of 50-50, and probability of predator dispersal should be low; [3i] resource-dependent dispersal and fixed allocation should be managed so that the probability of predator dipsersal is low but not zero, and the allocation should not be split 50-50; [3ii] with resource-dependent dispersal and proportional allocation, the probability of prey extinction is the same as a fixed allocation of 50-50, and the probability of predator dispersal should be kept as low as possible.

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\left.
\begin{aligned}
\frac{dN_1}{dt} &= rN_1\left(1-\frac{N_1}{K}\right)-\frac{aP_1\,N_1}{l+N_1} && (1)\\
\frac{dP_1}{dt} &= \frac{\gamma\,aP_1\,N_1}{l+N_1}-kP_1-\frac{\alpha\,BP_1}{m+\alpha\,B}-\delta\,\phi && (2)\\
\frac{dN_2}{dt} &= rN_2\left(1-\frac{N_2}{K}\right)-\frac{aP_2\,N_2}{l+N_2} && (3)\\
\frac{dP_2}{dt} &= \frac{\gamma\,aP_2\,N_2}{l+N_2}-kP_2-\frac{(1-\alpha)\,BP_2}{m+(1-\alpha)\,B}+\delta\,\phi && (4)
\end{aligned}
\right\}\ (5)
$$

Figure 1. The model.

2. INTRODUCTION

Introduced predators have a major impact on native species around the world, and have been identified as one of the greatest threats to biodiversity (Diamond 1989). They have invaded many environments and are continuing to spread. Native species in these environments are often naïve to such predators and can be more vulnerable to population decline and extinction as a result. To conserve these species, it is therefore important to control introduced predators.

Controlling introduced predators is a complex process. Many factors need to be taken into consideration in the design and implementation of control programmes. For example the type of predator, the number, location and connectivity of populations, the efficiency of control and the available budget all need to be taken into consideration to determine optimal control strategies and assess if the control is likely to be effective.

Models are an exploratory tool that are very useful in conservation ecology for understanding complex system dynamics. The relative success of predictions under various model scenarios can aid managers when planning a control programme by enabling us to explore the benefits of different control options.

Our aim in this study was to determine how the allocation of budgeted resources should be split between two habitat patches when the introduced predator populations are linked by dispersal and both patches have a prey population that is under threat from these predators. One of the most well-known theories of predator-prey interactions is summarised by the Lotka-Volterra equations, which form the basis of the model used in this paper.

3. METHOD

3.1 The Model

The model (5) was based on the Lotka-Volterra set of equations. The base equations (Lotka 1925, Volterra 1926) were adjusted to account for the existence of two habitat patches, density dependence in the prey population, a prey-predator functional response (Holling 1959), predator dispersal and our predator control strategy.

The variables in the set of equations are defined as follows: N_i and P_i are the population sizes in patch i of the prey and predator, respectively; r, the intrinsic rate of increase of the prey population; K_i, carrying capacity for prey in patch i; a, the maximum predatory attack rate; l, predation half-saturation constant; γ, the energy conversion efficiency of the predator; k, the predator's death rate in the absence of prey; α, the proportion of budgeted resources allocated to predator control in patch 1; B, the budgeted number of predators that can be removed at each time step; m, the half-saturation constant for predator control success; δ, predator dispersal function.

Therefore the prey population increases at a maximum rate, r, until the population approaches the carrying capacity of the patch, K_i. The prey population is also decreased via predation: predators in each patch eat prey found within their current patch. The rate of consumption of prey per predator in relation to prey density is represented by the $l + N_1$ term (see equation (1),(3)). Thus we use a type-II functional response to represent predatory inefficiencies at low prey densities (Holling 1959).

The predator populations grow by converting the consumed prey to new predator biomass with efficiency γ. In all biological systems, available energy is lost to the system as heat as it flows through the trophic levels so that on average only about 10% of the energy contained in one level is passed through to the next level (Begon *et al.* 1990; p.670). Predators starve in the absence of prey, and this model assumes that the predator population will decline with an exponential decay rate of k.

Predator control is built into the model as follows. B gives the total number of predators that can be killed in any one year, and so αB is the number of predators that can be removed from patch 1, and $(1 - \alpha)B$ is the number of predators from patch 2 that can be culled. To represent inefficiencies in predator removal at low densities, we employ a type-II functional response (Holling 1959) between managers and predators, with half-saturation constant m.

Predators can also move between the two patches. The net number of predators that leave patch 1 for patch 2 is given by δ (if $\delta < 0$, $-\delta$ is the number leaving patch 2 for patch 1) and φ is the probability of successful dispersal to the new patch.

To find a rule of thumb for the optimal allocation of budgeted resources between the two patches, we attempted to solve (5) for the sum of the equilibrium prey populations and maximise this with respect to α.

3.2 Case 1 – No Dispersal

In the first instance we took the case where there is no dispersal between the two predator populations, hence $\delta = 0$.

To get an expression for the optimal resource allocation between patches, first simplify equations (2) and (4) for N_1 and N_2 respectively. This yields the equilibrium prey populations for these patches, the sum of which is an expression for the total equilibrium in terms of α. From this we can find the resource division α^* that maximises the total equilibrium prey population size N.

3.3 Case 2 – Simple Dispersal

As a first step to investigating the effect of dispersal between the predator populations, we considered predators moving according to the relative density between the patches. In this case we assumed that the excess in one patch at each time step moved to the other patch, giving $\delta = (P_1 - P_2)$.

3.4 Case 3 – Resource-dependent Dispersal

A third case was investigated where dispersal was assumed to be dependent on the relative availability of prey items in either patch. Thus predators move when the other patch has more available food. This can be given by the function $\delta = (P_1N_2 - P_2N_1)/(N_1 + N_2)$. It is assumed that if $N_1 + N_2 = 0$, then $\delta = 0$.

3.5 Simulation

The other aspect of our investigation was to simulate the effects of various budget allocation options for all three dispersal cases. These simulations were included to help identify which allocation option is best. The first simulation allocated a fixed proportion of the budget to each patch for the entire management period, which was repeated across the full range of allocation options ($0 \le \alpha \le 1$). The second simulation assumed that budget resources are allocated dynamically in proportion to predator density in each patch at each time-step. In practice, this would mean that the predator densities would have to be monitored continually which would therefore add further cost to this control option. However, for simplicity we assumed that a monitoring program is ongoing independent of the management strategy so that the extra cost of monitoring was not included in the simulation.

Stochastic variability is inherent in real ecological systems, and has a fundamental effect on population dynamics and survival. Therefore it is important to include stochastic effects in the model. We included stochasticity in the model by defining r_i and k_i to be uniformly distributed random variables, and randomly choosing values between their upper and lower bounds at each time step. We simulated each scenario 1000 times. The parameter values chosen for the simulations are given in Table 1.

Table 1. Variables used in the stochastic simulations

r_1, r_2	$\sim U(2.45, 3.05)$
k_1, k_2	$\sim U(0.55, 0.95)$
K	350
a	10
B	11
l	50
m	25

γ	0.1
$N_1(t=0)$	150
$N_2(t=0)$	150
$P_1(t=0)$	15
$P_2(t=0)$	15

We optimised the sum of the equilibrium prey populations with respect to α, but consider the probability of extinction obtained through the simulation as a meaningful measure of risk to the prey population. Hence the results of the simulation are discussed in terms of probabilities of extinction.

4. RESULTS

4.1 No Dispersal

Finding the optimal value of α (to maximise the prey equilibrium populations) was analytically straightforward under the no-dispersal scenario, giving optimal $\alpha^* = \frac{1}{2}$.

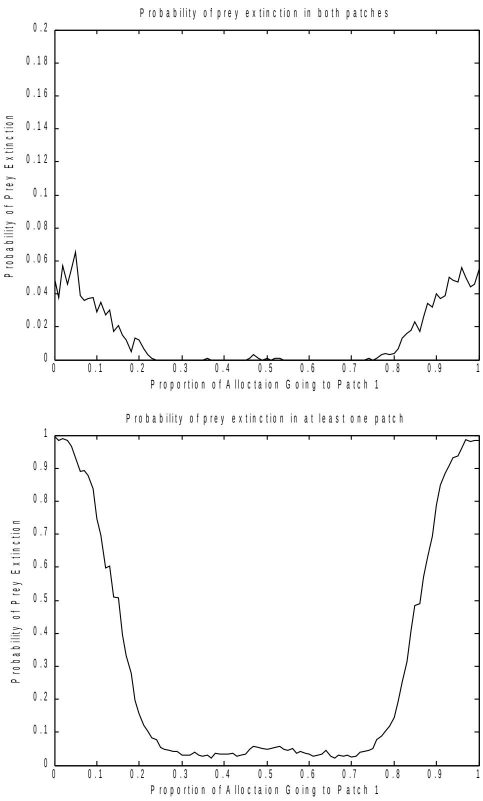


Figure 2. The probability of both prey populations (a) and at least one prey population (b, note different scale) going extinct for various allocation options and no dispersal.

Fixed Budget Allocation: The probability of both patches going extinct (Fig. 2a) is around 5% when the budget is allocated entirely to one patch (α = 0 or α = 1), decreasing towards zero when both patches are managed together (e.g. α = 0.25; the slight increase in extinction probability around α = 0.5 may be due to stochastic effects). In the absence of dispersal, the extinction probabilities are approximately symmetric about α = 0.5 so that at α » 0.75, the probability of extinction increases again, approaching 5% at α = 1. Similar trade-offs in patch-specific prey extinction probabilities can be seen by examining the probability that at least one prey population goes extinct (Fig. 2b). When almost all the budget is allocated to one patch we are almost guaranteed to loss at least one patch (p = 1, α = 0 and α = 0). When at least 25% of the budget is allocated to each patch then probability of losing at least one of these populations plateaus to approximately 0.05 (0.25 ≤ α ≤ 0.75).

Proportional Budget Allocation: When no dispersal occurs, the strategy of allocating the budget in proportion to the current predator population in each patch gives zero probability of both prey populations going extinct, and a probability of at least one population going extinct of only 5%. These results are also consistent with allocating half of the resources to each patch.

4.2 Simple Dispersal

When we included the simple dispersal function where predators move according to the relative density between the patches, $\delta = (P_1 - P_2)$, the additional model complexity was prohibitive to finding an analytic expression for the optimal allocation, α* which would maximise the sum of the equilibrium prey populations. We therefore focus on simulation results below.

Fixed budget allocation: When we consider the allocation of a fixed proportion of the budget to each patch, and that the predator populations in the two patches are linked with the simple dispersal function, higher prey extinction probabilities are observed (Fig. 3). These probabilities also increase with the probability of predator dispersal. Again the overall patterns are similar, but at different scales, for extinction probabilities either in both patches or in at least one patch. Budget allocation between patches seems to have little consequence on the probability of extinction of the prey populations when predator dispersal is above approximately 20%. The increase of prey extinction probability in both patches resulting from increased dispersal can be offset by more equal budget allocation between patches (Fig. 3a), indicated by a bell-shaped region of allocation and probability of dispersal where the probability of both patches going extinct is close to zero. The majority of the surface, however, has extinctions risks between 12 and 18% across the plane. For the most part, the probability of at least one patch going extinct is 100% (Fig. 3b). Nonetheless, there remains a region where extinction risk is significantly reduced by more equal allocation between patches, given approximately by the area under the curve running from $(\varphi, \alpha) = (0, 0.1)$ to $(0.175, 0.5)$ then $(0, 0.9)$.

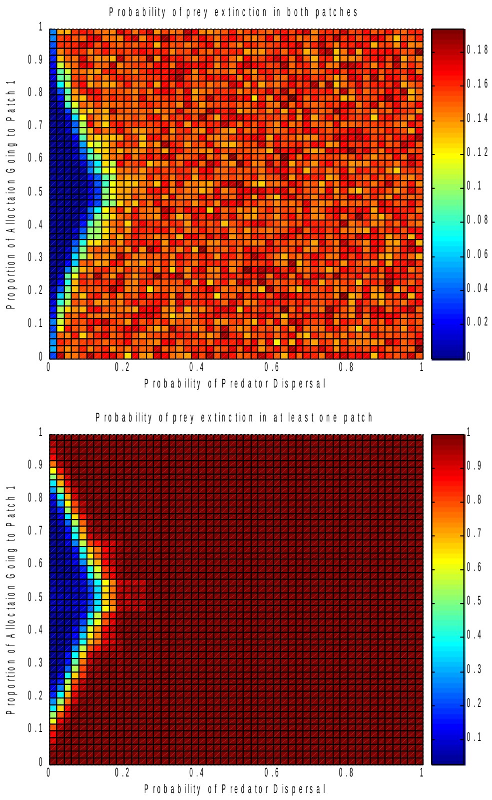


Figure 3. The probability of extinction of (a) both prey populations and (b) at least one prey population for fixed budget allocation options and various probabilities of 'simple' dispersal. (Note different scales.)

Proportional Budget Allocation: When the budget was proportionately allocated according to predator densities, the probability of extinctions have their minima in the dispersal probability range $0 < \varphi < \sim 0.2$ (Figure 4a, b). As seen in the fixed-budget allocation strategy there is a pronounced increase in extinction once dispersal probability exceeds 20%; however once dispersal reaches about 30% ($\varphi \approx 0.3$) the probability of extinction does not vary significantly. This relationship corresponds closely to that observed for the fixed budget allocation option where there is equal allocation ($\alpha = 0.5$).

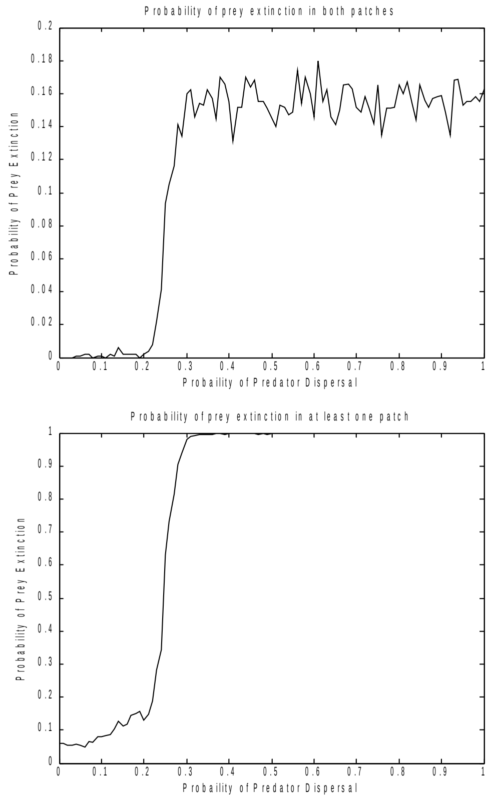
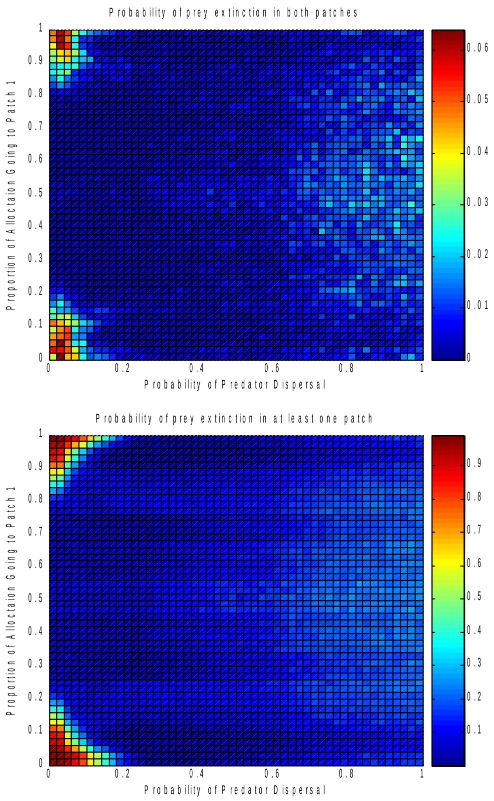


Figure 4. The probability of (a) both prey populations and (b) at least one prey population going extinct as the probability of 'simple' dispersal increases, when budget allocation is proportional to predator density in either patch.

4.3 Resource-dependent Dispersal

We next considered a more complex dispersal function, in which the number of predators dispersing between patches reflected the relative prey abundance available per predator. Once again, the extra complexity in the model meant that an optimal solution for α to maximise the prey equilibrium populations was elusive and therefore we concentrate on simulation results below.



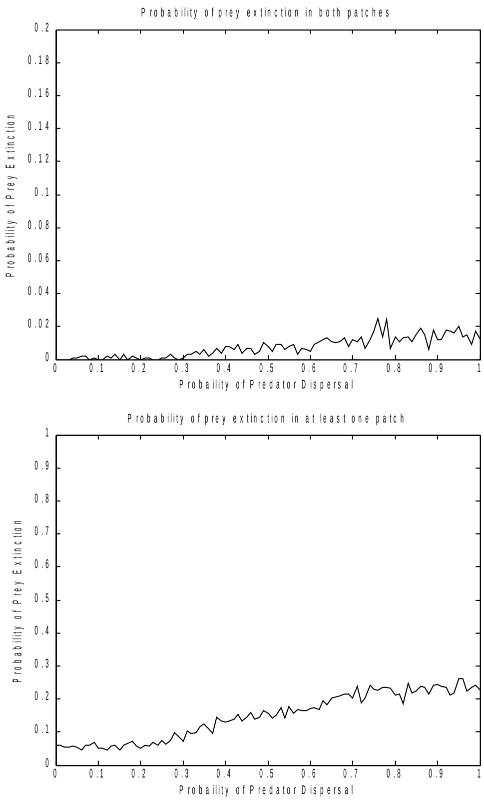


Figure 5. The probability of both prey populations (a) and at least one prey population (b, note different scale) going extinct as a function of fixed allocation and probability of resource-dependent dispersal.

Figure 6. The probability of both prey populations (a) and at least one prey population (b) going extinct for proportional allocation and various probabilities of 'more complex' dispersal.

Fixed budget allocation: Generally the threat to prey is reduced when dispersal responds to relative prey density per predator, compared to the simple predator dispersal scenario (Fig. 5). Again the probabilities of prey extinction in at least one (Fig. 5b), and in both (Fig. 5a), patches follow similar patterns. There is a region of increased probability of extinction when probability of dispersal is low and management is focussed mainly on one patch (higher and lower values of α). There is also a region of moderately increased probability of extinction when dispersal is high and α is intermediate. Over most of the phase-space, probability of extinction is relatively low (dark blue regions), as predators redistribute themselves according to the relative availability of prey. This redistribution lowers the prey extinction risk by reducing the net direct impact on the prey populations and by dampening the dynamics rendering the prey less vulnerable to stochastic effects.

Proportional budget allocation: The probabilities of extinction in both patches, and in at least one patch, again show a similar pattern as a function of predator dispersal when the budget is allocated in proportion to predator density (Fig. 6). The probability of extinction is lowest when the probability of dispersal is less than approximately 20%, increasing steadily as dispersal increases. These relationships are once again very similar to the fixed allocation option with equal allocation (α = 0.5). The sharp increase in prey extinction risk seen with simple-dispersal probabilities of 0.2 is much less pronounced when predator dispersal is resource-dependent (compare Figs. 4 and 6), reflecting the more damped dynamics of the system overall.

DISCUSSION

Managers of systems where there is no dispersal of predators between populations could aim for an equal division of resources between the patches, but if this was varied slightly there is no indication that adverse effects would follow. When there was no dispersal an allocation split of 50-50 was analytically optimal. This was further supported by the simulation, although there is a range of allocation options that also produced the same results. Managers of systems with density-dependent dispersal should also aim for splitting resources equally. However, this is only effective under low amounts of dispersal because once the probability of dispersal becomes too large, predator control becomes ineffective. Resource-dependent dispersal produces some results that may seem counter-intuitive at first. With a 50-50 budget split between patches, there is often a regional maxima for many values of φ, and the minima are around $\alpha = 0.3$ and 0.7. The reason for this is in the dispersal dynamics, and its occurrence is similar to the paradox of enrichment (Rosenzweig 1971).

Dynamic allocation of the budget produces results that are no better than a 50-50 split in all cases. So if management alternatives focused on either splitting the budget 50-50, or using dynamic allocation, then the 50-50 fixed alternative should be used to save money.

The probability of dispersal affected the outcome of results in both cases where the dispersal function allowed movement between the predator populations. Under density-dependent dispersal, an effective management option could be to keep predator dispersal as low as possible. This is because the probability of extinction increased significantly when φ became too large. Under resource-dependent dispersal, managers should allow some restricted movement between the populations. This is because under very low and high probabilities of dispersal, there are regions of increased extinction risk, whereas low to mid φ have regions of decreased risk.

A model that explicitly investigates the control of probability of dispersal (φ) can extend upon this paper. It would aid in determining whether altering connectivity between patches would be an effective management option to reduce the probability of extinction of endangered prey.

CONCLUSION

To efficiently manage two endangered prey populations, managers need to allocate the budget in a way that will maximise prey survival. The most effective budget allocation method differs under the various predator dispersal modes. Dynamic allocation of the budget is one option that managers can employ, but does not seem to be any more effective than a straightforward 50-50 split. Controlling the probability of dispersal between the predator populations could be an effective management option. More research focused on the explicit control of probability of dispersal could lead to further insights.

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