The Effect of Habitat Fragmentation on Cyclic Population Dynamics: A Numerical Study

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Abstract Through four spatially explicit models, we investigate how habitat fragmentation affects cyclic predator–prey population dynamics. We use a Partial Differential Equation (PDE) framework to describe the dispersal of predators and prey in a heterogeneous landscape made of high quality and low quality habitat patches, subject to increasing fragmentation through habitat separation and/or habitat loss. Our results show that habitat fragmentation decreases the amplitude of the predator–prey population cycles while average population density is not as strongly affected in general. Beyond these simple trends however, the four models show differing responses to fragmentation, indicating that when making predictions about population survival and persistence in the face of habitat fragmentation, the choice of model is important. Our results may inform conservation efforts in fragmented habitats for cyclic species such as the snowshoe hare and Canada lynx.

Keywords Population dynamics · Population cycles · Spatial ecology · Mathematical model · Partial differential equation · Canada lynx and snowshoe hare · Fragmentation · Habitat separation · Habitat loss

1. Introduction

In the northern hemisphere, several mammalian species and their predators show high-amplitude cyclic population dynamics in the northern portions of their range, but reduced or zero amplitude population dynamics toward the south (Akcakaya, 1992). Two examples are the snowshoe hare (Lepus americanus), with its specialist predator the Canada lynx (Lynx canadensis) (Murray, 2000; Ruggiero et al., 2000), and the meadow vole (Microtus agrestis) with its specialist predator the least weasel (Mustela nivalis) (Ylonen et al., 2003). For a more complete list of cyclic mammalian populations see Akcakaya (1992). For all of these populations, the southern habitats are subject to increased fragmentation

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due to forestry, conversion of land to agriculture, housing development and other anthropogenic activities (Ruggiero et al., 2000; Ylonen et al., 2003). Little is known about the interaction between cyclic population dynamics and habitat fragmentation. In this paper, we investigate the possibility that the north–south decrease in cycle amplitude is due to increased habitat fragmentation in the south. As at least one cyclic animal, the Canada lynx, is endangered or a species of special concern in its southern habitat (Poole, 2003), our question has relevance to conservation efforts.

The importance of spatial heterogeneity has been recognised in ecology for the past few decades (Kareiva, 1990). Important concepts such as metapopulations (Levin, 1974), source-sink populations (Pulliam, 1988), island–mainland populations (see references in Kareiva, 1990), and the refugium hypothesis (Ruggiero et al., 2000) are all linked to spatially nonuniform habitats and/or population distributions, and all have key consequences to the predicted survival of species. Indeed, links between the dynamics of mammalian cycles and habitat fragmentation have been found in experimental studies of both snowshoe hares (Akcakaya, 1992; Murray, 2000) and meadow voles (Ylonen et al., 2003).

Several mathematical studies of non-cyclic populations have suggested that fragmentation of habitat can affect the population dynamics of species in diverse ways (Van Kirk and Lewis, 1997; Cantrell and Cosner, 1991; Hanski and Ovaskainen, 2000). Poggiale (2005) found that global production can be increased by spatial heterogeneity in growth rates. That is, the number of individuals is greater in a heterogeneous environment than in the equivalent homogeneous environment. Cantrell and Cosner (1998) investigated the effect of the arrangement and location of prey refuges on predator invasibility (whether or not a predator would persist in a given patch). Prey refuges are patches where the prey experience decreased predation but also decreased reproduction. They found that if there was a sufficiently large contiguous subregion of habitat on which the predator was efficient (predation rate is high), the predator would persist regardless of the spatial arrangement and location of the prey refuges. If the size of the subregion and the effectiveness of the predator are of intermediate values then the spatial arrangement and location of prey refuges is critical. In another study, McKenzie (2006) showed that anthropogenic linear features, such as seismic lines, affect the rate at which wolves (predator) encounter ungulates (prey) in the central east slopes of the Rocky Mountains. The addition of linear features (a form of fragmentation) correlated to an increase in predation on ungulates by wolves with consequences to the dynamics of both populations.

Less mathematical work has been done to investigate how habitat fragmentation affects cyclic populations. Ecologists have suggested that cycles could be at least partially driven by the postulated presence of prey refuges (Ruggiero et al., 2000; Akcakaya, 1992). The prey might use these sub-optimal habitats to increase survival during years when population numbers are low. The predator population would subsequently decrease, allowing the prey population to increase again. Once it reaches a certain threshold, the prey population could disperse back into optimal reproductive habitats. In this scenario, increased fragmentation of habitat would result in fewer refuge patches and greater distances between refuge patches, and this could affect cyclic dynamics.

Many of the studies investigating how habitat fragmentation affects cyclic populations are reviewed by Fahrig (2003) and Ryall and Fahrig (2006). Fahrig (2003) defines two types of habitat fragmentation: habitat loss and habitat separation. Habitat loss occurs when patches of habitat that are suitable for predator and prey survival become smaller, but unsuitable patches remain the same size. Habitat separation occurs when patches of
habitat that are suitable for predator and prey stay the same size but become more distant from one another. Fahrig suggests that habitat loss has consistently negative effects on biodiversity while habitat separation can have both negative and positive effects on biodiversity. Ryall and Fahrig (2006) found that habitat loss had greater negative effects on the abundance of specialist predators than on the abundance of their prey. Furthermore, Ryall found that this decrease in specialist predator populations can increase prey populations. Habitat separation also negatively affected the abundance of specialist predators, but this did not necessarily result in consistent increases or decreases in prey and predator persistence: Five of the seven papers quoted by Ryall and Fahrig supported the increase of prey and predator persistence due to habitat separation, while the other two found that prey and predator persistence decreased.

In this paper we explore how habitat fragmentation affects cyclic population dynamics through a cyclic predator–prey model with spatially-explicit dispersal. For the spatial component we choose a diffusion equation approach, as such models have been successfully used to answer questions about dispersal of large organisms (McKenzie, 2006; Okubo and Levin, 2001; Murray, 1993; Turchin, 2001; Holmes et al., 1994; Ali and Coster, 1995). For our reaction terms, we use four different functions from the literature as described below. Our results are therefore a survey of model responses to habitat fragmentation, in parameter ranges where the models exhibit cyclic population dynamics.

In Section 2, we present the modelling framework and summarise the model dynamics in homogeneous domains where dispersal is ignored. The spatial domain and our manipulations of it are presented in Section 3, along with our simulation results. These are followed in Section 4 with a discussion of our findings and future directions for research.

2. The model

The population dynamics terms we use come from four different models in the predator–prey literature. These are the Lotka–Volterra (LV), Rosenzweig–MacArthur (RM), May and Variable Territory (VT) models. The LV model is the least realistic of the four but we include it in our study because it has a long history in the predator–prey literature (Murray, 1993; Okubo and Levin, 2001) and provides a basis for comparison with other models. The Rosenzweig–MacArthur model has been used to theoretically analyse cyclic population dynamics (Turchin, 2001; Rosenzweig and MacArthur, 1963) and recently has been applied to periodic-wave generation in cyclic predator–prey systems (Sherratt et al., 2002) and to oscillations and chaos in predator–prey invasions (Sherratt et al., 1997). The May model has been applied to mammalian predator–prey systems such as the Canada lynx and snowshoe hare (Tyson et al., In progress) and the meadow vole and least weasel (Hanski et al., 1993). The model was first used to study stability and complexity in model ecosystems (May, 1974) and has also been used in an analysis of ecological chaos in the wake of invasion (Sherratt et al., 1995). The May model is also referred to as the Holling–Tanner model because of seminal work by Tanner (1975). In this article Tanner studied the cyclic and non-cyclic dynamics of several populations, including the snowshoe hare and Canada lynx. The Variable Territory model was developed by Turchin and Batzli (2001) to study the cyclic population dynamics of arvicoline rodents.

Below we give the formulation of the full spatial model with dispersal terms, and then describe each of the four sets of predator–prey interaction terms.
2.1. The model

Following other researchers (Moorcroft and Lewis, 2006; Okubo and Levin, 2001), we assume that predator and prey movements can be modelled as random Fickian diffusion plus advection. In our model, advection is mediated through two visibility functions, $V_n(x)$ and $V_p(x)$, which describe the directed movement of prey and predator (respectively) toward high quality patches of habitat. We assume that the animals can see neighbouring patches of high quality habitat from within patches of low quality habitat, hence the name “visibility” function. Ideally, lynx movement should be directed up gradients of hare density, but such gradients may be less easy for the lynx to detect than habitat quality gradients. We assume therefore that the lynx can see (and/or smell) habitats that are likely to contain hares and orient themselves toward these habitats in a non-random way. We thus arrive at the model equations:

\[
\frac{\partial n}{\partial t} = D_n \frac{\partial^2 n}{\partial x^2} + \frac{\partial (V_n(x)n)}{\partial x} + f(n, p, x), \tag{1a}
\]

\[
\frac{\partial p}{\partial t} = D_p \frac{\partial^2 p}{\partial x^2} + \frac{\partial (V_p(x)p)}{\partial x} + g(n, p), \tag{1b}
\]

where, $D_n, D_p =$ the diffusivity coefficients for prey and predator, respectively; $V_n(x), V_p(x) =$ the visibility functions for prey and predator, respectively; $n, p =$ the population densities of prey and predator, respectively; $f(n, p, x), g(n, p) =$ the reaction terms for prey and predator, respectively.

Note that the reaction term $f(n, p, x)$ in (1a) depends explicitly on position, $x$. This is because we allow the prey growth rate to vary spatially with habitat quality. The general form of the reaction terms is

\[
\begin{align*}
    f(n, p, x) &= nH(n, x) - pF(n, p), \\
    g(n, p) &= pG(n, p).
\end{align*}
\tag{2}
\]

The function $H(n, p, x)$ is the intrinsic growth rate of prey, $F(n, p)$ is called the functional response of the predator to the prey, and $G(n, p)$ is the prey-dependent growth rate of the predator and is called the numerical response of the predator. If the numerical and functional response only depend upon $n$ then the reaction terms are called “laissez-faire” (Yodzis, 1994). In these models, per capita consumption of prey by the predator and the per capita growth rate of the predator depend only on the density of prey present. That is, the predators do not interfere with each other, either positively or negatively. If $G(n, p) = \chi F(n, p)$ then growth of predators is directly tied to consumption of prey with conversion rate $\chi$. In this case there is strict accounting of biomass in the system and the model can be said to follow the conversion rule (Abrams and Ginzburg, 2000).

We take the functions $f(n, p, x)$ and $g(n, p)$ from the LV, RM, May, and VT models. These are presented in Sections 2.1.1–2.1.4.

2.1.1. Lotka–Volterra

The Lotka–Volterra model (Murray, 1993) is a laissez-faire model that follows the conversion rule. The prey growth and predator death terms are linear and the predator–prey
interactions are based on the mass–action principle. The LV model reaction terms are

\[
\begin{align*}
    f(n, p, x) &= r(x)n - cnp, \\
    g(n, p) &= \chi cnp - \delta p,
\end{align*}
\]

where \( r(x) \) is the spatially varying intrinsic rate of prey population increase, \( c \) is the predation rate, \( \chi \) is the conversion rate of prey to predator, and \( \delta \) is the predator death rate.

2.1.2. Rosenzweig–MacArthur

The Rosenzweig–MacArthur model (Rosenzweig and MacArthur, 1963) is also a laissez-faire model that follows the conversion rule. Growth of the prey is logistic and predation is according to a hyperbolic functional response. The logistic growth limits prey densities to the carrying capacity of the region. The hyperbolic functional response, also known as a Holling Type 2 response, is the type of predation term most widely accepted for specialist predators (Turchin, 2001). As in the LV model, the predator has a constant per capita death rate. The RM model reaction terms are

\[
\begin{align*}
    f(n, p, x) &= r(x)n \left(1 - \frac{n}{k}\right) - \frac{cnp}{d + n}, \\
    g(n, p) &= \frac{\chi cnp}{d + n} - \delta p,
\end{align*}
\]

where \( r(x) \) is the spatially varying intrinsic rate of prey population increase, \( k \) is the carrying capacity of prey, \( c \) is the predator saturation kill rate, \( d \) is the predator half-saturation constant, \( \chi \) is the prey–predator conversion rate, and \( \delta \) is the predator death rate in absence of prey.

2.1.3. May

The prey equation in the May model (May, 1974) is exactly the same as the prey equation in the Rosenzweig–MacArthur (4) model. The May model however, is not laissez-faire, nor does it follow the conversion rule. Growth of the predator is logistic with carrying capacity of \( n/q \). That is, the carrying capacity of the predator is directly proportional to prey density. One can show that a consequence of this term is that predator territory size must increase as prey density decreases (Turchin, 2001). This is consistent with experimental observations of predatory mammals, and so the model is appropriate as long as \( n \) is not too small. This type of numerical response can be attributed to Leslie (1948) and has been criticised by several different authors for biological concerns and conservation of biomass (Yodzis, 1994; Ginzburg, 1998; Abrams and Ginzburg, 2000). Specifically, the \( n/q \) carrying capacity means that predators can continue to survive even when prey densities are very low, and the lack of biomass accounting can be problematic. Nonetheless, the model has a strong presence in the literature, and so we investigate its behaviour here. The May model reaction terms are

\[
\begin{align*}
    f(n, p, x) &= r(x)n \left(1 - \frac{n}{k}\right) - \frac{cnp}{d + n}, \\
    g(n, p) &= sp \left(1 - \frac{qp}{n}\right),
\end{align*}
\]
where \( r(x) \) is the spatially varying intrinsic rate of prey population increase, \( k \) is the carrying capacity of prey, \( c \) is the predator saturation kill rate, \( d \) is the predator half-saturation constant, \( s \) is the intrinsic rate of predator population increase, and \( q \) is the minimum prey biomass per predator.

### 2.1.4. Variable territory

Turchin and Batzli’s Variable Territory model (Turchin, 2001; Turchin and Batzli, 2001) is based on a model by Bazykin (1974), and shares features with both the RM and May models. The prey equation is the same for all three models. The predator equation in the VT model looks like the one in the RM model except for the addition of a second density-dependent death term (crowding term) that is inversely proportional to prey density. The effect of this crowding term is to make predator growth logistic-like, thus sharing similarities with the May model. This crowding term can be attributed to Leslie (1948). Turchin (2001) makes the observation that for \( n \gg d \), the VT model becomes the May model. With the parameter values we investigate below however, \( n \) and \( d \) are comparable in magnitude, so the condition for the VT model to reduce to the May model is not satisfied. The VT model, however, is similar to the May model in that the territory size of the predator changes with availability of prey. This model is not laissez-faire but it does follow the conversion rule. The VT model reaction terms are

\[
\begin{align*}
    f(n, p, x) &= r(x)n \left( 1 - \frac{n}{k} \right) - \frac{cnp}{d + n}, \\
    g(n, p) &= \frac{\chi cnp}{d + n} - \delta p - \frac{sqp^2}{n},
\end{align*}
\]

where \( r(x) \) is the spatially varying intrinsic rate of prey population increase, \( k \) is the carrying capacity of prey, \( c \) is the predator saturation kill rate, \( d \) is the predator half-saturation constant, \( s \) is the intrinsic rate of predator population increase, \( q \) is the minimum prey biomass per predator, \( \chi \) is the prey–predator conversion rate, and \( \delta \) is the predator death rate in absence of prey.

### 2.2. Non-spatial model dynamics

Ignoring the movement terms for the moment (that is, setting \( D_i = 0 \) and \( V_i(x) \equiv 0 \) in (1b)) and considering a homogeneous domain made of a single good patch (so \( r(x) \equiv r, \) a constant), we know that each of the four models we consider has a coexistence steady state for the prey and predator. That is, setting the time and spatial derivatives to zero (Murray, 1993) we obtain \( f(n^*, p^*) = 0 \) and \( g(n^*, p^*) = 0 \), where the steady state is given by \( (n, p) = (n^*, p^*) \) with \( n^* > 0 \) and \( p^* > 0 \). Table 1 gives the coexistence steady states for each model and its classification. The model behaviours about the coexistence steady state are illustrated in Fig. 1. For the LV model, \( (n^*, p^*) \) is a centre and so there are multiple closed solution trajectories about the steady state. All of the other models (VT, May, and RM) exhibit a limit cycle about \( (n^*, p^*) \). Recent studies have suggested that the May model has some additional dynamics and bifurcation structure depending on parameter values (Braza, 2003; Saez and Gonzalez-Olivares, 1999). The ODE results provide a reference point for the spatial work of this paper.
Table 1  Steady states and classifications of the SLV, SRM, SVT, and SM models. Note that the spiral source steady state of the SVT model is difficult to solve analytically, but it is the unique real solution to the equations given in the table.

<table>
<thead>
<tr>
<th>Model</th>
<th>Classification</th>
<th>((n, p))</th>
</tr>
</thead>
<tbody>
<tr>
<td>SLV</td>
<td>Centre</td>
<td>(\left( \frac{\delta}{r X}, \frac{r}{X} \right))</td>
</tr>
<tr>
<td>SRM</td>
<td>Spiral source</td>
<td>(\left( \frac{\delta d}{r + \delta}, \frac{r d}{r + \delta} \left( 1 + k \delta \right) \right))</td>
</tr>
<tr>
<td>SM</td>
<td>Spiral source</td>
<td>(\left( n_0, p_0 \right)), where (n_0) and (p_0) satisfy the equations:</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(p_0 = \frac{r (d + n_0) (k - n_0)}{c k}),</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0 = -n_0^3 + n_0^2 (k - 2d - \frac{c k}{r s q} (\chi c - \delta)) + n_0 \left( 2 dk - d^2 + \frac{4 d c k}{r s q} \right) + k d^2.)</td>
</tr>
<tr>
<td>SVT</td>
<td>Spiral source</td>
<td>((n_0, p_0)),</td>
</tr>
<tr>
<td></td>
<td></td>
<td>where (n_0) and (p_0) satisfy the equations:</td>
</tr>
</tbody>
</table>

2.3. The spatial models with reaction terms

Together with the diffusion and advection terms \((1b)\), the reaction terms \((3)–(6)\) give us four spatially-explicit predator–prey models, which we call the Spatial Lotka–Volterra (SLV), Spatial Rosenzweig–MacArthur (SRM), Spatial May (SM), and Spatial Variable Territory (SVT) models. We test the behaviour of all four models over a linear domain that is divided into good and bad patches. For the remainder of the paper we will refer to the “domain” as the composition of good and bad patches. “Good patches” are patches with enough cover for protection from predators and sufficient resources to sustain reproduction of prey. “Bad patches” designate habitats with inadequate cover and resources to allow prey growth.

The good and bad patches appear in the model (Eq. \((1b)\)) through the spatially-explicit functions \(V_i(x)\) and \(f(n, p, x)\). From Eqs. \((3)–(6)\) we see that the \(x\) dependence in \(f(n, p, x)\) comes from the spatially-varying growth rate of prey, \(r(x)\). The forms we used for these functions are illustrated in Fig. 2.

The visibility functions, \(V_i(x)\), model prey and predator directed movement toward patches of high quality habitat. They are consistent with studies of lynx and hare movement showing that these animals move quickly through low quality habitat, and spend most of their time in high quality habitat (Ruggiero et al., 2000). The visibility functions model the preferential movement of predators and prey toward the closest high-quality habitat. Movement is to the left if \(V_i(x) < 0\) and to the right if \(V_i(x) > 0\). Inside a good patch there is no advective movement and \(V_i(x) = 0\). The function \(V_i(x)\) is continuous throughout the domain and has odd symmetry within any bad patch about the centre of that patch.

Spatially varying growth rates have been used mathematically by several authors (Cantrell and Cosner, 1991; Poggiale et al., 2005) and ecological studies have shown that not all habitat patches are created equal where reproduction is concerned (Ruggiero et al., 2000; Poole, 2003; Mowat and Slough, 2003). Growth rate in our model is zero inside a bad patch since the resources and cover there are insufficient to sustain prey reproduction. In a good patch, \(r(x)\) is positive, increasing from 0 at the edges to a positive value, \(r_0\), inside the patch. Thus \(r(x)\) is continuous and first-order differentiable throughout the domain.
2.4. Parameter values

The parameter values we used for our four different models are listed in Tables 2, 3, and 4. Table 2 contains the parameters for spatial movement. We found that the magnitudes of $D_i$ and $V_i$ do not change the pattern of results reported below, as long as they are different from zero. That is, the patterns we report below depend critically on spatial movement being present, but not on the speed of this movement. Thus we simply used convenient values for these parameters.
Fig. 2 Patch type, visibility function (top), and spatially varying growth rate (bottom) in a $l_g, l_b = 10, n_g = 1, n_b = 2$ domain. “x” is the spatial position within the domain. The advective motion is to the left if $V_i(x) < 0$, to the right if $V_i(x) > 0$, and there is no advective movement if $V_i(x) = 0$. The prey birth rate $r(x)$ is zero in bad patches. $V_i(x)$ is negative for $0 > x > -L$ and positive for $0 < x < L$.

Table 2 Parameters, units, and default values for the advection and diffusion terms of the four models tested. The values of the diffusion and advection terms are the same throughout the four different models. “Good” refers to default values in good patches and “Bad” refers to default values in bad patches. Refer to Fig. 2 for a pictorial representation of these values. Note that $x$ is the position in space.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Units</th>
<th>Default values</th>
</tr>
</thead>
<tbody>
<tr>
<td>$D_n$</td>
<td>ha/yr</td>
<td>1.5 (constant)</td>
</tr>
<tr>
<td>$D_p$</td>
<td>ha/yr</td>
<td>2 (constant)</td>
</tr>
<tr>
<td>$V_i(x), i = n, p$</td>
<td>$\sqrt{ha/yr}$</td>
<td>0 for $</td>
</tr>
</tbody>
</table>

The remaining non-spatial parameter values are listed for the SLV model in Table 3, and for the SRM, SM and SVT models in Table 4. These parameters were chosen so that the cycles obtained from each model in homogeneous good habitat were similar, and yielded population cycles with reasonable prey average density and period based upon data from snowshoe hare and Canada lynx studies in the boreal forest. Thus, the cycle changes due to habitat fragmentation were all measured relative to homogeneous domain cycles that were similar. For the SRM, SM and SVT models, the periodic solutions are limit cycles and thus the actual values of the initial predator and prey densi-
Table 3  Parameters, units and default values for the SLV model. Parameter values were calculated based on the parameter values for the SM and SRM models (Tyson et al., In progress)

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Units</th>
<th>Default values</th>
</tr>
</thead>
<tbody>
<tr>
<td>$r_0$</td>
<td>/yr</td>
<td>0.75</td>
</tr>
<tr>
<td>$c$</td>
<td>ha/(predator·yr)</td>
<td>122</td>
</tr>
<tr>
<td>$\chi$</td>
<td>predator/prey</td>
<td>0.00197</td>
</tr>
<tr>
<td>$\delta$</td>
<td>/yr</td>
<td>0.85</td>
</tr>
</tbody>
</table>

Table 4  Parameters, units, and default values for the SRM, SM, and SVT models. The parameter values for the SRM and SM models were obtained from Tyson (In progress). The parameter values for the SVT model were deduced from the SRM and SM models

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Units</th>
<th>Rosenzweig–MacArthur</th>
<th>May</th>
<th>Variable territory</th>
</tr>
</thead>
<tbody>
<tr>
<td>$r_0$</td>
<td>/yr</td>
<td>2.1</td>
<td>1.75</td>
<td>1.75</td>
</tr>
<tr>
<td>$k$</td>
<td>prey/ha</td>
<td>11</td>
<td>8</td>
<td>8</td>
</tr>
<tr>
<td>$c$</td>
<td>prey/(pred·yr)</td>
<td>800</td>
<td>505</td>
<td>800</td>
</tr>
<tr>
<td>$d$</td>
<td>prey/ha</td>
<td>1.5</td>
<td>0.3</td>
<td>0.3</td>
</tr>
<tr>
<td>$\chi$</td>
<td>pred/prey</td>
<td>0.0040</td>
<td>n/a</td>
<td>0.0040</td>
</tr>
<tr>
<td>$\delta$</td>
<td>/yr</td>
<td>2.4</td>
<td>n/a</td>
<td>2.4</td>
</tr>
<tr>
<td>$s$</td>
<td>/yr</td>
<td>n/a</td>
<td>0.85</td>
<td>0.80</td>
</tr>
<tr>
<td>$q$</td>
<td>prey/pred</td>
<td>n/a</td>
<td>212</td>
<td>212</td>
</tr>
</tbody>
</table>

Table 5  Values for prey and predator amplitude, average and period in a homogeneous good patch for the SLV, SRM, SM, and SVT models. Field data from Canada (Poole, 2003; Krebs et al., 2001) finds the period of snowshoe hare and Canada lynx to be 8–11 years. Therefore, the models we use have the appropriate period. Note that the predator amplitudes and averages are multiplied by a factor of 1000 for readability

<table>
<thead>
<tr>
<th>Model</th>
<th>Prey amplitude</th>
<th>Predator amplitude</th>
<th>Prey average</th>
<th>Predator average</th>
<th>Period</th>
</tr>
</thead>
<tbody>
<tr>
<td>SLV</td>
<td>2.68</td>
<td>4.94</td>
<td>3.71</td>
<td>6.46</td>
<td>8</td>
</tr>
<tr>
<td>SRM</td>
<td>4.22</td>
<td>5.86</td>
<td>4.81</td>
<td>8.89</td>
<td>8</td>
</tr>
<tr>
<td>SM</td>
<td>2.36</td>
<td>7.28</td>
<td>1.37</td>
<td>4.90</td>
<td>9</td>
</tr>
<tr>
<td>SVT</td>
<td>7.03</td>
<td>8.07</td>
<td>3.71</td>
<td>4.30</td>
<td>9</td>
</tr>
</tbody>
</table>

ties are not important to the results. For the SLV model however, the coexistence steady state is a centre (Fig. 1), so the periodic solution trajectory is different for each set of initial conditions. We therefore chose initial conditions that gave cycles with appropriate period and prey average density. The initial conditions for the SLV model were $(n, p) = (5$ prey/ha, 0.01 predator/ha).

We initially tested all of the models on a homogeneous domain consisting of a single good patch. In this situation, the spatial models essentially collapse down to the original ODE models, as there is no spatial variation in population size or model parameters. The values of the five cycle attributes we monitor are summarised in Table 5. The periods obtained across all four models are very similar, but the other four attributes vary from one model to another.
3. Simulation experiments: testing the effect of habitat fragmentation

To investigate the behaviour of the SLV, SRM, SM, and SVT models in a fragmented domain, we explore two aspects of habitat fragmentation: the size of good habitat patches ($L_g$) and the distance between these patches, or bad patch size ($L_b$). Consideration of these individual variables leads to three different types of fragmentation as suggested by Fahrig (2003) and Ryall and Fahrig (2006):

- **Habitat loss** Increase $L_b$ while $L_g$ is held constant
- **Habitat separation** Increase $L_b$ while $L_g$ is held constant
- **Combined separation and loss** Increase $L_b$ and decrease $L_g$ while $L$ (domain size) is held constant—this is the paradigm most applicable to current anthropogenic habitat disturbance.

For our simulations we divided the domain into $n_g$ good and $n_b$ bad patches, with all good patches having the same length $l_g$, and all bad patches having the same length $l_b$. The total length of good patches, $L_g$, is $n_g l_g$ and the total length of bad patches, $L_b$, is $n_b l_b$. Total domain length is thus $L = n_g l_g + n_b l_b$. We manipulated domains by varying the size and number of good and bad patches according to the three different types of fragmentation listed above. Since domain size $L$ is fixed only for combined separation and loss, this is the only type of fragmentation that is a realistic representation of actual habitat disturbance. Examples of these three types of fragmentation are shown in Fig. 3, and Fig. 4 shows how they are related in the $(l_g, l_b)$ space.

In order to quantify the effect of habitat fragmentation there are a number of cycle attributes one could measure. For simplicity, we chose five attributes: cycle period, prey cycle amplitude, predator cycle amplitude, prey average density, and predator average density. Cycle period and amplitude are considered key properties of population cycles.

![Fig. 3](image-url) Examples of fragmented habitats of length $L$ ($0 \leq x \leq L$) using three different types of fragmentation. Note that black designates bad patches while white designates good patches. In the left column we have combined separation and loss. In the right column we have habitat loss (top) and habitat separation (bottom). Fragmentation increases in each example from (a) → (b) or from (a) → (c).
and are commonly measured by ecologists. We also included average densities since we found that these yielded interesting results. Cycle attributes were recorded at the centre of good patches after transients had disappeared. Average density was calculated as the mean of the maximum and the minimum densities of the cycles within one patch, and cycle period was measured as the time elapsed between consecutive peaks in the population cycle. The amplitude in a given patch was calculated by subtracting the minimum density from the maximum density (rather than dividing, as is done in the ecological literature).

In our simulations we used uniform initial conditions and homogeneous Neumann boundary conditions. Numerical solutions were obtained using the Matlab pde solver pdepe. This solver discretizes the equations spatially, and then solves the resulting ODEs using implicit multistep formulas with adaptive time-stepping (Shampine and Reichelt, 1997). The choice of uniform initial conditions means that the solutions in each patch are synchronised temporally, that is, the solution in each patch (especially good and bad patches) may be different, but they all oscillate with the same period and in phase with each other. The numerical solutions were tested for periodicity and sensitivity to initial conditions, and our results show that the solutions are indeed periodic, and that for the SRM, SM and SVT models the initial conditions chosen do not affect the results.

**Fig. 4** Fragmentation space as a function of good patch size, \( l_g \) and bad patch size, \( l_b \), showing how the three types of habitat fragmentation are related. Arrowheads indicated direction of increasing fragmentation.
3.1. Fragmented domains

In this section we present the results of our habitat fragmentation study. We first consider combined separation and loss (Section 3.1.1), since this type of fragmentation is most familiar from a practical point of view. We then consider habitat loss (Section 3.1.2) and habitat separation (Section 3.1.3) individually.

3.1.1. Combined separation and loss

We consider first a two-patch domain of size \( L = 20 \) (Fig. 3, pattern 1) where \( 1 \leq l_g \leq 20 \) and \( l_b = L - l_g \). Figure 5 shows the cycle amplitude and average population density for both prey and predator at the centre of the good patch as a function of good patch length. When \( l_g = 20 \) the 2-patch domain essentially collapses to a single good patch. Results are presented for all four models simultaneously. In order to make comparison across models possible, the results (y-axis values) are normalised to lie between 0 and 1.

The figure has two striking features. First, the effect of fragmentation on cycle amplitude is different for the different models tested. Cycle amplitude is most affected by fragmentation in the SLV model and least affected in the SVT model. The second striking feature is that the SM model predicts a steady decrease in average prey density with increasing fragmentation, while the SVT model is relatively insensitive to fragmentation, and the SLV and SRM models actually predict an increase in prey average as fragmentation increases. All four models behave similarly with regard to predator average density with increasing fragmentation, though the SRM model predicts the most significant decrease.

Together these results suggest that spatial movement in a heterogeneous domain strongly affects the limit cycle (or neutrally stable orbit) of all four models, but has much less effect on the average population densities in all but the SM model. The population cycles are illustrated in the phase plane in Fig. 6. We see that the spatial movement of predator and prey in the presence of fragmentation has a strong contraction effect on the phase plane trajectory in the SLV and SRM models. The trajectories contract in a fairly symmetric manner however, and so maintain approximately the same centre value until small \( l_g \). In contrast, spatial movement in the SM model contracts the limit cycle mostly in the high prey and high predator portion of the cycle, and thus moves the centre of the orbit. Fragmentation has relatively little effect on the phase plane trajectories of the SVT model.

We also tested the sensitivity of the cycle period to changes in good patch size. Cycle period is relatively insensitive to decreasing good patch size for all models except the SRM model (Table 6). Using the period obtained in the homogeneous good patch domain (labelled “20g” in the table) as the baseline value, the percent change in period for each new patch arrangement is within 9%. The one exception is the period obtained in the “5 good 15 bad” patch arrangement for the SRM model. In this case there is an 18% change from the baseline value.

Figure 7 is a plot of the same variables shown in Fig. 5, but this time on a 4-patch domain of size \( L = 40 \), consisting of an alternating arrangement of good and bad patches (Fig. 3, pattern 3). The variables are plotted against good patch size where \( 1 \leq l_g \leq 19 \) and \( l_b = (L - 2l_g)/2 \). The introduction of two additional patches means that one of the good habitat patches is a boundary patch on the edge of the domain, while the other one is a central patch flanked on either side by a bad habitat patch. Figure 7 illustrates the
Plots of amplitude and average (scaled between zero and one) of predator and prey against good patch size using the SLV, SRM, SM, and SVT models with combined separation and loss fragmentation. These plots are for a domain with $n_g, n_b = 1, 1 \leq l_g \leq 20$, and $l_b = L - l_g$ where $L = 20$. The figure shows prey amplitude (top left), prey average (top right), predator amplitude (bottom left), and predator average (bottom right). Fragmentation occurs from right to left as good patch size decreases.

Table 6 Cycle period under combined habitat fragmentation and loss. The domain of length 20 was divided into two patches, one good and one bad, in four different ways; $\alpha_g \beta_b$ indicates a domain with a good patch of length $\alpha$ and a bad patch of length $\beta$. Cycle period is relatively insensitive to decreasing good patch length.

<table>
<thead>
<tr>
<th>Patch arrangement</th>
<th>Period</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>SLV</td>
</tr>
<tr>
<td>20 g</td>
<td>8.11</td>
</tr>
<tr>
<td>15g 5b</td>
<td>7.88</td>
</tr>
<tr>
<td>10g 10b</td>
<td>7.91</td>
</tr>
<tr>
<td>5g 15b</td>
<td>8.60</td>
</tr>
</tbody>
</table>

cyclic population dynamics in both good habitat patches. The overall trends are the same as those observed in Fig. 5, but central patches are generally more sensitive to spatial
The Effect of Habitat Fragmentation on Cyclic Population Dynamics

Fig. 6 Phase plots of our four different spatial models in a homogeneous high quality habitat and in two-patch heterogeneous domains of length 20. The four different models pictured are SLV (top left), SRM (top right), SM (bottom left), and SVT (bottom right). The phase plots show the changes in the phase plane trajectory for the SLV and the limit cycles for the other three models (SRM, SM, and SVT) as fragmentation increases. We see that the SLV phase plane trajectory and the SRM limit cycles are significantly contracted by fragmentation. The limit cycle of the SM model is contracted and the centre of the periodic orbit is moved by fragmentation. Finally, the SVT model is relatively unaffected by fragmentation. All phase plots are simulated in a 2-patch domain with size $L = 20$ and $l_g = \{5, 10, 15, 20\}$. The entry “5g” denotes a 2-patch domain with $l_g = 5$ (and $l_b = 15$).

movement than boundary patches: In general, boundary patches have larger amplitude and average densities than central patches.

We also note that in the SLV and SRM models, the prey average increases in boundary patches but decreases in central patches. Thus, all of the models predict decreases in prey average densities for central patches, but in boundary patches the different models predict contradictory results for prey average density, as in the two-patch case.

Cycle amplitude and population average density behave similarly in 3-patch (Fig. 3, pattern 2) and 5-patch domains (Fig. 3, pattern 4) (results not shown).

3.1.2. Habitat loss

Habitat loss occurs when we fix $l_b$ and decrease $l_g$. Figure 8 is a plot of the same variables in the same type of 4-patch domain as Fig. 7, but with $l_b = 12$ and $1 \leq l_g \leq 19$. Comparing
Fig. 7  Plots of amplitude and average (scaled between zero and one) of predator and prey against good patch size using the SLV, SRM, SM, and SVT models with combined separation and loss fragmentation. These plots are for a domain with $n_g, n_b = 2$, $1 \leq l_g \leq 19$ and $l_b = (L - 2 * l_g)/2$ where $L = 40$. The figure shows prey amplitude (top left), prey average (top right), predator amplitude (bottom left), and predator average (bottom right). The legend entries SLV$_b$, SRM$_b$, SM$_b$, and SVT$_b$ denote boundary patches for the SLV, SRM, SM, and SVT models respectively. The legend entries SLV$_c$, SRM$_c$, SM$_c$, and SVT$_c$ denote central patches for the SLV, SRM, SM, and SVT models, respectively.

Figs. 7 and 8 we see that the overall trends are the same. So the results predicted by habitat loss are very similar to those predicted by combined separation and loss.

3.1.3. Habitat separation
Habitat separation occurs when $l_g$ is fixed and $l_b$ is increased. Figure 9 presents the results for a 4-patch domain with $l_g = 9$ and $1 \leq l_b \leq 19$. The y-axis variables are the same as in Fig. 8 but now the results are plotted against bad patch size instead of good patch size, since the latter is fixed. In this type of fragmentation, fragmentation increases as bad patch size increases. Note that bad patch size increases from right to left, so the direction of increasing fragmentation is the same as for Figs. 7 and 8.

Figure 9 reveals interesting results. The average densities of prey and predator are largely unaffected by fragmentation by separation. Prey and predator amplitudes in the
The Effect of Habitat Fragmentation on Cyclic Population Dynamics

Fig. 8 Plots of amplitude and average (scaled between zero and one) of predator and prey against good patch size using the SLV, SRM, SM, and SVT models with habitat loss fragmentation. These plots are for a domain with $n_g, n_b = 2, l_b = 12$, and $1 \leq l_g \leq 19$. The figure shows prey amplitude (top left), prey average (top right), predator amplitude (bottom left), and predator average (bottom right). The legend entries $SLV_b, SRM_b, SM_b, and SVT_b$ denote boundary patches for the SLV, SRM, SM, and SVT models respectively. The legend entries $SLV_c, SRM_c, SM_c, and SVT_c$ denote central patches for the SLV, SRM, SM, and SVT models, respectively.

SVT model are also minimally affected by separation. In contrast, the predator and prey amplitude of the other three models are strongly affected, with the greatest changes occurring in the interval $1 \leq l_b \leq 4$. The SLV and SRM models predict that amplitude decreases as bad patch size increases. In contrast, the SM model predicts that prey and predator amplitudes increase with increasing separation. As before, central patches are more affected by habitat separation (i.e. have lower densities and amplitudes) than boundary patches.

The trends in cycle amplitude are independent of the fixed good patch sizes chosen (results not shown). The choice of good patch size does, however, affect the magnitude of the changes in amplitude. The smaller the fixed good patch size, the more sensitive the amplitude to habitat fragmentation by habitat separation.

Average densities of prey and predator are relatively unaffected by habitat separation at the good patch size shown in the Fig. 9 ($l_g = 9$). But as $l_g$ decreases, the effects of habitat
Fig. 9  Plots of amplitude and average (scaled between zero and one) of predator and prey against bad patch size using the SLV, SRM, SM, and SVT models with habitat separation fragmentation. These plots are for a domain with $n_g, n_b = 2$, $l_g = 9$, and $1 \leq l_b \leq 19$. The figure shows prey amplitude (top left), prey average (top right), predator amplitude (bottom left), and predator average (bottom right). The legend entries SLV$_b$, SRM$_b$, SM$_b$, and SVT$_b$ denotes boundary patches for the SLV, SRM, SM, and SVT models respectively. The legend entries SLV$_c$, SRM$_c$, SM$_c$, and SVT$_c$ denotes central patches for the SLV, SRM, SM, and SVT models, respectively.

separation are more pronounced (results not shown). If the good patch size is fixed at $l_g \leq 4$, the averages in the central patch decrease while the average values in the boundary patch are relatively unaffected. In contrast, if the good patch size is fixed at a larger value, the effects of habitat separation on average densities is even less than shown in Fig. 9.

3.1.4. Comparing habitat separation and habitat loss
Here we summarise the results from Figs. 7 to 9. Since habitat loss has essentially the same results as combined habitat separation and loss, we compare habitat loss and habitat separation. The comparison of results between habitat loss and habitat separation is seen in Table 7. The trends in amplitude are the same for the SVT model, slightly different for the SLV and SRM models, and opposite for the SM model. The trends in average are different for both the central and boundary patches. The average in boundary patches is
Table 7: Comparison between habitat separation and habitat loss for the SLV, SRM, SM, and SVT models

<table>
<thead>
<tr>
<th>Quantity and model</th>
<th>Habitat loss</th>
<th>Habitat separation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amplitude</td>
<td></td>
<td></td>
</tr>
<tr>
<td>SLV</td>
<td>Decreasing</td>
<td>Decreasing then constant</td>
</tr>
<tr>
<td>SRM</td>
<td>Decreasing</td>
<td>Decreasing then constant</td>
</tr>
<tr>
<td>SM</td>
<td>Decreasing</td>
<td>Increasing</td>
</tr>
<tr>
<td>SVT</td>
<td>Decreasing</td>
<td>Decreasing</td>
</tr>
<tr>
<td>Prey average boundary</td>
<td></td>
<td></td>
</tr>
<tr>
<td>SLV</td>
<td>Increasing</td>
<td>Constant</td>
</tr>
<tr>
<td>SRM</td>
<td>Increasing</td>
<td>Constant</td>
</tr>
<tr>
<td>SM</td>
<td>Decreasing</td>
<td>Constant</td>
</tr>
<tr>
<td>SVT</td>
<td>Decreasing</td>
<td>Constant</td>
</tr>
<tr>
<td>Prey average central</td>
<td></td>
<td></td>
</tr>
<tr>
<td>SLV</td>
<td>Decreasing&lt;sup&gt;a&lt;/sup&gt;</td>
<td>Constant&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>SRM</td>
<td>Decreasing&lt;sup&gt;a&lt;/sup&gt;</td>
<td>Constant&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>SM</td>
<td>Decreasing</td>
<td>Constant</td>
</tr>
<tr>
<td>SVT</td>
<td>Decreasing</td>
<td>Constant</td>
</tr>
<tr>
<td>Predator average boundary</td>
<td></td>
<td></td>
</tr>
<tr>
<td>SLV</td>
<td>Decreasing</td>
<td>Constant</td>
</tr>
<tr>
<td>SRM</td>
<td>Decreasing</td>
<td>Constant</td>
</tr>
<tr>
<td>SM</td>
<td>Decreasing</td>
<td>Constant</td>
</tr>
<tr>
<td>SVT</td>
<td>Decreasing</td>
<td>Constant</td>
</tr>
<tr>
<td>Predator average central</td>
<td></td>
<td></td>
</tr>
<tr>
<td>SLV</td>
<td>Decreasing</td>
<td>Constant</td>
</tr>
<tr>
<td>SRM</td>
<td>Decreasing</td>
<td>Constant</td>
</tr>
<tr>
<td>SM</td>
<td>Decreasing</td>
<td>Constant</td>
</tr>
<tr>
<td>SVT</td>
<td>Decreasing</td>
<td>Constant</td>
</tr>
</tbody>
</table>

<sup>a</sup>The prey average in the SLV and SRM models in the central patch increases for \( l_b \leq 10 \) and decreases for \( l_b > 10 \)

<sup>b</sup>If \( l_g \leq 4 \) the averages are decreasing

relatively constant under fragmentation by habitat separation while it is either increasing or decreasing under fragmentation by habitat loss. In the central patches, the average stays roughly constant (until \( l_g \leq 4 \)) under habitat separation but decreases under habitat loss. We conclude that habitat loss has more consistently negative effects on amplitude and average than habitat separation (with the exception of prey average in a boundary patch).

3.1.5. The fragmentation space

In Sections 3.1.1 to 3.1.3 we investigated the three types of fragmentation along particular lines in the \((l_g, l_b)\) space as shown in Fig. 4. This allowed us to compare the responses of all four models to fragmentation. The behaviour along these particular fragmentation lines however, is not necessarily representative of behaviour throughout the fragmentation space, and so we also investigated model behaviour throughout the entire region defined by \( 1 \leq l_g \leq 19 \) and \( 1 \leq l_b \leq 19 \) in a four-patch domain.

We found that the patterns identified in the linear results held for all of the variables except prey averages in the central good patch for the SLV and SRM models. Contour plots of the prey averages in all four models are presented in Fig. 10. For all four models,
Fig. 10 Contour plots of good patch size against bad patch size of prey average for the SLV, SRM, SM, and SVT models in a central good patch. These plots are for a domain with \( n_g, n_b = 2 \), and \( 1 \leq l_g, l_b \leq 19 \). The figure shows a contour plot of prey average for the SLV model (top left), SRM model (top right), SM model (bottom left), and SVT model (bottom right). For a legend of the effects of habitat loss, habitat separation, and combined habitat separation and loss see Fig. 4. Since the contours mainly change from right to left, it implies that habitat loss has a greater effect on prey average (in the central patch) than habitat separation.

if \( l_b < 10 \) the prey average decreases with decreasing \( l_g \). If \( l_b > 10 \), the SM and SVT continue to predict decreasing prey average with decreasing \( l_g \), but the SLV and SRM models predict instead that prey average increases with decreasing \( l_g \). Our results in Section 3.1.1 correspond to values taken along a diagonal line going from \((l_g, l_b) = (19, 1)\) to \((l_g, l_b) = (1, 19)\) while the results in Section 3.1.2 correspond to values taken along the horizontal line \( l_b = 12 \) from \( l_g = 19 \) to 1. Along both of these transects, prey average in the SLV and SRM models increases as fragmentation increases, but with the full contour plot at our disposal, we can see that transects of the \((l_g, l_b)\) plane can be constructed along which prey average density will decrease with increasing fragmentation for all four models.

The four-model contour plots for the four cycle attributes (prey average, predator average, prey amplitude, and predator amplitude) in both central and boundary good patches can be found in the online supplemental material.
4. Discussion

4.1. Summary of results

In this paper we have investigated how habitat fragmentation affects the solution behaviour of four cyclic predator–prey models. To evaluate the solutions we focused on four test variables: cycle amplitude for prey and predator, and average density for prey and predator. We also noted the cycle period, but it changed very little under habitat fragmentation.

Our results show that habitat fragmentation can decrease predator and prey cycle amplitude and that the predicted magnitude of this change depends on the model used. Average population density can increase or decrease with decreasing good patch size, depending on the model, but decreases in central patches for all four models if \( l_g \) is sufficiently low and \( l_b \) is sufficiently large.

The different responses between the four models we studied may be partly explained by the structural stability of the closed solution orbits in the underlying non-spatial models (Fig. 1). One measure of this is the time required for a solution trajectory to return to the closed orbit solution when perturbed away from it. The closed orbits in the LV model are structurally unstable, since perturbations result in new closed solution trajectories that never return to the original one. The RM, May and VT models each admit a limit cycle, and so solution trajectories starting near the limit cycle eventually join it. Such solution trajectories are illustrated in Fig. 1. We observe that solution trajectories with initial values near the limit cycle rotate a number of times before becoming indistinguishable from the limit cycle. The number of rotations required before the limit cycle is reached is large in the RM model, less in the May model, and small in the VT model. This suggests that the limit cycle ranges in attractiveness and stability from being relatively weak in the RM model to very strong in the VT model. Of the four models the SVT model is least affected by fragmentation, while the models most affected are generally the SLV and SRM models, though occasionally the SM model shows the largest change in behaviour.

We investigated the effect of fragmentation through habitat loss and habitat separation considered separately and together (“combined separation and loss”). Habitat loss and combined separation and loss affect the solution behaviour in similar ways for each of the four models, with increasing fragmentation generally resulting in decreasing cycle amplitude and population average density. Habitat separation, however, resulted in both increases and decreases in the test variables. This contrast between the effects of habitat loss and habitat separation was also noticed by Fahrig (2003). Fahrig found that fragmentation by habitat loss had consistently negative effects on biodiversity while fragmentation by habitat separation had both positive and negative effects on biodiversity. Fahrig measures biodiversity in several different ways, but abundance is one biodiversity variable that we both included in our studies.

The trends in average population densities under habitat loss and combined habitat separation and loss are consistent with the trends predicted by Ryall and Fahrig (2006). In our results, predator densities always decrease whereas prey densities may increase or decrease depending upon the model, the good patch position, and the size of the bad patch, \( l_b \). Increased prey averages can be explained by simultaneous decreases in predator density as fragmentation increases. In this scenario, habitat fragmentation affects predator average densities more than prey average densities. This result has also been observed in competition systems, where habitat destruction and fragmentation is more detrimental to
the superior competitor than to the inferior competitor (Neuhauser, 1998; Ali and Cosner, 1995); and by Ryall and Fahrig (2006) for specialist predators and their prey.

Decreases in prey average in our simulations occurred in central patches for large enough bad patch size, \( l_b \). A possible explanation for decreasing prey average density is that at large \( l_b \) the effect of decreased predator density in the good patch competes with loss of prey to the bad patch. If the loss of prey to bad patches is large enough, the prey average densities will decrease even though the predator average densities also decrease. Poggiale (2005) found that the number of individuals in a heterogeneous domain can be greater than the number of individuals in the equivalent homogeneous domain. He was studying an ODE model for a single population distributed between two patches with migration between the patches. Our results are consistent with Poggiale’s only in the case for prey averages in the SLV and SRM models in a boundary good patch or in a central good patch with \( l_b \leq 10 \).

We also found that position of the patch in the domain affected the population density there. The cycle amplitude and average population densities were less affected by fragmentation in boundary patches than in central patches. We surmise that this difference is due to the additional loss of individuals that occurs through the two open edges of the central patch, as compared to the one open edge of the boundary patch. This result is in accordance with the results of Cantrell and Cosner (1991) who found that a patch near the boundary was the most favourable location for a good patch in a domain with a reflecting boundary. Cantrell and Cosner measured how favourable the patch location was by finding the principal eigenvalue of the model, which determines whether or not a species persists.

Our results for the SM model differ from results obtained by Tanner (1975). In his study, Tanner used an ODE model in which predation was reduced because of the existence of refugia for the prey. Thus he essentially had differential predation rates in good and bad patches (from the point of view of the prey, so good patches had no predation while bad patches did), rather than variations in prey reproduction as we have in our models. Tanner found that under his assumptions the existence of refugia would cause the stable limit cycle to collapse to a stable focus. In contrast, our populations continued to cycle in the presence of fragmentation, though amplitude and average density were affected.

Finally, we found that good patch size \( (l_g) \) is more important than the separation between good patches (or bad patch size, \( l_b \)) under fragmentation by habitat loss and combined habitat separation and loss. We plotted cycle amplitude and average population densities against bad patch size, and ratio of good patch size to bad patch size (results not shown) and found no consistent trends. While the results presented for habitat separation (Fig. 9) indicate that bad patch size is important, our analysis indicates that the most critical quantity is good patch size.

### 4.2. Ecological implications

Our ultimate goal is to determine what is the effect of habitat fragmentation on the population dynamics of real cyclic predator–prey populations. We base our conclusions upon the combined separation and loss (3.1.1) analysis since these results are the most immediately applicable to species conservation on real domains. We find that for all of the
different models considered, prey and predator amplitudes decrease with increasing frag-
mentation. The SLV model predicts rapid declines in cycle amplitude, the SM and SRM
models have intermediate declines, and the SVT model predicts much smaller declines.
It is thus possible that habitat fragmentation contributes to the north–south differences in
cycle amplitude for species such as the Canada lynx and snowshoe hare.

Central patches may be more appropriate than boundary patches for models of real
habitat patches, since many habitats do not have reflecting boundaries but are surrounded
by patches of bad habitat. Considerable further work is necessary before the effects we
have discovered can be quantified for real populations. Our study emphasises however,
the importance of considering a range of plausible models when doing predictions, as
fragmentation affects population cycles differently for different models. It is especially
important to note that in the SVT model the population cycles show little response to habi-
tat fragmentation, which could lead one to suppose that increases in habitat fragmentation
are not a conservation concern. Once good patch size decreases below a certain threshold
however, this model shows declines of both prey and predator populations, which could
threaten population persistence.

4.3. Future research

There are a number of open questions and future avenues of investigation suggested by
our model. There is a need to expand the model to two dimensions and determine whether
or not the one-dimensional results still hold. In two dimensions, dispersal can vary with
direction and the domain geometry may play a role in the solutions. From the point of
view of conservation, a two-dimensional dispersal model will allow for more realistic
simulations, and make it possible to define landscape structure at a finer scale in terms of
resources and types of habitat (Dunning et al., 1995).

Our theoretically-based study makes it clear that model details matter when consid-
ering cyclic predator–prey dynamics on fragmented domains. In order for any modelling
study to make reliable predictions concerning the effects of habitat fragmentation on par-
ticular species, it is essential that the model be biologically-motivated and closely match
observed population dynamics. Developing such models is a non-trivial task and may
necessitate the inclusion of additional factors, such as multiple predators (Tyson et al.,
In progress).

While Fickian diffusion is a reasonable model for mammalian dispersal, the extent
to which our results depend on this choice needs to be established. Density-dependent
dispersal may be a more realistic alternative for certain species (Travis and French, 2000;
Okubo and Levin, 2001; Turchin, 2001). It is possible that in fragmented habitats more
long-distance dispersal is necessary and more costly to the disperser (since dispersal will
often be through “bad” patches). Travis and French (2000) suggest that whenever there
is a cost to dispersal the probability of a given individual dispersing should depend upon
the population density. If the population density is low in a given patch there is likely to
be more resources and territory available with less intraspecific competition. However,
if there is a higher population density in the patch, the individual will be more likely to
disperse to a new patch to avoid starvation. The Canada lynx is very territorial (Poole,
1997) and so its foraging behaviour may be linked to the density of conspecifics.

Another area of research to explore is quality gradation in patch value. At this moment
patches are either “bad” or “good” in our model. But there may be patches that have
intermediate values, or which are good in some aspects (lower predation rate) but not so good in others (lower reproduction rates). This last type of spatial heterogeneity, termed the refugium hypothesis, has been used by several authors (Poggiale and Auger, 2004; Ylonen et al., 2003).

We have postulated that the nonuniform population distributions are obtained through diffusive movement of prey and predator out of bad patches and advective movement toward visible good patches (coupled with a zero birth rate for the prey in bad patches). Other mechanisms offer reasonable explanations as well. For example, predator movement may be up prey gradients, rather than toward habitats that potentially contain prey (Moorcroft and Lewis, 2006). Alternatively, a key mechanism might be spatially varying hunting efficiency of predators (Cantrell and Cosner, 1998). We also included advection toward high quality patches in our model, but we did find that some of the trends we report here can also be observed if the advective terms are eliminated. The extent to which orientation toward high quality patches is important, and the various forms this orientation may take, warrant further study.

The role played by the boundaries also needs to be investigated. We have shown that patches with open boundaries (those in central positions) behave differently from patches with a reflecting boundary. From a conservation point of view, it might be relevant to consider partially absorbing boundaries, that is, boundaries that wildlife cross only occasionally. As patch sizes decrease, the nature of the boundaries could become very important to the predictions of the model.

With more realistic models and experimentally measured parameter values, it will hopefully be possible to determine how habitat fragmentation affects the dynamics of real cyclic predator–prey systems. Studies of habitat fragmentation and critical patch size have been investigated previously for non-cyclic populations (Cantrell and Cosner, 1991, 1999, 2001; Cantrell et al., 1998, 2001). This paper is an initial investigation into the parallel problem of the dynamics and persistence of cyclic species.

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References

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