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Optimal population harvesting in a source–sink environment

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ABSTRACT

We derive optimal harvesting strategies for a single population in a simple two-habitat environment. We let one of the habitats function as a source with logistic population growth and the other habitat as a sink that cannot have positive equilibrium population density without immigration from the source. The dispersal between habitats is assumed to be density-independent and cost-free. The total yield function for simultaneous harvesting in the two habitats has no interior extreme point. Given that maximum sustainable yield is the management goal (not necessarily a very wise one), two possible harvesting policies emerge. Either the sink should be harvested at its optimal rate (provided that the yield function has a maximum), or the sink should be harvested at a maximal rate and the source at its optimal rate. In the former case, the yield from the sink always exceeds the yield from the source; in the latter case, the reverse is often, but not always, true. The relationship between maximum per capita growth rate in the source and the dispersal parameters determine which of the above two cases applies. Regardless of harvesting strategy, or if we harvest at all, the sink often has the highest population density. Harvesting the sink will always result in the highest yield. Both source and sink harvesting generally destabilize the dynamics of the total population. Although sources and sinks are real, it may be impossible to distinguish between them in the field. Our results are, therefore, not directly or easily applied to real harvesting situations. Given that there are habitat quality differences of the source–sink kind, however, harvesting decisions may result in unexpected and unwanted outcomes that population management should take into account.

Keywords: dispersal, harvesting theory, population harvesting, population management, population stability, source–sink dynamics.

INTRODUCTION

Most ecological systems are characterized by variation in habitat quality and spatial structure. The importance of spatial structure for the dynamics of most natural populations has recently received much attention (e.g. Kareiva, 1990; Fryxell and Lundberg, 1997; Hanski and Gilpin, 1997; Ranta *et al.*, 1997; Tilman and Kareiva, 1997).

In a heterogeneous environment, there is considerable variation in habitat quality – some are good, others bad. Although age- and stage-specific demographic rates have been widely explored by ecologists, less attention has been paid to the consequences of habitat-specific

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demographic rates (Pulliam, 1996). One approach has been the identification of sources and sinks (e.g. Holt, 1985; Pulliam, 1988; Pulliam and Danielson, 1991). A source is a population (or subpopulation) in which births exceed deaths and emigration exceeds immigration; in a sink, deaths and immigration exceed births and emigration (Pulliam, 1988). Hence, in the absence of immigration, a sink population would deterministically go extinct.

Many studies have considered harvesting in temporally fluctuating environments and in the face of uncertainty (e.g. Beddington and May, 1977; May *et al.*, 1978; Walters, 1986; Hilborn and Walters, 1992; Lande *et al.*, 1995). However, the harvested population is often assumed to be uniformly distributed in a uniform environment, which is often questionable. Recent research into population harvesting in non-uniform environments (McCullough, 1996) has considered spatial control of harvesting in continuous populations – refuges free from harvesting – and the effects of harvesting in a metapopulation. We believe that spatial structure of the environment may be very important for both population persistence and harvesting decisions. In this paper, we try to analyse a simple source–sink system for a single species subject to harvesting. We are primarily interested in how we optimally decide harvesting strategies when a population has two available habitats and we are free to harvest in either of them. We define an optimal harvesting strategy as a strategy that maximizes (sustainable) yield. In fisheries and wildlife management, this is unlikely to be desirable, but here it illustrates, in its simplicity, the very basic problems of harvesting or otherwise managing populations in spatially structured environments.

THEORY

Our assumptions are overly simple, yet capture some essential characteristics of many natural environments. We will assume a simple two-habitat environment and that individuals move between them passively and without costs. We will let the source population be characterized by the following growth equation:

$$\frac{\mathrm{d}S}{\mathrm{d}t} = rS\left(1 - \frac{S}{K}\right) - eS + dN - h_{\mathrm{s}}S \tag{1}$$

where S is the population density in the source habitat, r is maximum per capita growth rate in the source habitat, e is emigration rate from the source to the sink, d is immigration rate to the source from the sink habitat, N is population density in the sink habitat and h_{s} is harvesting rate in the source. The equilibrium population density in the source habitat in the absence of migration and harvesting is denoted by K. The only positive contribution to the sink is immigration from the source. The sink habitat is not able to sustain a positive equilibrium population density in the absence of immigration. The resulting equation for the dynamics in the sink is:

$$\frac{\mathrm{d}N}{\mathrm{d}t} = eS - mN - dN - h_{\mathrm{n}}N \tag{2}$$

where h_{n} is harvest rate in the sink habitat and m is per capita growth rate. Dispersal (e and d) is cost-free and density-independent in both habitats. Our task is to calculate equilibrium population densities, optimal harvest rates and the yield in both habitats.

Equilibrium population densities

The equilibrium population densities are found by setting equations (1) and (2) to zero and solving for the S and N that satisfy that condition. This is rather straightforward and we have:

$$
\begin{aligned}
S^* &= \frac{N^*(d + m + h_{\mathrm{n}})}{e} \\
N^* &= \frac{S^*(K(e + h_{\mathrm{s}}) - r(K - S^*))}{dK}
\end{aligned}
\tag{3}
$$

where S^* and N^* denote the equilibrium population densities. Equation (3) can be simplified and the equilibrium densities expressed in parameters only, such that:

$$
\begin{aligned}
S^* &= \frac{K}{r}\left(e\left(\frac{d}{d + m + h_{\mathrm{n}}} - 1\right) + r - h_{\mathrm{s}}\right) \\
N^* &= \frac{eK}{r(d + m + h_{\mathrm{n}})}\left(e\left(\frac{d}{d + m + h_{\mathrm{n}}} - 1\right) + r - h_{\mathrm{s}}\right)
\end{aligned}
\tag{4}
$$

The two equilibria in equation (4) will be positive provided that $r > (dh_{\mathrm{s}} + (e + h_{\mathrm{s}})(m + h_{\mathrm{n}}))/(d + m + h_{\mathrm{n}})$. In the absence of harvesting, that condition reduces to $r > em/(d + m)$ and we note that both the source and the sink potentially have positive equilibria.

Optimal harvest rates

We now calculate the optimal harvest rates in the two habitats. We will initially assume that we are able to direct harvesting to both habitats to maximize total yield. The optimal harvest rate is defined as a rate of harvesting that achieves that goal, given that the equilibrium population density in the habitat is positive. Assuming that harvesting is performed in both habitats, the total yield, Y, will be:

$$
Y = h_{\mathrm{s}}^* S^* + h_{\mathrm{n}}^* N^*
\tag{5}
$$

where h_i^* is the optimal harvest rate in the respective habitat. Maximizing Y with respect to h_{s}^* and h_{n}^* is done by letting $\partial Y/\partial h_{\mathrm{s}}^* = \partial Y/\partial h_{\mathrm{n}}^* = 0$ and solving for the respective harvesting rates (the necessary first-order condition). If the second-order conditions $\partial^2 Y/\partial h_{\mathrm{s}}^{*2} < 0$, $\partial^2 Y/\partial h_{\mathrm{n}}^{*2} < 0$ and $(\partial^2 Y/\partial h_{\mathrm{s}}^{*2})(\partial^2 Y/\partial h_{\mathrm{n}}^{*2}) > \partial(\partial Y/\partial h_n^*)/\partial h_{\mathrm{s}}^*$ are also fulfilled for equation (5), the first-order condition results in the optimal harvest rates:

$$
\begin{aligned}
h_{\mathrm{s}}^* &= \frac{dr - m(e - r)}{m} \\
h_{\mathrm{n}}^* &= \frac{m(e - r) - dr}{r}
\end{aligned}
\tag{6}
$$

Inspection of the numerators in equation (6) tells us that harvest rates > 0 cannot happen simultaneously in the two habitats. This means that there is no interior maximum of the total yield function. We therefore have to determine optimal harvest rates in the two habitats separately before we return to the problem of harvesting in both simultaneously.

Let us first assume that only the source habitat is harvested. Equation (1) is then intact and we have to modify equation (2) slightly, so that:

$$\frac{\mathrm{d}N}{\mathrm{d}t} = eS - mN - dN$$

The new equilibrium population densities are:

$$\begin{aligned} S^* &= \frac{K}{r}\left(e\left(\frac{d}{d+m} - 1\right) + r - h_\mathrm{s}\right) \\ N^* &= \frac{eK}{r(d+m)}\left(e\left(\frac{d}{d+m} - 1\right) + r - h_\mathrm{s}\right) \end{aligned} \tag{7}$$

The yield function (equation 5) now reduces to involve the source only, and calculation of the optimal harvest rate is simplified and is rather easily found to be:

$$h_\mathrm{s}^* = \frac{1}{2}\left(e\left(\frac{d}{d+m} - 1\right) + r\right) \tag{8}$$

The optimal harvest rate in the source increases with increasing migration rate back from the sink and with decreasing mortality rate in the sink habitat. $h_\mathrm{s}^* > 0$ provided that $r > em/(d+m)$. If there is no migration between habitats, $h_\mathrm{s}^* = r/2$; that is, the optimal harvest rate is equal to half the per capita growth rate in the source. This is the familiar result from analyses of single-population harvesting in uniform environments (Ricker, 1954; Schaefer, 1954; Beverton and Holt, 1957; Clark, 1990). We use S^* from equation (7) and the result of equation (8) to calculate the maximum yield in the source, Y_s $(= h_\mathrm{s}^* S^*)$:

$$Y_\mathrm{s} = \left(\frac{k}{4r}\right)\left(r - \frac{em}{d+m}\right)^2 \tag{9}$$

Alternatively, we may choose to harvest the sink habitat only. Following the same procedure as above, we arrive at the optimal harvest rate:

$$h_\mathrm{n}^* = \begin{cases} 0 & \text{if } r < \dfrac{em}{d+m} \\[2ex] \dfrac{rd^2 + dm(2r-e) - m^2(e-r)}{d(2e-r) + m(e-r)} & \text{if } \dfrac{em}{d+m} < r < \dfrac{e(2d+m)}{d+m} \\[2ex] \to \infty & \text{if } r > \dfrac{e(2d+m)}{d+m} \end{cases} \tag{10}$$

The first condition in equation (10) tells us that, if maximum per capita growth rate in the source (r) is too small, no sustainable harvesting in the sink is possible. If the middle condition is true, then the yield function for the sink ($Y_\mathrm{n}(h_\mathrm{n})$) does have an interior maximum with the corresponding optimal harvest rate. As r increases, the Y_n-function changes from being humped (as long as the middle condition is true) to a monotonically increasing function (when the third condition holds); hence, the harvesting rate is approaching infinity.

Let us now consider two different possible combinations of source and sink harvesting. First, let both habitats have yield functions with interior maxima – that is, equation (9) and the middle condition for equation (10) both apply. The corresponding expressions for the yield in the two habitats are:

$$\begin{aligned} Y_s &= \left(\frac{k}{4r}\right)\left(r - \frac{em}{d+m}\right)^2 \\ Y_n &= \left(\frac{k(d+m)}{4rd}\right)\left(r - \frac{em}{d+m}\right)^2 \end{aligned} \tag{11}$$

The two expressions differ only in the term $(d + m)/d$, which is > 1. Thus, the yield in the sink always exceeds that in the source. Since no interior maximum for the total yield function (equation 5) exists, the optimal harvesting strategy under these conditions is to harvest the sink only. Alternatively, parameter values are such that no maximum exists for the yield function in the sink. The yield in the sink as $h_n \to \infty$ is then:

$$Y(h_n \to \infty) = \frac{ek(r-e)}{r} \tag{12}$$

This expression should now be compared with equation (9). It is not obvious which habitat will give the highest yield (Fig. 1), but it is clear that the overall optimal harvesting policy is to harvest the sink at a maximum rate and the source at its optimal rate (equation 9).

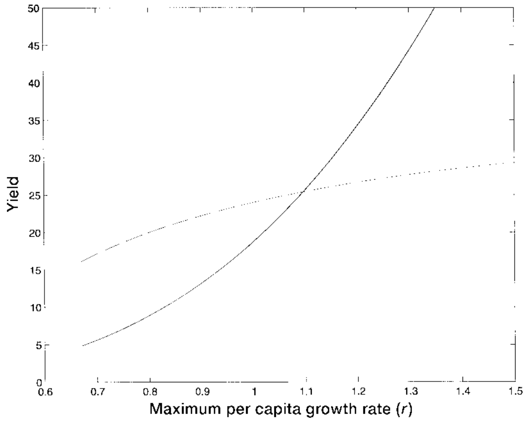

Fig. 1. Yield in the source (solid line) and sink (dashed line) in relation to the maximum per capita growth rate (r) in the source habitat. r is set such that the optimal harvest rate in the sink is maximal (equation 10) and the yield in the source and the sink is specified by equations (9) and (12), respectively. Parameter values: $e = 0.4$, $d = 0.2$, $K = 100$, $m = 0.1$.

RESULTS

Basic properties of the source–sink system

As expected, equilibrium population density increases in both habitats as the maximum per capita growth rate (r) in the source increases. The reverse is true for the mortality rate (m) in the sink (Fig. 2a,b). For many combinations of parameters, the highest density will be found in the sink. Figure 2c also shows how densities vary with the relative flux of individuals between the two habitats. If emigration from the source (e) greatly exceeds the migration back (d), the sink population will have a higher density than the source. As the migration back to the source increases, the density in the sink habitat will decrease relative to the source.

Source harvesting

The equilibrium population densities in the source and the sink decrease linearly with increasing harvest rate in the source (equation 7). As indicated in equation (8), the optimal harvest rate increases linearly as per capita growth rate in the source (r) increases. The optimal harvest rate in the source is also strongly dependent on the migration parameters (Fig. 3). Note that the optimal harvest rate decreases as the absolute magnitude of the migration increases. If the migration rate back to the source from the sink is low ($d = 0.1$), the sink acts as a refuge, permitting a higher harvesting rate in the source.

Sink harvesting

As noted above, sink harvesting involves two possible outcomes. If an optimal harvest rate in the sink exists (equation 10), then the optimal harvesting policy is to harvest the sink

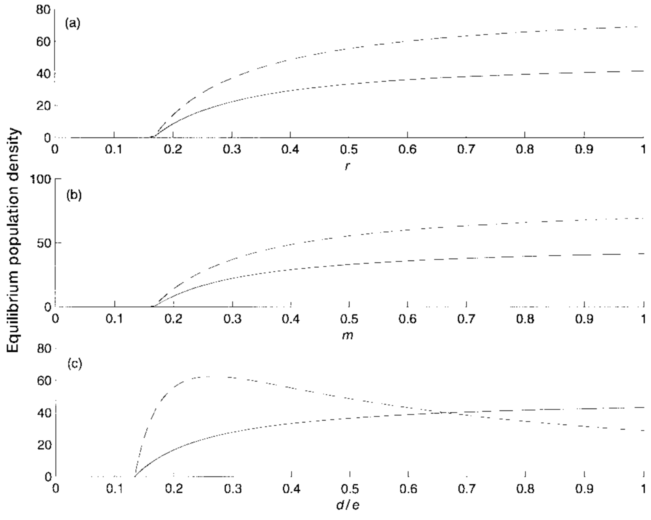

Fig. 2. Equilibrium population density without harvesting in the source (solid curve) and the sink (dashed curve) as functions of (a) r, (b) m and (c) the relative flow of dispersers (d/e) to and from the sink. Parameter values: $r = 0.5$, $K = 50$, $e = 0.5$, $d = 0.2$.

only at that rate (Fig. 4). If, on the other hand, the sink is a very poor habitat with very little migration back to the source (i.e. large m and very small d), then both habitats should be harvested; the sink at a maximal rate and the source according to equation (8).

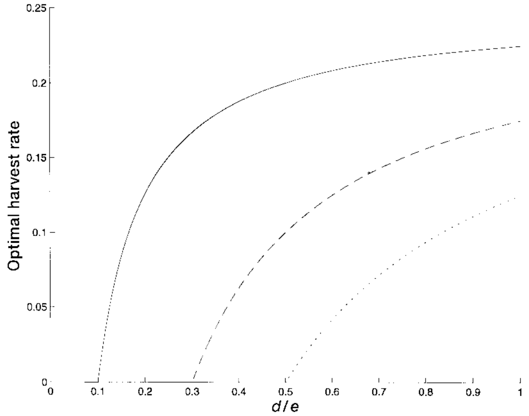

Fig. 3. Optimal harvest rate in the source in relation to the relative flow of dispersers (d/e) to and from the sink. Migration rate back to the source, d, was set to three different values: $d = 0.1$ (solid curve), $d = 0.2$ (dashed curve), $d = 0.3$ (dotted curve). Other parameter values: $r = 0.5$; in all three cases, $m = 0.1$, $K = 50$.

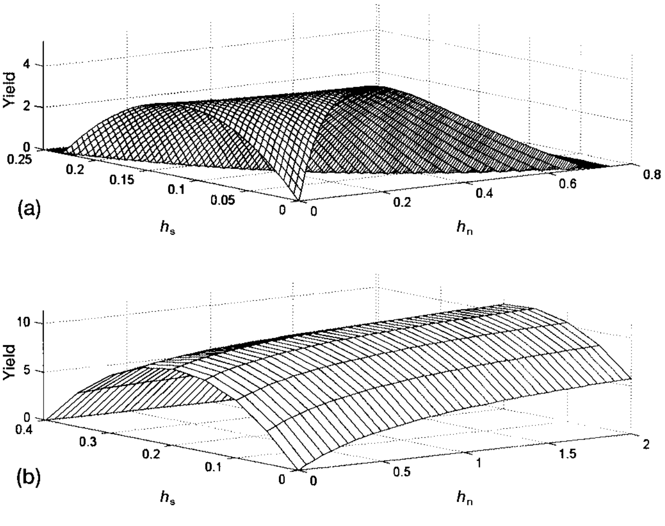

Fig. 4. The yield as a function of harvest rates in the source (h_s) and in the sink (h_n). (a) The case when optimal harvest rates exist for both the source and the sink. The yield has no interior extreme point and maximum yield is achieved by harvesting the sink only. Parameter values: $e = 0.4$, $d = 0.2$, $m = 0.1$, $r = 0.4$, $K = 100$. (b) The case when the optimal harvest rate in the sink is infinite. The optimal harvesting policy is to harvest the sink at the maximum rate and the source at its optimal harvesting rate. Parameter values: $e = 0.1$, $d = 0.001$, $m = 0.75$, $r = 0.5$, $K = 100$.

Population stability

In Fig. 5, we present the stability conditions for the harvesting scenarios (no harvesting, harvesting in the source only and harvesting in the sink only) in the r (intrinsic growth rate in the source) and m (mortality rate in the sink) plane. Note that both source and sink harvesting result in a more narrow parameter range for population stability and that sink harvesting has the narrowest range. Another aspect of stability is resilience – that is, how fast the system returns to equilibrium if displaced away from it. We calculated the characteristic return time (Pimm and Lawton, 1977), which is inversely proportional to resilience for combinations of parameters that result in locally stable dynamics. The change in return time in relation to r is shown in Fig. 6. In general, the case with no harvest has shorter return times (higher resilience) than when the population is harvested. We note also that harvesting in the source increases return time compared with sink harvesting. In fact, sink harvesting even stabilizes the dynamics relative to the situation without harvesting for r-values roughly between 0.5 and 0.8 (Fig. 6).

DISCUSSION

As clearly illustrated in Fig. 1, population density does not reflect reproduction in the habitat, and thus cannot be used for classification of a habitat as a source or a sink. This is consistent with the work of Pulliam (1988), who explored density-dependent dispersal between sources and sinks. Accepting the difficulties involved in the correct identification of sources and sinks from demographic and census data (e.g. Pulliam, 1988; Watkinson and

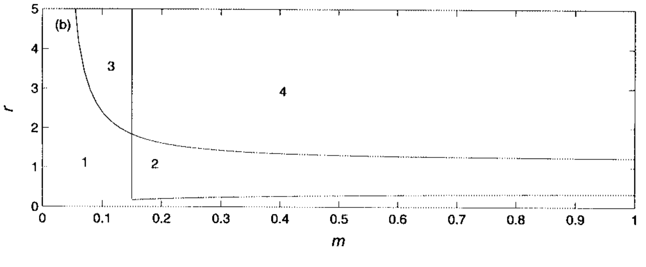

Fig. 5. Combinations of r (maximum per capita growth rate in the source) and m (mortality rate in the sink), and stability properties of the system under optimal harvesting in the source (a) and in the sink (b). Other parameter values: $e = 0.4$, $d = 0.2$, $K = 50$. Note the different r-scales in (a) and (b). The areas denoted 1–4 indicate stability properties such that 1 = both harvested and non-harvested systems non-persistent; 2 = only non-harvested systems stable and persistent; 3 = only harvested systems stable and persistent; 4 = both harvested and non-harvested systems stable and persistent.

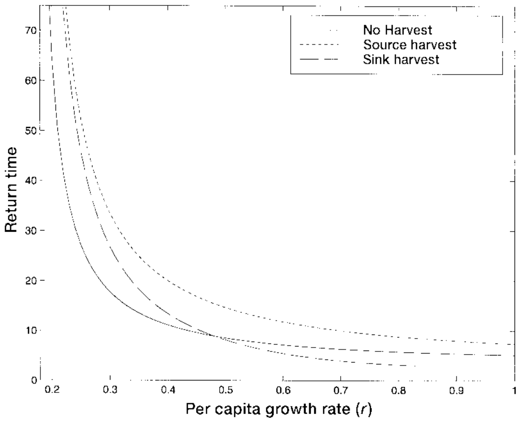

Fig. 6. The characteristic return time (= $1/\Lambda$, where $\Lambda = \min\{-\mathrm{Re}(\lambda_i)\}$, $i = 1, 2$. $\mathrm{Re}(\lambda_i)$ is the real part of the ith eigenvalue of the community matrix of equations (1) and (2) (with their appropriate changes according to the different harvesting cases)) for the source–sink system with and without harvesting. Return time decreases monotonically with r in all cases and harvesting in the source always results in the longest return time. Parameter values: $e = 0.5$, $d = 0.2$, $m = 0.1$, $K = 50$. The return times were calculated for combinations of parameters for which the system was locally stable and persistent.

Sutherland, 1995), it is somewhat disturbing how optimal harvesting decisions differ between a source and a sink. On the one hand, optimal harvesting in the source pushes down the equilibrium densities in the source and the sink, and optimal harvest rate increases linearly with per capita growth rate in the source, which seems to be a straightforward and intuitive result. Optimal harvest rate approaches infinity for increasing per capita birth rate in the source (r) and increasing relative migration from the sink to the source (d/e). In the sink, however, threshold values exist for r and d/e, respectively, above which no optimum exists in the sink and the sink should be harvested at the maximum rate.

If the migration rate back to the source from the sink (d) is low, the sink acts as a refuge, permitting a higher harvesting rate in the source. The virtue of refuges for harvested populations has recently been discussed by McCullough (1996). The difference here lies in the fact that McCullough considered designated areas as refuges, whereas our results indicate that some parts of the environment (i.e. the sinks) may automatically become refuges under certain harvesting strategies. The role of refuges in harvesting theory and practice is, however, yet to be fully explored.

One of the most important results from our analysis is that, whenever the optimal harvest rate in the sink is finite, then the yield is also higher in the sink. This means that population production and population harvesting should take place in spatially separate locations. If, on the other hand, optimal harvest rate in the sink is infinite, a substantial increase in yield is possible by source harvesting at its optimal rate. The practical ramifications of this result are yet unclear, but it suggests that we should reconsider much of current harvesting theory, which, almost in its entirety, is built on the assumption of uniformly distributed populations. Note that we have not considered seasonal migration in our model system. Migration between habitats is cost-free in all respects as opposed to seasonal return migration. Pelletier and Magal (1996) have also recently shown that the allocation of harvesting among seasons and locations in the environment may strongly influence the overall yield.

Harvesting in different habitats not only influences equilibrium population densities and yield, but also population stability. Our results show that harvesting under all conditions considered is destabilizing in the sense that the range of stable parameter combinations is smaller. Resilience can, on the other hand, be enhanced by harvesting in the sink (Fig. 6). Surprisingly few studies have addressed this problem. Beddington and May (1977) and May *et al.* (1978) showed that harvesting in a single-population model with noise (maximum per capita growth rate, r, being a stochastic variable in the logistic equation) increased the characteristic return time for the population, particularly in the vicinity of the maximum sustainable yield. By and large, our results confirm that observation, except for sink harvesting with relatively high r-values. The consequences for population persistence of this harvesting effect have not been explored in detail since (but see Krebs and May, 1990; Hilborn and Walters, 1992).

The model analysed in this paper is extremely simple. We have made a number of unrealistic and questionable assumptions about both the environment and the process of population growth and individual movements between patches in the landscape. Our aim was to highlight an often neglected problem in harvesting theory, the fact that the environment is rarely, if ever, spatially uniform. It is obvious from the vast body of literature on population dynamics in spatially heterogeneous environments that spatial structure matters. It is clear that harvesting theory has not caught up on this development in population ecology. Despite the many limitations of our simplified approach to the problem, we feel that harvesting theory eventually must be injected with spatial structure. One of the main problems with our model is the assumption that we are able to identify source and sink habitats. Sources and sinks may very well be real, but it is not easy to identify them (Watkinson and Sutherland, 1995). However, we have shown that, if there are differences in habitat quality, then the decision where and how to harvest the population will greatly influence equilibrium population density, population stability and yield. This must be of prime concern in all population management.

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