

Spatial structure and the control of invasive alien species

Justin M. J. Travis¹ and Kirsty J. Park²

¹ Centre for Conservation Science, The Observatory, Buchanan Gardens, University of St Andrews, St Andrews, Fife KY16 9LZ, UK

² Centre for Conservation Science, Department of Biological Sciences, University of Stirling, Stirling FK9 4LA, UK

(Received 4 March 2003; resubmitted 27 August 2003; accepted 28 February 2004)

Abstract

Invasive alien species pose a significant threat to biodiversity worldwide and many eradication programmes are now underway in an effort to reduce the impact they may have on native species and ecosystems. The spatial structure of such invasive species populations is likely to have important implications for designing effective control strategies. Here, a simple source–sink population model is used to address the following question: if a population of an invasive alien species is source–sink in nature, what is the best way of dividing limited resources for its control? Results from this model indicate that allocation of resources solely to the source population does not always result in the most effective control strategy. The most efficient control measure is determined by the relative strengths (net gains and losses) of the source and sink populations and, crucially, the nature of dispersal between them. We present a case study for the control of an invasive species illustrating the use of these types of model.

INTRODUCTION

Spatial variability in habitat quality is characteristic of natural ecological systems. This is reflected in the explosion of recent work that seeks to increase our understanding of how spatial structure influences the dynamics of populations and communities (e.g. Kareiva, 1990; Hassell, Comins & May, 1994; Ruxton & Doebeli, 1996; Thomas & Kunin, 1999; Harkonen & Harking, 2001; Focardi *et al.*, 2002; Mauritzen *et al.*, 2002). Differences in habitat quality may lead to inequality in the demography of populations occupying these different habitats. Categorising habitat into sources and sinks has become one popular theoretical approach for incorporating spatial environmental variability: habitats in which populations exhibit net positive growth rates can be classified as sources, whereas those in which populations incur net negative growth can be classified as sinks. Sinks persist only through the dispersal of individuals from source habitats. Holt (1985) used a mathematical model to demonstrate that dispersal from the source to the sink could maintain a population within the sink and that the total population in the source and sink could be greater than could be maintained in the source alone. Pulliam (1988) extended this work and found that: (1) sink habitats may contain very large populations, in some cases larger than the source that maintains them; (2) the realised niche of a

species may be larger than the fundamental niche, which is the opposite of what Hutchinson (1957) suggested was likely; (3) in the most extreme case, the species composition at a particular locality may be determined more by the nature and proximity of neighbouring habitats than by the environmental conditions of the location itself.

Implications of spatial structure for population management

The spatial structure of a population can have important implications for its management and this is now recognised when considering conservation of rare or vulnerable species (e.g. Tuck & Possingham, 1994; McCullough, 1996; Brawn, Robinson & Thompson, 2001; Dalle *et al.*, 2002; Schadt *et al.*, 2002). Although demonstrating the existence of source–sink populations in nature can be problematic (Dias, 1996), source–sink models have been applied to several conservation issues (e.g. Doak, 1995; Donovan *et al.*, 1995; Robinson *et al.*, 1995; McCoy *et al.*, 1999) and to the investigation of optimal harvesting in spatially-structured populations (Lundberg & Jonzen, 1999; Jonzen, Lundberg & Gårdmark, 2001). In several instances management recommendations have been based on model outcomes (e.g. Wootton & Bell, 1992; Gaona, Ferreras & Delibes, 1998; Donovan & Thompson, 2001).

Invasive alien species

The introduction of invasive alien species into novel environments is one of the most important factors

All correspondence to: Justin M. J. Travis. Centre for Ecology & Hydrology Banchory, Hill of Brathens, Banchory, Kincardineshire, AB31 4BW, Scotland. Tel: 01330 826345; E-mail: jmjt@ceh.ac.uk.

influencing dramatic population declines for many native species (IUCN Council, 2000). In many situations the optimal conservation action is to eradicate the species through removal or culling programmes, but this strategy can be very costly and may require long-term commitment, particularly if a population has been allowed to establish before action is taken (e.g. Courchamp, Chapuis & Pascal, 2003). For established populations, constructing population models of invasive species can help assess the requirements of any successful eradication strategy and highlight important areas of uncertainty in the species' ecology. Most species are spatially structured at one or more spatial scales and this is also likely to be true for invasive species populations, although few empirical studies have demonstrated this. A source–sink framework has been suggested for a number of invasive species and pest populations including molluscs, insects and mammals (Hudson & Cox, 1989; Horvath *et al.*, 1996; Portillo *et al.*, 1998). For example, North American mink (*Mustela vison*) have colonised much of the UK following escapes and deliberate releases from fur farms established in the 1930s (Dunstone, 1993). Results from numerous studies have indicated that spatial variability in habitat quality exists for this species (Dunstone & Birks, 1983; Hudson & Cox, 1989; Clode, Halliwell & Macdonald, 1995) and a study conducted in the Scottish Hebrides suggested that coastal populations may act as a source for lower quality riverine and lochan populations (Hudson & Cox, 1989). This potential spatial variation and the consequences for the effectiveness of control strategies is now being investigated by a trapping programme currently underway in the Hebrides (Scottish Natural Heritage, 2000).

Modelling source–sink populations

For conservation purposes the aim of source–sink models is to maximise the population size. Similarly, obtaining an optimal harvest from such a population requires a management strategy that allows individuals to be removed, whilst maintaining the population. In this paper, rapid and efficient population reduction is the objective – resulting either in eradication of the target population or reduction to very low density. It is obvious that if the population really is structured as a source and a sink, then by eliminating the source (and preventing its re-establishment), the sink will eventually go extinct on its own. However, it is not clear whether the most rapid and efficient control is achieved through focussing entirely on controlling the source. To provide a general answer to these questions we investigate a simple source–sink model that consists of one source population and one sink population linked by dispersal. We search for efficient control strategies for a range of different strength sources and sinks and for different rates and forms of dispersal.

METHODS

We constructed a simple model that represented two habitats, one a source and the other a sink, linked by

dispersal. We allowed this spatially-structured population to obtain equilibrium and then imposed a range of culling strategies. In this paper, therefore, we are concerned largely with established alien species, rather than those undergoing rapid range expansion. We varied both the total cull effort and the partitioning of the effort between source and sink. We looked to find the culling strategy that most rapidly reduced the total population to a target density.

The population models

We assumed that when it is isolated from the sink, the source population behaved according to the logistic growth model:

$$S_{t+1} = S_t + r \cdot S_t \cdot (1 - S_t/K)$$

where S_{t+1} is the population density of the source habitat post-reproduction, S_t is the population density of the source pre-reproduction, r is the maximum per capita growth rate in the source habitat and K is the equilibrium density of the source population in the absence of dispersal and with no culling. In the absence of immigration from the source, the sink population declines at a constant rate d , thus:

$$N_{t+1} = (1 + d) \cdot N_t$$

where N_{t+1} is the population density of the sink habitat post-reproduction and N_t represents the population density of the sink pre-reproduction. For the model presented, stable equilibrium dynamics were used with r varying between 0.2 and 1.4, while K was set at 2000. We deliberately limited our analyses to a range of r values that produced stable equilibrium dynamics. Many vertebrate species exhibit dynamics that are best characterised by these low values of r . In isolated populations, higher values of r produce cyclic or chaotic population dynamics. Spatial population structure can dampen the dynamics of populations with a high r value. However, the dynamics become complicated and are beyond the scope of this paper. Net reproductive deficit of the sink population (we use the term 'strength' here), d , varied between -0.5 (strong) and 0.0 (the latter representing the case where the sink does not truly represent a sink but results in no net loss or gain to the population).

Dispersal

In most of the simulations, we assumed that density-independent dispersal occurred between the two habitats: the rate of movement from source to sink being μ and from sink to source ϕ . Adults and juveniles were assumed to disperse with equal likelihood. Here, we allowed both μ and ϕ dispersal to vary independently between 0 and 1 (0 representing no movement). Dispersal was assumed to be free of costs.

Many organisms, however, exhibit density-dependent dispersal and to assess how this may influence the choice of control strategy we also ran simulations incorporating

density-dependent dispersal from the source to the sink. Density-dependent dispersal was modelled here using a simple linear function, where the rate of dispersal from source to sink is given by:

$$\mu = \eta + \frac{(S_t - K) \cdot \omega}{K}$$

where η is the rate of dispersal when $S_t = K$ and ω is the strength of density dependence. To bound the rate of dispersal between 0 and 1, when the above function gave $\mu < 0.0$, we set $\mu = 0$ and, similarly, when the function gave $\mu > 1.0$ we set $\mu = 1.0$.

Culling

We assumed that the total effort available to culling was given by H and that a proportion, γ , of the total effort was dedicated to reducing the source population. Increasing cull effort resulted in the same increase in the rate of reduction of the target population. The cull reduced the source population at rate $H \cdot \gamma$. Similarly the sink population was reduced at rate $H \cdot (1 - \gamma)$. For most of the simulations in this paper γ was kept constant through time. However, it is possible that the most efficient culling strategy is one where the proportion of the effort devoted to the source varies over time. We investigated two possible time-varying strategies. The first was very simple: every generation the largest population was identified and all of the available resources were put towards its control. The second involved the use of a simple genetic algorithm to search for the optimal time-varying culling strategy. The genetic algorithm was implemented as follows: 20 random numbers between 0 and 1 were generated 100 000 times. Each set of 20 numbers represented γ for the 20 years of control. The reduction in population density that was obtained using the 100 000 different sets of γ was calculated and the best performing set was selected for further refinement. At random, one of the γ values of the best performing set was replaced by a random number between 0 and 1. If the modified set of γ improved control it replaced the old set. This step was repeated 1000 000 times. To reduce the risk that local maxima were being identified all of the above steps were repeated 10 times. In most cases the 10 replicates converged to produce identical or extremely similar sets of γ . We compared the performance of these two time-varying strategies with those where the partitioning of effort between source and sink remained constant through time.

Ordering of events

We assumed that in one discrete generation, reproduction occurred at both sites simultaneously, followed rapidly by dispersal. Culling was applied to the populations post-dispersal. This led to the following functions that calculated the size of the source and sink populations pre-reproduction at time $t+1$ from the densities pre-

reproduction at time t :

$$\text{Source: } S_{t+1} = \{([S_t] + [r \cdot S_t \cdot (1 - S_t/K)]) \cdot [1 - \mu] \\ + (1 + d) \cdot N_t \cdot \phi\} \cdot (1 - H \cdot \gamma)$$

$$\text{Sink: } N_{t+1} = \{([S_t] + [r \cdot S_t \cdot (1 - S_t/K)]) \cdot \mu \\ + (1 + d) \cdot N_t \cdot (1 - \phi)\} \cdot [1 - H \cdot (1 - \gamma)]$$

This ordering of events was chosen as it seemed likely to best represent the behaviour of many species. However, if the model was developed for a particular scenario its formulation would have to depend on the species biology and the specific culling strategy employed.

The simulations

Our main question was how should we distribute culling effort between the source and the sink habitat for the most efficient reduction of total population density? Obtaining an analytical solution to this proved to be non-trivial as the population is not at equilibrium. Therefore, we used simulations here to explore the model's behaviour.

For each set of parameters explored, a simulation was started by introducing a small density of individuals to both source and sink populations. We allowed the population to reach equilibrium by running 500 iterations (generations) of the model in the absence of a cull. Culling was then applied and we recorded the time required for the cull to have the desired effect. If the cull did not achieve the target population density (in this case 5% of the carrying capacity or 100 individuals) within 200 iterations the simulation stopped. We found that in almost all cases if control had not been obtained within 200 iterations then it would never be obtained using that particular culling strategy.

RESULTS

Basic properties of the model

Increasing the reproductive growth of the source (r) from 0.2 to 1.4 results in an increase in the number of generations required for eradication. Similarly, an increase in the reproductive deficit rate of the sink (the strength of the sink, d) results in a decrease in the number of generations required for eradication. These results are true regardless of the values of the other model parameters.

Influence of dispersal

Generally, as the proportion of the source population dispersing to the sink (μ) increases, the increase in the sink population size (with accompanying decrease in source population size) causes a decrease in the number of generations required for eradication. The opposite is true for dispersal from the sink to the source (ϕ): the greater the dispersal from sink to source, the longer it takes to achieve population control. A change in the rate of sink to source dispersal generally has a far less dramatic effect on the eradication times than does dispersal from source to sink (e.g. Fig. 1).

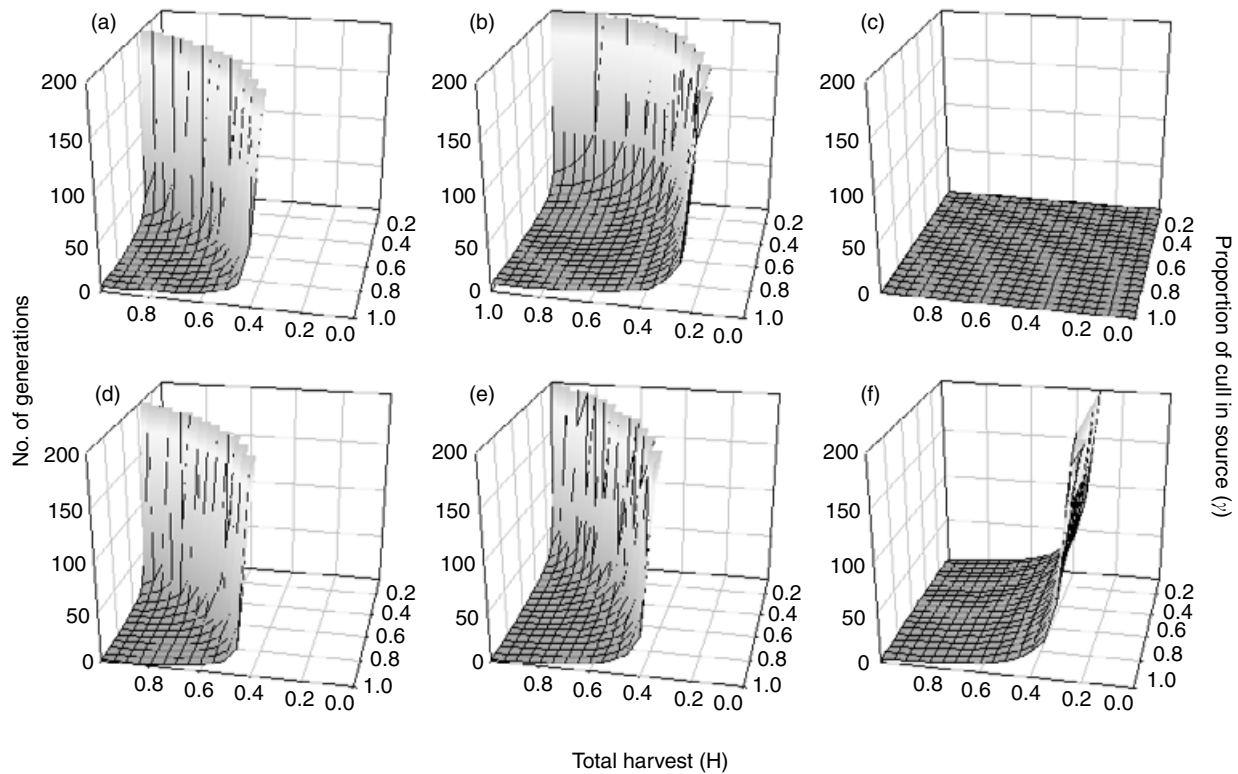


Fig. 1. The number of generations required to reach target population density (100 individuals) with varying culling levels (H) and a variable proportion of the cull being concentrated in the source population (γ). Dispersal rates differ between figures: moving left to right represents an increase in μ (source to sink dispersal), while moving top to bottom represents an increase in ϕ (sink to source dispersal). (a) – (c), $\phi = 0.1$, and $\mu = 0.1, 0.4$ and 0.8 , respectively. (d) – (f), $\phi = 0.8$ and $\mu = 0.1, 0.4$ and 0.8 , respectively. Other parameter settings are: $r = 0.8$, $d = -0.25$.

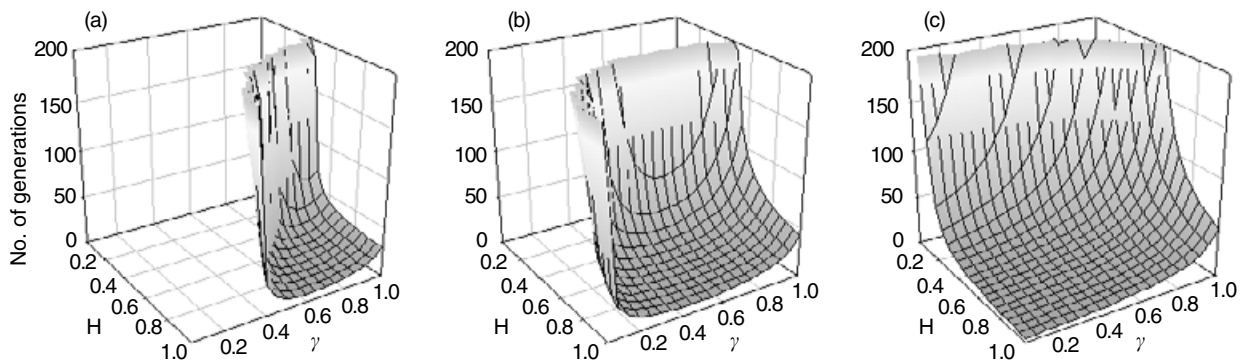


Fig. 2. The number of generations required to reach the target population density with changing cull levels (H) and proportion of cull in the source population (γ). Other parameter settings are $r = 0.8$, $d = 0.0$ and $\phi = 0.1$. The level of dispersal from the source to the sink (μ) differs between figures, with μ increasing from 0.1 (a) to 0.4 (b) to 0.8 (c).

However, as the strength of the sink decreases (d increases), the importance of sink to source dispersal (ϕ) increases and when d is zero, eradication is only possible if ϕ is low and resources are concentrated largely in the sink.

Optimal culling strategies

The proportion of cull effort that should be concentrated in the source population (γ) varies depending on the strength of the sink and the level of dispersal between the source

and sink populations. With a reasonably strong sink, it is optimal to cull solely in the source population, but if the sink is weak and the level of dispersal to the sink is high, an optimal culling strategy would be to cull solely in the sink.

An interesting situation arises where the sink is not, in fact, a sink at all but has a net reproductive deficit of zero (e.g. Fig. 2). If this is the case, the optimal strategy lies in a division of resources between the source and the sink, or if μ is very high the cull should be concentrated solely in the sink population (Fig. 2(c)).

Sensitivity analysis

We have investigated whether the results are sensitive to environmental variability. There are a number of ways in which environmental variability can affect population dynamics, acting perhaps to alter the equilibrium density (K) from year to year, or to modify the average productivity of a female (r). Here, we assessed how temporal variation in K affects the general results of the model presented. Temporal variation has been incorporated both as white (no temporal autocorrelation) and red (with positive temporal autocorrelation) noise (see Travis, 2001 for details on methods; see also Ranta, Kaitala & Lindstrom, 1997; Ripa, Lundberg & Kaitala, 1998 for further discussion on spatial and temporal environmental variability). We found that the results produced when environmental variability is incorporated are qualitatively similar to those when the environment is assumed to be constant. The main difference is that with environmental variability, the model becomes stochastic and in a set of simulations all using identical parameter values, control will be more effective in some simulations than in others. Environmental variability thus increases the uncertainty associated with a control programme. A particularly bad year for the target species can greatly assist control (as was the case for coypu eradication in the UK: e.g. see Gosling & Baker, 1987), while a particularly good year can set it back. With red noise this effect is heightened since several bad (or good) years are likely to come together.

Dynamic management strategies

So far, we have only considered fixed management strategies where γ , the proportion of cull in the source population, is constant through time. Now we will compare this fixed strategy with two alternative management strategies: the first of these concentrates all culling effort towards the largest population each year, while the second uses a simple genetic algorithm to search for the optimal time-varying culling strategy (γ can take any value between 0 and 1 each year).

For a range of different parameter combinations we compared the population sizes following 20 years of control by the different strategies (Fig. 3). In Fig. 3(a), γ has a large effect on the outcome of the fixed strategy and the optimal γ here is 1.0 (i.e. all culling in the source). This results in a final population size of 188, as do both the alternative management strategies (which in both cases prescribe that all the effort should always be devoted to the source). In Fig. 3(b), the optimal γ for the fixed strategy is 0.45, which gives a smaller final population size (474) than the strategy targeting the largest population (611), but is not as efficient as the time-varying culling strategy, which results in a population size of 414. Fig. 3(c) illustrates a scenario in which culling using the fixed strategy should be largely directed towards the sink ($\gamma = 0.36$), but again this is not as efficient as using the time-varying culling strategy. However, none of the strategies here is particularly successful in achieving a significant reduction in population density.

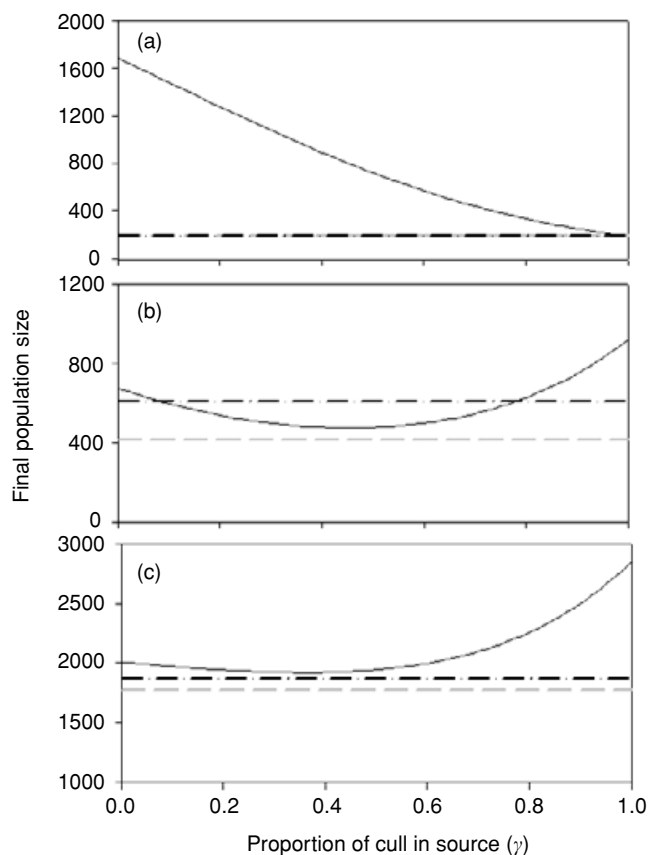


Fig. 3. Predicted final population sizes for three different management strategies (solid black line = fixed culling strategy (constant γ through time), broken black line = strategy targeting the biggest population each year, dash-dot grey line = optimal time-varying culling strategy identified by a genetic algorithm) under three different scenarios (a), (b) and (c). Parameter values for each scenario are: (a) $H = 0.2$, $r = 0.2$, $d = -0.2$, $\mu = 0.05$, $\phi = 0.05$; (b) $H = 0.2$, $r = 0.2$, $d = -0.05$, $\mu = 0.2$, $\phi = 0.05$; (c) $H = 0.2$, $r = 0.5$, $d = -0.05$, $\mu = 0.2$, $\phi = 0.05$. Increasing γ shown on the x-axis is only applicable to the fixed culling strategy. The genetic algorithm used for the optimal time-varying culling strategy was as follows: (a) $\gamma = 1$ every year; (b) 0, 0, 1, 0, 1, 1, 0, 1, 0, 1, 0, 1, 0, 1, 0, 1, 0, 1, 0, 0 ($\gamma = 0$ for the first 2 years and then again in years 4, 6, 8, 10, 12 and for the last 3 years. In all other years γ should equal 1); (c) 0, 0, 0, 0, 0, 0, 1, 0, 1, 1, 0, 1, 0, 1, 1, 0, 1, 1, 0, 1, 0, 0.

Density-dependent dispersal

Density-dependent dispersal tends to make effective control more difficult (Fig. 4). For a given culling effort, as the strength of the density dependence, ω , increases, a greater reduction in the sink population is obtained. This is because as population size is reduced through culling, a lower rate of dispersal occurs from the source to the sink population. However, control of the source population is far less effective (due to the lower rate of dispersal away from the source) and, overall, the total population size is reduced less for higher values of ω . Importantly, we find that if an organism exhibits density-dependent dispersal it becomes more likely that culling exclusively in the source habitat will be a more effective strategy. For higher values

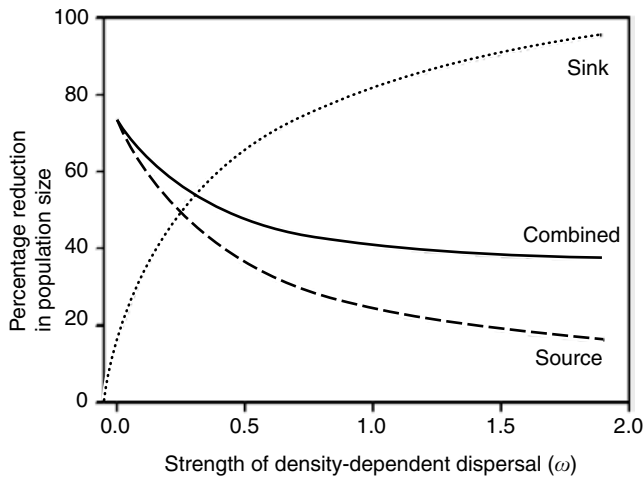


Fig. 4. Percentage reduction in population size after 20 generations of a culling strategy with differing strengths of density-dependent dispersal (ω). Resources are divided equally between the source and sink populations ($\gamma = 0.5$). Other parameter settings are: $H = 0.3$, $r = 0.6$, $d = -0.3$, η (dispersal from source at K) = 0.2, ϕ (sink to source dispersal) = 0.4. The dotted line represents percentage reduction in the sink population; the dashed line represents reductions in the source population; the solid line represents changes in the source and sink populations combined.

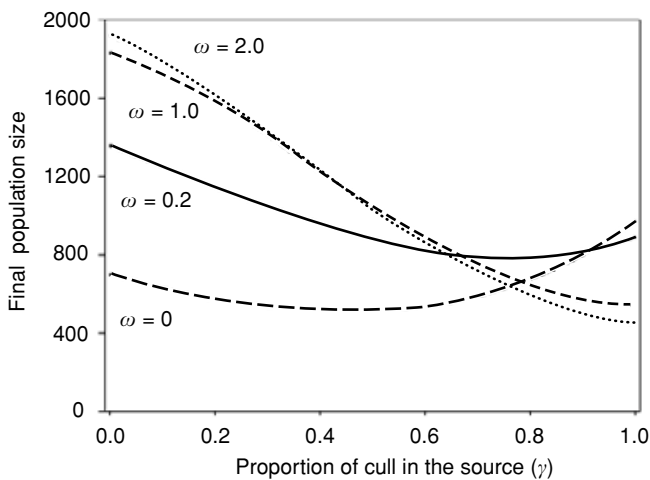


Fig. 5. Predicted sizes (source and sink combined) for populations with a range of density-dependent dispersal values (ω) under different culling strategies (γ). The different lines represent differing degrees of density-dependent dispersal from the source to the sink (long dashed line, $\omega = 0$, solid line, $\omega = 0.2$, short dashed line, $\omega = 1.0$, dotted line, $\omega = 2.0$). Simulations were run for 20 generations. See Methods section for description of incorporating density-dependent dispersal into the population models. Other parameter settings are: $H = 0.2$, $r = 0.2$, $d = -0.05$, η (dispersal from source at K) = 0.2.

of ω , allocating more of the resources to the source is likely to result in improved overall control (Fig. 5).

Case study: The European hedgehog in South Uist

An example of where consideration of spatial structure may be useful is the proposed control programme

for European hedgehogs (*Erinaceus europaeus*) in the Scottish Western Isles (Scottish Natural Heritage Scientific Advisory Committee 16/10/02, Perth, UK). *E. europaeus* were introduced from mainland Britain to South Uist, an island off the west coast of Scotland in the mid 1970s (Angus, 1993). Studies have indicated that the spread in the range and abundance of this species since then is responsible for large declines in internationally important breeding wader populations (Jackson & Green, 2000; Jackson, 2001). We present here some preliminary modelling work using data collected from the hedgehog population on the Uists (Jackson & Green, 2000; Jackson, 2001; D. B. Jackson, unpublished results). We use the same model structure as that described above to consider hedgehog populations in two habitats (machair and blackland) linked by dispersal. The low, sandy coastal plain known as machair lies along the west coast of the Western Isles. The blackland habitat, which separates machair from hill and moorland habitats, is formed from the mixing of the calcium-rich sands with the acidic peat of the moorland edge (Cummins *et al.*, 2002). Research has largely concentrated on hedgehogs in the machair habitat since this is where some of the highest densities of breeding waders can be found (e.g. Fuller *et al.*, 1986). Hedgehogs also, to some extent, inhabit moorland habitat but little is known about their density other than it appears to be much lower than in either the machair or blackland habitats (Jackson & Green, 2000). The model presented here is concerned only with these latter two habitat types. Machair and blackland habitats differ substantially in the resources they offer hedgehogs (food, shelter, etc.) and hedgehog densities on blackland habitat are thought to be approximately half of that on the machair (Jackson & Green, 2000). However, there is no evidence to suggest that hedgehog populations on the Uists have a source–sink structure and in the model presented here the demographic characteristics, fecundity and survival, in the two habitats are the same.

Parameter values for the model were derived from both published (Jackson & Green, 2000) and unpublished (D. B. Jackson, unpublished results) data. It should be noted that the values for mortality and fecundity are from preliminary analyses and the full analyses will be published elsewhere (D. B. Jackson, unpublished results).

The simulation model was run on a weekly time-step during the period May–October when hedgehogs are active (beginning of week 16 to the end of week 43). The ordering of events is the same as that used for the source–sink model (i.e. reproduction, dispersal and removal). The weekly mortality value for adults was 0.0080 and for juveniles it was 0.0256. In addition, subadults experienced a density-dependent mortality during the first few weeks following emergence from hibernation of $0.1 \cdot N/3000$ (where N is the total population abundance, 3000 is the assumed equilibrium population abundance of the combined habitats and 0.1 is a realistic, but arbitrary, value for this additional mortality when the population is at equilibrium). Overwinter mortality was included in the model at 35% of individuals entering hibernation. Fecundity was estimated to be: 2.85 offspring per female

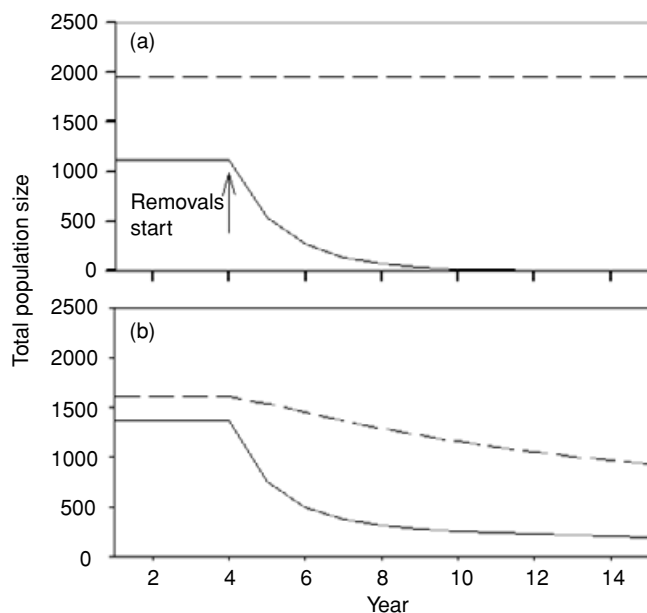


Fig. 6. Hedgehog abundance before and after the start of removal operations (starting in year 5) with levels of (density-independent) dispersal between machair and blackland habitat set at (a) zero and (b) 0.1. Output values are based on the removal of 10% of the population for the first 8 weeks of the active season. Starting values represent K for each habitat. In both figures, abundance in the machair is represented by the solid line, in the blackland by the broken line. Parameter values are as follows: weekly mortality value for adults = 0.0080; juveniles = 0.0256; subadult density-dependent mortality following emergence from hibernation = $0.1 * N / 3000$ (where N is the total population abundance, 3000 is the assumed equilibrium population abundance of the combined habitats and 0.1 is the value for this additional mortality when the population is at equilibrium). Overwinter mortality = 35% of individuals entering hibernation. Fecundity = 2.85 offspring per female for 59% of adult females during week 24 (first birthing period), = 2.85 offspring per female for 70% of adult females during week 32 (second birthing period), = 2.85 offspring per female for 43% of subadult females during week 32.

for 59% of adult females during week 24 (first birthing period), 2.85 offspring per female for 70% of adult females during week 32 (second birthing period) and 2.85 offspring per female for 43% of subadult females during week 32. Sample sizes on hedgehog movements on South Uist from telemetry studies (D. B. Jackson, unpublished results) were too small to allow us to estimate reliably the probability of an animal moving from blackland to machair or vice versa. We have, therefore, assumed that the probability of movement between the two habitat types is independent of density and we have explored the implications of a range of dispersal rates.

The dispersal rate between habitats is crucial for determining how successful the control strategy will be if it is implemented only on the machair. Dispersal between the two habitats means that removal of animals on the machair may also result in reduced densities in the blackland, albeit at a slower rate (Fig. 6). However, the model also indicates that the percentage reduction in population size in the machair decreases as the dispersal

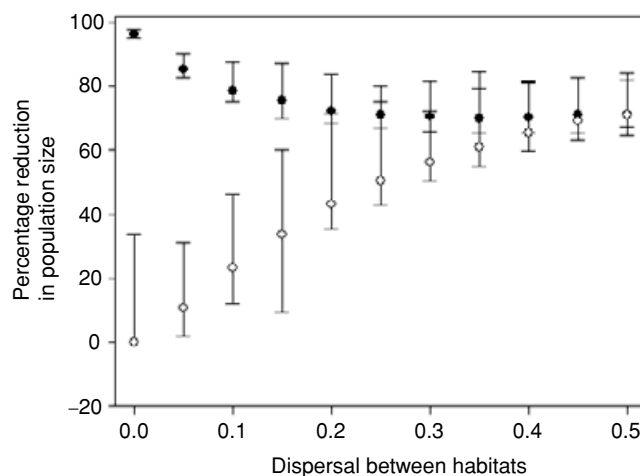


Fig. 7. Percentage reduction achieved in the machair (black circles) and blackland (white circles) habitats with differing levels of dispersal. Output values are based on the removal of 10% of the population each week for the first 8 weeks of the active season for 5 continuous years. Uncertainty in parameter estimates and demographic stochasticity was incorporated by resampling with replacement from the field data and by resampling from the parameter estimates respectively. Parameter values are as follows: weekly mortality value for adults = 0.0080; juveniles = 0.0256; subadult density-dependent mortality following emergence from hibernation = $0.1 * N / 3000$ (where N is the total population abundance, 3000 is the assumed equilibrium population abundance of the combined habitats and 0.1 is the value for this additional mortality when the population is at equilibrium). Overwinter mortality = 35% of individuals entering hibernation. Fecundity = 2.85 offspring per female for 59% of adult females during week 24 (first birthing period), = 2.85 offspring per female for 70% of adult females during week 32 (second birthing period) and = 2.85 offspring per female for 43% of subadult females during week 32.

rate increases, because the blackland provides a refuge from the control operations (Fig. 7): even with dispersal rates of as low as 10% per year, the reduction in hedgehog abundance on the machair will be considerably lower than if the machair was isolated.

DISCUSSION

Most populations are spatially structured at one or more spatial scale. Considerable theory already exists on the consequences of spatial processes for conservation biology (see Hanski, 1999) and recent work has begun to address the implications for sustainable harvesting (Lundberg & Jonzen, 1999). Here, we have shown that a consideration of the spatial structure of a population can also have important implications for designing efficient control strategies.

Control of populations with source–sink dynamics

During the planning of an eradication or control programme and in the absence of any knowledge regarding a population's demographic parameters, concentrating on the habitats containing the highest numbers of individuals

might be considered a sensible strategy. Similarly, if source–sink dynamics were suspected, the expectation might be that the most efficient eradication would be achieved by concentrating on the habitat thought to contain the source population. However, for some species these approaches may fail to provide the desired result (rapid eradication or control). Without some knowledge of the parameters governing a species' demography, employing what might seem to be an intuitively obvious strategy may be inefficient or even result in unwanted effects. The results from the model show that the outcome of a particular control strategy is highly dependent upon the populations' demographic parameters and, in particular, on the levels of dispersal between the source and the sink (or between areas in which control is being carried out and adjacent areas without control). Under certain conditions the optimal strategy can be far removed from what intuition would suggest it should be.

For a range of parameter values, the model indicated that the optimal strategy for the reduction of the total population is to concentrate all the available resources on culling the source population. Source-targeted control is likely to be more efficient if the sink is strong, if dispersal rate from the source to the sink is very low, or if dispersal is strongly density-dependent. For other scenarios the situation is less straightforward.

Pulliam (1988) demonstrated that under certain conditions a sink contains a greater number of individuals than a source. This is likely to occur when source to sink dispersal is relatively high, the sink is weak and the area of sink habitat is large relative to that of the source. It is under these conditions that our model exhibited the most interesting properties. For some regions of parameter space the model indicated that the most efficient static control strategy is to target only the sink population (see Fig. 2(c)). However, this result only occurs when the rate of dispersal from source to sink is very high, probably unrealistically so. For more realistic rates of dispersal, quite often the optimal static strategy involves partitioning some effort to both source and sink (e.g. Figs. 3(b) & (c)). If sufficient information is available for a population's demographic parameters then it may be possible to devise a dynamic strategy that is more efficient than any static strategy. The optimal time-varying strategies, as identified by the genetic algorithm, always consisted of a sequence of 1s and 0s. This implies that the best possible control is obtained by some particular pattern that involves switching between putting all the effort into the source and then into the sink and never splitting it between the two. Clearly with the fixed strategy, the value of γ has a large effect on the final population size. The optimal fixed strategy is generally equal to, or slightly better than, targeting the largest population and the optimal time-varying strategy is always equal to, or superior to, either of the other two strategies. The simplest dynamic strategy would be to target the largest population each generation and when the largest population is also the source population this is as efficient as the optimal time-varying strategy. Unfortunately, this is not always a reliable approach (Fig. 3(b)).

Practical applications of these models

The model described in this paper deals with hypothetical species on hypothetical habitat patches. As such, it is useful for providing some general results. Any particular control programme, however, would require the development of a model specifically for the species and habitat of concern. An important role for this type of model will be to suggest not only the single most rapid or efficient strategy, but also the safest strategy, whereby uncertainty in parameter estimation is accounted for. A further function will be to assist in identifying those parameters that are most important in determining the outcome. Resources can then be directed to working towards a reduction in the uncertainty of those critical parameters. We chose a target density of 100 individuals that represented 5% of the carrying capacity of the population. Although this is a fairly arbitrary value, once numbers in a population become very low, the main challenge to successful eradication will be in detection and capture at low densities. There are also likely to be species-specific Allee effects (e.g. Courchamp, Clutton-Brock & Grenfell, 1999) that would make general predictions about response to control at low population sizes unreliable.

The model presented here for hedgehogs indicates that by concentrating control on areas of high conservation value (i.e. those favoured by breeding waders), it may be possible to reduce the impact of egg predation on the waders but also to reduce densities in neighbouring habitats, even with relatively low dispersal rates between them. However, by adopting such a tactic the blackland habitat essentially acts as a refuge from removal operations: because of this, as dispersal between the two habitats increases, so does hedgehog abundance in the machair. The importance of this refuge will depend to a large extent on whether it represents a sink or a source habitat for hedgehogs. If the management aim is control rather than eradication then the existence of a refuge may not be of such great importance. Since there is insufficient information on dispersal between habitats or of density dependence in the population, the current model presented here cannot be used to derive predictions about the required length of removal operations or what the most effective control strategy may be.

Populations may frequently be suspected to fit the source–sink framework. However, in many cases, knowledge of the critical demographic parameters is unlikely to be sufficient to verify whether this really is the case. Indeed, several authors (e.g. Watkinson & Sutherland, 1995; Kadmon & Tielbörger, 1999) have commented on the paucity of empirical demonstrations of source–sink dynamics relative to the comparative abundance of source–sink models. This is indicative of the difficulties involved in obtaining reliable estimates of demographic parameters for a population. It must also be recognised that the demography of a population is likely to change throughout the culling process and, as such, an adaptive management approach should be adopted. The use of adaptive management for addressing ecological questions has long been considered a useful tool for managing

natural resources (e.g. Walters & Hollings, 1990), but is perhaps under used in the field of invasive species control (Shea *et al.*, 2002). Adaptive management or active adaptive management (Innes *et al.*, 1999; Shea *et al.*, 2002) can provide a means of testing hypotheses concerning the spatial distribution of populations (and thereby informing on the most efficient strategy for population reduction), whilst simultaneously alleviating the negative impact that the introduced species may be exerting.

Future directions

In this paper, we have presented the results from a very simple model in which the population is structured as a source and a sink. We assume that density-dependence acts on the source population, but not on the sink. Under certain conditions this assumption may be quite reasonable: a small area of high quality habitat (the source) may be surrounded by a very large area of poor quality habitat (the sink). However, some of the results shown in this paper, particularly those that indicate that the sink habitat should be targeted with the most control, are likely to be quite dependent on this assumption and so may not be true for all source-sink populations. Future work relaxing this assumption is needed. All the results shown in this paper arise from populations with stable equilibrium dynamics. The sensitivity analysis that we have carried out indicates that the general predictions are likely to be robust for populations exhibiting more complex dynamical behaviours. It is only recently that people have begun to consider the effect of environmental variability on source sink systems (Gonzalez & Holt, 2002) and work investigating potential interactions between different dynamical behaviours and different forms of environmental noise might be informative.

From a modelling point of view it is convenient to think of habitat as distinct patches. Here we have assumed just two patches. This type of approach could readily be extended to incorporate a greater number of discrete patches, perhaps using a lattice model framework (e.g. Travis & Dytham, 1999, 2002). However, in most natural systems the spatial configuration of a population will be far more complex and the quality of the environment will vary continuously through space (Thomas & Kunin, 1999). The further development of models that can account for this type of spatial structure (see Pacala, 1987; Bolker, Pacala & Levin, 2000; Berec, 2002; Law, Murrell & Dieckmann, 2003) is much needed, not only for the control of source-sink populations, but for understanding the dynamics of spatial populations in general.

In this paper, we limited ourselves to a consideration of the dynamics of populations characterised by relatively low intrinsic rates of growth (r). For many vertebrate species the choice of low values of r is appropriate, however many other species will exhibit dynamics that are better characterised by higher r values. Future work is needed to establish how spatially structured populations with high intrinsic growth rates should be optimally

controlled. It is possible that in some cases the rapid declines in population size that occur quite naturally with high r , might help efforts to reduce the abundance of a population. However, the rapid growth rate of high- r populations when density is low may render them particularly difficult to eradicate.

A considerable literature addresses the conservation of spatially-structured populations. In contrast, there is a paucity of theory devoted to understanding how spatially-structured populations can be efficiently controlled or eradicated. The work presented here has clearly demonstrated that the control of wild populations might be made more efficient by a proper consideration of the spatial structure of the population. Focussing on an idealised, source-sink population, we show that the optimal control strategy depends not only on the relative productivities of the two environments, but on the degree of dispersal between them. There is great scope for further work in this area and the results from this type of study might have a considerable impact on the way population control measures are implemented in the future.

Acknowledgements

Thanks to the RSPB and Digger Jackson for the use of unpublished data and to Jeremy Wilson and Digger Jackson for comments on the manuscript. We thank John Harwood, Jason Matthiopoulos, Len Thomas, Simon Wood, Sophie Smout and Christian Asseburg for trying to find an analytical solution to this problem and for their comments on earlier versions of the manuscript. Thanks also to Pete Hudson for comments on the manuscript and Tim Benton for useful discussions.

REFERENCES

- Angus, S. (1993). Hedgehogs in the Western Isles in 1991. *Hebridean Nat.* **11**: 73–76.
- Berec, L. (2002). Techniques of spatially explicit individual-based models: construction, simulation and mean-field analysis. *Ecol. Mod.* **150**: 55–81.
- Bolker, B. M., Pacala, S. W. & Levin, S. A. (2000). Moment methods for ecological processes in continuous space. In *The geometry of ecological interactions*: 388–411. Dieckmann, U., Law, R. & Metz, J. A. J. (Eds). Cambridge: Cambridge University Press.
- Brawn, J. D., Robinson, S. K. & Thompson, F. R. (2001). The role of disturbance in the ecology and conservation of birds. *Annu. Rev. Ecol. Syst.* **32**: 251–276.
- Clode, D., Halliwell, E. C. & Macdonald, D. W. (1995). A comparison of body condition in riverine and coastal mink (*Mustela vison*). *J. Zool. Lond.* **237**: 686–689.
- Courchamp, F., Clutton-Brock, T. & Grenfell, B. (1999). Inverse density dependence and the allee effect. *Trends Ecol. Evol.* **14**: 405–410.
- Courchamp, F., Chapuis, J. & Pascal, M. (2003). Mammal invaders on islands: impact, control and control impact. *Biol. Rev.* **78**: 347–383.
- Cummins, R. P., Hewison, R. L. H., French, D. D., Bacon, P. J., Gauld, J., Mills, C., Rees, T. & Elston, D. A. (2002). *Monitoring environmentally sensitive areas in Scotland: summary of monitoring. Programme and overview of results 1994–1999*. Banchory: CEH.
- Dalle, S. P., Lopez, H., Diaz, D., Legendre, P. & Potvin, C. (2002). Spatial distribution and habitats of useful plants: an initial assessment for conservation on an indigenous territory, Panama. *Biodivers. Conserv.* **11**: 637–667.

- Dias, P. C. (1996). Sources and sinks in population biology. *Trends Ecol. Evol.* **11**: 326–330.
- Doak, D. F. (1995). Source–sink models and the problem of habitat degradation: general models and applications to the Yellowstone grizzly. *Conserv. Biol.* **9**: 1370–1379.
- Donovan, T. M. & Thompson, F. R. (2001). Modeling the ecological trap hypothesis: a habitat and demographic analysis for migrant songbirds. *Ecol. Applic.* **11**: 871–882.
- Donovan, T. M., Thompson, F. R., Faaborg, J. & Probst, J. R. (1995). Reproductive success of migratory birds in habitat sources and sinks. *Conserv. Biol.* **9**: 1380–1395.
- Dunstone, N. (1993). *The mink*. London: Poyser Natural History.
- Dunstone, N. & Birks, J. (1983). Activity budget and habitat usage by coastal-living mink (*Mustela vison*, Schreber). *Acta Zool. Fenn.* **174**: 189–191.
- Focardi, S., Pelliccioni, E. R., Petrucco, R. & Toso, S. (2002). Spatial patterns and density dependence in the dynamics of a roe deer (*Capreolus capreolus*) population in central Italy. *Oecologia* **130**: 411–419.
- Fuller, R. J., Reed, T. M., Buxton, N. E., Webb, A., Williams, T. D. & Pienkowski, M. W. (1986). Populations of breeding waders Charadrii and their habitat on crofting lands of the Outer Hebrides, Scotland. *Biol. Conserv.* **37**: 333–361.
- Gaona, P., Ferreras, P. & Delibes, M. (1998). Dynamics and viability of a metapopulation of the endangered Iberian lynx (*Lynx pardinus*). *Ecol. Monogr.* **68**: 349–370.
- Gonzalez, A. & Holt, R. D. (2002). The inflationary effects of environmental fluctuations in source–sink systems. *Proc. Natl. Acad. Sci. USA* **99**: 14872–14877.
- Gosling, L. M. & Baker, S. J. (1987). Planning and monitoring an attempt to eradicate coypus from Britain. *Symp. Zool. Soc. Lond.* **58**: 99–113.
- Hanski, I. (1999). *Metapopulation ecology*. Oxford: Oxford University Press.
- Harkonen, T. & Harding, K. C. (2001). Spatial structure of harbour seal populations and the implications thereof. *Can. J. Zool.* **79**: 2115–2127.
- Hassell, M. P., Comins, H. N. & May, R. M. (1994). Species coexistence and self-organizing spatial dynamics. *Nature* **370**: 290–292.
- Holt, R. D. (1985). Population dynamics in two-patch environments: some anomalous consequences of an optimal habitat distribution. *Theoret. Pop. Biol.* **28**: 181–208.
- Horvath, T. G., Lamberti, G. A., Lodge, D. M. & Perry, W. L. (1996). Zebra mussel dispersal in lake-stream systems: source–sink dynamics. *J. N. Am. Benthol. Soc.* **15**: 564–575.
- Hudson, P. J. & Cox, R. (1989). Mink problems in the Outer Hebrides: a pilot study. *Game Conservancy Rev.* **1988**: 133–135.
- Hutchinson, G. E. (1957). Concluding remarks. *Cold Spring Harbor Symp. Quant. Biol.* **22**: 415–427.
- Innes, J., Hay, R., Flux, I., Bradfield, P., Speed, H. & Jansen, P. (1999). Successful recovery of North Island kokako *Callaeas cinerea wilsoni* populations, by adaptive management. *Biol. Conserv.* **87**: 201–214.
- IUCN Council (2000). *Guidelines for the prevention of biodiversity loss caused by alien invasive species*. Prepared by the IUCN/SSC Invasive Species Specialist Group (ISSG) and approved by the 51st Meeting of the IUCN Council, Gland Switzerland, February 2000. Gland: IUCN.
- Jackson, D. B. (2001). Experimental removal of introduced hedgehogs improves wader nest success in the Western Isles, Scotland. *J. Appl. Ecol.* **38**: 802–812.
- Jackson, D. B. & Green, R. E. (2000). The importance of the introduced hedgehog (*Erinaceus europaeus*) as a predator of the eggs of waders (Charadrii) on machair in South Uist, Scotland. *Biol. Conserv.* **93**: 333–348.
- Jonzen, N., Lundberg, P. & Gårdmark, A. (2001). Harvesting spatially distributed populations. *Wildl. Biol.* **7**: 197–203.
- Kadmon, R. & Tielbörger, K. (1999). Testing for source–sink population dynamics: an experimental approach exemplified with desert annuals. *Oikos* **86**: 417–429.
- Kareiva, P. (1990). Population dynamics in spatially complex environments – theory and data. *Phil. Trans. R. Soc. Ser. B.* **330**: 175–190.
- Law, R., Murrell, D. J. & Dieckmann, U. (2003). Population growth in space and time: spatial logistic equations. *Ecology* **84**: 252–262.
- Lundberg, P. & Jonzen, N. (1999). Optimal population harvesting in a source–sink environment. *Evol. Ecol. Res.* **1**: 719–729.
- Mauritzen, M., Derocher, A. E., Wiig, O., Belikov, S. E., Boltunov, A. N., Hansen, E. & Garner, G. W. (2002). Using satellite telemetry to define spatial population structure in polar bears in the Norwegian and western Russian Arctic. *J. Appl. Ecol.* **39**: 79–90.
- McCoy, T. D., Ryan, M. R., Kurzejeski, E. W. & Burger, L. W. (1999). Conservation Reserve Program: source or sink habitat for grassland birds in Missouri? *J. Wildl. Mgmt.* **63**: 530–538.
- McCullough, D. R. (1996). Spatially structured populations and harvest theory. *J. Wildl. Mgmt.* **60**: 1–9.
- Pacala, S. W. (1987). Neighborhood models of plant population dynamics. III. Models with spatial heterogeneity in the physical environment. *Theoret. Pop. Biol.* **31**: 359–392.
- Portillo, H. E., Pitre, H. N., Meckenstock, D. H. & Andrews, K. L. (1998). Performance of a lepidopteran pest complex (Langosta) (Lepidoptera : Noctuidae) on sorghum, maize, and noncrop vegetation in Honduras. *Environ. Entomol.* **27**: 70–79.
- Pulliam, H. R. (1988). Sources, sinks and population regulation. *Am. Nat.* **132**: 652–661.
- Ranta, E., Kaitala, V. & Lindstrom, J. 1997. Spatially autocorrelated disturbances and patterns in population synchrony. *Proc. R. Soc. Lond. Ser. B.* **266**: 1851–1856.
- Ripa, J., Lundberg, P. & Kaitala, V. (1998). A general theory of environmental noise in ecological food webs. *Am. Nat.* **151**: 256–263.
- Robinson, S. K., Thompson, F. R., Donovan, T. M., Whitehead, D. R. & Faaborg, J. (1995). Regional forest fragmentation and the nesting success of migratory birds. *Science* **267**: 1987–1990.
- Ruxton, G. D. & Doebeli, M. (1996). Spatial self-organization and persistence of transients in a metapopulation model. *Proc. Roy. Soc. Lond. Ser. B.* **263**: 1153–1158.
- Schadt, S., Knauer, F., Kaczensky, P., Revilla, E., Wiegand, T. & Trepl, L. (2002). Rule-based assessment of suitable habitat and patch connectivity for the Eurasian lynx. *Ecol. Applic.* **12**: 1469–1483.
- Scottish Natural Heritage (2000). *Mink control to protect important birds in SPAs in the Western Isles*. Application to EU-LIFE III-Nature.
- Shea, K., Possingham, H. P., Murdoch, W. W. & Roush, R. (2002). Active adaptive management in insect pest and weed control: intervention with a plan for learning. *Ecol. Applic.* **12**: 927–936.
- Thomas, C. D. & Kunin, W. E. (1999). The spatial structure of populations. *J. Anim. Ecol.* **68**: 647–657.
- Travis, J. M. J. (2001). The colour of noise and the evolution of dispersal. *Ecol. Res.* **16**: 157–163.
- Travis, J. M. J. & Dytham, C. (1999). Habitat persistence, habitat availability and the evolution of dispersal. *Proc. R. Soc. Lond. Ser. B.* **266**: 723–728.
- Travis, J. M. J. & Dytham, C. (2002). Dispersal evolution during invasions. *Evol. Ecol. Res.* **4**: 1119–1129.
- Tuck, G. N. & Possingham, H. P. (1994). Optimal harvesting strategies for a metapopulation. *Bull. Math. Biol.* **56**: 107–127.
- Walters, C. J. & Hollings, C. S. (1990). Large-scale management experiments and learning by doing. *Ecology* **71**: 2060–2068.
- Watkinson, A. R. & Sutherland, W. J. (1995). Sources, sinks and pseudo-sinks. *J. Anim. Ecol.* **64**: 126–130.
- Wootton, J. T. & Bell, D. A. (1992). A metapopulation model of the peregrine falcon in California: viability and management strategies. *Ecol. Applic.* **2**: 307–321.